

Life amidst Singularities

Proefschrift

ter verkrijging van
de graad van Doctor aan de Universiteit Leiden,
op gezag van Rector Magnificus Prof.mr. P.F. van der Heijden,
volgens besluit van het College voor Promoties
te verdedigen op woensdag 15 oktober 2008
klokke 15:00 uur

door
Michel Durinx
geboren te Borgerhout, België
in 1976

Promotiecommissie

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This study was supported by the Netherlands organisation for Scientific Research (NWO), through the Research Council for Earth and Life Sciences (ALW).

There is something to be learned from a rainstorm. When a sudden shower overtakes you in spring, you may try to keep dry by hurrying along the side of the road. Then you still get wet, from the water collected by the roofs, streaming off the eaves. But if your mind is set from the beginning, you will not be surprised by the downpour, though you get drenched just the same. This understanding extends to everything.

– Yamamoto Tsunetomo

I recoil with dismay and horror at this lamentable plague of functions that do not have derivatives.

– Charles Hermite

The study of non-linear systems is like the study of non-elephant biology.

– attributed to Stanislaw Ulam

Like most mathematicians, [Lotka] takes the hopeful biologist to the edge of a pond, points out that a good swim will help his work, and then pushes him in and leaves him to drown.

– Charles Elton

A girl and a boy bump into each other — surely an accident. A girl and a boy bump and her handkerchief drops — surely another accident. But when a girl gives a boy a dead squid — That HAD To Mean Something.

– S. Morganstern

Invisible Pink Unicorns are beings of great spiritual power. We know this because they are capable of being invisible and pink at the same time. Like all religions, the Faith of the Invisible Pink Unicorns is based upon both logic and faith. We have faith that they are pink; we logically know that they are invisible because we can't see them.

– Steve Eley

We know mathematics is a function mapping coffee onto theorems.
But is it invertible?

– after Alfred Rényi

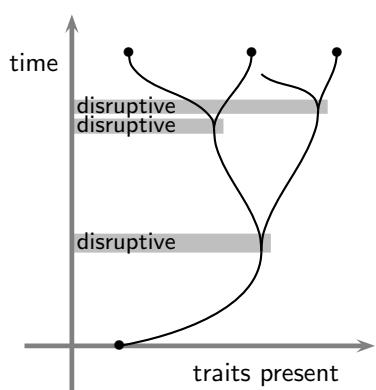
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General introduction

Adaptive dynamics is the study of evolution driven by rare mutations that are minor in effect. When these mutational steps are sufficiently rare and small, a situation like the one illustrated may occur: starting from a community with individuals that all show the same trait, this heritable characteristic may change gradually over time at varying rates. But following the timeline upwards from zero, we see three events where the variety of types present is increased, and a later event where the variety is decreased again. As such this is an appealing image to the biologist¹: starting from a simple ecosystem with a group of individuals of the same type, ecological pressures are such that subgroups start playing different, heritable roles, and eventually the community is made up of a collection of distinct populations. Also, if these groups evolve sufficiently far away from each other, they may become distinct species.



In the whole story above, though, there are a lot of tacit assumptions. Firstly, individuals must have some heritable trait that has an influence on their life history, i.e., those aspects of individuals' lives that determine their demographics: age at maturity, life expectancy, lifetime offspring number, offspring survival rate, In adaptive dynamics, this heritable trait is assumed to be passed on as a faithful copy nearly every time, the population to be locally well-mixed, and the genetical variation to be initially hardly segregating at all; only in very rare cases the trait may mutate, and those mutations should have but small effects. The consequence of having only rare mutation events in such a population is that there effectively are two timescales, the demographical one and a much slower evolutionary one that tracks the mutations — as the community reaches its population dynamical attractor long before the next mutation occurs, the whole population dynamics, from an evolutionary perspective, can be summed up by its attractor. If then furthermore the mutational steps are small, a neat (piecewise) smooth graph as in the illustration emerges.

In the picture we also see that the changing traits seem to zoom in on special

¹Though creationists and ID'ers may want to abstain.

points — the points where the population diversifies, and the three trait values that are eventually reached by the end of the time interval. These points are called “singularities”, or with their full name “evolutionarily singular traits”, and will play a central role in each of the chapters of this thesis. They come in several varieties with very different properties, as some are evolutionary endpoints while others are agents of diversification. As indicated in the illustration, selection is disruptive near points of the last type, driving the trait to change in two opposite directions at once. Such singular traits are called branching points, because they grow new branches on the evolutionary tree.

We also see that most of the time selection is not disruptive, but directional, exerting its influence so that traits change in a specific direction. And it is also important to note that whether a trait is singular or not depends on the community present. This is seen from the fact that before the first branching event, the trait value passes through the value at which the second branching event will take place later on, but nothing happens during this first pass. The essential difference is that when the second branching occurs, the world is a different place from when the first passing happened: there is a second branch of residents, that competes for resources with those on the other branch (as well as among themselves, of course). Therefore we say that the trait value where the second branching occurs is a singularity of the two-resident evolutionary dynamics, and (most probably) not of the one-resident dynamics. This goes to the heart of adaptive dynamics, namely the tenet that the fitness of a trait on its own is a meaningless concept.

The fitness concept which is central to adaptive dynamics is that of the invasion fitness. Explained in the first chapter with a careful definition and applied to Lotka-Volterra and other types of models, it essentially measures how many offspring a single individual of an ‘invading’ type is expected to make when introduced in a given community at equilibrium of ‘resident’ types. If this number is more than one, fitness is positive and the original invader’s descendants may establish a population; if it is less than one, fitness is negative and the invaders disappear. It can be shown that in general, during regimes of directional selection, the successful invasion of a type that is close to a resident type means that it will outcompete this ancestor (which it mutated from) and drive it to extinction, and conversely that two similar residents can only coexist near singular points. It is this property that makes the graph look like it does, with only very few branches even after a very large number of very small mutational steps (small and numerous enough to make the graph look smooth). Of course the graph looks as smooth as it does because it is an idealization, based on assumptions like infinite system size, infinitesimal mutation step size and complete timescale separation, which together remove all stochasticity.

Adaptive dynamics can be applied to a lot of different ecological model types and in many different contexts. Individuals may reproduce clonally (so that offspring are identical copies of their parent) or sexually (so that half the alleles are inherited from each parent), with time being discrete (e.g., if the population dynamics is strongly seasonal it makes sense to census only at one or a few points in time each year, often just before or just after reproduction) or continuous, with traits being scalars (as in the illustration) and thus controlling only one independent parameter, or being vectors and influencing several independent life history

parameters (or even being functions, e.g. in the case of reaction norms), with individuals having a complex multi-stage life cycle involving two sexes and several morphs with different ecological roles, or so simple that all they can do is give birth and die, with genetically identical individuals being born all alike or with different possible qualities, with the population dynamics formulated as a caricatural out-of-the-box ODE (ordinary differential equation) or carefully crafted from an individual-based scenario, with the community's population dynamical attractor being a fixed point, periodic, quasi-periodic or chaotic attractor, and so forth. These myriad possibilities within the adaptive dynamics framework are not obvious from most papers, leading a reviewer to assure me adaptive dynamics only tackles clonal reproduction. As this thesis contains mostly theoretical work and little work with specific models, very few actual models will be used. If a model family is given, it will often be either a Lotka-Volterra or a physiologically structured population model. The former are a well-known and mathematically tractable type of ODE (and hence continuous time) model, with nothing specified about the individuals except for how strongly they react, per capita, to competition and how fast they reproduce in a world with no competitors. The latter family of models allows for different sexes and morphs, age- or stage structuring, and actually all of the possibilities mentioned in this paragraph. They will explicitly and extensively occur in the first two chapters, implicitly in the third and not (or only in a severely restricted form) in the last.

No detailed description of the ins and outs of adaptive dynamics and physiologically structured population modelling, and all other concepts introduced in the preceding paragraphs, will be given here at the start of this thesis, because all of that can be found in the relatively long introduction to Chapter I — the reader is invited to skip to page 1 for explanations of the ideas introduced up to now. (Indeed, my initial idea was to slice that introduction off its chapter and make it the general introduction.) Let me give you instead an outline of the thesis along with some personal notes, and show how the chapters fit together.

Chapter I is a many-tentacled creature. It gives an estimate for the speed of change in traits of physiologically structured populations, in a generalization of the proof of what is known as the canonical equation of adaptive dynamics. This estimate holds only away from singularities, paradoxically making those the interesting points from the vantage point of the equation. As the equation shows that change must happen unless the community finds itself at an evolutionarily singular strategy, it calls for a study of communities near singularities.

The second part of Chapter I is such a study, and reveals a surprising truth: choose your favourite structured population model, and no matter how complicated the interactions between residents are in a multi-resident community, the one-resident fitness function that follows from your model already contains all the essential information on your multi-resident community. In slightly more technical terms, if the small parameter ϵ gauges the distance between the residents and between the residents and an invader, then all the terms of the multi-resident invasion fitness function up to and including order $O(\epsilon^2)$ are known at a glance from the one-resident fitness. On top of proving this property in a rather general scenario, some consequences of this fact are explored in this part, for example a mutual exclusion principle that gives an upper limit to the number of locally coexisting types,

and how the environmental feedback dimension pertains to this. All in all, a lot of technicalities (like the definition of said environmental dimension) and lemmata are juggled around and thrown at the reader. But what the central result means is that some cumbersome aspects of the study of communities near singularities for creatures with convoluted life histories (but with fixed-point ecological dynamics), can be replaced with that of any other creature, however caricaturally trivial its life history, as long as it has the same one-resident invasion function.

Where the first part of this chapter shows how a community evolves if it is not in the vicinity of a singularity, and the second part shows this community's population dynamics can be approximated by a simpler dynamics near a singularity, the third part shows how to tie these first two strands together. From the canonical equation we know that generally a community either ends up near a singularity, or at the edge of its trait space. In the second case, either the boundary is left after a while at a place where the boundary is locally repelling, or else the community stays on it forever; in any case, movement on the boundary is just movement in a lower dimensional trait space, subject to all the previous considerations.

The third part therefore shows how to extract the necessary life history parameters from a population dynamical model under consideration, to unleash the techniques developed in the first two parts. Then comes a stepwise description of what can happen during the phase of directional selection, and of some things to look out for. Tying the normal form found in the second part to results developed by others, the possibilities near singularities are listed together with criteria to decide which one is occurring plus the implications for the fate of such communities near singularities, such as their possible escape into a further regime of directional selection. Since this third part is written with a public of more (biologically) applied researchers in mind, it is as self-contained as possible with few theoretical digressions or links to the first two parts, and only such technical issues are discussed as the reader is expected to encounter in applications of this nature. To add to all the joy and comprehensibility, it is illustrated by an example that analyzes a classical model.

I can see the (anonymous) reviewer's motivation when proposing to chop this chapter up into separate pieces for publication in the Journal of Mathematical Biology. Historically it was planned as a set of separate papers, but now the advantages of keeping it as one whole should be considered. With a single paper, any reader interested in more than one part can easily switch between them as all notations are carefully chosen so as to be uniform throughout the chapter, and not to interfere with each other (note for example ε and ϵ , which are similar entities but not the same). It also means that there are no three overlapping but distinct introductions and discussions that one has to get through and puzzle over how they fit together. Essentially, in keeping with Pascal, I took more time so I could write less (but sadly fell short of my stated aim of a five page thesis accompanied by a twenty or thirty page explanatory booklet). This constitutes an obvious loss in academic output measures (assuming that all parts would be accepted as separate publications) in exchange for saving a lot of pages, with extra time and effort invested in leaving no gaps or repeats in the structure. All in all, the reviewer may have been onto something.

Chapter II explores whether a normal form as found in the second part of Chapter I, for structured populations near singularities, could be formulated such that it is valid up to one higher order of the small parameter. The answer turns out to be, ‘not really’. Here a discussion of the concept of a normal form is in order, something that could be avoided in the first chapter as a normal form naturally occurred. To paraphrase the US legal system on what does and does not constitute pornography²: if something is a normal form, you just know it when you see it ... let me explain this.

In mathematics, a canonical form of a given set relative to a given equivalence relation is generally defined as a subset that contains exactly one element from each equivalence class. This setup automatically provides a classification theorem, and it allows problems involving any particular element to be solved using its canonical representative. In many branches of mathematics the term is used interchangeably with the term ‘normal form’, though in dynamical systems theory this last one is usually taken to mean a similar arrangement of subset and equivalence relation, but with the subset possibly containing several elements of a given equivalence class. From the definition it follows that a canonical form always exists, as the subset can be the whole set and the relation can be the identity. In the normal form introduced in the first chapter, we work with the set of all multi-resident fitness functions of population models with fixed point dynamics; to be equivalent is to have the same one-resident fitness function up to second order terms in ε , and the representative subset is that of Lotka-Volterra models. The uniqueness necessary to be termed a canonical form follows if we restrict the subset to Lotka-Volterra models with a trait-independent virgin growth rate $r(Y) := 1$ and a homogenous quadratic polynomial $a(X^* + V, X^* + U) := U^\top C_{11} U + U^\top C_{10} V + V^\top C_{00} V$ as interaction function, for some matrices C_{11} , C_{10} and C_{00} (where $C_{11} + C_{10} + C_{10}^\top + C_{00} = 0$). However, to be useful and therefore worthy of the label, most dynamical systems theorists would agree that a normal form has to furthermore form a (relatively) small subset and that the equivalence relation must be such that no essential information is lost.

Clearly both of the last two criteria named lie to some extent in the eye of the beholder, leading to the earlier paraphrasing boutade, and hence the second chapter does not attempt to show that no general (useful) normal form exists. What it does is to show that the equivalence relation ‘has the same invasion fitness function up to terms of order $O(\varepsilon^3)$ ’ already fails our purpose within the set of Lotka-Volterra models: having the same one-resident fitness means having a different multi-resident fitness function, unless the (normalized) first derivative of virgin growth rate (r'/r^*) is the same as well. These third order differences among Lotka-Volterra models’ fitness functions are then studied, and a comparison is made with the expansion of an unrelated type of models, from which further conclusions can be drawn.

Chapter III turns the full attention to populations near singularities again. The context is that of scenarios for (the onset of) sympatric speciation, in which a phenotypically monomorphic population evolves until the trait it has is singular, from which moment onwards disruptive selection (possibly with the help of assortative mate choice) will split the population into two distinct groups that adapt to different ecological niches. The underlying idea is that if these groups evolve further and

²Supreme Court justice Potter Stewart, *Jacobellis v. Ohio*, 1964

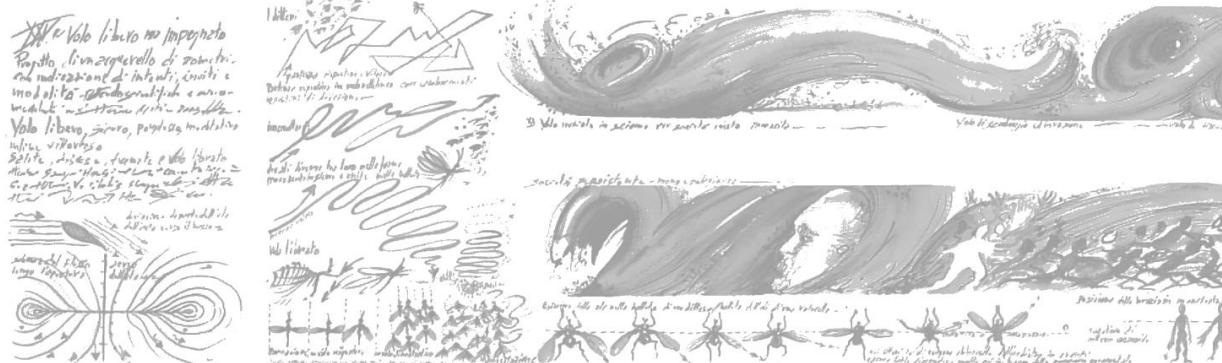
further away from each other, they may become what constitutes different species.

This chapter however shows that in sexually reproducing populations, if one allows for the male and female traits to evolve separately (essentially by considering genes with sex-specific expression), then in many evolutionary scenarios the males and females will occupy those ecological niches that are otherwise taken by the distinct subgroups, and will thus block the possibility of speciation as they necessarily keep breeding with one another.

Here a recipe is given to turn any simple model into one with two (potentially different) sexes, and we essentially show that any attracting singularity of the original model where selection is disruptive (a branching point) turns into a singularity of the sexual model, that attracts in certain directions but repells in others (a saddle point) and thus leads to the result described earlier. An analysis of two (slight variations on) models found in the literature illustrates these results, and moreover shows how further phenotypes may occur through branching within one sex.

Chapter IV grew out of a nagging feeling: repeatedly people have said, while discussing other issues, that of course in diploid populations just after branching the heterozygotes do worse than either of the homozygotes. Also in print one may come across this assertion (e.g., the introduction of Matessi *et al.*, 2001), but I didn't find any direct argument for this in the adaptive dynamics literature. When inquiring about this, argumentation about the heterozygotes' fitness (which is undefined) tends to follow, and my unease never cleared up. Don't misunderstand me, I'm sure everybody based their opinion on the fact that this situation occurred in every model analyzed up to now, and much later on I saw that the origin lies in fact with the reinforcement hypothesis of Dobzhanski (1940), bringing us all the way to the first youth of the sympatric speciation idea. But my reasoning was that if something is so obviously true, it must be rather easy to prove for a wide class of models, and indeed this turned out to be the case. For me personally this still is the heart of the fourth chapter, but it makes up only a minor part of it; after all, not much mileage can be gotten out of facts that are accepted for over three score years.

Therefore this chapter looks at a freely recombining diploid population near a singularity, and establishes criteria to see whether the heterozygote is at an advantage or not. In these situations the question is then posed whether mate choice (which tends to remove heterozygotes from the population) can invade or not, and evolve by small mutational steps or not, and whether dominance modification (where the phenotype of the heterozygotes becomes that of one of the homozygotes) can invade or not, and evolve by little steps or not. In those situations where both mate choice and phenotypical bias can invade, the relative strengths of the selection gradients are compared in order to see which strategy has the better chance to be a successful invader. As no model is specified here, this general comparison can only be made near branching points. The conclusion is that assortative mating is the more successful invader when the alternative alleles are equally frequent and mutational steps are small — a welcome result as these are features of many scenarios for the evolution of reproductive isolation in a sexual population through the coevolution of mate choice based on the ecological traits, but none of these scenarios have considered whether an alternative to mate choice could spoil the outcome. With an example, the previous points are illustrated and the relative numerical values of the selection gradients are shown for some parameter combinations.



ONE

Adaptive dynamics for physiologically structured population models

Abstract

We develop a systematic toolbox for analyzing the adaptive dynamics of multidimensional traits in physiologically structured population models with point equilibria (sensu Dieckmann *et al.*, TPB **63**:309–338, 2003). Firstly, we show how the canonical equation of adaptive dynamics (Dieckmann & Law, JMB **34**:579–612, 1996), an approximation for the rate of evolutionary change in characters under directional selection, can be extended so as to apply to general physiologically structured population models with multiple birth states. Secondly, we show that the invasion fitness function (up to and including second order terms, in the distances of the trait vectors to the singularity) for a community of N coexisting types near an evolutionarily singular point has a rational form, which is model-independent in the following sense: the form depends on the strategies of the residents and the invader, and on the second order partial derivatives of the one-resident fitness function at the singular point. This normal form holds for Lotka-Volterra models as well as for physiologically structured population models with multiple birth states, in discrete as well as continuous time and can thus be considered universal for the evolutionary dynamics in the neighbourhood of singular points. Only in the case of one-dimensional trait spaces or when $N = 1$ can the normal form be reduced to a Taylor polynomial. Lastly we show, in the form of a stylized recipe, how these results can be combined into a systematic approach for the analysis of the (large) class of evolutionary models that satisfy the above restrictions.

1 Introduction

This paper is concerned with the abstract geometry underlying the process of repeated invasions by novel mutants. Mutation limited near-continuous evolution will be our frame of reference, as we follow the so-called adaptive dynamics approach. Adaptive dynamics studies which rare mutants can establish themselves

Adapted with minor changes from: Michel Durinx, Hans J.A.J. Metz, and Géza Meszéna 2008. Adaptive dynamics of physiologically structured population models. Journal of Mathematical Biology **56** 673–742. © Springer-Verlag 2007

in an environment inhabited by a large equilibrium population of residents that they closely resemble, which invasions by similar mutants will lead to the demise of the original residents, and what the evolutionary outcome will be of a series of such substitution events. The tricks and tools of this trade are introduced in the following section.

The assumed magnitude of the resident population makes its dynamics deterministic, whereas the rarity of the invading mutant introduces a strong stochastic effect. This complication means that a positive average growth rate is a necessity, but no guarantee for a mutant's invasion success. To ask for the probability of such success is basically to ask what chance a given mutant has of being the ancestor of an unbroken line of descendants. This is analogous to the "surname" problem that led to the theory of branching processes, where the quantity we called for is termed the *establishment probability* of the given mutant (e.g. Haccou *et al.*, 2005).

The last major consideration we have in the setup of this enquiry is that we look for general geometric properties and not artifacts generated by specific models. Therefore we must consider as wide a class of models as we can technically handle. To that end, we derive our results within the context of general physiologically structured populations. This class of models is the ultimate generalization of resource competition models, allowing populations structured e.g. by size, and multiple birth states (think sexes, morphs, or size at birth). The third part of this introduction (1.2) points out the main assumptions and quantities pertaining to such models.

Gathering together the results of perturbation calculations, we are able to extend the so-called canonical equation derived by Dieckmann & Law (1996) to general physiologically structured populations. It is *the* adaptive dynamics tool, describing the rate of trait change in the case of directional selection. However, the canonical equation is an approximation that loses its validity in the close proximity of its equilibrium points. At such points, called evolutionarily singular points, a more precise analysis is required.

In this paper we also show that with regard to the invasion fitness function near evolutionarily singular points, all possible models are locally equivalent to Lotka-Volterra models (3.4, Proposition 3). Therefore the fitness function of these well-known and mathematically relatively tractable models provides a general normal form. Thus the derivation of this property is a step towards classifying the local geometrical properties of invasion functions. Geritz *et al.* (1998) showed that if the trait under evolutionary control is scalar, a full classification of nonexceptional cases consists of eight possibilities. When traits are multidimensional (as in this paper), it is unknown how many classes are needed to cover all nonexceptional cases nor what they would look like, let alone that there is an understanding of the bifurcations between those classes. F.J.A. Jacobs is engaged (together with one of the authors) in analyzing the latter for Lotka-Volterra models with scalar traits; this paper shows that a fair part of his results apply to all models with one-dimensional strategies.

1.1 Adaptive dynamics

Adaptive dynamics is concerned with evolutionary outcomes of community - dynamical processes where reproduction is nearly faithful (Metz *et al.*, 1996). The main assumptions are rarity of mutations (i.e., the ecological and evolutionary timescales are separated, and hence the community dynamics will settle on an attractor between mutation events), smallness of mutational steps (allowing sensible topological and geometrical inferences) and the initial rareness of mutants (implying a well-mixed resident population of large size).

A key insight of structured population models is given pride of place in adaptive dynamics: the separation of individual and *environment*, both influencing each other in a feedback loop (Metz & Diekmann, 1986). The idea is that individuals influence the environment in an additive manner. Given an environment, individuals are independent — any two particular individuals being exceedingly rare as a proportion of the total population, their mutual influence is effectively zero. This decoupling makes the equations linear when the environmental condition is given as a function of time.

The starting point of adaptive dynamics is the *invasion fitness function* (Metz *et al.*, 1992). By definition this is the long-term average per capita growth rate of a rare type (the *invader*) in an equilibrium community of a given set of types (the *residents*). Thus a resident type cast in the role of invader always has a zero invasion fitness, since it will on average neither grow nor diminish in abundance. One also sees that a negative fitness for a given type implies the impossibility for such an invader to gain a foothold in the population, whereas a positive fitness means a positive probability of establishment. But as this concerns a stochastic process with an initially very small amount of invaders, even a positive average growth rate will not prevent extinction in a fair amount of cases. However, as we consider gradual, mutation-driven evolution, the relevant invaders are the *mutants*: new types that differ but slightly from one of the residents. When a mutant has a positive invasion fitness, but due to stochasticity its attempt at establishment fails, this is not the end; evolution can bide its time and a later occurring similar mutation may get established due to other chance fluctuations.

Reviewing the technical setup of the framework, we start by considering the parameters under evolutionary control. We refer to this set of parameters as a *strategy* (which gives it a life history flavour), a *trait value* or *trait vector* (which sets the mind to a more technical, algebraic frame), a *point* in the strategy space (which hints at a graphical representation, or a geometrical argument), or simply the *type* of the individual. We call the set of all possible traits the *trait space* and denote it by \mathfrak{X} .

The invasion fitness function is also known as the *s*-function, to underline its heritage as a conceptual extension of the selection coefficient of population genetics. The *s*-function for a *monomorphic* community, denoted by $s_X(Y)$, describes the invasion fitness of a mutant with trait value Y in an environment set by a single resident of type X . The *s*-function for a *polymorphic* community, similarly denoted by $s_{\mathbb{X}}(Y)$, gives the invasion fitness of a Y -type mutant in an environment set by a community of N types $\{X_1, X_2, \dots, X_N\} =: \mathbb{X}$. That the community can (locally) be identified with the strategies present, comes from the convenient assumption of existence and (local) uniqueness of an attractor for the population dynamics of the community, plus the paucity and small effect of mutations.

The s -function generates further functions of central concern, namely the *invasion gradients*, which are the transposes of the derivatives of the fitness in the mutant direction at the trait value of a resident: $\left(\frac{\partial s_X(Y)}{\partial Y}\right)^\top$ for a monomorphic world, $\left(\frac{\partial s_X(Y)}{\partial Y}\Big|_{Y=x_i}\right)^\top$ for each i between 1 and N in the polymorphic case. The trait values where these invasion gradients are zero are called *evolutionarily singular strategies*. The study of evolutionary dynamics can thereby be split into two main parts. First, away from the zeros of the invasion gradient and under the restriction of well-behaved population dynamics, it can be shown that “*invasion implies substitution*” (Dercole, 2002; Dercole & Rinaldi, in press). What well-behaved entails, is considered by Geritz *et al.* (2002) and Geritz (2005), and substitution means that the mutant drives its ancestral resident to extinction if it succeeds in establishing itself. Hence the apparition of a new type, the mutant, does not usually lead to increased diversity — on the contrary, if there are several types coexisting in the resident community, on rare occasions the appearance of a mutant may lead to the demise of not only the resident that spawned it but also of other resident types, thereby actually reducing the diversity of resident types. Close to a singular strategy however, other phenomena come into play. Singularities fall into several categories, one possibility being the classical *ESS*, known i.a. from evolutionary game theory. What makes adaptive dynamics an interesting evolutionary framework, is the existence of other, naturally occurring, types of singularities. Foremost among them is the *branching point*, a singularity that is attracting (for the monomorphic dynamics) but in the proximity of which selection is disruptive. Here selection acts such that a newly established mutant does not drive its progenitor to kingdom come. Subsequent mutants do however wipe out their ancestors, so that after a few mutation events two distinct resident populations will sit on opposite sides of the singularity. Over evolutionary time, these populations form two “branches” of co-viable types, that evolve away from the singularity. Such a splitting of genetic lines through an intrinsic process has an obvious appeal as a model for (the initiation of) speciation.

Research into the mathematical properties of adaptive dynamics models has led to several insights. Foremost there is the canonical equation as formulated by Dieckmann & Law (1996), which predicts the speed of evolution as a function of the underlying individual processes. That formulation so far allows only community dynamics modelled by ODEs. The equation basically predicts evolution under directional selection, at some distance from singularities. In this paper we first extend the applicability of the canonical equation to physiologically structured populations, and later look what happens at those points where the approximation fails to hold true. To this end we devise an expansion near the singular points of the fitness function. The formalism in which we do the calculations is set down in the following subsection.

1.2 Physiologically structured population models

As described for example by Diekmann *et al.* (2003), general physiologically structured models assume few restrictions on population dynamical mechanisms other than (local) well-mixedness. We restrict our attention to the special case of structured populations with point equilibria in the resident population dynamics. In

that case, the following definitions shape the modelling framework:

- \mathbf{b} is the column vector of *birth rates*, with as components the steady rates at which individuals are born with state-at-birth specified by the component number.
- \mathbf{I} is a vector describing the *environmental conditions* as far as they play a role in the (direct or indirect) interactions between the individuals. The defining requirement is that individuals are independent of one another when \mathbf{I} is given. In this paper, we restrict our attention to community dynamics with point equilibria, so \mathbf{I} is time-independent.
- $\mathbf{L}(\mathbf{X}, \mathbf{I})$ is the *next-generation matrix*. The matrix component $\mathbf{L}(\mathbf{X}, \mathbf{I})_{lm}$ is the expected number of offspring with birth state l born over the lifetime of an individual with trait vector \mathbf{X} that was born with state m , given steady environmental conditions as specified by \mathbf{I} .
- $\mathbf{G}(\mathbf{X}, \mathbf{I})$ is the *feedback matrix*. The matrix component $\mathbf{G}(\mathbf{X}, \mathbf{I})_{tl}$ is the lifetime contribution to the t^{th} component of \mathbf{I} by an individual born in state l with trait vector \mathbf{X} , given steady environmental conditions as specified by \mathbf{I} .

The terminology above implies that we are only considering a finite number of possible birth states and of environmental dimensions, although there are no conceptual reasons for this restriction. For example, single celled organisms will inherit their size from their mother (about half her size at the time of division), which implies a continuous range of sizes for the newborns. Similarly, sexual reproduction leads to infinite dimensional environments usually, because each trait can potentially partner with infinitely many other traits to make up a diploid individual.

We restrict ourselves to finite dimensional environments and birth flows, to make sure that our formal calculations make mathematical sense; there is no a priori reason why a generalization would not be possible or desirable (see e.g. Diekmann & Gyllenberg (submitted) for modelling work without these limitations).

We actually do go out of our way to make such a generalization as natural as possible: by defining *generalized individuals* as those individuals born in one focal birth state plus all their descendants born in the remaining states, any population dynamics with a finite number of birth states can be mapped to one with a single birth state (cf. Roberts & Heesterbeek, 2003). While such a transformation would shorten some of the proofs here, we did not want to use it as it cannot be extended to infinitely many birth states. On top of that, the rewritten form would severely hamper the interpretation of the components in the formulæ to come.

For a community under the above conditions with N types present, equilibrium means that each generation precisely replaces the previous generation, and that the feedback is such that it exactly re-creates the environment as experienced by the organisms:

$$\begin{cases} \mathbf{b}_i &= \mathbf{L}(\mathbf{X}_i, \mathbf{I}) \mathbf{b}_i \quad (\forall i \in \{1, 2, \dots, N\}) \\ \mathbf{I} &= \sum_{j=1}^N \mathbf{G}(\mathbf{X}_j, \mathbf{I}) \mathbf{b}_j \end{cases} \quad (1)$$

It is clear that the first equation is equivalent to stating that at equilibrium, a population is either extinct or the expected lifetime offspring production R_0 of its indi-

viduals is one, since R_0 is the dominant eigenvalue of L . The second equation states nothing more than that all individuals together must contribute to the environment in such a way that it remains unchanged. Diekmann *et al.* (2003) have shown that the equilibrium conditions of most population models in the literature may be cast in the above form (1), a claim hinging on the considerations below about uncoupling the feedback loop that connects populations and individuals. It will however often be an arduous task to rewrite a given model representation into this form while the individual-based recipe for arriving at Equation (1) is easy.

It should be stressed that Equation (1) is an equilibrium equation, written in terms of the next-generation operator L together with the feedback operator G . Discrete time non-overlapping generations models are typically specified by giving matrix valued functions L and G for all possible environmental conditions, including non-equilibrium population states. Then Equation (1) is immediately found as the corresponding equilibrium condition. For continuous time models, Diekmann *et al.* (2001, in press) have shown how an extension into nonequilibrium conditions can be done through reformulating the dynamics using an integral kernel formulation, which can be a challenging task in concrete cases.

From a biological point of view, the environment I is more readily observed as the effect of the community on the world (the *environmental output* I_{out}) than vice versa (the *environmental input* I_{in}), as the rest of this subsection will elaborate.

The idea behind physiologically structured population models as put forward by Diekmann *et al.* (2001, 2003), is to characterize the populations by their birth flow vectors; that is, we register the flux of births b_i of the i^{th} population differentiated according to the possible birth states. The per capita lifetime offspring production depends on the condition of the world, I_{in} , and on the type X_i of the individual, so that in the special case where the world is constant, a given cohort b_i produces $L(X_i, I_{in})b_i$ offspring over its lifetime, for some matrix function L .

The output I_{out} registers the total influence the individuals have on the environment. This clearly depends on the state of the community; for example, an individual in a virgin (i.e., devoid of competitors) environment may consume more and have far more offspring than an identically born individual that is put in an overcrowded world. It is also clear that this output should scale with the number of individuals there are, as it is an instantaneous output: two individuals will have exactly twice the influence of a single individual if they are kept under exactly the same conditions. Furthermore, this influence depends on the type of the individuals concerned. Therefore we postulate that the output must depend on the input in the following way that accounts for the scaling argument: $I_{out} = \sum_j G(X_j, I_{in})b_j$.

All other things being equal, the state of the world must be the result of the compounded influence of all the individuals. Thus the condition I_{in} depends only on the output I_{out} of the population, through some conversion function F that accounts for the effect of the environmental dynamics. Hence the feedback loop of the community's influence on itself is closed.

All told, we have the following system to solve, where the last equation is the equilibrium condition:

$$I_{out} = \sum_j G(X_j, I_{in})b_j \quad I_{in} = F(I_{out}) \quad \forall i: b_i = L(X_i, I_{in})b_i$$

Here we see that we can eliminate one equation and have only I_{out} and \mathbf{b} as unknowns, since

$$I_{out} = \sum_j \tilde{G}(X_j, I_{out}) \mathbf{b}_j \quad \forall i: \mathbf{b}_i = \tilde{L}(X_i, I_{out}) \mathbf{b}_i$$

where the matrix functions \tilde{G} and \tilde{L} are the compositions $G \circ (\text{id} \times F)$ and $L \circ (\text{id} \times F)$ respectively. We will denote I_{out} simply as I and drop the tilde in the notation of G and L , which gives us the equations introduced at the beginning of this subsection. It is clear that an arbitrarily complicated amount of biological detail can be put in the functions G and L , justifying the claim that this is a very flexible modelling framework. We do however assume a certain level of smoothness (namely that G and L are thrice continuously Fréchet differentiable functions), to guarantee the existence of chain rules and to justify our expansion arguments by the implicit function theorem.

1.3 Notations

Throughout this paper, we will deal with communities where a finite number of types are present. These are numbered from 1 to N and denoted by their respective trait vectors X_1 up to X_N . The community as a whole is denoted by \mathbb{X} and it is interpreted either as a set of trait vectors $\mathbb{X} := \{X_1, X_2, \dots, X_N\}$, or as an N -column matrix $\mathbb{X} := [X_1 \ X_2 \ \dots \ X_N]$, depending on the context. As a convention,

- the indices i, j, k will exclusively refer to resident types (which were said to range from 1 to N),
- the indices l, m, n are reserved for denoting birth states in a structured population model, and if only a finite number of different birth states exist they are numbered from 1 to d ,
- the indices a, b will only be used to indicate the scalar trait components that make up a trait vector, which we take to be z -dimensional,
- the indices s, t always relate to environmental components, where the dimension of the environment I is r (cf. Subsection 1.2).

Thanks to these rules, a summation index implicitly has a range attached to it, as for example \sum_i can be unambiguously read as $\sum_{i=1}^N$. Our aim however was not a slight notational simplification, but to make calculations easier to verify.

As far as possible, we adhere to the convention (e.g. Beccari, 1997) that matrices and tensors are denoted by an upright, sans serif capital like M , vectors with a bold Italic letter like \mathbf{b} or V , and scalars with a Greek or Roman letter like λ, Π, t or R_0 . A consequence of this convention is that for example the l^{th} component of the birth flow vector \mathbf{b} must be written as b_l , and one cannot mistake the matrix C_{11} for the first diagonal element C_{11} of another matrix C .

To help the reader, brackets around matrix-valued expressions are square, while vector- or scalar-valued expressions are signalled by round brackets; thus matrix components are indicated as e.g. $[C_{11}]_{ab}$.

Furthermore, column vectors with all entries equal to 1 (resp. 0) will be denoted by **1** (resp. **0**), where the dimension will be clear from the context. Similarly, the zero matrix is denoted by 0 and the identity matrix by id.

Please see Subsection 3.1 for additional notations restricted to Section 3.

1.4 Assumptions

Here we present an overview of the assumptions scattered throughout this paper. The impact of some of these conditions cannot be meaningfully discussed at this point, as the relevant concepts have not been presented yet. Hence we refer the reader to the subsections where the assumptions are stated as preliminary to specific calculations. One notes that most are stated in the Introduction, and hence are necessarily active from there onwards until the end. Assumptions made in one of Sections 2 or 3 do not apply to the other section, but are necessarily active in Section 4.

First and foremost we abide by the core premises of the adaptive dynamics framework: individuals have heritable traits that influence their life histories, the resident community is large and well-mixed while both mutants and mutation events are rare (1.1), plus the additional assumption that the community has a global point attractor, or alternatively that it has locally unique point attractors while mutational steps are sufficiently small so as to guarantee that after a successful invasion the community moves to a natural continuation of its earlier attractor (1.1, 1.2, 2.2). The basic process from which the deliberations start is derived in the following manner, as a limit of a fully individual-based community dynamics. Introducing a parameter Ω called *system size* that scales inversely with the effects of interactions between the individuals in the community, the number of individuals must be about proportional to Ω . The limit to consider is that where Ω becomes large while the mutation probability per birth event gets so small that a mutant strategy reaching establishment becomes a rare event on the community dynamical timescale. To compensate for this rarity, time is rescaled so that the number of different established mutants per unit of time stays $O(1)$; this new timescale is called the *evolutionary timescale*. (With increasing Ω , the rescaling must be such that the rate of mutations reaching establishment decays sufficiently slowly to guarantee that the rescaled asymptotic rate at which the community goes extinct through demographic fluctuations, decreases to zero.) On the ecological timescale, the community relaxes to its deterministic attractor before the next mutant comes along. This attractor can be calculated from the equilibrium equations (1) scaled by $1/\Omega$, i.e., when b is read as a density per time and I as a density. The described combination of a limit and a rescaling allows a reduced process description, where at almost all times there is but a small set \mathbb{X} of trait values around, in densities given by the corresponding deterministic community attractor. Such a process has been variously referred to as adaptive dynamics (Metz *et al.*, 1996), oligomorphic dynamics (Dieckmann & Law, 1996) and trait substitution process (Geritz *et al.*, 1998). The validity of the limit has been proven for some specific Markovian models by Champagnat (2006). For general physiologically structured populations there is as yet no proof for the step from the underlying stochastic models to the deterministic models considered by Diekmann *et al.* (2001, 2003). In our paper, we take the

existence of the limit on faith, and from this vantage point study situations where mutational steps are small and all types present in the population are very similar. All order statements refer to the scale of the differences in the traits under consideration, between mutant and ancestor in Section 2 and mutant and residents in Section 3. In Section 4 however we also consider situations with similar residents and mutational steps that are of an even smaller order.

In addition, we impose regularity conditions that are inherent to our modelling approach: a thrice continuously differentiable dependence of the demographic parameters on trait values and environment (1.2, 3.3), offspring distributions that decay sufficiently quickly to have uniformly bounded third moments (which amounts to the thrice differentiability of the generating function) (2.5), and no birth states with zero birth flow for the sole singular resident (3.4). Finiteness of the number of birth states (1.2) can also be put into this class of requirement, although it is fundamental to our approach only in the sense that it is required by our specific machinery (i.e. vectors and matrices, instead of distributions and operators).

Lastly, we inherit assumptions made by Dieckmann & Law (1996), as one of our aims is to see how the canonical equation changes when their premise of ODE population regulation is dropped: unbiased mutations (2.6), and a stochastic trait substitution process that becomes deterministic when the mutational steps become small while time is rescaled such that on the new scale the rate of trait change stays $O(1)$ (2.3).

2 The canonical equation of directional adaptive dynamics

2.1 Unstructured populations

The *canonical equation of adaptive dynamics*, first derived by Dieckmann & Law (1996) for ODE population models, is a first order approximation for the average speed of evolution. The rate of trait change per time of the i^{th} type in a community is

$$\frac{dX_i}{dt} \approx \frac{1}{2} \hat{n}_i \mu_i(X_i) M(X_i) \left. \frac{\partial s_{\mathbb{X}}(Y)}{\partial Y} \right|_{Y=X_i}^T \quad (2)$$

where the *mutational covariance matrix* M at trait value X_i is defined as $M(X_i) := \int VV^T \mathcal{M}(V, X_i) dV$, an expression that depends on the multivariate *distribution of mutational steps* $\mathcal{M}(V, X_i)$ from X_i to $X_i + V$. The speed of evolution is thus seen to be proportional to the mutation probability per birth event μ_i , the equilibrium population size \hat{n}_i in the given N -resident community \mathbb{X} , and the fitness gradient $\left(\left. \frac{\partial s_{\mathbb{X}}(Y)}{\partial Y} \right|_{Y=X_i} \right)^T$.

At the singular strategies the fitness gradient becomes zero. Hence, close to the singular strategies the first and second order terms are of similar size, and the approximation embodied by the canonical equation loses its descriptive power. Champagnat (2003, 2004) has proven that under some additional technical conditions, trait substitution processes that are based on population models with ODE deterministic skeletons sporting globally attracting point equilibria do converge

weakly to the deterministic process captured by the canonical equation. His proof applies without change to the general case except for some small changes in the formulas, to be provided in the next subsections. Simulations suggest that away from the singular points, the pictures derived by solving the canonical equation capture the temporal development of the trait composition of the underlying individual-based process rather well (e.g. Fig. 2 in Dieckmann & Law, 1996; Fig. 10 in Metz *et al.*, 1996) in a fair-sized parameter volume close to the origin of the three-dimensional parameter space spanned by mutational step size, inverse system size and mutation probability per birth event.

2.2 Aims of this section

Where Dieckmann & Law (1996) formulated the canonical equation for ODE models, we aim here to relax that limitation by considering the far wider class of physiologically structured population models, and thus to recover a generalized form of Equation (2). As the canonical equation (in both formulations) fails to capture the trait substitution behaviour of systems near evolutionary singularities, a separate part of this paper will deal with singularities (Section 3).

Our goal is to find out how a community (or more precisely, a set of trait values) will evolve, and at what rate. The basic scenario is the following: we start by considering a coalition of N different trait values that are the strategies of residents, which form a community that is at equilibrium. This fixed point attractor is presumed to exist for the community as a whole, as a unique set of positive equilibrium densities for all N trait values. When a mutant with positive invasion fitness appears, several things may happen. Usually, it will fail to get established in the community due to stochasticity, and will disappear. However, if it does get established, it will remove its parent from the population through competitive exclusion. Then the $N - 1$ remaining residents plus the invader will have their densities equilibrate at new values, assumed to be positive and unique to the given set of N strategies. The first situation means that the community returns to its earlier state, the second that a small evolutionary step has taken place. Mutation events are by assumption so rare, that the community has relaxed to its attractor before the next mutation event takes place. As the cycle of mutation followed by possible invasion and equilibration can occur over and over again, this invasion/replacement dynamics provides a scenario where evolution proceeds through a great number of small trait changes.

The above setting assumes that the mutating trait value is not (close to) singular nor close to the boundary of the coexistence region, and that the population dynamics is sufficiently well-behaved, so that the dictum “invasion implies substitution” holds (Geritz *et al.*, 2002; Dercole, 2002; Meszéna *et al.*, 2005; Geritz, 2005; Dercole & Rinaldi, in press). We stress here that we restrict ourselves to point attractors, as it is not clear yet to which extent the rule holds for more complicated attractors than fixed points and limit cycles. Thus special situations, where either the mutant co-exists indefinitely with its parent or where it drives several residents to extinction, are explicitly excluded from this paper’s analysis. Also, in higher dimensional trait spaces there are unavoidable exceptions to the dictum: several selectively neutral mutants (in directions orthogonal to the invasion gradient) may briefly establish a

foothold, until the next successful mutant in the direction of the invasion gradient kills off its progenitor along with those recent invaders. But these problematic scenarios are essentially negligible, as they represent a fraction of the total invasion events that vanishes in the limit of infinitesimal mutation steps.

From Geritz *et al.* (2002), Meszéna *et al.* (2005) and Dercole & Rinaldi (in press) one learns that the assumption of uniqueness of the community fixed point is only made for mathematical convenience, as the community attractors before and after successful invasions are arbitrarily close for sufficiently small mutation steps. Thus the invader inherits the attractor of the resident it replaces, as the new attractor lies on the continuation of the older. The existence and (local) uniqueness is therefore guaranteed under the mild restrictions put forward by Geritz *et al.* (2002), which essentially are absence of population dynamical bifurcations and sufficient smoothness of the model ingredients. If several fixed point attractors exist for a given set of trait vectors, they necessarily lie on distinct branches of solutions to the population dynamical equilibrium equations. Distinguishing such multiple attractors is therefore an administrative rather than mathematical problem, as the initial conditions (specifically, the earlier community attractors) determine in which basin of attraction the community finds itself.

The appearance of mutants, governed by the probability per birth event of a mutation and the distribution \mathfrak{M} of mutational steps, and their eventual success or failure at establishment is inherently stochastic. This means that trait values are stochastic and time-dependent variables that we can characterize by the probability of the community being in a given state at a given time. The essential information to determine this probability is the rate at which the community's state is expected to change from one state to another, an issue we will turn our attention to over the following paragraphs.

2.3 The deterministic path

We can now view the change in community composition as a Markov process, with a probability $\Pi(\mathbb{X}, t)$ that the population is in state \mathbb{X} at a given time $t > 0$. From the interpretation as a Markovian dynamics, there are instantaneous transition rates $\pi(B, A)$ from any state A to any B . The connection between probability distribution and transition rates is found by observing that the rate of change in Π must consist of two terms at any time, a gain in probability mass from other states into \mathbb{X} , and a loss from transitions to other states (the Kolmogorov forward equation):

$$\frac{\partial \Pi(\mathbb{X}, t)}{\partial t} = \int (\pi(\mathbb{X}, \mathbb{X}') \Pi(\mathbb{X}', t) - \pi(\mathbb{X}', \mathbb{X}) \Pi(\mathbb{X}, t)) d\mathbb{X}' \quad (3)$$

For any observable ψ of our dynamical system, the expected value at time t is defined as the ensemble average

$$\mathbb{E}(\psi(\mathbb{X})) := \int \psi(\mathbb{X}) \Pi(\mathbb{X}, t) d\mathbb{X}$$

Applying the above definition with ψ the identity and using the Markov property above, we find the following equality:

$$\begin{aligned}\frac{d}{dt} \mathbb{E}(\mathbb{X}) &= \int \mathbb{X} \frac{\partial \Pi(\mathbb{X}, t)}{\partial t} d\mathbb{X} \\ &= \iint \mathbb{X} (\pi(\mathbb{X}, \mathbb{X}') \Pi(\mathbb{X}', t) - \pi(\mathbb{X}', \mathbb{X}) \Pi(\mathbb{X}, t)) d\mathbb{X}' d\mathbb{X} \\ &= \iint (\mathbb{X}' - \mathbb{X}) \pi(\mathbb{X}', \mathbb{X}) \Pi(\mathbb{X}, t) d\mathbb{X}' d\mathbb{X} \\ &= \mathbb{E}(\mathbb{A}_\epsilon(\mathbb{X}))\end{aligned}\tag{4}$$

where we introduce the operator $\mathbb{A}_\epsilon(\mathbb{X}) := \int (\mathbb{X}' - \mathbb{X}) \pi(\mathbb{X}', \mathbb{X}) d\mathbb{X}'$, and the parameter ϵ that is proportional to the mutation step size (so the distance between a mutant and its ancestor is $O(\epsilon)$). The solution to Equation (4) is called the *mean path* of \mathbb{X} . Sadly this equation is not a self-contained equation in $\mathbb{E}(\mathbb{X})$, causing much mathematical grief (or joy, depending on one's disposition). To dodge this issue, the *deterministic path* is introduced, which is the solution to this variation on Equation (4):

$$\frac{d}{dt} \bar{\mathbb{X}} = \mathbb{A}_\epsilon(\bar{\mathbb{X}})\tag{5}$$

The mean and deterministic paths would coincide if the distribution of \mathbb{X} is concentrated in a point or if the integral on the right hand side is linear in \mathbb{X} , but neither is true in general. Whether the deterministic path is a valid approximation of the mean path clearly depends on whether it is dominated by the first order term of \mathbb{A}_ϵ or not. Intuitively one expects this to be true, as the adaptive dynamics modelling approach has evolution proceeding through very many very small steps. Thus with decreasing mutational step size, it takes more and more mutation steps to cover the same distance in trait space and a law-of-large-numbers effect should hold sway in the limit $\epsilon \rightarrow 0$. Dieckmann & Law (1996) assumed this to be a valid approximation, relying on simulations plus the considerations of van Kampen (1981). More recently Champagnat (2003, 2004) has proven the weak convergence of the stochastic trait substitution process to the solution of Equation (6). Apart from a number of more technical assumptions, all papers mentioned assume ODE population dynamics and the existence of a global point attractor for the deterministic community dynamics. Furthermore, the many-small-steps argument suggests that the error around the deterministic approximation is Gaussian with variance proportional to ϵ . This heuristic argument is confirmed by Champagnat (2003, 2004) who derives the full equations for this Gaussian error process as well.

We will simplify the notations $\mathbb{E}(X)$ and \bar{X} to X henceforth, and similarly for the community \mathbb{X} , so Equation (5) is rewritten as

$$\frac{d}{dt} \bar{X} = \mathbb{A}_\epsilon(\bar{X})\tag{6}$$

One should not lose sight of the fact that for the remainder of this section, any strategy or community not marked by a prime (' \prime ') should be read as the value predicted by the deterministic limit; hence the mutation step $V := X'_i - X_i$ is the difference between a potential stochastically realized new strategy and its deterministically calculated originator.

The next step in capturing the dynamics is to divide and conquer the transition probabilities.

2.4 The transition probabilities

Since we consider rare mutations, any transition must be a mutation affecting a single strategy vector. Therefore nontrivial transition rates are of the form $\pi_o(\mathbf{X}'_i, \mathbf{X}_i, \mathbb{X})$, representing the rate at which the i^{th} resident in a given community \mathbb{X} switches from state \mathbf{X}_i to \mathbf{X}'_i . Thus if we interpret \mathbb{X} as the matrix $[\mathbf{X}_1 \mathbf{X}_2 \cdots \mathbf{X}_N]$, then the i^{th} column of the matrix equation describing the deterministic path (5) simplifies to

$$\frac{d}{dt} \mathbf{X}_i = \mathbb{A}_e^i(\mathbb{X}) = \int (\mathbf{X}'_i - \mathbf{X}_i) \pi_o(\mathbf{X}'_i, \mathbf{X}_i, \mathbb{X}) d\mathbf{X}'_i \quad (7)$$

Our next aim must therefore be to derive analytical expressions for the right hand side of Equation (7). As a first step, we split π_o into separate factors by observing that mutation and selection are independent processes, hence these transition probabilities are the product of the appearance rate of mutants and their probability of establishment:

$$\begin{aligned} \pi_o(\mathbf{X}'_i, \mathbf{X}_i, \mathbb{X}) &= (\text{production rate of mutants } \mathbf{X}'_i) (\text{establishment chance of } \mathbf{X}'_i) \\ &= \overbrace{(\text{birth rate of } \mathbf{X}_i \text{ types}) (\text{mutation chance } \mathbf{X}_i \rightarrow \mathbf{X}'_i)}^{} P(\mathbf{X}'_i, \mathbb{X}) \\ &= \overbrace{\lambda(\mathbf{X}_i, \mathbb{X})}^{} \hat{n}_i \overbrace{\mu(\mathbf{X}_i)}^{} \overbrace{\mathfrak{M}(\mathbf{X}'_i - \mathbf{X}_i, \mathbf{X}_i)}^{} P(\mathbf{X}'_i, \mathbb{X}) \end{aligned} \quad (8)$$

We stress again that the values above are population averages, while \hat{n}_i stands for the equilibrium density of the i^{th} type. The probability P of establishment is the expected outcome of a branching process. This rather complicated beast, which depends heavily on the underlying population model, will be resolved in the next subsection. The other factors are easy to understand. The appearance rate of mutants (that is, \mathbf{X}'_i -type individuals that have \mathbf{X}_i -type parents) is just the total offspring production by \mathbf{X}_i -type parents, times the mutation rate of \mathbf{X}_i into \mathbf{X}'_i . This comes from the fact that we have assumed the mutational steps to be small, so only the i^{th} type can be the ancestor of our mutant. The total production of \mathbf{X}_i individuals is (by definition) the instantaneous per capita birth rate of such individuals, times their equilibrium density. The mutation chance $\mathbf{X}_i \rightarrow \mathbf{X}'_i$ is the probability per birth event of mutating for an \mathbf{X}_i -type individual, times the mutation distribution around this trait value; $\mathfrak{M}(V, \mathbf{X}_i)$ is the probability density of a mutation from \mathbf{X}_i to $\mathbf{X}_i + V$.

In a closed system at equilibrium, the per capita birth rate is the inverse of the expected lifespan. This was termed the “microcosm principle” by Mollison (1995), and it holds for the stochastic systems we consider. The argument is that in a large population ergodically fluctuating around its attracting density, the density is the product of the influx of new individuals and the time they stay in the population. Since the population is closed, the newborns correspond to the influx of residents,

and only death ends a resident's stay. Hence

$$\begin{aligned}\mathbb{E}(\text{density}) &= \mathbb{E}(\text{influx of individuals per area}) \mathbb{E}(\text{duration of stay}) \\ &= \mathbb{E}(\text{per capita birth rate} \times \text{density}) \mathbb{E}(\text{lifespan}) \\ &= \mathbb{E}(\text{per capita birth rate}) \mathbb{E}(\text{density}) \mathbb{E}(\text{lifespan})\end{aligned}\quad (9)$$

where the last step follows from our assumptions of large system size and thrice differentiable model ingredients. So we conclude that the expected lifespan T_s is the inverse of the birth rate:

$$T_s := T_s(X_i, \mathbb{X}) = (\mathbb{E}(\text{per capita birth rate}))^{-1} = \lambda(X_i, \mathbb{X})^{-1} \quad (10)$$

We can substitute this result in our breakdown of π_o (8) and move on to a study of $P(X'_i, \mathbb{X})$.

2.5 The establishment probability

To determine the establishment probability of a given mutant, we recall from the introduction on adaptive dynamics (Subsection 1.1) a statement about the link between branching processes and adaptive dynamics: under very general conditions, the probability $P(Y, \mathbb{X})$ of an individual with strategy Y establishing itself in a given community \mathbb{X} , is related to that type's invasion fitness by

$$P(Y, \mathbb{X}) > 0 \Leftrightarrow s_{\mathbb{X}}(Y) > 0 \quad (11)$$

(cf. Haccou *et al.*, 2005)

We now require a quantitative relationship between these entities. We will derive this relation in two steps: first we relate P to the lifetime offspring production R_0 , and then R_0 to the fitness s . For the first part, we will use some techniques from the theory of branching processes. By assumption we started with the large equilibrium community \mathbb{X} and a single mutant. Thus the community resides on its attractor as its size makes deviations from the mean too small to be significant, and a deterministic description is valid. This constitutes the environment of the branching process that describes the demography of the initial mutant and its (still rare) offspring, which are too rare to influence each other. An approximation first heuristically derived (as a generalization of a result of Haldane (1927)) by Ewens (1969) for single type branching processes (12), and its multitype counterpart (14), gives our first relation as we shall presently see.

If there is only a single possible birth state in our (at this timescale) constant environment, and a small but positive scalar ϱ so that the lifetime reproductive output is $R_0 = 1 + \varrho$, then our single-type process is called *slightly supercritical*. If the probability generating function $g(z, \varrho)$ of the offspring distribution is three times continuously differentiable in its arguments, then

$$P(X'_i, \mathbb{X}) = \frac{2\varrho}{\sigma^2} + O(\varrho^2) = \frac{2 \log R_0}{\sigma^2} + O(\varrho^2) \quad (12)$$

where R_0 and σ^2 are respectively the mean and variance of the mutant's offspring distribution in the community. For further information see Athreya (1992), and also Eshel (1981) and Hoppe (1992).

Unfortunately the above result does not suffice, as we want to include population dynamics where multiple birth states are possible. In cases where there are d possible birth states, we denote by the stochastic variable ξ_{lm} the number of offspring born in state l to a parent that was itself born in state m . Then $\mathbb{E}(\xi_{lm}) = [\mathbf{L}]_{lm}$ relates these random variables to the reproduction matrix we introduced at the start of Subsection 1.2. Furthermore, R_0 is in such multitype models the dominant eigenvalue of the \mathbf{L} matrix, and we denote by \mathbf{u} and \mathbf{v}^\top respectively the right- and left eigenvectors of \mathbf{L} belonging to R_0 :

$$R_0 = \lambda_d(\mathbf{L}) = \mathbf{v}^\top \mathbf{L} \mathbf{u} \quad (13)$$

where we normalized \mathbf{u} and \mathbf{v} by requiring $\sum_l |u_l| = 1$ and $\mathbf{v}^\top \mathbf{u} = 1$ (see e.g. Caswell, 2001).

One should be mindful that this notation for ξ_{lm} reverses the order of the subscripts with respect to the traditional branching processes notation. The definition of \mathbf{u} and \mathbf{v} is similarly reversed, so that in both notations \mathbf{u} is the stable type distribution, and \mathbf{v} the vector of the (generationwise) *reproductive values*.

Similarly, in the above d -type situation for a slightly supercritical process, the chance P_l for a single mutant born in state l of establishing itself can be written as

$$P_l(\mathbf{X}'_i, \mathbb{X}) = \frac{2\varrho}{B} v_l + O(\varrho^2) = \frac{2 \log R_0}{B} v_l + O(\varrho^2) \quad (14)$$

with $B := \sum_{l'mn} u_{l'} v_m v_n \mathbb{E}(\xi_{ml'} (\xi_{nl'} - \delta_{mn}))$ where δ is the Kronecker delta (i.e., $\delta_{ll} = 1$ and $\delta_{lm} = 0$ if $l \neq m$) and conditions similar to those of the single state case (12) are assumed to be satisfied (see Athreya (1993) and Eshel (1984) for further details). Clearly B and both eigenvectors depend on ϱ , as does R_0 . It is easily seen that if $d = 1$, the earlier version is recovered, as it should be. We have mainly stated the (better known) single-type result (12) earlier on, to hint at an interpretation of B as a variance. Bearing in mind that \mathbf{u} and \mathbf{v}^\top are the right- and left eigenvectors of \mathbf{L} , we find

$$\begin{aligned} B &= \sum_l u_l \mathbb{E} \left(\sum_{mn} v_m v_n \xi_{ml} \xi_{nl} \right) - \sum_{lm} u_l v_m^2 \mathbb{E}(\xi_{ml}) \\ &= \sum_l u_l \mathbb{E} \left(\left(\sum_m v_m \xi_{ml} \right)^2 \right) - \sum_{lm} v_m^2 \mathbb{E}(\xi_{ml}) u_l \\ &= \sum_l u_l \left(\text{Var} \left(\sum_m v_m \xi_{ml} \right) + \left(\mathbb{E} \left(\sum_m v_m \xi_{ml} \right) \right)^2 \right) - \sum_m v_m^2 R_0 u_m \\ &= \sum_l u_l \text{Var} \left(\sum_m v_m \xi_{ml} \right) + \sum_l u_l v_l^2 R_0^2 - \sum_m v_m^2 R_0 u_m \\ &= \sum_l u_l \text{Var} \left(\sum_m v_m \xi_{ml} \right) + O(\varrho^2) \end{aligned} \quad (15)$$

where the $O(\varrho^2)$ approximation holds since $R_0^2 - R_0 = \varrho^2 + \varrho$. By defining

$$\sigma^2 := \sum_l u_l \text{Var} \left(\sum_m v_m \xi_{ml} \right) \quad (16)$$

we can replace B with the variance-like quantity σ^2 to bring out the close similarity of the multiple birth state case (14) with the simpler case (12):

$$P(\mathbf{X}'_i, \mathbb{X}) = \sum_n P_n(\mathbf{X}'_i, \mathbb{X}) u_n = 2 \frac{\log R_0}{\sigma^2} + O(\epsilon^2) \quad (17)$$

since $\sum_n v_n u_n = 1$, which concludes the first step in quantifying the relation (11) between establishment chance $P(\mathbf{Y}, \mathbb{X})$ and invasion fitness $s_{\mathbb{X}}(\mathbf{Y})$.

The second step is to determine the relation between R_0 and $s_{\mathbb{X}}(\mathbf{Y})$. To derive this, we consider the *birth kernel* notation of a general model. If we denote the environment set by the community \mathbb{X} as $I_{\mathbb{X}} := I(\mathbf{X}_1, \mathbf{X}_2, \dots, \mathbf{X}_N)$, then there exists a matrix function Λ with entries $[\Lambda(\mathbf{X}'_i, I_{\mathbb{X}}, a)]_{lm}$ that are the expected number of offspring born in state l to a \mathbf{X}'_i -type invader, newly born in state m , before the invader reaches age a , in the equilibrium community \mathbb{X} (cf. Diekmann *et al.*, 2003). The link with the lifetime offspring production matrix is obviously that $[\Lambda(\mathbf{X}'_i, I_{\mathbb{X}}, \infty)]_{lm} = [\mathbf{L}]_{lm} = \mathbb{E}(\xi_{lm})$. Using this notation, the invasion fitness $s_{\mathbb{X}}(\mathbf{X}'_i)$ is the (generally unique) solution for ρ of the Euler-Lotka equation

$$\lambda_d \left(\int_0^\infty e^{-\rho a} \Lambda(\mathbf{X}'_i, I_{\mathbb{X}}, da) \right) = 1 \quad (18)$$

where λ_d is the dominant eigenvalue operator. In Appendix A we show how to extract from Equation (18) the following relationship:

$$\log R_0 = T_f(\mathbf{X}_i, \mathbb{X}) s_{\mathbb{X}}(\mathbf{X}_i + \mathbf{V}) + O(||\mathbf{V}||^2) \quad (19)$$

where T_f is the *average age at giving birth* (100). If we approximate $s_{\mathbb{X}}(\mathbf{X}'_i)$ using the fitness gradient, we can finally formulate the establishment probability (in both single (12) and multitype (17) cases) as

$$P(\mathbf{X}'_i, \mathbb{X}) = \frac{2 T_f s_{\mathbb{X}}(\mathbf{X}'_i)}{\sigma^2} + O(\epsilon^2) \quad (20)$$

$$= \frac{2 T_f}{\sigma^2} (\mathbf{X}'_i - \mathbf{X}_i)^T \frac{\partial s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}} \Big|_{\mathbf{Y}=\mathbf{X}_i} + O(\epsilon^2) \quad (21)$$

As this last expression contains the factor $\mathbf{X}'_i - \mathbf{X}_i$, we are free to evaluate T_f and σ^2 at \mathbf{X}_i without changing the order of the approximation. Hence the mutant trait value \mathbf{X}'_i only appears in the mutation step $\mathbf{V} := \mathbf{X}'_i - \mathbf{X}_i$.

Bear in mind that this result only holds for positive P , as such is the starting point of the approximation formula (14).

2.6 The canonical equation for physiologically structured population models

After this divide-and-conquer campaign, we can substitute the factors that make up the transition rates (8), (10), (21) into the equation describing the deterministic

path (7):

$$\begin{aligned}\mathbb{A}_\epsilon^i(\mathbb{X}) &= \int (\mathbf{X}'_i - \mathbf{X}_i) \pi_o(\mathbf{X}'_i, \mathbf{X}_i, \mathbb{X}) d\mathbf{X}'_i \\ &= \frac{\hat{n}_i \mu}{T_s} \int (\mathbf{X}'_i - \mathbf{X}_i) \mathfrak{M}(\mathbf{X}'_i - \mathbf{X}_i, \mathbf{X}_i) P(\mathbf{X}'_i, \mathbb{X}) d\mathbf{X}'_i \\ &= \frac{T_f}{T_s} \frac{2 \hat{n}_i \mu}{\sigma^2} \int V \mathfrak{M}(V, \mathbf{X}_i) V^\top \left. \frac{\partial s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}} \right|_{\mathbf{Y}=\mathbf{X}_i} dV + O(\epsilon^3)\end{aligned}\quad (22)$$

where ϵ is the average mutation step size. The order term comes from the estimate of the establishment probability (21) that introduces an error equal to a constant times $\int V \mathfrak{M}(V, \mathbf{X}_i) O(||V||^2) dV$.

Equation (22) allows us finally to formulate the canonical equation for structured population models with unbiased mutation distributions, giving an approximate rate of change under evolutionary selection for traits of the i^{th} resident in a multitype community \mathbb{X} in the limit of infinitesimal mutational step size, as

$$\mathbb{A}_0^i(\mathbb{X}) = \frac{T_f}{T_s} \frac{\hat{n}_i \mu}{\sigma^2} \mathbf{M} \left. \frac{\partial s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}} \right|_{\mathbf{Y}=\mathbf{X}_i} \quad (23)$$

We repeat that all factors in Equation (23) are expected values, and that the canonical equation characterizes the deterministic, not the mean, path. One sees that most of the parameters in the canonical equation (23) depend both on the strategy \mathbf{X}_i and the entire community \mathbb{X} ; the exceptions are μ and \mathbf{M} , which only depend on the strategy.

In the last transition, a factor 2 may seem to be lost. Its disappearance stems from the fact that the approximation formula (14) only holds for supercritical processes, where $\log R_0 > 0$, but in other cases we must substitute a zero. As the sign of $\log R_0$ is that of $V^\top \left. \frac{\partial s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}} \right|_{\mathbf{Y}=\mathbf{X}'_i}$, we can correctly account for the subcritical cases by integrating over a halfspace. If the mutation distribution is unbiased, this comes down to dividing by two. In case this assumption is not met, one has to stick to Equation (22). Alternative formulations when mutations are biased are given by Champagnat *et al.* (2001) and Champagnat (2004).

All the quantities in Eq. (22), including the order estimate, are still on the original community dynamical timescale. The reason for not changing to expressions in evolutionary time, is that doing so lets the biological interpretation of model ingredients disappear from sight. The speeded up timescale necessary for deriving a proper limit process is constructed by equating one unit of evolutionary time to $1/\epsilon$ units of community dynamical time. The order estimate becomes $O(\epsilon)$ in evolutionary time, which is higher than the $O(\sqrt{\epsilon})$ estimate for the approximation to the stochastic process using the deterministic path (cf. the paragraph preceding Eq. (6)). Hence the overall order of the approximation is dominated by the process noise and not by the calculation of the mean speed of change of \mathbb{X} , and is $O(\sqrt{\epsilon})$.

One sees that the only difference between the canonical equation for unstructured (2) and for structured populations (23) is that a factor $1/2$ becomes a factor $T_f/(T_s \sigma^2)$. As an illustration, we now bridge this gap by recovering the canonical equation for unstructured population models from the general result for structured

models. The unstructured case deals with ODE models, which implies the absence of any historical dependence of the individual birth and death rates. Hence in such models the initial invasion of a mutant is described by a linear birth-and-death process. If we denote birth and death rates respectively by λ and μ , we can calculate the ratio $T_f/(T_s \sigma^2)$. First, the ratio of the average age at giving birth to the life expectancy can be computed since

$$T_f = \frac{\int_0^\infty \lambda e^{-\mu t} t dt}{\int_0^\infty \lambda e^{-\mu t} dt} = \frac{1}{\mu} = \frac{\int_0^\infty \mu e^{-\mu t} t dt}{\int_0^\infty \mu e^{-\mu t} dt} = T_s$$

Second, the offspring distribution follows from the observation that a lifetime number of i children means i successive birth events (each with relative probability $\lambda/(\lambda + \mu)$), followed by a death event (with probability $\mu/(\lambda + \mu)$). All events being independent, the probability of having i offspring is the product of all these probabilities:

$$P(\xi = i) := p_i = \left(\frac{\lambda}{\lambda + \mu} \right)^i \frac{\mu}{\lambda + \mu}$$

This geometric distribution has variance $\sigma^2 = \lambda(\lambda + \mu)/\mu^2$, so the factor we try to calculate is

$$\frac{T_f}{T_s} \frac{1}{\sum_l u_l \text{Var}(\sum_m v_m \xi_{ml})} = \frac{\mu^2}{\lambda(\lambda + \mu)} = \frac{1}{2} + O(\varrho)$$

since $\lambda = \mu + O(\varrho)$ in a slightly supercritical situation. This completes our recovery of the result of Dieckmann & Law (1996).

3 The normal form of the invasion fitness function at a singularity

When trying to figure out the nature of the invasion function for a community close to a singularity, the first naive attempts usually fail. A clear example is the formulation of the general form of the s -function for a community of three or more residents, close to a singular strategy. If one assumes the existence of a Taylor expansion up to quadratic terms and checks some consistency conditions that must surely hold, a single page of calculations (Appendix C) gives the clean-but-nonsensical result that $s = O(\varepsilon^3)$ at the singularity, no matter what model or parameters.

When we look at a community of two residents that are similar and close to a singular strategy, we can see the root of the problem. At the limit where the residents' strategies are equal to the singular strategy, the population densities show a line of neutrally stable equilibria (Fig. 1); any other combination of trait vectors shows an attracting point equilibrium. Thus a bifurcation that is unusual for general dynamical systems, is generic in the context of invasion analysis. The illustration shows the essential nature of the beast: even though a derivative does not exist, the directional derivatives do. What this suggests, is to blow up singularities by separating the directional components of a strategy from its norm. The notations that follow are natural implementations of this idea.

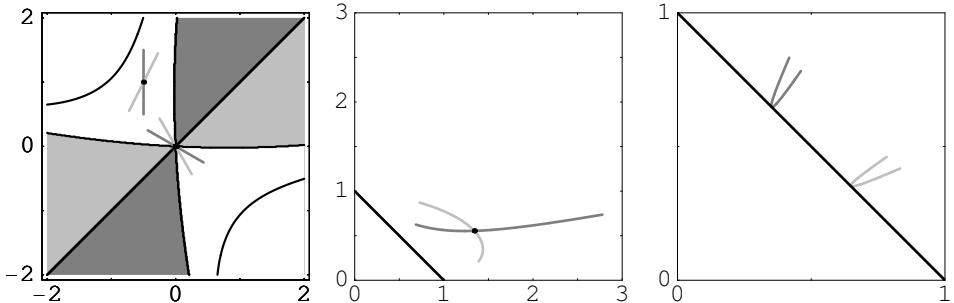


Figure 1: The nature of the beast. We consider here an N -resident Lotka-Volterra system with scalar strategies. The population dynamics for the i^{th} type is given by $d \log n_i/dt = 1 - \sum_j a(X_i, X_j)n_j - a(X_i, Y)m$ and similarly for the mutant's density $d \log m/dt = 1 - \sum_j a(Y, X_j)n_j - a(Y, Y)m$, where the interaction function was chosen as $a(X, X') := 1 + (X - X')(0.05X + 1.00X' - 0.03X^2 - 0.02XX' + 0.1X'^2)$. In the first plot, strategy X_1 is plotted against strategy X_2 , the dark gray area is defined by $s_{X_1}(X_2) < 0$, the light gray one by $s_{X_2}(X_1) < 0$. In the white zone the equilibrium densities of both residents have the same sign, positive on the origin's side of the black curve and negative on the other. Thus all points on the four straight lines drawn in gray represent strategy combinations that can coexist in a protected manner (since they are mutually invadable). The second and third graph plot the equilibrium density of X_1 strategists against that of X_2 strategists. The black dot in the second plot corresponds to the coalition $(-0.5, 1)$ indicated on the first plot, and the gray curves on the second plot correspond to the identically colored lines through $(-0.5, 1)$ in the first plot. The same correspondence holds between the two lines through the singularity at $(0, 0)$ in the first plot, and the curves in the third plot. The aim of these figures is to point out what happens as the community approaches the singularity: one sees that there exists no limit for the densities when both strategies converge to the singular trait value, although in each direction this limit exists. Hence the black point on the second plot is the normal situation where the density equations have a stable fixed point solution, but in the third plot we see that this point degenerates into a line of neutrally stable equilibria when both populations are at the singular trait value. Note that the system is scaled such that the equilibrium density is always 1 for a monomorphic population. As all the curves in the second and third plot are above the line $\hat{n}_1 + \hat{n}_2 = 1$, the total density in a community with two residents is always higher than in one with a single resident. From the third plot, we expect that the total density in a community "close" to the singularity in terms of some distance measure, will have a zero linear part when expanded in terms of this distance; the analysis we present will show that this holds true in general.

3.1 Additional notations for this section

On top of the notations we presented in Subsection 1.3, we introduce the following conventions.

As we are interested in the form of the fitness function for a community near an evolutionarily singular strategy, we choose a parametrization centered around it. Denoting the singular trait value by X^* , a resident has strategy vector $\mathbf{X} = \mathbf{X}^* + \mathbf{U}$, or $\mathbf{X}_i = \mathbf{X}^* + \mathbf{U}_i$ if there are several residents. Likewise an invader has trait value $\mathbf{Y} = \mathbf{X}^* + \mathbf{V}$.

We introduce the small (bifurcation) parameter ε to scale the set of resident traits: for each i from 1 to N there is a vector ξ_i so that the i^{th} resident has strategy $\mathbf{X}_i = \mathbf{X}^* + \mathbf{U}_i = \mathbf{X}^* + \varepsilon \xi_i$.

Any quantity with an asterisk will refer to a community at equilibrium with only the singular strategy present: e.g. \mathbf{b}^* is the equilibrium birth flow and \mathbf{I}^* the equilibrium environment when only \mathbf{X}^* is present. Furthermore, all derivatives in this section will be evaluated for exactly that community. Thus a very substantial notational simplification is the systematic suppression of variable names and the location of evaluation: we see that without ambiguity, we can denote e.g. the average of the lifetime reproductive output $\mathbf{L} = \mathbf{L}(\mathbf{Y}, \mathbf{I})$, derived first for its second argument then for its first and evaluated at the singular strategy and environment, as the $z \times r$ matrix¹

$$\frac{\partial^2 \lambda_d(\mathbf{L})}{\partial \mathbf{Y} \partial \mathbf{I}} := \left[\frac{\partial}{\partial \mathbf{Y}} \left(\frac{\partial \lambda_d(\mathbf{L}(\mathbf{Y}, \mathbf{I}))}{\partial \mathbf{I}} \right)^T \Big|_{\substack{\mathbf{Y}=\mathbf{X}^* \\ \mathbf{I}=\mathbf{I}^*}} \right]^T \quad (24)$$

where λ_d is the dominant eigenvalue operator.

Since no third order derivatives occur in this paper, all partial derivatives of scalar functions (s , r and λ_d) are either row vectors or matrices. A minor complication is however the occurrence of tensors of rank 3 as derivatives of matrix functions (\mathbf{G} and \mathbf{L}). Instead of solving this issue by treating them componentwise and thus cluttering the notation, we interpret these tensors as matrices with row vectors as elements by introducing an additional notation: to take the derivative of \mathbf{L} in the mutant direction as an example, we define it componentwise as

$$\left[\frac{\partial \mathbf{L}}{\partial \mathbf{Y}} \right]_{lm} := \frac{\partial [\mathbf{L}]_{lm}}{\partial \mathbf{Y}} \quad (25)$$

Whenever this symbol occurs, it will always be in an expansion and acting on an appropriately dimensioned vector like \mathbf{U} , so that we have a $d \times d$ matrix $\frac{\partial \mathbf{L}}{\partial \mathbf{Y}}(\mathbf{U})$ that gives no further complications. The slightly different layout serves as a reminder that the vector-and-matrix notation cannot be used when the tensor is separated

¹This notation is the transpose of the one used in the published version of this chapter. The improvement is that here higher order derivative notation is a more logical continuation of first order notation: since $\frac{d^2 f(x)}{dx^2} := \frac{d}{dx} \frac{df(x)}{dx}$, one prefers to see $\frac{\partial^2 f(x,y)}{\partial x \partial y} := \frac{\partial}{\partial x} \frac{\partial f(x,y)}{\partial y}$ for scalar variables x and y , so that the order of derivation reads from right to left. The change has no influence on the appearance or correctness of any of the following equations, only on the interpretation of their terms. For the continuous partial derivatives we are dealing with, the point is anyhow moot.

from its argument in parentheses. Whenever possible, we opt not to use this unfamiliar notation: e.g. since \mathbf{b}^* is a constant vector, $\frac{\partial L}{\partial Y}(\mathbf{U}) \mathbf{b}^*$ may be replaced by $\frac{\partial L \mathbf{b}^*}{\partial Y} \mathbf{U}$.

In the case of a double subscript, parentheses are added to remove ambiguity: e.g. $(\mathbf{b}_i)_l$ is the l^{th} component of the i^{th} resident's birth flow; without parentheses, b_{il} might just as well be a component of some matrix \mathbf{b} .

3.2 Aims of this section

In the introduction we have defined the invasion fitness of type Y in an N -resident community $\mathbb{X} = \{X_1, X_2, \dots, X_N\}$ as the long-term average per capita growth rate of a rare Y -type individual in a large equilibrium community made up of all the resident types, X_1 to X_N . In this section we show that for such an N -resident community, the invasion fitness function $s_{\mathbb{X}}(Y)$ up to quadratic terms can be constructed using only the trait values present plus the second order derivatives at the singularity of the simpler fitness function $s_X(Y)$.

The effect is that the task of formulating the fitness function for a polymorphic community in the neighbourhood of an evolutionarily singular strategy for an arbitrarily complicated structured population model, is reduced to formulating the one-resident s -function, and either fitting the corresponding Lotka-Volterra model (Proposition 1) or substituting the simple s -functions into the normal form (75) that we will present below. Both procedures yield an invasion fitness function $s_{\mathbb{X}}(Y)$ which is correct up to quadratic terms in the small parameter ε .

For example, assume one knows the simple fitness function $s_X(Y)$ for some model and one has resident strategies X_1 and X_2 (with $N = 2$). First we calculate the second order partial derivatives of $s_X(Y)$ at the singularity:

$$C_{11} := \frac{1}{2} \frac{\partial^2 s_X(Y)}{\partial X^2} \quad C_{10} := \frac{1}{2} \frac{\partial^2 s_X(Y)}{\partial X \partial Y} \quad C_{00} := \frac{1}{2} \frac{\partial^2 s_X(Y)}{\partial Y^2} \quad (26)$$

Using the additional notations $\bar{U} := \frac{U_1+U_2}{2}$ and $\Delta := \frac{U_1-U_2}{2}$ where the deviations U_1, U_2 and V are $O(\varepsilon)$, we will show in Subsection 3.5 that the invasion fitness of any mutant Y is

$$\begin{aligned} s_{X_1 X_2}(Y) &= V^T C_{00} V + 2\bar{U}^T C_{10} V + \bar{U}^T C_{11} \bar{U} - \Delta^T C_{00} \Delta \\ &\quad + 2\Delta^T C_{10} (\bar{U} - V) \frac{\Delta^T [C_{00} + C_{10}^T] \bar{U}}{\Delta^T C_{10} \Delta} + O(\varepsilon^3) \end{aligned} \quad (27)$$

Therefore we can consider the equation above to be a normal form. It immediately shows that a Taylor expansion of $s_{X_1 X_2}$ does not exist and explains why calculations like those in Appendix C are doomed to fail, with the exception of the case where strategies are scalar so that the equation above simplifies to $s_{X_1 X_2}(Y) = (X_1 - Y)(X_2 - Y)C_{00} + O(\varepsilon^3)$.

One available route for deriving the normal form for general N -resident population dynamics close to a singular strategy and showing the mentioned niceties, is to first prove the general case, then cast a general Lotka-Volterra system in that form and show what it reduces to, and lastly demonstrate that this form only depends

on the mentioned strategies and derivatives. The unpleasant reality however is, that casting Lotka-Volterra models into the form of physiologically structured population models requires us in general to introduce an infinite dimensional vector as description of the environmental conditions \mathbf{I} (one environmental dimension for every possible trait value). The proof for the infinite dimensional case requires more sophisticated mathematical tools than we use here, like operators and distributions instead of finite dimensional matrices and vectors. We fully expect, though, that the same techniques as used in this paper still hold for any model on a space supporting a chain rule and an inverse function theorem.

For clarity's sake and given our own more limited mathematical expertise, we have opted for another route: we restrict ourselves to the case of structured populations with a finite dimensional environment, and show that the same normal form is found as derived separately for Lotka-Volterra systems. We will start with a detailed exposition of the Lotka-Volterra case in view of its familiarity, followed by the corresponding calculations for the structured case.

3.3 The normal form for Lotka-Volterra systems

The following is a general form for Lotka-Volterra systems, where $r(\mathbf{Y})$ is the per capita growth rate in a virgin environment (i.e., the growth rate in the absense of competitors), and the interaction is fully determined by the interaction function $a(\mathbf{Y}, \mathbf{X})$ plus the trait value and the densities of the interacting types. We assume that r and a are C^3 functions, to guarantee the existence of an expansion of the fitness function up to order $O(\varepsilon^3)$. If the community has N residents plus an invading type, the equations that govern growth can be formulated as

$$\left\{ \begin{array}{lcl} \forall j: \frac{1}{n_j} \frac{dn_j}{dt} & = & r(\mathbf{X}_j) \left(1 - \sum_i a(\mathbf{X}_j, \mathbf{X}_i) n_i - a(\mathbf{X}_j, \mathbf{Y}) m \right) \\ \frac{1}{m} \frac{dm}{dt} & = & r(\mathbf{Y}) \left(1 - \sum_i a(\mathbf{Y}, \mathbf{X}_i) n_i - a(\mathbf{Y}, \mathbf{Y}) m \right) \end{array} \right. \quad (28)$$

We will first perform a trait-dependent rescaling and some calculations pertaining to monomorphic communities.

We first add a tilde to indicate rescaled quantities, and later drop the tilde once convinced that rescaling has no effect on the fitness value. We multiply the density of any type with the strength of its self-competition and similarly divide the interaction function:

$$\forall \mathbf{X}, \mathbf{Y}: \tilde{a}(\mathbf{Y}, \mathbf{X}) := \frac{a(\mathbf{Y}, \mathbf{X})}{a(\mathbf{X}, \mathbf{X})} \quad \forall i: \tilde{n}_i := a(\mathbf{X}_i, \mathbf{X}_i) n_i \quad \tilde{m} := a(\mathbf{Y}, \mathbf{Y}) m \quad (29)$$

Thus for any strategy \mathbf{X} we have that $\tilde{a}(\mathbf{X}, \mathbf{X}) = 1$ and consequently the equilibrium density in a monomorphic world is always $\hat{n} = 1$, as seen from the equilibrium equation $0 = r(\mathbf{X})(1 - \tilde{a}(\mathbf{X}, \mathbf{X})\hat{n})$. We see that for example $a(\mathbf{X}_i, \mathbf{X}_j)n_j$ equals $\tilde{a}(\mathbf{X}_i, \mathbf{X}_j)\tilde{n}_j$, so that the per capita growth rate, and therefore the invasion fitness $s_{\mathbf{X}}(\mathbf{Y})$, is independent of this rescaling. So without loss of generality, we assume from here onwards that $a(\mathbf{X}, \mathbf{X}) = 1$ for any \mathbf{X} and hence that $\hat{n} = 1$ if there is a sole resident type.

By a literal translation of the definition of the s -function (see 1.1) into symbols, we calculate the invasion fitness for a monomorphic community as

$$s_X(Y) = \lim_{T \rightarrow \infty} \lim_{m \rightarrow 0} \frac{1}{T} \int_0^T \frac{1}{m} \frac{dm}{dt} \Big|_{n=\hat{n}} dt = r(Y)(1 - a(Y, X)) \quad (30)$$

Proposition 1 *For every single-resident fitness function $s_X(Y)$ and every strictly positive growth rate in a virgin environment $r(Y)$, there exists an interaction function $a(Y, X)$ such that the resultant Lotka-Volterra model (28) has the same single-resident s -function.*

proof As we comply to the rescaling (29), the suitable interaction function can be found from the formula for the invasion fitness in a Lotka-Volterra model (30) as $a(Y, X) := 1 - s_X(Y)/r(Y)$. \square

In practice, a constant growth rate $r(Y) := 1$ is usually preferable as it tends to simplify calculations.

Once we have fitted an interaction function to a simple fitness function and growth rate, the corresponding fitness for a mutant of type Y invading in a polymorphic Lotka-Volterra community $\{X_1, X_2, \dots, X_N\}$ is found as in Equation (30), by combining the definitions of its dynamics (28) and of s -functions:

$$s_X(Y) = r(Y) \left(1 - \sum_i a(Y, X_i) \hat{n}_i \right) \quad (31)$$

Then we simply solve the equilibrium densities \hat{n}_i from the growth equations and find that

$$s_X(Y) = r(Y) \left(1 - (a(Y, X_1) \ a(Y, X_2) \ \cdots \ a(Y, X_N)) A^{-1} \mathbf{1} \right) \quad (32)$$

where A is the interaction matrix for the given community, with entries $[A]_{ij} := a(X_i, X_j)$, and we recall that $\mathbf{1}$ is a column vector of 1's (cf. 1.3).

From Equation (32) we see that except for the non-Lotka-Volterra case, there will in general not exist a well-defined interaction function $a(Y, X)$ that satisfies this equation for all communities and invaders:

Proposition 2 *Proposition 1 does not hold if the words single-resident are replaced by N -resident.*

proof Equation (32) shows that Lotka-Volterra systems only allow pairwise interactions (that are scaled by a specific type of density regulation). Any multiresident s -function that fails these requirements can therefore serve as a counterexample. In principle, the only constraint on s -functions is that they have to satisfy the following consistency conditions (Metz *et al.*, 1996): zero fitness for each of the residents (i.e., $s_X(X_i) = 0$ for all i) and invariance under the renaming of residents (i.e., $s_{X_i X_j}(Y) = s_{X_j X_i}(Y)$ for all i, j). The simplest example, with scalar traits, would be

$$s_{X_1 X_2}(Y) := (X_1 - Y)(X_2 - Y) \quad (33)$$

where the reader can verify that no choice of growth rate and interaction function will lead to a Lotka-Volterra model with this two-resident s -function. A slightly less

caricatural example starts from the fitness function of an N -resident Lotka-Volterra model (31), and adds interaction terms between triples of strategies

$$s_X(Y) := r(Y) \left(1 - \sum_i a(Y, X_i) \hat{n}_i - \sum_{ij} b(Y, X_i, X_j) \hat{n}_i \hat{n}_j \right) \quad (34)$$

through an appropriate function $b(Y, X, X')$. For nontrivial choices of b , it is clearly impossible get the above fitness function from a Lotka-Volterra model. \square

How to relate N -resident Lotka-Volterra and physiologically structured population models instead, will be the central question of this section. To address it we return our attention to the simple fitness function (30) we found, which can be expanded in the small parameter ε as

$$\begin{aligned} s_X(Y) &= r(X^* + V)(1 - a(X^* + V, X^* + U)) \\ &= \left(r(X^*) + r'(X^*)V + \frac{1}{2}V^\top r''(X^*)V + O(\varepsilon^3) \right) \\ &\quad \times \left(1 - \alpha - \beta_1 U - \beta_0 V - U^\top \Gamma_{11} U - 2U^\top \Gamma_{10} V - V^\top \Gamma_{00} V + O(\varepsilon^3) \right) \\ &= r(X^*)(1 - \alpha) - (r(X^*)(\beta_1 U + \beta_0 V) + r'(X^*)V(1 - \alpha)) \\ &\quad - r(X^*)(U^\top \Gamma_{11} U + 2U^\top \Gamma_{10} V + V^\top \Gamma_{00} V) + r'(X^*)V(\beta_1 U + \beta_0 V) \\ &\quad + \frac{1}{2}V^\top r''(X^*)V(1 - \alpha) + O(\varepsilon^3) \end{aligned} \quad (35)$$

were all terms of the same order in ε are grouped together.

As Γ_{11} and Γ_{00} are always pre- and postmultiplied by the same vector, their antisymmetric parts are irrelevant. Thus there is an equivalence class of matrix choices for which the evaluation of Expansion (35) is the same, and from this class we choose a unique element by demanding that Γ_{11} and Γ_{00} are symmetric. As an aside we note that while it is highly nongeneric for Γ_{10} to be symmetric as well, this phenomenon happens often in simple models: either as a result of special symmetries (cf. our example, Subsection 4.6), or since the model is formulated so that the environmental input is effectively one-dimensional, and monotonically influences the invasion fitness (cf. Metz *et al.*, 1996).

Several consistency conditions can be used to simplify Equation (35). As a result of its definition, $s_X(X)$ is zero for any value of X . So for any $U = V$, the four parts of the right hand side of (35) — constant, linear, quadratic and higher order in ε — must be separately zero. Without loss of generality we may assume that $r(X^*)$ is strictly positive, as else the singular type would not be viable. The constant, linear and quadratic parts of the equation then respectively imply that $\alpha = 1$, $\beta_1 = -\beta_0$ and $\Gamma_{11} + \Gamma_{10} + \Gamma_{10}^\top + \Gamma_{00} = 0$.

Since X^* is singular, by definition $\theta^\top = \frac{\partial s_{X^*}(Y)}{\partial Y}|_{Y=X^*} = -r(X^*)\beta_0$ and hence $-\beta_1 = \beta_0 = \theta^\top$. We rename the matrices using $C := -r(X^*)\Gamma$ so that the expansion (35) simplifies to

$$s_X(Y) = U^\top C_{11} U + 2U^\top C_{10} V + V^\top C_{00} V + O(\varepsilon^3) \quad (36)$$

From this we see that renaming and rescaling the Γ -matrices into the C -matrices was consistent with the earlier definition (26) of those as second order partial derivatives at the singularity.

We can now start considering N -resident invasion fitness functions close to singular points. Starting from Equation (31), we see that we can express some parts of the multiresident s -function immediately in terms of single-resident invasion functions:

$$\begin{aligned} s_{\mathbb{X}}(\mathbf{Y}) &= r(\mathbf{Y}) \left(1 - \sum_i a(\mathbf{Y}, \mathbf{X}_i) \hat{n}_i \right) \\ &= r(\mathbf{Y}) \left(1 - \sum_i \left(1 - \frac{s_{\mathbf{X}_i}(\mathbf{Y})}{r(\mathbf{Y})} \right) \hat{n}_i \right) \\ &= r(\mathbf{Y}) \left(1 - \sum_i \hat{n}_i \right) + \sum_i s_{\mathbf{X}_i}(\mathbf{Y}) \hat{n}_i \end{aligned} \quad (37)$$

We will now expand this last equality up to but not including $O(\varepsilon^3)$ -terms. In view of the considerations at the start of this section, we change our coordinates from densities \hat{n}_i to fractional densities p_i plus the difference in total density from the monomorphic equilibrium density:

$$p_i := \frac{\hat{n}_i}{\sum_j \hat{n}_j} \quad \Delta_n := \sum_i \hat{n}_i - 1 \quad (38)$$

Note that the constant term of Δ_n is zero since $\varepsilon = 0$ corresponds to a monomorphic community $\mathbb{X} = \{\mathbf{X}^*\}$. Introducing a shorthand notation,

$$c(\mathbf{U}, \mathbf{V}) := \mathbf{U}^\top \mathbf{C}_{11} \mathbf{U} + 2\mathbf{U}^\top \mathbf{C}_{10} \mathbf{V} + \mathbf{V}^\top \mathbf{C}_{00} \mathbf{V} \quad (39)$$

we see that terms like $c(\mathbf{U}_i, \mathbf{V})\Delta_n$ will be discarded, since $c(\mathbf{U}, \mathbf{V})$ itself is already purely second order in ε . Using the new coordinates, we see that

$$s_{\mathbb{X}}(\mathbf{Y}) = -(r(\mathbf{X}^*) + \mathbf{r}'(\mathbf{X}^*)\mathbf{V})\Delta_n + \sum_i c(\mathbf{U}_i, \mathbf{V}) p_i + O(\varepsilon^3)$$

From the above we also note that only the constant part of the fractions p_i matters in the calculation of $s_{\mathbb{X}}(\mathbf{Y})$ up to the given order. We expand the density difference as $\Delta_n = e_1\varepsilon + e_2\varepsilon^2 + O(\varepsilon^3)$. Since $s_{\mathbb{X}}(\mathbf{X}_i)$ is zero for each resident, we have for each $i \in \{1, 2, \dots, N\}$ that

$$0 = -r(\mathbf{X}^*)(e_1\varepsilon + e_2\varepsilon^2) - \mathbf{r}'(\mathbf{X}^*)\mathbf{U}_i e_1\varepsilon + \sum_j c(\mathbf{U}_j, \mathbf{U}_i) p_j + O(\varepsilon^3) \quad (40)$$

From the part that is linear in ε , we see that e_1 too is zero, and from the quadratic part we have that $r(\mathbf{X}^*)e_2\varepsilon^2 = \sum_j c(\mathbf{U}_j, \mathbf{U}_i)p_j$. Thus $N+1$ unknowns (p_1, p_2, \dots, p_N and e_2) have to be solved using the consistency condition $\sum_i p_i = 1$ plus the requirement that for each i from 1 to N

$$\underbrace{\sum_j 2\mathbf{U}_j^\top \mathbf{C}_{10} \mathbf{U}_i}_{[\mathbf{E}]_{ij}} \underbrace{p_j}_{(P)_j} + \underbrace{\sum_j \mathbf{U}_j^\top \mathbf{C}_{11} \mathbf{U}_j}_{\sigma} p_j - r(\mathbf{X}^*)e_2\varepsilon^2 = \underbrace{-\mathbf{U}_i^\top \mathbf{C}_{00} \mathbf{U}_i}_{(T)_i} \quad (41)$$

Together these equations contain the componentwise definitions of the scalar σ , the column vectors T and P , and the matrix E . We can also gather together all N equations into a single vectorial one, using the vector $\mathbf{1}$ that has all its components equal to one (cf. 1.3 Notations). The fact that the proportions necessarily sum up to 1 gives us an additional (scalar) equation, so we have altogether $N + 1$ equations in $N + 1$ unknowns:

$$\begin{cases} EP + \sigma \mathbf{1} = T \\ \mathbf{1}^T P = 1 \end{cases} \quad (42)$$

If we treat σ as an unknown (equivalent to the unknown e_2 once P is solved), these are linear equations. Hence we extend E , P and T to

$$E^* := \begin{bmatrix} E & \mathbf{1} \\ \mathbf{1}^T & 0 \end{bmatrix} \quad P^* := \begin{pmatrix} P \\ \sigma \end{pmatrix} \quad T^* := \begin{pmatrix} T \\ 1 \end{pmatrix}$$

so that we can straightforwardly solve σ and the proportions p_i in terms of second order derivatives of simple s -functions from

$$P^* = E^{*-1} T^* \quad (43)$$

to come to the final conclusion that

$$\begin{aligned} s_X(Y) &= -r(X^*)\Delta_n + \sum_i c(U_i, V)p_i + O(\varepsilon^3) \\ &= \sigma + 2 \left(\sum_i p_i U_i^T \right) C_{10} V + V^T C_{00} V + O(\varepsilon^3) \end{aligned} \quad (44)$$

where each term or factor is expressed in second order partial derivatives of the simple s -function, or a strategy difference vector (U_i or V , of respectively a resident or the invader), since σ and the proportions are solved from

$$\begin{pmatrix} p_1 \\ \vdots \\ p_N \\ \sigma \end{pmatrix} = \begin{bmatrix} 2U_1^T C_{10} U_1 & \cdots & 2U_N^T C_{10} U_1 & 1 \\ \vdots & \ddots & \vdots & \vdots \\ 2U_1^T C_{10} U_N & \cdots & 2U_N^T C_{10} U_N & 1 \\ 1 & \cdots & 1 & 0 \end{bmatrix}^{-1} \begin{pmatrix} -U_1^T C_{00} U_1 \\ \vdots \\ -U_N^T C_{00} U_N \\ 1 \end{pmatrix} \quad (45)$$

The invertibility of the matrix E^* is clearly an important issue here. It will be treated in Subsection 3.6 (and touched upon in 3.5), but the gist is that generically E^* is invertible if the community $\{X_1, X_2, \dots, X_N\}$ exists.

3.4 The normal form for physiologically structured population models

As explained in Subsection 1.2, the equilibrium equations for a physiologically structured community are

$$\begin{cases} b_i = L(X_i, I) b_i & (\forall i) \\ I = \sum_i G(X_i, I) b_i \end{cases} \quad (46)$$

In Appendix B we show that if the residents and the invader are near the singularity \mathbf{X}^* , the invasion fitness is²

$$s_{\mathbb{X}}(\mathbf{Y}) = \frac{\log R_0(\mathbf{Y}, \mathbf{I})}{T_f(\mathbf{X}^*, \mathbf{I}^*)} + O(\varepsilon^3) \quad (47)$$

where R_0 is the dominant eigenvalue $\lambda_d(\mathbf{L})$ of the next-generation matrix \mathbf{L} , \mathbf{I} the equilibrium environment set by the community $\mathbb{X} := \{\mathbf{X}_1, \mathbf{X}_2, \dots, \mathbf{X}_N\}$, and T_f the average age at giving birth (cf. Eq. (100)).

As before, we will use an invertible, trait-dependent rescaling. In this case, we do not rescale population densities at equilibrium to 1 (while compensating by rescaling the interaction function, or vice versa) as these do not appear in the equilibrium equations. Instead we rescale the birth flow such that, for the monomorphic equilibrium community set by any strategy X in the trait space,

$$\mathbf{b} = \mathbf{b}^* \quad (48)$$

where \mathbf{b}^* is the equilibrium birth flow for a community with only the singular strategy X^* present. We do this by defining for each strategy X the rescaled birth flow $\tilde{\mathbf{b}} := D\mathbf{b}$ where D is the diagonal $d \times d$ matrix with components $[D]_{ll} := b_l^*/b_l$, where b_l is the l^{th} component of the unscaled equilibrium birth flow in the monomorphic community set by X . This transformation clearly ensures that Equation (48) is satisfied. If all components of \mathbf{b}^* are strictly positive, there is a neighbourhood of the singularity in which the birth flow b_l in each state is nonzero, so the matrix D is well-defined. The invertibility of the rescaling is guaranteed as well if all components of \mathbf{b}^* are strictly positive. So we assume henceforth that $b_l^* > 0$, which we can do essentially without loss of generality since models flouting this assumption should be rare indeed. As in the Lotka-Volterra case (29), we compensate the first rescaling by rescaling the interaction; here by choosing $\tilde{\mathbf{L}} := D\mathbf{L}D^{-1}$ and $\tilde{\mathbf{G}} := G\mathbf{D}^{-1}$. The matrices $\tilde{\mathbf{L}}$ and \mathbf{L} necessarily have the same eigenvalues, hence the rescaling does not affect $s_{\mathbb{X}}(\mathbf{Y})$ while it allows us to greatly simplify the calculations. From here on we revert to the old notations while assuming the rescaling has happened.

To expand a structured population's invasion fitness function (47) near a singularity, we have to look at the lower orders of dependence on ε for all unknowns. To that end, we start by defining \mathbf{I}_i as the monomorphic environment set solely by strategy X_i , so that $\mathbf{I}_i = G(\mathbf{X}_i, \mathbf{I}_i)\mathbf{b}^*$ (note that the rescaling has been used here). We then expand respectively the polymorphic environment set by \mathbb{X} and the monomorphic environment set by X_i as follows:

$$\begin{aligned} \mathbf{I} &= \mathbf{I}^* + \varepsilon \mathbf{I}' + \varepsilon^2 \mathbf{I}'' + O(\varepsilon^3) \\ \forall i: \mathbf{I}_i &= \mathbf{I}_i^* + \varepsilon \mathbf{I}_i' + \varepsilon^2 \mathbf{I}_i'' + O(\varepsilon^3) \end{aligned} \quad (49)$$

In order to establish a relation between the N -resident environment \mathbf{I} and its N monomorphic counterparts $\mathbf{I}_1, \mathbf{I}_2, \dots, \mathbf{I}_N$, we introduce first some new coordinates, similar to those we used in the Lotka-Volterra case (38). We will need to

²This expression differs from the one in the Jour. Math. Biol. version of this chapter, but both are correct as the differences are of order $O(\varepsilon^3)$. The version here is what is found in Appendix B and shortens the proof of Expression (69), but the other version is correct up to one more order of ε as shown in Section II.B.

calculate the relative abundance of each type of resident in the community. But as we now look from a generational perspective, we define this time a vector \mathbf{p}_i that is the proportional abundance at birth of the i^{th} type in the respective birth states, plus a difference vector $\Delta\mathbf{b}$ that is the proportional change in total births from the monomorphic equilibrium: for each birth state from 1 to d and for each resident from 1 to N ,

$$\forall l, \forall i: (\mathbf{p}_i)_l := \frac{(\mathbf{b}_i)_l}{\sum_j (\mathbf{b}_j)_l} \quad 1 + (\Delta\mathbf{b})_l := \frac{\sum_j (\mathbf{b}_j)_l}{b_l^*} \quad (50)$$

We expand the N proportion vectors \mathbf{p}_i and $\Delta\mathbf{b}$ with respect to ε as

$$\begin{aligned} \forall i: \mathbf{p}_i &= \mathbf{p}_i^0 + \mathbf{q}_i \varepsilon + O(\varepsilon^2) \\ \Delta\mathbf{b} &= \Delta_b^0 + \Delta_b^1 \varepsilon + O(\varepsilon^2) \end{aligned} \quad (51)$$

defining vectors $\Delta_b^0, \Delta_b^1, \mathbf{p}_1^0, \mathbf{p}_2^0, \dots, \mathbf{p}_N^0, \mathbf{q}_1, \mathbf{q}_2, \dots, \mathbf{q}_N$ in the process. As happens with the density difference Δ_n in the Lotka-Volterra case (Eq. (38)), the constant part of the birth flow difference automatically disappears: $\Delta_b^0 = \mathbf{0}$ since $\varepsilon = 0$ corresponds to a monomorphic case. Note that for each birth state l separately these proportions sum up to one, since $\sum_i (\mathbf{p}_i)_l = \sum_i (\mathbf{b}_i)_l / \sum_j (\mathbf{b}_j)_l = 1$. Expanding both sides of these equalities with respect to ε , we find two times d consistency conditions

$$\sum_i \mathbf{p}_i^0 = \mathbf{1} \quad \sum_i \mathbf{q}_i = \mathbf{0} \quad (52)$$

As we only have the equilibrium equations (46) to start from, let's begin by expanding all parts of the first equation:

$$(\mathbf{b}_i)_l = (\mathbf{p}_i)_l \sum_j (\mathbf{b}_j)_l = ((\mathbf{p}_i^0)_l + (\mathbf{q}_i)_l \varepsilon) (1 + (\Delta_b^1)_l \varepsilon) b_l^* + O(\varepsilon^2) \quad (53)$$

$$\mathcal{L}(\mathbf{X}_i, \mathbf{I}) = \mathcal{L}(\mathbf{X}^*, \mathbf{I}^*) + \frac{\partial \mathcal{L}}{\partial \mathbf{Y}}(\varepsilon \xi_i) + \frac{\partial \mathcal{L}}{\partial \mathbf{I}}(\varepsilon \mathbf{I}') + O(\varepsilon^2) \quad (54)$$

where e.g. $\frac{\partial \mathcal{L}}{\partial \mathbf{I}}(\varepsilon \mathbf{I}')$ is the $d \times d$ matrix with entries $\left(\frac{\partial \mathcal{L}(\mathbf{X}^*, \mathbf{I})_{lm}}{\partial \mathbf{I}} \Big|_{\mathbf{I}=\mathbf{I}^*} \right) \varepsilon \mathbf{I}'$ in accordance with the conventions introduced in Subsection 3.1.

From Equations (53) and (54) we see that $\mathbf{b}_i = \mathcal{L}(\mathbf{X}_i, \mathbf{I}) \mathbf{b}_i$ can be rewritten for each i as

$$\begin{aligned} & \left((\mathbf{p}_i^0)_l + \varepsilon (\mathbf{q}_i)_l + \varepsilon (\mathbf{p}_i^0)_l (\Delta_b^1)_l \right) b_l^* + O(\varepsilon^2) \\ &= \sum_m \left[\mathcal{L}(\mathbf{X}^*, \mathbf{I}^*) + \frac{\partial \mathcal{L}}{\partial \mathbf{Y}}(\varepsilon \xi_i) + \frac{\partial \mathcal{L}}{\partial \mathbf{I}}(\varepsilon \mathbf{I}') \right]_{lm} \left((\mathbf{p}_i^0)_m + \varepsilon (\mathbf{q}_i)_m + \varepsilon (\mathbf{p}_i^0)_m (\Delta_b^1)_m \right) b_m^* \\ &= \sum_m \left[\mathcal{L}(\mathbf{X}^*, \mathbf{I}^*) \right]_{lm} (\mathbf{p}_i^0)_m b_m^* \\ & \quad + \sum_m \varepsilon \left[\frac{\partial \mathcal{L}}{\partial \mathbf{Y}}(\xi_i) + \frac{\partial \mathcal{L}}{\partial \mathbf{I}}(\mathbf{I}') \right]_{lm} (\mathbf{p}_i^0)_m b_m^* \\ & \quad + \sum_m \left[\mathcal{L}(\mathbf{X}^*, \mathbf{I}^*) \right]_{lm} \left(\varepsilon (\mathbf{q}_i)_m + \varepsilon (\mathbf{p}_i^0)_m (\Delta_b^1)_m \right) b_m^* \end{aligned} \quad (55)$$

As this equality has to hold for all ε , it has to hold for all orders of ε separately. Thus the constant part tells us that for each i the vector with components $(\mathbf{p}_i^0)_l b_l^*$ is an eigenvector of $\mathbf{L}(\mathbf{X}^*, \mathbf{I}^*)$ with eigenvalue 1. Since this eigenvalue was assumed to be simple, with corresponding eigenvector \mathbf{b}^* , necessarily there must exist some scalars p_i such that

$$\forall i: \mathbf{p}_i^0 = p_i \mathbf{1} \quad (56)$$

This fact helps us simplify the part of Equation (55) that is linear in ε . We can transform it further by summing over i , so that the \mathbf{q}_i -components disappear (52):

$$\begin{aligned} (\Delta_{\mathbf{b}}^1)_l b_l^* &= \sum_i \sum_m \left[\frac{\partial \mathbf{L}}{\partial \mathbf{Y}}(\xi_i) + \frac{\partial \mathbf{L}}{\partial \mathbf{I}}(\mathbf{I}') \right]_{lm} p_i b_m^* \\ &\quad + \sum_m [\mathbf{L}(\mathbf{X}^*, \mathbf{I}^*)]_{lm} (\Delta_{\mathbf{b}}^1)_m b_m^* \end{aligned} \quad (57)$$

If we define a “help” vector \mathbf{h}_{eb} componentwise as $(\mathbf{h}_{eb})_l := (\Delta_{\mathbf{b}}^1)_l b_l^*$, we have

$$\mathbf{h}_{eb} = \sum_i p_i \frac{\partial \mathbf{L} \mathbf{b}^*}{\partial \mathbf{Y}} \xi_i + \frac{\partial \mathbf{L} \mathbf{b}^*}{\partial \mathbf{I}} \mathbf{I}' + \mathbf{L}(\mathbf{X}^*, \mathbf{I}^*) \mathbf{h}_{eb} \quad (58)$$

$$\mathbf{0} = \frac{\partial \mathbf{L} \mathbf{b}^*}{\partial \mathbf{Y}} \xi_i + \frac{\partial \mathbf{L} \mathbf{b}^*}{\partial \mathbf{I}} \mathbf{I}' \quad (59)$$

where the second equation is the monomorphic case, for which we scaled the equilibrium birth flow to \mathbf{b}^* so $\Delta_{\mathbf{b}}^1 = \mathbf{h}_{eb} = \mathbf{0}$.

Let’s now look at the second equilibrium equation, $\mathbf{I} = \sum_i \mathbf{G}(\mathbf{X}_i, \mathbf{I}) \mathbf{b}_i$. If we here too expand both \mathbf{I} and \mathbf{b}_i while using the new coordinates (50), we can combine the per-state summation rules (52) with the fact that $\mathbf{p}_i^0 = p_i \mathbf{1}$, to find that

$$\begin{aligned} \mathbf{I}^* + \varepsilon \mathbf{I}' + O(\varepsilon^2) &= \sum_i \left[\mathbf{G}(\mathbf{X}^*, \mathbf{I}^*) + \frac{\partial \mathbf{G}}{\partial \mathbf{I}}(\varepsilon \mathbf{I}') + \frac{\partial \mathbf{G}}{\partial \mathbf{Y}}(\varepsilon \xi_i) \right] \begin{pmatrix} (p_i + \varepsilon (\mathbf{q}_i)_1 + \varepsilon p_i (\Delta_{\mathbf{b}}^1)_1) b_1^* \\ \vdots \\ (p_i + \varepsilon (\mathbf{q}_i)_d + \varepsilon p_i (\Delta_{\mathbf{b}}^1)_d) b_d^* \end{pmatrix} \\ &= \mathbf{G}(\mathbf{X}^*, \mathbf{I}^*) \mathbf{b}^* + \varepsilon \mathbf{G}(\mathbf{X}^*, \mathbf{I}^*) \mathbf{h}_{eb} + \varepsilon \frac{\partial \mathbf{G}}{\partial \mathbf{I}}(\mathbf{I}') \mathbf{b}^* + \sum_i p_i \varepsilon \frac{\partial \mathbf{G}}{\partial \mathbf{Y}}(\xi_i) \mathbf{b}^* \end{aligned} \quad (60)$$

The part of this equation that is independent of ε does not tell us anything new, but the part that is linear in ε gives the following relation:

$$\mathbf{I}' = \mathbf{G}(\mathbf{X}^*, \mathbf{I}^*) \mathbf{h}_{eb} + \frac{\partial \mathbf{G} \mathbf{b}^*}{\partial \mathbf{I}} \mathbf{I}' + \sum_i p_i \frac{\partial \mathbf{G} \mathbf{b}^*}{\partial \mathbf{Y}} \xi_i$$

From this we solve \mathbf{I}' and \mathbf{I}'_i (where again $\Delta_{\mathbf{b}}^1 = \mathbf{0}$ so \mathbf{h}_{eb} disappears), as

$$\mathbf{I}' = \left[\text{id} - \frac{\partial \mathbf{G} \mathbf{b}^*}{\partial \mathbf{I}} \right]^{-1} \left(\mathbf{G}(\mathbf{X}^*, \mathbf{I}^*) \mathbf{h}_{eb} + \sum_i p_i \frac{\partial \mathbf{G} \mathbf{b}^*}{\partial \mathbf{Y}} \xi_i \right) \quad (61)$$

$$\mathbf{I}'_i = \left[\text{id} - \frac{\partial \mathbf{G} \mathbf{b}^*}{\partial \mathbf{I}} \right]^{-1} \frac{\partial \mathbf{G} \mathbf{b}^*}{\partial \mathbf{Y}} \xi_i \quad (62)$$

where id represents the identity matrix, and taking the inverse is allowed as this transformation is nonsingular provided we stay away from bifurcation points of the population dynamics.

With the shorthand notations $L^* := L(X^*, \mathbf{I}^*)$ and $G^* := G(X^*, \mathbf{I}^*)$, we have as a consequence of Equations (61) and (62) that

$$\mathbf{I}' = \sum_i p_i \mathbf{I}'_i + \left[\text{id} - \frac{\partial G \mathbf{b}^*}{\partial \mathbf{I}} \right]^{-1} G^* \mathbf{h}_{eb} \quad (63)$$

which we substitute into Equation (58) so that we can use Equality (59):

$$\begin{aligned} & [\text{id} - L^*] \mathbf{h}_{eb} \\ &= \sum_i p_i \frac{\partial L \mathbf{b}^*}{\partial Y} \xi_i + \frac{\partial L \mathbf{b}^*}{\partial \mathbf{I}} \mathbf{I}' \\ &= \sum_i p_i \left(\frac{\partial L \mathbf{b}^*}{\partial Y} \xi_i + \frac{\partial L \mathbf{b}^*}{\partial \mathbf{I}} \mathbf{I}'_i \right) + \frac{\partial L \mathbf{b}^*}{\partial \mathbf{I}} \left[\text{id} - \frac{\partial G \mathbf{b}^*}{\partial \mathbf{I}} \right]^{-1} G^* \mathbf{h}_{eb} \\ &= \frac{\partial L \mathbf{b}^*}{\partial \mathbf{I}} \left[\text{id} - \frac{\partial G \mathbf{b}^*}{\partial \mathbf{I}} \right]^{-1} G^* \mathbf{h}_{eb} \end{aligned} \quad (64)$$

After a slight rewrite we find that

$$\mathbf{0} = \left[[L^* - \text{id}] + \frac{\partial L \mathbf{b}^*}{\partial \mathbf{I}} \left[\text{id} - \frac{\partial G \mathbf{b}^*}{\partial \mathbf{I}} \right]^{-1} G^* \right] \mathbf{h}_{eb} \quad (65)$$

As there is no a priori, fixed connection between L and G — changing one without changing the other (while not violating consistency conditions) results in an equally valid population model — we see that the matrix in this equation generically (within the set of local equivalence classes of models characterized by L , G , $\partial L / \partial \mathbf{I}$ and $\partial G / \partial \mathbf{I}$) has full rank. In the special case of a single birth state model, clearly $\text{id} = L^* = 1$, and hence $\Delta_b^1 = e^1 = 0$. In general, $L^* - \text{id}$ always has rank $d - 1$ as $[L^* - \text{id}] \mathbf{b}^* = \mathbf{0}$ and this eigenvalue is simple. Other examples corroborating the intuition that the matrix in Eq. (65) generically is invertible, are models where $G(\mathbf{X}_i, \mathbf{I})$ is independent of \mathbf{I} .

Therefore $\Delta_b^1 = \mathbf{h}_{eb} = \mathbf{0}$ is generically the only possible solution, since all entries of \mathbf{b}^* are strictly positive as argued in the justification of the birth flow rescaling (48). Hence Equation (63) shows that the relation we sought between the linear parts of the environments \mathbf{I}_i and \mathbf{I} is simply

$$\mathbf{I}' = \sum_i \mathbf{I}'_i p_i \quad (66)$$

With this, we can formulate an expansion of the multitype s -function at the singularity \mathbf{X}^* , up to $O(\varepsilon^3)$. For that, we start by recalling the single-resident invasion fitness for structured population models (47),

$$s_{\mathbf{X}}(\mathbf{Y}) = \frac{\log \lambda_d(L(\mathbf{X}^* + \mathbf{V}, \mathbf{I}^* + \varepsilon \mathbf{I}' + \varepsilon^2 \mathbf{I}'') + O(\varepsilon^3))}{T_f(\mathbf{X}^*, \mathbf{I}^*)} + O(\varepsilon^3)$$

where we know from Equation (102) that the numerator has no constant or linear terms, so the logarithm can be replaced by a first order approximation. Introducing the shorthand $T_f^* := T_f(\mathbf{X}^*, \mathbf{I}^*)$, this gives us

$$s_{\mathbf{X}_i}(\mathbf{Y}) = \frac{\lambda_d(L(X^* + V, I^* + \varepsilon I'_i + \varepsilon^2 I''_i)) - 1}{T_f^*} + O(\varepsilon^3) \quad (67)$$

where the absence of first order terms implies that $(\partial \lambda_d(L)/\partial I)I' = 0$ (while in general $\partial \lambda_d(L)/\partial I \neq 0^\top$). Thus the second order expansion looks like

$$\begin{aligned} & s_{\mathbf{X}}(\mathbf{Y}) + O(\varepsilon^3) \\ &= \frac{1}{T_f^*} \left(\varepsilon^2 \frac{\partial \lambda_d(L)}{\partial I} I'' + \frac{1}{2} \varepsilon^2 I'^\top \frac{\partial^2 \lambda_d(L)}{\partial I^2} I' + \varepsilon I'^\top \frac{\partial^2 \lambda_d(L)}{\partial I \partial Y} V + \frac{1}{2} V^\top \frac{\partial^2 \lambda_d(L)}{\partial Y^2} V \right) \end{aligned} \quad (68)$$

If we compare this expansion, in the case of a single resident X_i , with the Taylor series of the simple s -function at a singularity, $s_{\mathbf{X}_i}(\mathbf{Y}) = \frac{1}{2} \mathbf{U}_i^\top \frac{\partial^2 s}{\partial X^2} \mathbf{U}_i + \mathbf{U}_i^\top \frac{\partial^2 s}{\partial X \partial Y} V + \frac{1}{2} V^\top \frac{\partial^2 s}{\partial Y^2} V + O(\varepsilon^3)$, we can link the partial derivatives of simple s -functions to the terms just found:

$$\begin{aligned} \mathbf{U}_i^\top \frac{\partial^2 s}{\partial X^2} \mathbf{U}_i &= \frac{1}{T_f^*} \left(2\varepsilon^2 \frac{\partial \lambda_d(L)}{\partial I} I'' + \varepsilon^2 I'^\top \frac{\partial^2 \lambda_d(L)}{\partial I^2} I' \right) \\ \mathbf{U}_i^\top \frac{\partial^2 s}{\partial X \partial Y} V &= \frac{1}{T_f^*} \varepsilon I_i^\top \frac{\partial^2 \lambda_d(L)}{\partial I \partial Y} V \\ V^\top \frac{\partial^2 s}{\partial Y^2} V &= \frac{1}{T_f^*} V^\top \frac{\partial^2 \lambda_d(L)}{\partial Y^2} V \end{aligned} \quad (69)$$

To simplify the notation and to bring out the similarity to the Lotka-Volterra case (36), we use the matrices C_{11} , C_{00} and C_{10} introduced before (cf. Eq. (26)), which consist of the second order partial derivatives of $s_{\mathbf{X}}(\mathbf{Y})$ at $\mathbf{X} = \mathbf{Y} = \mathbf{X}^*$. In addition, we use a shorthand notation

$$\sigma := \frac{\varepsilon^2}{T_f^*} \left(\frac{\partial \lambda_d(L)}{\partial I} I'' + \frac{1}{2} I'^\top \frac{\partial^2 \lambda_d(L)}{\partial I^2} I' \right) \quad (70)$$

Since for each resident necessarily $s_{\mathbf{X}}(X_i) = 0$, we see from combining the expansion of $s_{\mathbf{X}}(\mathbf{Y})$ (69) with Equality (66) that for each i

$$\begin{aligned} 0 &= \varepsilon^2 \frac{\partial \lambda_d(L)}{\partial I} I'' + \frac{1}{2} \varepsilon^2 I'^\top \frac{\partial^2 \lambda_d(L)}{\partial I^2} I' + \varepsilon^2 I'^\top \frac{\partial^2 \lambda_d(L)}{\partial I \partial Y} \xi_i + \frac{1}{2} \varepsilon^2 \xi_i^\top \frac{\partial^2 \lambda_d(L)}{\partial Y^2} \xi_i \\ &= T_f^* \left(\sigma + 2 \sum_j \mathbf{U}_j^\top C_{10} \mathbf{U}_i p_j + \mathbf{U}_i^\top C_{00} \mathbf{U}_i \right) \end{aligned} \quad (71)$$

As for the Lotka-Volterra case (41), we can formulate these N equalities as

$$\forall i: \underbrace{\sum_j \underbrace{2\mathbf{U}_j^\top C_{10} \mathbf{U}_i}_{[\mathbf{E}]_{ij}} \underbrace{p_j}_{(\mathbf{P})_j}}_{(T)_i} + \sigma = \underbrace{-\mathbf{U}_i^\top C_{00} \mathbf{U}_i}_{(T)_i} \quad (72)$$

From here onwards, we can paraphrase all steps that led us to the result in the Lotka-Volterra case, since we have the same set of equations and all terms and factors have exactly the same meaning.

To reiterate succinctly, our set of N equations (72) can be used to define componentwise an $N \times N$ matrix E and vectors P and T , so that we can write the N equations in a vectorial form: $E P + \sigma \mathbf{1} = T$. Treating σ as an independent unknown, we have $N + 1$ linear equations (since additionally we know $\mathbf{1}^\top P = \sum_i p_i = 1$) in the $N + 1$ unknowns σ and p_1, p_2, \dots, p_N . We then gather the vectorial and the scalar equation together by extending E , P and T as

$$E^* := \begin{bmatrix} E & \mathbf{1} \\ \mathbf{1}^\top & 0 \end{bmatrix} \quad P^* := \begin{pmatrix} P \\ \sigma \end{pmatrix} \quad T^* := \begin{pmatrix} T \\ 1 \end{pmatrix} \quad (73)$$

so that σ and the proportions p_i are solved from $P^* = E^{*-1} T^*$ using only the C-matrices and the strategy differences U_i . Componentwise this gives

$$\begin{pmatrix} p_1 \\ \vdots \\ p_N \\ \sigma \end{pmatrix} = \begin{bmatrix} 2U_1^\top C_{10} U_1 & \cdots & 2U_N^\top C_{10} U_1 & 1 \\ \vdots & \ddots & \vdots & \vdots \\ 2U_1^\top C_{10} U_N & \cdots & 2U_N^\top C_{10} U_N & 1 \\ 1 & \cdots & 1 & 0 \end{bmatrix}^{-1} \begin{pmatrix} -U_1^\top C_{00} U_1 \\ \vdots \\ -U_N^\top C_{00} U_N \\ 1 \end{pmatrix} \quad (74)$$

The issue of the invertibility of E^* will be explored in Subsection 3.6. Note however, that a full rank of E^* is a necessity for the structurally stable existence of the community $\{X_1, X_2, \dots, X_N\}$.

Finally, we have to cast the second order approximation of $s_X(Y)$ close to X^* (47) in the form we found for Lotka-Volterra systems (44). To that end, we use Equality (69), the relationship $I' = \sum_i p_i I'_i$ (66), and the definitions of σ and the C-matrices. Then we find the following form for the invasion fitness function of any structured population model with N resident types:

$$\begin{aligned} s_X(Y) &= \frac{\log(\lambda_d(L(Y, I)))}{T_f^*} + O(\varepsilon^3) \\ &= \frac{1}{T_f^*} \left(\varepsilon^2 \frac{\partial \lambda_d(L)}{\partial I} I'' + \frac{1}{2} \varepsilon^2 I'^\top \frac{\partial^2 \lambda_d(L)}{\partial I^2} I' \right) \\ &\quad + \frac{1}{T_f^*} \left(\varepsilon I'^\top \frac{\partial^2 \lambda_d(L)}{\partial I \partial Y} V + \frac{1}{2} V^\top \frac{\partial^2 \lambda_d(L)}{\partial Y^2} V \right) + O(\varepsilon^3) \\ &= \sigma + 2 \left(\sum_i p_i U_i^\top \right) C_{10} V + V^\top C_{00} V + O(\varepsilon^3) \end{aligned} \quad (75)$$

which is exactly the same equation as we found for the invasion fitness in Lotka-Volterra models (44), and leads us to the following proposition:

Proposition 3 *The invasion fitness function of a general physiologically structured population model with N resident strategies near an evolutionarily singular strategy, can be approximated by that of an N -resident Lotka-Volterra system, up to terms of order $O(\varepsilon^3)$ for distances between residents and singularity of order $O(\varepsilon)$.*

proof By comparing the multiresident s -functions of the Lotka-Volterra case (44–45) with the physiologically structured population case (74–75), it is seen that both depend in exactly the same way on the second order derivatives of the single-resident s -function at \mathbf{X}^* (i.e., the C-matrices) and the deviations \mathbf{U}_i of the resident strategies $\mathbf{X}^* + \mathbf{U}_i$ from the singular strategy. Applying Proposition 1, we can fit a Lotka-Volterra model with the same N -resident fitness function as the given physiologically structured population model, up to quadratic terms in ε . \square

As remarked before, adding the requirement that the fitted Lotka-Volterra model has a trait-independent growth rate r in virgin environments, makes the approximating system unique since $a(\mathbf{Y}, \mathbf{X}) = 1 - s_{\mathbf{X}}(\mathbf{Y})/r$.

Proposition 3 may be read as follows: *The s -function for N -resident Lotka-Volterra models (31) is a second order normal form for multiresident fitness functions*, since for any given structured population model for which we can write down the simple invasion function $s_{\mathbf{X}}(\mathbf{Y})$, we can easily fit a Lotka-Volterra model by defining the growth rate in a virgin environment and the interaction function as

$$\forall \mathbf{Y}: r(\mathbf{Y}) := 1 \quad \forall \mathbf{X}, \mathbf{Y}: a(\mathbf{Y}, \mathbf{X}) := 1 - s_{\mathbf{X}}(\mathbf{Y}) \quad (76)$$

The single-resident fitness function of this Lotka-Volterra model is exactly the same as that of the given model, and the multiresident s -function for Lotka-Volterra models (31) was found to be

$$s_{\mathbf{X}}(\mathbf{Y}) = 1 - (a(\mathbf{Y}, \mathbf{X}_1) \cdots a(\mathbf{Y}, \mathbf{X}_N)) \mathbf{A}^{-1} \mathbf{1} \quad (77)$$

where the interaction matrix \mathbf{A} was defined as

$$\mathbf{A} := \begin{bmatrix} a(\mathbf{X}_1, \mathbf{X}_1) & a(\mathbf{X}_1, \mathbf{X}_2) & \cdots & a(\mathbf{X}_1, \mathbf{X}_N) \\ a(\mathbf{X}_2, \mathbf{X}_1) & a(\mathbf{X}_2, \mathbf{X}_2) & \cdots & a(\mathbf{X}_2, \mathbf{X}_N) \\ \vdots & \vdots & \ddots & \vdots \\ a(\mathbf{X}_N, \mathbf{X}_1) & a(\mathbf{X}_N, \mathbf{X}_2) & \cdots & a(\mathbf{X}_N, \mathbf{X}_N) \end{bmatrix} \quad (78)$$

with necessarily each diagonal element $a(\mathbf{X}_i, \mathbf{X}_i)$ equal to one.

Proposition 3 guarantees that the difference between the N -resident fitness function (77) and the correct function for the given population model is of order $O(\varepsilon^3)$.

3.5 The case of two residents

We found a normal form for fitness functions that is generally applicable to any N -resident Lotka-Volterra (44) or physiologically structured (75) community near a singularity. It is however not a very perspicacious relation between the model ingredients.

If there are only two residents, we can come to a more insightful form by choosing as coordinates $\bar{\mathbf{U}} := (\mathbf{U}_1 + \mathbf{U}_2)/2$ and $\Delta := (\mathbf{U}_1 - \mathbf{U}_2)/2$ (so conversely $\mathbf{U}_1 = \bar{\mathbf{U}} + \Delta$ and $\mathbf{U}_2 = \bar{\mathbf{U}} - \Delta$). Translating \mathbf{T}^* and \mathbf{E}^* , we have

$$\mathbf{T}^* := \begin{pmatrix} -\mathbf{U}_1^\top \mathbf{C}_{00} \mathbf{U}_1 \\ -\mathbf{U}_2^\top \mathbf{C}_{00} \mathbf{U}_2 \\ 1 \end{pmatrix} = \begin{pmatrix} -\bar{\mathbf{U}}^\top \mathbf{C}_{00} \bar{\mathbf{U}} - 2\Delta^\top \mathbf{C}_{00} \bar{\mathbf{U}} - \Delta^\top \mathbf{C}_{00} \Delta \\ -\bar{\mathbf{U}}^\top \mathbf{C}_{00} \bar{\mathbf{U}} + 2\Delta^\top \mathbf{C}_{00} \bar{\mathbf{U}} - \Delta^\top \mathbf{C}_{00} \Delta \\ 1 \end{pmatrix}$$

and (after some computing)

$$\mathbf{E}^{*-1} = -\frac{1}{8\Delta^T C_{10}\Delta} \begin{bmatrix} -1 & 1 & 4\bar{\mathbf{U}}^T C_{10}\Delta - 4\Delta^T C_{10}\Delta \\ 1 & -1 & -4\bar{\mathbf{U}}^T C_{10}\Delta - 4\Delta^T C_{10}\Delta \\ 4\Delta^T C_{10}\bar{\mathbf{U}} & -4\Delta^T C_{10}\bar{\mathbf{U}} & 16\Delta^T C_{10}\Delta \bar{\mathbf{U}}^T C_{10}\bar{\mathbf{U}} \\ -4\Delta^T C_{10}\Delta & -4\Delta^T C_{10}\Delta & -16\bar{\mathbf{U}}^T C_{10}\Delta \Delta^T C_{10}\bar{\mathbf{U}} \end{bmatrix}$$

Through adding the second row or column to the first, we can easily calculate that $\det \mathbf{E}^{*-1} = -8\Delta^T C_{10}\Delta$. Thus we find p_1 , p_2 and σ from $\mathbf{E}^{*-1} \mathbf{T}^*$ to be

$$\begin{pmatrix} p_1 \\ p_2 \\ \sigma \end{pmatrix} = \begin{pmatrix} \frac{1}{2} - \frac{1}{2} \frac{\bar{\mathbf{U}}^T C_{00}\Delta + \bar{\mathbf{U}}^T C_{10}\Delta}{\Delta^T C_{10}\Delta} \\ \frac{1}{2} + \frac{1}{2} \frac{\bar{\mathbf{U}}^T C_{00}\Delta + \bar{\mathbf{U}}^T C_{10}\Delta}{\Delta^T C_{10}\Delta} \\ -\Delta^T C_{00}\Delta - \bar{\mathbf{U}}^T C_{00}\bar{\mathbf{U}} - 2\bar{\mathbf{U}}^T C_{10}\bar{\mathbf{U}} \\ + 2 \frac{\Delta^T [C_{00} + C_{10}^T] \bar{\mathbf{U}}}{\Delta^T C_{10}\Delta} \end{pmatrix} \quad (79)$$

Substituting these three in the normal form (75) presented before, we find

$$\begin{aligned} s_{X_1 X_2}(\mathbf{Y}) &= \mathbf{V}^T C_{00} \mathbf{V} + 2\bar{\mathbf{U}}^T C_{10} \mathbf{V} - \bar{\mathbf{U}}^T [C_{00} + 2C_{10}] \bar{\mathbf{U}} - \Delta^T C_{00} \Delta \\ &\quad + 2\Delta^T C_{10} (\bar{\mathbf{U}} - \mathbf{V}) \frac{\Delta^T [C_{00} + C_{10}^T] \bar{\mathbf{U}}}{\Delta^T C_{10}\Delta} + O(\varepsilon^3) \end{aligned} \quad (80)$$

which is Equation (27) as presented in Subsection 3.2, “Aims”. As an aid to the reader, we remark that most of the correspondence between the general (75) and the two-resident normal form (80) is seen by observing that

$$\sum_i p_i \mathbf{U}_i^T = \bar{\mathbf{U}}^T - \frac{\Delta^T [C_{00} + C_{10}^T] \bar{\mathbf{U}}}{\Delta^T C_{10}\Delta} \Delta^T$$

For two strategies close to \mathbf{X}^* , to be mutually invadable (a requirement for stable coexistence) implies that $\Delta^T C_{10}\Delta$ is negative:

$$\begin{aligned} 0 < s_{X_1}(\mathbf{X}_2) + s_{X_2}(\mathbf{X}_1) &= \mathbf{U}_1^T C_{11} \mathbf{U}_1 + 2\mathbf{U}_1^T C_{10} \mathbf{U}_2 + \mathbf{U}_2^T C_{00} \mathbf{U}_2 + O(\varepsilon^3) \\ &\quad + \mathbf{U}_2^T C_{11} \mathbf{U}_2 + 2\mathbf{U}_2^T C_{10} \mathbf{U}_1 + \mathbf{U}_1^T C_{00} \mathbf{U}_1 + O(\varepsilon^3) \\ &= 2\bar{\mathbf{U}}^T [C_{11} + C_{00}] \bar{\mathbf{U}} + 2\Delta^T [C_{11} + C_{00}] \Delta \\ &\quad + 2\bar{\mathbf{U}}^T [C_{10} + C_{10}^T] \bar{\mathbf{U}} - 2\Delta^T [C_{10} + C_{10}^T] \Delta + O(\varepsilon^3) \\ &= -8\Delta^T C_{10}\Delta + O(\varepsilon^3) \end{aligned} \quad (81)$$

Equation (80) shows that the relative densities can at least be calculated, as long as the denominator $\Delta^T C_{10} \Delta$ is nonzero. However, this does not amount to coexistence when one of the proportions p_i is negative. From (79) we see that coexistence (the positiveness of both p_1 and p_2) is equivalent to

$$\left| \frac{\bar{U}^T C_{00} \Delta + \bar{U}^T C_{10} \Delta}{\Delta^T C_{10} \Delta} \right| < 1 \quad (82)$$

To see how likely it is that this inequality is fulfilled, consider the case where X_1, X_2 and X^* are collinear, so $U_2 = \alpha U_1$ for some value of α . Typically residents will be on opposite sides of the singularity (corresponding to a negative α), although shortly after a branching event we may find them on the same side (positive α). We see that

$$E = 2U_1^T C_{10} U_1 \begin{bmatrix} 1 & \alpha \\ \alpha & \alpha^2 \end{bmatrix} \quad \det E^* = -2U_1^T C_{10} U_1 (\alpha - 1)^2 \quad (83)$$

so there is no unique solution if α is one; T^* then lies in the range of E^* and the linear system $E^* P^* = T^*$ is underdetermined. This much was expected (cf. Fig. 1) since the residents are indistinguishable in this case and coexist at a neutrally stable equilibrium, their relative abundances dependent on initial conditions.

Thus for a nonsingular E^* , the condition for true coexistence is

$$\left| \frac{1 + \alpha}{1 - \alpha} \right| < \left| \frac{U_1^T C_{10} U_1}{U_1^T C_{00} U_1 + U_1^T C_{10} U_1} \right| = \left| \frac{1 + \frac{U_1^T C_{11} U_1}{U_1^T C_{00} U_1}}{1 - \frac{U_1^T C_{11} U_1}{U_1^T C_{00} U_1}} \right| \quad (84)$$

By plotting the left hand side of the inequality, we can draw some conclusions. For two residents to lie on the same side of a singularity ($\alpha > 0$), it is necessary that the right hand side of the inequality is larger than one. The pole at $\alpha = 1$ shows that the closer two such residents are, the less likely it is that the condition is satisfied. On the other hand, we see that $\alpha = -1$ is always a solution, and the closer two residents are to being each other's opposite ($U_1 \approx -U_2$), the likelier it is that the condition is fulfilled.

If X^* is invadable, C_{00} has positive eigenvalues. We can then choose U_1 such that $U_1^T C_{00} U_1 > 0$. Moreover, we concluded that $U_1^T C_{10} U_1$ is negative (cf. Eq. (81)), so necessarily the right hand side of Inequality (84) is larger than one and any $\alpha < 0$ suffices. If however X^* is uninvadable, the right hand side of the inequality is smaller than one and only a narrow interval around $\alpha = -1$ will lead to coexistence.

3.6 Limits to the level of local polymorphism

We have solved σ and the proportions P by inverting E^* . To justify this approach, we show first that by excluding singular matrices E^* , we have only excluded structurally unstable communities.

Let us first point out that the frame of reference in Propositions 4 and 5 and Lemmata 3–6 below, is the set of all systems in the product of the space of strategy deviations $\{U_1, U_2, \dots, U_N\}$ and the space of local equivalence classes of communities specified by the matrices C_{11}, C_{10} and C_{00} ; within this context the qualification “generically” must be understood.

Proposition 4 Generically, if the strategies $\{X^* + \varepsilon \zeta_i \mid i = 1, 2, \dots, N\}$ can coexist in the limit $\varepsilon \rightarrow 0$, then E^* is nonsingular.

proof If E^* is singular, there exists a nontrivial vector μ such that

$$(\mu_1 \mu_2 \cdots \mu_N \mu_{N+1}) E^* = \mathbf{0}^\top$$

or in another form

$$\begin{cases} (\mu_1 \mu_2 \cdots \mu_N) E = -\mu_{N+1} \mathbf{1}^\top \\ (\mu_1 \mu_2 \cdots \mu_N) \mathbf{1} = 0 \end{cases}$$

If we now apply the equalities $\mathbf{1} = \mathbf{1}^\top P$ and $E P = T - \sigma \mathbf{1}$ (which we found for both Lotka-Volterra (42) and physiologically structured models (72)), we see that

$$-\mu_{N+1} = -\mu_{N+1} \mathbf{1}^\top P = (\mu_1 \mu_2 \cdots \mu_N) E P = (\mu_1 \mu_2 \cdots \mu_N) T$$

which is generically a contradiction since μ only relates to E^* whereas T has no direct connection to E^* since they depend on different C-matrices that can be varied independently, by slight changes in the model specification. \square

We will now formulate some results about the influence of the system ingredients on the invertibility of E^* (Lemma 1–4). Proposition 4 then provides a recipe for translating those results into upper bounds to the possible complexity of communities (Proposition 5–Lemma 6). Finally, Proposition 7 relates these results to some very general ideas floating around in the literature about the abstract generalization of the theorem by Levin (1970) that N limiting resources can robustly support the coexistence of at most N types.

Lemma 1 If $\det E \neq 0$, then $\det E^* = -(\det E) \mathbf{1}^\top E^{-1} \mathbf{1}$.

Lemma 2 If $\text{rank } E \leq N - 2$, then E^* is singular.

Lemma 3 If $\text{rank } E = N - 1$, then generically E^* is invertible.

Lemma 4 If $\text{rank } E = N$, then generically E^* is invertible.

The first three lemmata are proven in Appendix D, while the last statement is verified by a look at Lemma 1 plus the realization that the sum $\mathbf{1}^\top E^{-1} \mathbf{1}$ of all the elements of the inverse matrix is typically nonzero.

Proposition 5 Generically, the number of residents N near a singularity is at most one higher than the dimension m of the trait vectors.

This proposition generalizes a result of Christiansen & Loeschke (1987).

proof First we define an $m \times N$ trait matrix $U := [U_1 \ U_2 \ \cdots \ U_N]$ from the trait vectors (or componentwise $[U]_{ai} := (U_i)_a$). We then see that E is a product of matrices,

$$[E]_{ij} := 2U_j^\top C_{10} U_i = [2U^\top C_{10}^\top U]_{ij}$$

As the rank of a product of matrices is never higher than the rank of any of its constituent matrices, the rank of E is at least two below maximal if $N \geq m + 2$, in which case E^* is not invertible according to Lemma 2 and the conclusion follows from Proposition 4. \square

Lemma 5 When two resident strategies are linearly dependent on the other $N - 2$ in a set of strategies close to a singularity, this set of N strategies generically cannot coexist.

proof In this case \mathbf{U} has a rank at least two below N , and by Lemma 2 this holds for \mathbf{E} too; applying Proposition 4 concludes the proof. \square

Lemma 6 Near a singularity, the number of residents is generically at most one higher than the rank of \mathbf{C}_{10} .

This is a corollary of Lemma 2 and Proposition 4 as well.

Lemma 7 Even if both \mathbf{U} and \mathbf{C}_{10} have full rank, \mathbf{E}^* may still be singular.

This statement is proven in Appendix D. We remark however that a small perturbation of \mathbf{U} and/or \mathbf{C}_{10} will suffice to make \mathbf{E}^* invertible.

We will now point out in Proposition 7 an indirect connection between $\mathbf{E} = 2\mathbf{U}^\top \mathbf{C}_{10} \mathbf{U}$ and the dimension of the feedback environment (Meszéna *et al.*, 2006; Dieckmann & Metz, 2006). As a corollary, Proposition 5 may be recovered, as at most N types can stably coexist in an N -dimensional environment (Meszéna & Metz, 1999; Meszéna *et al.*, 2006). As a preliminary we show how to find the exceptions to the rule that Lotka-Volterra models generate infinite dimensional environments:

Proposition 6 A Lotka-Volterra model with interaction function $a(\mathbf{Y}, \mathbf{X})$ has feedback dimension e , if and only if e is the minimal number for which we can write $a(\mathbf{Y}, \mathbf{X}) = \sum_{q=1}^e b_q(\mathbf{Y}) c_q(\mathbf{X})$, for some functions b_q and c_q .

A proof is given in Appendix E.

Proposition 7 (local environmental dimension) Near singularities, environments are locally at most $(z + 1)$ -dimensional when the strategies are z -dimensional.

proof In this section we showed that an adaptive dynamics model near a singularity can be approximated, up to quadratic terms, by a Lotka-Volterra model with any interaction function of the form

$$a(\mathbf{X}^* + \mathbf{V}, \mathbf{X}^* + \mathbf{U}) := 1 - \mathbf{U}^\top \mathbf{C}_{11} \mathbf{U} - 2\mathbf{U}^\top \mathbf{C}_{10} \mathbf{V} - \mathbf{V}^\top \mathbf{C}_{00} \mathbf{V} + O(\varepsilon^3)$$

and growth rate $r(\mathbf{Y}) := 1$, where the \mathbf{C} -matrices are determined by the model to be approximated. The fitted model then has the same s -function as the original model, up to quadratic terms in ε . Making the specific choice

$$a(\mathbf{X}^* + \mathbf{V}, \mathbf{X}^* + \mathbf{U}) := 1 - \mathbf{U}^\top \mathbf{C}_{11} \mathbf{U} - 2\mathbf{U}^\top \mathbf{C}_{10} \mathbf{V} - \mathbf{V}^\top \mathbf{C}_{00} \mathbf{V} + \mathbf{U}^\top \mathbf{C}_{11} \mathbf{U} \mathbf{V}^\top \mathbf{C}_{00} \mathbf{V}$$

and using the following definitions,

$$\begin{aligned} b_0(\mathbf{Y}) &:= 1 - (\mathbf{Y} - \mathbf{X}^*)^\top \mathbf{C}_{00} (\mathbf{Y} - \mathbf{X}^*) \\ c_0(\mathbf{X}) &:= 1 - (\mathbf{X} - \mathbf{X}^*)^\top \mathbf{C}_{11} (\mathbf{X} - \mathbf{X}^*) \\ \forall a: b_a(\mathbf{Y}) &:= 2 \sum_b [\mathbf{C}_{10}]_{ab} (\mathbf{Y} - \mathbf{X}^*)_b \\ c_a(\mathbf{X}) &:= (\mathbf{X} - \mathbf{X}^*)_a \end{aligned}$$

we see that $a(\mathbf{Y}, \mathbf{X}) = \sum_{a=0}^z b_a(\mathbf{Y}) c_a(\mathbf{X})$. Proposition 6 then shows us that the feedback dimension of the approximating model is at most $z + 1$. \square

4 The meaning of it all

What is the relation between the canonical equation (Section 2) and the fitness function near singularities (Section 3)? How can they aid in interpreting a model? Or in other words, why do these sections appear together in a single paper? We will address these questions here, by describing a recipe for analysing concrete models and illustrating it with an example from the literature.

The starting point should be a model that satisfies the assumptions of adaptive dynamics: a large system size and a population dynamics where the individuals have heritable life history parameters that are under evolutionary control through a low rate of mutations with relatively small effect. In this situation, the ecology typically is dominated by a few, markedly different, strategy vectors. The distribution of the strategies thus has a few distinct peaks, with almost all individuals having a trait very close to the position of one of the peaks. If there are one or two such trait values, for example, the community is termed *quasi-monomorphic* or *quasi-dimorphic*. Interesting evolutionary dynamics are those where the number of peaks increases over time, as such increasing diversity and specialization has an obvious interpretation as (the onset of) (sym- or parapatric) speciation. Of course, it is just as important to know when this buildup of diversity does not and/or cannot occur.

The evolutionary analysis of such a model starts by setting up a resident population at equilibrium, with all individuals of a single type. Typically the trait finds itself under directional selection and evolves as predicted by the canonical equation (23). The community is then quasi-monomorphic at an evolutionary timescale, as the appearance of a successful mutant is immediately followed by the disappearance of the former resident (cf. Section 2.2, “invasion implies substitution”). This substitutional regime only comes to an end when the population finds itself near a singular trait value (cf. Introduction 1.1). Near singular trait values the invasion/replacement dynamics acts differently with other behaviours possible: resident traits may stop evolving, or the quasi-monomorphic population may diversify into a quasi-dimorphic community after a brief polymorphic phase. If we find that the population does branch into several populations with differing strategies, these branches must be followed until they go extinct or until they are a safe distance away from the singularity, so that one knows whether several types of residents coexist in a protected manner or whether the polymorphism quickly disappears again. Once the branches have evolved out of the proximity of the singularity, a canonical equation again governs the evolution of the subpopulation associated with each branch, and the analysis can proceed as before.

This process is possibly repeated, with further evolutionary branching, until all branches have reached evolutionary endpoints (i.e., attracting, uninvadable trait values): only then a final evolutionary outcome has been found. In some cases however, evolution does not proceed towards a definite endpoint but ends up on a limit cycle or on a more complicated attractor (e.g. Dieckmann *et al.*, 1995).

A recipe for studying the evolutionary behaviour of a model, from random initial resident until the final outcome(s), can be broken down in the following steps.

4.1 Model (re)formulation

The adaptive dynamics approach requires that the basic model assumptions are formulated in terms of the behaviour of individuals. These must possess near-faithfully inherited traits (Metz *et al.*, 1996) influencing their reproduction, survival, change in spatial and physiological states, and impact on their environment. (The environment was introduced in Subsection 1.1 and described further in 1.2. It is a concept of which the utility lies in the fact that in a given environment the growth dynamics of any clone is linear with an asymptotic relative growth rate depending on both the strategy and the environment.) Such a description requires i.a. postulates for how individuals convert resources into offspring (depending on the state and inherited strategy of the organism, and the state of the resources), but also for the dynamics of the resources consumed by individuals. Therefore the vector of heritable traits will appear as a parameter of the individual dynamics (and hence of the population dynamics), and the population distribution will appear as an input of the environmental dynamics.

4.2 Life history parameters

Once the model is formulated in individual-based terms, the necessary life history parameters can be calculated: for a resident with strategy \mathbf{X} in the environment \mathbf{I} , there is the expected lifetime offspring production $\mathbf{L}(\mathbf{X}, \mathbf{I})$ and the feedback matrix $\mathbf{G}(\mathbf{X}, \mathbf{I})$ (cf. Subsection 1.2), the life expectancy $T_s(\mathbf{X}, \mathbf{I})$ and the average age-at-giving-birth $T_f(\mathbf{X}, \mathbf{I})$ (100), the equilibrium population densities $T_s(\mathbf{X}, \mathbf{I}) ||\mathbf{b}||$ where \mathbf{b} is the birth flow vector (1), and the offspring variance σ^2 (16). Notice that these are all observables, with a clear biological interpretation.

From Appendix A we know that the invasion fitness of a mutant that resembles the i^{th} resident type has the following form in general:

$$s_{\mathbf{X}}(\mathbf{X}_i + \mathbf{V}) = \frac{\log \lambda_d(\mathbf{L}(\mathbf{X}_i + \mathbf{V}, \mathbf{I}_{\mathbf{X}}))}{T_f(\mathbf{X}_i, \mathbf{I}_{\mathbf{X}})} + O(||\mathbf{V}||^2)$$

where λ_d is the dominant eigenvalue operator. Notice how in this context one can avoid solving the characteristic equation to find $\lambda_d(\mathbf{L})$: the dominant eigenvalue of \mathbf{L} for any resident \mathbf{X}_i is necessarily 1. Therefore the right- and left eigenvectors \mathbf{b}_i and \mathbf{v}_i^T of \mathbf{L} are the (unique, up to a scalar) solutions to $[\text{id} - \mathbf{L}(\mathbf{X}_i, \mathbf{I}_{\mathbf{X}})]\mathbf{b}_i = \mathbf{0}$ and $\mathbf{v}_i^T [\text{id} - \mathbf{L}(\mathbf{X}_i, \mathbf{I}_{\mathbf{X}})] = \mathbf{0}^T$. This allows us to approximate the a^{th} component of the fitness gradient $\left(\frac{\partial s_{\mathbf{X}}(Y)}{\partial Y_a} \Big|_{Y=X_i} \right)^T$ by $\mathbf{v}_i^T \left[\frac{\partial \mathbf{L}(Y, \mathbf{I}_{\mathbf{X}})}{\partial Y_a} \Big|_{Y=X_i} \right] \mathbf{b}_i / (T_f \mathbf{v}_i^T \mathbf{b}_i)$. Hence we see that for the fitness gradient we only have to solve the next-generation and environmental feedback equations (1) for \mathbf{b}_i (and $\mathbf{L}(\mathbf{X}_i, \mathbf{I}_{\mathbf{X}})$), and to find \mathbf{v}_i .

For each i , the eigenvectors are normalized so that $||\mathbf{u}_i|| = 1$ and $1 = \mathbf{v}_i^T \mathbf{u}_i$ (13). This allows us to calculate T_f (100) and T_s ; the life expectancy for example is

$$T_s := \sum_i u_i \int_0^\infty F_i(\mathbf{X}, \mathbf{I}, a) da \tag{85}$$

with $F_i(\mathbf{X}, \mathbf{I}, a)$ the probability that an individual with trait value \mathbf{X} and born in state i , survives to at least age a .

Depending on model type, the previously described steps in the analysis may be numerical or analytical. Clearly an analytical approach has many advantages, like showing how life histories depend on strategy parameters. However, even when this treatment is theoretically possible, it may be so cumbersome as to be unfeasable: finding the dominant eigenvalue of L where there are three or four possible birth states would be a case in point.

We remark furthermore that this description of the second step of the analysis is written so as to be as general as possible. In practice life tends to be simpler, and often parts of this step may be skipped: e.g., for an ODE or difference equation model, the population dynamical equilibrium and per capita growth rate are found directly, making the explicit formulation of G and L (and its derivatives and eigenvectors) redundant. Furthermore the community will be starting from a single resident, so that $1 = i = N$ and the number of equations to solve simultaneously may be low.

4.3 The monomorphic dynamics under directional selection

The canonical equation (23) predicts how the trait vectors in a community will change over time. This prediction is valid as long as the fitness gradient stays nonzero, allowing a deterministic approximation of the path a community will follow from any given initial state. Here we assume that the mutational covariance matrix is nonsingular. (It may become singular, for example when the traits under evolutionary control are subject to constraints. For trait vectors on the surface that then forms the boundary of the attainable trait space, the null space of the covariance matrix is locally orthogonal to that surface. The equation shows that at equilibrium the fitness gradient must lie in that null space. This scenario may be treated in the same way as that of a bounded trait space, discussed below.) From the canonical equation, we see that a state is transient if the fitness gradient is nonzero. As it is derived from an approximation that fails in the proximity of singular points, the canonical equation does not help the analysis close to those interesting points towards which evolution drives the community. Paradoxically, we will use the (one-resident) canonical equation to find the strategy values where it fails as an approximation, and subsequently use the (multiple-resident) equation to predict how the community will evolve around those strategies.

A major exception to the above scenario occurs when the trait space is bounded in one or more directions. In that case, a distinction must be made between the dynamics tangential and orthogonal to the boundary. If the fitness gradient points outward at the boundary, the dynamics orthogonal to the boundary will trap any approaching community. Hence the analysis can be continued in a lower-dimensional strategy space, looking for singularities of the dynamics constrained to the boundary. Some care must be taken if the fitness gradient points outward only along part of the boundary, as the community may evolve for a while along the boundary, but later stray away from it.

After locating those points where the fitness gradient is zero — the so-called *singular points* (1.1) — we can use the canonical equation to find out whether they are attracting or not, and if so, to find their basin of attraction. Singular points that are repelling or have inappreciable domains of attraction are clearly not that inter-

esting, as the community will normally not approach such points. In principle, the equation can be as rich in dynamical features as any ODE. As such, the appropriate numerical tools, or theorems about the qualitative behaviour of solutions, will depend on the specifics of the model under consideration.

At this point we still lack one ingredient of the canonical equation: the mutational covariance matrix $M(X)$ near the trait value X (cf. Eq. (2), (23)). The influence of M can be understood in the following way: selection impels traits to change in the direction of the steepest increase in fitness, but the covariances are changing the direction of movement away from this “optimal” direction. Covariance matrices are the great unknowns in evolutionary biology. There is little or no understanding of which choices of M (or, equivalently, of the mutational distribution \mathfrak{M}) are the reasonable ones for each type of biological model, as the covariances are footprints of deeper developmental, physiological and biophysical processes (cf. Pigliucci, 2006). The safest conclusion to draw is that any complicated dynamical features found from the canonical equation should be dismissed as biologically irrelevant, unless they are robust against changes in M . When there is no further information about it, most people in practice choose $M = \text{id}$, the identity matrix. However, it is never a bad idea to do simulations for a few other values of M . The best possible result would then be that one can classify the potential evolutionary outcomes as dependent on M . Then the theoretical analysis leads to a potentially empirically answerable question: “Is M expected to lie in this or that domain?”.

If we are satisfied that evolution is towards a singularity, whether of the full trait space or of a constrained subspace, we continue to the next step. If there is no such singularity, the community will stay monomorphic indefinitely while the resident trait keeps changing according to the canonical equation.

4.4 Near singularities

When a resident strategy moves closer and closer to a singularity, the first order approximation of fitness by the selection gradient breaks down, and so do a number of other approximations that were made so far. Around a singularity, several zones can be distinguished in which different refinements come into play.

In the most convenient (and hence generally emphasized) case, there exists an outer zone where the second order terms start to dominate the s -function, while the radius of curvature of the local fitness contours is still large in comparison with the average mutational step length. We note here that the existence of such a region depends on the separation of two scales: that of the distance of the residents from the singular point and that of the distance of the mutants from their resident progenitors, where the relative effects on the two scales have to be gauged through the s -function. Whether or not the singular point attracts throughout this outer zone can be determined through recourse to the canonical equation. The only difference with the earlier discussion is that here standard analytic tools from linearized stability theory can be used, as the second order terms of the invasion fitness function fully determine the local linearization of the canonical equation. The one snag is that the canonical equation still contains the mutational covariance matrix. Leimar (2001, 2005, to appear) analyzed the extent to which the stability of a singular point can be determined without any knowledge of that matrix. In this analysis, the

eigenvalues of the matrix $\partial^2 s_X(Y)/\partial Y^2 - \partial^2 s_X(Y)/\partial X^2$ (or $C_{00} - C_{11}$ in our earlier notation (26)) play the key role in the classification of the evolutionary possibilities relatively close to a singularity X^* . The possibilities are as follows:

- If $C_{00} - C_{11}$ is positive definite (i.e., has only strictly positive eigenvalues), X^* is repelling. Thus the community can only find itself close to X^* if the initial resident was close to X^* as well. In such cases, the community will evolve away from the singularity and the canonical equation will quickly become valid, so that the analysis can proceed in accordance with 4.3.
- If $C_{00} - C_{11}$ is negative definite (i.e., has only strictly negative eigenvalues), convergence to X^* is assured. In this case the next step of this recipe, Subsection 4.5, applies. Different outcomes are possible, as X^* may be an evolutionary endpoint or a branching point.
- If $C_{00} - C_{11}$ is indefinite (i.e., has both strictly positive and negative eigenvalues), the covariance matrix $M(X^*)$ is decisive. Firstly, for a given M the singularity may be a saddlepoint, so that at first the resident can approach X^* but later grow more and more distinct from X^* . Thus the regime of directional selection stays intact and the analysis of 4.3 applies. Secondly, for a given M the singularity may be an attractor so that the analysis can continue at the next step in this analysis. Thirdly, for a given M the singularity may be a repellor, and hence be disregarded as unattainable.

The model under consideration may constrain M to one of the three cases and thus simplify the analysis, or several cases may occur depending on parameter values.

Closer to the singular point where the curvature of the fitness contours starts to have its effects, it is also no longer possible to assume permanent quasi-monomorphism, as it may be that mutants are no longer able to oust their progenitor. A discussion of the final convergence to an unininvadable singular point (characterized by C_{00} being negative definite) under a still mutation limited regime, can be found in Appendix B of Dieckmann & Metz (2006). Although the problem of the final convergence is far from solved, in this case it turns out to be both independent of the mutational covariance matrix and an all-or-none property. Hence the problem can be solved in principle by a single extended simulation run, of a type similar to those described in the next subsection. A final problem is that sufficiently close to the singular point, the timescale of selective takeovers will in any concrete case become so slow that the assumption of mutation limitation will break down, thus necessitating an approach along the lines of quantitative genetics (cf. Schneider, 2006).

4.5 At attracting singularities

Once we know that the singularity X^* is an attractor, we can start wondering whether selection will be stabilizing (so that the resident distribution will forever have the shape of a single peak close to X^*), or disruptive (so that distinct (sub-) populations may form near X^* and evolve away from each other).

When C_{00} is negative definite then X^* is unininvadable and selection is stabilizing close to X^* . Hence the first requirement for branching to occur is that X^* must be invadable: C_{00} must have at least one positive eigenvalue. If increasingly differentiating polymorphisms indeed do arise, we once again have to distinguish between the zones discussed in the previous subsection.

For the zone where both the canonical equation and the second order approximation to the s -function hold, the following conjecture is floating around (Stefan Geritz, lecture given at the International Conference on Computational and Mathematical Population Dynamics, Trento 2004): in those cases where C_{00} has a simple positive maximal eigenvalue, there will remain only a single pair of branches if $e_M^\top [C_{00} + C_{11}]e_M > 0$, where e_M is an eigenvector corresponding to the maximal eigenvalue; else all but one branch will eventually go extinct. When there are two co-maximal positive eigenvalues, then in principle three branches can grow away from each other at 120 degree angles, without any two of them driving the remaining third to extinction (Vukics *et al.*, 2003). But even in the particular case of co-maximality, it appears that three-way splitting happens only under special conditions. (The authors welcome any counterexamples!)

As an aside we note that in finite populations, the largest positive eigenvalue of C_{00} has to be sufficiently large for branching to really occur. Moreover, several other processes may obstruct diversification. Consider for example a diploid, sexual organism and assume some diversity has arisen. If a male and female of differing types mate, their offspring will be of a type close to the average of the parental types. Hence unless a preference for assortative mating is present already, sexual reproduction and the recombination it engenders will tend to average out strategies and thus prevent the buildup of specialized subpopulations through what could be called the “Mendelian mixer”.

Before we can with some confidence rely on the canonical equation, evolution has to get the resident community out of the region where the radius of curvature of the local fitness contours is small relative to the average mutational step length. It is in the analysis of what happens in this region that Section 3 is useful in our recipe: since (up to quadratic terms in the mutation step size) all models behave as Lotka-Volterra models (28) near singularities, we can fit such a model and study it instead of the original model. As explained after Proposition 3 and applied in the Example 4.6 below, to construct a Lotka-Volterra model with the same N -resident fitness function as the model under consideration, we merely have to define the per capita growth rate in a virgin environment and the interaction function as

$$\forall Y: r(Y) := 1 \quad \forall X, Y: a(Y, X) := 1 - s_X(Y) \quad (86)$$

This model is now fitted so as to have the same single-resident fitness function as the original model, for any combination of resident and invader. As mentioned above, Section 3 shows that fitness functions of communities close to a singularity are model-independent in a sense, so we can proceed our analysis with either model. Whatever the nature of the original model, the new one is an ODE model, so a possible advantage is that we can study its dynamics with standard packages. Furthermore Lotka-Volterra models are mathematically rather straightforward (e.g. Hofbauer & Sigmund, 1998), as for example the equilibrium population sizes in a community of N types is easily calculated (Formula 32). Finally, stochastic simu-

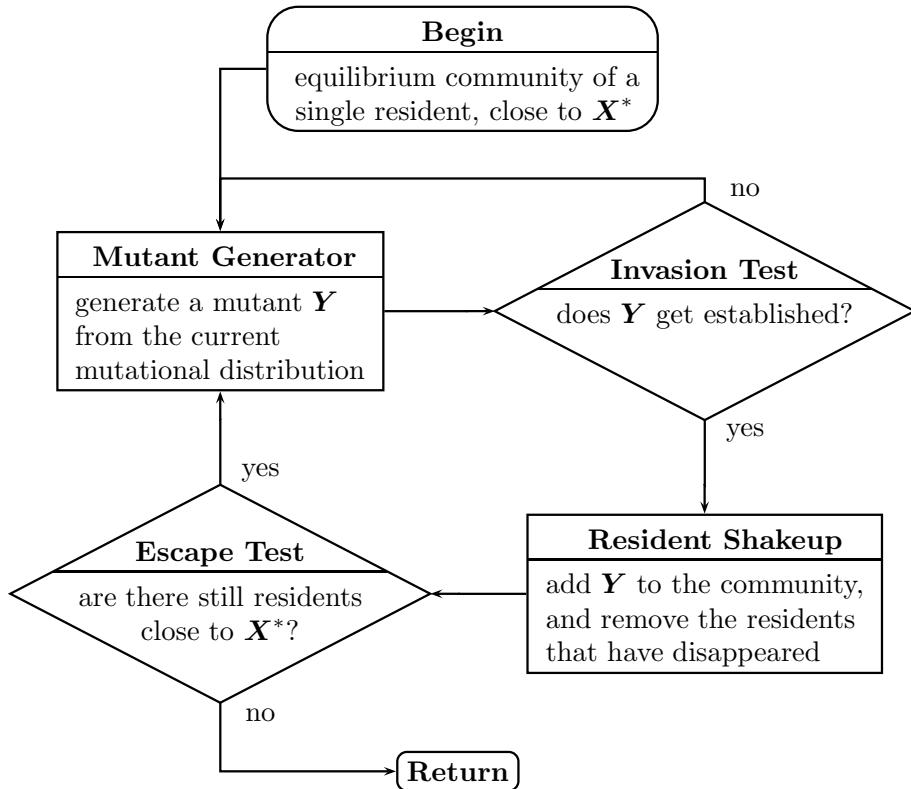


Figure 2: Steps in simulating the evolutionary dynamics close to a singularity.

lations of their individual-based counterparts are easily performed using the Gillespie (1976) algorithm (see e.g. the appendix to Dieckmann *et al.*, 1995; and Champagnat *et al.*, 2006).

To explore the evolutionary behaviour of a system near an invadable attracting singularity X^* , simulations can be run along the following lines:

1. Choose an initial resident near the singularity: for some small U_1 , this resident's strategy is $X_1 = X^* + U_1$. Its density is set at the (nontrivial) equilibrium, and the number N of resident types in the community is set at 1.
2. Draw a mutant from the mutational distribution associated with the community. To do this straightforwardly, we just have to think about the mutant's ancestor. If N types are present in the community at densities \hat{n}_i , then with probability $p_i = \hat{n}_i / \sum_j \hat{n}_j$ the mutant derives from the i^{th} resident. From the mutational step distribution $\mathcal{M}(X_i)$ around this progenitor we draw a muta-

tion step V , generating a mutant of type $Y := X_i + V$.

If the invasion fitness of the newly found mutant is negative, we discard it and draw another mutant according to the above recipe. Once we have a mutant with positive fitness, we have to see whether it will get established or not. For this we turn the Wheel of Fortune a second time, where the chance of success scales with the mutant's fitness as required by Equality (21). If our mutant is unlucky, we go back to generating mutants until one successfully invades.

3. See which of the original residents survive the invasion of our mutant. This is done by initializing the Lotka-Volterra ODEs at the community attractor, adding a small number of invaders — enough to avoid disappearance of the mutants by roundoff errors — and then following the community dynamics to its new equilibrium.

After the transition from (close to) the equilibrium of the former to that of the new community, we will usually find that the mutant's progenitor has disappeared. In some situations however, several residents may have disappeared, while in the case of disruptive selection it is possible that no residents disappear at all. Thus the community \mathbb{X} may have lost residents $X_{d_1}, X_{d_2}, \dots, X_{d_k}$ but gained a new resident $X_{N-k+1} := Y$, where the equilibrium densities are easily found analytically or numerically, using the interaction function and the resident strategies (cf. Eq. 32).

4. Go back to Step 2, as long as there still are residents in a close neighbourhood of X^* .

In some cases however, the singularity is invadable but does not allow a polymorphism to build up. This happens when the zone of mutual invadability (and hence stable coexistence) is so narrow that a mutant will be outside of this area after very few mutation steps, and therefore drive all close by residents to extinction. The trajectory will then hover close to the singularity, while neither really closing in on X^* nor branching. Thus, if any polymorphism in the community only remains for a brief period while the trajectory makes no progress towards the nearby singularity within a reasonable time, the algorithm must be interrupted and X^* be proclaimed an evolutionary endpoint.

At the last step, there is no hard and fast rule to work out what a safe distance is for concluding that all branches present have evolved away from the proximity of the singularity. Out of hand, we would say ten mutation steps. The underlying idea is that away from a singularity, the “invasion implies substitution” dictum holds sway for each of the separate branches, so we can be confident that no buildup of diversity is possible beyond our chosen boundary. Similarly, what constitutes a “reasonable time” at Step 2 is not exactly defined; we would call it a day when a thousand successive mutants fail to invade. Given these inexactitudes, it is clear that our story relies on the common sense of the programmer. A summary of the algorithm as a flow diagram is given in Fig. 2.

If we are convinced there is no diversification occurring while the resident creeps ever closer to X^* , we label this strategy an evolutionary endpoint. If on the other

hand branching has occurred, then the branches come under a regime of directional selection once they have outgrown the influence of X^* . Thus we find ourselves back at Subsection 4.3 to repeat the entire analysis, this time in a more complicated fashion since equilibria of the canonical equation for several residents have to be found, and equilibria of a community dynamics with several residents. The invasion analysis, however, keeps studying the singular points separately, with the other (faraway) strategists being part of the background that determines part of the environment \mathcal{I} when examining the evolution of a resident.

To illustrate our recipe, we conclude with an example from the literature.

4.6 A fitting example

As an example we will consider a one-locus model for intraspecific competition (Christiansen & Loeschke, 1987). Diploid additive genetics is assumed in a discrete time, non-overlapping generations analogue to Lotka-Volterra dynamics. There are multiple resources, and the trait under evolutionary control is the modus of the utilization function:

- Resources are distributed as a z -variate Gaussian with mean 0 and covariance matrix Ψ , where Ψ is real, symmetric and positive definite.
- Each existing allele $A_i \in \{A_1, A_2, \dots, A_N\}$ has a trait value X_i associated with it, such that for a diploid with genotype (A_i, A_j) , the optimal resource type is $D_{ij} := D + X_i + X_j$ and the diploid has a Gaussian resource utilization function $U_{ij}(\mathbf{r}) := \alpha \exp\left(-\frac{1}{2}(D_{ij} - \mathbf{r})^\top \Phi^{-1}(D_{ij} - \mathbf{r})\right)$. The scaling constants α and D , and the symmetrical, positive definite covariance matrix Φ are shared by all genotypes.

Diploid individuals (A_i, A_j) and (A_k, A_l) interact through the competition coefficient $\gamma_{ij,kl} := \exp\left(-\frac{1}{4}(D_{ij} - D_{kl})^\top \Phi^{-1}(D_{ij} - D_{kl})\right)$ while the carrying capacity is given as $k_{ij} := \exp\left(-\frac{1}{2}D_{ij}^\top [\Phi + \Psi]^{-1}D_{ij}\right)$.

Genotypes are formed by random mating under free recombination. Between generations, a genotype (A_i, A_j) changes in abundance as

$$n_{ij}(t+1) = n_{ij}(t) \left(1 + \beta \left(k_{ij} - \sum_{kl} \gamma_{ij,kl} n_{kl}(t) \right) \right) \quad (87)$$

for some scaling constant β .

For an adaptive dynamics analysis of this model, it is important to realize at this point that the alleles, not the diploids, are the individuals to consider. This is seen by contemplating who is faithfully replicating (Metz *et al.*, 1996) in this community: in the extreme situation where the population is made up of homozygotes (A_1, A_1) and (A_2, A_2) , half of the offspring is of a brand new type so that the heterozygote per capita growth rate is infinite.

We can now interpret the model ingredients in an adaptive dynamics context. Firstly, the strategy of an allele A_i is the allelic trait value X_i associated with it.

Secondly, for a rare allele A_j that is introduced in this monomorphic community, the number of alleles A_j is actually n_{ij} as mutant homozygotes are exceedingly rare. Thus we find the one-resident invasion fitness (i.e., the per capita growth rate of a rare mutant in a monomorphic equilibrium community) as the logarithm of the mutant heterozygote's growth rate. From these considerations plus the model ingredients and Equation (87), we see that

$$\begin{aligned} s_X(Y) = \log & \left(1 + \beta e^{-\frac{1}{2}(D+X+Y)^T[\Phi+\Psi]^{-1}(D+X+Y)} \right. \\ & \left. - \beta e^{-\frac{1}{2}(D+2X)^T[\Phi+\Psi]^{-1}(D+2X)} e^{-\frac{1}{4}(X-Y)^T\Phi^{-1}(X-Y)} \right) \end{aligned} \quad (88)$$

From the selection gradient

$$\left(\frac{\partial s_X(Y)}{\partial Y} \Big|_{Y=X} \right)^T = -\beta e^{-\frac{1}{2}(D+2X)^T[\Phi+\Psi]^{-1}(D+2X)} [\Phi + \Psi]^{-1}(D + 2X) \quad (89)$$

we see that the unique singularity lies at $X^* := -D/2$, so we translate the origin of our coordinate system to X^* and use the (not necessarily small) strategy difference vectors $U := D/2 + X$ and $V := D/2 + Y$.

The singularity is globally attracting, as can be seen in the following way. First we note that the inverse of the sum of real, positive definite, symmetric matrices has these three properties as well, so that $0 < X^T[\Phi + \Psi]^{-1}X$ for any nontrivial vector X . If we look at the canonical equation (23), we see that it predicts the resident trait to change according to

$$\frac{dX}{dt} = \alpha(X) M(X) \frac{\partial s_X(Y)}{\partial Y} \Big|_{Y=X} =: f(X) \quad (90)$$

for some positive function $\alpha(X)$. Considering only small mutations in the direction of the singularity (i.e., $V := (1 - \gamma)U$ with $\gamma > 0$ and $V - U = O(\varepsilon)$), we see that such a mutant has positive fitness, while a step away from the singularity ($\gamma < 0$) implies negative fitness:

$$\begin{aligned} s_{X^*+U}(X^* + V) &= 0 + \frac{\partial s_X(Y)}{\partial Y} \Big|_{Y=X^*+U} (-\gamma U) + O(\varepsilon^2) \\ &= 2\beta\gamma e^{-2U^T[\Phi+\Psi]^{-1}U} U^T[\Phi + \Psi]^{-1}U + O(\varepsilon^2) > 0 \end{aligned} \quad (91)$$

Given this inequality, it is easy to find a Lyapunov function for $f(X)$: e.g., $L(X) := X^T[\Phi + \Psi]^{-1}X$ is positive, continuously differentiable and for every nontrivial U

$$\nabla L(U) f(X^* + U) = -\alpha_2(X^* + U) U^T[\Phi + \Psi]^{-1}M[\Phi + \Psi]^{-1}U < 0 \quad (92)$$

where α_2 is a positive function. Hence the singular point always is a global attractor for the one-resident canonical equation, and there is no separate need to check the conditions described in Subsection 4.4.

We draw attention here to the fact that C_{10} is symmetric, as often happens in simple models (cf. the paragraph following Equation (35)).

As the sign of $s_X(Y)$ is not influenced by the value of $\beta > 0$, we can put this proportionality constant at $\beta := 1$. For strategies close to the singularity, where U

and \mathbf{V} are $O(\varepsilon)$, we approximate the invasion fitness function as

$$\begin{aligned} & s_{\mathbf{X}^* + \mathbf{U}}(\mathbf{X}^* + \mathbf{V}) \\ &= \log \left(1 + e^{-\frac{1}{2}(\mathbf{U} + \mathbf{V})^\top [\Phi + \Psi]^{-1}(\mathbf{U} + \mathbf{V})} - e^{-2\mathbf{U}^\top [\Phi + \Psi]^{-1}\mathbf{U}} e^{-\frac{1}{4}(\mathbf{U} - \mathbf{V})^\top \Phi^{-1}(\mathbf{U} - \mathbf{V})} \right) \\ &= \mathbf{U}^\top \left[\frac{3}{2}[\Phi + \Psi]^{-1} + \frac{1}{4}\Phi^{-1} \right] \mathbf{U} + 2\mathbf{U}^\top \left[-\frac{1}{2}[\Phi + \Psi]^{-1} - \frac{1}{4}\Phi^{-1} \right] \mathbf{V} \\ &\quad + \mathbf{V}^\top \left[-\frac{1}{2}[\Phi + \Psi]^{-1} + \frac{1}{4}\Phi^{-1} \right] \mathbf{V} + O(\varepsilon^3) \end{aligned} \quad (93)$$

from which form we can read off C_{11} , C_{10} and C_{00} .

In the case of scalar traits, the invadability of \mathbf{X}^* now settles the rest: if $0 < C_{00}$ we find a branching point, else a CSS. The first case corresponds to $\Phi < \Psi$, the second to the reverse. This is the classical result that for branching to occur, the resource utilization kernel must be narrower than the resource abundance spectrum (Christiansen, 1991).

In the case of vectorial traits, \mathbf{X}^* is an evolutionary endpoint if C_{00} is negative (semi)definite, and a branching point if C_{00} is positive (semi)definite. In Appendix G we show that C_{00} is positive definite if and only if $\Psi - \Phi$ is positive definite, and that the same holds for indefiniteness, (non)negative and nonpositive definiteness. Hence a similar result holds for the relation between resource utilization kernel and resource abundance spectrum as in the scalar case. However, that C_{00} has a single positive eigenvalue is not sufficient for branching, as a protected polymorphism is not guaranteed to arise. Even if it does arise, the region of coexistence may be so narrow that the dimorphic population quickly strays out of it.

In the case where C_{00} has both positive and negative eigenvalues, we should resort to the algorithm suggested in Figure 2 and use a Lotka-Volterra model to simulate the evolutionary dynamics. This is a valid approach, since the dynamics (up to $O(\varepsilon^3)$) of the proportions p_i are identical in all models with the same single-resident fitness function, as argued in Appendix F: two different community dynamics that yield the same one-resident fitness functions up to terms of order $O(\varepsilon^3)$ will arrive at an equilibrium with the same set of types surviving, whenever they start with the same N -resident community at equilibrium plus the same invader at a low density. Therefore, instead of the original discrete time equations (87) for diploids, we switch to a Lotka-Volterra system that has a sign-equivalent fitness function for any community of alleles, up to terms of order $O(\varepsilon^3)$. If alleles with trait values $\mathbf{X}^* + \mathbf{U}_1$, $\mathbf{X}^* + \mathbf{U}_2$, ..., $\mathbf{X}^* + \mathbf{U}_N$ are present in the community, their respective densities change over time as

$$\frac{d \log n_i}{dt} = 1 - \sum_j (\mathbf{U}_j^\top C_{11} \mathbf{U}_j + 2\mathbf{U}_j^\top C_{10} \mathbf{U}_i + \mathbf{U}_i^\top C_{00} \mathbf{U}_i) n_j$$

from which we can calculate the equilibrium densities of the residents. Consequently, the initial conditions for an invasion event consist of the resident community at this attractor in addition to an invading allele, with associated trait vector $\mathbf{X}^* + \mathbf{V}$, at a very small density. By running the population dynamical equations with $N + 1$ types present, we get to know the fate of the invader and all the resident types.

However, where do the invaders come from? At this point, we have to postulate a mutational process, as there is none given by Christiansen & Loeschke (1987). Then we can follow the algorithm given in Subsection 4.1, which involves generating a new mutant after each invasion attempt and running a similar invasion experiment, with the surviving community as initial condition. This is repeated until the branches have escaped the close proximity of the singularity and we are satisfied that the polymorphism is either protected or unstable.

As an example, using the notations $\Delta := (\mathbf{U}_1 - \mathbf{U}_2)/2$ and $\bar{\mathbf{U}} := (\mathbf{U}_1 + \mathbf{U}_2)/2$, we turn to Equation (27) which approximates the invasion function for dimorphic communities with both residents near a singularity \mathbf{X}^* :

$$\begin{aligned}s_{X_1, X_2}(\mathbf{X}^* + \mathbf{V}) &= \mathbf{V}^\top \mathbf{C}_{00} \mathbf{V} + 2\bar{\mathbf{U}}^\top \mathbf{C}_{10} \mathbf{V} + \bar{\mathbf{U}}^\top \mathbf{C}_{11} \bar{\mathbf{U}} - \Delta^\top \mathbf{C}_{00} \Delta \\ &\quad + 2\Delta^\top \mathbf{C}_{10} (\bar{\mathbf{U}} - \mathbf{V}) \frac{\Delta^\top [\mathbf{C}_{00} + \mathbf{C}_{10}^\top] \bar{\mathbf{U}}}{\Delta^\top \mathbf{C}_{10} \Delta} + O(\varepsilon^2)\end{aligned}$$

Note that at the singularity, $s_{X^*}(\mathbf{X}^* + \mathbf{V}) = \mathbf{V}^\top \mathbf{C}_{00} \mathbf{V}$ so mutants in the direction of the largest (positive) eigenvalue of \mathbf{C}_{00} have the highest probability of invading. When branching indeed occurs, there are almost always two branches on opposite sides of the singularity that move at the same pace in opposite directions, along the steepest fitness gradient (cf. 4.5). Approximating this situation by $\mathbf{U}_1 = -\mathbf{U}_2$, we have $\bar{\mathbf{U}} = \mathbf{0}$ and $\Delta = \mathbf{U}_1$ and find ourselves in the special case

$$s_{X^* + \mathbf{U}_1, X^* + \mathbf{U}_2}(\mathbf{X}^* + \mathbf{V}) = \mathbf{V}^\top \mathbf{C}_{00} \mathbf{V} - \mathbf{U}_1^\top \mathbf{C}_{00} \mathbf{U}_1 + O(\varepsilon^3)$$

in which any more extreme mutant ($\mathbf{V} := \alpha \mathbf{U}_1$ with $|\alpha| > 1$) can invade and replace its ancestor, while $\alpha < 1$ implies negative fitness. This shows that branches initially indeed grow away from the singularity.

If we are convinced that branching indeed does occur (either from a simulation as described above or because \mathbf{C}_{00} is positive definite), one starts by formulating the two-resident fitness function

$$\begin{aligned}s_{X^* + \mathbf{U}_1, X^* + \mathbf{U}_2}(\mathbf{X}^* + \mathbf{U}_3) \\ = \log \left(\max_{j=1,2} \left(1 + \beta (k_{j3} - \gamma_{j3,11} \hat{n}_{11} - \gamma_{j3,12} \hat{n}_{12} - \gamma_{j3,22} \hat{n}_{22}) \right) \right) \quad (94)\end{aligned}$$

where the equilibrium densities are calculated from

$$\begin{pmatrix} k_{11} \\ k_{12} \\ k_{22} \end{pmatrix} = \begin{bmatrix} 1 & \gamma & \gamma^4 \\ \gamma & 1 & \gamma \\ \gamma^4 & \gamma & 1 \end{bmatrix} \begin{pmatrix} \hat{n}_{11} \\ \hat{n}_{12} \\ \hat{n}_{22} \end{pmatrix} \quad (95)$$

with $\gamma := \exp(-\frac{1}{4}(\mathbf{U}_1 - \mathbf{U}_2)^\top \Phi^{-1}(\mathbf{U}_1 - \mathbf{U}_2))$.

If the traits are scalar, we can calculate from the above expression (95) the X_1 -isocline defined by $\frac{\partial s_{X_1, X_2}(Y)}{\partial Y} \Big|_{Y=X_1} = 0$, and the similarly defined X_2 -isocline. These allow *trait evolution plots* (TEPs) to be drawn, which are basically *pairwise invasibility plots* (PIPs) with added information related to the s -function of dimorphic communities. For an easy explanation on how to plot and interpret PIPs consult

Diekmann (2004), for examples of TEPs with some explanations including properties of the isolines see Geritz *et al.* (1999). The usefulness of TEPs lies in the fact that one can tell from them at a glance whether the community will evolve towards the edge of the coexistence region (so that the community reverts to a monomorphic state), towards the edge of the trait space (an evolutionary endpoint) or towards a singularity (with a possibility for secondary branching where the same analysis as before applies again).

5 Discussion

While superficially the first two parts of this paper are wildly disparate, we hope that the last part has shown their fundamental connexion by addressing one of the open problems the evolutionary biologist faces, namely how to systematically treat long-term evolutionary behaviour.

To the more mathematically inclined, Section 3 shows that classifying the bifurcation patterns that the s -functions of quadratic Lotka-Volterra models can exhibit is not just a niche hobby, but in the case of codimension-1 singularities amounts to a full classification of these singularities for models of evolution driven by small mutations. Furthermore we have revealed how the local geometry of coexistence (3.5, 3.6) and the residents' proportional density dynamics (Appendix F) are model independent (up to a given order), in the sense that they only depend on the geometry of the one-resident fitness function near the singularity and on the strategies present in the community.

To the more biologically inclined, Section 4 gives a handle on the systematic analysis of concrete evolutionary models from scratch. The approach can also prove useful in the interpretation of any odd pattern one has encountered, by showing a straightforward way to explore the geometry close to the location of the oddity and hence to figure out what model features cause the pattern. The approach on the whole allows the reader to focus on the phenomena at hand instead of the specific mathematical problems that are encountered: as models are shown to be interchangeable in some ways, computational difficulties may be avoided e.g. by switching between continuous and discrete time versions of a model, or a similar sleight of hand.

The biologist will note how similar the canonical equation is to Lande's equation (Lande, 1979) which in turn derives from the breeder's equation (Lush, 1937) in the animal sciences. Except for the population density which does not appear in Lande's equation as a factor, all visible differences with the canonical equation amount to differences in the interpretation of parameters. Where they differ is in interpretation, as Lande's equation describes changes in the genetical makeup of a population through selection on standing genetic variation. This variation can for example be accumulated in a population near to a (weak) optimal strategy in a stable environment. Some have cast doubts on the sufficiency of the mutation/selection balance for the generation of the observed levels of variation (e.g. Turelli (1984); Kondrashov & Turelli (1992)), though our feeling is that the associated problems are of greater mathematical than biological interest (see Zhang & Hill (2005) for some mathematical counterarguments). Changing the environmental pa-

rameters that a population close to an evolutionary optimum is subjected to, leads to a rapid evolution in the genetical makeup. However, Haldane (1927) already realized that in the next phase, true innovations and long-term changes must come from mutations. He also made plain that mutation limited evolution is a slower process than naive analytical models would suggest since most advantageous mutants will fail to establish themselves due to stochasticity, an effect that is quantitatively captured by Ewens' approximation (14) of the establishment probability. The canonical equation builds on those ideas to derive a quantitative relation between the factors involved, establishing in particular how the ecology determines the selective pressures. The extended form presented in Section 2 is applicable to a very wide variety of discrete and continuous time models, instead of only to ODE models as is the original version by Dieckmann & Law (1996).

The analysis as presented in Sections 2 and 3 is ready for extension in several directions. In terms of content, the third order terms of the normal form (27), (44) should be worked out and compared between the different model types. While they do show differences, it is not yet clear to the authors whether those are substantial enough to translate into differences in bifurcation patterns.

In terms of rigour, we note that the calculations are presented in a heuristic and biologically slanted manner, at a cost to mathematical precision and exhaustiveness. We have followed most of the biological literature by treating mutations as unbiased, as if tacitly assuming the genotype-phenotype map to be linear and mutations to be unbiased at the genotype level. Since we are treating exceedingly small mutation steps, the mapping is indeed linear, but the possibility of bias remains (cf. Dieckmann & Law, 1996). A discussion of this topic can be found in the more mathematical treatment of the canonical equation by Champagnat *et al.* (2001, 2006) and Champagnat (2006). A far more complicated issue is the one underlying timescale separation and the several latent limits (of system size, mutation step size and mutation probability) which are not commutative, as Metz *et al.* (1996) explained. How quasi-monomorphicity (and by extension, quasi- N -morphicity) is maintained under some not-too-restrictive assumptions is being addressed more recently (e.g. Cressman & Hofbauer, 2005; Meszéna *et al.*, 2005). More specifically, the latter authors show for general ODE population models with small differences between the types, that away from evolutionary singularities the dynamics of the relative frequencies p_i follows (up to the lowest order of approximation) the familiar population genetics equations for the density independent case. Furthermore they show that near singularities the dynamics mimics that of Lotka-Volterra models, with fitnesses approximated along the same lines as in this paper.

In terms of applicability, the collection of models covered should be extended to physiologically structured populations with infinite numbers of birth states. Biologically this is a small step, for example not just allowing a few classes of birth weights but allowing a continuum of sizes at birth. Mathematically however, this means that the matrix operations of Section 3 should be rewritten in terms of operators and norms, which we happily leave as a problem for more accomplished non-linear analysts. Additionally, this requires an extension of Equality (14) to branching processes with infinitely many types, where the d -type version was provided by Athreya (1993) and Eshel (1984).

In continuous time, the extension to infinite numbers of birth states would au-

tomatically remove our restriction to fixed point attractors, as individuals born in a community on a periodic attractor can be assigned the phase of the attractor as (a component of) their birth state. Thus the attractor can be interpreted as a fixed point attractor and all analysis goes through. (In discrete time this trick does not even require the suggested extension.) Analytically, we have no clear idea how to extend our treatment to nonperiodic attractors. Heuristic explorations by Ulf Dieckmann (pers. comm.) for ergodically fluctuating environments with linear birth-and-death population dynamics for the invaders, suggest that the canonical equation is robust against such extension: by approximating the fixation probabilities as calculated by Kendall (1948), it is found that the establishment probability is still approximately proportional to the fitness (cf. Relation (20)).

The analysis of this paper is valid for models where the population is spread over a finite number of patches, as long as the local resident densities are large enough to ensure local infinite dilution of individual effects and a branching process approximation for the initial phase of the invasion process. The patch an individual inhabits is then expressed in a component of its (birth) state. More research is badly needed on more complicated spatial models to see under which conditions the probability of establishment scales linearly with changes in strategy, as then an equation similar to the canonical equation will apply.

Acknowledgements Michel Durinx is supported by the Dutch national science organization (NWO) through PhD grant 809.34.002. Michel Durinx and Hans Metz received funding from the European Research Training Network ModLife. Géza Meszéna benefited from OTKA grants T049689 and TS049885. All authors received support from the NWO through the Dutch-Hungarian exchange grant 048.011.039.

The authors would like to thank Mats Gyllenberg and both referees for extensive suggestions and very detailed criticism that has benefited this paper immensely. We would also like to thank Frans Jacobs for discussions and a counterexample.

Appendices

A The relationship between $s_{\mathbb{X}}(Y)$ and R_0 . I. Away from singularities

To derive a relationship between the N -resident invasion fitness $s_{\mathbb{X}}(X_i + V)$ and the lifetime offspring production R_0 , we define ϕ as

$$\phi(\rho, V) := \log \left(\lambda_d \left(\int_0^\infty e^{-\rho a} \Lambda(X_i + V, I_{\mathbb{X}}, da) \right) \right) \quad (96)$$

where Λ is the birth kernel (see Eq. (18) and preceding lines). Then the invasion fitness of a mutant $X_i + V$ in a given community \mathbb{X} is the (generally unique) solution ρ to $\phi(\rho, V) = 0$ (known as the Euler-Lotka equation (18)).

We can expand ϕ as a function of its first argument,

$$\phi(\rho, V) = \phi(0, V) + f(V)\rho + O(\rho^2) \quad (97)$$

As $\partial\phi(\rho, V)/\partial\rho$ is (generically, in the space of all models that allow a birth kernel notation (96)) nonzero, the implicit function theorem may be applied to ρ . Hence we can furthermore expand s as a function of V , where the constant term is zero since residents have zero fitness. Thus

$$\begin{aligned} 0 &= \phi(s_{\mathbb{X}}(\mathbf{X}_i + V), V) \\ &= \phi(0, V) + f(V)s_{\mathbb{X}}(\mathbf{X}_i + V) + O(s_{\mathbb{X}}(\mathbf{X}_i + V)^2) \\ &= \log R_0 + f_0 s_{\mathbb{X}}(\mathbf{X}_i + V) + O(||V||^2) \end{aligned} \quad (98)$$

where we have used the fact that $\phi(0, V) = \log \lambda_d(L(\mathbf{X}_i + V, I_{\mathbb{X}})) = \log R_0$, and $f(V)$ was replaced by its the lowest order part $f_0 := f(\mathbf{0})$. To calculate f_0 , observe that it is a partial derivative of ϕ for ρ at 0:

$$f_0 = \frac{\partial\phi(0, \mathbf{0})}{\partial\rho} = \frac{1}{\lambda_d(\int_0^\infty \Lambda(\mathbf{X}_i, I_{\mathbb{X}}, da))} \frac{\partial}{\partial\rho} \lambda_d(\int_0^\infty e^{-\rho a} \Lambda(\mathbf{X}_i, I_{\mathbb{X}}, da))|_{\rho=0}$$

Since \mathbf{X}_i is a resident, the first factor is one. The last factor can be resolved, as derivatives of simple eigenvalue $\lambda(x)$ of a matrix $M(x)$ are found from

$$\frac{\partial\lambda(x_0)}{\partial x} = v^\top \frac{\partial M(x_0)}{\partial x} u \quad (99)$$

where u and v^\top are respectively right- and left eigenvectors of $M(x_0)$, normalized such that $v^\top u = 1$ (e.g. Magnus & Neudecker, 1988; Caswell, 2001). Since $\int_0^\infty e^{-\rho a} \Lambda(\mathbf{X}_i, I_{\mathbb{X}}, da)$ is nonnegative and primitive, λ_d is an isolated eigenvalue and we can use Property (99) to decide that

$$\begin{aligned} f_0 &= \left. \frac{\partial\lambda_d(\int_0^\infty e^{-\rho a} \Lambda(\mathbf{X}_i, I_{\mathbb{X}}, da))}{\partial\rho} \right|_{\rho=0} \\ &= v^\top \left(\left. \frac{\partial \int_0^\infty e^{-\rho a} \Lambda(\mathbf{X}_i, I_{\mathbb{X}}, da)}{\partial\rho} \right|_{\rho=0} \right) u \\ &= -v^\top \left(\int_0^\infty a \Lambda(\mathbf{X}_i, I_{\mathbb{X}}, da) \right) u =: -T_f(\mathbf{X}_i, I_{\mathbb{X}}) \end{aligned} \quad (100)$$

where u and v^\top now are normalized right- and left eigenvectors of $L(\mathbf{X}_i, I_{\mathbb{X}})$ (cf. Eq. (13)). The (nonzero) quantity T_f has a natural interpretation as the *average age at giving birth*, since the integral is a lifetime census of the parent's age at each birth event while the expected lifetime offspring production is one (as $\mathbf{X}_i \in \mathbb{X}$). Substituting this value for f_0 into our expansion (98), we conclude that

$$s_{\mathbb{X}}(\mathbf{X}_i + V) = \frac{\log R_0(\mathbf{X}_i + V, I_{\mathbb{X}})}{T_f(\mathbf{X}_i, I_{\mathbb{X}})} + O(||V||^2)$$

B The relationship between $s_{\mathbb{X}}(Y)$ and R_0 . II. Near singularities

In Appendix A, a relationship between invasion fitness and lifetime reproductive output was formulated, up to $O(\varepsilon^2) = O(||V||^2)$. Near a singularity however, we

can redo the analysis to show that the approximate relation is correct up to terms of order $O(\varepsilon^3)$.

When all residents are close to a singular strategy \mathbf{X}^* , we can describe the community in terms of strategy deviations ξ_i and a scaling factor ε as $\mathbb{X} := \{\mathbf{X}^* + \varepsilon \xi_i \mid i \leq N\}$. We expand the multiresident fitness function as dependent on the mutation step \mathbf{V} and the community scaling factor ε as

$$s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V}) = s_{\mathbf{X}^*}(\mathbf{X}^*) + \beta \mathbf{V} + \varepsilon B(\xi_1, \xi_2, \dots, \xi_N) + O(||\mathbf{V}||^2 + ||\mathbf{V}||\varepsilon + \varepsilon^2) \quad (101)$$

The constant term is necessarily zero, and β too since $s_{\mathbb{X}}(\mathbf{Y}) = s_{\mathbf{X}^*}(\mathbf{Y})$ at $\varepsilon = 0$. Furthermore, any resident strategy is a zero of the N -resident fitness function, so we find from any choice $\mathbf{V} = \varepsilon \xi_i$ that $B(\xi_1, \xi_2, \dots, \xi_N)$ is zero as well. Thus for any mutant $\mathbf{X}^* + \mathbf{V}$ where $\mathbf{V} = O(\varepsilon)$, we have that

$$s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V}) = O(\varepsilon^2) \quad (102)$$

When we define

$$\phi(\rho, \mathbf{V}) := \log \left(\lambda_d \left(\int_0^\infty e^{-\rho a} \Lambda(\mathbf{X}^* + \mathbf{V}, \mathbf{I}_{\mathbb{X}}, da) \right) \right) \quad (103)$$

we may expand this ϕ again as a function of ρ and thus solve the Euler-Lotka equation $\phi(\rho, \mathbf{V}) = 0$ for $\mathbf{V} = O(\varepsilon)$ as

$$\begin{aligned} 0 &= \phi(s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V}), \mathbf{V}) \\ &= \phi(0, \mathbf{V}) + f(\mathbf{V}) s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V}) + O(s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V})^2) \\ &= \log R_0(\mathbf{X}^* + \mathbf{V}, \mathbf{I}_{\mathbb{X}}) + f_0 s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V}) + O(\varepsilon^3) \end{aligned} \quad (104)$$

where $f_0 := f(\mathbf{0}) = -T_f(\mathbf{X}^*, \mathbf{I}^*) =: -T_f^*$, as shown at Eq. (100). Hence we conclude that

$$s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V}) = \frac{\log R_0(\mathbf{X}^* + \mathbf{V}, \mathbf{I}_{\mathbb{X}})}{T_f^*} + O(\varepsilon^3)$$

for communities and mutants near a singularity \mathbf{X}^* .

C Miscalculating $s_{\mathbb{X}}(\mathbf{Y})$

Let us consider a singular strategy \mathbf{X}^* , and try to express the s -function in case there are N resident strategies close to \mathbf{X}^* . For each i from 1 to N , we can express resident trait values as $\mathbf{X}_i = \mathbf{X}^* + \mathbf{U}_i$ for some small vector \mathbf{U}_i , and similarly for invading mutants $\mathbf{Y} = \mathbf{X}^* + \mathbf{V}$. We now take the Taylor expansion around \mathbf{X}^* up to quadratic terms, and can start to figure out the coefficients:

$$\begin{aligned} s_{\mathbf{X}_1 \mathbf{X}_2 \dots \mathbf{X}_N}(\mathbf{Y}) &= \alpha + \beta \mathbf{V} + \sum_i \beta_i \mathbf{U}_i + \mathbf{V}^T \mathbf{C}_{00} \mathbf{V} \\ &\quad + 2 \sum_i \mathbf{U}_i^T \mathbf{C}_{i0} \mathbf{V} + \sum_{ij} \mathbf{U}_i^T \mathbf{C}_{ij} \mathbf{U}_j + O(\varepsilon^3) \end{aligned}$$

where \mathbf{C}_{00} and each matrix \mathbf{C}_{ii} is taken to be symmetric.

Any resident has zero growth in an equilibrium population, so for each k we have the consistency condition $s_{X_1 X_2 \dots X_N}(X_k) = 0$. Thus for all k we must have that

$$0 = \alpha + \beta U_k + \sum_i \beta_i U_i + U_k^\top C_{00} U_k + 2 \sum_i U_i^\top C_{i0} U_k + \sum_{ij} U_i^\top C_{ij} U_j + O(\varepsilon^3)$$

As this has to hold independently of the strategy deviations U_1 to U_N , we can split the equation into several equations like

$$0 = \alpha + (\beta + \beta_k) U_k + \sum_{i \neq k} \beta_i U_i \quad (105)$$

$$0 = U_k^\top (C_{00} + 2C_{k0} + C_{kk}) U_k \quad (106)$$

$$0 = \sum_{i \neq k} U_i^\top (2C_{i0} + C_{ki}^\top + C_{ik}) U_k \quad (107)$$

$$0 = \sum_{i,j \neq k} U_i^\top C_{ij} U_j \quad (108)$$

Equation (105) shows that $\alpha = 0$, and for each $i \neq k$ we see $\beta_i = \mathbf{0}^\top$ while $\beta_k = -\beta$. So if we first choose $k = 1$ and then $k = 2$, we conclude that for *all* the residents $\beta = \beta_i = \mathbf{0}^\top$. Note that in the monomorphic case, this argumentation does not hold as $k = 2$ is impossible then.

We deduce from Equality (108) that $C_{ij} = 0$, if both i and j differ from k . So taking an initial choice of $k = 1$ shows that all C_{ij} are zero except if i or j is one, and a further choice of $k = 2$ shows that all are zero except C_{12} and C_{21} . If $N > 2$, we can take $k = 3$ to prove that for any i and j the matrix C_{ij} is zero. The case $N = 2$ is worked out below, where C_{12} and C_{21} may be nonzero.

For $N > 2$ we substitute our results into Equation (107) and see in a similar way that $C_{i0} = 0$ for any i . From Equation (106) we deduce that the symmetric matrix C_{00} is zero as well. Hence we conclude that for any model where $N > 2$

$$s_{X_1 X_2 \dots X_N}(\mathbf{Y}) = 0 + O(\varepsilon^3) \quad (109)$$

which is clearly false. (By repeating the argumentation for higher order terms we can “show” that $s_{X_1 X_2 \dots X_N}(\mathbf{Y}) = O(\varepsilon^{M+1})$ when $N > M$.) The false result can be traced back to one implicit assumption: the existence of partial derivatives, a basic requirement for the applicability of Taylor approximations.

For $N = 2$ we find that $C_{10} + C_{10}^\top = -C_{00} = C_{20} + C_{20}^\top$ and $2C_{10} = 2C_{20}^\top = -[C_{12} + C_{21}^\top]$, so that

$$s_{X_1 X_2}(\mathbf{Y}) = (\mathbf{V} - \mathbf{U}_1)^\top [C_{12} + C_{21}^\top] (\mathbf{V} - \mathbf{U}_2) + O(\varepsilon^3) \quad (110)$$

This equation suggests that the s -function for any two resident model would be locally quadratic at X^* . If one compares this equation to the correct solution in this paper (27), we see that it is correct only if we are dealing with scalar strategies.

D Proofs of Lemma 1–3 and 7

The following lemmata were mentioned without proof in Section 3.6. They are useful in making some points about upper bounds to the number of types that can locally coexist. The (non)invertibility of E^* plays a central role in this issue, not

just because our route to calculating the multiresident fitness function depends on the invertibility of E^* (74), but because invertibility is a necessary condition for the population dynamical stability of the community. Since the proofs are of a technical nature, they were moved to this appendix, as they merely divert the attention from the real issues in Section 3.6.

Lemma 8 *If $\det E \neq 0$, then $\det E^* = -(\det E) \mathbf{1}^\top E^{-1} \mathbf{1}$.*

proof We start by recalling the general formula for the inverse of a nonsingular $N \times N$ matrix:

$$(\det E)E^{-1} = \begin{bmatrix} (-1)^{1+1}e_{1,1} & \cdots & (-1)^{1+N}e_{N,1} \\ \vdots & \ddots & \vdots \\ (-1)^{N+1}e_{1,N} & \cdots & (-1)^{N+N}e_{N,N} \end{bmatrix}$$

where the minor $e_{i,j}$ is defined as the determinant of the matrix obtained by deleting the i^{th} row and j^{th} column of E .

We encounter the same minors, when we calculate the determinant of E^* by expanding first from the bottom row and then from the rightmost column:

$$\begin{aligned} \det E^* &= \sum_j (-1)^{N+1+j} \det \begin{bmatrix} E_{1,1} & \cdots & E_{1,j-1} & E_{1,j+1} & \cdots & E_{1,N} & 1 \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & \vdots \\ E_{N,1} & \cdots & E_{N,j-1} & E_{N,j+1} & \cdots & E_{N,N} & 1 \end{bmatrix} \\ &= \sum_{ij} (-1)^{N+1+j} (-1)^{N+i} \det \begin{bmatrix} E_{1,1} & \cdots & E_{1,j-1} & E_{1,j+1} & \cdots & E_{1,N} \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ E_{i-1,1} & \cdots & E_{i-1,j-1} & E_{i-1,j+1} & \cdots & E_{i-1,N} \\ E_{i+1,1} & \cdots & E_{i+1,j-1} & E_{i+1,j+1} & \cdots & E_{i+1,N} \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ E_{N,1} & \cdots & E_{N,j-1} & E_{N,j+1} & \cdots & E_{N,N} \end{bmatrix} \\ &= \sum_{ij} (-1)^{i+j+1} e_{i,j} \\ &= -(\det E) \mathbf{1}^\top E^{-1} \mathbf{1} \end{aligned}$$

□

Lemma 9 *If $\text{rank } E \leq N - 2$, then E^* is singular.*

proof If the rank of E is $N - 2$ or less, we can transform it by elementary row operations into an $N \times N$ matrix with the last two rows equal to zero. After applying the same sequence of elementary operations to E^* instead, one of its last two rows is a multiple of the other (since only their last coefficients possibly differ from zero). Thus E^* is singular since the determinant is not affected by elementary row operations. □

Lemma 10 *If $\text{rank } E = N - 1$, then generically E^* is invertible.*

proof [by contradiction] If E^* is singular, there exists a nontrivial vector μ such that the $N + 1$ equations $(\mu_1 \mu_2 \cdots \mu_{N+1}) E^* = \mathbf{0}^\top$ are simultaneously satisfied.

If $\mu_{N+1} = 0$, then μ is the unique (up to a scalar) nonzero vector such that $(\mu_1 \mu_2 \cdots \mu_N) E = \mathbf{0}^\top$, where uniqueness comes from the rank of E . This situation is nongeneric as the independent $(N + 1)^{\text{st}}$ equation $\sum_i \mu_i = 0$ is satisfied as well.

If on the other hand $\mu_{N+1} \neq 0$, we rescale μ by setting $\mu_{N+1} := -1$, thus finding a solution to the N equations $(\mu_1 \mu_2 \cdots \mu_N) E = \mathbf{1}^\top$. Generically such a solution does not exist however, as E has an $(N - 1)$ -dimensional range. \square

Lemma 11 *Even if both U and C_{10} have full rank, E^* can still be singular. In fact, all four combinations of invertible or singular E and E^* can occur.*

proof Only in cases where $N = m$ we know offhand whether $E = U^\top C_{10} U$ is singular or not, as the determinant of a matrix product is the product of the determinants.

As an example of the case that both E and E^* are singular, consider

$$[\mathbf{u}_1 \quad \mathbf{u}_2 \quad \mathbf{u}_3 \quad \mathbf{u}_4] := \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \quad C_{10} := \begin{bmatrix} 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{bmatrix}$$

We see that for any combination of two residents, both U and C_{10} have full rank (respectively two and four). For two out of the six possible combinations (namely $\{\mathbf{u}_1, \mathbf{u}_4\}$ and $\{\mathbf{u}_2, \mathbf{u}_3\}$), both E and E^* are invertible. But for the other four pairs of residents (namely $\{\mathbf{u}_1, \mathbf{u}_2\}$, $\{\mathbf{u}_1, \mathbf{u}_3\}$, $\{\mathbf{u}_2, \mathbf{u}_4\}$ and $\{\mathbf{u}_3, \mathbf{u}_4\}$), matrix E has rank zero and E^* is singular, so that such strategy couples cannot coexist: if $[C_{00}]_{ii} \neq [C_{00}]_{jj}$, the system $E P = T$ (72) is contradictory; if $[C_{00}]_{ii} = [C_{00}]_{jj}$, there is a continuum of neutrally stable solutions.

If we add any of the remaining two as a third resident type, coexistence becomes possible again as E^* is invertible (but E is singular). Notice that $T_i := -U_i^\top C_{00} U_i = -[C_{00}]_{ii}$, so that there is no a priori relation whatsoever between the vector T and the matrix E . If we consider the community $\{\mathbf{u}_1, \mathbf{u}_2, \mathbf{u}_3\}$ for example, the proportions p_1, p_2, p_3 will respectively be $1 + 2T_1 - T_2 - T_3, T_3 - T_1$ and $T_2 - T_1$. Values of T that result in strictly positive proportion vectors are $(1/4 \quad 1/2 \quad 1/2)^\top$ or $(-1/2 \quad -1/3 \quad -1/6)^\top$. Similarly, there are generic solutions with all four given strategies present.

Considering another possible resident, $\mathbf{u}_0^\top := (1 \ 0 \ 0 \ 1)$, we encounter the fourth possibility, as the resident duo $\{\mathbf{u}_1, \mathbf{u}_0\}$ has a singular E^* matrix yet $E = \begin{bmatrix} 0 & 1 \\ 1 & 2 \end{bmatrix}$ is invertible. \square

E The environmental dimension and finite dimensional Lotka-Volterra environments

We will first precisely define the environmental dimension, as relevant in an evolutionary context and differing from the dimension concept used in physiologically structured models. In such models, the environment is used to describe the full

population dynamics. In the adaptive dynamics context however, the interest is reduced to a time-averaged growth rate of an individual in that environment (as testified by the definition of invasion fitness). Moreover, it is not the environments themselves that are of central concern here, but the collection of ergodic probability measures on functions that map time to environments.

A closer inspection of this topic reveals there is an observability issue. Whether for reasons of didactical clearness, mathematical manipulability, interpretability or ineptitude, the environment will not always be formulated in a minimal form. In addition one must realize that not the dimension of the set of environments is relevant, but the dimension of the subspace of feasible environments.

To do away with these potential deficiencies, we use the following definitions. For the trait space \mathfrak{X} and the set of all possible environments \mathcal{I} , we define the *growth operator* as

$$\rho : \mathcal{I} \rightarrow C(\mathfrak{X}) \quad (111)$$

such that $\rho(\mathbf{I})(\mathbf{Y})$ is the instantaneous per capita growth rate of a given type \mathbf{Y} in a given environment \mathbf{I} , as dependent on the model under consideration. In this setting we define the *environmental dimension* of that model as

$$\dim_E := \dim \rho(\mathcal{I}) \quad (112)$$

From the definition we straightforwardly see why Lotka-Volterra type models by default have infinite dimensional environments, as opposed to e.g. resource dynamics models (cf. Eq. (121)):

Lemma 12 *Generically, the environment of a Lotka-Volterra model is infinite dimensional.*

proof Let us consider a strategy space \mathfrak{X} with an infinite number of elements. Using the growth operator (111), for an N -resident Lotka-Volterra model (28) we formally have that

$$\rho(\mathbf{I})(\mathbf{Y}) = r(\mathbf{Y}) \left(1 - \sum_i a(\mathbf{Y}, \mathbf{X}_i) n_i \right)$$

or for more general Lotka-Volterra models

$$\rho(\mathbf{I})(\mathbf{Y}) = r(\mathbf{Y}) \left(1 - \int_{\mathfrak{X}} a(\mathbf{Y}, \mathbf{X}) d\nu(\mathbf{X}) \right)$$

where N -resident models are made by taking the population distribution ν to be a weighted sum of N Dirac delta distributions $\nu(\mathbf{X}) := \sum_j n_j \delta(\mathbf{X} - \mathbf{X}_j)$.

To separate the focal individual \mathbf{Y} from the environment \mathbf{I} , we have to define the environment as (something isomorphic to) the real-valued function

$$\mathbf{I} : \mathbf{Y}' \mapsto \int_{\mathfrak{X}} a(\mathbf{Y}', \mathbf{X}) d\nu(\mathbf{X}) \quad (113)$$

Now the growth rate can indeed be put in the form $\rho(\mathbf{I})(\mathbf{Y})$, with \mathbf{I} independent of \mathbf{Y} . Thus we see that the dimension of \mathbf{I} is at most the cardinality of \mathfrak{X} .

As there is no a priori reason for a smaller set than \mathfrak{X} to suffice as domain for a function similar to Expression (113), generically \mathbf{I} is infinite dimensional. \square

Proposition 8 A Lotka-Volterra model with interaction function $a(\mathbf{Y}, \mathbf{X})$ has finite feedback dimension e , if and only if e is the minimal number for which there exist functions b_q and c_q such that $a(\mathbf{Y}, \mathbf{X}) = \sum_{q=1}^e b_q(\mathbf{Y})c_q(\mathbf{X})$.

proof Firstly, by Definition (112) we have

$$e := \dim \rho(\mathcal{J}) = \dim A(\mathfrak{D}) \quad (114)$$

where \mathfrak{D} is the space of all Borel measures on \mathfrak{X} and the operator A is defined as

$$A(\nu) : \mathbf{Y} \mapsto \int_{\mathfrak{X}} a(\mathbf{Y}, \mathbf{X}) d\nu(\mathbf{X}) \quad (115)$$

Therefore $A(\mathfrak{D})$ has a basis $\{b_1(\mathbf{Y}), b_2(\mathbf{Y}), \dots, b_e(\mathbf{Y})\}$, and for any $\nu \in \mathfrak{D}$ there are coefficients γ_q such that $A(\nu)(\mathbf{Y}) = \sum_{q=1}^e b_q(\mathbf{Y})\gamma_q$. By choosing Dirac distributions $\nu(\mathbf{X}) := \delta(\mathbf{X} - \mathbf{X}_0)$, we see that for any strategy combination $(\mathbf{X}_0, \mathbf{Y})$ the interaction term can be written as

$$a(\mathbf{Y}, \mathbf{X}_0) = \int_{\mathfrak{X}} a(\mathbf{Y}, \mathbf{X}) d\nu(\mathbf{X}) = \sum_{q=1}^e b_q(\mathbf{Y})\gamma_q \quad (116)$$

Thus the c_q -functions are defined pointwise from Equality (116) as $c_q(\mathbf{X}_0) := \gamma_q$. That e is the minimal number of functions b_q and c_q , follows from the second part of this proof.

Conversely, if $a(\mathbf{Y}, \mathbf{X})$ can be written as a finite sum $\sum_{q=1}^e b_q(\mathbf{Y})c_q(\mathbf{X})$, then

$$\rho(\mathbf{Y})(\mathbf{I}) = r(\mathbf{Y}) \left(1 - \int_{\mathfrak{X}} \sum_{q=1}^e b_q(\mathbf{Y})c_q(\mathbf{X}) d\nu(\mathbf{X}) \right) = r(\mathbf{Y}) \left(1 - \sum_{q=1}^e b_q(\mathbf{Y})I_q \right)$$

where $I_q := \int_{\mathfrak{X}} c_q(\mathbf{X}) d\nu(\mathbf{X})$. Thus we see that the environment is at most e -dimensional. In fact, \mathbf{I} is exactly e -dimensional: if \mathbf{I} were e' -dimensional with $e' < e$, then the first part of the proof shows that e was not minimal.

To finish the first half of the proof, we note that there cannot exist an interaction operator $a(\mathbf{Y}, \mathbf{X}) = \sum_{q=1}^{e'} b_q(\mathbf{Y})c_q(\mathbf{X})$ with environments of dimension $e > e'$, as the second half of the proof shows that $e \leq e'$. \square

F The dynamics of fractions p_i

We have seen, through the equality $P^* = E^{*-1}T^*$ (43), that the equilibrium fractions for all models depend in an identical way on the simple fitness function $s_X(\mathbf{Y})$ and the strategies of the players, up to but not including terms of order $O(\varepsilon^3)$. But there is more than that: in this appendix we argue that for a given fitness function, the dynamics of the fractions is model-independent in the same sense as well.

To show this, we first analyze a general Lotka-Volterra system. Later on we repeat the analysis with a resource dynamics model, as the relevant singular perturbation theory for the dynamical analogues of the equilibrium equations (1) for general structured populations has not yet been developed. (We note that for the

single birth state case, an obvious research plan would be to apply the approach in the third chapter of the thesis of Getto (2005) to the conjecture of Greiner *et al.* (1994); see also Diekmann *et al.* (in press)).

First we consider a Lotka-Volterra community $\{X_1, X_2, \dots, X_{N-1}\}$ at equilibrium, to which we add a small number $n_N = O(\varepsilon^2)$ of mutants with strategy X_N . We recall that for the $(N-1)$ -resident community at equilibrium, the density is of the form $\hat{n} = 1 + O(\varepsilon^2)$ (40), so at least initially $n = 1 + O(\varepsilon^2)$ for our N -resident community as well. That this actually holds at all times, is shown in the following way.

Writing $r_i := r(X_i)$ and $a_{ij} := a(X_i, X_j) = 1 + \varepsilon^2 \alpha_{ij} + O(\varepsilon^3)$ for some constants α_{ij} (35), the dynamics of each of the N densities is

$$\frac{dn_i}{dt} = n_i r_i \left(1 - \sum_j a_{ij} n_j \right) \quad (117)$$

and therefore the dynamics of the total density is

$$\begin{aligned} \frac{d\Delta_n}{dt} &= \frac{dn}{dt} = \sum_j \frac{dn_j}{dt} = \sum_j n_j r_j \left(1 - \sum_k a_{jk} n_k \right) \\ &= n \sum_j p_j r_j \left(1 - \sum_k \left(1 + \varepsilon^2 \alpha_{jk} \right) p_k n \right) + O(\varepsilon^3) \\ &= n \sum_j p_j r_j (-\Delta_n) + O(\varepsilon^2) \end{aligned} \quad (118)$$

Since the solution to this ODE is continuous, there exists some half open time interval $[0, \tau]$ during which $\Delta_n = O(\varepsilon)$. Then the sign of $d\Delta_n/dt$ is the opposite of that of Δ_n , so Δ_n cannot escape from an $O(\varepsilon^2)$ -neighbourhood of zero and $\tau = \infty$.

Bearing the above in mind, we expand the dynamics of a fraction p_i as

$$\begin{aligned} \frac{dp_i}{dt} &= \frac{dn_i}{dt} \frac{1}{n} - \frac{n_i}{n^2} \frac{dn}{dt} \\ &= p_i r_i \left(1 - \sum_k a_{ik} p_k n \right) - p_i \sum_j p_j r_j \left(-\Delta_n - \varepsilon^2 n \sum_k \alpha_{jk} p_k \right) + O(\varepsilon^3) \\ &= p_i r_i \left(-\Delta_n - \sum_k \varepsilon^2 \alpha_{ik} p_k n \right) + p_i \sum_j p_j r_j \left(\Delta_n + \varepsilon^2 n \sum_k \alpha_{jk} p_k \right) + O(\varepsilon^3) \\ &= -p_i r(\mathbf{X}^*) \varepsilon^2 n \sum_k \alpha_{ik} p_k + p_i r(\mathbf{X}^*) \varepsilon^2 n \sum_{jk} \alpha_{jk} p_j p_k + O(\varepsilon^3) \end{aligned} \quad (119)$$

where the Δ_n -terms cancelled each other out because $r_i, r_j = r(\mathbf{X}^*) + O(\varepsilon)$ and thus the difference is absorbed by the order term $O(\varepsilon^3)$ since $\Delta_n = O(\varepsilon^2)$ at all times. Similarly we can replace n by 1 in the remaining terms, which both have ε^2 as a factor. From the calculations following Equation (35) we know that $\alpha_{kj} = \xi_j^\top \Gamma_{11} \xi_j + 2\xi_j^\top \Gamma_{10} \xi_k + \xi_k^\top \Gamma_{00} \xi_k$, so using the renaming $C := -r(\mathbf{X}^*) \Gamma$ (cf. Eq. (36)) we

rewrite Equation (119) as

$$\begin{aligned} \frac{dp_i}{dt} &= -p_i r(\mathbf{X}^*) \varepsilon^2 \sum_k (\xi_k^\top \Gamma_{11} \xi_k + 2\xi_k^\top \Gamma_{10} \xi_i + \xi_i^\top \Gamma_{00} \xi_i) p_k \\ &\quad + p_i r(\mathbf{X}^*) \varepsilon^2 \sum_{jk} (\xi_j^\top \Gamma_{11} \xi_k + 2\xi_k^\top \Gamma_{10} \xi_j + \xi_j^\top \Gamma_{00} \xi_j) p_j p_k + O(\varepsilon^3) \\ &= p_i \sum_{jk} (2\mathbf{U}_k^\top C_{10}(\mathbf{U}_i - \mathbf{U}_j) + (\mathbf{U}_i + \mathbf{U}_j)^\top C_{00}(\mathbf{U}_i - \mathbf{U}_j)) p_j p_k + O(\varepsilon^3) \quad (120) \end{aligned}$$

We will now argue that this dynamics (120) is a shared property of all population dynamical models. However, as mentioned in the first lines of this appendix, there is no dynamical equivalent of the equilibrium equations available for physiologically structured populations (1). Therefore we will show that the dynamics found for Lotka-Volterra models (120), is also found for the most general subclass of the structured population models where the dynamical equivalent of the equilibrium equations (1) is of ODE form. The subclass in question is that of resource dynamics models, generally formulated as follows: for each trait value X_i , per capita growth is given by

$$\frac{1}{n_i} \frac{dn_i}{dt} = g \left(\mathbf{X}_i, \sum_j h_1(\mathbf{X}_j) n_j, \sum_j h_2(\mathbf{X}_j) n_j, \dots, \sum_j h_r(\mathbf{X}_j) n_j \right) \quad (121)$$

for some C^3 functions g and h_1, h_2, \dots, h_r . The multiresident invasion fitness is by definition

$$s_{\mathbb{X}}(\mathbf{Y}) := g(\mathbf{Y}, I_1, I_2, \dots, I_r) \quad (122)$$

where the environment \mathbf{I} is defined componentwise as

$$(\mathbf{I})_s = I_s := \sum_j h_s(\mathbf{X}_j) n_j \quad (123)$$

Like we did for Lotka-Volterra (29) and general structured population models (48), we simplify the calculations through a trait-dependent rescaling that does not influence the s -function:

$$\forall \mathbf{X}: 0 = g(\mathbf{X}, h_1(\mathbf{X}), h_2(\mathbf{X}), \dots, h_r(\mathbf{X})) \quad (124)$$

The effect is that the equilibrium density \hat{n} is one in every monomorphic community.

Once again we need to know that $\Delta_n = O(\varepsilon^2)$ at all times. For that we combine a first-order expansion of the environmental differences,

$$\begin{aligned} I_s - h_s(\mathbf{X}^*) &= \sum_j \left(h_s(\mathbf{X}^*) + \frac{\partial h_s}{\partial \mathbf{X}} \mathbf{U}_j \right) p_j (1 + \Delta_n) - h_s(\mathbf{X}^*) + O(\varepsilon^2) \\ &= h_s(\mathbf{X}^*) \Delta_n + \sum_j \frac{\partial h_s}{\partial \mathbf{X}} \mathbf{U}_j p_j (1 + \Delta_n) + O(\varepsilon^2) \quad (125) \end{aligned}$$

with a first-order expansion of g

$$\begin{aligned} g(\mathbf{X}^* + \mathbf{V}, I_1, I_2, \dots, I_r) \\ = g(\mathbf{X}^*, h_1(\mathbf{X}^*), h_2(\mathbf{X}^*), \dots, h_r(\mathbf{X}^*)) + \frac{\partial g}{\partial \mathbf{Y}} \mathbf{V} + \sum_s \frac{\partial g}{\partial I_s} (I_s - h_s(\mathbf{X}^*)) \\ + O(\varepsilon^2) + \sum_{st} O((I_s - h_s(\mathbf{X}^*))(I_t - h_t(\mathbf{X}^*))) \end{aligned} \quad (126)$$

where the derivatives are taken at $I_s = h_s(\mathbf{X}^*)$ ($\forall s$) and $\mathbf{V} = \mathbf{0}$. Note that the first term is zero because of the rescaling, and the second because \mathbf{X}^* is a singular strategy.

Because of the rescaling (124), Δ_n is zero in monomorphic equilibrium communities, and hence $I_s - h_s(\mathbf{X}^*) = \sum_j (\partial h_s / \partial \mathbf{X}) \mathbf{U} + O(\varepsilon^2)$ there. If we combine this expansion with that of g (126), and observe that the linear terms (in ε) are zero in the normal form for s -functions near singularities (75), we see that

$$\sum_s \frac{\partial g}{\partial I_s} \frac{\partial h_s}{\partial \mathbf{X}} = \mathbf{0}^\top \quad (127)$$

As we have shown in the paragraph preceding Equation (66), $\Delta_n = O(\varepsilon^2)$ for a community at equilibrium with $N - 1$ types present. If we then add a small number $n_N = O(\varepsilon^2)$ of invaders, then there is an open time interval $[0, \tau)$ during which $\Delta_n = O(\varepsilon)$. During this interval, by combining Expansions (125) and (126) and Equality (127), we find

$$\begin{aligned} \frac{d\Delta_n}{dt} &= \frac{dn}{dt} = n \sum_i p_i g(\mathbf{X}^* + \mathbf{U}_i, I_1, I_2, \dots, I_r) \\ &= (1 + \Delta_n) \sum_s \frac{\partial g}{\partial I_s} h_s(\mathbf{X}^*) \Delta_n + O(\varepsilon^2) \end{aligned} \quad (128)$$

From this we can conclude that either $\Delta_n = O(\varepsilon^2)$ or its sign is the opposite of that of $d\Delta_n/dt$, so the time interval $[0, \tau)$ is actually unbounded and $\Delta_n = O(\varepsilon^2)$ at all times. The sign difference is easy to show, as the assumption of the existence of a fixed point attractor (1.1) holds for this singular community at equilibrium, so

$$0 > \left. \frac{\partial g(\mathbf{X}^*, I_1, I_2, \dots, I_r)}{\partial n} \right|_{\substack{\forall s: I_s = h_s(\mathbf{X}^*)n \\ n=1}} = \sum_s \frac{\partial g}{\partial I_s} h_s(\mathbf{X}^*) \quad (129)$$

To find the dynamics of the fractions p_i , we need a second-order expansion of the both the environmental differences,

$$I_s - h_s(\mathbf{X}^*) = h_s(\mathbf{X}^*) \Delta_n + \sum_j \left(\frac{\partial h_s}{\partial \mathbf{X}} \mathbf{U}_j + \mathbf{U}_j^\top \frac{\partial^2 h_s}{\partial \mathbf{X}^2} \mathbf{U}_j \right) p_j + O(\varepsilon^3) \quad (130)$$

and the community dynamics,

$$\begin{aligned} g(\mathbf{X}^* + \mathbf{V}, I_1, I_2, \dots, I_r) \\ = \sum_s \frac{\partial g}{\partial I_s} (I_s - h_s(\mathbf{X}^*)) + \frac{1}{2} \sum_{st} \frac{\partial^2 g}{\partial I_s \partial I_t} (I_s - h_s(\mathbf{X}^*))(I_t - h_t(\mathbf{X}^*)) \\ + \sum_s (I_s - h_s(\mathbf{X}^*)) \frac{\partial^2 g}{\partial I_s \partial \mathbf{Y}} \mathbf{V} + \frac{1}{2} \mathbf{V}^\top \frac{\partial^2 g}{\partial \mathbf{Y}^2} \mathbf{V} + O(\varepsilon^3) \end{aligned} \quad (131)$$

The dynamics of the fractions is then approximated as

$$\begin{aligned}
\frac{dp_i}{dt} &= \frac{dn_i}{dt} \frac{1}{n} - \frac{n_i}{n^2} \frac{dn}{dt} \\
&= p_i \left(g(\mathbf{X}_i, \mathbf{I}_1, \mathbf{I}_2, \dots, \mathbf{I}_r) - \sum_j p_j g(\mathbf{X}_j, \mathbf{I}_1, \mathbf{I}_2, \dots, \mathbf{I}_r) \right) \\
&= p_i \left(\sum_s \left(\sum_k p_k \frac{\partial h_s}{\partial \mathbf{X}} \mathbf{U}_k \right) \frac{\partial^2 g}{\partial I_s \partial \mathbf{Y}} \mathbf{U}_i + \frac{1}{2} \mathbf{U}_i^\top \frac{\partial^2 g}{\partial \mathbf{Y}^2} \mathbf{U}_i \right) \\
&\quad - p_i \left(\sum_j p_j \left(\sum_s \left(\sum_k p_k \frac{\partial h_s}{\partial \mathbf{X}} \mathbf{U}_k \right) \frac{\partial^2 g}{\partial I_s \partial \mathbf{Y}} \mathbf{U}_j + \frac{1}{2} \mathbf{U}_j^\top \frac{\partial^2 g}{\partial \mathbf{Y}^2} \mathbf{U}_j \right) \right) + O(\varepsilon^3) \\
&= p_i \sum_{jk} p_j p_k \left(2 \mathbf{U}_k^\top C_{10} (\mathbf{U}_i - \mathbf{U}_j) + (\mathbf{U}_i + \mathbf{U}_j)^\top C_{00} (\mathbf{U}_i - \mathbf{U}_j) \right) + O(\varepsilon^3) \quad (132)
\end{aligned}$$

where we have used the correspondences

$$C_{00} = \frac{1}{2} \frac{\partial^2 g}{\partial \mathbf{Y}^2} \quad C_{10} = \frac{1}{2} \sum_s \frac{\partial}{\partial \mathbf{Y}} \left(\frac{\partial g}{\partial I_s} \frac{\partial h_s}{\partial \mathbf{X}} \right)^\top = \frac{1}{2} \sum_s \frac{\partial h_s}{\partial \mathbf{X}}^\top \frac{\partial^2 g}{\partial I_s \partial \mathbf{Y}} \quad (133)$$

which are straightforward to derive, given the definition of $s_X(\mathbf{Y})$ (122) and the expansion of g (131). Our last result (132) is identical to that for Lotka-Volterra systems (120) and shows that the dynamics of the fractions is the same, up to and including terms of order $O(\varepsilon^2)$, for all systems near evolutionary singularities.

G Resource utilization and abundance, in relation to invadability

We will show here that in our example (Subsection 4.6), the matrix C_{00} is positive definite (resp. indefinite, negative, nonnegative or nonpositive definite) if and only if $\Psi - \Phi$ is positive definite (resp. indefinite, negative, nonnegative or nonpositive definite).

proof We start by decomposing the symmetric, positive definite matrix Φ using a matrix V of normalized, orthogonal eigenvectors:

$$\exists V, \Lambda: \Phi V = V \Lambda \quad \text{for which} \quad \text{id} = V^\top V = VV^\top \quad (134)$$

where id is the identity and Λ is a diagonal matrix containing the (strictly positive) eigenvalues of Φ . Using the above, we decompose Φ and find

$$\Psi + \Phi = V \Lambda^{\frac{1}{2}} \left[\Lambda^{-\frac{1}{2}} V^\top \Psi V \Lambda^{-\frac{1}{2}} + \text{id} \right] \Lambda^{\frac{1}{2}} V^\top \quad (135)$$

so that

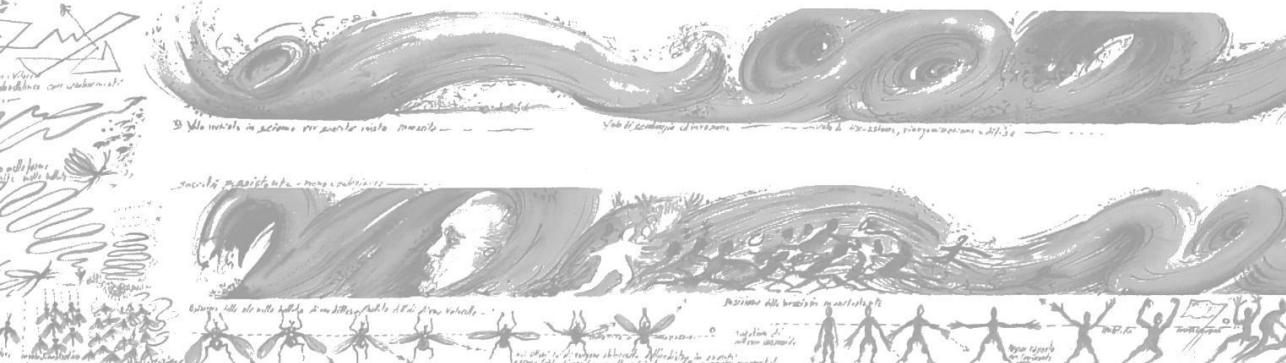
$$\begin{aligned}
C_{00} &= \frac{\Phi^{-1}}{4} - \frac{[\Psi + \Phi]^{-1}}{2} \\
&= V \Lambda^{-\frac{1}{2}} \left[\frac{1}{4} \text{id} - \frac{1}{2} \left[\text{id} + \Lambda^{-\frac{1}{2}} V^\top \Psi V \Lambda^{-\frac{1}{2}} \right]^{-1} \right] \Lambda^{-\frac{1}{2}} V^\top \quad (136)
\end{aligned}$$

Defining $C_{00}^* := \frac{1}{4}\text{id} - \frac{1}{2}\left[\text{id} + \Lambda^{-\frac{1}{2}}V^\top \Psi V \Lambda^{-\frac{1}{2}}\right]^{-1}$, it is easy to see that C_{00} has a positive (resp. negative, zero) eigenvalue for each positive (resp. negative, zero) eigenvalue of C_{00}^* : for any vector v , consider $w := V^\top \Lambda^{\frac{1}{2}} v$ so that $w^\top C_{00}^* w = v^\top C_{00} v$. The same correspondence holds between $[\Psi - \Phi]^* := \Lambda^{-\frac{1}{2}}V^\top \Psi V \Lambda^{-\frac{1}{2}} - \text{id}$ and $\Psi - \Phi$.

To conclude the proof, it suffices to remark that the matrices $[\Psi - \Phi]^*$ and C_{00}^* have the same eigenvectors, and more importantly that the signs of their eigenvalues coincide:

$$\begin{aligned} & \left[\Lambda^{-\frac{1}{2}}V^\top \Psi V \Lambda^{-\frac{1}{2}} - \text{id}\right]v = \lambda v \\ \Leftrightarrow & \left[\Lambda^{-\frac{1}{2}}V^\top \Psi V \Lambda^{-\frac{1}{2}} + \text{id}\right]^{-1}v = (\lambda + 2)^{-1}v \\ \Leftrightarrow & C_{00}^*v = \left[\frac{1}{4} - \frac{1}{2}(\lambda + 2)^{-1}\right]v = \frac{1}{4} \frac{\lambda}{\lambda + 2}v \end{aligned}$$

where $\lambda + 2$ is necessarily positive, as it is an eigenvalue of a sum of positive definite matrices. \square



TWO

Third order expansions of invasion fitness functions near singular strategies

Abstract

The invasion fitness function close to singularities is analyzed for different model families, up to terms of order $O(\varepsilon^3)$ where ε is a measure for the distance between resident traits. As such this chapter is an extension of the work by Durinx *et al.* (2008), and it negatively answers the question whether a third order normal form for N -resident invasion fitness functions near singularities can be derived from the one-resident invasion fitness.

1 Introduction

Since I continue in this chapter the analysis of the fitness function of N -resident population models close to singularities, I will adhere to all but one of the assumptions and notational conventions of Chapter I that are used in the calculation of the normal form for fitness functions close to singularities (Sections I.3 and I.3.1). Therefore I do not restate those assumptions and conventions, but only highlight changes and additional notations in the following subsection. Similarly, the reader is referred to Sections I.1 (Introduction) and I.3.2 (Aims) for the how and why of the present chapter, as the necessary context for most of what follows can be found there.

This chapter's existence in its own right, however, is justified by the fact that the study of codimension-1 bifurcations of evolutionarily singular strategies requires the invasion fitness function to be known up to and including third order terms in the small parameter that scales with the distance between resident strategies. For singularities of models with scalar strategies, for example, the fitness function up to second order terms suffices to determine for all nonexceptional cases only to which of the eight basic categories they belong (Metz *et al.*, 1996; Geritz *et al.*, 1998). However, if Proposition I.3,

Proposition *The invasion fitness function of a general physiologically structured population model with N resident strategies near an evolutionarily singular strategy is the same as that of an N -resident Lotka-Volterra system, up to but not including terms of order $O(\varepsilon^3)$ for distances between residents and singularity of order $O(\varepsilon)$,*

can be extended to include terms of order $O(\varepsilon^3)$, then a classification of the codimension-1 bifurcations of Lotka-Volterra models between those eight cases (as F.J.A. Jacobs is engaged in developing) automatically becomes a general (i.e., model type agnostic) classification of codimension-1 bifurcations. And if Proposition I.3 does not lend itself to extending, then a precise study of the differences may reveal whether or not other types of bifurcations are possible for non-Lotka-Volterra models.

Let us therefore shortly look at the new conventions and then immediately start on the analysis.

2 Notations and assumptions

In addition to those assumptions that apply to the Section I.3, I assume that the dependence of the demographic parameters on trait values and environment is four times continuously differentiable. This assumption, of four instead of three times, obviously stems from the fact that here we study the terms of the fitness function up to one more order of ε .

A consequence of dealing with one more order of the small parameter ε is that additional indices must be reserved. Since no multiple birth states will occur in this chapter, we can recycle the first birth state index, l , as a species index:

- i, j, k, l are indices for species (1 to N),
- a, b, c are indices for trait components (1 to z),
- s, t, u are indices for the environmental feedback components (1 to r).

For derivatives a new notation has to be introduced since the scheme used in Chapter I only works for first and second order derivatives (as was pointed out there). To uniformly address arbitrary orders of derivation in this chapter, let us denote by

$$\frac{\partial^n f(x_1, x_2, \dots, x_N)}{\partial x_{a_n} \cdots \partial x_{a_2} \partial x_{a_1}} \Big|_{(x'_1, x'_2, \dots, x'_N)} \quad (1)$$

the N -variable function f derived respectively for x_{a_1}, x_{a_2}, \dots and x_{a_n} , and evaluated at $(x'_1, x'_2, \dots, x'_N)$. Given that the derivative will always be evaluated at the singularity, that part of the notation will be dropped systematically as will be the names of the variables of f . In a square bracket notation as is often used for (multi)linear functions, the arguments are gathered from left to right in order of derivation. As an example of this notational convention, the Taylor expansion of $f(x, y)$ at (a, b) may be written down as

$$\begin{aligned} f(x, y) &= f(a, b) + \frac{\partial f}{\partial x}[x - a] + \frac{\partial f}{\partial y}[y - b] + \frac{1}{2} \frac{\partial^2 f}{\partial x^2}[x - a, x - a] \\ &\quad + \frac{\partial^2 f}{\partial y \partial x}[x - a, y - b] + \frac{1}{2} \frac{\partial^2 f}{\partial y^2}[y - b, y - b] + O((||x - a|| + ||y - b||)^3) \end{aligned}$$

3 Third order expansion of the N -resident invasion fitness function for Lotka-Volterra models

The population dynamical equations of a Lotka-Volterra system with an N -resident community $\mathbb{X} := \{X_1, X_2, \dots, X_N\}$ plus an invader type Y can be written as

$$\begin{cases} \forall j: \frac{1}{n_j} \frac{dn_j}{dt} = r(X_j) \left(1 - \sum_i a(X_j, X_i) n_i - a(X_j, Y) m \right) \\ \frac{1}{m} \frac{dm}{dt} = r(Y) \left(1 - \sum_i a(Y, X_i) n_i - a(Y, Y) m \right) \end{cases} \quad (2)$$

where $r(Y)$ is the per capita growth rate in a virgin environment (i.e., the growth rate in the absense of competitors of any type), and $a(Y, X)$ is the interaction function. By assumption, r and a are C^4 functions here, to guarantee the existence of an expansion of the fitness function up to order $O(\varepsilon^4)$. We may also assume that $a(X, X) = 1$ for any X , thanks to a rescaling (I.29).

At a singular strategy X^* , we know from the consistency conditions (cf. I.35) that $\partial a / \partial Y = \partial a / \partial X = \mathbf{0}^\top$, so the fitness function of a single-resident Lotka-Volterra model (I.30) is expanded in the small parameter ε as

$$\begin{aligned} s_{\mathbb{X}}(Y) &= r(Y)(1 - a(Y, X)) \\ &= r(X^* + V)(1 - a(X^* + V, X^* + U)) \\ &= \left(r^* + \frac{\partial r}{\partial Y}[V] + \frac{1}{2} \frac{\partial^2 r}{\partial Y^2}[V, V] + \frac{1}{6} \frac{\partial^3 r}{\partial Y^3}[V, V, V] + O(\varepsilon^4) \right) \\ &\quad \times \left(\begin{array}{l} -\frac{\partial a}{\partial X}[U] - \frac{\partial a}{\partial Y}[V] - \frac{1}{2} \frac{\partial^2 a}{\partial X^2}[U, U] - \frac{2}{2} \frac{\partial^2 a}{\partial Y \partial X}[U, V] - \frac{1}{2} \frac{\partial^2 a}{\partial Y^2}[V, V] \\ -\frac{1}{6} \frac{\partial^3 a}{\partial X^3}[U, U, U] - \frac{3}{6} \frac{\partial^3 a}{\partial Y \partial X^2}[U, U, V] - \frac{3}{6} \frac{\partial^3 a}{\partial Y^2 \partial X}[U, V, V] \\ -\frac{1}{6} \frac{\partial^3 a}{\partial Y^3}[V, V, V] + O(\varepsilon^4) \end{array} \right) \\ &= -r^* \left(\frac{1}{2} \frac{\partial^2 a}{\partial X^2}[U, U] + \frac{\partial^2 a}{\partial Y \partial X}[U, V] + \frac{1}{2} \frac{\partial^2 a}{\partial Y^2}[V, V] \right) \\ &\quad - r^* \left(\begin{array}{l} -\frac{1}{6} \frac{\partial^3 a}{\partial X^3}[U, U, U] - \frac{1}{2} \frac{\partial^3 a}{\partial Y \partial X^2}[U, U, V] \\ -\frac{1}{2} \frac{\partial^3 a}{\partial Y^2 \partial X}[U, V, V] - \frac{1}{6} \frac{\partial^3 a}{\partial Y^3}[V, V, V] \end{array} \right) \\ &\quad - \frac{\partial r}{\partial Y}[V] \left(\frac{1}{2} \frac{\partial^2 a}{\partial X^2}[U, U] + \frac{\partial^2 a}{\partial Y \partial X}[U, V] + \frac{1}{2} \frac{\partial^2 a}{\partial Y^2}[V, V] \right) + O(\varepsilon^4) \end{aligned} \quad (3)$$

where $r^* = r(X^*)$. From this expansion we can find the second order partial deriva-

tives of $s_{\mathbb{X}}(\mathbf{Y})$,

$$\begin{aligned}\frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^2}[\mathbf{U}, \mathbf{U}] &= -r^* \frac{\partial^2 a}{\partial \mathbf{X}^2}[\mathbf{U}, \mathbf{U}] \\ \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}}[\mathbf{U}, \mathbf{V}] &= -r^* \frac{\partial^2 a}{\partial \mathbf{Y} \partial \mathbf{X}}[\mathbf{U}, \mathbf{V}] \\ \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2}[\mathbf{V}, \mathbf{V}] &= -r^* \frac{\partial^2 a}{\partial \mathbf{Y}^2}[\mathbf{V}, \mathbf{V}]\end{aligned}\quad (4)$$

and those of third order

$$\begin{aligned}\frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^3}[\mathbf{U}, \mathbf{U}, \mathbf{U}] &= -r^* \frac{\partial^3 a}{\partial \mathbf{X}^3}[\mathbf{U}, \mathbf{U}, \mathbf{U}] \\ \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}^2}[\mathbf{U}, \mathbf{U}, \mathbf{V}] &= -r^* \frac{\partial^3 a}{\partial \mathbf{Y} \partial \mathbf{X}^2}[\mathbf{U}, \mathbf{U}, \mathbf{V}] - \frac{\partial r}{\partial \mathbf{Y}}[\mathbf{V}] \frac{\partial^2 a}{\partial \mathbf{X}^2}[\mathbf{U}, \mathbf{U}] \\ \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2 \partial \mathbf{X}}[\mathbf{U}, \mathbf{V}, \mathbf{V}] &= -r^* \frac{\partial^3 a}{\partial \mathbf{Y}^2 \partial \mathbf{X}}[\mathbf{U}, \mathbf{V}, \mathbf{V}] - 2 \frac{\partial r}{\partial \mathbf{Y}}[\mathbf{V}] \frac{\partial^2 a}{\partial \mathbf{Y} \partial \mathbf{X}}[\mathbf{U}, \mathbf{V}] \\ \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^3}[\mathbf{V}, \mathbf{V}, \mathbf{V}] &= -r^* \frac{\partial^3 a}{\partial \mathbf{Y}^3}[\mathbf{V}, \mathbf{V}, \mathbf{V}] - 3 \frac{\partial r}{\partial \mathbf{Y}}[\mathbf{V}] \frac{\partial^2 a}{\partial \mathbf{Y}^2}[\mathbf{V}, \mathbf{V}]\end{aligned}\quad (5)$$

To expand the N -resident fitness function up to but not including $O(\varepsilon^4)$ -terms, a change of coordinates is made from densities \hat{n}_i to fractional densities p_i plus the difference Δ_n in total density from the monomorphic equilibrium density, both of which must be themselves expanded in ε :

$$\begin{aligned}p_i^0 + q_i \varepsilon + O(\varepsilon^2) &:= p_i := \frac{\hat{n}_i}{\sum_j \hat{n}_j} \\ \Delta_n^0 + \Delta_n^1 \varepsilon + \Delta_n^2 \varepsilon^2 + \Delta_n^3 \varepsilon^3 + O(\varepsilon^4) &:= \Delta_n := \sum_i \hat{n}_i - 1\end{aligned}\quad (6)$$

where we have that $\sum_i p_i^0 = 1$, $\sum_i q_i = 0$, and $\Delta_n^0 = 0$ since ε is zero in a monomorphic community $\mathbb{X} = \{\mathbf{X}^*\}$. But as shown before (Eq. (I.40)), Δ_n^1 is zero as well so that a third order expansion of the N -resident Lotka-Volterra fitness (I.31) close to

the singular point \mathbf{X}^* looks like

$$\begin{aligned}
 s_{\mathbf{X}}(\mathbf{Y}) &= \sum_i s_{\mathbf{X}_i}(\mathbf{Y}) \hat{n}_i + r(\mathbf{Y}) \left(1 - \sum_i \hat{n}_i \right) \\
 &= \sum_i \left(\begin{array}{l} \frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i] + \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{V}] + \frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2} [\mathbf{V}, \mathbf{V}] \\ + \frac{1}{6} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{X}^3} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_i] + \frac{1}{2} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{V}] \\ + \frac{1}{2} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2 \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{V}, \mathbf{V}] + \frac{1}{6} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^3} [\mathbf{V}, \mathbf{V}, \mathbf{V}] \end{array} \right) (p_i^0 + q_i \varepsilon) \\
 &\quad - \left(r^* + \frac{\partial r}{\partial \mathbf{Y}} [\mathbf{V}] \right) (\Delta_n^2 \varepsilon^2 + \Delta_n^3 \varepsilon^3) + O(\varepsilon^4) \\
 &= \sum_i p_i^0 \left(\begin{array}{l} \frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i] + \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{V}] + \frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2} [\mathbf{V}, \mathbf{V}] \\ + \frac{1}{6} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{X}^3} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_i] + \frac{1}{2} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{V}] \\ + \frac{1}{2} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2 \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{V}, \mathbf{V}] + \frac{1}{6} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^3} [\mathbf{V}, \mathbf{V}, \mathbf{V}] \end{array} \right) \\
 &\quad + \sum_i q_i \varepsilon \left(\frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i] + \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{V}] \right) \\
 &\quad - \left(r^* \Delta_n^2 \varepsilon^2 + \frac{\partial r}{\partial \mathbf{Y}} [\mathbf{V}] \Delta_n^2 \varepsilon^2 + r^* \Delta_n^3 \varepsilon^3 \right) + O(\varepsilon^4)
 \end{aligned} \tag{7}$$

In Chapter I we have seen (Eq. (I.44)–(I.45)) that this expansion can be rewritten, up to second order terms, as

$$s_{\mathbf{X}}(\mathbf{Y}) = \sigma + \sum_i p_i^0 \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{V}] + \frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2} [\mathbf{V}, \mathbf{V}] + O(\varepsilon^3) \tag{8}$$

where

$$\begin{pmatrix} p_1^0 \\ \vdots \\ p_N^0 \\ \sigma \end{pmatrix} = \begin{bmatrix} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_1, \mathbf{U}_1] & \dots & \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_N, \mathbf{U}_1] & 1 \\ \vdots & \ddots & \vdots & \vdots \\ \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_1, \mathbf{U}_N] & \dots & \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_N, \mathbf{U}_N] & 1 \\ 1 & \dots & 1 & 0 \end{bmatrix}^{-1} \begin{pmatrix} -\frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2} [\mathbf{U}_1, \mathbf{U}_1] \\ \vdots \\ -\frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2} [\mathbf{U}_N, \mathbf{U}_N] \\ 1 \end{pmatrix} \tag{9}$$

and $r^* \Delta_n^2 \varepsilon^2 = \sum_i p_i^0 \partial^2 s_{\mathbf{X}}(\mathbf{Y}) / \partial \mathbf{X}^2 [\mathbf{U}_i, \mathbf{U}_i] - \sigma$ (I.41), which shows that knowing either of the variables Δ_n^2 or σ suffices to calculate the other one, given the fractions p_i . It also shows that the quadratic density difference Δ_n^2 scales inversely with the virgin growth rate of the singular strategy.

To rewrite the third order part we must similarly find $N + 1$ unknowns (Δ_n^3 and q_1, q_2, \dots, q_N), where we can use the equality $\sum_i q_i = 0$ and the N consistency

conditions $\forall j : s_{\mathbb{X}}(\mathbf{X}_j) = 0$. As these last mean that each order of ε separately is zero, we have N conditions from the third order part of the N -resident fitness (7),

$$0 = \sum_i p_i^0 \left(\begin{array}{l} \frac{1}{6} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^3} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_i] + \frac{1}{2} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_j] \\ + \frac{1}{2} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2 \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{U}_j, \mathbf{U}_j] + \frac{1}{6} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^3} [\mathbf{U}_j, \mathbf{U}_j, \mathbf{U}_j] \end{array} \right) \\ + \sum_i q_i \varepsilon \left(\frac{1}{2} \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i] + \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{U}_j] \right) \\ - \left(\frac{\partial r}{\partial \mathbf{Y}} [\mathbf{U}_j] \Delta_n^2 \varepsilon^2 + r^* \Delta_n^3 \varepsilon^3 \right) \quad (10)$$

or slightly rearranged

$$\sum_i \underbrace{\frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{U}_j]}_{[\mathbf{E}]_{ji}} \underbrace{q_i \varepsilon}_{(\mathbf{Q})_i} \\ + \underbrace{\frac{1}{6} \sum_i p_i^0 \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^3} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_i] + \frac{1}{2} \sum_i q_i \varepsilon \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i] - r^* \Delta_n^3 \varepsilon^3}_{\theta} \\ = \frac{\partial r}{\partial \mathbf{Y}} [\mathbf{U}_j] \Delta_n^2 \varepsilon^2 - \sum_i p_i^0 \left(\begin{array}{l} \frac{1}{2} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_j] + \frac{1}{2} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2 \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{U}_j, \mathbf{U}_j] \\ + \frac{1}{6} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^3} [\mathbf{U}_j, \mathbf{U}_j, \mathbf{U}_j] \end{array} \right) \underbrace{(\mathbf{T}')_j}_{(11)}$$

where we indicate how a matrix \mathbf{E} , vectors \mathbf{Q} and \mathbf{T}' , and a scalar θ are defined (where the unknown Δ_n^3 can be calculated from θ , and vice versa, when \mathbf{Q} is known). With these notations the $N + 1$ consistency conditions can be written as $\mathbf{E}\mathbf{Q} + \theta\mathbf{1} = \mathbf{T}'$ plus $\mathbf{T}'^T \mathbf{Q} = 0$, or after extending the vectors and matrix (almost) as before (I.43),

$$\mathbf{Q}^* = \mathbf{E}^{*-1} \mathbf{T}'^* \quad (12)$$

where $\mathbf{E}^* := \begin{bmatrix} \mathbf{E} & \mathbf{1} \\ \mathbf{1}^T & 0 \end{bmatrix}$, $\mathbf{Q}^* := \begin{pmatrix} \mathbf{Q} \\ \theta \end{pmatrix}$ and $\mathbf{T}'^* := \begin{pmatrix} \mathbf{T}' \\ 0 \end{pmatrix}$. Thus we can rewrite the N -resident fitness function for Lotka-Volterra models (I.31) as

$$s_{\mathbb{X}}(\mathbf{Y}) = \sigma + \theta + \sum_i \left(p_i^0 + q_i \varepsilon \right) \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{V}] + \frac{1}{2} \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2} [\mathbf{V}, \mathbf{V}] \\ + \sum_i p_i^0 \left(\frac{1}{2} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{V}] + \frac{1}{2} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2 \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{V}, \mathbf{V}] + \frac{1}{6} \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^3} [\mathbf{V}, \mathbf{V}, \mathbf{V}] \right) \\ + \frac{\partial r}{\partial \mathbf{Y}} [\mathbf{V}] \frac{1}{r^*} \left(\sigma - \sum_i p_i^0 \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i] \right) + O(\varepsilon^4) \quad (13)$$

As the vector \mathbf{T}' depends on the virgin growth rate in the underlying Lotka-Volterra model in such a manner that this dependence cannot be removed through a transformation of the trait space, we see that the first order parts q_i of the proportions, as well as the remainder-term θ , do not strictly depend on partial derivatives of the one-resident fitness function and on the resident and invader strategies as do their lower order counterparts p_i^0 and σ (8). Furthermore the r -dependent term in \mathbf{T}' reappears as the last term in the expansion.

Since θ is the only term of order $O(\varepsilon^3)$ that is independent of the invader's strategy, we see that the third order part of the fitness function is not model-agnostic in the sense that the second order part was, as it depends on additional properties of the underlying ecological model beyond the one-resident fitness' derivatives plus the resident and mutant strategies. This means that as a consequence, a generally applicable formula as found in Chapter I cannot exist for third order expansions of the fitness function.

The expansion also strongly suggests, but does not unequivocally prove at first sight, that there are further r -dependent terms in the expansion, since it is highly unlikely that for Lotka-Volterra models with different virgin growth rates $r(\mathbf{Y})$ but identical one-resident fitness functions $s_{\mathbb{X}}(\mathbf{Y})$, the differences in the r -dependent part of \mathbf{T}' change the q_i in exactly the right way to have the changes in

$$\sum_i q_i \varepsilon \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_i, \mathbf{V}] \quad (14)$$

generically cancel those in

$$\frac{\partial r}{\partial \mathbf{Y}} [\mathbf{V}] \frac{1}{r^*} \left(\sigma - \sum_i p_i^0 \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i] \right) \quad (15)$$

This issue is settled at the end of Appendix A which analyzes the changes in θ , and coincidentally shows that the above terms do not cancel each other.

4 Third order expansion of the N -resident invasion fitness function for consumer resource dynamics models

To look for differences of order $O(\varepsilon^3)$ from the Lotka-Volterra case in fitness functions, we can study consumer resource dynamics models (I.121), which are of the following form (Tilman, 1982; Grover, 1997): for each trait value X_i , per capita growth is given by

$$\frac{1}{n_i} \frac{dn_i}{dt} = g \left(X_i, \sum_j h_1(X_j) n_j, \sum_j h_2(X_j) n_j, \dots, \sum_j h_r(X_j) n_j \right) \quad (16)$$

for the growth rate function g and r (positive) resource functions h_s , which are all C^4 functions. The multi-resident invasion fitness is by definition

$$s_{\mathbb{X}}(\mathbf{Y}) := g(\mathbf{Y}, \hat{I}_1, \hat{I}_2, \dots, \hat{I}_r) \quad (17)$$

where the environment \mathbf{I} is defined componentwise as

$$(\mathbf{I})_s = I_s := \sum_j h_s(X_j) n_j \quad (18)$$

Note that the underlying individual-based model of such an ODE population model is necessarily a stochastic birth-and-death process (or rather a generalized b.a.d. process as multiple births can be allowed). However, specifying the ODE (here by the function g (16)) does not provide sufficient information to calculate for example the expected lifetime offspring number L . When given both the average rate of giving birth $b(\mathbf{Y}, \mathbf{I})$ and death rate $d(\mathbf{Y}, \mathbf{I})$, the expected lifetime offspring production is found as

$$L(\mathbf{Y}, \mathbf{I}) = L(\mathbf{Y}, \mathbf{I}) = \frac{b(\mathbf{Y}, \mathbf{I})}{d(\mathbf{Y}, \mathbf{I})} = 1 + \frac{g(\mathbf{Y}, \mathbf{I})}{d(\mathbf{Y}, \mathbf{I})} \quad (19)$$

and similarly T_f is calculated, allowing us to treat this dynamics as a structured population model (61). However, we were only given the difference $g(\mathbf{Y}, \mathbf{I})$ between the birth and death rates.

We do a trait-dependent rescaling of the densities (I.124) that has no influence on the s -function,

$$\forall \mathbf{X}: 0 = g(\mathbf{X}, h_1(\mathbf{X}), h_2(\mathbf{X}), \dots, h_r(\mathbf{X})) \quad (20)$$

so that the equilibrium density \hat{n} is one in every monomorphic community. It is possible to do this rescaling such that additionally $h_s(\mathbf{X}^*) = 1$ for all s , but this is not done here as it obscures more than it simplifies.

As before, we change the coordinate system from absolute densities to fractions and total density,

$$\begin{aligned} p_i^0 + q_i \varepsilon + q_i^2 \varepsilon^2 + q_i^3 \varepsilon^3 + O(\varepsilon^4) &:= p_i := \frac{\hat{n}_i}{\sum_j \hat{n}_j} \\ \Delta_n^0 + \Delta_n^1 \varepsilon + \Delta_n^2 \varepsilon^2 + \Delta_n^3 \varepsilon^3 + O(\varepsilon^4) &:= \Delta_n := \sum_i \hat{n}_i - 1 \end{aligned} \quad (21)$$

where we know that $\Delta_n^0 = 0$ from the rescaling. We note that here the second and third order components of the fractions seem to be needed (as opposed to the Lotka-Volterra case (6)), but terms in the expansion having this component will quickly cancel each other. For example, if we expand the environmental components at

population-dynamical equilibrium,

$$\begin{aligned}
 \hat{I}_s &= \sum_i h_s(\mathbf{X}_i) p_i \sum_j \hat{n}_j \\
 &= \sum_i \left(h_s(\mathbf{X}^*) + \frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_i] + \frac{1}{2} \frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}_i, \mathbf{U}_i] + \frac{1}{6} \frac{\partial^3 h_s}{\partial \mathbf{X}^3}[\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_i] \right) \\
 &\quad \times \begin{pmatrix} p_i^0 + p_i^0 \Delta_n^1 \varepsilon + q_i \varepsilon + p_i^0 \Delta_n^2 \varepsilon^2 + q_i \Delta_n^1 \varepsilon^2 + q_i^2 \varepsilon^2 \\ p_i^0 \Delta_n^3 \varepsilon^3 + q_i \Delta_n^2 \varepsilon^3 + q_i^2 \Delta_n^1 \varepsilon^3 + q_i^3 \varepsilon^3 \end{pmatrix} + O(\varepsilon^4) \\
 &= h_s(\mathbf{X}^*) + h_s(\mathbf{X}^*) \Delta_n^1 \varepsilon + \sum_i \frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_i] p_i^0 + h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2 \\
 &\quad + \sum_i \frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_i] p_i^0 \Delta_n^1 \varepsilon + \sum_i \frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_i] q_i \varepsilon + \frac{1}{2} \sum_i \frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}_i, \mathbf{U}_i] p_i^0 \\
 &\quad + h_s(\mathbf{X}^*) \Delta_n^3 \varepsilon^3 + \sum_i \frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_i] p_i^0 \Delta_n^2 \varepsilon^2 + \sum_i \frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_i] q_i \Delta_n^1 \varepsilon^2 \\
 &\quad + \sum_i \frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_i] q_i^2 \varepsilon^2 + \frac{1}{2} \sum_i \frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}_i, \mathbf{U}_i] p_i^0 \Delta_n^1 \varepsilon + \frac{1}{2} \sum_i \frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}_i, \mathbf{U}_i] q_i \varepsilon \\
 &\quad + \frac{1}{6} \sum_i \frac{\partial^3 h_s}{\partial \mathbf{X}^3}[\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_i] p_i^0 + O(\varepsilon^4)
 \end{aligned} \tag{22}$$

all terms containing q_i^3 disappear since $\sum_i q_i = \sum_i q_i^2 = \sum_i q_i^3 = 0$. Using the lower order terms of this expansion in a first order one of the N -resident invasion fitness function, we have

$$\begin{aligned}
 s_{\mathbb{X}}(\mathbf{Y}) &= g(\mathbf{Y}, \hat{I}_1, \hat{I}_2, \dots, \hat{I}_r) \\
 &= 0 + 0 + \sum_s \frac{\partial g}{\partial I_s} [h_s(\mathbf{X}^*) \Delta_n^1 \varepsilon] + \sum_i \left(\sum_s \frac{\partial g}{\partial I_s} \frac{\partial h_s}{\partial \mathbf{X}} \right) [p_i^0 \mathbf{U}_i] + O(\varepsilon^2)
 \end{aligned} \tag{23}$$

where the zeros stem from the consistency condition $s_{\mathbb{X}^*}(\mathbf{X}^*) = 0$ and from the fact that $\frac{\partial s_{\mathbb{X}^*}(\mathbf{X}^*)}{\partial \mathbf{Y}} = \mathbf{0}^\top$. But if we apply this equality to a one-resident community (where $\Delta_n^1 = 0$ due to the rescaling (20)), then it follows from the consistency condition $s_{\mathbb{X}}(\mathbf{X}) = 0$ that $\sum_s \frac{\partial g}{\partial I_s} \frac{\partial h_s}{\partial \mathbf{X}} = \mathbf{0}^\top$. Thus we see that for any resident \mathbf{X}_i

$$0 = s_{\mathbb{X}}(\mathbf{X}_i) = \sum_s \frac{\partial g}{\partial I_s} [h_s(\mathbf{X}^*) \Delta_n^1 \varepsilon] + O(\varepsilon^2) \tag{24}$$

which means that (within the set of local equivalence classes of models characterized by $\partial g / \partial I$) generically $\Delta_n^1 = 0$. Another consequence of $\sum_s \frac{\partial g}{\partial I_s} \frac{\partial h_s}{\partial \mathbf{X}} = \mathbf{0}^\top$ is that also q_i^2 -terms disappear, as promised. Using these observations to simplify \hat{I}_s (22), we see that the third order expansion of the N -resident fitness for resource compe-

tition models is

$$\begin{aligned}
 s_{\mathbb{X}}(\mathbf{Y}) &= g(\mathbf{Y}, \hat{l}_1, \hat{l}_2, \dots, \hat{l}_r) \\
 &= \sum_s \frac{\partial g}{\partial I_s} [h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2 + h_s(\mathbf{X}^*) \Delta_n^3 \varepsilon^3] + \frac{1}{2} \sum_{js} \frac{\partial g}{\partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}_j, \mathbf{U}_j] p_j^0 \right] \\
 &\quad + \sum_{js} \frac{\partial g}{\partial I_s} \left[\frac{1}{2} \frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}_j, \mathbf{U}_j] q_j \varepsilon + \frac{1}{6} \frac{\partial^3 h_s}{\partial \mathbf{X}^3} [\mathbf{U}_j, \mathbf{U}_j, \mathbf{U}_j] p_j^0 \right] + \frac{1}{2} \frac{\partial^2 g}{\partial \mathbf{Y}^2} [\mathbf{V}, \mathbf{V}] \\
 &\quad + \sum_{js} \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] p_j^0, \mathbf{V} \right] + \sum_s \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} [h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2, \mathbf{V}] \\
 &\quad + \sum_{js} \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] q_j \varepsilon, \mathbf{V} \right] + \frac{1}{2} \sum_{js} \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}_j, \mathbf{U}_j] p_j^0, \mathbf{V} \right] \\
 &\quad + \frac{1}{2} \sum_{jkst} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] p_j^0 + 2h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0 \right] \\
 &\quad + \sum_{jkst} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] q_j \varepsilon + \frac{1}{2} \frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}_j, \mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0 \right] \\
 &\quad + \frac{1}{6} \frac{\partial^3 g}{\partial \mathbf{Y}^3} [\mathbf{V}, \mathbf{V}, \mathbf{V}] + \frac{3}{6} \sum_{js} \frac{\partial^3 g}{\partial \mathbf{Y}^2 \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] p_j^0, \mathbf{V}, \mathbf{V} \right] \\
 &\quad + \frac{3}{6} \sum_{jkst} \frac{\partial^3 g}{\partial \mathbf{Y} \partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0, \mathbf{V} \right] \\
 &\quad + \frac{1}{6} \sum_{jklstu} \frac{\partial^3 g}{\partial I_u \partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0, \frac{\partial h_u}{\partial \mathbf{X}} [\mathbf{U}_l] p_l^0 \right] + 0(\varepsilon^4) \quad (25)
 \end{aligned}$$

Applying this to the one-resident case (where $q_1 = \Delta_n^2 = \Delta_n^3 = 0$ and $p_1 = 1$), the second order parts of the one-resident fitness function are

$$\begin{aligned}
 \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^2} [\mathbf{U}, \mathbf{U}] &= \sum_s \frac{\partial g}{\partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}, \mathbf{U}] \right] + \sum_{st} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}], \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}] \right] \\
 \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}, \mathbf{V}] &= \sum_s \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}], \mathbf{V} \right] \\
 \frac{\partial^2 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2} [\mathbf{V}, \mathbf{V}] &= \frac{\partial^2 g}{\partial \mathbf{Y}^2} [\mathbf{V}, \mathbf{V}] \quad (26)
 \end{aligned}$$

and the third order parts are

$$\begin{aligned}
 \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{X}^3}[\mathbf{U}, \mathbf{U}, \mathbf{U}] &= \sum_s \frac{\partial g}{\partial I_s} \left[\frac{\partial^3 h_s}{\partial \mathbf{X}^3}[\mathbf{U}, \mathbf{U}, \mathbf{U}] \right] + 3 \sum_{st} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}, \mathbf{U}], \frac{\partial h_t}{\partial \mathbf{X}}[\mathbf{U}] \right] \\
 &\quad + \sum_{stu} \frac{\partial^3 g}{\partial I_u \partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}], \frac{\partial h_t}{\partial \mathbf{X}}[\mathbf{U}], \frac{\partial h_u}{\partial \mathbf{X}}[\mathbf{U}] \right] \\
 \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}^2}[\mathbf{U}, \mathbf{U}, \mathbf{V}] &= \sum_s \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}, \mathbf{U}], \mathbf{V} \right] \\
 &\quad + \sum_{st} \frac{\partial^3 g}{\partial \mathbf{Y} \partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}], \frac{\partial h_t}{\partial \mathbf{X}}[\mathbf{U}], \mathbf{V} \right] \\
 \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2 \partial \mathbf{X}}[\mathbf{U}, \mathbf{V}, \mathbf{V}] &= \sum_s \frac{\partial^3 g}{\partial \mathbf{Y}^2 \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}], \mathbf{V}, \mathbf{V} \right] \\
 \frac{\partial^3 s_{\mathbb{X}}(\mathbf{Y})}{\partial \mathbf{Y}^3}[\mathbf{V}, \mathbf{V}, \mathbf{V}] &= \frac{\partial^3 g}{\partial \mathbf{Y}^3}[\mathbf{V}, \mathbf{V}, \mathbf{V}]
 \end{aligned} \tag{27}$$

There are twice N consistency conditions to exploit, as $s_{\mathbb{X}}(\mathbf{X}_i) = 0$ for each resident \mathbf{X}_i , so the expansion terms must sum up to zero for each order separately:

$$\begin{aligned}
 0 &= \sum_s \frac{\partial g}{\partial I_s} [h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2] + \frac{1}{2} \sum_{js} \frac{\partial g}{\partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}_j, \mathbf{U}_j] p_j^0 \right] + \frac{1}{2} \frac{\partial^2 g}{\partial \mathbf{Y}^2}[\mathbf{U}_i, \mathbf{U}_i] \\
 &\quad + \sum_{js} \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_j] p_j^0, \mathbf{U}_i \right] + \frac{1}{2} \sum_{jkst} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}}[\mathbf{U}_k] p_k^0 \right]
 \end{aligned} \tag{28}$$

and

$$\begin{aligned}
 0 &= \sum_s \frac{\partial g}{\partial I_s} [h_s(\mathbf{X}^*) \Delta_n^3 \varepsilon^3] + \sum_{js} \frac{\partial g}{\partial I_s} \left[\frac{1}{2} \frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}_j, \mathbf{U}_j] q_j \varepsilon + \frac{1}{6} \frac{\partial^3 h_s}{\partial \mathbf{X}^3}[\mathbf{U}_j, \mathbf{U}_j, \mathbf{U}_j] p_j^0 \right] \\
 &\quad + \sum_s \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} [h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2, \mathbf{U}_i] + \sum_{js} \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_j] q_j \varepsilon, \mathbf{U}_i \right] \\
 &\quad + \frac{1}{2} \sum_{js} \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}_j, \mathbf{U}_j] p_j^0, \mathbf{U}_i \right] + \sum_{jkst} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2, \frac{\partial h_t}{\partial \mathbf{X}}[\mathbf{U}_k] p_k^0 \right] \\
 &\quad + \sum_{jkst} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_j] q_j \varepsilon + \frac{1}{2} \frac{\partial^2 h_s}{\partial \mathbf{X}^2}[\mathbf{U}_j, \mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}}[\mathbf{U}_k] p_k^0 \right] \\
 &\quad + \frac{1}{6} \frac{\partial^3 g}{\partial \mathbf{Y}^3}[\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_i] + \frac{1}{2} \sum_{js} \frac{\partial^3 g}{\partial \mathbf{Y}^2 \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_j] p_j^0, \mathbf{U}_i, \mathbf{U}_i \right] \\
 &\quad + \frac{1}{2} \sum_{jkst} \frac{\partial^3 g}{\partial \mathbf{Y} \partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}}[\mathbf{U}_k] p_k^0, \mathbf{U}_i \right] \\
 &\quad + \frac{1}{6} \sum_{jklstu} \frac{\partial^3 g}{\partial I_u \partial I_l \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}}[\mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}}[\mathbf{U}_k] p_k^0, \frac{\partial h_u}{\partial \mathbf{X}}[\mathbf{U}_l] p_l^0 \right]
 \end{aligned} \tag{29}$$

We can neatly rearrange the second order part if we define a scalar constant,

$$\begin{aligned}\sigma := & \sum_s \frac{\partial g}{\partial I_s} [h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2] + \frac{1}{2} \sum_{js} \frac{\partial g}{\partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}_j, \mathbf{U}_j] p_j^0 \right] \\ & + \frac{1}{2} \sum_{jkst} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0 \right]\end{aligned}\quad (30)$$

then recognize two parts of the single resident fitness (26), and once more define a matrix \mathbf{E} and two vectors \mathbf{P} and \mathbf{T} componentwise (cf. (I.41), (11)),

$$\sum_j \underbrace{p_j^0}_{(\mathbf{P})_j} \underbrace{\frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_j, \mathbf{U}_i]}_{(\mathbf{E})_{ij}} + \sigma = - \underbrace{\frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2} [\mathbf{U}_i, \mathbf{U}_i]}_{(\mathbf{T})_i}\quad (31)$$

which solves the second order part of the N -resident fitness as before (8, 9). Defining another scalar constant,

$$\begin{aligned}\theta = & \sum_s \frac{\partial g}{\partial I_s} [h_s(\mathbf{X}^*) \Delta_n^3 \varepsilon^3] + \sum_{js} \frac{\partial g}{\partial I_s} \left[\frac{1}{2} \frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}_j, \mathbf{U}_j] q_j \varepsilon + \frac{1}{6} \frac{\partial^3 h_s}{\partial \mathbf{X}^3} [\mathbf{U}_j, \mathbf{U}_j, \mathbf{U}_j] p_j^0 \right] \\ & + \sum_{jkst} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0 \right] \\ & + \sum_{jkst} \frac{\partial^2 g}{\partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] q_j \varepsilon + \frac{1}{2} \frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}_j, \mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0 \right] \\ & + \frac{1}{6} \sum_{jklstu} \frac{\partial^3 g}{\partial I_u \partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0, \frac{\partial h_u}{\partial \mathbf{X}} [\mathbf{U}_l] p_l^0 \right]\end{aligned}\quad (32)$$

and another vector, which consists purely of (now) known parts,

$$\begin{aligned}(\mathbf{T}')_i = & - \sum_s \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} [h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2, \mathbf{U}_i] - \frac{1}{2} \sum_{js} \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}_j, \mathbf{U}_j] p_j^0, \mathbf{U}_i \right] \\ & - \frac{1}{2} \sum_{jkst} \frac{\partial^3 g}{\partial \mathbf{Y} \partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0, \mathbf{U}_i \right] \\ & - \frac{1}{2} \sum_j p_j^0 \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2 \partial \mathbf{X}} [\mathbf{U}_j, \mathbf{U}_i, \mathbf{U}_i] - \frac{1}{6} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^3} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{U}_i]\end{aligned}\quad (33)$$

we can similarly rearrange the third order part as

$$\mathbf{E} \mathbf{Q} + \theta \mathbf{1} = \mathbf{T}' \quad (34)$$

where \mathbf{Q} is the vector made up of the first order parts $q_i \varepsilon$ of the proportions.

We can conclude from these calculations that the N -resident fitness for consumer resource dynamics models looks like

$$\begin{aligned} s_{\mathbf{X}}(\mathbf{Y}) = & \sigma + \theta + \sum_j \left(p_j^0 + q_j \varepsilon \right) \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}} [\mathbf{U}_j, \mathbf{V}] + \frac{1}{2} \frac{\partial^2 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2} [\mathbf{V}, \mathbf{V}] \\ & + \frac{1}{2} \sum_{jkst} \frac{\partial^3 g}{\partial \mathbf{Y} \partial I_t \partial I_s} \left[\frac{\partial h_s}{\partial \mathbf{X}} [\mathbf{U}_j] p_j^0, \frac{\partial h_t}{\partial \mathbf{X}} [\mathbf{U}_k] p_k^0, \mathbf{V} \right] \end{aligned} \quad (35)$$

$$+ \frac{1}{2} \sum_{js} \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} \left[\frac{\partial^2 h_s}{\partial \mathbf{X}^2} [\mathbf{U}_j, \mathbf{U}_j] p_j^0, \mathbf{V} \right] \quad (36)$$

$$\begin{aligned} & + \frac{1}{2} \sum_j p_j^0 \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^2 \partial \mathbf{X}} [\mathbf{U}_j, \mathbf{V}, \mathbf{V}] + \frac{1}{6} \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y}^3} [\mathbf{V}, \mathbf{V}, \mathbf{V}] \\ & + \sum_s \frac{\partial^2 g}{\partial \mathbf{Y} \partial I_s} [h_s(\mathbf{X}^*) \Delta_n^2 \varepsilon^2, \mathbf{V}] + O(\varepsilon^4) \end{aligned} \quad (37)$$

Comparing this formula with that for Lotka-Volterra models (13), we see that the missing $\frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}^2}$ -term is replaced by a similar (cf. Eq. (27)) two-part term (35)+(36). The same thing happens with \mathbf{T}' : for Lotka-Volterra models (11) this vector's components consist of one leftover term that reappears in the expansion, plus three third order derivatives of the one-resident fitness. For resource competition models there is such a leftover term in \mathbf{T}' (33) as well, which similarly reappears in the expansion, as well as two of the three partial derivatives. But the third of these partial derivatives is replaced by two terms that together almost (but not quite) are $\sum_i p_i^0 \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{Y} \partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i, \mathbf{V}]$. This phenomenon occurs again in θ , and once more in its second order equivalent σ (but not in \mathbf{T} , as then the second order fitness expansions (I.44, I.75) of Chapter I would not coincide): for example, in resource competition models the last two terms of σ (30) almost, but not exactly, form the partial derivative term $\sum_i p_i^0 \frac{\partial^3 s_{\mathbf{X}}(\mathbf{Y})}{\partial \mathbf{X}^2} [\mathbf{U}_i, \mathbf{U}_i]$ (26) which is found in σ for Lotka-Volterra models (I.41).

Naturally, the same difference from Lotka-Volterra models in multi-resident invasion fitness occurs for general physiologically structured population models, as we see from the connection between their value of σ (I.72) and their second order partial derivatives (I.69).

5 Discussion

The key to the differences between model types in third order fitness function near singularities, highlighted in the paragraph following Equation (37), probably lies in the structure of the environment. If we expand the N -resident environment as $\mathbf{I} = \mathbf{I}^* + \mathbf{I}' \varepsilon + \mathbf{I}'' \varepsilon^2 + O(\varepsilon^3)$, where \mathbf{I}^* is the environment with only the singular strategy present, and the environment when only X_i -strategists are present as $\mathbf{I}_i = \mathbf{I}^* + \mathbf{I}'_i \varepsilon + \mathbf{I}''_i \varepsilon^2 + O(\varepsilon^3)$, then we have that for all models at equilibrium $\hat{\mathbf{I}}' = \sum_i p_i^0 \hat{\mathbf{I}}'_i$ (I.66). From the definition of environmental dimension in Appendix I.E, we know

that a possible representation of the environment of a Lotka-Volterra model is the real-valued function

$$I : Y' \mapsto \int_{\mathfrak{X}} a(Y', X) d\nu(X)$$

where \mathfrak{X} is the trait space and ν the density distribution (I.113). In the case of N -resident communities, the density is just a weighted sum of delta peaks, $\nu(X) = \sum_i n_i \delta(X - X_j)$, and therefore $I = \sum_i n_i I_i$. That is to say, the N -species environment is nothing more than the weighted sum of the N one-species environments, a consequence of the fact that Lotka-Volterra dynamics only contain pairwise interaction terms (cf. Proposition I.2 and its second example (I.34)). Thus the relation between second order parts of the environment is $\hat{I}'' = \sum_i p_i^0 \hat{I}_i'' + \sum_i q_i \hat{I}_i'$. In contrast, Equation (22) shows us that for resource competition models $\hat{I}'' = \sum_i p_i^0 \hat{I}_i'' + \sum_i q_i \hat{I}_i' + h_s(X^*) \Delta_n^2$.

Two-resident, instead of N -resident, Lotka-Volterra systems near singularities are studied in Appendix A, because they constitute a rather natural case since branching events do very rarely lead to three or more branches (Vukics *et al.*, 2003). Furthermore, by comparing Equations (I.32) and (48), we see that additional resident types do not make the calculations essentially more complex, but just add more terms of the types already present. On the other hand, restricting ourselves to scalar traits allows some powerful simplifications (Jacobs *et al.*, in prep.) that are not available for multi-dimensional strategies. Therefore the first system considered (39, 40) can be taken as representative for all Lotka-Volterra systems near singularities. Given two different Lotka-Volterra systems with the same one-resident fitness function, Equation (55) shows that they will always have the same N -resident invasion function up to second order terms (as we knew from Chapter I), Equation (44) that they will differ at some order of ε , and Equation (56) that they will differ already in terms of order $O(\varepsilon^3)$ unless they have the same value of r'/r^* . Similarly, they will have the same fitness up to terms of order $O(\varepsilon^4)$ if furthermore they have the same value of r''/r^* ; this can be seen when considering two systems such that

$$R(Y)(1 - A(Y, X)) = r(Y)(1 - a(Y, X)) \quad (38)$$

with

$$\begin{aligned} r(Y) &= r^* + r'[V] + r''[V, V] + O(V^3) \\ R(Y) &= R^* + \frac{R^*}{r^*} r'[V] + \frac{R^*}{r^*} r''[V, V] + O(V^3) \end{aligned}$$

so that all second, third and fourth order partial derivatives of $A(Y, X)/R^*$ and $a(Y, X)/r^*$ coincide, as seen from the combination of Equations (4) and (5) and their extrapolation to fourth order. I would conjecture therefore that to have identical N -resident fitness functions up to terms of order $O(\varepsilon^{k+2})$, two systems with identical one-resident fitness must have virgin growth rates with identical (normalized) derivatives $\frac{r'}{r^*}, \frac{r''}{r^*}, \dots, \frac{r^{(k)}}{r^*}$.

Underlying the second order normal form (Prop. I.3) is the equivalence relation *has locally the same one-resident fitness function as*, the Lotka-Volterra models with virgin growth rate $r(Y) := 1$ form a basis, and each equivalence class contains infinitely many Lotka-Volterra models with differing growth rates. Thus an

obvious idea when looking for a third order normal form is to see if we can fit a Lotka-Volterra system to an arbitrary physiologically structured population (Proposition (I.1)), such that their N -resident fitnesses coincide up to third order terms. In Appendix A the viability of this idea is checked by fitting one Lotka-Volterra system to another. There we see that there cannot exist a third order normal form for the multi-resident invasion fitness of Lotka-Volterra models that does not unravel the population dynamical model into its constituent ingredients $r(Y)$ and $a(Y, X)$. Hence Proposition I.3 cannot be extended to one more order: there cannot exist a third order normal form for $s_X(Y)$ that only depends on $s_X(Y)$ and the community X . Given that to have identical N -resident fitnesses up to third order terms, two Lotka-Volterra models with identical one-resident fitnesses must even have the same normalized first derivative r'/r^* of the growth rate, and given that population models can have very different interactions among residents (cf. the counterexamples accompanying Proposition (I.2)), there exists no recipe to fit a Lotka-Volterra model to an arbitrary population model such that their third order fitnesses coincide.

The main purpose of this chapter has been to show that there is a definite limit to using Lotka-Volterra models as universal representatives for communities near singularities, as well as to explore some consequences of the programme started in Chapter I, and last but not least to document some useful formulæ for future use. I stop at the present stage, however, as the time for unbounded PhD research is over, and leave several open ends behind.

Acknowledgements I'd like to thank Frans Jacobs for discussions on the expansion of Lotka-Volterra fitness functions, and Hans Metz for relentless questioning and commenting that has improved this chapter no end.

Appendices

A Re-fitting Lotka-Volterra models

A two-resident Lotka-Volterra system specified by its virgin growth rate $r(Y)$ and interaction function $a(Y, X)$ (and scaled such that $a(X, X) = 1$ for all X) has equilibrium densities (I.32)

$$\begin{pmatrix} \hat{n}_1 \\ \hat{n}_2 \end{pmatrix} = \frac{1}{1 - a(X_1, X_2) a(X_2, X_1)} \begin{pmatrix} 1 - a(X_1, X_2) \\ 1 - a(X_2, X_1) \end{pmatrix} \quad (39)$$

and invasion fitness function

$$\begin{aligned} s_{X_1 X_2}(Y) &= r(Y) \left(1 - a(Y, X_1) \hat{n}_1 - a(Y, X_2) \hat{n}_2 \right) \\ &= r(Y) \left(1 - \frac{a(Y, X_1)(1 - a(X_1, X_2)) + a(Y, X_2)(1 - a(X_2, X_1))}{1 - a(X_1, X_2) a(X_2, X_1)} \right) \end{aligned} \quad (40)$$

To this system we can fit a Lotka-Volterra model with the same one-resident fitness function, by specifying a virgin growth rate and interaction function (in capital

letters, to distinguish it from the original),

$$R(\mathbf{Y}) := 1 \quad A(\mathbf{Y}, \mathbf{X}) := 1 - r(\mathbf{Y})(1 - a(\mathbf{Y}, \mathbf{X})) \quad (41)$$

which shares its one-resident fitness function with the older Lotka-Volterra system:

$$S_{\mathbf{X}}(\mathbf{Y}) = R(\mathbf{Y})(1 - A(\mathbf{Y}, \mathbf{X})) = r(\mathbf{Y})(1 - a(\mathbf{Y}, \mathbf{X})) \quad (42)$$

If we calculate the equilibrium densities from Formula (39),

$$\begin{aligned} \begin{pmatrix} \hat{N}_1 \\ \hat{N}_2 \end{pmatrix} &= \frac{\begin{pmatrix} 1 - A(\mathbf{X}_1, \mathbf{X}_2) \\ 1 - A(\mathbf{X}_2, \mathbf{X}_1) \end{pmatrix}}{1 - A(\mathbf{X}_1, \mathbf{X}_2)A(\mathbf{X}_2, \mathbf{X}_1)} \\ &= \frac{\begin{pmatrix} r(\mathbf{X}_1)(1 - a(\mathbf{X}_1, \mathbf{X}_2)) \\ r(\mathbf{X}_2)(1 - a(\mathbf{X}_2, \mathbf{X}_1)) \end{pmatrix}}{r(\mathbf{X}_1)(1 - a(\mathbf{X}_1, \mathbf{X}_2)) + r(\mathbf{X}_2)(1 - a(\mathbf{X}_2, \mathbf{X}_1))} \\ &\quad - r(\mathbf{X}_1)r(\mathbf{X}_2)(1 - a(\mathbf{X}_1, \mathbf{X}_2))(1 - a(\mathbf{X}_2, \mathbf{X}_1)) \end{aligned} \quad (43)$$

then we see that the two-resident fitness function is

$$\begin{aligned} S_{\mathbf{X}_1 \mathbf{X}_2}(\mathbf{Y}) &= R(\mathbf{Y}) \left(1 - A(\mathbf{Y}, \mathbf{X}_1)\hat{N}_1 - A(\mathbf{Y}, \mathbf{X}_2)\hat{N}_2 \right) \\ &\quad r(\mathbf{X}_1)(1 - a(\mathbf{X}_1, \mathbf{X}_2)) + r(\mathbf{X}_2)(1 - a(\mathbf{X}_2, \mathbf{X}_1)) \\ &\quad - r(\mathbf{X}_1)r(\mathbf{X}_2)(1 - a(\mathbf{X}_1, \mathbf{X}_2))(1 - a(\mathbf{X}_2, \mathbf{X}_1)) \\ &= \frac{- (1 - r(\mathbf{Y})(1 - a(\mathbf{Y}, \mathbf{X}_1)))r(\mathbf{X}_1)(1 - a(\mathbf{X}_1, \mathbf{X}_2))}{r(\mathbf{X}_1)(1 - a(\mathbf{X}_1, \mathbf{X}_2)) + r(\mathbf{X}_2)(1 - a(\mathbf{X}_2, \mathbf{X}_1))} \\ &\quad - (1 - r(\mathbf{Y})(1 - a(\mathbf{Y}, \mathbf{X}_2)))r(\mathbf{X}_2)(1 - a(\mathbf{X}_2, \mathbf{X}_1)) \\ &= \frac{r(\mathbf{Y})(1 - a(\mathbf{Y}, \mathbf{X}_1))r(\mathbf{X}_1)(1 - a(\mathbf{X}_1, \mathbf{X}_2))}{r(\mathbf{X}_1)(1 - a(\mathbf{X}_1, \mathbf{X}_2)) + r(\mathbf{X}_2)(1 - a(\mathbf{X}_2, \mathbf{X}_1))} \\ &\quad + r(\mathbf{Y})(1 - a(\mathbf{Y}, \mathbf{X}_2))r(\mathbf{X}_2)(1 - a(\mathbf{X}_2, \mathbf{X}_1)) \\ &= \frac{- r(\mathbf{X}_1)r(\mathbf{X}_2)(1 - a(\mathbf{X}_1, \mathbf{X}_2))(1 - a(\mathbf{X}_2, \mathbf{X}_1))}{r(\mathbf{X}_1)(1 - a(\mathbf{X}_1, \mathbf{X}_2)) + r(\mathbf{X}_2)(1 - a(\mathbf{X}_2, \mathbf{X}_1))} \\ &= \frac{r(\mathbf{X}_1)(1 - a(\mathbf{X}_1, \mathbf{X}_2)) + r(\mathbf{X}_2)(1 - a(\mathbf{X}_2, \mathbf{X}_1))}{- r(\mathbf{X}_1)r(\mathbf{X}_2)(1 - a(\mathbf{X}_1, \mathbf{X}_2))(1 - a(\mathbf{X}_2, \mathbf{X}_1))} \end{aligned} \quad (44)$$

which is clearly different from the original system's fitness (40), as for example $r(\mathbf{Y})$ is not a factor anymore.

However, it is not clear at first look, from which order of the small parameter ε the two N -resident fitness functions (40, 44), start to differ. To answer that question, we calculate the term of order $O(\varepsilon^3)$ which does not depend on the invader's strategy, in the N -resident invasion fitness function of both the original (40) and the fitted (44) Lotka-Volterra model.

Schematically, if we split the numerator and denominator of the original two-resident fitness (40) into parts that are homogenous in $\{\mathbf{X}_1, \mathbf{X}_2\}$, it looks like

$$s_{\mathbf{X}_1 \mathbf{X}_2}(\mathbf{Y}) = \frac{\mathcal{N}}{\mathcal{D}} = \frac{\mathcal{N}_0 + \mathcal{N}_1 + \mathcal{N}_2 + \mathcal{N}_3 + \mathcal{N}_4 + \mathcal{N}_5 + O(\varepsilon^6)}{\mathcal{D}_0 + \mathcal{D}_1 + \mathcal{D}_2 + \mathcal{D}_3 + \mathcal{D}_4 + \mathcal{D}_5 + O(\varepsilon^6)} \quad (45)$$

where a subscript is used to indicate the order of the homogenous polynomials. From the second order expansion in the case of two residents (I.80) we know that we must find $\mathcal{D}_0 = \mathcal{D}_1 = 0$ while (generically) $\mathcal{D}_2 \neq 0$, as well as $\mathcal{N}_0 = \mathcal{N}_1 = \mathcal{N}_2 = \mathcal{N}_3 = 0$. Thus we have for precision up to cubic terms in ε , by expanding the denominator around \mathcal{D}_2 , that

$$\frac{\mathcal{N}}{\mathcal{D}} = \frac{\mathcal{N}_4 + \mathcal{N}_5}{\mathcal{D}_2 + \mathcal{D}_3 + \mathcal{D}_4 + \mathcal{D}_5} + O(\varepsilon^4) = \frac{\mathcal{N}_4 + \mathcal{N}_5}{\mathcal{D}_2} \left(1 - \frac{\mathcal{D}_3}{\mathcal{D}_2} \right) + O(\varepsilon^4) \quad (46)$$

As we need the parts that only depend on resident strategies, we delete all terms that contain V (which is equivalent to setting $Y := X^*$), but do not change the notations of Equation (46). From this equation we see that the part shared by all models with the same one-resident fitness is $\mathcal{N}_4/\mathcal{D}_2$, and the part that possibly differs is the third order part, $\mathcal{N}_5/\mathcal{D}_2 - \mathcal{N}_4\mathcal{D}_3/\mathcal{D}_2^2$. We know that $a(Y, X)$ has no linear part near the singularity (3), so we can expand the interaction function as

$$\begin{aligned} a(X^* + \mathbf{U}_1, X^* + \mathbf{U}_2) \\ = 1 + A_2(\mathbf{U}_1, \mathbf{U}_2) + A_3(\mathbf{U}_1, \mathbf{U}_2) + A_4(\mathbf{U}_1, \mathbf{U}_2) + A_5(\mathbf{U}_1, \mathbf{U}_2) + O(\varepsilon^6) \end{aligned} \quad (47)$$

where each term A_i is a homogenous polynomial of order i . Thus up to $O(\varepsilon^4)$, the invader-independent part \mathcal{N}/\mathcal{D} of the fitness for the original two-resident Lotka-Volterra model (40) is

$$r^* \left(1 + \frac{\left(1 + A_2(\mathbf{0}, \mathbf{U}_1) + A_3(\mathbf{0}, \mathbf{U}_1) + A_4(\mathbf{0}, \mathbf{U}_1) + A_5(\mathbf{0}, \mathbf{U}_1) \right) \times \left(A_2(\mathbf{U}_1, \mathbf{U}_2) + A_3(\mathbf{U}_1, \mathbf{U}_2) + A_4(\mathbf{U}_1, \mathbf{U}_2) + A_5(\mathbf{U}_1, \mathbf{U}_2) \right) + \left(1 + A_2(\mathbf{0}, \mathbf{U}_2) + A_3(\mathbf{0}, \mathbf{U}_2) + A_4(\mathbf{0}, \mathbf{U}_2) + A_5(\mathbf{0}, \mathbf{U}_2) \right) \times \left(A_2(\mathbf{U}_2, \mathbf{U}_1) + A_3(\mathbf{U}_2, \mathbf{U}_1) + A_4(\mathbf{U}_2, \mathbf{U}_1) + A_5(\mathbf{U}_2, \mathbf{U}_1) \right)}{1 - \left(1 + A_2(\mathbf{U}_1, \mathbf{U}_2) + A_3(\mathbf{U}_1, \mathbf{U}_2) + A_4(\mathbf{U}_1, \mathbf{U}_2) + A_5(\mathbf{U}_1, \mathbf{U}_2) \right) \times \left(1 + A_2(\mathbf{U}_2, \mathbf{U}_1) + A_3(\mathbf{U}_2, \mathbf{U}_1) + A_4(\mathbf{U}_2, \mathbf{U}_1) + A_5(\mathbf{U}_2, \mathbf{U}_1) \right)} \right) \quad (48)$$

To put this expression on a common denominator, we first determine the denominator up to fifth order terms,

$$\begin{aligned} \mathcal{D} = & -A_2(\mathbf{U}_1, \mathbf{U}_2) - A_3(\mathbf{U}_1, \mathbf{U}_2) - A_4(\mathbf{U}_1, \mathbf{U}_2) - A_5(\mathbf{U}_1, \mathbf{U}_2) \\ & - A_2(\mathbf{U}_2, \mathbf{U}_1) - A_3(\mathbf{U}_2, \mathbf{U}_1) - A_4(\mathbf{U}_2, \mathbf{U}_1) - A_5(\mathbf{U}_2, \mathbf{U}_1) \\ & - A_2(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) \\ & - A_3(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) - A_2(\mathbf{U}_2, \mathbf{U}_1)A_3(\mathbf{U}_1, \mathbf{U}_2) + O(\varepsilon^6) \end{aligned} \quad (49)$$

and use this formula in finding the numerator up to fifth order terms,

$$\mathcal{N} = r^* \left(\begin{array}{l} -A_2(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) - A_3(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) \\ - A_2(\mathbf{U}_2, \mathbf{U}_1)A_3(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) \\ + A_2(\mathbf{0}, \mathbf{U}_1)A_3(\mathbf{U}_1, \mathbf{U}_2) + A_3(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) \\ + A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) + A_2(\mathbf{0}, \mathbf{U}_2)A_3(\mathbf{U}_2, \mathbf{U}_1) \\ + A_3(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) \end{array} \right) + O(\varepsilon^6) \quad (50)$$

As anticipated $\mathcal{N}_0 = \mathcal{N}_1 = \mathcal{N}_2 = \mathcal{N}_3 = \mathcal{D}_0 = \mathcal{D}_1 = 0$, and separating the parts of \mathcal{N} and \mathcal{D} per order, we find the second order part

$$\frac{\mathcal{N}_4}{\mathcal{D}_2} = r^* \frac{-A_2(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2)}{+A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) - A_2(\mathbf{U}_1, \mathbf{U}_2) - A_2(\mathbf{U}_2, \mathbf{U}_1)} \quad (51)$$

which we use to calculate the third order part:

$$\begin{aligned} & \frac{\mathcal{N}_5}{\mathcal{D}_2} - \frac{\mathcal{N}_4}{\mathcal{D}_2} \frac{\mathcal{D}_3}{\mathcal{D}_2} \\ &= r^* \frac{A_2(\mathbf{0}, \mathbf{U}_1)A_3(\mathbf{U}_1, \mathbf{U}_2) + A_3(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2)}{-A_3(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) - A_2(\mathbf{U}_2, \mathbf{U}_1)} \\ & \quad + A_2(\mathbf{0}, \mathbf{U}_2)A_3(\mathbf{U}_2, \mathbf{U}_1) + A_3(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) \\ & \quad - A_2(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) \\ & \quad - r^* \frac{-A_2(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1)}{-A_2(\mathbf{U}_1, \mathbf{U}_2) - A_2(\mathbf{U}_2, \mathbf{U}_1)} \\ & \quad \times \frac{-A_3(\mathbf{U}_1, \mathbf{U}_2) - A_3(\mathbf{U}_2, \mathbf{U}_1)}{-A_2(\mathbf{U}_1, \mathbf{U}_2) - A_2(\mathbf{U}_2, \mathbf{U}_1)} \\ &= r^* \frac{-A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_2, \mathbf{U}_1)A_3(\mathbf{U}_1, \mathbf{U}_2)}{(A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{U}_2, \mathbf{U}_1))^2} \\ & \quad + A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2)A_3(\mathbf{U}_2, \mathbf{U}_1) \\ & \quad - A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_1, \mathbf{U}_2)A_3(\mathbf{U}_2, \mathbf{U}_1) \\ & \quad + A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1)A_3(\mathbf{U}_1, \mathbf{U}_2) \\ & \quad - A_3(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_1, \mathbf{U}_2) \\ & \quad - A_3(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) \\ & \quad - A_3(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) \\ & \quad - A_3(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_2, \mathbf{U}_1) \\ & \quad + A_2(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_1, \mathbf{U}_2)A_3(\mathbf{U}_2, \mathbf{U}_1) \\ & \quad + A_2(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_2, \mathbf{U}_1)A_3(\mathbf{U}_1, \mathbf{U}_2) \end{aligned} \quad (52)$$

To calculate the corresponding term for the fitted system (41), we go through the same steps of expanding the numerator and denominator of the two-resident fitness in homogenous parts, using a prime (' \prime ') to distinguish those parts from the originals. The denominator of the two-resident fitness function (44), without Y -dependent terms, is

$$\begin{aligned} \mathcal{D}' = & -r^* A_2(\mathbf{U}_1, \mathbf{U}_2) - r^* A_2(\mathbf{U}_2, \mathbf{U}_1) - r^* A_3(\mathbf{U}_1, \mathbf{U}_2) \\ & - r^* A_3(\mathbf{U}_2, \mathbf{U}_1) - r' \mathbf{U}_1 A_2(\mathbf{U}_1, \mathbf{U}_2) - r' \mathbf{U}_2 A_2(\mathbf{U}_2, \mathbf{U}_1) + O(\varepsilon^4) \end{aligned} \quad (53)$$

and the numerator, without invader-dependent terms, is

$$\begin{aligned}
\mathcal{N}' &= r^*(A_2(\mathbf{0}, \mathbf{U}_1) + A_3(\mathbf{0}, \mathbf{U}_1))(r^* + \mathbf{r}' \mathbf{U}_1)(A_2(\mathbf{U}_1, \mathbf{U}_2) + A_3(\mathbf{U}_1, \mathbf{U}_2)) \\
&\quad + r^*(A_2(\mathbf{0}, \mathbf{U}_2) + A_3(\mathbf{0}, \mathbf{U}_2))(r^* + \mathbf{r}' \mathbf{U}_2)(A_2(\mathbf{U}_2, \mathbf{U}_1) + A_3(\mathbf{U}_2, \mathbf{U}_1)) \\
&\quad - (r^* + \mathbf{r}' \mathbf{U}_1)(r^* + \mathbf{r}' \mathbf{U}_2)(A_2(\mathbf{U}_1, \mathbf{U}_2) + A_3(\mathbf{U}_1, \mathbf{U}_2)) \\
&\quad \times (A_2(\mathbf{U}_2, \mathbf{U}_1) + A_3(\mathbf{U}_2, \mathbf{U}_1)) + O(\varepsilon^6) \\
&= r^{*2}(A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) + A_3(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2)) \\
&\quad + r^{*2}A_2(\mathbf{0}, \mathbf{U}_1)A_3(\mathbf{U}_1, \mathbf{U}_2) + r^{*2}A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) \\
&\quad + r^{*2}(A_3(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) + A_2(\mathbf{0}, \mathbf{U}_2)A_3(\mathbf{U}_2, \mathbf{U}_1)) \\
&\quad + r^*\mathbf{r}'\mathbf{U}_1A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) + r^*\mathbf{r}'\mathbf{U}_2A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) \\
&\quad - r^{*2}(A_2(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) + A_3(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1)) \\
&\quad - r^{*2}A_2(\mathbf{U}_1, \mathbf{U}_2)A_3(\mathbf{U}_2, \mathbf{U}_1) - r^*\mathbf{r}'\mathbf{U}_1A_2(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) \\
&\quad - r^*\mathbf{r}'\mathbf{U}_2A_2(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) + O(\varepsilon^6)
\end{aligned} \tag{54}$$

so that the second order part of the fitness without Y -dependent terms is

$$\frac{\mathcal{N}'_4}{\mathcal{D}'_2} = \frac{r^{*2}A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) + r^{*2}A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1)}{-r^{*2}A_2(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2)} = \frac{\mathcal{N}_4}{\mathcal{D}_2} \tag{55}$$

which neatly coincides with the result found before, as it should. The third order part differs though, as it is

$$\begin{aligned}
&\frac{\mathcal{N}'_5}{\mathcal{D}'_2} - \frac{\mathcal{N}'_4}{\mathcal{D}'_2} \frac{\mathcal{D}'_3}{\mathcal{D}'_2} \\
&- r^*(A_3(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{0}, \mathbf{U}_1)A_3(\mathbf{U}_1, \mathbf{U}_2)) \\
&- r^*(A_3(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) + A_2(\mathbf{0}, \mathbf{U}_2)A_3(\mathbf{U}_2, \mathbf{U}_1)) \\
&- \mathbf{r}'\mathbf{U}_1A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) - \mathbf{r}'\mathbf{U}_2A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) \\
&+ r^*(A_3(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) + A_2(\mathbf{U}_1, \mathbf{U}_2)A_3(\mathbf{U}_2, \mathbf{U}_1)) \\
&+ r'\mathbf{U}_1A_2(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) + r'\mathbf{U}_2A_2(\mathbf{U}_1, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) \\
&= r^* \frac{r^*A_2(\mathbf{U}_1, \mathbf{U}_2) + r^*A_2(\mathbf{U}_2, \mathbf{U}_1)}{r^*A_2(\mathbf{U}_1, \mathbf{U}_2) + r^*A_2(\mathbf{U}_2, \mathbf{U}_1)} \\
&+ r^* \frac{A_2(\mathbf{0}, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{0}, \mathbf{U}_2)A_2(\mathbf{U}_2, \mathbf{U}_1) - A_2(\mathbf{U}_2, \mathbf{U}_1)A_2(\mathbf{U}_1, \mathbf{U}_2)}{A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{U}_2, \mathbf{U}_1)} \\
&\times \frac{r^*A_3(\mathbf{U}_1, \mathbf{U}_2) + r^*A_3(\mathbf{U}_2, \mathbf{U}_1) + \mathbf{r}'\mathbf{U}_1A_2(\mathbf{U}_1, \mathbf{U}_2) + \mathbf{r}'\mathbf{U}_2A_2(\mathbf{U}_2, \mathbf{U}_1)}{r^*A_2(\mathbf{U}_1, \mathbf{U}_2) + r^*A_2(\mathbf{U}_2, \mathbf{U}_1)} \\
&= \dots
\end{aligned}$$

$$\begin{aligned}
& -r^* A_2(\mathbf{0}, \mathbf{U}_1) A_2(\mathbf{U}_2, \mathbf{U}_1) A_3(\mathbf{U}_1, \mathbf{U}_2) \\
& + r^* A_2(\mathbf{0}, \mathbf{U}_1) A_2(\mathbf{U}_1, \mathbf{U}_2) A_3(\mathbf{U}_2, \mathbf{U}_1) \\
& - r^* A_2(\mathbf{0}, \mathbf{U}_2) A_2(\mathbf{U}_1, \mathbf{U}_2) A_3(\mathbf{U}_2, \mathbf{U}_1) \\
& + r^* A_2(\mathbf{0}, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) A_3(\mathbf{U}_2, \mathbf{U}_1) \\
& - r^* A_3(\mathbf{0}, \mathbf{U}_1) A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_1, \mathbf{U}_2) \\
& - r^* A_3(\mathbf{0}, \mathbf{U}_1) A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& - r^* A_3(\mathbf{0}, \mathbf{U}_2) A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& - r^* A_3(\mathbf{0}, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& + r^* A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_1, \mathbf{U}_2) A_3(\mathbf{U}_2, \mathbf{U}_1) \\
& + r^* A_2(\mathbf{U}_2, \mathbf{U}_1) A_2(\mathbf{U}_2, \mathbf{U}_1) A_3(\mathbf{U}_1, \mathbf{U}_2) \\
& - r' U_1 A_2(\mathbf{0}, \mathbf{U}_1) A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& + r' U_2 A_2(\mathbf{0}, \mathbf{U}_1) A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& - r' U_2 A_2(\mathbf{0}, \mathbf{U}_2) A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& + r' U_1 A_2(\mathbf{0}, \mathbf{U}_2) A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& + r' U_1 A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& + r' U_2 A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
\ldots = & \frac{(A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{U}_2, \mathbf{U}_1))^2}{(A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{U}_2, \mathbf{U}_1))^2} \tag{56}
\end{aligned}$$

which has the same denominator as the original system's term \mathcal{N}/\mathcal{D} (52), and the numerator has all ten terms of \mathcal{N} as well as six new terms that depend on the first derivative r' of the virgin growth rate.

To calculate and compare the third order term that depends once on the invader's strategy, for the two Lotka-Volterra systems we consider here, is done in exactly the same way. For example, in the numerator \mathcal{N} (50) we need to just replace r^* by $(r^* + r'V)$ and each $A_i(\mathbf{0}, \mathbf{U}_j)$ by $A_i(V, \mathbf{U}_j)$, while the denominator \mathcal{D} (49) is unchanged. Hence the term we are looking for is

$$\begin{aligned}
& -\frac{\partial^2 a}{\partial X \partial Y} [\mathbf{V}, \mathbf{U}_1] A_2(\mathbf{U}_2, \mathbf{U}_1) A_3(\mathbf{U}_1, \mathbf{U}_2) \\
& + \frac{\partial^2 a}{\partial X \partial Y} [\mathbf{V}, \mathbf{U}_1] A_2(\mathbf{U}_1, \mathbf{U}_2) A_3(\mathbf{U}_2, \mathbf{U}_1) \\
& - \frac{\partial^2 a}{\partial X \partial Y} [\mathbf{V}, \mathbf{U}_2] A_2(\mathbf{U}_1, \mathbf{U}_2) A_3(\mathbf{U}_2, \mathbf{U}_1) \\
& + \frac{\partial^2 a}{\partial X \partial Y} [\mathbf{V}, \mathbf{U}_2] A_2(\mathbf{U}_2, \mathbf{U}_1) A_3(\mathbf{U}_1, \mathbf{U}_2) \\
& - \frac{1}{2} \frac{\partial^3 a}{\partial X^2 \partial Y} [\mathbf{V}, \mathbf{U}_1, \mathbf{U}_1] A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_1, \mathbf{U}_2) \\
& - \frac{1}{2} \frac{\partial^3 a}{\partial X^2 \partial Y} [\mathbf{V}, \mathbf{U}_1, \mathbf{U}_1] A_2(\mathbf{U}_1, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& - A_2(\mathbf{U}_2, \mathbf{U}_1) A_2(\mathbf{U}_1, \mathbf{U}_2) \\
& - A_2(\mathbf{0}, \mathbf{U}_1) A_2(\mathbf{U}_1, \mathbf{U}_2) \\
& - A_2(\mathbf{0}, \mathbf{U}_2) A_2(\mathbf{U}_2, \mathbf{U}_1) \\
& r' V \frac{A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{U}_2, \mathbf{U}_1)}{(A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{U}_2, \mathbf{U}_1))} + r^* \frac{-\frac{1}{2} \frac{\partial^3 a}{\partial X^2 \partial Y} [\mathbf{V}, \mathbf{U}_2, \mathbf{U}_2] A_2(\mathbf{U}_2, \mathbf{U}_1) A_2(\mathbf{U}_2, \mathbf{U}_1)}{(A_2(\mathbf{U}_1, \mathbf{U}_2) + A_2(\mathbf{U}_2, \mathbf{U}_1))^2}
\end{aligned}$$

where the partial derivatives stem from the fact that $A_2(\mathbf{V}, \mathbf{U}) := \frac{1}{2} \frac{\partial^2 a}{\partial Y^2} [\mathbf{V}, \mathbf{V}] + \frac{\partial^2 a}{\partial X \partial Y} [\mathbf{V}, \mathbf{U}_1] + \frac{1}{2} \frac{\partial^2 a}{\partial X^2} [\mathbf{U}_1, \mathbf{U}_1]$ and similarly for A_3 . Note that the first term is just $(r'V/r^*)(\mathcal{N}_4/\mathcal{D}_2)$.

Similarly, for the fitted system nothing changes in \mathcal{D}' (53), and in the numerator \mathcal{N}' (54) we must replace each instance of $A_i(\mathbf{0}, \mathbf{U}_j)$ with $A_i(V, \mathbf{U}_j)$, of r^{*2} with $r^*(r^* + r'V)$ and of $r^*r'U_i$ with $(r^* + r'V)r'U_i$, to find that the term we are looking

for is

$$\begin{aligned}
 & -r^* \frac{\partial^2 a}{\partial X \partial Y} [V, U_1] A_2(U_2, U_1) A_3(U_1, U_2) \\
 & + r^* \frac{\partial^2 a}{\partial X \partial Y} [V, U_1] A_2(U_1, U_2) A_3(U_2, U_1) \\
 & - r^* \frac{\partial^2 a}{\partial X \partial Y} [V, U_2] A_2(U_1, U_2) A_3(U_2, U_1) \\
 & + r^* \frac{\partial^2 a}{\partial X \partial Y} [V, U_2] A_2(U_2, U_1) A_3(U_1, U_2) \\
 & - \frac{1}{2} r^* \frac{\partial^3 a}{\partial X^2 \partial Y} [V, U_1, U_1] A_2(U_1, U_2) A_2(U_1, U_2) \\
 & - \frac{1}{2} r^* \frac{\partial^3 a}{\partial X^2 \partial Y} [V, U_1, U_1] A_2(U_1, U_2) A_2(U_2, U_1) \\
 & - \frac{1}{2} r^* \frac{\partial^3 a}{\partial X^2 \partial Y} [V, U_2, U_2] A_2(U_1, U_2) A_2(U_2, U_1) \\
 & - \frac{1}{2} r^* \frac{\partial^3 a}{\partial X^2 \partial Y} [V, U_2, U_2] A_2(U_2, U_1) A_2(U_2, U_1) \\
 & - r' U_1 \frac{\partial^2 a}{\partial X \partial Y} [V, U_1] A_2(U_1, U_2) A_2(U_2, U_1) \\
 & + r' U_2 \frac{\partial^2 a}{\partial X \partial Y} [V, U_1] A_2(U_1, U_2) A_2(U_2, U_1) \\
 & - r' U_2 \frac{\partial^2 a}{\partial X \partial Y} [V, U_2] A_2(U_1, U_2) A_2(U_2, U_1) \\
 & + r' U_1 \frac{\partial^2 a}{\partial X \partial Y} [V, U_2] A_2(U_1, U_2) A_2(U_2, U_1) \\
 & \frac{A_2(U_2, U_1) A_2(U_1, U_2)}{A_2(U_1, U_2) + A_2(U_2, U_1)} - \frac{A_2(\mathbf{0}, U_1) A_2(U_1, U_2)}{A_2(U_1, U_2) + A_2(U_2, U_1)} \\
 & - \frac{A_2(\mathbf{0}, U_2) A_2(U_2, U_1)}{A_2(U_1, U_2) + A_2(U_2, U_1)} + \frac{(r' V - A_2(U_1, U_2) - A_2(U_2, U_1))}{(A_2(U_1, U_2) + A_2(U_2, U_1))^2}
 \end{aligned}$$

We see that this term differs between the two Lotka-Volterra systems with the same one-resident fitness, answering the question posed at the end of Section 3.

B The relationship between $s_{\mathbb{X}}(Y)$ and R_0 near singularities, revisited

A first step towards a third order expansion of the multi-resident fitness function near a singular strategy for physiologically structured population models is to have this fitness function in terms of model ingredients. In Chapter I there is a formula (I.47) in terms of lifetime reproductive output R_0 and expected age at giving birth T_f , but it is only correct up to quadratic terms in ε . Therefore the fitness function is calculated here up to and including terms of order $O(\varepsilon^3)$.

From Equation (I.102),

$$s_{\mathbb{X}}(X^* + V) = O(\varepsilon^2) \quad (57)$$

we know that the invasion fitness near the singularity X^* has no constant nor linear terms in ε . We defined a function (I.103)

$$\phi(\rho, V) := \log \left(\lambda_d \left(\int_0^\infty e^{-\rho a} \Lambda(X^* + V, I_{\mathbb{X}}, da) \right) \right) \quad (58)$$

which we may expand here once more as a function of ρ , and thus solve the Euler-

Lotka equation $\phi(\rho, \mathbf{V}) = 0$ for $\mathbf{V} = O(\varepsilon)$ as

$$\begin{aligned} 0 &= \phi(s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V}), \mathbf{V}) \\ &= \phi(0, \mathbf{V}) + \frac{\partial \phi(0, \mathbf{V})}{\partial \rho} s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V}) + O(s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V})^2) \\ &= \log R_0(\mathbf{X}^* + \mathbf{V}, \mathbf{I}_{\mathbb{X}}) + \frac{\partial \phi(0, \mathbf{V})}{\partial \rho} s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V}) + O(\varepsilon^4) \end{aligned} \quad (59)$$

The remaining expansion coefficient is

$$\frac{\partial \phi(0, \mathbf{V})}{\partial \rho} = \frac{1}{\lambda_d(\int_0^\infty \Lambda(\mathbf{X}^* + \mathbf{V}, \mathbf{I}_{\mathbb{X}}, da))} \left. \frac{\partial \lambda_d(\int_0^\infty e^{-\rho a} \Lambda(\mathbf{X}^* + \mathbf{V}, \mathbf{I}_{\mathbb{X}}, da))}{\partial \rho} \right|_{\rho=0} \quad (60)$$

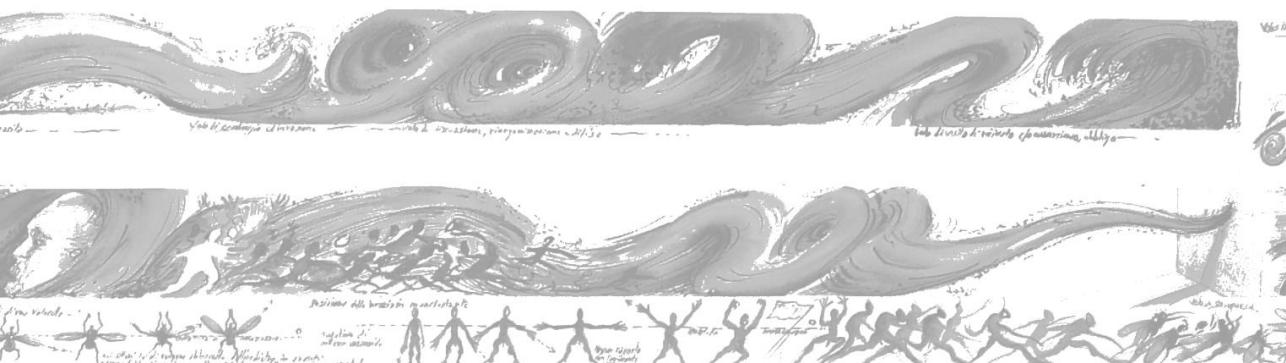
As Equations (57) and (59) together show that $\log R_0 = O(s_{\mathbb{X}}(\mathbf{X}^* + \mathbf{V})) = O(\varepsilon^2)$, we only need to know this coefficient up to first order terms. We can ignore the first factor that makes up $\partial \phi(0, \mathbf{V})/\partial \rho$ since $R_0(\mathbf{X}^* + \mathbf{V}, \mathbf{I}_{\mathbb{X}}) = 1 + O(\varepsilon^2)$ (because $\exp(x) = 1 + x + O(x^2)$). The last factor is defined as $-T_f(\mathbf{X}^* + \mathbf{V}, \mathbf{I}_{\mathbb{X}})$ (I.100), i.e., minus the average age at giving birth of the invader $\mathbf{X}^* + \mathbf{V}$ in the community \mathbb{X} .

Putting everything together, we see that the N -resident fitness for physiologically structured population models can be written as

$$s_{\mathbb{X}}(\mathbf{Y}) = \frac{\log R_0(\mathbf{X}^* + \mathbf{V}, \mathbf{I}_{\mathbb{X}})}{-\frac{\partial \phi(0, \mathbf{V})}{\partial \rho}} + O(\varepsilon^4) = \frac{\log R_0(\mathbf{Y}, \mathbf{I}_{\mathbb{X}})}{T_f(\mathbf{Y}, \mathbf{I}_{\mathbb{X}})} + O(\varepsilon^4) \quad (61)$$

This formula is the analog of Equation (17) with $\log(R_0)/T_f$ in the role of g , and of Equation (I.47) but correct up to one more order of ε .

When generalizing the calculations of Section 4 from resource competition to physiologically structured population models, the main complication is that the matrix G , which is the analog of the resource functions (h_1, h_2, \dots, h_r) , depends itself on the environment \mathbf{I} : compare $I_s = \sum_i h_s(\mathbf{X}_i) n_i$ to $\mathbf{I} = \sum_i G(\mathbf{X}_i, \mathbf{I}) \mathbf{b}_i$. This creates some technical difficulties (e.g., showing that generically Δ_n^1 is zero (24) takes far less effort than showing the same for its analog Δ_b^1 (I.65)), and a comparison of the above result (61) to the second order approximation (I.75) tells us that some extra terms come into play, but essentially no new phenomena occur (Michel Durinx, unpublished; but see as well the last lines of Section 4, and compare Equations (I.69) and (26)).



THREE

Sexual dimorphism or evolutionary branching?

Abstract

Disruptive selection due to ecological causes can lead to different types of phenotypic polymorphism. For a broad range of ecological scenarios, we investigate the odds that disruptive selection leads to sexual dimorphism versus to polymorphisms that appear after evolutionary branching. These are genetic polymorphisms, such as sympatric species or Mendelian genes with strong dominance-recessivity. When models that allow for sexual dimorphism are compared to constrained models with equal phenotypes in males and females, a sexual dimorphism is expected to evolve instead of any evolutionary branching in the constrained model, whereas one noninvadable attracting singularity is replaced by another. This is an important general result on the odds of different types of ecological polymorphism as it implies that the possibility for sympatric speciation caused by ecological selection pressures can be removed by the evolution of ecological differences between the sexes. Evolutionary branching becomes more likely if (A) there is a strong constraint on sex differentiation, (B) secondary branching events occur after sexual dimorphism has already evolved, or (C) assortative mate choice occurs before trait divergence starts. The possibility of sexual selection driving sympatric speciation is not affected by our conclusions.

1 Introduction

Sexual dimorphism is widespread in the animal kingdom. Sexual selection is generally seen as the major driving force behind these differences (Shine, 1989), but ecological selection can also play a role (Temeles *et al.*, 2000; Temeles & Kress, 2003). In theoretical studies, there is a similar focus on sexual selection. Many studies (e.g., Lande, 1980; Iwasa *et al.*, 1991; Pomiankowski *et al.*, 1991) have examined how sexual and natural selection both contribute to the evolution of sexual dimorphism, whereas Slatkin (1984) focussed on its ecological causes. One of the selection scenarios he considered was one of character displacement, in which competition over a limiting resource causes disruptive selection and phenotypic differences between

Adapted with minor changes from: Tom J.M. Van Dooren, Michel Durinx & Inez Demon 2004. Sexual dimorphism or evolutionary branching? *Evolutionary Ecology Research* 6 857–871.
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the sexes. Thus, Slatkin (1984) had already drawn parallels between sympatric speciation models and models for sexual dimorphism. The ecological conditions that lead to dimorphic sexes or diverging species were identical in his models, but he never compared the odds for either outcome directly.

Recently, the evolution of sympatric speciation due to ecological causes is again receiving a lot of attention (Dieckmann & Doebeli, 1999; Matessi *et al.*, 2001; van Doorn & Weissing, 2001; Doebeli & Dieckmann, 2003), with the same resource competition scenario playing a prominent role in several studies. There is a growing consensus among theoreticians (Dieckmann & Doebeli, 1999; van Doorn & Weissing, 2001; Gavrilets & Waxman, 2002) that sympatric speciation often requires evolutionary branching (Metz *et al.*, 1996; Geritz *et al.*, 1998). In that evolutionary scenario, an ecological generalist with intermediate trait values usually evolves first, but once it has become common in the population, competition intensifies. It then pays to specialize again and the generalist gets replaced by a genetic and phenotypic polymorphism of more specialized strategies. In ecological selection models, selection occurs on the use of available resources. With sexual selection, it is the distribution of potential mates that is the resource that individuals can specialize on. Evolutionary branching occurs at the phenotypic value of the generalist strategy that is replaced by co-existing specialists. It is defined as convergence of the evolutionary process to a point in trait space where directional selection disappears and disruptive selection dominates (Metz *et al.*, 1996; Geritz *et al.*, 1998). At that point in trait space, disruptive selection drives the emergence of a polymorphism of very different major genes (Kisdi & Geritz, 1999a; Van Dooren, 1999) or an increase in the genetic variance when there are only polygenes with small effects (Bulmer, 1980). That increase in the amount of standing genetic variation can trigger the evolution of assortative mate choice (Dieckmann & Doebeli, 1999), with the origin of two new species as a consequence. There is a snag, however, when major genes appear. Many traits and properties of the genetic system start to evolve differently in the presence of major genes (Dickinson & Antonovics, 1973), and not all of them lead to sympatric species. For instance, Balkau & Feldman (1973), Meszéna *et al.* (1997), and Kisdi & Geritz (1999b) have suggested that evolutionary branching can trigger the evolution of reduced migration, inducing parapatric or allopatric speciation. Van Dooren (1999) has shown that major genes that appear after evolutionary branching can evolve pronounced dominance interactions, which eliminates the selective advantage of assortative mate choice and speciation. If completely assortative mate choice is already present before evolutionary branching, two species must emerge instantly (van Doorn & Weissing, 2001), but there is a possibility that dominance evolution might still occur in a population with incomplete assortative mating.

Considering the existence of alternative evolutionary outcomes in the same ecological context, it becomes important to investigate the odds among different evolutionary outcomes. The odds of evolutionary branching, relative to those of phenotypic polymorphisms where a genetic or environmental switch provokes alternative phenotypes from a single set of genes, are also important. In this paper, we investigate the odds for the evolution of sexual dimorphism, modelled as a reaction norm with two alternative states, versus polymorphisms that require evolutionary branching. We generalize the resource competition model of Slatkin (1984) to a

broad range of ecological scenarios. Then we focus on a specific question: Starting from a constrained model in which phenotypic differentiation between the sexes is not allowed, will evolutionary branching still occur at the same trait values as before, once dimorphic sexes are allowed to evolve? Bolnick & Doebeli (2003) consider a specific model within our modelling framework and conclude that sexual dimorphism is more likely to evolve than sympatric species. The distinction addressed here between phenotypic polymorphism requiring evolutionary branching and sexual dimorphism is more fundamental. Moreover, the results presented are analytical and do not depend on model details, such as the independent diallele loci sometimes assumed in sympatric speciation models (Dieckmann & Doebeli, 1999; Bolnick & Doebeli, 2003), or specific ecological functions used (Slatkin, 1984; Bolnick & Doebeli, 2003).

2 Invasion fitness

We assume that sex-specific phenotypic traits of females and males are determined by a single set of autosomal genes with potentially pleiotropic effects or sex-specific expression. One can therefore consider these genes to specify a reaction norm with two alternative states (i.e., for the phenotypes expressed in each sex). An unspecified environmental or genetic switch controls sex determination, independent of the genes for sex-specific phenotypes. We assume there is an even sex ratio at birth, because it is the evolutionarily stable strategy (ESS) sex ratio of the models we consider.

The calculations presented use the invasion fitness of rare mutants (Fisher, 1930; Metz *et al.*, 1992; Rand *et al.*, 1994; Diekmann *et al.*, 2003), since that fitness measure is used to characterize evolutionary branching (Metz *et al.*, 1996; Geritz *et al.*, 1998). Invasion fitness is a property of a strategy in a given ecological environment. The effects of such an environment on demographic parameters are summarized in a vector E , which has to be determined from a population dynamical model for all common strategies in the population. Usually, populations with a single common strategy are considered to determine the existence and location of evolutionary branching points.

We will look at environments $E(z)$, set by a single common resident strategy with trait vector z , assume that $E(z)$ is constant over time (i.e., that the population dynamics of common phenotypes is at equilibrium) and that the population is not spatially structured in a manner that creates local mating pools. The population can still be age-, stage- or otherwise structured. We consider two-sex models where the resident trait vector is $z = (z_f, z_m)$, with a continuous phenotypic trait in females and in males. The trait vector of the invading mutant is written as z' . Invasion fitness, defined as the per capita number of mutant individuals contributed to the next generation by the mutant strategy z' in the equilibrium environment set by the resident strategy z , then has the form (Shaw & Mohler, 1953; Charnov, 1982; Diekmann *et al.*, 2003)

$$\lambda(z', z) = \frac{1}{2} \left(\frac{R^{\text{female}}(z'_f, E(z))}{R^{\text{female}}(z_f, E(z))} + \frac{R^{\text{male}}(z'_m, E(z))}{R^{\text{male}}(z_m, E(z))} \right) \quad (1)$$

where functions $R^i(z, E)$ denote the number of offspring contributed to the next generation, by a phenotypic strategy z taking the reproductive role of females ($i = \text{female}$) or males ($i = \text{male}$) in environment E . When phenotypic differentiation between males and females is ignored, the trait vector is equivalent to a scalar trait and the invasion fitness becomes

$$\lambda(z', z) = \frac{R(z', E(z))}{R(z, E(z))} \quad (2)$$

There are two obvious cases where an invasion fitness as in Equation (1) simplifies and becomes more similar to the form in Equation (2). One is when there are no intrinsic differences in reproductive roles between the sexes, numbers of offspring only depend on phenotypic values. Functions R^i are then identical in both sexes, such that invasion fitness simplifies to

$$\lambda(z', z) = \frac{1}{2} \left(\frac{R(z'_f, E(z))}{R(z_f, E(z))} + \frac{R(z'_m, E(z))}{R(z_m, E(z))} \right) \quad (3)$$

When the phenotypes of females and males are constrained to be equal, we obtain Equation (2). The complete reproductive symmetry of Equation (3) is unrealistic for many organisms. However, if the traits in the mating process and focus on the number of times or the probability that offspring enter the mating pool. In that case, we also obtain an invasion fitness with the symmetry of Equation (3).

3 Evolutionary dynamics

Assuming large population sizes and small mutation rates, ecological and evolutionary timescales become separated (Roughgarden, 1979). The common strategies in the population then determine the environments E in which novel mutants will invade or not, and after each successful invasion the resident environment will have reached equilibrium before a new successful mutant rises in frequency. With a single common strategy and a unique equilibrium of the population dynamics, we can write environments as functions of the strategy present: $E(z)$. We can then use the invasion fitness functions (1)–(3) to study the evolutionary dynamics of sex-specific phenotypes.

Additionally, assuming small mutational effects, a multivariate equation similar to the breeder's equation can be derived, which describes gradual phenotypic change over evolutionary time if fitness depends on the state of the population (Dieckmann & Law, 1996, and Chapter I of this thesis). This equation (4), known as the canonical equation, describes the rate of change of the resident phenotype in a population,

$$\frac{\partial z}{\partial t} = G \beta(z) \quad (4)$$

where G is the mutational variance-covariance matrix times a scaling factor for the rate of appearance of mutants (which depend on z as well, but keeping that implicit does not affect our conclusions) and β is the selection gradient (given by Equation (5) below). In contrast to the approach of Iwasa *et al.* (1991) and Abrams *et al.*

(1993), the matrix G does not incorporate any standing genetic variation among the residents, because the separation of evolutionary and ecological timescales has eliminated that.

The selection gradient (5) is the vector of partial derivatives of invasion fitness with respect to the mutant traits, evaluated at equal mutant and resident traits. We can write the fitness gradient vector as

$$\beta(z) = \nabla' \lambda(z', z) = \begin{pmatrix} \frac{\partial}{\partial z'_f} \lambda(z', z) \Big|_{z'=z} \\ \frac{\partial}{\partial z'_m} \lambda(z', z) \Big|_{z'=z} \end{pmatrix} \quad (5)$$

where the notation ∇' stresses that we (only) take partial derivatives with respect to the mutant traits. When the fitness gradient (5) is zero, directional selection is absent (4), and the trait vector in question is a potential endpoint of evolution, a candidate ESS (Metz *et al.*, 1996) called a singular or critical point. For a two-sex model with invasion fitness as in Equation (3), if a singular strategy z^* has equal phenotypes in females and males we denote it by $z^*_{\equiv} = (z^*, z^*)$; if there is a sexual dimorphism we denote the critical strategy by $z^*_{\neq} = (z^*_f, z^*_m)$, where $z^*_m \neq z^*_f$. Whether evolution will really halt at such a point depends on the pattern of invasion fitness over trait space, and on the mutational variances and covariances that can make paths of evolution deviate from the direction in which the fitness gradient points (Leimar, 2001).

4 Sexual dimorphism or evolutionary branching?

Symmetric two-sex models (cf. Eq. (3)) reduce to models without differentiated sexes when phenotypes of females and males are equal. This property makes it easy to turn many models that do not allow for sexual dimorphism into variants that do. In a model without separate sexes, individuals can be equally partitioned in two classes that may be interpreted as males and females, without introducing any differences in total equilibrium densities and so forth. Such partitioning also creates specifications of the environment E , to be used in a simple two-sex model.

In this section, we use reproductive success functions R as if they have three ordered arguments: the mutant trait value z' , and the trait values of resident females z_f and males z_m . Specifying partial derivatives of R can be done by writing indicators of the three arguments. For example, the second-order partial derivative for the mutant trait, evaluated at the point where all three phenotypes are equal to z^* , can be written as $R_{11}(z^*, z^*, z^*)$ as it requires taking a partial derivative for the first argument twice.

Singular points z^* of models with differentiated sexes (cf. Eq. (3)) were defined as points where the selection gradient (5) is zero. In terms of partial derivatives of the function R , this translates into $R_1(z^*, z^*, z^*) = 0$ and $R_1(z^*, z^*_f, z^*_m) = 0$. For the constrained model with undifferentiated females and males, a singular point z^* satisfies $R_1(z^*, z^*, z^*) = 0$. This immediately shows that singular points of the constrained model are equivalent to singular points $z^*_{\equiv} = (z^*, z^*)$ in the unconstrained

model which lie on the diagonal in the trait space where phenotypes z_f and z_m are equal (Fig. 1).

With a supply of the appropriate mutational variation, evolutionary branching occurs at a point z^* that attracts evolutionary orbits from nearby, which at the same time is a local fitness minimum in at least one direction (Metz *et al.*, 1996; Geritz *et al.*, 1998; Leimar, 2001, to appear). The main question we want to address here is whether rewriting a constrained model that does not allow for sexual dimorphism, such that it allows phenotypic differences between the sexes, maintains the evolutionary branching of the original model or not. Hence singular points z_* with equal phenotypes in females and males are of special interest.

In the constrained model, those z^* that are evolutionary branching points are invadable by similar strategies (Metz *et al.*, 1996; Geritz *et al.*, 1998). Invadability requires that the curvature h of invasion fitness is positive at z^* , with h given by

$$h = \frac{R_{11}(z^*, z^*, z^*)}{R(z^*, z^*, z^*)} \quad (6)$$

so that invadability corresponds to the condition $R_{11}(z^*, z^*, z^*) > 0$.

For the unconstrained model, a two-by-two matrix called the fitness Hessian $H(z^*)$ (Leimar, 2001, to appear) specifies the curvature of the invasion fitness at z^* and determines whether a singular point can be invaded by mutants. This Hessian consists of second-order partial derivatives

$$H_{ij}(z^*) = \frac{\partial^2}{\partial z'_i \partial z'_j} \lambda(z', z)|_{z'=z=z^*} \quad (7)$$

where the indices i and j take on the values female or male (f, m). If the Hessian has two eigenvalues with negative real parts, then the singular point is a local fitness maximum and uninvadable, regardless of the mutational variance-covariance matrix (Leimar, 2001, to appear). Otherwise, there is at least one direction where selection is neutral or disruptive. When disruptive selection is present, the strategy z^* is invadable. If the Hessian has only positive eigenvalues, invasion fitness has a local minimum at z^* , invadable by any phenotypically similar mutant strategy. At z_* the hessian is a diagonal matrix with two eigenvalues equal to $h/2$ (6). The invasion fitness therefore has a local minimum at z_* if the singular point of the constrained model was an evolutionary branching point.

The matrix $J(z^*)$ (8) (Leimar, 2001, to appear), together with the mutational variance-covariance matrix, determines whether a singular point is evolutionarily attracting. This fitness Jacobian is used to decide whether mutants can invade that bring the population closer to z^* if starting nearby. $J(z^*)$ is the derivative of the selection gradient for the resident traits, evaluated at the point z^* . One finds that the Jacobian $J(z^*)$ is the sum of two matrices,

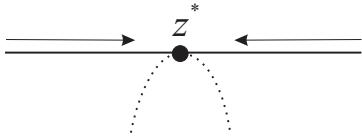
$$J(z^*) = H(z^*) + Q(z^*) \quad (8)$$

namely the Hessian from Equation 7 and a square matrix $Q(z^*)$ consisting of elements

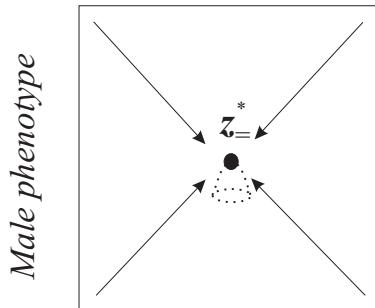
$$Q_{ij}(z^*) = \frac{\partial^2}{\partial z'_i \partial z_j} \lambda(z', z)|_{z'=z=z^*} \quad (9)$$

One Phenotypic Trait

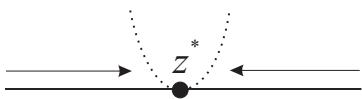
*Convergence Stable
Local Fitness Maximum*

*Sex - Specific Phenotypes*

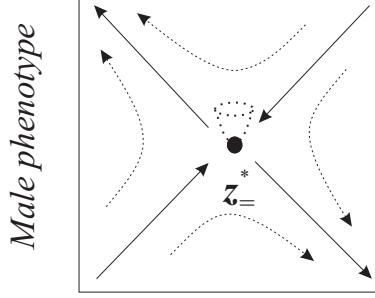
*Convergence Stable
Local Fitness Maximum*



*Convergence Stable
Local Fitness Minimum*



*Evolutionary Saddle Point
Local Fitness Minimum*



Female phenotype

Figure 1: Separate phenotypes for each sex. Diagram showing changes in convergence stability and invadability that are expected when sex-specific phenotypes are introduced in an evolutionary model with a singular point z^* . A strategy $z_* = (z^*, z^*)$ with equal phenotypes in the two sexes appears as a singular point. Non-invadability at z^* or z_* corresponds to a local fitness maximum at the singular point (drawn as an attached parabola or dome respectively), invadability to a local fitness minimum. If z^* was convergence stable and non-invadable in the original model, then z_* has these properties too. For those z^* that were evolutionary branching points, z_* is an invadable strategy that lacks convergence stability, with the typical pattern of evolutionary trajectories as indicated by the dotted arrows.

When all eigenvalues of the Jacobian have negative real parts, then the singular point is attracting from all directions and for any mutational covariance matrix. This property is called strong convergence stability (Leimar, 2001, to appear) and extends the convergence stability (Eshel & Motro, 1981; Eshel, 1983; Christiansen, 1991) used in single-trait models to multiple traits. Here we will call both convergence stability. When all eigenvalues of J have positive real parts, then z^* is repelling for any mutational covariance matrix. In the case of indefinite J , different choices of mutational covariance can affect convergence to z^* .

In the constrained model, a local stability analysis shows that convergence stability holds at z^* when the scalar $j = h + q_2 + q_3$ is negative, with h defined by Equation (6) and q_2, q_3 by Equation (10):

$$q_2 = \frac{R_{12}(z^*, z^*, z^*)}{R(z^*, z^*, z^*)} \quad q_3 = \frac{R_{13}(z^*, z^*, z^*)}{R(z^*, z^*, z^*)} \quad (10)$$

Parameters q_2 and q_3 will be equal when a small change in the phenotype of resident females or males affects the environment E equally. The combination of a negative Jacobian j and a negative Hessian h is called a continuously stable strategy (CSS) (Eshel & Motro, 1981; Eshel, 1983). Figure 1 also depicts the pattern of invasion fitness in the neighbourhood of that type of convergence stable strategy.

The Jacobian of the unconstrained model at a point z_-^* has the form

$$J(z_-^*) = \frac{1}{2} \begin{pmatrix} h & 0 \\ 0 & h \end{pmatrix} + \frac{1}{2} \begin{pmatrix} q_2 & q_3 \\ q_2 & q_3 \end{pmatrix} \quad (11)$$

This matrix has eigenvalues $h/2$ and $j/2$. Convergence to z_-^* depends on the convergence stability parameter j of the constrained model in the direction where male and female ecological phenotypes are kept equal (Fig. 1). Convergence in another direction depends on invadability parameter h , such that a branching point implies a repelling direction in the two-sex model (Fig. 1). Summarizing, convergence stability of z^* is inherited by z_-^* if z^* is non-invadable in the unconstrained model, but is lost when the constrained model has an evolutionary branching point. Figure 1 illustrates that the fitness gradient then points towards the two-sex candidate ESS z_-^* in one direction and away from it in another. Evolutionary branching becomes therefore unlikely when phenotypic differentiation between the sexes is allowed: evolutionary trait substitution sequences veer away from z_-^* into an area where females have either larger or smaller phenotypic values than males. Using the Ordinary Differential Equation (4) to describe the evolutionary dynamics around z_-^* , this strategy turns out to be a saddle point. This point is not approached even though fitness is a local minimum exactly at z_-^* . One can calculate from the eigenvalues of the product $GJ(z_-^*)$ that z_-^* only attracts when the genetic correlation between the female and male trait values equals -1 or $+1$. That situation, in fact, corresponds to constrained models not allowing any change in the amount of sexual dimorphism yet allowing different mutational variances in females and males.

Our results show the generality of the pattern observed by Bolnick & Doebeli (2003), where the evolution of sexual dimorphism greatly hampers evolutionary branching and potentially leads to sympatric speciation. For cases of sex-linked inheritance with dosage compensation, Lande (1980) has shown that the selection

gradient is not affected by the genetic mechanism of sex differentiation as only the variance-covariance matrix becomes rescaled relative to genetics with autosomal inheritance. Our results therefore hold for sex-linked inheritance with dosage compensation too.

The Appendix generalizes the results of this section to multivariate phenotypes for each sex.

5 Examples

We will show by means of two examples that evolutionary branching remains a possibility after the evolution of sexual dimorphism. The first example is a version of a time-honoured model of resource competition (Roughgarden, 1979; Slatkin, 1984; Metz *et al.*, 1996). A peculiarity of the model by Bolnick & Doebeli (2003) is that it never has an evolutionarily stable sexual dimorphism. We modified their resource competition model to demonstrate that it does allow for ESS sexual dimorphisms after a minor change. We also provide an example of asymmetric competition, showing the intuitive pattern that the number of coexisting phenotypes each time increases or decreases by one when an ecological parameter is varied in small steps.

5.1 Symmetric competition

Figure 2 contains results from a resource competition model without competitive asymmetries. Phenotypic values are limited to the interval $(1, 1)$. The number of offspring is controlled by females. Each female has r offspring of which half are males. Offspring viability is a function of their phenotype z , of the vector N of population densities of offspring of different types, and of the vector y of all corresponding phenotypes in the population,

$$R(z, (N, y)) := \left(1 + \frac{r-1}{k(z)} \sum_i \alpha(z, y_i) N_i \right)^{-1} \quad (12)$$

with a competition intensity function and carrying capacity

$$\alpha(z, y) := \exp(-(z - y)^2 / 2\sigma_\alpha^2) \quad k(z) := 1 - z^2 \quad (13)$$

(as in Metz *et al.*, 1996) that can be interpreted as the distribution of a limiting resource. Equilibrium densities and invasion fitnesses are calculated from Equations (3), (12) and (13). Note that Bolnick & Doebeli (2003) use a Gaussian for the function k .

In the example of Fig. 2, we fixed parameter r at a value of 3. Figure 2A shows the pattern of the invasion fitness gradient (5) for three values of the parameter σ_α controlling the range over which phenotypes compete. The convergence stable singular points are either a single monomorphic one, or two sexually dimorphic singular points. However, a dimorphic convergence stable trait vector can still be invadable (Fig. 2B). It can be seen that the singular point is a local fitness minimum

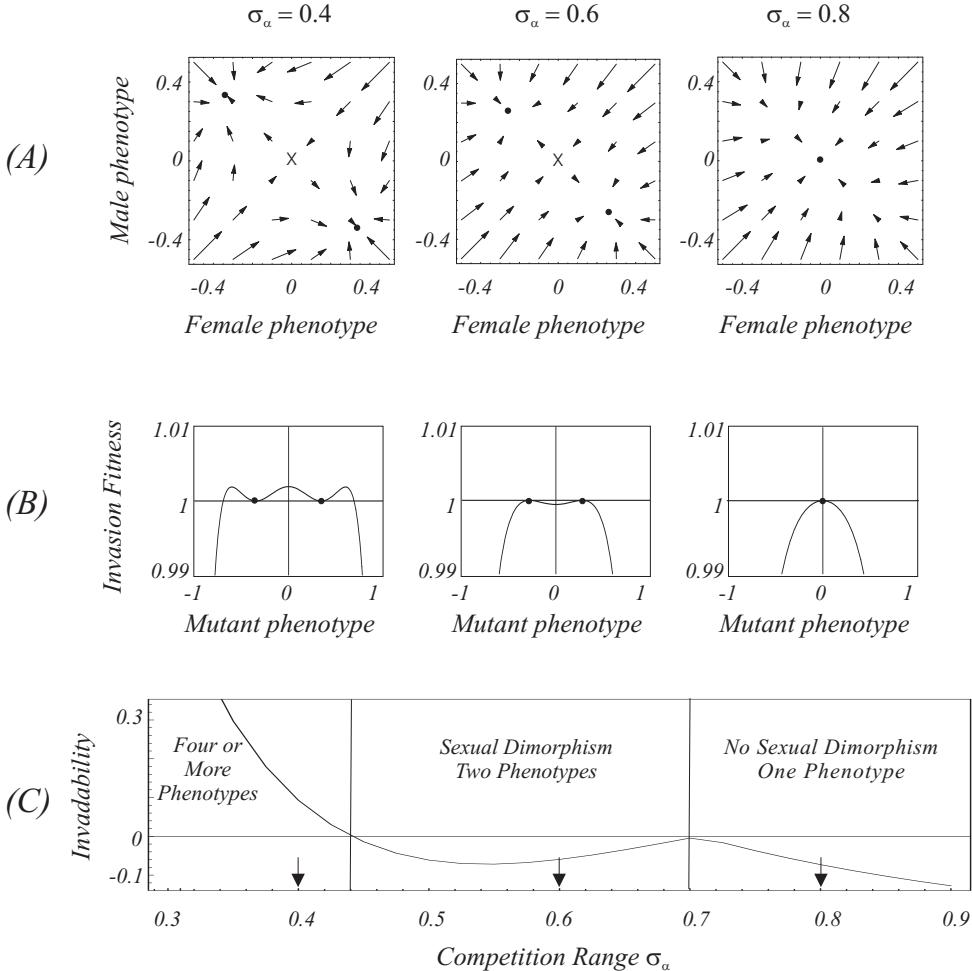


Figure 2: Model example. Results from a resource competition model with symmetric competition. (A) Pattern of the invasion fitness gradient for three values of the parameter σ_α , which controls the range of competition of the phenotypes. These three values are also indicated with arrows in Panel (C). The convergence stable singular points are either a monomorphic convergence stable strategy, or two dimorphic singular points. Convergence stable singular points are indicated by a dot, evolutionary saddles by a cross. (B) Invasion fitness functions at the singular points seen in Panel (A). Because of the symmetry in the functions used to model competition, these are equal for mutants with a change in either the female or the male trait. Resident trait values at convergence stable singular points are indicated by dots. (C) Values of the Hessian parameter determining invadability, calculated at the convergence stable singular points (with $z_f \leq z_m$). When this curvature measure is positive, the singular points are local fitness minima. When increasing the range of competition between phenotypes from the minimum, a polymorphism of four morphs (or higher-order polymorphisms for the smallest values), a dimorphism and a single phenotype are the evolutionary outcomes.

for the ecological parameter value $\sigma_\alpha = 0.4$, and secondary evolutionary branching is expected in both sexes simultaneously. This joint secondary branching of the sexes is a consequence of the symmetry in competition. Figure 2C shows the eigenvalue of the Hessian at convergence stable critical points, which determines invadability.

5.2 Asymmetric competition

We present a simple example of a model with asymmetric competition, similar to Kisdi (1999). The viabilities are calculated from Equation (12) but we use

$$\alpha(z, y) := 1 - \frac{1}{1 + e^{-\nu(z-y)}} \quad k(z) := \frac{1}{\sqrt{2\pi\sigma_k^2}} e^{-\frac{z^2}{2\sigma_k^2}} \quad (14)$$

The trait space ranges over the positive real numbers in this example. The competition intensity function α assumes that individuals have a competitive advantage when they are larger. Parameter ν controls the competition intensity between different phenotypes. Parameter σ_k controls the width of the resource distribution function k . One can calculate that the constrained version of this model has an attracting singular point at $z^* = \nu\sigma_k^2/2$. The Hessian h is positive when $\sigma_k > 1$ and then z^* is invadable; otherwise it is not.

Figure 3 shows results from this model, with $r = 3$ and $\nu = 2$. When σ_k is smaller than one, the singular point z_-^* for the two-sex model attracts and is non-invadable. When σ_k is larger than one, this singular point with equal phenotypes in males and females becomes an evolutionary saddle and two new singular points appear that have different phenotypes for males and females. These singular points are noninvadable for a small range of σ_k . In Fig. 3B, we see that at a dimorphic singular point for larger values of σ_k , fitness can be a local minimum for the phenotype of one sex and a maximum for the other. In such cases, a secondary polymorphism in only one sex originates through evolutionary branching. Such evolutionary branching can potentially lead to speciation with species-specific phenotypes in a single sex.

6 Discussion

Our results show that constraints play an important role in ecological diversification via evolutionary branching. When two classes of individuals can become phenotypically different and reduce competition in that manner, it becomes much less likely that the evolutionary dynamics passes through an evolutionary branching point. We derived this conclusion from a study of the evolution of sexual dimorphism, but the same phenomenon might also be relevant when there are other types of classes of individuals with facultatively different phenotypes. Evolutionary branching appears to thrive on constraints that keep these classes phenotypically equal, so that the only route towards phenotypic polymorphism and reduced competition is via a genetic polymorphism.

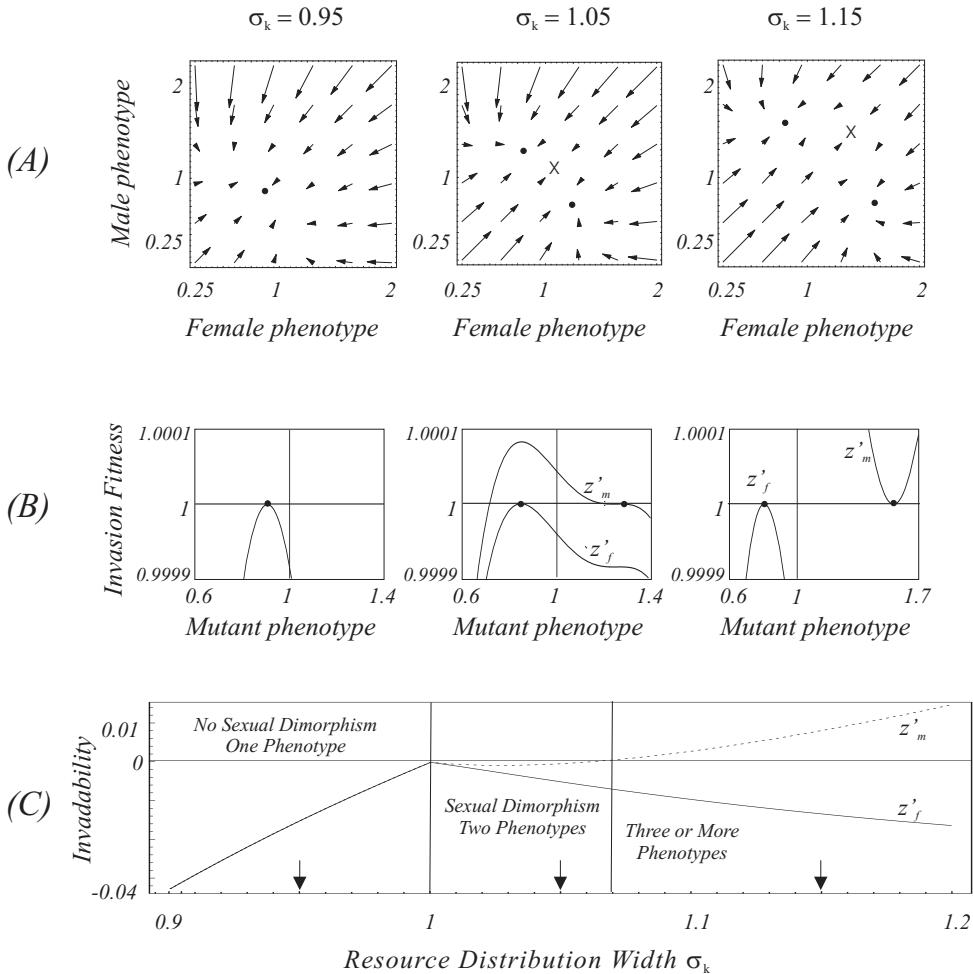


Figure 3: Model example. Results from a resource competition model with asymmetric competition. (A) Pattern of the invasion fitness gradient for three values of a parameter σ_k that controls the width of resource distribution function k . (B) Invasion fitness functions at the singular points shown in Panel (A), calculated at those where $z_f \leq z_m$. Resident trait values at convergence stable singular points are indicated by dots. Mutants with changes in the female (indicated by z'_f) or in the male trait (indicated by z'_m) have different invasion fitness functions. (C) Values of the double partial derivatives of the Hessian that determine invadability, calculated at convergence stable singular points. For dimorphic singular points, we chose the one with the largest male phenotype. With increasing σ_k , a single phenotype, a dimorphism, and three morphs or a higher-order polymorphism are expected.

With autosomal genes for alternative sex phenotypes, some sort of gene regulation must occur to provoke the right phenotype in each situation. Severe genetic constraints on this plasticity can make the evolution of sexual dimorphism impossible, but the evolution of regulatory modifier sequences does not seem to be very restricted (Badyaev, 2002). Merilä *et al.* (1998) show that genetic correlations between undifferentiated sex phenotypes can sometimes be equal to +1. However, not all evidence for strong genetic correlations between sex phenotypes excludes the possibility of sex differentiation. Some studies have reported strong positive genetic correlations between already dimorphic sex phenotypes (Rogers & Mukherjee, 1992). In that case, one can only conclude that the scope of further sex differentiation is limited, once sexual dimorphism is present. We also must keep in mind that, strictly speaking, our model requires a strong constraint on the mutational variance to prevent the evolution of sexual dimorphism. Little is known about such constraints (Mackay, 2001), and the main study in this respect did not find it (Mackay *et al.*, 1992). Bolnick & Doebeli (2003) simulate the effects of a genetic constraint by modifying the ratio of loci with sex-specific expression to loci without, and derive the same conclusion concerning constraints and sympatric speciation as we do with respect to evolutionary branching: sexual dimorphism evolves unless a genetic constraint prevents it. Additionally, they show that stochastic effects from finite population sizes affect the probability of sexual dimorphism versus branching, indicating that the adaptive dynamics approximation (Dieckmann & Law, 1996) we used to investigate the evolutionary dynamics has its limitations. Bolnick & Doebeli (2003) also note in their simulations that a partial constraint limiting sex differentiation, as used by Rogers & Mukherjee (1992), can lead to the loss of sexual dimorphism followed by sympatric speciation. This could depend on the amount of standing genetic variation in the simulated populations and on the sexual selection it creates, which allows for the evolution of assortative mate choice even when evolutionary branching for ecological reasons has not occurred (Lande, 1981).

Our examples show that evolutionary branching remains possible after the evolution of dimorphic sexes. Intuitively, this must occur less often than evolving sexual dimorphism. Competition parameters must be more extreme to obtain it, if the character displacement between the sexes already manages to annihilate disruptive selection caused by competition. Surprisingly, Bolnick & Doebeli (2003) find that the evolution of sexual dimorphism in their model comes together with disruptive selection and potential secondary branching at the dimorphic candidate ESS. However, genetic constraints from the diallele model they use generally prevent what they call "adaptive splitting". For some parameter combinations though, the evolution of (dis)assortative mating does seem to make secondary branching possible. When the Gaussian carrying capacity function in their model is replaced by a different function, such as a parabola, the coupling between sexual dimorphism and secondary branching disappears. Selection can then be stabilizing at a convergence stable sexual dimorphism. When competition is asymmetric, selection can be stabilizing for one sex and disruptive for the other. In that case, secondary branching will occur in a single sex, leading to three co-existing phenotypes. In any case, the route to speciation via secondary branching is not implausible.

Another possibility that will lead to evolutionary branching, and sympatric

species by necessity, is the presence of (completely) assortative mate choice before phenotypic sex differentiation evolves. Females only mating with phenotypically equal males inhibit the emergence of sexual dimorphism, and the only way ecological differentiation can occur is through sympatric speciation. This can imply that branching will be restored, but van Doorn & Weissing (2001) have shown that the presence of assortative mate choice also reduces the likelihood of evolutionary branching, because it stabilizes selection.

Sexual selection has been put forward as another driving force behind evolutionary branching leading to sympatric speciation (e.g. van Doorn & Weissing, 2001). We did not consider it here, but we do note that our conclusions do not directly affect the plausibility of sympatric speciation via sexual selection. In sexual selection models, evolutionary branching occurs in traits that are already specific to a single sex. That rules out the possibility for the appearance of a new phenotypic difference between the sexes capable of preventing branching caused by sexual selection. Thus, using our results indirectly, the odds for sexual selection versus ecological selection as the force driving sympatric speciation seem to veer towards sexual selection because the evolution of sexual dimorphism reduces the likelihood of the ecological route to speciation.

Acknowledgements Hans Metz provided many stimulating comments, which let us strengthen our case. Dan Bolnick and Michael Doebeli shared their unpublished work. Sander van Doorn inquired about the odds for sympatric speciation through sexual selection and Claus Rueffler provided detailed comments that improved readability. This research was supported by the European Modlife Research Training Network, funded through the Human Potential Programme of the EU (Contract HPRN-CT-2000-00051) and a Dutch NWO-VENI grant to Tom Van Dooren. Michel Durinx is supported by the Dutch national science organization (NWO) through PhD grant 809.34.002.

A Appendix

With multivariate ecological phenotypes per sex, say n traits, the complete trait vector becomes $\mathbf{z} = (z_f, z_m)$, which is a vector of length $2n$.

Selection gradient Singular points are determined using Equation (5), but with partial derivatives for each element in the trait vector \mathbf{z} . When the fitness gradient $\nabla' \lambda(\mathbf{z}', \mathbf{z})$ is a zero vector, evolution is potentially halted.

Invadability At a singular point with equal male and female multivariate phenotypes, the Hessian $H(z_{\pm}^*)$ (7) becomes a block diagonal matrix with two blocks $h/2$, and off-diagonal zero matrices. The eigenvalues of each h are determined by a constrained model without sex differentiation. If we append a vector $\mathbf{0}$ of n zeroes to an eigenvector \mathbf{u}_h of such an eigenvalue λ_h , then that extended vector, $\mathbf{u} := (\mathbf{u}_h^T, \mathbf{0}^T)^T$ (where “ T ” stands for transpose), solves the eigenvalue equation $H(z_{\pm}^*)\mathbf{u} = \lambda \mathbf{u}$ of the two-sex model with $\lambda = \lambda_h/2$. The similarly extended vector $(\mathbf{0}^T, \mathbf{u}_h^T)^T$ also

solves this equation, with the same λ found. Therefore each eigenvalue of the constrained model corresponds to an eigenvalue of the Hessian of the two-sex model with double multiplicity.

Convergence stability The Jacobian $J(z_-^*)$ of the two-sex model is a real matrix with blocks of second-order (mixed) partial derivatives corresponding to the entries in matrices $H(z_-^*)$ and $Q(z_-^*)$ (7)–(9). Concerning convergence stability, we first show that the eigenvalues of the Hessian h are always equal to two times an eigenvalue of the Jacobian $J(z_-^*)$. The eigenvalues of $J(z_-^*)$ are equal to those of its transpose. These solve the equality $J(z_-^*)^\top u = \lambda u$, which is

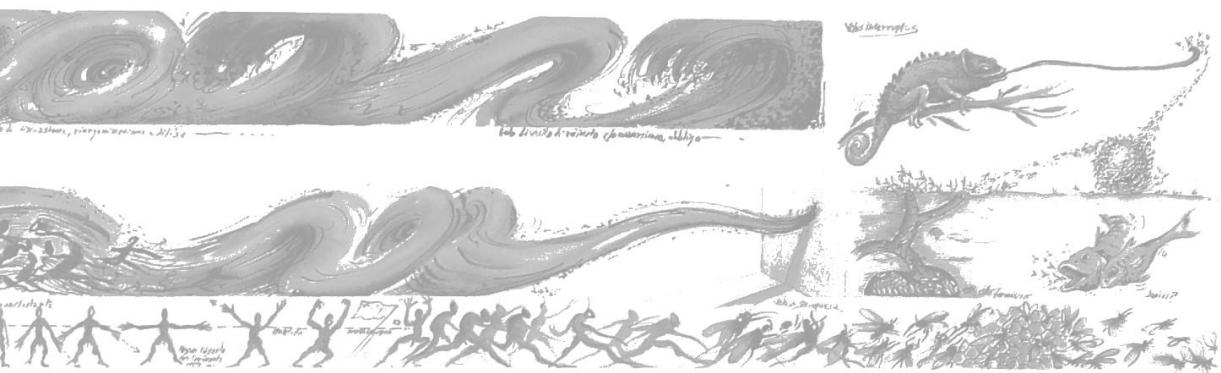
$$\frac{1}{2} \begin{pmatrix} q_2^\top + h^\top & q_2^\top \\ q_3^\top & q_3^\top + h^\top \end{pmatrix} u = \lambda u$$

If we take a (right) eigenvector u_h of h^\top (with eigenvalue λ_h) and concatenate it with $-u_h$, we see that this extended vector $u = (u_h^\top, -u_h^\top)^\top$ solves the equality. Its eigenvalue λ equals $\lambda_h/2$, where λ_h was an eigenvalue of the Hessian h .

Second, to show that halves of the eigenvalues of the Jacobian $j = q_2 + q_3 + h$ of the model without sex differentiation also occur in the two-sex model, we rewrite the eigenvalue equation of the two-sex Jacobian $J(z_-^*)$ as

$$\frac{1}{2} \begin{pmatrix} -q_3 & q_3 \\ q_2 & -q_2 \end{pmatrix} u + \frac{1}{2} \begin{pmatrix} q_2 + q_3 + h & 0 \\ 0 & q_2 + q_3 + h \end{pmatrix} u = \lambda u$$

If we use a vector $u = (u_j^\top, u_j^\top)^\top$, which is a twice repeated eigenvector u_j of the Jacobian j , and plug it into the eigenvalue equation of the two-sex Jacobian $J(z_-^*)$, the elements in the first matrix clearly cancel. Thus we see that u solves the two-sex eigenvalue equation and its eigenvalue is one-half that of the eigenvalue of u_j in the original model.



FOUR

Assortative mate choice and dominance modification: alternative ways of removing heterozygote disadvantage

Abstract

In genetic polymorphisms of two alleles, heterozygous individuals may contribute to the next generation on average more or fewer descendants than the homozygotes. Two different evolutionary responses that remove a disadvantageous heterozygote phenotype from the population are the evolution of strictly assortative mate choice, and that of a modifier making one of the two alleles completely dominant. We derive invasion fitnesses of mutants introducing dominance or assortative mate choice in a randomly mating population with a genetic polymorphism for an ecological trait. Mutations with small effects as well as mutants introducing complete dominance or perfect assorting are considered. Using adaptive dynamics techniques, we are able to calculate the ratio of fitness gradients for the effects of a dominance modifier and a mate choice locus, near evolutionary branching points. With equal resident allele frequencies, selection for mate choice is always stronger. Dominance is more strongly selected than assortative mating when the resident (common) alleles have very unequal frequencies at equilibrium. With female mate choice the difference in frequencies where dominance is more strongly selected is smaller than when mutants of both sexes can choose without costs. A symmetric resource-competition model illustrates the results; it shows that the mating system will have a decisive effect on relative selection pressures, also for mutations of large effect.

1 Introduction

When populations experience frequency-dependent disruptive selection from ecological causes for a prolonged time period, the distribution of phenotypic trait values will show an increase in the phenotypic variance. Disruptive selection favours extremes, and an increase in phenotypic variation in a population tends to remove the disruptivity of selection. Such a response can result from different underlying

Adapted, with minor corrections plus two additional appendices, from: Michel Durinx & Tom J.M. Van Dooren. Assortative mate choice and dominance modification: alternative ways of removing heterozygote disadvantage. *Evolution* (in revision)

processes (Rueffler *et al.*, 2006): those that increase the amount of genetic variation, those that increase the amount of phenotypic variation without increasing genetic variation, or those that combine purely phenotypic and genetic modifications. Several authors have investigated relative selection pressures on different types of response, to calculate the odds of observing specific types of response. This leads to general predictions that may have to be modified in their application, for example to account for system-specific constraints which affect distributions of mutational effects.

Most theoretical studies so far compare a purely phenotypic response with one that involves an increase in genetic variation. Bolnick & Doebeli (2003) studied the odds for the evolution of sexual dimorphism versus sympatric speciation, and Van Dooren *et al.* (2004) similarly probed the evolution of sexual dimorphism in comparison with the increase in genetic variation by evolutionary branching (*sensu* Metz *et al.*, 1996). Ackermann & Doebeli (2004) calculated the odds of all individuals becoming more generalist by broadening their niche, versus evolution towards a community of several specialists. Leimar (2005) investigated the likelihood of the evolution of random phenotype determination (bet-hedging) as opposed to an increase in genetic variation. Similarly, Matessi & Gimelfarb (2006) investigated an increase in phenotypic variation by genetic changes at a single polymorphic locus and evolution at loci controlling developmental stability. A study by Leimar *et al.* (2006) allowed for responses combining increased phenotypic variation per genotype with an increased number of genotypes in the population, the idea being that developmental processes integrate environmental and genetic information adaptively in order to predict selective conditions the individual will experience and that the process adjusts the phenotype accordingly.

In this paper, we compare two responses that both involve an increase in the amount of genetic variation in the population: the evolution of assortative mate choice, which may lead to sympatric speciation (Dieckmann & Doebeli, 1999), and the evolution of dominance-recessivity starting from additive genetics (Van Dooren, 1999). This pair of evolutionary responses was already considered in a seminal simulation study by Dickinson & Antonovics (1973), but they saw them much less as contenders as we do. We will consider a different range of models than Dickinson & Antonovics (1973) do, without an explicit spatial structure, and we aim for analytical results as much as possible.

The likelihood of sympatric speciation has been hotly debated in recent years (see Waxman & Gavrilets (2005) and attached commentaries), where the debate was mainly concerned with the plausibility of model assumptions and the number of speciation events for which the data support a sympatric explanation (Coyne & Orr, 2004). Here we want to investigate the likelihood of sympatric speciation in another way, namely by treating dominance evolution and reproductive isolation by assortative mate choice as different evolutionary responses to the disadvantage of producing heterozygotes. We investigate the odds of either response becoming established by the invasion of mutant alleles in a population with random mating and additive genetics. To assess the relative selection pressures as cleanly as possible, we ensure that the models are as symmetric as possible with respect to causes for the two responses, and try to introduce as few modelling constraints as keeps the calculations manageable.

Assuming that mate choice induces no cost whatsoever for mutants while they are rare, we will show that whether strictly assortative mate choice or complete dominance of a particular allele can invade purely depends on the pattern of heterozygote disadvantage, i.e., whether heterozygotes contribute on average less to the next generation than homozygotes. The same holds for the invasion of mutants with a weak tendency to choose assortatively. In contrast, the invasion of dominance modifiers with small effects on the phenotype of the heterozygote strongly depends on the demographic effects of such small changes.

There are populations where individuals show quantitative trait values that are of special interest, called evolutionary branching points (Metz *et al.*, 1996; Geritz *et al.*, 1998). At such points, disruptive frequency-dependent selection causes the emergence of a genetic polymorphism from a population originally containing a single common allele. A mutant allele which can invade such a population does not go to fixation, but coexists with the formerly single resident in a protected polymorphism. Continued disruptive selection on the polymorphism will cause the pair of alleles to be replaced by other pairs, which increases the phenotypic variance in the population further. Similarly to previous studies investigating the odds of other pairs of alternative evolutionary responses, we can determine the ratio of selection pressures on mutations in dominance modifiers versus those on the mate choice locus, when the resident population is near an evolutionary branching point. It turns out that dominance modification is favoured when the resident allele frequencies are unequal. When the frequencies of the resident alleles are equal, selection on mate choice is always stronger. The boundary between resident allele frequencies where dominance becomes more strongly selected than mate choice depends on how mated pairs are formed: with female mate choice the difference in frequencies is smaller than when rare mutants of both sexes choose assortatively.

A symmetric resource competition model used as an example shows that for mutations inducing a complete modification in mate choice or heterozygote phenotype, as well as for mutations that induce only a small modification, the relative strengths of selection on dominance modification and mate choice evolution depend on the mating system.

2 Model family, notations and assumptions

We consider populations of randomly mating diploid individuals, with a single category (class) of reproducing adults. It is assumed that selection pressures on ecological trait values cannot differ between sexes or sex roles in the population, so that it is not necessary to model the sexes separately and explicitly in the dynamics (cf. Appendix A).

We consider evolution at three different loci with free recombination. Firstly, an ecological locus with two alleles present in the population, which induce the (vectorial) *allelic traits* X_1 and X_2 respectively. These are considered to be given for the calculations, since we are not immediately interested in their evolution, and they determine the genotypic values of the homozygotes: $2X_1$ and $2X_2$ respectively. Secondly, a locus where the presence of the resident allele a ensures random mating. Here we want to study whether rare alleles that induce a tendency for assorta-

tive mating can invade. Thirdly, a locus where the presence of the resident allele d gives equal weight to both alleles on the ecological locus in heterozygotes, i.e., their genotypic value equals $X_1 + X_2$. Here we are interested in the invasion of rare alleles that bias the genotypic value towards either $2X_1$ or $2X_2$. Since we do not consider environmental effects on phenotypes explicitly, we will simply call genotypic values *phenotypes* in this paper. For simplicity's sake, we assume that no loss of mating opportunities (and hence no cost) follows from the pickiness induced by the tendency to mate assortatively.

We made our assumptions such that the underlying evolutionary and population dynamical model fits in the adaptive dynamics framework for mutation-limited evolution (Metz *et al.*, 1996; Geritz *et al.*, 1998), i.e., such that the resident population is sufficiently large and locally well-mixed to allow for a deterministic description of its dynamics, and that mutations occur sufficiently rarely to ensure that there is no interference between different invading mutants. To predict the fate of the invaders, we first of all need to study their dynamics while still rare. Most of our conclusions are based on such investigations. Because of the well-mixedness, individuals that are homozygous for the mutant alleles are vanishingly rare in comparison to heterozygous mutants and their numbers can therefore be disregarded. Additionally, in several calculations we assume mutation steps to be small. The population dynamics is assumed to have (locally) unique point equilibria, and to be sufficiently well-behaved to preclude sudden bifurcations (Geritz *et al.*, 2002; Geritz, 2005) which would cause the extinction of an ecological allele during one of the invasions we consider. Following standard allele notations, lower case letters refer to the “wild” or initial resident types, and upper case letters to “mutant” or invading types. The densities n_{11} , n_{12} and n_{22} refer respectively to the resident populations of parents of type X_1X_1aadd , X_1X_2aadd and X_2X_2aadd . When considering an invading allele A on the second locus, the invaders’ densities N_{11} , N_{12} and N_{22} refer to types X_1X_1Aadd , X_1X_2Aadd and X_2X_2Aadd . The same three names will be used when dealing with a mutant D on the third locus, as the correct meaning will be clear from the context. In an obvious manner, we gather these six densities in two density vectors \mathbf{n} and \mathbf{N} , and rescale those into frequency vectors $\mathbf{p} := (p_{11}, p_{12}, p_{22})^\top$ and $\mathbf{P} := (P_{11}, P_{12}, P_{22})^\top$.

3 Random mating and selection

When the resident population is at equilibrium, with no invaders present, random mating ensures that a resident of type X_1X_1aadd mates with the three types of resident at a ratio of $p_{11} : p_{12} : p_{22}$, so that zygotes of the three ordered ecological genotypes are produced in proportions $P_{\text{rnd}}(t)$ $\mathbf{p}(t)$ where P_{rnd} is defined as

$$P_{\text{rnd}} := \begin{bmatrix} p_{11} + \frac{p_{12}}{2} & \frac{1}{2} \left(p_{11} + \frac{p_{12}}{2} \right) & 0 \\ p_{22} + \frac{p_{12}}{2} & \frac{1}{2} & p_{11} + \frac{p_{12}}{2} \\ 0 & \frac{1}{2} \left(p_{22} + \frac{p_{12}}{2} \right) & p_{22} + \frac{p_{12}}{2} \end{bmatrix} \quad (1)$$

or, using allele frequencies $p_1 := p_{11} + p_{12}/2$ and $p_2 := p_{22} + p_{12}/2$ instead of the diploid frequencies (p_{11} , p_{12} , p_{22}),

$$P_{\text{rnd}} = \begin{bmatrix} p_1 & p_1/2 & 0 \\ p_2 & 1/2 & p_1 \\ 0 & p_2/2 & p_2 \end{bmatrix} \quad (2)$$

We note that the first and last columns add up to twice the middle one, so the determinant of P_{rnd} is 0 and its eigenvalues are relatively easy to calculate, a property which will turn out to be crucial.

After the formation of zygotes, competition solely determines how many of each of the three resident (plus possibly three invading) phenotypes will make up the next breeding generation. To allow as wide a class of models as possible within the assumptions, we only demand that selection is governed by a positive *lifetime (adult) reproductive output* function. It is the expected number of adults which an adult contributes to the mating pool of the next generation, denoted as the function $L(\phi, I)$ which depends on the phenotype ϕ of the zygote and on the ecological feedback environment I . This environment is a concept from physiologically structured populations theory: it is that quantity which closes the feedback loop and makes the population equations, for a given I , linear in the population density (Metz & Diekmann, 1986). I will typically depend on the densities and traits of the respective resident phenotypes, but possibly also on other (time-dependent) factors like temperature and resource density. Being a solution to a balance equation, it is only known implicitly.

In the absence of any non-additive dominance interactions, ϕ is just the sum of the two traits on the first locus, i.e. $\phi = X_1 + X_2$ for a heterozygote. Therefore the residents' next-generation operator L_{rnd} , for which $\mathbf{n}(t+1) = L_{\text{rnd}}(t) \mathbf{n}(t)$, looks like

$$L_{\text{rnd}} := \begin{bmatrix} L_1 & 0 & 0 \\ 0 & L_2 & 0 \\ 0 & 0 & L_3 \end{bmatrix} \begin{bmatrix} p_1 & p_1/2 & 0 \\ p_2 & 1/2 & p_1 \\ 0 & p_2/2 & p_2 \end{bmatrix} \quad (3)$$

where $L_1 := L(X_1 + X_1, I)$, $L_2 := L(X_1 + X_2, I)$ and $L_3 := L(X_2 + X_2, I)$. Appendix B shows that at a stable equilibrium, necessarily one of the three following relations between the $L(\phi, I)$ -values holds:

1. $L_1 = L_2 = L_3 = 1$: in this context an uninteresting special case.
2. $L_1 < 1$ & $L_3 < 1$: then $L_2 = 1 + \sqrt{(L_1 - 1)(L_3 - 1)} > 1$ and $p_1 = \sqrt{1 - L_3} / (\sqrt{1 - L_1} + \sqrt{1 - L_3})$. We call this situation *heterozygote advantage*. Note from the formula that necessarily $L_2 < 2$.
3. $L_1 > 1$ & $L_3 > 1$: then $L_2 = 1 - \sqrt{(L_1 - 1)(L_3 - 1)} < 1$ and $p_1 = \sqrt{L_3 - 1} / (\sqrt{L_1 - 1} + \sqrt{L_3 - 1})$. We call this situation *heterozygote disadvantage*.

Using the allele frequencies just found, and noting that L can still implicitly depend on allele frequencies, we can use Equation (3) to write the equilibrium frequencies

of adult genotypes as

$$\begin{pmatrix} p_{11} \\ p_{12} \\ p_{22} \end{pmatrix} = \begin{bmatrix} L_1 p_1 & L_1 p_1/2 & 0 \\ L_2 p_2 & L_2/2 & L_2 p_1 \\ 0 & L_3 p_2/2 & L_3 p_2 \end{bmatrix} \begin{pmatrix} p_{11} \\ p_{12} \\ p_{22} \end{pmatrix} = \begin{pmatrix} L_1 p_1^2 \\ 2L_2 p_1 p_2 \\ L_3 p_2^2 \end{pmatrix} \quad (4)$$

4 Assortative mating

We start our investigation of the evolution of assortative mate choice by considering an extreme case, which we use as a benchmark: we consider the invasion fitness of a mutant at the mate choice locus, A , inducing perfect assortative mate choice in all its carriers. We assume that such mutants are not losing any mating opportunities due to their choosiness, and that there are no other costs to choosiness. In this manner, the mutant can obtain the maximum benefit of assortative mate choice, without costs. (How such a model relates to models with mate choice functions is shown in Appendix G.)

Given a large, well-mixed resident population at equilibrium, let us study the invasion dynamics of such a rare allele A by tracking the individuals that are heterozygous for the assortative locus, as the number of AA -individuals is vanishingly small while A is still rare. Subsequently, the next-generation matrix L_A of the assortatively mating heterozygotes is

$$L_A := \begin{bmatrix} L_1 & 0 & 0 \\ 0 & L_2 & 0 \\ 0 & 0 & L_3 \end{bmatrix} \begin{bmatrix} 1 & 1/4 & 0 \\ 0 & 1/2 & 0 \\ 0 & 1/4 & 1 \end{bmatrix} \quad (5)$$

and the set of eigenvalues of L_A is $\{L_1, L_2/2, L_3\}$. The logarithm of the largest eigenvalue among these three is the invasion fitness of the allele A (Metz *et al.*, 1992). It can invade if and only if the dominant eigenvalue is larger than 1 (positive invasion fitness). Therefore, in case of heterozygote advantage (Case 2 at the end of last section), all three eigenvalues are less than 1 and the allele A cannot invade. In case of heterozygote disadvantage, both L_1 and L_3 are larger than 1 so that the invader has positive invasion fitness (regardless of the genotype in which the mutation appears). We will use the logarithm of the dominant eigenvalue of the next-generation matrix of a mutant allele as invasion fitness throughout this paper.

Similar to the approach of the O'Donald (1960) model, one can instead consider an allele $A(\alpha)$ that causes mutant heterozygotes of both sexes to mate assortatively in a proportion α of the total number of matings, while still avoiding any costs of choosiness. While $A(\alpha)$ is still rare, the next-generation matrix of invaders with this allele is

$$L_{A(\alpha)} := (1 - \alpha)L_{\text{rnd}} + \alpha L_A = L_{\text{rnd}} + \alpha(L_A - L_{\text{rnd}}) \quad (6)$$

It is not feasible to calculate the dominant eigenvalue λ_d of the matrix $L_{A(\alpha)}$ in general, and tell if it is smaller or larger than 1. However, this last question can be answered for small values of α , as we show in Appendix C that

$$\frac{\partial \lambda_d}{\partial \alpha} \Big|_{\alpha=0} = p_1 p_2 \left(1 - \frac{L_2}{2}\right) (L_1 + L_3 - 2L_2) \quad (7)$$

Since L_2 is smaller than 2 in all cases, we see that for any small value α the allele $A(\alpha)$ cannot invade in the case of heterozygote advantage, but it has positive invasion fitness and can invade in the case of heterozygote disadvantage.

For females, the assumption of no loss of mating opportunities is reasonable as long as p_1 is not too close to 0 or 1. However, in models where the males can also be choosy and can have an unlimited number of mating opportunities, the assumption is generally untenable for males: a choosy male of type X_1X_1 accepts only a fraction p_{11} of the mating opportunities offered to him, while all would be accepted by his non-choosy peers. Without any compensatory mechanism restoring overall mating success for choosy males, that constitutes a severe mating disadvantage which the ecological selective differences usually cannot make up for. Note that if the choosiness allele A is already present in the population but not equally prevalent in the three genotypes, then female carriers mate disproportionately often with male carriers. Conversely, when male mating opportunities are unlimited, the disadvantage to choosy males decreases with increasing prevalence of A and obviously vanishes when all female (or all male) individuals are carriers.

In models where only the females take the decision to mate with a specific male or not, (6) still appears in invasion fitness expressions. For mutations which induce complete assortative mate choice in females, L_A has to be replaced by $(1 - \rho_f)L_{\text{rnd}} + \rho_f L_A$ where ρ_f is the proportion of females among the adults. Consequently, for mutations inducing choosiness in a fraction α of females, $L_{A(\alpha)}$ (6) is replaced by $L_{A(\rho_f\alpha)}$, and we see that the (dis)advantage of choosiness in one sex in terms of invasion fitness has the same sign as that of choosiness in both sexes, when mutation steps are small. (For large mutational steps, exactly the same problem as before arises that prevents us from calculating the dominant eigenvalue. Here it does not make sense to give analytical solutions for $\rho_f \approx 0$ or $\rho_f = 1$.) Also, in this female choice scenario, males can experience sexual selection due to the preferences of females for a certain phenotype when female assortative mate choice becomes common. Polymorphism at the mate choice locus can also be maintained in this case if the disadvantage of heterozygotes is relatively weak (Matessi *et al.*, 2001). However, if the mutant also increases in frequency when a has become rare, and differences between resident and mutant alleles are small and selection therefore weak, then A will go to fixation regardless of the precise model under consideration (Dercole & Rinaldi, *in press*; Metz *et al.*, 1996; Geritz *et al.*, 1998; Geritz, 2005). Both for mutations expressed in two sexes and in females only, when a small value of α can invade a randomly mating population, then by continuity there necessarily is a (small) neighbourhood around $\alpha = 0$ of resident levels of assortativeness, where any allele inducing a higher level α' can invade.

In case of heterozygote disadvantage and female choice, can assortativeness evolve by repeated invasions and fixations until $\alpha = 1$? To address this question, we have to consider that it is not possible to calculate the zygote frequencies p_{ij} and the values of L_1 , L_2 and L_3 analytically if the residents are mating nonrandomly, even in the simpler case where only one sex is choosy; the problem is that the equivalent of Appendix B yields much higher order polynomial equations. But looking at the other end of the scale, we can consider a community where the resi-

dents are all mating completely assortative, so their transition matrix is

$$L_{\text{ass}} = \begin{bmatrix} L_1 & L_1/4 & 0 \\ 0 & L_2/2 & 0 \\ 0 & L_3/4 & L_3 \end{bmatrix} \quad (8)$$

(Note that this is not the same matrix as L_A , whose values of L_1 , L_2 and L_3 are determined from L_{rnd} , even though both matrices superficially look the same; cf. Appendix D.) If both sexes would choose assortatively, it is obvious at a glance that any mutant allele $a(\omega)$ inducing a small probability ω of random mating has negative invasion fitness: residents would rebuff any attempts by mutants at mating nonassortatively. If alternatively only the females can choose, then the mutants are indistinguishable from the residents for a fraction $1 - \rho_f \omega$ of the matings, but for a fraction $\rho_f \omega$ they are females that mate randomly. So the mutant transition matrix is

$$L_{a(\omega)} = L_{\text{ass}} + \rho_f \omega (L_a - L_{\text{ass}}) \quad (9)$$

where L_a looks the same as L_{rnd} but its values for L_1 , L_2 and L_3 are determined from L_{ass} . An additional complication is that in many scenarios, there will be no resident heterozygotes to mate with; then $L_{a(\omega)}$ must be altered to reflect this, as mutant heterozygotes are too rare to encounter each other in a well-mixed population. In Appendix D we show that either L_{ass} has a double (or even triple, if additionally $L_2 = 2$) dominant eigenvalue $L_1 = L_3 = 1$, in which case there are no resident heterozygotes and the mutant $a(\omega)$ has negative invasion fitness, or else $L_2 = 2$ and $L_1, L_3 < 1$ so 1 is the simple dominant eigenvalue, in which case there are resident heterozygotes and the mutant has positive invasion fitness. (In this second case, a tendency for random mating can invade the strictly assortatively mating population, or more importantly, fully assortative mating cannot evolve.) The last case ($L_2 = 2; L_1, L_3 < 1$) implies that the heterozygote has a drastically different ecology from the two homozygotes, a situation that cannot occur when X_1 and X_2 are sufficiently close (as they are near branching points for example, cf. Section 6). We also expect this situation to occur but very rarely if the population has started evolving gradually from random mating and heterozygote disadvantage.

5 Dominance modifiers

If a dominance-modifying allele D arises that causes a heterozygote X_1X_2aaDd to be ecologically indistinguishable from a X_1X_1aadd homozygote, then the only difference between L_{rnd} and this mutant's next-generation matrix L_D is that L_2 is replaced by L_1 . In Appendix E we show that the dominant eigenvalue of L_D is therefore easily calculated (47). Invasion fitness is positive in case of heterozygote disadvantage, since a switch to the homozygote phenotype implies the avoidance of disadvantage, but negative in case of heterozygote advantage.

We also want to model modifiers with small effects next to mutations introducing complete dominance, just like we did for the evolution of assortative mating. Whereas we could model small changes in mating preference as a linear combina-

tion of two extreme cases, we cannot do that here because

$$L_{D(\delta)} \neq (1 - \delta)L_{\text{rnd}} + \delta L_D \quad (10)$$

as that would be a linear interpolation of the *ecology* instead of the *type* of the diploid. Therefore we parametrize phenotype by

$$\phi_\delta(X_1, X_2) = X_1 + X_2 + \delta(X_1 - X_2) \quad (11)$$

where we assume that $\delta \in [-1, 1]$, i.e., phenotypic over- and underdominance are not considered. The case $\delta = 0$ corresponds to additive effects of the two ecological alleles. $\delta = 1$ is total dominance of the X_1 allelic trait so that $L_{D(1)} = L_D$ (and $\delta = -1$ is complete dominance of the X_2 allele). The next-generation matrix of a mutant with dominance bias δ is then

$$L_{D(\delta)} = \begin{bmatrix} L_1 & 0 & 0 \\ 0 & L_2^\delta & 0 \\ 0 & 0 & L_3 \end{bmatrix} \begin{bmatrix} p_1 & p_1/2 & 0 \\ p_2 & 1/2 & p_1 \\ 0 & p_2/2 & p_2 \end{bmatrix} \quad (12)$$

where $L_2^\delta = L(\phi_\delta(X_1, X_2), I)$ with I the ecological feedback environment set by the resident population at equilibrium. One correctly expects here that for any $\delta \in [-1, 1]$ such that $L_2^\delta > L_2$, the dominant eigenvalue is larger than 1 (and smaller if $L_2^\delta < L_2$; proof in Appendix E). Furthermore, the above also holds true if the unbiased (“wild”) type allele d has been replaced as unique resident by $D(\delta)$: any mutant inducing a different degree of dominance bias $\delta + \delta'$ will be able to invade if and only if $L_2^{\delta'} > L_2$ (where L_2 is calculated for the resident level of bias δ).

Equation (48) gives us the derivative of the dominant eigenvalue of $L_{D(\delta)}$ as

$$\frac{\partial \lambda_d}{\partial \delta} = 2 p_1 p_2 D_1 L(X_1 - X_2) \quad (13)$$

where $D_1 L$ is the first order partial derivative of L for its first argument, evaluated at $(\phi_\delta(X_1, X_2), I)$. Because this factor depends on the model in question, we cannot immediately compare with evolution towards assortative mating (7), but we see that in general the local slope of L at the heterozygote phenotype determines invasion success; the exception being those points where $D_1 L(X_1 - X_2) = 0$. These points are critical points of the function L restricted to the direction $X_1 - X_2$: at a maximum, no further dominance evolution can take place; at a minimum, the heterozygote phenotype can be modified in both directions; in degenerate cases the point is a half-stable equilibrium (saddlepoint), which allows modification in one direction, just like noncritical points.

6 Relative strengths of selection

At first sight, one might expect invasion fitness for mutants inducing strictly assortative mate choice to be about half as large as that for mutants inducing complete phenotypic dominance, if the two ecological alleles are equally common. The first

only affects about half the offspring of about half the individuals carrying the mutation (the homozygotes of the ecological alleles substitute their heterozygous offspring with ecological homozygotes), while the second affects about half the carriers directly (all the ecological heterozygotes change phenotype). The mistake here, however, is to equate the distribution of mutant mate choice alleles over ecological genotypes with that of the randomly mating resident. In any case, a few generations after its appearance, all or nearly all carriers of the mutation inducing strictly assortative mate choice are by necessity homozygotes on the ecological locus.

For “benchmark” models where mutant females and males can be choosy, the table in Appendix E shows that it is impossible to say in general whether a mutant inducing perfectly assortative mate choice or one inducing complete dominance modification has the better chance of invading: in most models units or parameters can be rescaled so that five qualitatively different situations may occur, with the answer then depending on the ecological type where the assortative mutant first appears and on which allele is dominant, as well as on the underlying ecological model (cf. table at end of Appendix E). In general, the selection pressure for assortative mate choice will be weaker with female mate choice only than when mutant males also choose assortatively (cf. Eq. (9)), so that the odds for dominance versus assortativeness depend on the mating system as well as other factors.

If diversification on the ecological locus occurs by a process of evolutionary branching, X_1 and X_2 are very similar shortly after branching, as disruptive selection has not yet caused a substantial increase in the difference between the resident allelic traits. In Appendix F we exploit the fact that the ecological phenotypes are not very different, using some adaptive dynamics results, to obtain the following expression 14 for the relative strength of selection on dominance modification and mate choice by both mutant males and females. It is the ratio ρ of their fitness gradients just after a branching event:

$$\rho = 2(p_2 - p_1) + O(\varepsilon) \quad (14)$$

From this the following classification can be derived:

1. if $p_1 < 1/4$ then the selection gradient of dominance bias towards X_1 is larger than those of other mutations,
2. if $p_1 > 3/4$ then dominance bias towards X_2 has the highest selection gradient,
3. if $1/4 < p_1 < 3/4$ then selection is strongest for a tendency for assortative mating.

The first two cases require that the reproductive output of one homozygote is at least nine times more sensitive to changes in the ecological trait than the other (from Eq. (63)), which seems a rather strong requirement that one intuitively expects not to occur very often. If there is female mate choice instead, then ρ gets divided by the proportion of females ρ_f (cf. Section 4). This makes it less likely that assortative mating has the larger selection gradient, since the requirement is now that $(2 - \rho_f)/4 < p_1 < (2 + \rho_f)/4$ (which is between 3/8 and 5/8 for $\rho_f = 0.5$), or equivalently that the reproductive outputs of the homozygotes differ at most by a factor $(2 + \rho_f)^2/(2 - \rho_f)^2$ in sensitivity (which is about 2.8 when $\rho_f = 0.5$).

However, at the edge of the zone of stable coexistence of X_1 and X_2 (called P_2 by e.g. (Metz *et al.*, 1996)), one of the two necessarily goes extinct. This means that close to this edge the allele frequencies are very unequal so that the conditions for dominance bias to triumph always do exist, even arbitrarily close to a singularity.

The ratio ρ should not be taken as the relative probability for the establishment of mutants bearing one of the respective traits, but it can be used to approximate the ratio of those odds for a given pair of mutants. The appropriate measure for the expected relative amount of change in the two traits should be the ratio of the canonical equations for evolutionary change in each trait (Dieckmann & Law, 1996). Durinx *et al.* (2008) have shown that if the models considered in this paper satisfy some further conditions necessary to derive the canonical equation of adaptive dynamics, the expected relative rate of change in dominance bias compared to that in mating behaviour will be

$$\frac{\mu_\delta}{\mu_\alpha} \frac{\text{Var}_\delta}{\text{Var}_\alpha} \rho \quad (15)$$

where μ stands for the probability per birth event of the respective mutations occurring, and Var for the variance of the respective mutation distributions.

7 Resource competition

Initially, the evolution of dominance and of assortative mate choice have been studied mostly separately in two-patch models with patch-specific selection (Dickinson & Antonovics, 1973; Van Dooren, 1999; Geritz & Kisdi, 2000). In such models, migration parameters show a tendency to decrease under the same conditions as favour genetic polymorphism, so that parapatric speciation seems the most likely outcome (Balkau & Feldman, 1973). Since much of the discussion concerning the likelihood of sympatric speciation is based on resource competition models, we illustrate here the results of the previous sections with numerical fitness calculations for a model of that kind, with discrete generations, similar to the ones by Van Dooren (2000) and by Peischl & Bürger (in press). An advantage of our example is that it can be easily derived from an individual-based ecological scenario, and it allows some analytical results.

The reproductive output function L is a product of fecundity f and the effect of competition which depends on the (scalar) phenotype ϕ . Competition between individuals is described by two bell-shaped functions k and a , their widths scaled respectively by parameters μ_k and μ_a . Function k describes the strength of competition between phenotypically identical individuals, which is assumed to be minimal when the phenotype $\phi = 2$. Function a describes how fast competition diminishes when individuals become phenotypically different. The parameter s (Van Dooren, 2000) sets the intensity of competition between individuals with phenotype $\phi = 2$ (i.e., allelic strategy $X = 1$ in a homozygote) in this example.

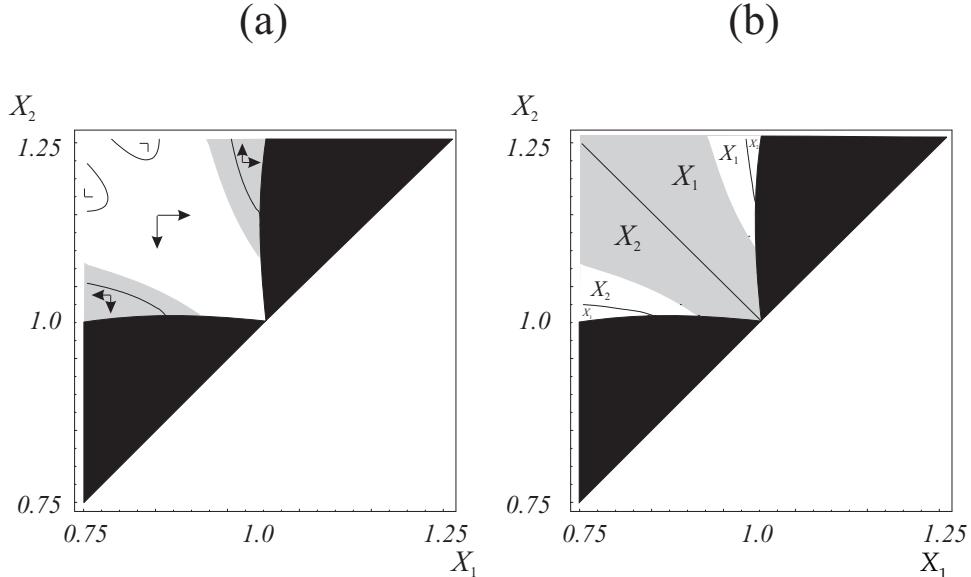


Figure 1: Patterns of heterozygote disadvantage and invasion fitnesses in dimorphic populations, for mutations with small effects and parameter values $\mu_k = 1$, $\mu_a = 7$ and $s = 0.9$. Here $X^* = 1$ is an unininvadable, attracting singularity. Because the graph is symmetric along the $X_1 = X_2$ line, only the top left half is shown. The black region consists of those trait combinations that cannot coexist in a protected polymorphism. Fig. 1a: Isoclines separate areas with different directions of selection on allelic effects X_1 and X_2 as indicated by the arrows. Area with heterozygote disadvantage in grey. Fig. 1b: Region with selection against assortative mating indicated by grey. Note that areas with heterozygote disadvantage correspond to areas with an advantage to mate assortatively. Isoclines separate regions with selection for either the allele with strategy X_1 or X_2 to become dominant.

$$\mathbf{I} = \{(\boldsymbol{\phi}_1, N_{\boldsymbol{\phi}_1}), (\boldsymbol{\phi}_2, N_{\boldsymbol{\phi}_2}), (\boldsymbol{\phi}_3, N_{\boldsymbol{\phi}_3})\} \quad (16)$$

$$L(\boldsymbol{\phi}', \mathbf{I}) := f \exp \left(- \sum_i (1 - s k(\boldsymbol{\phi}')) a(\boldsymbol{\phi}', \boldsymbol{\phi}_i) N_{\boldsymbol{\phi}_i} \right) \quad (17)$$

$$k(\boldsymbol{\phi}') := \exp(-\mu_k(\boldsymbol{\phi}' - 2)^2) \quad (18)$$

$$a(\boldsymbol{\phi}', \boldsymbol{\phi}_i) := \exp(-\mu_a(\boldsymbol{\phi}' - \boldsymbol{\phi}_i)^2) \quad (19)$$

For this model, a singular point is present at the trait value $X^* = 1$ of the ecological locus, and invasibility and convergence stability there can be determined analytically. The probability of assortative mating, and the dominance deviation parameter, were determined in an additive way from the values at the respective loci.

We iterated the population dynamics of residents to find population dynamical

equilibria. In these simulations we did not model separate sexes but simultaneous hermaphrodites, with mate choice in the female function determined by the female preference trait. The population dynamics of a specific mutant in a given equilibrium population was iterated to estimate invasion fitness. In the female choice scenario, mutants which for example mate completely assortatively, contribute to the next generation also through their male role and therefore according to the preferences of the residents. For comparison, we also calculated the invasion fitness of “benchmark” mutants in a given resident population according Equations (5) and (6).

We first calculated patterns of invasion fitness in dimorphic populations with random mating and additive genetics for the ecological traits. Figures 1a and 2a give representative patterns of invasion fitness in the set of dimorphic resident populations with random mating and additive genetics at the ecological locus. In these figures, contour lines are based on invasion fitness landscapes for mutants of the mating locus which mate assortatively in 5% of their matings (i.e., $\alpha = 0.05$). For mutations affecting dominance, invasion fitnesses were similarly calculated for $|\delta| = 0.05$.

To help interpret the results, we also calculated heterozygote (dis)advantage as $L_2 - (L_1 + L_3)/2$ and show this information on Figures 1a and 2a together with the pattern of invasion fitness for mutations on the ecological locus (i.e., affecting the trait value X_1 or X_2). From these pairs of figures, it is clear that assortative mate choice evolves in response to the pattern of heterozygote (dis)advantage. Dominance evolution however is completely independent from this pattern, as can be expected from Equation (13).

Figure 3a shows the dependence of the reproductive output function $L(\phi, I)$ (17) on the phenotype of the mutant, for a range of resident trait combinations along the line $X_1 + X_2 = 2$. One can see that a local maximum appears when the difference between the ecological phenotypes becomes larger. As this local maximum becomes more pronounced, heterozygotes obtain an advantage (in terms of $L(\phi, I)$) relative to the two homozygotes. Along the line $X_1 + X_2 = 2$, which allele becomes more dominant also changes with increasing distance between homozygote phenotypes. When polymorphisms right next to the line $X_1 + X_2 = 2$ are inspected (Fig. 3b), the cause is seen to be the sign switch of the slope of $L(\phi, I)$ (17) at the phenotype of the heterozygote in these polymorphisms, while the difference between phenotypes is still insufficient to cause heterozygote advantage or an intermediate maximum for the nearby polymorphisms on the line $X_1 + X_2 = 2$.

Figure 4 compares the strength of selection on dominance and assortative mate choice. For mutations with small effects (Fig. 4a and 4b), one sees that dominance evolution has much smaller invasion fitnesses close to the singularity and near the line $X_1 + X_2 = 2$, i.e., when allele frequencies in the resident population are similar. When mate choice occurs by females only (Fig. 4a), selection on assortative mate choice is weaker than in the case where mutant males also choose assortatively, a fact that is reflected in a smaller area where dominance is at a disadvantage, in Fig. 4a as compared to Fig. 4b. When there is heterozygote advantage in the polymorphism and the resident alleles are not near the line $X_1 + X_2 = 2$, the strength of selection for dominance modification is stronger than that against assortative mating. For reference, we also compare absolute values of invasion fitnesses

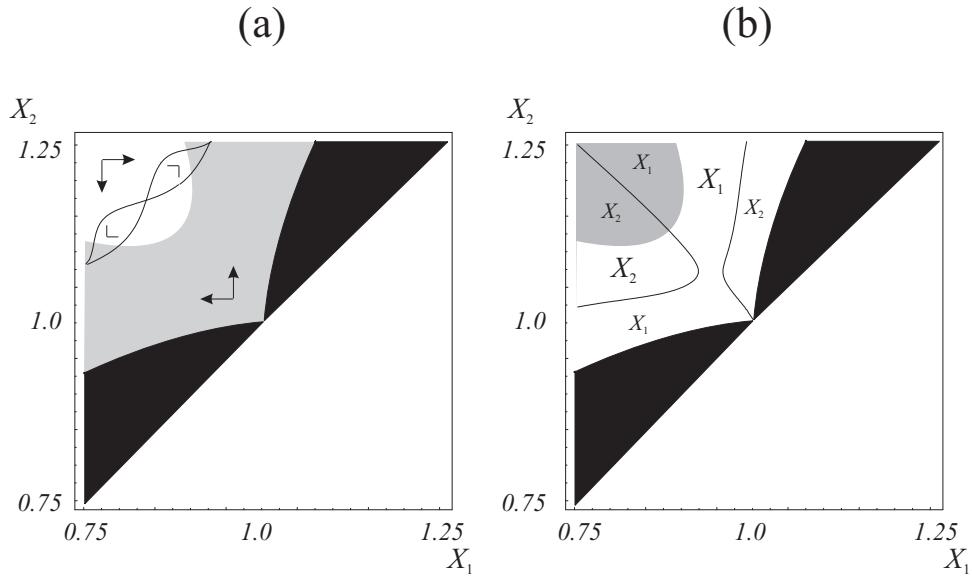


Figure 2: Patterns of heterozygote disadvantage and invasion fitnesses in dimorphic populations, for mutations with small effects and parameter values $\mu_k = 1$, $\mu_a = 15$ and $s = 0.9$. Here $X^* = 1$ is a branching point. Colouring, isoclines and labelling as in Figures 1a and 1b. The dimorphic singular strategy is seen at the top left of Figure 2a, at the intersection of the two isoclines.

In Figure 2b, the fitness isoclines for dominance modifiers would coincide in a single point on the line $X_1 + X_2 = 2$ if dominance mutations were of infinitesimally small effect, or if signs of fitness gradients were plotted. However, since this graph is based on calculations for mutants with small but discrete trait changes, invasion fitnesses at the location where these two isoclines would coincide are all positive for mutants increasing dominance of X_1 . This is the only instance where the mutational step size we used has a qualitative effect on the dominance isoclines.

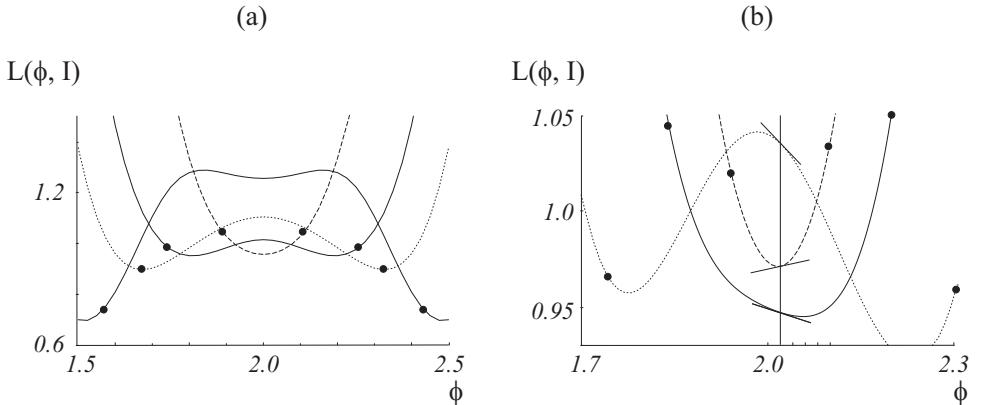


Figure 3: The shape of the offspring production function $L(\phi, I)$, depending on the population composition and with parameter values such as in Figure 2.

Fig. 3a: Four different populations along the line $X_1 + X_2 = 2$ are shown where $L_1 = L_3$, with the phenotypes of the homozygotes indicated by dots on the corresponding function. Due to symmetry, the slope of L at the heterozygote is always 0. We see that for a small difference between homozygotes (dashed line), selection is purely disruptive. With increasing differences, the minimum of L splits into two minima with an intermediate local maximum at the heterozygote phenotype. For even larger differences, the local minima move out of the plotted range, and the local maximum turns again into a local minimum that is now surrounded by two local maxima. L is also given for the dimorphic singular strategy (dotted line), given additive genetics, where the homozygote phenotypes are at local minima and the heterozygote at the local maximum. Fig. 3b: L is given as in Fig. 3a (with parameters as in Figure 2), for three populations on the $X_1 + X_2 = 2.02$ line. The resident populations have allelic trait combinations $(0.97, 1.05)$, $(0.92, 1.10)$ and $(0.87, 1.15)$. The phenotype of the heterozygote is indicated by a vertical line, and the tangent indicates the slope of L there. One can see that in case of heterozygote disadvantage, evolution by small mutational steps modifies the phenotype in the direction away from the local minimum of L ; in case of advantage, it is towards the local maximum. In the first two populations, the minimum of L lies on different sides of the heterozygote. Thus gradual evolution is independent of which homozygote phenotype has the higher L -value (L_1 or L_2), whereas large mutation steps inducing complete dominance clearly favour dominance by the allele with the higher homozygote L -value.

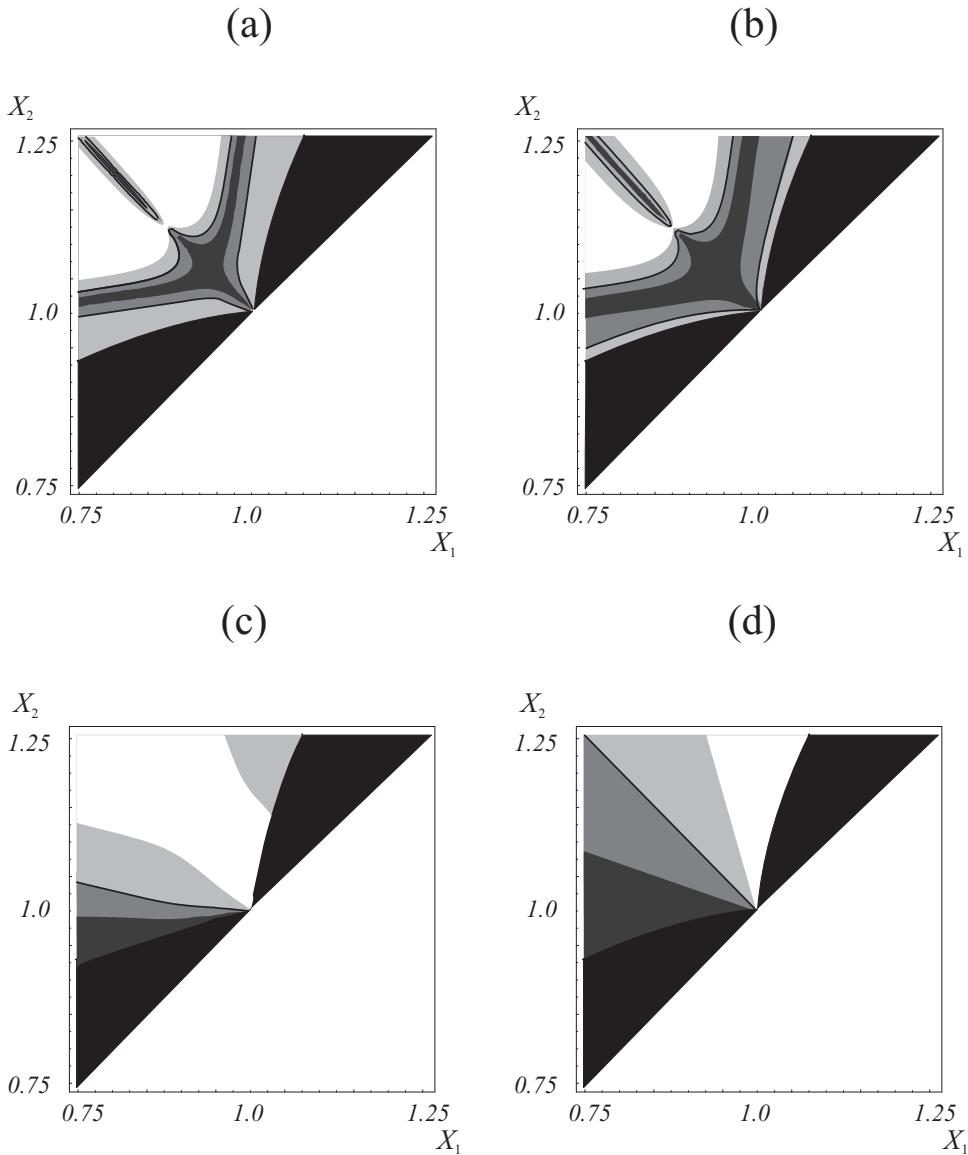


Figure 4: Contour plots of differences between the logarithms of absolute values of invasion fitness for a mutant increasing dominance of the largest allele, and for a mutant increasing the probability to mate assortatively. Parameters as in Fig. 2, with randomly mating residents without dominance bias, and therefore (in black) the same region of noncoexistence. Contours are plotted at the values -1 , 0 and 1 . A dark shading indicates that selection for or against assortative mate choice is stronger than selection on the dominance modifier locus. Therefore the shading indicates relative strengths of selection, not in which direction assortative mate choice or dominance modification will evolve. The solid line indicates the 0 -contour of the log-ratio, where ... [continued]

Figure 4 [Continued]: . . . absolute values of invasion fitnesses for dominance and assorting are equal. In the white area, dominance has invasion fitness at least e ($= 2.718\ldots$) times larger than assortative mate choice; in the dark grey area, that ratio is smaller than $1/e$. Fig. 4a: Simultaneous hermaphrodites with female mate choice. Mutations on the second locus induce a tendency $\alpha = 0.05$ of mating assortatively in mutant heterozygotes. Mutations on the dominance modifier locus shift the phenotype of heterozygotes 5% towards that of homozygotes for the allele with the largest value at the ecological locus (i.e., X_2X_2). Fig. 4b: Mate choice by mutant males and females. Mutations on the second locus induce a tendency $\alpha = 0.05$ of mating assortatively. Mutations on the dominance modifier locus shift the phenotype of heterozygotes 5% towards that of homozygotes for the allele with the largest value at the ecological locus. Fig. 4c: Simultaneous hermaphrodites with female mate choice. Mutations induce either fully assortative mate choice in the female role or full dominance of the allele with the largest ecological trait value. Fig. 4d: Mate choice by mutant males and females. Mutations induce either fully assortative mate choice by the homozygote X_1X_1 or full dominance of the allele with the largest ecological trait value.

of mutants originating in the X_1X_1 homozygote that would induce complete assortative mating or complete dominance (Fig. 4c and 4d). For the scenario of female choice (Fig. 4c), it seems that dominance is more strongly selected than assortative mate choice in a large subset of polymorphic populations. When both sexes of mutant can choose assortatively (Fig. 4d), dominance has the advantage above the line $X_1 + X_2 = 2$, in polymorphisms where the initial mutation inducing complete assorting occurs in the homozygote with the smallest value of L . However, in that area mutants for assortativeness occurring in the other homozygote would do better so that there is always a mutation for strictly assortative mate choice which is more strongly selected than those for complete dominance. The conclusion here is that the mating system as well as the magnitude of mutational steps can have a decisive influence on relative selection pressures.

Additionally, we iterated the dynamics of resident populations with either female choice and partial assortative mating or partial dominance to obtain their population dynamical equilibria, and calculated invasion fitnesses of mutants with small and large effects on either dominance or assortative mate choice. These simulations show that once partial assortative mating has evolved, evolution of the dominance modifier in small steps halts due to the strongly stabilizing sexual selection this mate choice exerts. For the parameter values used in Figure 1, we see these effects already when 20% of matings are assortative. However, dominance modifiers which can induce complete dominance can still invade in some ecological polymorphisms, but their invasion fitness is always smaller than that of a mutant inducing complete assortative mating. Mate choice evolves towards stronger assortment in response to heterozygote disadvantage, as before. When partial dominance has evolved while mating is still random, invasion fitnesses for dominance modifiers with small (resp. large) effects are always larger in magnitude than for mutants of mate choice with small (resp. large) effects. Further evolution of dominance also seems to be determined mostly by the pattern of heterozygote (dis)advantage. If an allele comes closer and closer to complete dominance, then the patterns of demo-

graphic differences between heterozygote and dominant homozygote and of heterozygote (dis)advantage coincide more and more. Overall, these results suggest that dominance and assortative mate choice can act as valid alternatives: as soon as one of these two responses has appeared, the probability that this response will evolve further by invasion of a mutant with a more extreme trait value increases in comparison to that of the other response appearing by invasion of a mutant in the appropriate locus. We did not investigate evolution in populations with both partial dominance and partially assortative mate choice, which is an issue that deserves further study.

8 Discussion

When two alleles are present at a locus with an ecological impact, complete assortative mating and complete dominance by one allele are two strategies which remove an intermediate phenotype from a randomly mating population. This phenotype is then removed respectively by avoiding its production, or by changing it to a more advantageous one. The invasion of both strategies is shown to be selectively favoured when there is heterozygote disadvantage, a condition which necessarily holds close to an evolutionary branching point. Evolutionary branching points play an important role in models of diversification: they are points in the trait space where disruptive frequency-dependent selection will lead to the emergence of a genetic polymorphism, from a population originally containing only one genotype. Near evolutionary branching points, the resident population will remain polymorphic throughout subsequent allele substitutions. However, whether dominance modification or assortative mate choice is the more advantageous strategy to remove an “unfit” heterozygote in such polymorphisms turns out to depend on the mating system, on the allele frequencies in the resident population and on the magnitude of mutational steps towards dominance or completely assortative mate choice. It is also shown that the invasion of assortative mating, both by small and very large steps but on condition of no costs to choosiness, purely depends on the pattern of heterozygote disadvantage, whereas this only holds for the invasion of complete dominance and not for modifiers with a small influence on the phenotype. In the last case, the demographic contribution of the modified heterozygote phenotype relative to the original heterozygote phenotype determines invasion fitness.

The results we have derived for polymorphisms near evolutionary branching points, where the heterozygote is at or near a fitness minimum, give conditions for which type of modification of the heterozygote gets a head start relative to the other. This advantage can be such that it tilts the balance between these two alternatives decisively. Our results from the numerical example suggest that dominance modification and assortative mate choice are indeed not just different evolutionary responses in randomly mating ecological polymorphisms, but valid alternatives where an already established response decreases the probability that the other type of response will appear. However, further study should assess whether that is always the case and whether in populations with both partial dominance and partial assortative mate choice one of these two responses usually evolves away. We be-

lieve that dominance modification should go more easily towards complete dominance than mate choice towards perfect assortment. Assortative mate choice often engenders sexual selection against choosiness, which can halt assortative mate choice evolution in a polymorphism or at partially assortative choice. Costs of choosiness might also make it more difficult to reach fully assortative choice gradually than in a single step. A further possibility that may occur in scenarios where individuals of both sexes can be choosy, is that all homozygotes of one ecological type carry only the random mating allele while those of the other type only carry the assortative choice allele, which results in a strictly assortatively mating population even though only about half the population has the strict mate choice strategy. When assortative mate choice or dominance of either of the two original alleles do evolve to completion, the results are superficially identical in all three situations — an equilibrium population with two distinct phenotypes, — but may mask rather large genetical differences. For example, if the (homozygous) phenotypes occur at a 3:1 ratio at equilibrium, then the three situations lead respectively to p_1 values of 0.75, 0.5 and 0.866. In the first scenario there will be reproductive isolation of two subpopulations, while dominance evolution can cause very unequal frequencies of the two alleles. In real and finite populations, this can influence persistence of the community under study as alleles become more or less prone to effects of demographic stochasticity depending on the outcome. On top of the consequences of differences in strengths of selection, such stochastic processes may affect the probability that sympatric species or ecological polymorphisms with dominance are observed.

The evolution of assortative mate choice and the reproductive isolation it engenders has been studied in many similar scenarios of sympatric speciation in recent years (e.g., Dieckmann & Doebeli, 1999). The plausibility of assortative mate choice evolution actually leading to sympatric speciation in scenarios with disruptive frequency-dependent selection is an issue of ongoing debate (e.g., Gavrilets, 2005; Pennings *et al.*, 2008), and such discussions should always consider the alternative responses, of which we investigated dominance evolution here. It is fortuitous that assortative mating turns out to be the more probable invader immediately after an evolutionary branching event, if the two resident ecological alleles are equally frequent and one sex is responsible for mate choice: these are exactly the conditions occurring in the mutation-limited implementation of the much-discussed Dieckmann & Doebeli (1999) symmetric competition model. Many models (e.g., Dieckmann & Doebeli, 1999; Gavrilets & Boake, 1998; Matessi *et al.*, 2001; Pennings *et al.*, 2008) use a mating function to regulate the acceptance or rejection of partners, which is often based on phenotypic distance. Appendix G shows that mating functions can easily be implemented in our modelling, by adjusting the values in the pair matrix (5). This appendix goes on to show that only at symmetric equilibria and on condition that the mating function is such that a homozygote rejects heterozygotes and homozygotes of the other type at the same rate, there is a strict correspondence between parameter values in our models with or without a mating function. Dieckmann & Doebeli (1999), Matessi *et al.* (2001), and Pennings *et al.* (2008) restrict themselves to such equilibria, thus allowing for direct numerical comparisons. Equivalent results are expected for general mating functions, as the differences are rather small from the models we treated up to here, even though

is no direct correspondence: if heterozygotes perform badly then it is clearly advantageous for one homozygote to reject the other type of homozygote at an even higher rate than heterozygotes, representing a selective advantage over the assortative mutants as modelled here; but again the same qualitative results follow since either type of rejection is advantageous. We have not considered any cost to choosiness, as for example Bolnick (2006), Schneider (2006) and Kopp & Hermisson (submitted) do. Kopp & Hermisson (submitted) find that this cost is negligible as long as the individuals have about ten mating opportunities, but this number might be an optimistic estimate as they only consider the symmetric case $p_1 = p_2$. Unless empirical observations confirm that most ecological dimorphisms have symmetric allele frequencies, one should be aware that assuming equal allele frequencies (e.g., Dieckmann & Doebeli, 1999; Pennings *et al.*, 2008 treats the asymmetric case in an appendix; Kopp & Hermisson, submitted) constrains models in such a way that selection gradients for dominance modification are minimized.

We also briefly compare our results for models without spatial structure with spatially structured situations. Dickinson & Antonovics (1973) investigated the evolution of dominance, assortative mating and also selfing or linkage in a two-niche model with limited migration between the patches. They found different strengths of selection on for example linkage and dominance or assortative mate choice, but considered dominance and assortative mate choice much less as alternative evolutionary outcomes as we do here. The most probable cause for this difference is that we consider the possibility that traits at the modifier and mating loci evolve gradually by mutation and invasion, while Dickinson & Antonovics (1973) were more concerned with finding ranges of trait values able to invade a given resident population. The most well-known prediction for dominance evolution in spatially structured populations is that common alleles can become dominant so that locally adapted populations avoid the phenotypic effects of relatively rare, maladapted immigrants (Otto & Bourguet, 1999). Similarly, in our modelling of a well-mixed population, selection on dominance modification seems strongest when an allele is at high frequency in a polymorphism. However, with heterozygote disadvantage, homozygotes of the most common allele will contribute much less per capita to the next generation (in terms of L) than homozygotes of the least common allele in the polymorphism. Given that the conditions apply which hold near evolutionary branching points, the relatively rare allele will evolve to become dominant and not the most common allele.

We have tried to carry out the analysis of a general model, but had to accept several restrictive assumptions to achieve analytical results, on top of the typical assumptions of adaptive dynamics approximations Waxman & Gavrillets (2005). We therefore have to carefully reconsider the assumptions made throughout this paper, and express our confidence in the validity of the results for cases where these assumptions will not hold.

If differences in the roles of females and males cannot be ignored in the equations for the population dynamics, we expect selection pressures on assortative mate choice to require more elaborate calculations. However, the strength of selection on assortative mate choice traits must in general depend on the proportion of individuals, within the population, in which the traits are actually expressed and functional. Therefore selection will be stronger for traits which induce assortative

mate choice in more classes of individuals. We thus suggest that in general, the odds for the establishment of assortative mate choice are largest when mate choice traits can be expressed and functional in all individuals in the mating pool, while avoiding fitness costs incurred by choosiness. Equations for the population dynamics were written with the adults as census population. To switch from adult to newborn frequencies (as is implicitly done at the start of the calculations in Appendix B) is trivial, as allele frequencies of reproducing adults and their offspring are the same with random mating, and newborn zygote frequencies are Hardy-Weinberg distributed. One can therefore simply choose one's census point for the calculations as the results will not differ. However, genotype frequencies of adults are relatively easy to estimate in a genetic polymorphism with discrete categories. Rewriting the results in terms of newborn genotype frequencies requires using the demographic functions L as well, and such demographic functions are usually difficult to estimate.

From our analysis of the ratio of the selection gradients, it is clear that those are often similar in magnitude. Therefore genetic constraints like the variance and frequency of the mutations under consideration (15) will usually play a major role. One way to eliminate strong effects of genetic constraints on predictions is to limit comparisons of different populations to those populations and species where one expects genetic constraints not to differ very much, which seems a reasonable assumption for comparisons limited to closely related species. Therefore, our predictions based on relative strengths of selection, are conditional on the assumption of similar genetic constraints in the systems compared.

Our calculations were in terms of the phenotypic effects of mutant heterozygotes. Whether mutant modifier or assortative mate choice alleles were dominant or not relative to the resident modifier or mate choice allele was left open. We only considered invasion dynamics, which does not involve mutant homozygotes. If disruptive selection on the ecological phenotypes is strong enough (Matessi *et al.*, 2001) and when mutant alleles are not completely dominant, we expect that mutants on the modifier and mating loci in many cases will also go to fixation if they can invade. However, there must be cases possible where a polymorphism at the modifier and mating loci gets established as well. Next to cases where choosiness leads to a disadvantage in terms of the range of potential mating partners, polymorphisms of that kind become more plausible if another cost of assorting would be introduced, or with linkage between the ecological and modifier loci in a spatially structured population (Otto & Bourguet, 1999). The choice of modelling dominance modification by a single, scalar parameter while the ecological trait is multidimensional can be relaxed by using a diagonal matrix allowing for trait-specific dominance instead (Van Dooren, 2006). In a population with an exactly intermediate heterozygote phenotype, selection on a dominance modifier which changes dominance in only a subset of traits is probably usually weaker than for a dominance modifier which affects all relevant ecological traits simultaneously. With dominance changes in all ecological traits of comparable magnitude, the results should be similar to the ones we present. If modifiers can change dominance in the ecological traits in a trait-specific manner, such that there are as many modifier traits as ecological ones, and if additionally these modifier traits show trait-specific dominance in the way modifier alleles determine modifier traits, then antagonis-

tic pleiotropy at the modifier locus can occur. In that case our approach can break down since such cases are especially prone to lead to polymorphism at modifier loci. Assortative mate choice as we chose to model it is not affected by this issue, as it can work perfectly with mate choice depending on a single polymorphic trait for distinguishing genotypes. However, when assortative mate choice depends on a function of different phenotypic distances, then similar phenomena might occur.

To summarize, our results yield the following predictions: (1) assortative mate choice has a larger chance of establishment than dominance modification when resident allele frequencies are symmetric, (2) assortative mate choice is more strongly selected when mate choice traits are effective in a larger proportion of individuals in the mating pool, and (3) dominance modification is more likely to appear than mate choice when allele frequencies are very asymmetric in a polymorphism and evolution acts only through a gradual increase in trait values.

Acknowledgements Michael Kopp, Pleuni Pennings, Hans Metz, and an anonymous reviewer gave plenty of helpful comments on the manuscript. Michel Durinx is supported by the Dutch national science organization (NWO) through PhD grant 809.34.002 and Tom Van Dooren received a Dutch NWO-VENI post-doc grant.

Appendices¹

A Parental roles and investments

At the start of this paper we have assumed that the phenotype or genotype of the parents does not directly influence the number of their offspring, nor their birth state and hence their initial survival. As a consequence, zygotes are produced in accordance with the proportions operator P_{rnd} (1). For example, there are four possible types of parent couples that create X_1X_1 -type zygotes, a fact reflected by the first two columns of the first row of P_{rnd} ; these four distinct influxes were subsequently assimilated into two components by using allele frequencies instead of diploid frequencies (2). In most scenarios where the parents' genotype matters, none of this can happen: if for example the female's body mass strongly influences the offspring number (as it does for e.g. fishes and arthropods) and there is a size difference between X_1X_1 and X_1X_2 females then the entries in the pair matrix must change, given that here it matters who is the female in each pairing as well as what relative (dis)advantage the female's genotype represents.

To see if we can allow some influence by one or both parents' genotype, let us look what would change in the next-generation operator. By putting the proportions of females in the three (zygotic) states ρ_{f_1} , ρ_{f_2} and ρ_{f_3} in a diagonal matrix R_f , the female population (vector) can be written as $R_f n$. Dividing the average offspring number of each maternal type by the population's average, we can formulate relative maternal influences f_1 , f_2 and f_3 (respectively, for mothers of type X_1X_1 , X_1X_2 and X_2X_2), and gather these in another diagonal matrix, F . (Obviously by the same token differences in offspring quality instead of quantity can be

¹Appendices A and G were not included in the manuscript as accepted by *Evolution*.

accounted for, as needed for example in those cases where differing birth weights correlate with differing offspring survival rates.)

Using the male genotype frequencies p_{11}^m , p_{12}^m and p_{22}^m which are calculated as e.g.

$$p_{11}^m := \frac{(1 - \rho_{f_1})n_{11}}{(1 - \rho_{f_1})n_{11} + (1 - \rho_{f_2})n_{12} + (1 - \rho_{f_3})n_{22}} \quad (20)$$

each female will pair with males according to the pair matrix

$$P_{rnd}^m = \begin{bmatrix} p_{11}^m m_1 + \frac{p_{12}^m}{2} m_2 & \frac{p_{11}^m}{2} m_1 + \frac{p_{12}^m}{4} m_2 & 0 \\ p_{22}^m m_3 + \frac{p_{12}^m}{2} m_2 & \frac{p_{11}^m}{2} m_1 + \frac{p_{12}^m}{2} m_2 + \frac{p_{22}^m}{2} m_3 & p_{11}^m m_1 + \frac{p_{12}^m}{2} m_2 \\ 0 & \frac{p_{22}^m}{2} m_3 + \frac{p_{12}^m}{4} m_2 & p_{22}^m m_3 + \frac{p_{12}^m}{2} m_2 \end{bmatrix} \quad (21)$$

where the relative male genotype-dependent influences m_1 , m_2 and m_3 on offspring quantity (or quality) are already taken into account and are calculated similar to the female influences f_i . (Here we note that P_{rnd}^m , just like P_{rnd} , has determinant zero since its middle column is the average of the first and last.)

From the preceding considerations, the next-generation equation now looks like

$$\mathbf{n}(t+1) = L P_{rnd}^m F R_f \mathbf{n}(t) \quad (22)$$

To make this equation resemble the original population dynamics more, the densities could be rescaled as $\tilde{\mathbf{n}}(t+1) := F R_f \mathbf{n}(t+1)$ and the (diagonal) survival matrix as $\tilde{L} := F R_f L$, so the next-generation equation becomes

$$\tilde{\mathbf{n}}(t+1) = \tilde{L} P_{rnd}^m \tilde{\mathbf{n}}(t) \quad (23)$$

However, there is no way to solve this in general, as there now are many more unknowns as before (the male and female frequencies which are equivalent to four independent variables, and similarly the male and female relative fertility rates). Furthermore, we can now not switch from zygote to allele frequencies, nor something similar, to reduce the number of unknowns by one (cf. Eq. (2)). Therefore such rescalings, while bringing an outward resemblance to the original dynamics, do not help in the search for a solution and we should stick with Equation (22).

If all sex ratios are equal ($\rho_{f_1} = \rho_{f_2} = \rho_{f_3} = \rho_f$) and all male and female relative fertility rates are at the same values ($m_1 = m_2 = m_3 = 1$ necessarily, and $f_1 = f_2 = f_3 = 1$), then same system of equations as the original dynamics is found (up to ρ_f , to be absorbed into L , with the difference stemming from the fact that all individuals in the original system were implicitly hermafrodites). But as long as either the male or the female fertility rates differ from one another, there are too many variables to solve the equation system (22). While it was a choice in this appendix to model the parental influences multiplicatively, other choices will lead to the same problem of having too little equations to solve sufficiently many variables, so the conclusions of this appendix are general.

B The resident population dynamics

That the resident population of randomly mating diploids is at a stable equilibrium is equivalent to the simple dominant eigenvalue of L_{rnd} being 1; for this matrix $\mathbf{n} = L_{\text{rnd}} \mathbf{n}$ or alternatively

$$\mathbf{p} = L_{\text{rnd}} \mathbf{p} \quad (24)$$

To solve this equation analytically (for the five unknowns L_1 , L_2 , L_3 , p_{11} and p_{12} , as p_1 , p_2 and p_{22} follow from these) is not immediately feasible. It can be done by the following trick: although the parents are not necessarily distributed at Hardy-Weinberg frequencies, the zygotes always are:

$$\begin{bmatrix} p_1 & p_1/2 & 0 \\ p_2 & 1/2 & p_1 \\ 0 & p_2/2 & p_2 \end{bmatrix} \begin{pmatrix} p_{11} \\ p_{12} \\ p_{22} \end{pmatrix} = \begin{bmatrix} p_1 \left(p_{11} + \frac{p_{12}}{2} \right) \\ p_2 p_{11} + (p_1 + p_2) \frac{p_{12}}{2} + p_1 p_{22} \\ p_2 \left(p_{22} + \frac{p_{12}}{2} \right) \end{bmatrix} = \begin{pmatrix} p_1^2 \\ 2p_1 p_2 \\ p_2^2 \end{pmatrix}$$

Instead of $\mathbf{p} = L_{\text{rnd}} \mathbf{p}$ (24), we can equivalently solve $P_{\text{rnd}} \mathbf{p} = P_{\text{rnd}} L_{\text{rnd}} \mathbf{p}$,

$$\begin{pmatrix} p_1^2 \\ 2p_1 p_2 \\ p_2^2 \end{pmatrix} = \begin{bmatrix} L_1 p_1 & L_2 p_1/2 & 0 \\ L_1 p_2 & L_2/2 & L_3 p_1 \\ 0 & L_2 p_2/2 & L_3 p_2 \end{bmatrix} \begin{pmatrix} p_1^2 \\ 2p_1 p_2 \\ p_2^2 \end{pmatrix} \quad (25)$$

This set of third order equations in p_1 (and p_2) can be simplified to

$$\begin{cases} 0 &= p_1^2(L_1 p_1 + L_2 p_2 - 1) \\ 0 &= p_1 p_2(L_1 p_1 + L_2 + L_3 p_2 - 2) \\ 0 &= p_2^2(L_2 p_1 + L_3 p_2 - 1) \end{cases} \quad (26)$$

As we are looking at the situation where two different alleles X_1 and X_2 occur together, we know that $p_1 \neq 0$ and $p_2 \neq 0$. Therefore we have the three following useful properties,

$$L_2 p_2 = 1 - L_1 p_1 \quad (27)$$

$$L_2 = 2 - L_1 p_1 - L_3 p_2 \quad (28)$$

$$L_2 p_1 = 1 - L_3 p_2 \quad (29)$$

where the second is just the sum of the other two. After eliminating $p_2 = 1 - p_1$ from the equations, the first equation can be rewritten into

$$p_1(L_1 - L_2) = 1 - L_2$$

So if $L_1 = L_2$ then $L_2 = 1$ and hence $L_3 = 1$ as well, and we end up in the Hardy-Weinberg case. If however $L_1 \neq L_2$ then p_1 can be eliminated from (29) to find

$$L_2 = 1 \pm \sqrt{(L_1 - 1)(L_3 - 1)} \quad (30)$$

which shows that $L_1 \neq 1$ and for similar reasons $L_3 \neq 1$, as that would put us again in the Hardy-Weinberg situation. Thus L_1 and L_3 are either both strictly smaller or

both strictly larger than 1, since L_2 is necessarily real. If both are smaller, then the smaller solution for L_2 (30) leads to an improper value of p_1 ,

$$\frac{1 - L_2}{L_1 - L_2} = \frac{1 - 1 + \sqrt{(1 - L_1)(1 - L_3)}}{\sqrt{(1 - L_1)(1 - L_3)} - (1 - L_1)} = \frac{\sqrt{(1 - L_3)}}{\sqrt{(1 - L_3)} - \sqrt{(1 - L_1)}} > 1$$

while the larger solution

$$L_2 = 1 + \sqrt{(1 - L_1)(1 - L_3)} \quad (31)$$

leads to

$$p_1 = \frac{1 - 1 - \sqrt{(L_1 - 1)(L_3 - 1)}}{(L_1 - 1) - \sqrt{(L_1 - 1)(L_3 - 1)}} = \frac{\sqrt{1 - L_3}}{\sqrt{1 - L_1} + \sqrt{1 - L_3}} \quad (32)$$

so that $0 < p_1 < 1$ and $L_2 > 1$ if $L_1, L_3 < 1$.

On the other hand, when both L_1 and L_3 are larger than 1, then it is the larger solution for L_2 that leads to an impossible value $p_1 = (1 - L_2)/(L_1 - L_2) < 0$. Therefore the unique solution in this case is

$$L_2 = 1 - \sqrt{(L_1 - 1)(L_3 - 1)} \quad (33)$$

which leads to a feasible value $0 < p_1 < 1$ of

$$p_1 = \frac{1 - 1 + \sqrt{(L_1 - 1)(L_3 - 1)}}{(L_1 - 1) + \sqrt{(L_1 - 1)(L_3 - 1)}} = \frac{\sqrt{L_3 - 1}}{\sqrt{L_1 - 1} + \sqrt{L_3 - 1}} \quad (34)$$

Note that in the last case $p_1 < p_2$ if $L_1 > L_3$, which is the opposite of the case before. An important caveat is that one must keep in mind that Equations (31)–(34) only hold for randomly mating populations.

From equation (25) we know that 1 is an eigenvalue of L_{rnd} at the above values of L_2 and p_1 , but we still need to prove that it is the dominant one. To that end, we solve the characteristic equation of L_{rnd} directly (feasible as 0 is another eigenvalue), and find that the nonzero eigenvalues satisfy

$$\lambda_{1,2} = \frac{1}{4}(L_2 + 2L_1 p_1 + 2L_3 p_2) \pm \frac{1}{4}\sqrt{\mathbb{D}} \quad (35)$$

where $\mathbb{D} := (L_2 + 2L_1 p_1 + 2L_3 p_2)^2 - 8(L_1 L_2 p_1^2 + L_2 L_3 p_2^2 + 2L_1 L_3 p_1 p_2)$. Using (27–29) it is straightforward to simplify this to

$$\lambda_{1,2} = \frac{1}{4}(4 - L_2) \pm \frac{1}{4}L_2 \quad (36)$$

so since $0 < L_2 < 2$ it is clear that the largest eigenvalue is 1 and the smallest 0, with the third at $1 - L_2/2$. Thus we know furthermore that the dominant eigenvalue is simple (as required to calculate its derivative (37)).

C Derivatives of $L_{A(\alpha)}$ at $\alpha = 0$

The derivative for α of the (simple, cf. (36)) dominant eigenvalue λ_d of matrix $L_{A(\alpha)}$ at $\alpha = 0$ is

$$\frac{\partial \lambda_d}{\partial \alpha} \Big|_{\alpha=0} = \frac{1}{v^\top u} v^\top \frac{\partial L_{A(\alpha)}}{\partial \alpha} \Big|_{\alpha=0} u \quad (37)$$

where u and v^\top are respectively the dominant right and left eigenvectors of $L_{A(0)}$ (e.g., Magnus & Neudecker, 1988). Those eigenvectors are

$$\begin{aligned} v^\top &= (1 \ 1 \ 1) \\ u &= (p_1^2 L_1 \ 2p_1 p_2 L_2 \ p_2^2 L_3)^\top \\ &= (p_1 - p_1 p_2 L_2 \ 2p_1 p_2 L_2 \ p_2 - p_1 p_2 L_2)^\top \end{aligned} \quad (38)$$

where u was given as the stable genotype distribution (4); its alternative form, following from the Equations (27) & (29), shortens the next calculation (39). The same two equations also let us easily show that $(1 \ 1 \ 1) L_{\text{rnd}} = (1 \ 1 \ 1)$.

Obviously $(\partial L_{A(\alpha)} / \partial \alpha)|_{\alpha=0} = L_A - L_{\text{rnd}}$. So we have, since $v^\top u = 1$, that

$$\begin{aligned} \frac{\partial \lambda}{\partial \alpha} \Big|_{\alpha=0} &= v^\top (L_A - L_{\text{rnd}}) u \\ &= (L_1 \ L_2 \ L_3) \begin{bmatrix} p_2 & \frac{1-2p_1}{4} & 0 \\ -p_2 & 0 & -p_1 \\ 0 & \frac{2p_1-1}{4} & p_1 \end{bmatrix} \begin{pmatrix} p_1 - p_1 p_2 L_2 \\ 2p_1 p_2 L_2 \\ p_2 - p_1 p_2 L_2 \end{pmatrix} \\ &= p_1 p_2 (L_1 - 2L_2 + L_3) - \frac{1}{2} p_1 p_2 L_2 (L_1 - 2L_2 + L_3) \\ &= p_1 p_2 \left(1 - \frac{L_2}{2}\right) (L_1 + L_3 - 2L_2) \end{aligned} \quad (39)$$

D Calculations for strictly assortative residents

When the residents are mating strictly assortatively, the transition matrix is L_{ass} (8). Note that the conversion rules (27)–(29) do not apply, so L_2 is not known in function of L_1 and L_3 as before.

We can see that the set of eigenvalues of L_{ass} is $\{L_1, L_2/2, L_3\}$ and that there are only two possible cases in which both X_1 and X_2 are present:

1. $L_2 = 2, L_1 < 1, L_3 < 1$, with stable equilibrium frequencies

$$\begin{pmatrix} p_{11} \\ p_{12} \\ p_{22} \end{pmatrix} = \frac{1}{4 - 3L_1 - 3L_3 + 2L_1 L_3} \begin{pmatrix} L_1(1 - L_3) \\ 4(1 - L_1)(1 - L_3) \\ L_3(1 - L_1) \end{pmatrix} \quad (40)$$

2. $L_2 \leq 2, L_1 = L_3 = 1$, with stable equilibrium frequencies $(p_{11}, p_{12}, p_{22})^\top = (p_1, 0, p_2)^\top$. Note that here the values of L_2 and p_1 depend on the model in question.

Note that in the second case, the (absent) heterozygote may or may not have an ecological advantage, so we cannot classify these cases with the labels *heterozygote (dis)advantage*. In the second case, even a heterozygote with an ecological advantage will gradually disappear from the population due to the assortative choices individuals make.

As remarked before, if residents of both sexes are choosy then no mutation inducing a tendency for random mating can invade, so only those models where one sex is potentially choosy have to be considered. In Case 1, we can use the technique in Appendix C to find the derivative of the dominant eigenvalue of $L_{a(\omega)}$ at $\omega = 0$. Here $v^T := (0 \ 1 \ 0)$ is a suitable left eigenvector of L_{ass} , and for the right eigenvector u we use the frequency vector p (40). Then we see that $L_{a(\omega)}$ can invade since

$$\begin{aligned} \frac{\partial \lambda_d}{\partial \omega} \Big|_{\omega=0} &= \frac{1}{v^T u} v^T \frac{\partial L_{a(\omega)}}{\partial \omega} \Big|_{\omega=0} u \\ &= \frac{1}{2p_{12}} (0 \ 1 \ 0) \begin{bmatrix} L_1 & 0 & 0 \\ 0 & 2 & 0 \\ 0 & 0 & L_3 \end{bmatrix} \begin{bmatrix} -p_2 & \frac{2p_1-1}{4} & 0 \\ p_2 & 0 & p_1 \\ 0 & \frac{2p_2-1}{4} & -p_1 \end{bmatrix} \begin{pmatrix} p_{11} \\ p_{12} \\ p_{22} \end{pmatrix} \\ &= \frac{2p_2 p_{11} + 2p_1 p_{22}}{2p_{12}} > 0 \end{aligned} \quad (41)$$

In Case 2, there are no resident heterozygotes. Thus a choosy mutant heterozygote cannot reproduce, and we have to alter the middle column of $L_{a(\omega)}$ to reflect this:

$$L_{a(\omega)} = \begin{bmatrix} L_1 & 0 & 0 \\ 0 & L_2 & 0 \\ 0 & 0 & L_3 \end{bmatrix} \begin{bmatrix} 1 - \frac{\omega}{2} p_2 & \frac{\omega}{4} p_1 & 0 \\ \frac{\omega}{2} p_2 & \frac{\omega}{4} & \frac{\omega}{2} p_1 \\ 0 & \frac{\omega}{4} p_2 & 1 - \frac{\omega}{2} p_1 \end{bmatrix}$$

In the limit $\omega = 0$, this mutant is a resident although the transition matrix differs due to our considerations, and the dominant eigenvalue still is 1 as it should be. However, this is a double eigenvalue, so we cannot use the technique we used in Case 1. Therefore we do a perturbation expansion instead, which starts from the characteristic polynomial of $L_{a(\omega)}$,

$$\begin{aligned} CP(L_{a(\omega)}, \lambda) &= \left(1 - \frac{\omega}{2} p_2 - \lambda\right) \left(\left(\frac{\omega}{4} L_2 - \lambda\right) \left(1 - \frac{\omega}{2} p_1 - \lambda\right) - \left(\frac{\omega}{4} p_2\right) \frac{\omega}{2} L_2 p_1\right) \\ &\quad - \frac{\omega}{2} L_2 p_2 \left(\frac{\omega}{4} p_1\right) \left(1 - \frac{\omega}{2} p_1 - \lambda\right) \\ &= -\lambda^3 + \frac{\lambda^2}{4} (8 - (2 - L_2)\omega) - \frac{\lambda}{8} (8 + 4(L_2 - 1)\omega - (L_2 + 2(L_2 - 1)p_1 p_2)\omega^2) \\ &\quad + \frac{\omega}{8} L_2 (2 - \omega(1 + 2p_1 p_2) + \omega^2 p_1 p_2) \end{aligned} \quad (42)$$

If we assume that eigenvalues can be written as $\lambda = c_0 + c_1\omega + c_2\omega^2 + O(\omega^3)$ for some coefficients c_i , we can calculate these coefficients one by one as needed. Replacing λ by c_0 and setting $\omega = 0$, the polynomial reduces to $-c_0(c_0 - 1)^2$ which

only gives us the three eigenvalues of L_{ass} we already knew (not exactly, as $L_2/2$ has been replaced by 0 due to changing the middle column of $L_{a(\omega)}$). To expand around the dominant eigenvalue of L_{ass} , we replace λ by $1 + \omega c_1$. Then the polynomial can be divided by ω^2 , and evaluating it subsequently at $\omega = 0$ reduces it to $-(4c_1^2 + 2c_1 + p_1 p_2)/4$. Solving this, we find that the dominant eigenvalue of $L_{a(\omega)}$ is one of

$$\lambda_1 = 1 - \frac{\omega}{2} p_1 + O(\omega^2), \quad \lambda_2 = 1 - \frac{\omega}{2} p_2 + O(\omega^2) \quad (43)$$

and hence smaller than 1, implying negative invasion fitness.

E Eigenvalues of $L_{D(\delta)}$ and their derivatives

Clearly the characteristic polynomial of

$$L_{D(\delta)} = \begin{bmatrix} L_1 & 0 & 0 \\ 0 & L_2^\delta & 0 \\ 0 & 0 & L_3 \end{bmatrix} \begin{bmatrix} p_1 & p_1/2 & 0 \\ p_2 & 1/2 & p_1 \\ 0 & p_2/2 & p_2 \end{bmatrix} \quad (44)$$

has the same solutions as that of L_{rnd} when replacing L_2 by L_2^δ , so the eigenvalues are 0 and, from Equation (35),

$$\lambda_{1,2} = \frac{1}{4}(L_2^\delta + 2L_1 p_1 + 2L_3 p_2) \pm \frac{1}{4}\sqrt{\mathbb{D}} \quad (45)$$

where $\mathbb{D} := (L_2^\delta + 2L_1 p_1 + 2L_3 p_2)^2 - 8(L_1 L_2^\delta p_1^2 + L_2^\delta L_3 p_2^2 + 2L_1 L_3 p_1 p_2)$. As L_1 , L_3 and p_1 are determined by the resident dynamics, we can use their conversion rules (27)–(29) in the same way as before (Eq. (36)):

$$\begin{aligned} \lambda_{1,2} &= \frac{1}{4}(4 + L_2^\delta - 2L_2) \\ &\quad \pm \frac{1}{4}\sqrt{(4 + L_2^\delta - 2L_2)^2 - 8L_2^\delta p_1(1 - L_2 p_2)} \\ &= \frac{1}{4}(4 + L_2^\delta - 2L_2) \pm \frac{1}{4}\sqrt{(2L_2 - L_2^\delta)^2 + 16p_1 p_2 L_2(L_2^\delta - L_2)} \quad (46) \end{aligned}$$

where the dominant eigenvalue is necessarily the $(+\sqrt{\cdot})$ -form. From Eq. (46) we see that for any $L_2^\delta > L_2$, the dominant eigenvalue is

$$\lambda_1 > \frac{1}{4}(4 + L_2^\delta - 2L_2) + \frac{1}{4}|2L_2 - L_2^\delta| \geq 1 \quad (47)$$

(and similarly $\lambda_1 < 1$ if $L_2^\delta < L_2$). This gives a criterium for the sign of invasion fitness for small mutational steps when the resident population has no phenotypic bias ($\delta = 0$). It also shows that mutations inducing complete dominance of one allele over the other ($\delta = 1, -1$) have positive fitness in case of heterozygote disadvantage but negative in case of advantage (cf. Eq. 5).

Completely assortative mutant that appears in X_1X_1 or X_1X_2		Mutant that turns $\phi(X_1, X_2)$ into $\phi(X_1, X_1)$		Example (L_1, L_3)
X_1X_1 or X_1X_2	X_2X_2	$\phi(X_1, X_1)$	$\phi(X_2, X_2)$	
1	2	3	4	(1.10, 1.05)
1	3	2	4	(1.20, 1.10)
1	4	2	3	(1.40, 1.10)
3	4	1	2	(1.50, 1.45)
2	4	1	3	(1.60, 1.50)
2	3	1	4	impossible

Table IV.1: size ranking of fitness gradients of mutants.

If there is heterozygote disadvantage, it is not possible to say offhand whether a mutant that mates strictly assortatively or one with a completely dominant allele has a higher selection gradient, and hence better chance of invading and establishing itself in the population. In fact, if we consider the case where mutants of both sexes can be choosy and assume (without loss of generality) that $L_1 > L_3$, five distinct rankings are possible (out of a hypothetical $4! = 24$) of the selection gradients for the four types of “strict” mutations: inducing complete dominance of X_1 , complete dominance of X_2 , or strictly assortative mate choice while first appearing in an individual of type X_2X_2 , or strictly assortative mate choice but appearing in one of type X_1X_2 or X_1X_1 . Half of those 24 orderings are impossible because mutations causing strict assortative mating and appearing first in a X_2X_2 individual can never spread to the X_1X_2 or X_1X_1 subpopulations if both partners can be choosy, which results in the lower fitness value $\log(L_3)$ instead of $\log(L_1)$ for those that can spread to the other X_1X_1 zygotes. Since the fitness of the third and fourth type of mutant is the logarithm of the $+\sqrt{-}$ -variant of Expression (46) with L_2^δ replaced by L_1 and L_3 respectively, a further six rankings are excluded because mutations modifying the phenotype of the heterozygote do worse if they modify it into $\phi(X_2, X_2)$ than into $\phi(X_1, X_1)$ since $L_{D(\delta)}$ is an increasing function of L_2^δ . The remaining orderings in fitness are summarized, and illustrated if possible, in Table IV.1. That the sixth and last possibility cannot occur, is easily shown by plotting the 0-contour of the inequalities in the viable zone ($L_1 > L_3 > 1, L_2 > 0$).

If we take the biologically reasonable view that individuals cannot choose perfectly according to their preference and that mistakes will be made, then the strict mate choice trait can spread between homozygotes and the second column of the table disappears. After adjusting the rankings to reflect this change, the first three cases become a single case and the fifth case merges with the impossible sixth case, so that three distinct rankings remain.

An important thing to realize is the following: the above dominant eigenvalue calculations also hold if the resident allele is $D(\delta)$ with a nonzero δ . In that situation L_1, L_2, L_3 and hence the resident transition matrix then have other values than in the original situation, but the three conversion rules (27)–(29) still apply, and the same criterium (47) holds for the invasion of mutants with a different dominance bias $D(\delta + \delta')$. Thus positive invasion fitness for this new mutant is equivalent to

$L_2^{\delta'} > L_2$ (where L_2 here is calculated for resident allele $D(\delta)$, not d).

Note that in general and for small differences δ' , either $L_2^{\delta'} > L_2$ or $L_2^{-\delta'} > L_2$ and one of either types of dominance bias can invade for some given resident bias level δ . Thus there is either a stepwise trait change until complete dominance has evolved, or evolution stops at a point where $\partial L(\phi_{\delta+\delta'}(X_1, X_2), I) / \partial \delta|_{\delta'=0} = 0$ (with I set by the resident dominance bias δ). We can call values δ such that this derivative is 0 *singular* values, and it is exactly those that were excluded by the qualification “in general”, two sentences ago. Thus we need to check whether at $\delta = 0$ dominance bias towards X_1 or X_2 can invade, find the nearest singular dominance bias level in that direction, and check whether it is an evolutionary endpoint or branching point. In that last case (which may also occur if $\delta^* = 0$), the singular values must be found for the more complicated situation of two co-occurring resident dominance biases.

To numerically compare with the case of assortative mating, we need to calculate the derivative $\partial \lambda_d / \partial \delta$ of the dominant eigenvalue of $L_{D(\delta)}$ (with no resident dominance bias) at $\delta = 0$. From Equation (46) we see that

$$\begin{aligned} \frac{\partial \lambda_d}{\partial \delta} \Big|_{\delta=0} &= \frac{1}{4} \frac{\partial L_2^\delta}{\partial \delta} \Big|_{\delta=0} + \frac{1}{4} \frac{1}{2} \left(\frac{(2L_2^\delta - 4L_2 + 16p_1 p_2 L_2) \frac{\partial L_2^\delta}{\partial \delta} \Big|_{\delta=0}}{\sqrt{(2L_2 - L_2^\delta)^2 + 16p_1 p_2 L_2 (L_2^\delta - L_2)}} \right) \Big|_{L_2^\delta = L_2} \\ &= 2p_1 p_2 \frac{\partial L_2^\delta}{\partial \delta} \Big|_{\delta=0} = 2p_1 p_2 D_1 L(X_1 - X_2) \end{aligned} \quad (48)$$

where $D_1 L$ is the partial derivative of L for its first argument, evaluated at $(X_1 + X_2, I)$ where I is set by the resident population. From this we see that whatever the resident level of dominance bias is, some mutant with a slightly different level (lower or higher) can always invade, unless $D_1 L(X_1 - X_2) = 0$.

F Invasion fitness $s_{\mathbb{X}}(Y)$ and success $L(\phi, I)$

In the following, we will compare strategies by their effects on invasion fitness (Metz *et al.*, 1992). The invasion fitness function $s_{\mathbb{X}}(Y)$ is defined as the long-term average per capita growth rate of the type Y (called the invader) in an equilibrium community $\mathbb{X} := \{X_1, X_2, \dots, X_N\}$ so that only these N types (called the residents) are present. All types are assumed to be characterized by the heritable, quantitative traits they share, i.e., these types correspond to phenotypes of clonal organisms, or values of alleles. For the randomly mating populations we are dealing with, this definition translates into

$$s_{\mathbb{X}}(Y) = \log \left(\sum_{i=1}^N L(Y + X_i, I) p_i \right) \quad (49)$$

where p_i is the frequency of the allele with strategy X_i . In the special case where there is a single resident, the formula

$$s_{\mathbb{X}}(Y) = \log(L(Y + X, I)) \quad (50)$$

also holds when there is a heterozygote phenotype with dominance bias or a tendency for assortative mating (with no cost to choosiness). Some of the immediate consequences of the definition are that a nonzero probability of invading implies and is implied by positive fitness, and that any resident type has fitness 0.

Points of special interest called evolutionarily singular points are those where the gradient (in the direction of the invader) of the fitness function is 0, since this gradient is nothing but the selection gradient. One type of singular points already mentioned are the evolutionary branching points, but others exist like the continuously stable strategies which are evolutionarily attracting but noninvadable (and hence evolutionary endpoints).

Resident alleles can only be close to each other in the neighbourhood of a singular strategy (Metz *et al.*, 1996; Geritz *et al.*, 1998), and conversely if the ecological alleles X_1 and X_2 arose from a single ancestor through evolutionary branching, then they will still be similar shortly after the branching event. In that case we can exploit this similarity, to obtain an expression for the relative strength of selection on mate choice versus dominance modification. We will also show in this appendix, through an expansion of the invasion fitness function, that heterozygote advantage or disadvantage is linked to the type of singular point we are dealing with.

The strategies being close to singular, we can introduce a small parameter ε and some vectors ξ_1 and ξ_2 such that $X_1 = X^* + U_1 = \varepsilon\xi_1$ and $X_2 = X^* + U_2 = X^* + \varepsilon\xi_2$, and consider invaders of the form $\mathbf{Y} = X^* + V$ with $V = O(\varepsilon)$. We denote by I^* the environment when only X^* occurs. When other alleles occur, the environment is expanded as $\mathbf{I} = I^* + \varepsilon I' + \varepsilon^2 I'' + O(\varepsilon^3)$. If we denote by D_1L and D_2L the partial derivatives of L at $(2X^*, I^*)$ respectively to its first and second argument, a first order expansion of the multiresident invasion fitness function (49) at X^* is

$$\begin{aligned} s_{\mathbb{X}}(\mathbf{Y}) &= \log \left(\sum_{i=1}^N L(\mathbf{Y} + \mathbf{X}_i, \mathbf{I}) p_i \right) \\ &= \log \left(L(2X^*, I^*) + D_1L \left(V + \sum_{i=1}^N p_i U_i \right) + D_2L \varepsilon I' + O(\varepsilon^2) \right) \\ &= D_1L \left(V + \sum_{i=1}^N p_i U_i \right) + D_2L \varepsilon I' + O(\varepsilon^2) \end{aligned} \quad (51)$$

Given that X^* is singular, the above expression must be 0 for any V when ε (and hence each U_i) is 0, so D_1L is the zero vector. Because each resident has fitness 0 by definition, we have furthermore that $D_2L \varepsilon I' = 0$ and hence an expansion of $\log(L)$ around $(2X^*, I^*)$ has no constant or linear terms in ε .

Similarly denoting the second order partial derivatives of L at $(2X^*, I^*)$ respectively as $D_{11}L$, $D_{12}L$ and $D_{22}L$, we see that a second order expansion of L for resident strategies X_a and X_b looks like

$$\begin{aligned} L(X_a + X_b, \mathbf{I}) &= L(2X^*, I^*) + D_2L \varepsilon^2 I'' + \frac{1}{2} (\mathbf{U}_a + \mathbf{U}_b)^T D_{11}L (\mathbf{U}_a + \mathbf{U}_b) \\ &\quad + (\mathbf{U}_a + \mathbf{U}_b)^T D_{12}L \varepsilon I' + \frac{1}{2} (\varepsilon I')^T D_{22}L \varepsilon I' + O(\varepsilon^3) \end{aligned} \quad (52)$$

Plugging this expression into the one-resident fitness function (50), we see that $D_{11}L$ is the term that depends twice on the invader. In other words,

$$D_{11}L = \frac{\partial^2 s_X(Y)}{\partial Y^2} \quad (53)$$

i.e., the one-resident fitness function twice derived in the mutant direction and evaluated at the singular strategy. This observation is useful because Equation (52) shows that the heterozygote (dis)advantage is linked to the derivative (53) by

$$\begin{aligned} L_1 + L_3 - 2L_2 &= (1+1-2) \left(L(2X^*, I^*) + D_{2L} \varepsilon^2 I'' + \frac{1}{2} (\varepsilon I')^\top D_{22}L \varepsilon I' \right) \\ &\quad + \frac{1}{2} (2U_1^\top D_{11}L 2U_1 + 2U_2^\top D_{11}L 2U_2 - 2(U_1 + U_2)^\top D_{11}L (U_1 + U_2)) \\ &\quad + (2U_1 + 2U_2 - 2(U_1 + U_2))^\top D_{12}L \varepsilon I' + O(\varepsilon^3) \\ &= 2U_1^\top D_{11}L U_1 + 2U_2^\top D_{11}L U_2 - (U_1 + U_2)^\top D_{11}L (U_1 + U_2) + O(\varepsilon^3) \\ &= (U_1 - U_2)^\top D_{11}L (U_1 - U_2) + O(\varepsilon^3) \end{aligned} \quad (54)$$

and similarly one can check that

$$L_1 - L_3 = 2(U_1 + U_2)^\top D_{11}L (U_1 - U_2) + 2(U_1 - U_2)^\top D_{12}L \varepsilon I' + O(\varepsilon^3) \quad (55)$$

Thus in a randomly mating population without dominance modification and with resident allelic traits $X_1 := X^* + \varepsilon \xi_1$ and $X_2 := X^* + \varepsilon \xi_2$, the values of L_1 , L_2 and L_3 are bound by the relationship

$$L_1 + L_3 - 2L_2 = (X_1 - X_2)^\top \frac{\partial^2 s_X(Y)}{\partial Y^2} (X_1 - X_2) + O(\varepsilon^3) \quad (56)$$

where we see that the small parameter ε measures the distance between residents and the evolutionarily singular strategy X^* , and $\partial^2 s_X(Y)/\partial Y^2$ obviously depends on the underlying ecological/population-dynamical model.

For one-dimensional strategies, Equation (56) shows that there necessarily is heterozygote disadvantage near a branching point and heterozygote advantage near a continuously stable strategy (Metz *et al.*, 1996; Geritz *et al.*, 1998), facts illustrated respectively by Figures 2a and 1a in Section 7. For higher-dimensional strategies the same dichotomy holds: if selection near X^* is stabilizing in all directions, then $\partial^2 s_X(Y)/\partial Y^2$ has only negative eigenvalues (Leimar, 2001, to appear) and the right hand side of Eq. (56) is negative; if X^* is a branching point, the right hand side of Eq. (56) is positive because the ecological strategies grow away from each other in the direction of the largest positive eigenvalue of $\partial^2 s_X(Y)/\partial Y^2$ (Stefan Geritz, lecture given at the International Conference on Computational and Mathematical Population Dynamics, Trento 2004; Hans Metz and Stefan Geritz, pers. comm.) so that $X_1 - X_2$ is also (close to) an eigenvector with the dominant eigenvalue. (Note that even in the special case where there is a multiple dominant eigenvalue, the linear combination $X_1 - X_2$ of two dominant eigenvectors returns a positive value of the right hand side of Equation (56).)

Close to a branching point we can further specify the derivative of the dominant eigenvalue for a dominance-inducing mutant (13), and similarly find how the ecological success L_2^δ of the new heterozygote depends on δ , by an expansion of L :

$$\begin{aligned} L_2^\delta &= L(\mathbf{X}_1 + \mathbf{X}_2 + \delta(\mathbf{X}_1 - \mathbf{X}_2), \mathbf{I}) \\ &= L(2\mathbf{X}^*, \mathbf{I}^*) + \frac{1}{2}(\mathbf{U}_1 + \mathbf{U}_2 + \delta(\mathbf{U}_1 - \mathbf{U}_2))^\top \mathbf{D}_{11}\mathbf{L} (\mathbf{U}_1 + \mathbf{U}_2 + \delta(\mathbf{U}_1 - \mathbf{U}_2)) \\ &\quad + (\mathbf{U}_1 + \mathbf{U}_2 + \delta(\mathbf{U}_1 - \mathbf{U}_2))^\top \mathbf{D}_{12}\mathbf{L}\varepsilon\mathbf{I}' + \frac{1}{2}\varepsilon\mathbf{I}'^\top \mathbf{D}_{22}\mathbf{L}\varepsilon\mathbf{I}' + \mathbf{D}_2\mathbf{L}\varepsilon^2\mathbf{I}'' + O(\varepsilon^3) \\ &= L_2 + \delta(\mathbf{U}_1 + \mathbf{U}_2)^\top \mathbf{D}_{11}\mathbf{L} (\mathbf{U}_1 - \mathbf{U}_2) + \frac{\delta^2}{2}(\mathbf{U}_1 - \mathbf{U}_2)^\top \mathbf{D}_{11}\mathbf{L} (\mathbf{U}_1 - \mathbf{U}_2) \\ &\quad + \delta(\mathbf{U}_1 - \mathbf{U}_2)^\top \mathbf{D}_{12}\mathbf{L}\varepsilon\mathbf{I}' + O(\varepsilon^3) \\ &= L_2 + \frac{\delta^2}{2}(L_1 + L_3 - 2L_2) + \frac{\delta}{2}(L_1 - L_3) + O(\varepsilon^3) \end{aligned} \quad (57)$$

where the last transition uses both Equations (54) and (55). Therefore the derivative of the dominant eigenvalue λ_d of $\mathbf{L}_{D(\delta)}$ at $\delta = 0$ is

$$\frac{\partial \lambda_d}{\partial \delta} \Big|_{\delta=0} = p_1 p_2 (L_1 - L_3) + O(\varepsilon^3) \quad (58)$$

$$= (p_2 - p_1)(1 - L_2) + O(\varepsilon^3) \quad (59)$$

with the second transition following from the conversion rules (27)–(29). We see that mutations distorting the heterozygote phenotype towards that of one of the two homozygotes can always invade (except in the special, symmetrical case where $L_1 = L_3$), independent of whether selection is disruptive or stabilizing at \mathbf{X}^* . Bias is always towards the homozygote that has the higher L -value. If for example L_1 is initially larger than L_3 , dominance bias towards \mathbf{X}_1 invades and increases until either $|\delta| = 1$ or a balance is reached where L_3 is larger than L_1 (cf. Equation (61)). In the special symmetrical case where $L_1 = L_3$, dominance bias cannot invade by small steps even when it would be beneficial to exhibit a nonzero amount of bias either way. From Eq. (59) we also see that if we switch from a situation with heterozygote disadvantage to one with advantage, then the direction of modifier evolution switches, from towards the more common allele to the rarer allele.

If some degree δ of dominance bias is already established in the randomly mating population, Equation (55) still holds (with changing values of L_1 , L_3 and \mathbf{I}') while Equation (54) changes into

$$\begin{aligned} L_1 + L_3 - 2L_2 &= (1 - \delta^2)(\mathbf{U}_1 - \mathbf{U}_2)^\top \mathbf{D}_{11}\mathbf{L} (\mathbf{U}_1 - \mathbf{U}_2) \\ &\quad - 2\delta(\mathbf{U}_1 - \mathbf{U}_2)^\top (\mathbf{D}_{11}\mathbf{L} (\mathbf{U}_1 + \mathbf{U}_2) + \mathbf{D}_{12}\mathbf{L}\varepsilon\mathbf{I}') + O(\varepsilon^3) \end{aligned} \quad (60)$$

A mutant with a slightly different bias $\delta + \delta'$ then has

$$L_2^{\delta'} = L_2 + \frac{\delta'}{2}(L_1 - L_3) + (2\delta'\delta + \delta'^2)(\mathbf{U}_1 - \mathbf{U}_2)^\top \mathbf{D}_{11}\mathbf{L} (\mathbf{U}_1 - \mathbf{U}_2)$$

so that the derivative of the dominant eigenvalue around δ is

$$\frac{\partial \lambda_d}{\partial \delta} = p_1 p_2 (L_1 - L_3 + 4\delta(\mathbf{U}_1 - \mathbf{U}_2)^\top \mathbf{D}_{11}\mathbf{L} (\mathbf{U}_1 - \mathbf{U}_2)) \quad (61)$$

where the last term is necessarily positive near a branching point (see Section 6). Thus either δ will reach the boundary of its trait space ($|\delta| = 1$), or the sign of $L_1 - L_3$ must change before δ reaches its final value (cf. Eq. (58)).

Near a branching point, there is heterozygote disadvantage and according to the conversion rule (33) therefore

$$L_1 + L_3 - 2L_2 = (L_1 - 1) + (L_3 - 1) + 2\sqrt{L_1 - 1}\sqrt{L_3 - 1} = \left(\sqrt{L_1 - 1} + \sqrt{L_3 - 1}\right)^2$$

and similarly

$$L_1 - L_3 = (L_1 - 1) - (L_3 - 1) = \left(\sqrt{L_1 - 1} - \sqrt{L_3 - 1}\right)\left(\sqrt{L_1 - 1} + \sqrt{L_3 - 1}\right)$$

We substitute these in the ratio ρ of the fitness derivatives for dominance bias (58) and assortativeness (39), to find the following expression:

$$\begin{aligned} \rho &:= \frac{(L_1 - L_3 + O(\varepsilon^3))}{(1 - L_2/2)(L_1 + L_3 - 2L_2)} = \frac{(\sqrt{L_1 - 1} - \sqrt{L_3 - 1})}{1/2(\sqrt{L_1 - 1} + \sqrt{L_3 - 1})} + O(\varepsilon) \\ &= 2(p_2 - p_1) + O(\varepsilon) \end{aligned} \quad (62)$$

where the approximation $L_2 = 1 + O(\varepsilon^2)$ is used as we are close to the singularity, as well as the appropriate conversion rule for frequencies (34).

If ρ is larger than 1 then selection for dominance bias towards $2X_1$ is stronger than that for a tendency for assortative mating (and bias towards $2X_2$ cannot invade), and mutatis mutandis the same holds for bias towards $2X_2$ if ρ is smaller than -1 (with bias towards $2X_1$ having negative fitness). If ρ is between 0 and 1 then dominance bias towards $2X_2$ cannot invade, towards $2X_1$ is a possible invader, but the selection gradient is largest for a tendency for assortative mating; and similarly for ρ between 0 and -1.

We can connect this classification to model ingredients, using Equation (62) and ignoring the order term, since

$$\begin{aligned} \rho > 1 &\Leftrightarrow \sqrt{L_1 - 1} > 3\sqrt{L_3 - 1} \Leftrightarrow p_1 < 1/4 \\ \rho < -1 &\Leftrightarrow \sqrt{L_3 - 1} > 3\sqrt{L_1 - 1} \Leftrightarrow p_1 > 3/4 \end{aligned} \quad (63)$$

From these conditions we see that for phenotypic dominance bias to be the better invader, requires the population dynamics to be far more sensitive in one homozygote than in the other to changes in strategy: just before branching $L_1 = L_3 = 1$ (since $X_1 = X_2 \approx X^*$ and the population is at equilibrium; but note that the frequencies are undefined, as they form a line of neutrally stable equilibria at a singularity (Fig. 1 in Durinx *et al.*, 2008)), just after branching these values change by $L_1 - 1$ and $L_3 - 1$, and the condition $\rho > 1$ implies that $(L_1 - 1) > 9(L_3 - 1)$. We remark here that symmetry means the same at the level of allele frequencies, zygote frequencies and reproductive output: we can easily find that

$$p_1 = p_2 \Leftrightarrow L_1 = L_3 \Leftrightarrow p_{11} = p_{22} \quad (64)$$

from the calculation rules for allele frequencies (32, 34) together with those for zygote frequencies (4). And then by consequence $L_2 = 1 - \sqrt{(L_1 - 1)^2} = 2 - L_1$.

If we are instead near a continuously stable singularity (that is, an uninvadable attracting singularity), we must use Equations (31) and (32) to find eventually the equivalent formula,

$$\rho = 2 \frac{\sqrt{1-L_1} - \sqrt{1-L_3}}{\sqrt{1-L_1} + \sqrt{1-L_3}} + O(\varepsilon) = 2(p_2 - p_1) + O(\varepsilon) \quad (65)$$

from which the same conditions (63) for ρ in terms of frequencies are found.

G Mate choice functions

We have modelled assortative mating by giving choosy individuals a probability α of mating assortatively, and hence a probability $1 - \alpha$ of mating randomly. This means that homozygotes of one type do not distinguish between homozygotes of the other type and heterozygotes, just classifying both as “different”.

An alternative way of modelling mate choice is by using a mate choice function (O’Donald, 1980; Janetos, 1980), and in this appendix we will show how to use these functions within our formalism. In such models a choosy individual with phenotype X is supposed to randomly pair off with a partner drawn from the population, say of type X' , and accept this partner with probability $\mu(X, X')$ as given by the mating function μ . If there is no cost of choosiness, then this pairing off will be repeated until a suitable partner is found; in other models only a limited number of draws is allowed. Typically the rejection rate increases with increasing differences between the partners, starting from complete acceptance of identical partners. (Note that mate choice functions can as easily model the reverse, negative assortative mating.) The typical mating function for these so-called distance-based mate choice models is a Gaussian,

$$\mu(X, X') := \exp\left(-\frac{||X - X'||^2}{2\sigma_m^2}\right) \quad (66)$$

with the variance σ_m^2 either given or under evolutionary control.

However, for our modelling we do not need to specify the entire function μ , but just the value for each possible pairing of the three diploids. Without loss of generality, we may assume that $\mu(X, X) = 1$ for any phenotype X since the rescaled choice function $\tilde{\mu}(X, X') := \mu(X, X') / \mu(X, X)$ leads to the same rejection rates as μ . If we follow the literature and let μ be symmetric, then we need to only specify two parameters: μ_h for the probability of a homozygote accepting a heterozygote partner (or vice versa), and μ_H for that of one homozygote accepting the other type of heterozygote. We see that any relation between μ_h and μ_H can follow from a suitable choice of μ , but with a Gaussian function μ we always have $\mu_H = (\mu_h)^4$.

Instead of matrix $L_{A(\alpha)}$ (6) we found for the tendency α of mating assortatively, here the next-generation matrix resembles that of the randomly mating residents,

L_{rnd} (3), but with each pairing in P_{rnd} (1) weighted by the suitability score:

$$P'_{\mu_h, H} := \begin{bmatrix} p_{11} + \mu_h \frac{p_{12}}{2} & \mu_h \frac{p_{11}}{2} + \frac{p_{12}}{4} & 0 \\ \mu_H p_{22} + \mu_h \frac{p_{12}}{2} & \mu_h \frac{p_{11}}{2} + \frac{p_{12}}{2} + \mu_h \frac{p_{22}}{2} & \mu_H p_{11} + \mu_h \frac{p_{12}}{2} \\ 0 & \frac{p_{12}}{4} + \mu_h \frac{p_{22}}{2} & p_{22} + \mu_h \frac{p_{12}}{2} \end{bmatrix}$$

However, as we assumed there is no cost to choosiness, the above pair matrix is rescaled so that each column sums up to 1, to account for retries until a suitable partner is found. Thus the actual pair matrix is

$$P_{\mu_h, H} := \begin{bmatrix} \frac{p_{11} + \mu_h p_{12}/2}{p_{11} + \mu_h p_{12} + \mu_H p_{22}} & \frac{\mu_h p_{11}/2 + p_{12}/4}{\mu_h p_{11} + p_{12} + \mu_h p_{22}} & 0 \\ \frac{\mu_H p_{22} + \mu_h p_{12}/2}{p_{11} + \mu_h p_{12} + \mu_H p_{22}} & 1/2 & \frac{\mu_H p_{11} + \mu_h p_{12}/2}{\mu_h p_{11} + \mu_h p_{12} + p_{22}} \\ 0 & \frac{p_{12}/4 + \mu_h p_{22}/2}{\mu_h p_{11} + p_{12} + \mu_h p_{22}} & \frac{p_{22} + \mu_h p_{12}/2}{\mu_h p_{11} + \mu_h p_{12} + p_{22}} \end{bmatrix} \quad (67)$$

It is clear that calculating the dominant eigenvalue of the next-generation matrix $L_{\mu_h, H}$ found from this pair matrix is just as hopeless an endeavour as calculating that of $L_{A(\alpha)}$, so we follow the path of Appendix C and calculate the derivative of the dominant eigenvalue of $L_{\mu_h, H}$ for μ_h and μ_H in a randomly mating resident population (i.e., at $\mu_h = \mu_H = 1$), as

$$\frac{\partial \lambda_d}{\partial \mu_h} \Big|_{\mu_h=\mu_H=1} = \frac{1}{v^\top u} v^\top \begin{pmatrix} L_1 & 0 & 0 \\ 0 & L_2 & 0 \\ 0 & 0 & L_3 \end{pmatrix} \frac{\partial P_{\mu_h, H}}{\partial \mu_h} \Big|_{\mu_h=\mu_H=1} u \quad (68)$$

and similarly for μ_H , with u and v (38) as before. Calculating the derivatives of the two pair matrices, and eliminating L_1 , L_3 and the zygote frequencies using the conversion rules (27)–(29), we find

$$\begin{aligned} \frac{\partial P_{\mu_h, H}}{\partial \mu_h} \Big|_{\mu_h=\mu_H=1} &= \begin{bmatrix} \frac{p_{12}}{2} - p_1 p_{12} & \frac{p_{11}}{2} - \frac{p_1}{2}(p_{11} + p_{22}) & 0 \\ \frac{p_{12}}{2} - p_2 p_{12} & 0 & \frac{p_{12}}{2} - p_1 p_{12} \\ 0 & \frac{p_{22}}{2} - \frac{p_2}{2}(p_{11} + p_{22}) & \frac{p_{12}}{2} - p_2 p_{12} \end{bmatrix} \\ &= \frac{p_1 p_2}{2} \begin{bmatrix} 2L_2 - 4p_1 L_2 & p_1 L_2 - p_2 L_2 & 0 \\ 2L_2 - 4p_2 L_2 & 0 & 2L_2 - 4p_1 L_2 \\ 0 & p_2 L_2 - p_1 L_2 & 2L_2 - 4p_2 L_2 \end{bmatrix} \end{aligned} \quad (69)$$

and similarly

$$\frac{\partial P_{\mu_h, H}}{\partial \mu_H} \Big|_{\mu_h=\mu_H=1} = p_1 p_2 \begin{bmatrix} -1 + p_1 L_2 & 0 & 0 \\ 1 - p_1 L_2 & 0 & 1 - p_2 L_2 \\ 0 & 0 & -1 + p_2 L_2 \end{bmatrix} \quad (70)$$

The factor $p_1 p_2$ that appears in both cases is best used to eliminate L_1 and L_3 from $(L_1 \ L_2 \ L_3) = v^T \begin{pmatrix} L_1 & 0 & 0 \\ 0 & L_2 & 0 \\ 0 & 0 & L_3 \end{pmatrix}$. Then the respective derivatives of the dominant eigenvalues are found as

$$\begin{aligned}
& v^T \frac{\partial L_{\mu_h, H}}{\partial \mu_h} \Big|_{\mu_h=\mu_H=1} u \\
&= \frac{1}{2} (p_2 - p_2^2 L_2 \quad p_1 p_2 L_2 \quad p_1 - p_1^2 L_2) \\
&\quad \times \begin{bmatrix} 2L_2 - 4p_1 L_2 & p_1 L_2 - p_2 L_2 & 0 \\ 2L_2 - 4p_2 L_2 & 0 & 2L_2 - 4p_1 L_2 \\ 0 & p_2 L_2 - p_1 L_2 & 2L_2 - 4p_2 L_2 \end{bmatrix} u \\
&= \frac{1}{2} \begin{pmatrix} (p_2 - p_2 L_2)(2L_2 - 4p_1 L_2) \\ (p_2 - p_2^2 L_2 - p_1 + p_1^2 L_2)(p_1 L_2 - p_2 L_2) \\ (p_1 - p_1 L_2)(2L_2 - 4p_2 L_2) \end{pmatrix}^T u \\
&= \frac{p_1 p_2}{2} [(1 - L_2)(4L_2 - 4p_1 L_2 - 4p_2 L_2) + 2L_2^2(1 - L_2)(6p_1 p_2 - 1 - p_1^2 - p_2^2)] \\
&= 2p_1 p_2 (L_2 - 1)(1 - 4p_1 p_2) L_2^2
\end{aligned} \tag{71}$$

and

$$\begin{aligned}
& v^T \frac{\partial L_{\mu_h, H}}{\partial \mu_H} \Big|_{\mu_h=\mu_H=1} u \\
&= (p_2 - p_2^2 L_2 \quad p_1 p_2 L_2 \quad p_1 - p_1^2 L_2) \begin{bmatrix} -1 + p_1 L_2 & 0 & 0 \\ 1 - p_1 L_2 & 0 & 1 - p_2 L_2 \\ 0 & 0 & -1 + p_2 L_2 \end{bmatrix} u \\
&= \begin{pmatrix} p_2(1 - L_2)(-1 + p_1 L_2) \\ 0 \\ p_1(1 - L_2)(-1 + p_2 L_2) \end{pmatrix}^T \begin{pmatrix} p_1 - p_1 p_2 L_2 \\ 2p_1 p_2 L_2 \\ p_2 - p_1 p_2 L_2 \end{pmatrix} \\
&= 2p_1 p_2 (L_2 - 1)(1 - L_2 + p_1 p_2 L_2^2) \\
&= 2p_1 p_2 (L_2 - 1)(1 - p_1 L_2)(1 - p_2 L_2)
\end{aligned} \tag{72}$$

In the special case where μ is Gaussian, the total derivative for μ_h at $\mu_h = 1$ is $\frac{d}{d\mu_h} = \frac{\partial}{\partial \mu_h} + 4 \frac{\partial}{\partial \mu_H}$, so the derivative of the dominant eigenvalue at $\mu_h = 1$ is

$$\begin{aligned}
\frac{d\lambda_d}{d\mu_h} &= 2p_1 p_2 (L_2 - 1) [(1 - 4p_1 p_2) L_2^2 + 4(1 - p_1 L_2)(1 - p_2 L_2)] \\
&= 2p_1 p_2 (L_2 - 1)(2 - L_2)^2
\end{aligned} \tag{73}$$

but in general it is

$$\frac{d\lambda_d}{d\mu_h} = 2p_1 p_2 (L_2 - 1) \left[(1 - 4p_1 p_2) L_2^2 + \left(\frac{\partial \mu_H}{\partial \mu_h} \Big|_{\mu_h=1} \right) (1 - L_2 + p_1 p_2 L_2^2) \right] \tag{74}$$

where $\frac{\partial \mu_H}{\partial \mu_h} > 1$ means that more different partners get rejected with a higher probability.

Looking only at the evolution of μ_h separately from that of μ_H (i.e., only at the first term (71) of the last equation), we immediately find the expected result that mutants with a small tendency to reject dissimilar partners (i.e., $\mu_h \lesssim 1$) have positive invasion fitness if and only if there is heterozygote disadvantage, since $p_1 p_2 \leq 1/4$. However, in the symmetric case (64) such mutants have zero fitness and can therefore not invade (except through random drift). Both results are easy to understand: each mating with a heterozygote that a homozygote avoids has in this case an equal chance of being replaced by one with either type of homozygote, and therefore the expected number of heterozygote offspring stays the same. In the asymmetric case however, a homozygote that avoids pairing with a heterozygote tends to get the more populous type of homozygote as a replacement partner — in case of heterozygote disadvantage this is per capita a benefit to the more common homozygote, of equal size as the disadvantage to the less common homozygote, so one average a benefit for the mutants; and the reverse in case of heterozygote advantage.

Looking only at the evolution of μ_H , we see that in case of heterozygote disadvantage the derivative of the dominant eigenvalue is negative (72) so mutants with $\mu_H \lesssim 1$ can invade. In case of heterozygote advantage and for reasonably symmetric distributions ($1 - 1/L_2 < p_1, p_2 < 1/L_2$), invasion fitness is negative.

Solving the full derivative (74) for L_2 , we see that for $0 < \frac{\partial \mu_H}{\partial \mu_h} < 4$ the quadratic part only has imaginary roots or the double, unreachable root $\tilde{L}_2 = 2$, so the analysis of $\frac{\partial \lambda_d}{\partial \mu_h}$ (71) applies. For $4 < \frac{\partial \mu_H}{\partial \mu_h}$, the partial derivative $\frac{\partial \lambda_d}{\partial \mu_H}$ dominates and its analysis applies to the sum (74). So we conclude that if there is heterozygote disadvantage then a mutant with any mate choice function μ can invade, but if there is heterozygote advantage then the mutant will have a negative fitness except for the more asymmetric zygote frequencies (or higher L_2) together with a much more sensitive μ_H than μ_h .

We can calculate ρ (62) for different functions μ , to find the strength of selection for assortative mating modelled with mating functions, relative to phenotypic bias. The conversion rules show that $L_1 - L_3 = (p_2 - p_1)(1 - L_2)/(p_1 - p_2)$, so for a Gaussian function μ we have

$$\rho = -\frac{p_2 - p_1}{2p_1 p_2 (2 - L_2)^2} + O(\varepsilon) \quad (75)$$

where the minus sign is accounted for by the fact that a positive $\partial/\partial \alpha$ corresponds to a negative $\partial/\partial \mu_h$. So we see that in the symmetric case (64) with heterozygote disadvantage, the same value of ρ is found as before but divided by a factor $(2 - L_2)^2 > 1$. This means that assortative mating modelled with a Gaussian mating function scores better than our model of assortative mating, as expected. However, choosing $\mu_h = \mu_H$ to resemble most closely our situation, we get

$$\rho = -\frac{p_2 - p_1}{2p_1 p_2 ((1 - 3p_1 p_2)L_2^2 + 1 - L_2)} + O(\varepsilon) \quad (76)$$

Here again we see that in the symmetric case with heterozygote disadvantage, the same value of ρ is found as before, but divided by a factor $(1 - L_2/2)^2 < 1$. (That

the last result differs in the symmetric case by a factor four from the preceding result (75) is of course seen immediately from the fitness derivative (74).)

While both μ_h and α range between zero and one, and random mating corresponds to $\mu_h = 1$ and $\alpha = 0$ while conversely strict assortative mating corresponds to $\mu_h = 0$ and $\alpha = 1$, the relation between these two parameters is not straightforward. This can immediately be seen from the difference between the two expressions for ρ , the first involving α (62) and the second with $\mu_h = \mu_H$ (76). The importance of establishing this relation lies in the comparison of this chapter's results with other modelling work (e.g., Pennings *et al.*, 2008; Kopp & Hermisson, submitted).

A closer look shows that at the level of individuals there is no value of μ_h ($= \mu_H$) corresponding to a given value of α : in the first modelling approach a mutant X_1X_1 homozygote mates with the three types of zygotes at a ratio

$$(p_{11}(1 - \alpha) + \alpha, p_{12}(1 - \alpha), p_{22}(1 - \alpha)) \quad (77)$$

and in the second at a ratio

$$\frac{(p_{11}, \mu_h p_{12}, \mu_h p_{22})}{p_{11} + \mu_h(p_{12} + p_{22})} \quad (78)$$

Comparing these two triples, we find in each position the relation

$$\alpha = \frac{p_{11}(1 - \mu_h)}{p_{11} + \mu_h(p_{12} + p_{22})} \quad (79)$$

which cannot account for the differences in value for ρ we found, as the derivative $\partial\alpha/\partial\mu_h$ at $\mu_h = 1$ is $-p_{11} = -p_1^2 L_1 = -p_1(1 - p_2 L_2)$. And making the same derivation but focussing on an $X_2\bar{X}_2$ homozygote leads to a different relation

$$\alpha = \frac{p_{22}(1 - \mu_h)}{p_{22} + \mu_h(p_{12} + p_{11})} \quad (80)$$

Equating the two solutions found for α leads to $p_1 = p_2$, which means that only in the symmetric case there can be an exact correspondence between the two approaches of modelling assortative mating. However, focussing on the heterozygotes a third value $\alpha = p_{12}(1 - \mu_h)/(p_{12} + \mu_h(p_{11} + p_{22}))$ is found, which is different unless $(2L_2 - L_1)(L_2 + L_1) = 0$. Since $L_2 + L_1 = 0$ cannot be satisfied, we must have $2L_2 = L_1$, but in the symmetrical case (64) we have $L_2 = 2 - L_1$, which brings us to the very specific case $L_1 = L_3 = 4/3$. Thus we conclude that in general, the two modelling approaches involving α and μ_h differ at the level of the individuals' behaviour.

On the other hand, to have an identical population dynamics, the requirement is that the pair matrices $P_{A(\alpha)} := (1 - \alpha)P_{\text{rnd}} + \alpha \begin{pmatrix} 1 & 1/4 & 0 \\ 0 & 1/2 & 0 \\ 0 & 1/4 & 1 \end{pmatrix}$ (6) and $P_{\mu_h, H}$ (67) are identical. Trivially, of these nine conditions three are fulfilled (namely, the entries that are on the second diagonal). It is now easy to verify that the remaining two entries of the second row coincide if and only if Equations (79) and (80) are satisfied, which implies that $p_1 = p_2$. Since in both matrices the entries of each column sum up to 1, the remaining two entries on the main diagonal do not lead to additional

conditions. Furthermore, we see that in both matrices and in the symmetrical case, the first and last entries of the middle column are identical (and therefore equal to 1/4). Thus we can conclude that in the symmetrical case (64) both modelling approaches are equivalent, if and only if

$$\alpha = \frac{p_{11}(1 - \mu_h)}{p_{11} + \mu_h(p_{12} + p_{22})} = \frac{L_1(1 - \mu_h)}{L_1 + \mu_h(4 - L_1)} \quad (81)$$

Since many models for the evolution of assortative mating only deal with symmetric equilibria (e.g., Dieckmann & Doebeli, 1999; Pennings *et al.*, 2008; Kopp & Hermisson, submitted), this relation allows us to compare results side by side.

As a check we can verify that for α and $\mu_h = \mu_H$ satisfying the above relation (81), indeed $\partial\lambda_d/\partial\alpha = 4p_1p_2(1 - L_2/2)(1 - L_2)$ (39) coincides with $\partial\lambda_d/\partial\mu_h = 2p_1p_2(L_2 - 1)(1 - L_2/2)^2$ (74), since

$$\left. \frac{\partial\alpha}{\partial\mu_h} \right|_{\mu_h=1} = \frac{-L_1(L_1 + \mu_h(4 - L_1)) - L_1(1 - \mu_h)(4 - L_1)}{(L_1 + \mu_h(4 - L_1))^2} \Big|_{\mu_h=1} = \frac{L_2 - 2}{2} \quad (82)$$

Around Kamigata they have a special, layered type of lunch box, used once a year when watching the cherry blossoms in spring. When you return, you throw it away and crush it with your feet; rightly you guess this image stayed with me from my trip to Kyoto. The end is important in all things.

– Yamamoto Tsunetomo

BIBLIOGRAPHY

- Abrams, P.A., Harada, Y. & Matsuda, H. (1993). On the relationship between quantitative genetic and ess models. *Evolution*, **47**, 982–985.
- Ackermann, M. & Doebeli, M. (2004). Evolution of niche width and adaptive diversification. *Evolution*, **58**, 2599–2612.
- Athreya, K.B. (1992). Rates of decay for the survival probability of a mutant gene. *J. Math. Biol.*, **30**, 577–581.
- Athreya, K.B. (1993). Rates of decay for the survival probability of a mutant gene. II. The multitype case. *J. Math. Biol.*, **32**, 45–53.
- Badyaev, A.V. (2002). Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends Ecol. Evol.*, **17**, 369–378.
- Balkau, B. & Feldman, M.W. (1973). Selection for migration modification. *Genetics*, **74**, 171–174.
- Beccari, C. (1997). Tutorial: typesetting maths for science and tech according to ISO 31/XI. Tech. rep., TeX Users Group.
- Bolnick (2006). Waiting time to speciation. *Evolution*.
- Bolnick, D.I. & Doebeli, M. (2003). Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. *Evolution*, **57**, 2433–2449.
- Bulmer, M.G. (1980). *The Mathematical Theory of Quantitative Genetics*. Oxford University Press, Oxford (UK).
- Caswell, H. (2001). *Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland (Mass.), 2nd edn.
- Champagnat, N. (2003). Convergence of adaptive dynamics n-morphic jump processes to the canonical equation and degenerate diffusion approximation. *Prépublication de l'Université de Nanterre (Paris X)*, **no. 03/7**.
- Champagnat, N. (2004). *Etude mathématique de modèles stochastiques d'évolution issus de la théorie écologique des dynamiques adaptives*. PhD thesis: Paris X, Paris (F).
- Champagnat, N. (2006). A microscopic interpretation for adaptive dynamics trait substitution sequence models. *Stochastic Processes and their Applications*, **116**, 1127–1160.
- Champagnat, N., Ferrière, R. & Ben Arous, G. (2001). The canonical equation of adaptive dynamics: a mathematical view. *Selection*, **2**, 71–81.
- Champagnat, N., Ferrière, R. & Méléard, S. (2006). Unifying evolutionary dynamics: From individual stochastic processes to macroscopic models. *Theor. Popul. Biol.*, **69**, 297–321.

- Charnov, E.L. (1982). *The Theory of Sex Allocation*. Princeton University Press, Princeton (NJ).
- Christiansen, F.B. (1991). On conditions for evolutionary stability for a continuously varying character. *Am. Nat.*, **138**, 37–50.
- Christiansen, F.B. & Loeschke, V. (1987). Evolution and intraspecific competition. III. One-locus theory for small additive gene effects and multidimensional resource qualities. *Theor. Popul. Biol.*, **31**, 33–46.
- Coyne, J.A. & Orr, A.H. (2004). *Speciation*. Sinauer Associates, Sunderland (Mass.).
- Cressman, R. & Hofbauer, J. (2005). Measure dynamics on a one-dimensional continuous trait space: Theoretical foundations for adaptive dynamics. *Theor. Popul. Biol.*, **67**, 47–59.
- Dercole, F. (2002). *Evolutionary Dynamics through Bifurcation Analysis: Methods and Applications*. PhD thesis: Department of Electronics and Information, Politecnico di Milano, Milano (Italy).
- Dercole, F. & Rinaldi, S. (in press). *Analysis of Evolutionary Processes: The Adaptive Dynamics Approach and its Applications*. Princeton University Press, Princeton (NJ).
- Dickinson, H. & Antonovics, J. (1973). Theoretical considerations of sympatric divergence. *Am. Nat.*, **107**, 256–274.
- Dieckmann, U. & Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature*, **400**, 354–357.
- Dieckmann, U. & Law, R. (1996). The dynamical theory of coevolution: A derivation from stochastic ecological processes. *J. Math. Biol.*, **34**, 579–612.
- Dieckmann, U. & Metz, J.A.J. (2006). Surprising evolutionary predictions from enhanced ecological realism. *Theor. Popul. Biol.*, **69**, 263–281.
- Dieckmann, U., Marrow, P. & Law, R. (1995). Evolutionary cycling in predator-prey interactions: Population dynamics and the red queen. *J. Theor. Biol.*, **176**, 91–102.
- Diekmann, O. (2004). A beginner's guide to adaptive dynamics. *Math. Mod. Pop. Dyn.*, **63**, 47–84.
- Diekmann, O. & Gyllenberg, M. (submitted). Abstract delay equations inspired by population dynamics
- Diekmann, O., Gyllenberg, M., Huang, H., Kirkilionis, M., Metz, J.A.J. & Thieme, H.R. (2001). On the formulation and analysis of general deterministic structured population models. II. Nonlinear theory. *J. Math. Biol.*, **43**, 157–189.
- Diekmann, O., Gyllenberg, M. & Metz, J.A.J. (2003). Steady-state analysis of structured population models. *Theor. Popul. Biol.*, **63**, 309–338.
- Diekmann, O., Getto, P. & Gyllenberg, M. (in press). Stability and bifurcation analysis of Volterra functional equations in the light of suns and stars. *SIAM Jour. Math. Anal.*.
- Dobzhanski, T. (1940). Speciation as a stage in evolutionary divergence. *Am. Nat.*, **74**, 312–321.
- Doebeli, M. & Dieckmann, U. (2003). Speciation along environmental gradients. *Nature*, **421**, 259–264.
- Durinx, M., Metz, J.A.J. & Meszéna, G. (2008). Adaptive dynamics for physiologically structured population models. *J. Math. Biol.*, **56**, 673–742.

- Eshel, I. (1981). On the survival probability of a slightly advantageous mutant gene with a general distribution of progeny size - a branching process model. *J. Math. Biol.*, **12**, 355–362.
- Eshel, I. (1983). Evolutionary and continuous stability. *J. Theor. Biol.*, **103**, 99–111.
- Eshel, I. (1984). On the survival probability of a slightly advantageous mutant gene in a multitype population: A multidimensional branching process model. *J. Math. Biol.*, **19**, 201–209.
- Eshel, I. & Motro, U. (1981). Kin selection and strong evolutionary stability of mutual help. *J. Pop. Biol.*, **19**, 420–433.
- Ewens, W.J. (1969). *Population Genetics*. Methuen, London (UK).
- Fisher, R.A. (1930). *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford (UK).
- Gavrilets, S. (2005). “Adaptive speciation”: It is not that simple. *Evolution*, **59**, 696–699.
- Gavrilets, S. & Boake, C.R.B. (1998). On the evolution of premating isolation after a founder event. *Am. Nat.*, **152**, 706–716.
- Gavrilets, S. & Waxman, D. (2002). Sympatric speciation by sexual conflict. *PNAS*, **99**, 10533–10538.
- Geritz, S.A.H. (2005). Resident-invader dynamics and the coexistence of similar strategies. *J. Math. Biol.*, **50**, 67–82.
- Geritz, S.A.H. & Kisdi, E. (2000). Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. *Proc. R. Soc. Lond. B*, **267**, 1671–1678.
- Geritz, S.A.H., Kisdi, E., Meszéna, G. & Metz, J.A.J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**, 35–57.
- Geritz, S.A.H., van der Meijden, E. & Metz, J.A.J. (1999). Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Popul. Biol.*, **55**, 324–343.
- Geritz, S.A.H., Gyllenberg, M., Jacobs, F.J.A. & Parvinen, K. (2002). Invasion dynamics and attractor inheritance. *J. Math. Biol.*, **44**, 548–560.
- Getto, P. (2005). *On some quasilinear structured population models*. thesis: Utrecht University, Utrecht (NL).
- Gillespie, D.T. (1976). A general method for numerically simulating the stochastic time evolution of coupled chemical reactions. *J. Comp. Phys.*, **22**, 403–434.
- Greiner, G., Heesterbeek, J.A.P. & Metz, J.A.J. (1994). A singular perturbation theorem for evolution equations and time-scale arguments for structured population models. *Canadian Applied Mathematics Quarterly*, **2**, 435–459.
- Grover, J.P. (1997). *Resource Competition*. Chapman & Hall, London (UK).
- Haccou, P., Jagers, P. & Vatutin, V.A. (2005). *Branching Processes - Variation, Growth, and Extinction of Populations*. Cambridge Studies in Adaptive Dynamics, Cambridge University Press, Cambridge (UK).
- Haldane, J.B.S. (1927). A mathematical theory of natural and artificial selection. V. Selection and mutation. *Proc. Cam. Phil. Soc.*, **23**, 838–844.
- Hofbauer, J. & Sigmund, K. (1998). *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge (UK).
- Hoppe, F.M. (1992). Asymptotic rates of growth of the extinction probability of a mutant gene. *J. Math. Biol.*, **30**, 547–566.

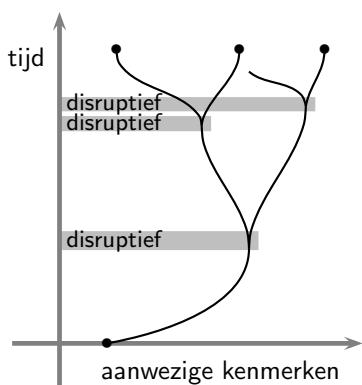
- Iwasa, Y., Pomiankowski, A. & Nee, S. (1991). The evolution of costly mate preferences. II. The "handicap principle". *Evolution*, **45**, 1431–1442.
- Jacobs, F.J.A., Metz, J.A.J. & Meszéna, G. (in prep.). A bifurcation analysis for adaptive dynamics based on lotka-volterra community dynamics.
- Janetos, A.C. (1980). Strategies of female mate choice: a theoretical analysis. *Behav. Ecol. Sociobiol.*, **7**, 107–112.
- Kendall, D.G. (1948). On the generalized "birth-and-death" process. *Annals of mathematical statistics*, **19**, 1–15.
- Kisdi, E. (1999). Evolutionary branching under asymmetric competition. *J. Theor. Biol.*, **197**, 149–162.
- Kisdi, E. & Geritz, S.A.H. (1999a). Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment. *Evolution*, **53**, 993–1008.
- Kisdi, E. & Geritz, S.A.H. (1999b). Evolutionary branching and sympatric speciation in diploid populations. *IIASA Interim Report*, IR-99-048.
- Kondrashov, A.S. & Turelli, M. (1992). Deleterious mutations, apparent stabilizing selection and the maintenance of quantitative variation. *Genetics*, **132**, 603–618.
- Kopp, M. & Hermisson, J. (submitted). Competitive speciation and costs of choosiness. (*submitted to: Journal of Evolutionary Biology*).
- Lande, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution*, **33**, 402–416.
- Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**, 292–305.
- Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *PNAS*, **78**, 3721–3725.
- Leimar, O. (2001). Evolutionary change and darwinian demons. *Selection*, **2**, 65–72.
- Leimar, O. (2005). The evolution of phenotypic polymorphism: randomized strategies versus evolutionary branching. *Am. Nat.*, **165**, 669–681.
- Leimar, O. (to appear). *Multidimensional convergence stability and the canonical adaptive dynamics*. In: Dieckmann, U. and Metz, J. A. J. (eds.), Elements of adaptive dynamics. Cambridge Studies in Adaptive Dynamics, Cambridge University Press, Cambridge (UK).
- Leimar, O., Hammerstein, P. & Van Dooren, T.J.M. (2006). A new perspective on phenotypic plasticity and the principles of adaptive morph determination. *Am. Nat.*, **167**, 367–376.
- Levin, S.M. (1970). Community equilibria and stability, and an extension of the competitive exclusion principle. *Am. Nat.*, **104**, 413–423.
- Lush, J.L. (1937). *Animal breeding plans*. Iowa State College Press, Ames (Iowa).
- Mackay, T.F.C. (2001). The genetic architecture of quantitative traits. *Annual Review of Genetics*, **35**, 303–339.
- Mackay, T.F.C., Lyman, R.F. & Jackson, M.S. (1992). Effects of p element insertions on quantitative traits in drosophila melanogaster. *Genetics*, **130**, 315–332.
- Magnus, J. & Neudecker, H. (1988). *Matrix Differential Calculus with Applications in Statistics and Econometrics*. J. Wiley & Sons, New York (NY).

- Matessi, C. & Gimelfarb, A. (2006). Discrete polymorphisms due to disruptive selection on a continuous trait. i: The one-locus case. *Theoretical Population Biology*, **69**, 283–295.
- Matessi, C., Gimelfarb, A. & Gavrilets, S. (2001). Long term buildup of reproductive isolation promoted by disruptive selection: how far does it go? *Selection*, **2**, 41–64.
- Merilä, J., Sheldon, B.C. & Ellegren, H. (1998). Quantitative genetics of sexual size dimorphism in the collared flycatcher *Ficedula albicollis*. *Evolution*, **52**, 870–876.
- Meszéna, G. & Metz, J.A.J. (1999). Species diversity and population regulation: the importance of environmental feedback dimensionality. *IIASA Interim Report*, IR-99-045.
- Meszéna, G., Czibula, I. & Geritz, S.A.H. (1997). Adaptive dynamics in a 2-patch environment: a toy model for allopatric and parapatric speciation. *J. Biol. Sys.*, **5** (2), 265–284.
- Meszéna, G., Gyllenberg, M., Jacobs, F.J.A. & Metz, J.A.J. (2005). Link between population dynamics and dynamics of darwinian evolution. *Phys. Rev. Lett.*, **95** (078105), 1–4.
- Meszéna, G., Gyllenberg, M., Pásztor, L. & Metz, J.A.J. (2006). Competitive exclusion and limiting similarity: a unified theory. *Theor. Popul. Biol.*, **69**, 68–87.
- Metz, J.A.J. & Diekmann, O. (1986). *The Dynamics of Physiologically Structured Populations*, vol. 68 of *Lecture Notes in Biomathematics*. Springer, Berlin (D).
- Metz, J.A.J., Nisbet, R.M. & Geritz, S.A.H. (1992). How should we define fitness for general ecological scenarios? *Trends Ecol. Evol.*, **7**, 198–202.
- Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. & Van Heerwaarden, J.S. (1996). *Adaptive Dynamics, a geometrical study of the consequences of nearly faithful reproduction*. In: Van Strien, S.J. and Verduyn Lunel, S.M. (eds). *Stochastic and spatial structures of dynamical systems*, vol. 45 of *KNAW Symposium Lectures, Section Science, First Series*, 183–231. North Holland, Amsterdam (NL).
- Mollison, D. (1995). *The structure of epidemic models*. In: *Epidemic Models: their structure and relation to data*, 27–28. Cambridge University Press, Cambridge (UK).
- O'Donald, P. (1960). Assortative mating in a population in which two alleles are segregating. *Heredity*, **15**, 389–396.
- O'Donald, P. (1980). *Genetic models of sexual selection*. Cambridge University Press, New York (NY).
- Otto, S.P. & Bourguet, D. (1999). Balanced polymorphisms and the evolution of dominance. *Am. Nat.*, **153**, 561574.
- Peischl, S. & Bürger, R. (in press). Evolution of dominance under frequency-dependent intraspecific competition. *J. Theor. Biol.*.
- Pennings, P.S., Kopp, M., Meszéna, G., Dieckmann, U. & Hermisson, J. (2008). An analytically tractable model for competitive speciation. *Am. Nat.*, **171**, E44–E71.
- Pigliucci, M. (2006). Genetic variance-covariance matrices: a critique of the evolutionary quantitative genetics research program. *Biology and Philosophy*, **21**, 1–23.
- Pomiankowski, A., Iwasa, Y. & Nee, S. (1991). The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution*, **45**, 1422–1430.
- Rand, D.A., Wilson, H.B. & McGlade, J.M. (1994). Dynamics and evolution: stable attractors, invasion exponents and phenotype dynamics. *Proc. R. Soc. Lond. B*, **343**, 261–283.

- Roberts, M.G. & Heesterbeek, J.A.P. (2003). A new method for estimating the effort required to control an infectious disease. *Proc. R. Soc. Lond. B*, **270**, 1359–1364.
- Rogers, A.R. & Mukherjee, A. (1992). Quantitative genetics of sexual dimorphism in human body size. *Evolution*, **46**, 226–234.
- Roughgarden, J. (1979). *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. Macmillan, New York (NY).
- Rueffler, C., Van Dooren, T.J.M., Leimar, O. & Abrams, P.A. (2006). Disruptive selection and then what? *Trends Ecol. Evol.*, **21**, 238–245.
- Schneider, K.A. (2006). A multilocus-multiallele analysis of frequency-dependent selection induced by intraspecific competition. *J. Math. Biol.*, **52**, 483–523.
- Shaw, R.F. & Mohler, J.D. (1953). The selective significance of the sex ratio. *Am. Nat.*, **87**, 337–342.
- Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Annual Review of Ecological Systems*, **64**, 419–441.
- Slatkin, M. (1984). Ecological causes of sexual dimorphism. *Evolution*, **38**, 622–630.
- Temeles, E.J. & Kress, W.J. (2003). Adaptation in a plant-hummingbird association. *Science*, **300**, 630–633.
- Temeles, E.J., Pan, I.L., Brennan, J.L. & Horwitt, J.N. (2000). Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science*, **289**, 441–443.
- Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press, Princeton (NJ).
- Turelli, M. (1984). Heritable genetic variation via mutation-selection balance: Lerch's ζ meets the abdominal bristle. *Theor. Popul. Biol.*, **25**, 138–193.
- Van Dooren, T.J.M. (1999). The evolutionary ecology of dominance-recessivity. *J. Theor. Biol.*, **198**, 519–532.
- Van Dooren, T.J.M. (2000). The evolutionary dynamics of direct phenotypic over-dominance — emergence possible, loss probable. *Evolution*, **54**, 1899–1914.
- Van Dooren, T.J.M. (2006). Protected polymorphism and evolutionary stability in pleiotropic models with trait-specific dominance. *Evolution*, **60**, 1991–2003.
- Van Dooren, T.J.M., Durinx, M. & Demon, I. (2004). Sexual dimorphism or evolutionary branching? *Evol. Ecol. Res.*, **6**, 857–871.
- van Doorn, G.S. & Weissing, F.J. (2001). Ecological versus sexual selection models of sympatric speciation. *Selection*, **2**, 17–40.
- van Kampen, N.G. (1981). *Stochastic Processes in Physics and Chemistry*. North Holland, Amsterdam (NL).
- Vukics, A., Asbóth, J. & Meszéna, G. (2003). Speciation in multidimensional evolutionary space. *Physical Review E*, **68** (041903), 1–10.
- Waxman, D. & Gavrillets, S. (2005). 20 questions about adaptive dynamics. *J. Evol. Biol.*, **18**, 1139–1154.
- Zhang, X.S. & Hill, W.G. (2005). Genetic variability under mutation selection balance. *Trends Ecol. Evol.*, **20**, 468–470.

Leven nabij Singulariteiten (Nederlandse samenvatting)

De adaptieve dynamica bestudeert hoe kenmerken veranderen met het verloop van tijd, door mutaties met een beperkte impact. Wanneer deze mutatiestapjes voldoende klein en zeldzaam zijn, dan kunnen situaties als in de schets hieronder voorkomen: te beginnen met een gemeenschap van individuen die allen hetzelfde kenmerk hebben, zien we dat dit erfelijke kenmerk geleidelijk aan wijzigt, niet altijd met dezelfde snelheid noch in dezelfde richting. Als we de tijdlijn volgen van beneden naar boven, dan zien we dat er drie momenten zijn waarbij het aantal aanwezige kenmerkenwaarden toeneemt, en een vierde waarbij het aantal weer afneemt. Alles gezamenlijk is dit een aantrekkelijk beeld voor biologen (op een paar mallotige creationisten en ID'ers na): te beginnen met een simpel ecosysteem dat een enkel type individuen bevat, is de invloed van de ecologie dusdanig dat er subgroepen ontstaan die verschillende, erfelijke, rollen spelen, met als eindresultaat een ingewikkelder systeem dat meerdere onderscheiden populaties omvat. Daarbij, als deze populaties voldoende verschillend worden, dan kunnen het mettertijd aparte soorten worden.



In dit hele verhaal zijn er echter een aantal aannames verzwegen. Om te beginnen dat individuen erfelijke kenmerken hebben met invloed op hun "life history", wat zoveel is als het geheel van demografische parameters dat de levensloop van de bestudeerde levensvorm kenmerkt: het aantal jongen dat een gemiddeld individu krijgt tijdens zijn leven, de leeftijd waarop ze volwassen worden en de kans die ze hebben om die leeftijd te halen, hoe lang ze daarna nog leven, enzovoorts.

In de adaptieve dynamica wordt daarbovenop aangenomen dat de populaties lokaal goed gemengd zijn, dat het erfelijke materiaal bijna altijd 100% getrouw doorgegeven wordt, en dat bij aanvang de genetische variatie gering is. Enkel in zeldzame gevallen mag een kopieerfout een kenmerkwaarde wijzigen tijdens de overdracht, en deze mutaties mogen maar weinig effect hebben. Het gevolg van de zeldzaamheid van mutaties in een dergelijk systeem is dat er effectief twee tijdschalen zijn: een snelle demografische en een veel tragere evolutieaire. Aangezien de populatiedynamica van de gemeenschap haar attractor bereikt lang voordat een

volgende mutatie optreedt, kan vanuit een evolutionair perspectief de toestand van deze gemeenschap afdoende beschreven worden door haar evenwichtswaarde. Als de mutatiestappen dan ook nog eens klein zijn, komt er een ordelijke, nette grafiek tevoorschijn zoals in de illustratie.

In dat prentje zien we ook dat de kenmerkenwaarden aangetrokken lijken door speciale punten: de drie punten waar een tak zich splitst, en de drie waarden die in de populatie voorkomen op het einde van het tijdsinterval. Zulke speciale punten spelen een belangrijke rol in alle hoofdstukken van dit proefschrift, en worden kortweg “singulariteiten” genoemd, of voluit “evolutionair singuliere strategieën”. Een handvol verschillende types worden hierbij onderscheiden, die elk hun karakteristieke eigenschappen hebben; sommige zijn bijvoorbeeld evolutaire eindpunten, terwijl andere net de plekken zijn waar de populatie zich diversifieert. Zoals de illustratie aangeeft, is selectie “disruptief” bij deze laatste punten, dat wil zeggen dat ze druk uitoefent op een kenmerk zodanig dat het tegelijkertijd in twee (of meer) verschillende richtingen evolueert. Dit type singulariteit noemen we een “vertakkingspunt”, omdat het de plek is waar er een nieuwe tak spruit aan de evolutionaire stamboom.

We zien ook dat selectie over het algemeen niet disruptief is, maar “directiveel”, wat zoveel wil zeggen als dat ze op elk kenmerk in een enkele richting druk uitoefent. Wat ook niet uit het oog verloren mag worden, is dat het afhangt van het ecosysteem of een kenmerkwaarde al dan niet singulier is. Dit is duidelijk te zien aan de waarde bij dewelke de tweede vertakking gebeurt: de populatie heeft deze kenmerkwaarde al eens gehad, nog voor de eerste vertakking, maar niets speciaals gebeurde. Deze observatie raakt aan de kern van de adaptieve dynamica, namelijk het inzicht dat het verwachte succes (oftewel de “fitness”) van een type op zichzelf geen werkzaam begrip is. De essentie van het verschil is dat bij die eerste passage het ecosysteem fundamenteel versilde, met een enkel type in aanwezigheid waar er ten tijde van de tweede vertakking een tweede groep van individuen is waarmee er om dezelfde voedselbronnen en mogelijkheden gestreden moet worden. Daarom zeggen we dat de kenmerkwaarde waar de tweede vertakking gebeurt een singulariteit is voor de evolutionaire dynamica met twee residenten, en (hoogstwaarschijnlijk) niet voor die met een enkele resident. Dat we dit verschil nu duidelijk kunnen zien is een voordeel van mijn keuze om te illustreren met een éendimensionaal kenmerk. Een verder voordeel is dat elke extra dimensie een extra dimensie in de grafiek vereist, wat problematisch is met een plat medium als papier.

Het “invasiefitnessconcept” staat centraal in de adaptieve dynamica. Dit concept wordt nauwkeurig gedefinieerd in het eerste hoofdstuk, en aan de hand van verschillende modeltypes geïllustreerd. In essentie is het een telling van het aantal afstammelingen dat een enkel individu van een “invaderend” type gemiddeld zal hebben, als het aan een ecosysteem-in-evenwicht van “residente” types wordt toegevoegd. Als dit aantal meer dan één is, is de fitness positief en is het mogelijk dat het nageslacht van de binnendringer een populatie zal vormen; is het aantal minder dan één dan is de fitness negatief en de binnendringers zullen weer verdwijnen. We kunnen aantonen dat in het algemeen, wanneer selectie directiveel is, het succesvol binnendringen door een mutant die slechts weinig verschilt van een bepaald type resident, onafwendbaar betekent dat deze voorvader het moet

afleggen tegen zijn nageslacht en uit het systeem zal verdwijnen, en omgekeerd dat twee gelijkaardige residenten enkel samen kunnen voorkomen nabij singuliere punten. Het zijn deze eigenschappen die maken dat het grafiekje er zo uitziet, met maar een handvol takken, zelfs na een zeer groot aantal zeer kleine mutatiestappen — zoals eerder gezegd gebeurt het verschijnen en weer verdwijnen van onsuccesvolle mutanten en het binnendringen van succesvolle mutanten (ten koste van residenten) op de snelle demografische tijdschaal, zodat we enkel de uitkomsten van deze veranderingen zien op de illustratie. Natuurlijk ziet het prentje er ook zo gladjes uit omdat het een idealisatie is, waarbij alle toevalelementen uitgeschakeld zijn door aan te nemen dat het systeem een oneindig aantal residenten omvat, de mutatiestappen infinitesimaal zijn en de tijdschalen volledig gescheiden.

De technieken en resultaten van de adaptieve dynamica gelden voor een groot aantal verschillende types van modellen, en zijn bruikbaar in zeer verschillende kaders. Zo kunnen de individuen zich clonaal vermenigvuldigen (waarbij het nageslacht een identieke kopie van het ouderlijke genoom heeft) of seksueel (waarbij de helft van de genen van elke ouder komen). De tijdstappen kunnen diskreet zijn (bijvoorbeeld omdat er enkel gegevens zijn op één of enkele punten in het jaar zoals voor passerende trekvogels, of door telling net voor of net na de jaarlijkse voortplanting) of continu. De kenmerken kunnen scalair zijn zoals in de illustratie en dus maar een enkele onafhankelijke parameter beïnvloeden, of vectoriel zijn en verscheidene life history parameters apart beïnvloeden, of zelfs functies zijn (zoals bij de zogeheten “reactienormen”). De individuen kunnen een complexe levenscyclus doorlopen met verschillende stadia, geslachten en morfen (vormen) die een verschillende ecologische rol spelen, of kunnen juist een schematisch levensverloop hebben met als enige mogelijke gebeurtenissen “ik sterf” en “ik krijg een kind”, zodat alle genetisch identieke individuen uitwisselbaar zijn. De populatiedynamica kan een arbitrair gekozen differentiaalvergelijking zijn, maar kan ook zorgvuldig afgeleid zijn van een individugebaseerd scenario. De populatiedynamische attractor van de gemeenschap kan een evenwichtspunt zijn, een periodieke cyclus, een quasiperiodische cyclus of een chaotische attractor....

Omdat in dit proefschrift voornamelijk theoretisch werk wordt verricht, komen er weinig concrete modellen in voor. Vaak zal enkel de modelfamilie aangegeven worden, die dan meestal die van de Lotka-Volterra modellen danwel die van de populatiemodellen met een fysiologische structurering al zijn. Deze eerste familie is een veelbestudeerde en wiskundig makkelijk te hanteren type van differentiaalvergelijkingen (en dus continuutijdsmodellen) waarbij er enkel wordt aangegeven hoe sterk individuen reageren op andere aanwezigen (in aantal nakomelingen meer of minder per tijdseenheid), en hoe snel ze zich voortplanten als ze alleen op de wereld zijn. De tweede familie van modellen daarentegen laat alle opties toe die in de vorige alinea vermeld werden; ze komt expliciet en herhaaldelijk aan bod in de eerste twee hoofdstukken, impliciet in het derde maar niet in het laatste.

Hoofdstuk I begint met een lange en gedetailleerde inleiding over adaptieve dynamica en fysiologischgestructureerde populatiemodellen¹ en bestaat verder uit drie grote stukken.

¹Een docent spelling kwam tot het besluit dat dit de momenteel correcte spellingswijze is. Mijn excuses voor dit gedrocht.

Het eerste stuk is een afschatting van de snelheid waarmee kenmerkenwaarden van gestructureerde populaties wijzigen, wat een veralgemening is van de zogenaamde “canonische vergelijking van de adaptieve dynamica”. Deze schatting geldt enkel weg uit de buurt van singuliere punten, waardoor deze met het oog op de vergelijking parodoxaal genoeg de enige interessante punten zijn. Omdat de vergelijking toont dat de aanwezige kenmerkwaarden zullen blijven wijzigen tenzij ze allen singulier zijn, noopt ze tot de studie van systemen nabij singuliere punten.

Het tweede deel van dit hoofdstuk is zo’n studie, en komt tot een vreemde conclusie: voor elk gestructureerdepopulatiemodel bevat de invasiefitnessfunctie voor een enkel type resident alle essentiële informatie om die met willekeurige aantallen types te kunnen berekenen, hoe ingewikkeld de interacties ook zijn tussen de residenten in het systeem met meerdere types. Iets technischer uitgedrukt: voor de kleine parameter ε die schaalt met de afstand zowel tussen de residente types als tussen de residenten en de mutant, geldt dat de termen van de invasiefunctie voor meerdere residenten, tot en met de orde $O(\varepsilon^2)$, allemaal zijn af te leiden van de invasiefunctie voor een enkel type resident. Naast een vrij algemeen bewijs van deze stelling wordt een aantal gevolgen ervan bekeken, zoals bijvoorbeeld een principe van wederzijdse uitsluiting dat een bovengrens stelt aan het aantal types dat lokaal tezamen kan voorkomen en daarbij ondermeer toont dat in onze illustratie een tak zich nooit in drieën kan splitsen, en verder worden er verbanden aangegeven met andere concepten zoals de dimensie van de terugkoppelingslus van de individuen via hun omgeving. Al bij al wordt er gejongleerd met een hoop technische aspecten die dan op het hoofd van de lezer terechtkomen. Het belangrijkste gevolg van de eerder genoemde stelling is dat een aantal moeilijk te hanteren berekeningen voor soorten met een ingewikkelde levenscyclus vervangen kunnen worden door berekeningen voor een veel eenvoudigere soort, zolang ze maar dezelfde éénresidentfitness hebben.

Het derde deel van dit hoofdstuk toont hoe het eerste tezamen met het tweede gebruikt kan worden om een volledig beeld te geven van de evolutie binnen een bepaald modelsysteem. De canonische vergelijking toont ons namelijk dat een gemeenschap altijd zal eindigen bij een singulariteit, of op de rand van de kenmerkruimte. Maar in dat laatste geval zal het systeem deze rand weer verlaten op een plek waar hij afstotend is, tenzij het systeem voor altijd op deze rand gevangen is. Welk van de twee gevallen zich ook voordoet, evolutie binnen dit grensgebied is niets meer dan evolutie binnen een lagerdimensionale kenmerkruimte dan voorheen, waarbij alle voorgaande en volgende overwegingen blijven gelden.

In dit derde stuk wordt getoond hoe de noodzakelijke lifehistoryparameters uit een populatiedynamisch model afgeleid kunnen worden om de canonische vergelijking toe te kunnen passen en de singulariteiten te lokaliseren. Een stapsgewijze beschrijving geeft aan wat er kan gebeuren onder het regime van directionele selectie, en welke complicaties kunnen optreden. Met de normaalvorm die in het bewijs van het tweede stuk gevonden wordt, gekoppeld aan resultaten van andere onderzoekers, volgt er een lijst van mogelijkheden nabij singuliere punten, plus criteria om vast te stellen dewelke zich voordoen en implicaties voor de verdere evolutie van systemen nabij singuliere punten (zoals hun mogelijke ontsnappen waardoor ze weer in een fase van directionele selectie terechtkomen). Omdat dit deel van het hoofdstuk geschreven is met een publiek van meer (biologisch) toegepaste on-

derzoekers in het achterhoofd, staat het voor zover mogelijk op zichzelf, met een minimum aan theoretische uitweidingen en verwijzingen naar de eerdere stukken, en worden enkel die technische haken en ogen besproken die we vermoeden dat de lezer zal tegenkomen als hij/zij het voorgaande in de praktijk brengt. Als afsluiter volgt er nog een heranalyse van een klassiek model uit de literatuur.

Hoofdstuk II draait om de vraag of er ook een normaalvorm bestaat, zoals die in het tweede deel van Hoofdstuk I gevonden werd, maar dan geldig voor extra orde in de parameter ϵ . Dit blijkt niet zo te zijn. Hier blijkt dat zelfs Lotka-Volterra modellen met identieke éénresidentfitnessfuncties meestal verschillen in hun derdeordetermen. Deze derdeordeverschillen worden daarna verder uitgeplozen, en de vergelijking wordt gemaakt met de derdeorde-expansie van een onverwacht type modellen.

Hoofdstuk III bekijkt scenario's die leiden tot (de aanvang van) sympatrische speciatie, waarbij de populatie evolueert tot bij een vertakingspunt, waarna de disruptieve selectie (al dan niet geholpen door assortieve, ofte "soort zoekt soort", partnerkeuze) de populatie in twee verschillende groepen splitst die zich dan elk aan een andere ecologische niche aanpassen.

Hier wordt aangetoond dat als we in het bovenstaande verhaal echter genen met geslachtspecifieke expressie toelaten, zodat mannetjes en vrouwtjes kunnen verschillen, dit verhaal vaak niet meer opgaat. Als er bijvoorbeeld twee verschillende ecologische niches zijn, dan zullen die niet meer door twee genetisch verschillende subpopulaties worden ingenomen, maar door de mannetjes en de vrouwtjes. Aangezien die twee groepen noodzakelijkerwijze met elkaar blijven paren, kunnen ze geen twee soorten vormen.

In dit hoofdstuk wordt er een recept gegeven om een willekeurig model om te zetten in eentje met twee (mogelijk verschillende) geslachten, en de essentie van wat we tonen is dat elk vertakingspunt van het originele model dan een zadelpunt wordt, oftewel een singulariteit die in sommige richtingen aantrekt maar in andere richtingen afstoot. De analyse van twee (lichte variaties op) modellen uit de literatuur illustreert dit hoofdstuk, waarbij ook te zien is dat er nog verdere types kunnen ontstaan door vertakking binnen een enkel geslacht.

Hoofdstuk IV bekijkt situaties waar er twee allelen zijn voor een bepaald gen in een seksueel voorplantende populatie. Dan zijn er drie types aanwezig — twee "homozygoten" die twee dezelfde exemplaren hebben, en een "heterozygoot" die een kopie van beide allelen heeft. Vaak doet die heterozygoot het slechter dan beide homozygoten (in aantalen nakomelingen), soms beter.

Als een eerste stap wordt hier voor een vrij algemene familie van modellen aangetoond dat bij een vertakingspunt de heterozygoot altijd in het nadeel is, maar in het voordeel bij een evolutionair eindpunt (een "CSS"). Als de heterozygoot in het nadeel is (of we nu dicht bij een singulariteit zijn of niet), dan zouden mutanten met een strategie om relatief meer homozygoten te maken in het voordeel zijn. De rest van dit hoofdstuk onderzoekt de relatieve kansen op invasiesucces voor twee van dit soort strategieën: positieve assortieve partnerkeuze (homozygoten die met een gelijke partner paren, krijgen enkel homozygote kinderen; heterozygoten die paren krijgen voor de helft homozygote kinderen die later assortatief zullen paren). Alles bijeen worden er elke generatie minder heterozy-

gotten geproduceerd zodat er twee reproductief gescheiden populaties ontstaan) en dominantiemodificatie (waarbij een van de twee allelen dominant wordt, zodanig dat de heterozygoot ecologisch niet te onderscheiden is van een homozygoot die twee exemplaren van het dominante allele heeft). Dit soort veranderingen gebeurt veelal stapsgewijs, met eerst een lichte voorkeur voor gelijkende partners (in plaats van een enkele mutatie die een random parenke plots enkel toelaat te paren met gelijkende partners) of een aanvankelijk slechts licht verhoogde invloed van het ene allele ten opzichte van het andere. Daarom zoeken we ook uit in welke omstandigheden welk van beide strategieën kan invaderen, en hoe de selectiegradiënten zich verhouden in die gevallen waar ze beiden kunnen binnendringen.

Vele van deze vergelijkingen kunnen we enkel uitvoeren nabij vertakkingspunten, omdat we geen model gespecificeerd hebben. Gelukkig blijkt dat assortiatieve partnerkeuze de meest succesvolle strategie is, als beide allelen even vaak voorkomen en de mutatiestapjes klein zijn: dit zijn net de voorwaarden die gelden in de meeste modellen waar er reproductieve isolatie ontstaat in een geslachtelijk voortplantende populatie door de co-evolutie van partnerkeuze met ecologische kenmerken (als prelude voor soortsvorming), maar geen van deze modellen heeft tot nu toe gecontroleerd of er alternatieve strategieën zijn die roet in het eten zouden kunnen gooien. Verder worden de voorgaande punten geïllustreerd met een model, waardoor we de relatieve sterktes van de selectie tonen voor een aantal parameter-combinaties.

Curriculum vitæ

Michel Durinx was born on the last night of April 1976 in Borgerhout, near Antwerp. Almost all of his school years were spent at St. Stanislas College in Berchem, which was renamed St. Willebrord College upon fusing with four uniform-wearing all-girls schools in 1990. Because of the gradual introduction of a school uniform for boys, he left the institution in 1993 and spent this last year of high school in the Latin-Mathematics class of Onze-Lieve-Vrouwe College in Edegem. After spending 1997–1998 as an Erasmus exchange student at Glasgow University, he received in 1998 a Masters of Science degree in fundamental mathematics from the University of Antwerp (with ‘grote onderscheiding’). He then spent two years in the Dynamical Systems group of Hasselt University in Diepenbeek (B). At the Institute of Biology Leiden he started in 2000 the research reported in this thesis. Subsequently he is weighing his options between postdoctoral research on good genes sexual selection theory, and llama herding in Chile Chico.

Publications

- Van Dooren, T.J.M., Durinx, M. & Demon, I. (2004). Sexual dimorphism or Evolutionary branching? *Evol. Ecol. Research*, **6**, 857–871.
- Durinx, M. & Metz, J.A.J. (2005). Multi-type branching processes and adaptive dynamics of structured populations. IIASA WP IR-05-075.
- Durinx, M. & Metz, J.A.J. (2005). Multi-type branching processes and adaptive dynamics of structured populations. In: Haccou, P. Jagers, P. & Vatutin, V. *Branching Processes: Variation, Growth, and Extinction of Populations*. Cambridge University Press, Cambridge (UK), 266–277.
- Durinx, M., Metz, J.A.J. & Meszéna, G. (2007). Adaptive dynamics for physiologically structured population models. IIASA WP IR-07-027.
- Durinx, M., Metz, J.A.J. & Meszéna, G. (2008). Adaptive dynamics for physiologically structured population models. *J. Math. Biol.*, **56**, 673–742
- Durinx, M. & Van Dooren, T.J.M. (accepted by *Evolution*). Assortative mate choice and dominance modification: alternative ways of removing heterozygote disadvantage.

Thanks

A special thanks in the finishing of this thesis goes out to Tine Wouters, who pointed out several dozen errors in the Dutch summary (and is solely to blame for the remaining ones, if any). Apparently there have been two spelling revisions (1995, 2005), but nobody sent me a memo.

Life in Leiden was much improved by the inhabitants of the EEW building, and specifically by those joining the weekly pilgrimage to 't Keizertje; you know who you are. More frequent though less observantly attended, the respective coffee, tea and cake breaks have added much merriment and some kilos to life; being a very mixed bunch as a section making said breaks all the more...ah...interesting. Its tolerance for seamonkies, praying mantises, baby daygeckos, ant colonies and other office pets can only be called exemplary. It was also good to share an office with Claus and Joost, though it has made me hate kohlrabi for the rest of my days, which seems like a fair price to pay. Probably much to their relief I later moved to my own office, incidentally saving their belongings from the subsequent Espresso Incident.

A big thanks must also go to Gé Boskamp, who not only kept my *Phelsuma quadriocellata* fed with weekly doses of leftover *Drosophila*, but also in my absense cleaned up the mess from the unfortunate Maggot Incident, for which Elisabeth Van Ast may not yet have forgiven me.

To me, a very important strain of Leiden life is Rob van der Hoorn's judo club. Look no further if you are searching for a fun bunch of people with their hearts in the right place, striking a balance between training, educating and insanity. Sometimes known as the Locust People, they can gather in large numbers and work for charity, or just hang out, or help you move house; this, however, will cost you a few crates of beer plus all the food you possess...

Last but not least there's Sabina, who provided most of the motivation for finishing this thesis, by making risotto every single day until I stopped fiddling with the manuscript.

xx

Thanks

Notes

This thesis was typeset using pdfL^AT_EX in combination with the Palatino text font and Pazo math font, and printed by Ipkamp Printpartners. The thesis cover was made with GIMP on Ubuntu, using part of Luca Leonelli's "Paradossi del Volo" (watercolour, 101 × 151cm, © the artist 2004); the same illustration recurs at each chapter's start. The scientific chapters as a whole carry AMS subject classification (2000) 70K45 - 92D15 - 92D25. No animals were harmed in this study.