Working Paper

Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction

J.A.J. Metz, S.A.H. Geritz,
G. Meszéna, F.J.A. Jacobs, and
J.S. van Heerwaarden

WP-95-99
September 1995

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IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 1

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The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

These and many more problems possess a common source: the interactions of individuals are bound to change the environments these individuals live in. By closing the feedback loop in the evolutionary explanation, a new mathematical theory of the evolution of complex adaptive systems arises. It is this general theoretical option that lies at the core of the emerging field of adaptive dynamics. In consequence a major promise of adaptive dynamics studies is to elucidate the long-term effects of the interactions between ecological and evolutionary processes.

A commitment to interfacing the theory with empirical applications is necessary both for validation and for management problems. For example, empirical evidence indicates that to control pests and diseases or to achieve sustainable harvesting of renewable resources evolutionary deliberation is already crucial on the time scale of two decades.

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Adaptive Dynamics, a geometrical study of the consequences of nearly faithful reproduction

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Adaptive Dynamics, a geometrical study of the consequences of nearly faithful reproduction

Abstract

We set out to explore a class of stochastic processes, called "adaptive dynamics", which supposedly capture some of the essentials of long term biological evolution. These processes have a strong deterministic component. This allows a classification of their qualitative features which in many aspects is similar to classifications from the theory of deterministic dynamical systems. But they also display a good number of clear-cut novel dynamical phenomena.

The sample functions of an adaptive dynamics are piece-wise constant functions from $\mathbb{R}_+$ to the finite subsets of some "trait" space $\mathbb{X} \subset \mathbb{R}^k$. Those subsets we call "adaptive conditions". Both the range and the jumps of a sample function are governed by a function s, called "fitness", mapping the present adaptive condition and the trait value of a potential "mutant" to $\mathbb{R}$. Sign(s) tells which subsets of $\mathbb{X}$ qualify as adaptive conditions, which mutants can potentially "invade", leading to a jump in the sample function, and which adaptive condition(s) can result from such an invasion.

Fitnesses supposedly satisfy certain constraints derived from their population/community dynamical origin, such as the fact that all mutants which are equal to some "resident", i.e., element of the present adaptive condition, have zero fitness. Apart from that we suppose that s is as smooth as can possibly be condoned by its community dynamical origin. Moreover we assume that a mutant can differ but little from its resident "progenitor".

In sections 1 and 2 we describe the biological background of our mathematical framework. In section 1 we deal with the position of our framework relative to present and past evolutionary research. In section 2 we discuss the community dynamical origins of s, and the reasons for making a number of specific simplifications relative to the full complexity seen in nature.

In sections 3 and 4 we consider some general, mathematical as well as biological, conclusions that can be drawn from our framework in its simplest guise, that is, when we assume that $\mathbb{X}$ is 1-dimensional, and that the cardinality of the adaptive conditions stays low. The main result is a classification of the adaptively singular points. These points comprise both the adaptive point attractors, as well as the points where the adaptive trajectory can branch, thus attaining its characteristic tree-like shape.

In section 5 we discuss how adaptive dynamics relate through a limiting argument to stochastic models in which individual organisms are represented as separate entities. It is only through such a limiting procedure that any class of population or evolutionary models can eventually be justified. Our basic assumptions are (i) clonal reproduction, i.e., the resident individuals reproduce faithfully without any of the complications of sex or Mendelian genetics, except for the occasional occurrence of a mutant, (ii) a large system size and an even rarer occurrence of mutations per birth event, (iii) uniqueness and global attractiveness of any interior attractor of the community dynamics in the limit of infinite system size.

In section 6 we try to delineate, by a tentative listing of "axioms", the largest possible class of processes that can result from the kind of limiting considerations spelled out in section 5. And in section 7 we heuristically derive some very general predictions about macro-evolutionary patterns, based on those weak assumptions only.

In the final section 8 we discuss (i) how the results from the preceding sections may fit into a more encompassing view of biological evolution, and (ii) some directions for further research.

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1. The larger context

1.1. *Evolutionary basics*

The most conspicuous, if not the defining, properties of life are that living objects (1) reproduce almost faithfully, and (2) die. It is a mathematical necessity that the independent reproduction of particles leads to exponential population growth (or to rapid extinction, but such populations habitually escape our attention) (Jagers, 1975, 1991, 1995). Therefore in any finite world organisms will (3) interact, both directly through jostling or fighting, and indirectly through the consumption of resources and the sharing of predators. The consequence of (1) to (3) is that life evolves: Those types that do a better job in contributing to future generations will inherit the earth. Until a copying error during the reproductive act creates a still "better adapted" type. Evolution will grind to a halt only when it has reached a combination of types which cannot be bettered under the current condition of the environment.

Simple though it may seem, this scenario becomes interestingly complicated due to the fact that those same types are (co-)instrumental in creating the current environmental condition.

Remark: That there is no sign yet that evolution on this earth is going to freeze has two causes. The easy one is that the physical configuration of the world keeps changing. But it usually does so relatively slowly. Much to the biologist's luck, since it allows him/her (sometimes) to predict organismal properties from evolutionary considerations.

The second cause is more involved: (a) There is no need that ecology drives evolution to a point attractor, even in models which only consider simple external (phenotypic) representations of organisms. But if we assume that too extreme phenotypes are weak survivors, as is generally the case in the real world, we may expect at least convergence to some nice attractor. However, there is a snag. (b) Since the internal (genotypic) representation of organisms is almost infinitely complicated, the map from genotype to any simple phenotypic representation is very many to one. Dolphins, Ichthyosaurs, tuna, and sharks may look similar, but underneath they are very different creatures. Consequently the mutational supply (due to copying errors of the genetic material) of new phenotypic variation shows considerable history dependence. (a) and (b) together make that when the evolutionary process is looked at in somewhat greater detail, it appears that non-point attractors with some recurrence property just don't exist. Evolution either halts, or progresses indefinitely, though not necessarily progressively. Luckily, here again, proper modes of abstraction as well as time scale differences come to the rescue of those who nevertheless want to make predictions.

1. 2. *History: the changes in attention paid to ecological and genetic complexity*

The mechanistic theory of evolution started public life with the publication of Charles Darwin's "On the Origin of Species" in 1859. The one flaw in the reasoning of the early Darwinists was their, lukewarm, adherence to the concept of blending inheritance (the blending of the properties of the parents in their offspring), since by mathematical necessity evolution can only occur among particles which reproduce sufficiently faithfully. But they clearly saw evolution as driven by the interaction between individuals, as is proved by Darwin's statement that he owed his idea of the "struggle for existence" to the writings of Thomas Malthus.

At the turn of the century the inheritance problem was solved by the rediscovery of a piece of contract research by a Moravian monk with physicist leanings, Gregor Mendel. It aren't the organisms which reproduce almost faithfully, but their genes. This considerably complexifies the logic, since the genes inhabiting one organism affect each other's reproductive potential. In the twenties a reconciliation of the Mendelian and Darwinian paradigms was effected by the three great mathematical population geneticists, Sir Ronald Fisher, J.B.S Haldane, and Sewall Wright. The hand-waving linking up in the forties and fifties of the resulting circle of ideas with those of the paleontologists and taxonomists of the day is now referred to as the Modern Synthesis. The strength of that link is still among the biologists' articles of faith.

Ironically the mathematical framework underlying the Modern Synthesis dealt almost exclusively with the genetics of populations of non-interacting individuals. For this was one of the main simplifications made by the early theoretical population geneticists in order to cope with the complexities of realistic inheritance laws. It is even more ironical that this assumption of non-interaction makes it particularly hard on model populations to split into lines going their separate ways. The origin of species was, and is, still one of the less well understood problems of population genetics.

The second point on which the population genetics of the time fell short as a cornerstone for the theory of adaptive evolution is that it almost exclusively concentrated on the changes in the relative frequencies of types from a fixed genetic repertoire. For this is the scale where contact could be made between theory and genetic observations on real populations. Yet, the overall features of long term adaptive evolution crucially depend on the existence of a continual trickle of new mutants. The stream of novel adaptive variation is that small and fickle, that it is essentially beyond direct observation. But its effects can be seen in overwhelming profusion. We are but one instance

Around 1970 both conceptual omissions were rectified by W.D. Hamilton (1967), G.R. Price and John Maynard Smith (Maynard Smith & Price, 1973; Maynard Smith, 1982), who put to the fore the concept of Evolutionarily Unbeatable Strategy. An EUS is a strategy which when played by everybody prevents all comparable strategies from increasing in numbers. Such strategies are the natural longer term evolutionary traps. (By now EUSes are more often called Evolutionarily Stable Strategies. Unfortunately this is a misnomer as EUSes need not be stable in the dynamic sense.) Of course there was a price. Only the statics of adaptive evolution was considered. Moreover, it became common usage to assume clonal reproduction (i.e., the almost faithful reproduction of individuals), in order to concentrate on behavioural interactions. Luckily later research has shown that a good number of the general results kept their ground for more realistic types of inheritance. But exceptions that are neither trivial nor contrived have been found as well.

1.3. *About this paper*

In this paper we set out to construct in a general manner the simplest possible dynamical counterpart to the EUS concept. Since we primarily want to cope with general types of ecological complexities we stick to the by now time-honoured assumption of clonal reproduction. Moreover we assume that the ecological and evolutionary time scales are clearly separated. Finally we shall assume that the types can be characterised by a finite number of numerical traits, that the ecology satisfies some continuity conditions (to be expounded below) and that mutation only produces small steps in trait space.

1.4. *Relation to present day views of the evolutionary process*

No doubt red-blooded biologists will find our assumptions artificial. To them we have the following three remarks to make in our defence. (i) It is always better to start hunting for patterns in some well chosen caricature of reality, and to leave it for a second stage to see to how those patterns modify when additional realism is added, than not to see any wood for the trees. (However, till we reach that second stage our conclusions about long term evolution should be taken with a pinch of salt.) (ii) The least we do is develop an internally consistent picture of a class of evolutionary processes, well worth of study in their own right. It is only by studying various classes of evolutionary processes that one may ever hope to bring out their essence. (iii) Our picture is the simplest one allowing the eventual development of a bifurcation theory of EUSes. Anyone who knows what bifurcation theory has done for differential equations will appreciate the usefulness of such a development.

For mathematicians we may add that there is a wholly new, and rather unusual, class of dynamical systems waiting to be explored.

As a final point we should make clear that we are by no means the first to venture on the present path. Some notable forerunners are Ilan Eshel (1983, 1991,1995; - & Feldman, 1982, 1984), Jonathan Roughgarden (1976, 1979, 1983), Freddy Bugge Christiansen (1984, 1988, 1991; - & Loeschcke, 1980, 1987, Loeschcke & -, 1984a,b), Peter Taylor (1989), Karl Sigmund (Hofbauer & -, 1990, Nowak & -, 1990), Si Levin (Cohen & -, 1987; Ludwig & -, 1992), Peter Hammerstein (1995, - & Selten, 1994), and Carlo Matessi (- & Di Pascuale, 1995). The main difference of our effort from theirs is that we strive to construct a clear mathematical framework that should abstractly encompass a greater deal of ecological complexity (but at the cost of highly oversimplifying the genetical end). Tom Vincent and co-workers (1990; - & Brown, 1984, 1987, 1988, 1989; Brown & -, 1987a,b, 1992; - & Fisher, 1988; - et al., 1993) followed a line of thought that superficially is rather similar to ours. Our approach differs from theirs both in its greater formal abstraction and in that we try to stick to formalisms that consistently allow an interpretation in individual-based terms concordant with the basic philosophy with which we started this discourse (see also Metz & De Roos, 1992).

2. Reconciling the population dynamical and taxonomical viewpoints

2.1. *Fitness*

The catch phrase of the theory of evolution by natural selection is "fitness". Definitions abound, most of them rather special or not very clear. Here we shall stick to the definition expounded in Metz et al. (1992), as this is the only one coping with a range of ecological scenario's which is sufficient for our purpose: Fitness is the asymptotic average rate of exponential growth ρ which results from a thought experiment in which we let a clone of the type under consideration grow in an ergodic environment. This definition immediately makes clear that the fitness of a type, say X, also depends on the environment in which it lives, E. We shall bring this out in our notation by writing $\rho_E(X)$.

Remark: The underlying mathematical idea is: (i) The dynamics of a sufficiently large (spatially and/or physiologically structured) population can, for a given time dependence of the environmental conditions, be described by a positivity-preserving linear evolutionary (in the mathematical sense) system. For ergodic environmental conditions, and subject to some biologically innocent regularity conditions, there exists a unique number ρ such that

$$\frac{\log |N(t)|}{t} \xrightarrow{a.s.} \rho,$$

$|N(t)|$ the total population mass. (This has not been proven yet in as much generality as we would wish. But the special model classes that so far have yielded to analysis all show the same pattern; see Tuljapurkar 1990; Inaba 1989; Ferrière & Gatto, 1995). In mathematics ρ is better known as the dominant Lyapunov exponent.
(ii) What results there are for special classes of branching processes (Jagers, 1975, 1991, 1995; Athreya & Karlin, 1971a,b) all tell that (i) a branching process starting with a single individual either goes extinct, or starts growing exponentially with a growth rate ρ equal to that of its mean process, (ii) the probability of non-extinction is zero when $\rho \leq 0$, and positive when $\rho > 0$.

In a non-virgin world the current environment is necessarily (co-)determined by those types that are already in residence. Let those types be denoted by $X_1,\ldots,X_n$ (we confine the discussion to situations where that number of types is finite), let $C := (X_1,\ldots,X_n)$ denote the combination of those types, and let a unique environment E(C) be created by the resulting interactions. If we interpret "being resident" as "staying bounded away from zero population size (on the population dynamical time scale!)" we expect E(C) to be ergodic with $\rho_{E(C)}(X_i) = 0$, $i = 1,\ldots,n$. For (a) by assumption the masses of none of the types goes to zero, (b) in a finite world none of those masses can go to infinity either.

Remark: We always think of the world as intrinsically noisy. This not only does away with some considerable mathematical complications (see e.g. Ruelle 1989 and Rand et al., 1994), but it also has the advantage of being realistic.

Let Y generically denote a mutant type. In our discussion of the determination of the environmental condition by the resident population we implicitly assumed that population to be numerically large. (Populations which stay numerically small quickly go extinct by chance fluctuations.) Mutants arrive as single individuals. Therefore the effect of the mutant population on the environment is that diluted that its initial growth is the same as that of a Y population in the ergodic environment E(C).

We shall denote the fitness of Y in a C population dynamical background as

$$s_C(Y) := \rho_{E(C)}(Y). \tag{2.1}$$

We assume that (i) mutants for which $s_C(Y) < 0$ are unable to invade a C community, (ii) mutants with $s_C(Y) > 0$ can invade (but will not necessarily always do so as a result of random fluctuations due to the small initial size of the mutant population; see sections 4 and 5.4).

Mutants that do indeed invade are traditionally referred to as successful.

2.2. *Traits*

We shall assume that the types come parametrised by some compact and simply connected subset $\mathbb{X}$ of $\mathbb{R}^k$. Moreover we shall assume that a mutant Y differs but slightly from the type X_i from which it derives. The components of X_i, Y stand for the values of some numerical traits, like leg length, metabolic rate, duration of juvenile period, etc..

Communities with only one evolving type are called monomorphic, with two evolving types dimorphic, etc.. (To keep the arguments simple we assume that the remaining species of the community don't evolve. We surmise that the theory can be extended to multi-species coevolution by making appropriate notational changes; see also Dieckmann & Law, 1995.)

The trait values determine the population dynamical characteristics of a type. Simple trait evolution in an n-morphic community, in which every successful mutant just oust its progenitor, can therefore be visualised as a movement through the parameter space of a community dynamical model.

It also can occur that the new mutant and all the old resident types can coexist, or that replacement of one of the former resident types by a mutant drives some other resident type(s) to extinction. In the first case evolution leads to an enriched, (n+1)-morphic, community, in the second case to an impoverished, (n-m)-morphic, $1 \leq m < n$, community. See also figure 8.

2.3. *The "taxonomic" perspective*

Many traits are easy observables, even on fossils (think of leg length). This in direct opposition to the population dynamical characteristics which they engender (think of the issue of determining in the field the probability of outrunning a predator). Therefore much biological research focusses on trait evolution per se, with little attention for the population dynamical gears of the evolutionary machinery. One of our goals is to accommodate this viewpoint to the greatest possible extent. This was the overriding reason for the assumptions that (i) there is a separation between the population dynamical and the evolutionary time scales, (ii) any combination of residents C engenders a unique E. For these two assumptions justify the introduction of the function

$$s: (C,Y) \mapsto s_C(Y),$$

thereby making it possible to talk about the relation of trait values and fitness per se.

The theoretical framework that we shall develop below is based on the Ansatz that such a function s (i) exists, (ii) provides an evolutionarily sufficient summary of the underlying community dynamics, and (iii) satisfies some appropriate smoothness properties.

The whole of section 6, setting out a tentative axiom system for a theory of Adaptive Dynamics, is devoted to staking out the land concealed behind (ii) and (iii) of the Ansatz. In sections 3 and 4 we explore some of its more immediate landmarks.

2.4. *More about the community dynamical justification*

The recent spate of attention for the non-linear phenomena occurring already in simple population dynamical models may have given the impression that multiple attractors are almost the rule in community dynamics. We believe that this impression is wrong, at least when it comes to evolutionary considerations. Deterministic community models are idealisations made with a purpose, the charting of particular types of community phenomena. More realistic models incorporating environmental noise usually have unique attractors, here to be interpreted as stationary probability measures on the set of functions mapping time to environmental conditions.

The following example may illustrate our point. A famous model for the outbreaks of the Canadian spruce bud-worm (Ludwig, Jones & Holling, 1978) gives rise to two stable equilibria. Yet the very reason that the model was built, was to explain the observed occurrences of shifts between two rather extreme defoliation regimes. On a slightly longer time scale we also have to account for the factors bringing about these shifts.

The introduction of noise also tends to smoothen the deterministic bifurcation of an attractor into a more gradual change of the probability measure on the set of functions mapping time to environmental conditions.

2.5. *Aside: a helpful special class of community dynamical models*

If one wants to develop a general theory it helps to have some simple examples to guide one's way. Unfortunately it is rarely possible to calculate s for a specific community dynamical model other than by doing a direct simulation to determine E(C). To compound our misfortune those cases where we can find an explicit expression for s almost invariably give rise to relatively trivial types of adaptive dynamics. However, there is an outstanding exception, which goes by the name of generalised Lotka-Volterra models (Hofbauer et al., 1987; Rand et al., 1994). These are models with community equations which can be written as either

$$\frac{dn_i}{dt}(t) \;=\; \left[r(X_i,E_0(t)) \;-\; \sum_{j=1}^{m} a(X_i,X_j)\, g(X_j,n_j(t),E_0(t))\right] n_i(t), \tag{2.2}$$

or

$$n_i(t+1) \;=\; \exp\left[r(X_i,E_0(t)) \;-\; \sum_{j=1}^{m} a(X_i,X_j)\, g(X_j,n_j(t),E_0(t))\right] n_i(t), \tag{2.3}$$

where n_i is the population density of the individuals of type X_i, and E_0 some ergodic driver (think of the weather). For such a model let $C = (X_1,\ldots,X_m)$ be a trait combination such that all m types can coexist, i.e., for any initial condition with all $n_j(0) > 0$, $\liminf n_i(t) > \varepsilon_i > 0$, $i = 1,\ldots,m$, then

$$s_C(Y) \;=\; \left[\rho(Y) \;-\; \sum_{j=1}^{m} a(Y,X_j)\, \gamma_j(X_1,\ldots,X_m)\right], \tag{2.4}$$

with $\rho(Y)$ the time average of $r(Y,E_0(t))$, and $\gamma_j(X_1,\ldots,X_m)$ the time average of $g(X_j,n_j(t),E_0(t))$. The latter can be calculated from the equations

$$\sum_{j=1}^{m} a(X_i,X_j)\, \gamma_j(X_1,\ldots,X_k) \;=\; \rho(X_i), \tag{2.5}$$

derived by setting $s_C(X_i) = 0$.

Note that for the Lotka-Volterra models $s_C(Y)$ is well defined even when the dynamics of the C community has multiple attractors.

2.6. *About this paper*

Below you find the prolegomena to a formal theory of Adaptive Dynamics. In section 3 we treat the only well established part: evolution close to monomorphism for one dimensional trait spaces. This is the one area where the barest possible of assumptions already give strong results. In section 4 we discuss, with the help of an example, the natural extension of the theory from section 3 to higher degrees of polymorphism. Near the end of that section it is found that a number of imminently relevant points have to remain undecided unless further assumptions are introduced. Luckily population dynamical considerations of a very general kind can guide us when we pick these assumptions. However, the maximal set of assumptions that can be derived in this manner is just a little less than is needed to get into some really interesting arguments. Therefore we in one place also introduce an assumption pertaining to the production of mutations by individual organisms, which, though fair, is less firmly supported by basic biological laws.

In section 5 we consider, with the help of the same example as in section 4, the relation of our taxonomically abstracted schemes to the fully individual-based point of view. This section should provide a background for judging the tentative "axiom system" for Adaptive Dynamics that we

present in section 6. There we aim at listing a set of assumptions that are mathematically sufficiently weak to have a certain minimum amount of biological firmness and yet are mathematically sufficiently strong, and sufficiently many, to erect an interesting theory on, leading to novel biological insights. In section 7 we list some provisional conclusions from that theory.
In the final section we discuss some pro's and con's of our approach in a wider biological perspective, and indicate some directions for future research.

3. Adaptive Dynamics in one dimension: I evolution close to monomorphism

3.1. *Graphical constructions*

In this section we shall heuristically treat Adaptive Dynamics for one dimensional trait spaces. To keep things simple we shall moreover assume that the trait space $\mathbb{X}$ coincides with the set $\mathbb{P}_1 :=$ $\{x \in \mathbb{X} \mid s(x) > 0\}$, where s(x) denotes the fitness of x in a (relatively) virgin world.

3.1.1. Monomorphic populations

We begin with a consideration of the monomorphic situation. Figure 1 shows two potential sign structures for $s_x(y)$. (Notice that $s_x(x) = 0$, so that generically s changes sign on the diagonal of the (x,y)-plane.) We start with discussing two situations where successful mutants oust their progenitors without arguing as yet why they may be supposed to do this.

We first consider figure 1a. For any x to the left of x* only smaller mutants can invade, for any x to the right of x* only larger mutants can do so. Therefore each subsequent successful mutation moves x further away from x*. The situation is analogous to the cobwebbing (or rather staircasing!) construction used to analyse recurrence relations in one variable. Only this time the steps come at random times and have stochastic sizes.

In figure 1b the opposite happens. For all x to the left of x* only larger, and for all x to the right of x* only smaller mutants can invade. If the mutational step size is bounded by ε, and if the process does not run out of successful mutations, evolution will eventually bring x within an ε-distance of x*. And here the analogy with recurrence relations ends.

3.1.2. Dimorphisms

As a next step we consider the conditions which make a mutant oust or not oust its progenitor. To find these conditions we return to the underlying community dynamical scenario. When a mutant ousts its progenitor the community necessarily passes through a phase during which the progenitor is present only in very low densities. Therefore that progenitor no longer contributes to the setting of the environmental stage. This is done by the mutant in its stead; population dynamically yestertime's resident and mutant have switched roles. We conclude that for a successful mutant y to oust its progenitor x, it is necessary that $s_y(x) \le 0$. We shall assume that this condition is also sufficient, as this accords best with our earlier assumption that the community dynamics always has a global attractor.

To construct the subset of $\mathbb{X}^2$ for which both $s_{x_1}(x_2) > 0$ and $s_{x_2}(x_1) > 0$, we flip copies of the diagrams of figure 1 over the diagonal and superimpose them on the originals. See figure 2. The intersection of the regions marked "+" we call $\mathbb{P}_2$. $\mathbb{P}_2$ parametrises the so-called "protected" dimorphisms.

Remark: Our choice not to include in $\mathbb{P}_2$ the points $C = (X_1, X_2)$ characterised by $s_{X_1}(X_2)=0$ or $s_{X_2}(X_1)=0$, is based on the usual pattern of soft bifurcation of community dynamical equilibria: If a parameter change moves a globally stable interior equilibrium of some decent community dynamics smoothly onto the boundary of the positive cone, then at the bifurcation point the community dynamics has a boundary equilibrium attracting the whole interior of the positive cone.

To have both the monomorphisms and the dimorphisms represented in one picture we embed $\mathbb{X}$, and with it $\mathbb{P}_1$, as the diagonal in $\mathbb{X}^2$. After all, a combination of two identical types is ecologically indistinguishable from a single type. The potential adaptive conditions of the population, up to and including dimorphisms, correspond to the union of $\mathbb{P}_1$ and $\mathbb{P}_2$. Its representation as a subset of $\mathbb{X}^2$ we shall refer to as $\mathbb{A}_2$. The example in figure 3 indicates how such a representation can help us portray patterns of evolutionary movement.

The invasion of a y mutant into a dimorphic population consisting of the type combination (x_1,x_2) is determined by the sign of $s_{x1,x2}(y)$. If y is successful, and if, say, $(x_1,y) \in \mathbb{P}_2$, $(y,x_2) \notin \mathbb{P}_2$, $s_{x1,y}(x_2) < 0$, then a step is made to (x_1,y). When the mutational steps are only small the most usual pattern is that a mutant ousts its progenitor. This is the situation hinted at in figure 3. If ousting the progenitor results in a jump over the boundary of $\mathbb{P}_2$ only the mutant remains. The cases in which mutant and progenitor will coexist will be discussed in section 4.

3.1.3. More about the space of adaptive conditions

A neater way of looking at our embedding trick is by noticing that the real objects of evolutionary interests are sets, not ordered lists, of trait values. This observation produces a natural equivalence between the diagonal of $\mathbb{X}^2$ and $\mathbb{X}$. By the same token the labelling as 1 and 2 of the two types making up a point in $\mathbb{X}^2$ is arbitrary. Therefore $\mathbb{P}_2$ should be invariant under a permutation of the indices of the x_i. In figure 3 this symmetry is seen as a mirror symmetry around the diagonal.

Terminological remark: We call the elements of $\mathbb{A}_2$ adaptive "conditions", instead of adaptive "states" since we customarily tie the notion of state to being Markovian, and we don't want to assume yet that the distribution of the mutational steps is determined in full by the adaptive condition.

3.2. *The classification of evolutionarily singular points*

3.2.1. Evolutionarily Singular Strategies

The consideration of figures 1 to 3 makes clear that a very special role is played by points x* where a(n other) 0-level set of the function $s_x(y)$ crosses the diagonal. We shall refer to such points as Evolutionarily Singular Strategies, or just as singular points. Such points correspond to the rest points of the movement in $\mathbb{P}_1$. Moreover $\mathbb{P}_2$ and $\mathbb{P}_1$ connect only in singular points x* ($\equiv$ (x*,x*) $\in \partial\mathbb{P}_2$) of $\mathbb{P}_1$: It is only near such points x* that evolution can step up from $\mathbb{P}_1$ to $\mathbb{P}_2$. (Stepping down from $\mathbb{P}_2$ to $\mathbb{P}_1$ is possible from all points near $\partial\mathbb{P}_2$ for which mutants in the direction of the nearby part of $\partial\mathbb{P}_2$ are potentially successful.)

Singular points can be characterised by

$$\left.\frac{\partial s_x(y)}{\partial y}\right|_{x=y=x*} = 0. \tag{3.1}$$

Remark: Please notice that, contrary to the usual situation in dynamical systems, evolutionarily singular strategies, as defined by us, aren't the rest points of the adaptive dynamics. The rest points are the (globally) Evolutionarily Unbeatable Strategies, i.e., the strategies X* such that $s_{X*}(Y) < 0$ for all $Y \neq X*$. The local variant of EUSes are characterised by

$$\left.\frac{\partial s_X(Y)}{\partial Y}\right|_{X=Y=X*} = 0 \quad \text{and} \quad \left.\frac{\partial^2 s_X(Y)}{\partial Y^2}\right|_{X=Y=X*} \text{negative definite,}$$

i.e., in addition to (3.1) a second order condition should be satisfied. All rest points of an adaptive dynamics are local EUSes. And any local EUS can be made into a rest point by sufficiently restraining the size of the mutational steps.

3.2.2. The expansion of $s_x(y)$

To classify the different types of singular points we linearise. To this end we define

$$u := x-x^*, \qquad v := y-x^*. \tag{3.2}$$

We shall with a slight abuse of notation use the same symbol s for the local coordinate version of the fitness function. Our assumption that s is sufficiently smooth allows us to write

$$s_u(v) = a + b_1u + b_2v + c_{11}u^2 + 2c_{12}uv + c_{22}v^2 + \text{h.o.t..} \tag{3.3}$$

The fact that any mutation indistinguishable from the resident should be selectively neutral, i.e., have zero fitness, translates into

$$s_u(u) = 0 \quad \text{for all } u, \tag{3.4}$$

allowing us to conclude that

$$a = 0, \qquad b_1+b_2 = 0, \qquad c_{11}+ 2c_{12}+c_{22} = 0. \tag{3.5}$$

Finally (3.1) tells us that

$$b_2 = 0. \tag{3.6}$$

Therefore

$$s_u(v) = c_{11}\, u^2 - (c_{11}+c_{22})\, uv + c_{22}\, v^2 + \text{h.o.t..} \tag{3.7}$$

Apparently we need only two parameters, c_{11} and c_{22}, at this stage of the classification (and only the ratio of c_{11} and c_{22} really matters, since all the pictures locally are invariant under scaling).

Figure 4 shows the dependence of the local sign structures of s on c_{11} and c_{22}. The local direction of evolutionary movement in $\mathbb{P}_1$ and the local configuration of $\mathbb{P}_2$, both deduced from the local sign structure of s in figure 4, are depicted in figure 5.

3.2.3. The expansion of $s_{x1x2}(y)$

To complete the picture we need the pattern of movement in $\mathbb{P}_2$. From now on we confine attention to the cases $c_{22} > -c_{11}$ to ensure that $\mathbb{P}_2$ is not locally empty (see fig. 5). We define

$$u_1 := x_1-x^*, \qquad u_2 := x_2-x^*, \qquad v := y-x^*, \tag{3.8}$$

and write

$$\begin{aligned} s_{u1u2}(v) = {} & \alpha + \beta_1u_1 + \beta_2u_2 + \beta_3v + \gamma_{11}u_1{}^2 + 2\gamma_{12}u_1u_2 + \gamma_{22}u_2{}^2 \\ & + 2\gamma_{13}u_1v + 2\gamma_{23}u_2v + \gamma_{33}v^2 + \text{h.o.t..} \end{aligned} \tag{3.9}$$

The numbering of the resident types is arbitrary. Therefore s should be invariant under a permutation of those numbers:

$$s_{u1u2}(v) \;=\; s_{u2u1}(v). \tag{3.10}$$

Another invocation of the principle of selective neutrality of the resident types gives

$$s_{u1u2}(u_1) \;=\; s_{u1u2}(u_2) \;=\; 0. \tag{3.11}$$

As a final step we use that there is a single point, $u_1 = u_2 = 0$, where $\mathbb{P}_2$ touches the diagonal of $\mathbb{X}^2$. In that point u_1 and u_2 are equal, so that we are back in the monomorphic case. Therefore

$$s_{00}(v) \;=\; s_0(v). \tag{3.12}$$

Combining all this information leads to

$$s_{u1u2}(v) \;=\; (v-u_1)\,(v-u_2)\,[c_{22} + \text{ h.o.t.}]. \tag{3.13}$$

Apparently the whole classification can be done in terms of the two parameters c_{11} and c_{22} only!

Remark: The above derivation was based on the, in afterthought somewhat unwarranted, assumption that the smoothness of s on $\mathbb{P}_2$ extends to the point $(x^*,x^*) \in \partial\mathbb{P}_2$ In section 6 we shall argue that in general the behaviour of community dynamical equilibria under parameter changes only condones assuming (i) that s is smooth on the closure of $\mathbb{P}_2$ with the exception of the points of $\partial\mathbb{P}_2$ where $\mathbb{P}_2$ touches the diagonal of $\mathbb{X}^2$, and (ii) that $s_{\bullet}(y)$ has continuous first and second (and higher) directional derivatives in the directions pointing to the interior of $\mathbb{P}_2$. In the points where $\mathbb{P}_2$ touches the diagonal of $\mathbb{X}^2$ full higher order derivatives fail to exist generally. However, for the case considered above it so happens that the condition that the resident types should be evolutionarily neutral together with (ii), implies that s is twice differentiable for (x_1,x_2,y) on $(\text{closure}\mathbb{P}_2)\times \mathbb{X}$, the points (x^*,x^*,y) not excepted.

3.2.4. Local evolution

From figure 4 we immediately see that locally the monomorphic substitutions bring the adaptive condition of the population closer to x* when $c_{22} < c_{11}$, and move the adaptive condition away from x* when $c_{22} > c_{11}$. Figure 5 shows that $\mathbb{P}_2$ is locally non-empty when $c_{22} > -c_{11}$ and empty when $c_{22} > -c_{11}$. From a consideration of both figures together we conclude that locally around x* transitions from the monomorphic condition to a dimorphic condition occur almost surely when and only when $-c_{11}< c_{22} < c_{11}$, and never when $c_{22} > c_{11}$, or $c_{22} < -c_{11}$.(Assuming, of course, that the process never runs out of mutational variation.)

To see how evolution proceeds from points in $\mathbb{P}_2$ we observe that, according to (3.13) $s_{u1u2}(v)$ for given values of u_1 and u_2 is a parabola in v which crosses the v-axis in the points $v = u_1$ and $v = u_2$.

We first consider the case $- c_{11} < c_{22} < 0$. In that case only mutants v between u_1 and u_2 can invade. A consideration of the local geometry of $\mathbb{P}_2$ tells that v will oust at least that u_i for which $\text{sign}(u_i) = \text{sign}(v)$. The other resident may or may not be ousted. A more detailed calculation shows that, if there is a continuous supply of mutations, (i) $\mathbb{P}_2$ will almost surely be left for $\mathbb{P}_1$, (ii) the distance to 0 decreases by at least a factor $\theta < 1$ for every excursion that is made from $\mathbb{P}_1$ into $\mathbb{P}_2$ and back. Every step from $\mathbb{P}_1$ into $\mathbb{P}_1$ also leads to a decrease of the distance to 0. Therefore the linearised adaptive dynamics almost surely converges to 0.

When $c_{22} > 0$ only mutants v outside the interval (u_1,u_2) can invade. A consideration of the local geometry of $\mathbb{P}_2$ tells that v will always oust the nearest resident. When in addition $c_{11} > 0$ the linearised adaptive dynamics (i) stays in $\mathbb{P}_2$ and (ii) keeps increasing the distance between u_1 and u_2. When $c_{11} < 0$ the linearised adaptive dynamics can also jump over the boundary of $\mathbb{P}_2$, to $\mathbb{P}_1$; once in $\mathbb{P}_1$ it moves away from x* (and from $\mathbb{P}_1$ it never enters $\mathbb{P}_2$ again).

In figure 5 the arrows in $\mathbb{P}_2$ symbolically summarise the results about the evolutionary movement in $\mathbb{P}_2$ locally near (x*,x*) which we have just described.

3.2.5. Types of singular points

The main classification resulting from a combined consideration of the movement in $\mathbb{P}_1 \cup \mathbb{P}_2$ is threefold: (i) evolutionary repellers characterised by $c_{22} > c_{11}$, (ii) evolutionary attractors characterised by $c_{22} < c_{11}$ and $c_{22} < 0$, and (iii) branching points characterised by $0 < c_{22} < c_{11}$. A look forward to figure 7 will explain our choice of the latter name.

Of course we may everywhere replace c_{11} and c_{22} by

$$\left.\frac{\partial^2 s_x(y)}{\partial x^2}\right|_{x=y=x^*} = 2\,c_{11}, \qquad \left.\frac{\partial^2 s_x(y)}{\partial y^2}\right|_{x=y=x^*} = 2\,c_{22}. \tag{3.14}$$

The classification shown in figure 5 underscores our remark in subsection 1.2 that Evolutionarily Unbeatable Strategies are not necessarily evolutionarily attracting, a point first made by Ilan Eshel in 1983 (see also Eshel, 1995). Intriguingly the condition which locally characterises an EUS, a singular strategy with $c_{22} < 0$, in retrospect turns out to be also the condition for attractivity in $\mathbb{P}_2$. For an EUS to be a locally asymptotically stable fixed point of the adaptive dynamics it has to be locally attractive in $\mathbb{P}_1$ as well, i.e., it is also needed that $c_{22} < c_{11}$. In the literature such fully attractive EUSes are called Continuously Stable Strategies (Eshel, 1983; as opposed to the "Evolutionarily Stable Strategies" which correspond to what we here call EUSes).

The general classification of singular points for one dimensional trait spaces was first derived by Peter Taylor (1989), though in a rather different disguise, and from a very different perspective.

4. Adaptive Dynamics in one dimension: II polymorphic evolution

4.1. *An example*

The following community equations should exemplify the results from the previous section .

$$\frac{dn(x_i)}{dt} = \left[1 - \frac{\sum_j a(x_i,x_j)n(x_j)}{k(x_i)}\right] n(x_i), \tag{4.1a}$$

with

$$a(x_i,x_j) = e^{\alpha(x_i - x_j)^2}, \qquad k(x) = 1 - x^2, \qquad -1 < x < 1, \tag{4.2b}$$

and the summation extending over all values of the trait x supporting a non-zero population mass. In subsection 2.5 it was indicated how (4.1) translates into a fitness function s. (This example is a slight adaptation of a time honoured model for competition along a resource axis, first introduced by Robert MacArthur and Richard Levins (1964; see also MacArthur, 1970, 1972) and extensively studied by i.a. Freddy Bugge Christiansen and Volker Loeschcke (1980, 1987; see also Christiansen, 1984, 1988; Loeschcke, 1984; Loeschcke & Christiansen, 1984).)

The left panes of figure 6 to 8 show $\mathbb{P}_1 \cup \mathbb{P}_2$ together with the directions of adaptive movement. The middle panes show the result of numerically solving the differential equation (4.1), with the following modifications: (i) The trait axis was discretised. (ii) Any trait bin with zero population mass adjacent to one with positive mass, had a fixed probability per unit of time to receive a small population mass of size ν_1. (iii) Any population mass which dropped below $\nu_0 < \nu_1$ was instantaneously set to zero. The panes show, in a style conventionally used by paleontologists, those populations which had masses either larger than ν_2 or than ν_3, $\nu_3 > \nu_2 > \nu_1$. Finally the right hand panes show the instantaneous fitness, $1 - \Sigma_i a(y,x_i)n(x_i)$, of a potential mutant in the community indicated with an arrow in the middle pane. Figures 6 to 8 only differ in the value of α (respectively 1/3, 2, and 3).

The most conspicuous feature of figures 7 and 8 is the occurrence of branching events, one in figure 7 and several in figure 8. All these branching events are dichotomies, in accordance with the graphical results from subsection 3.2.

Remark: Instantaneous fitness is a useful concept for non-structured populations only. In a constant environment such populations immediately start growing, or declining, exponentially. The instantaneous fitness $r_{E(t)}(Y)$, at time t of a type Y in an environment E, is the relative growth rate of Y clone in an environment which is forever kept in condition E(t). For non-structured populations, and generically only for them, the fitness $\rho_E(Y)$ can be calculated from these instantaneous fitnesses as

$$\rho_E(Y) \;=\; \lim_{t\to\infty} t^{-1} \int_0^t r_{E(\tau)}(Y)\, d\tau.$$

Remark: Preliminary explorations of an extension of the theory to higher dimensional trait spaces indicate that there polytomies should be possible, at least in principle. The maximum number of branches that can sprout from a single very small (a term in need of explanation, see section 7.1 for some ideas on this topic) region in trait space, after a line of descent has entered that region, is one plus the dimension of the trait space.

4.2. *Stagnation sets*

In the left panes of figures 7 and 8 we also have drawn the lines defined by

$$\left.\frac{\partial s_{x_1,x_2}(y)}{\partial y}\right|_{y=x_i} \;=\; 0, \qquad\qquad i = 1, 2. \tag{4.2}$$

From these lines the adaptive condition either cannot make local jumps in the x_i-direction, or can equally jump in positive or negative x_i-directions. This can be deduced from the following thought experiment: When we forbid x_j, j = 2, 1, to mutate, we are back in a monomorphic adaptive dynamics, with only x_i, i = 1, 2, evolving. (4.2) corresponds to the equation for the singular points of that monomorphic x_i-dynamics, parametrised by x_j.

For one dimensional trait spaces the stagnation sets are somewhat comparable to the isoclines of a differential equation. More in particular, if we let the jump size go to zero, and the mutation rate to infinity in such a manner that [mean mutation distance]×[mutation rate] goes everywhere to the same constant we end up with a set of differential equations for the x_i, which have the stagnation sets for their isoclines (Dieckmann & Law, 1995). Moreover, the intersection of the x_1- and x_2-stagnation sets in $\mathbb{P}_2$ corresponds to the rest points of the dimorphic adaptive dynamics. This is well illustrated in figure 7, where that rest point is also stable towards higher degrees of polymorphism.

Terminological remark: When we speak of the dimorphic dynamics in situations where trimorphisms aren't naturally excluded, we refer to the adaptive dynamics conditioned on the sample path staying dimorphic.

4.3. *Colour-coding the stagnation sets*

It is of course tempting to try to extend the classification of singular points from subsection 3.2 to the points $({}_ix_1,{}_ix_2)$ of an x_i-stagnation set. But we should be a little careful. Those parts of the classification that referred to attractivity or repulsivity in $\mathbb{P}_1$ are not particularly meaningful in a $\mathbb{P}_2$ context, due to the potential for movements of the remaining coordinate.

Let

$$ {}_ic_{11} = \frac{1}{2}\left.\frac{\partial^2 s_{x_1,x_2}(y)}{\partial x_i^{\,2}}\right|_{\substack{y=x_i\\ x_1={}_ix_1,\ x_2={}_ix_2}} , \qquad {}_ic_{22} = \frac{1}{2}\left.\frac{\partial^2 s_{x_1,x_2}(y)}{\partial y^2}\right|_{\substack{y=x_i\\ x_1={}_ix_1,\ x_2={}_ix_2}} . \tag{4.3}$$

We shall call points of an x_i-stagnation set black when ${}_ic_{22} < -{}_ic_{11}$, and coloured when ${}_ic_{22} > -{}_ic_{11}$. Coloured x_i-stagnation points with ${}_ic_{22} < 0$ we call green, and coloured x_i-stagnation points with ${}_ic_{22} > 0$ we call red. In figures 7 and 8 the red parts of the stagnation sets are drawn as interrupted lines.

The thought experiment in which we forbade one of the two types to mutate also tells us that the coloured parts of a stagnation set in $\mathbb{P}_2$ make contact with the set of protected trimorphisms $\mathbb{P}_3$.

Remark: The term contact should be interpreted in terms of the threefold embedding of $\mathbb{X}^2$ in $\mathbb{X}^3$, as the three diagonal planes $x_1=x_2$, $x_1=x_3$, $x_2=x_3$, which follows from the natural equivalence relation $(x_1,\ldots,x_n) \sim (x_1,\ldots,x_m) :\Leftrightarrow \{x_1,\ldots,x_n\} = \{x_1,\ldots,x_m\}$. By the same token $\mathbb{P}_3$ should be invariant under permutations of the indices of (x_1,x_2,x_3), and the three diagonal planes should divide $\mathbb{X}^3$ up in six segments, each of which contains a canonical piece of $\mathbb{P}_3$, see figure 9. Each diagonal plane consists of two equivalent parts, just as did $\mathbb{X}^2$, plus the diagonal line $x_1=x_2=x_3$, separating them. These two parts each connect a different pair of segments of $\mathbb{X}^3$.

For the green parts of the stagnation sets this contact is inconsequential, as can be seen from figure 7, but near to the red part of an x_1-stagnation set there is the possibility that a transition $({}_1x_1+\varepsilon_1, {}_1x_2+\delta) \to ({}_1x_1+\varepsilon_1,\ {}_1x_1+\varepsilon_2,\ {}_1x_2+\delta)$ is followed by steps moving the adaptive condition further and further away from the diagonal plane, and the same holds true for the x_2-stagnation sets. In other words, from, and only from, near to a red x_i-stagnation point there may occur a visible dichotomy in the line descending from x_i. This effect is illustrated in figure 8. Whether we really will see a fully developed dichotomy depends on the relative speeds of the movement in the directions parallel and orthogonal to the diagonal plane. In the example from figure 8 the branchings occur near a rest point of the dimorphic adaptive dynamics, so that the motion orthogonal to the diagonal plane dominates. Local domination of the component of adaptive motion parallel to the diagonal plane will lead in a few adaptive steps to a jump across $\partial\mathbb{P}_3$, back to $\mathbb{P}_2$.

4.4. *Extinctions and treeness*

Reductions in the number of types are results of jumps over the boundary of $\mathbb{P}_n$. When a disappearing type differs appreciably (a term in need of explanation, see section 7.1 for some ideas on this topic) from any of the remaining types we shall speak of an extinction.

An example of an extinction can be seen in the middle pane of figure 8, where the sample path jumps $\partial\mathbb{P}_4$ to $\mathbb{P}_3$.

The particular extinction event from figure 8 owes its occurrence to a geometrical peculiarity which directly relates to our earlier classification of the singular points. In the four-type stage the various members of the community are seen evolving in such a manner that the two middle branches are pushed towards each other. Geometrically this corresponds to a movement towards the diagonal plane $x_2 = x_3$ (assuming that we number the types from left to right). To see what happens geometrically we consider the slice through $\mathbb{X}^4$ which results from keeping x_1 and x_4 constant. From the direction of movement of the middle two branches, we infer that the geometry of that slice is locally similar to the diagram depicted in figure 5 between three o'clock and four thirty. This conclusion is corroborated by the right hand pane of figure 8, second graph from above. Therefore we may imagine the trajectory in $\mathbb{P}_4$ as descending from some fixed height into a narrow furrow, with a codimension 1 bottom. Since the adaptive movement has a considerable stochastic slack there is essentially zero chance that the trajectory ever hits precisely that bottom.

To develop the last argument a little further we assume that the mutational steps have length less than ε, and that we consider a family of adaptive dynamics parametrised with ε, where ε acts as a scaling factor for the distribution of the mutational steps. Otherwise the distribution of the mutational steps is assumed to be fixed. Moreover we assume that mutations in the different types occur in independent Poisson processes with rates scaling as ε^{-1}, and otherwise only dependent on the composition of the community. Finally we assume that these rates are for fixed ε bounded away from both infinity and zero, the latter with the exception of points near to a boundary of the $\mathbb{P}_n$ under consideration where that type is pushed to extinction. (These assumptions are the simplest ones compatible with our wish to accommodate general types of community dynamics; see subsection 6.4.1).

Our new assumptions imply that the crossing of a unit distance by our descending trajectory brings with it a sideways wobble scaling as $\varepsilon^{0.5}$. Therefore we predict that it hits the side walls of the furrow at a distance from the bottom which scales as ε^{θ}, with $0 \leq \theta \leq 0.5$ depending on the particular assumptions that we make about its starting point.

The argument which we just developed applies to any situation in which evolution of the members of a community pushes two lines of descent towards each other. Except for a set of initial conditions with vanishing measure the chance that two lines of descent will ever come within an ε-distance from each other, once they have diverged further than that distance, should go to zero faster than ε.

The pleasant conclusion is that the trajectories of an adaptive dynamics in which the sizes of the mutational steps are bounded by ε, ε small, should, when observed at a resolution coarser than ε, look like good trees, without any merging branches.

4.5. *About the speeds of adaptive movement, and, again, branching*

In the polymorphic situation, as in more species co-evolution, the relative speeds of stepping in different directions starts to matter. (For higher dimensional trait spaces this is already the case for monomorphic evolution.) Biologically this speed is determined by two classes of processes: Intra-individual ones, determining (i) the probability that a birth event produces a mutated individual as well as (ii) the sizes of the mutational steps (and for higher dimensional trait spaces also the correlations between the various directions in which that step may be made). And ecological ones, determining (iii) the birth rate into a population and (iv) the probability that a mutant gets established.

We shall argue below that population dynamical considerations suggest that in nature the latter probability is roughly proportional to the fitness of the mutant, as long as that fitness is but small. Therefore we shall make an assumption to this effect in section 6 where we describe the directions in which we think that taxonomic level theory should be developed. For the time being we only point to one important effect of this assumption: It makes the initial development of a dichotomy a relatively slow process, and thereby usually precludes the development of full blown dichotomies when a sample path gets in the neighbourhood of a red stagnation set, except near rest points of the n-type adaptive dynamics under consideration.

Remark: In the simulations from figures 6 to 8, the probability of a mutant with positive fitness getting established was set equal to a constant. For the combination of the particular initial condition chosen and the fitness function deriving from (4.1), this difference in assumptions effectively only affects the time scale of the middle panes.

5. The individual based justification

5.1. *Two examples of the justification of deterministic population models at the level of the individuals comprising the population*

The middle pane of figure 10 shows the results of a simulation of a stochastic population model, in which the individuals are counted in integers $N(x_i)$, that may be thought as underlying the model from subsection 4.1.

The individual-based models underlying the differential equation (4.1) have in common that, conditional on the present condition of their environment E(t), with

$$E = \{(x_j,n(x_j))\}, \qquad n(x_j) := N(x_j)/\Omega, \qquad \Omega \text{ the "system size"}, \tag{5.1}$$

(i) individuals are independent, (ii) die at random, with death rate $\mu(x_i,E(t))$, (iii) a living individual gives birth in a Poisson process with rate $\lambda(x_i,E(t))$, and (iv)

$$\lambda(x_i,E(t)) - \mu(x_i,E(t)) = \left[1 - \frac{\sum_j a(x_i,x_j)n(x_j)}{k(x_i)}\right]. \tag{5.2}$$

As a result the counts form a continuous time Markov process with transition rates

$$N(x_i) \xrightarrow{\mu(x_i,E(t))\,N_i} N(x_i)-1, \qquad N(x_i) \xrightarrow{\lambda(x_i,E(t))\,N_i} N(x_i)+1. \tag{5.3}$$

(4.1) is interpreted as the large number limit of such processes, i.e., the limit in distribution of a sequence of processes $\{n(x_i) = N(x_i)/\Omega\}$, for $\Omega \to \infty$ (see e.g. van Kampen, 1981; Kurtz, 1981 ; Ethier & Kurtz, 1986).

To speed up the simulations we chose to set the birth rates uniformly equal to one and put all dependence on E in the death rates. Moreover we discretised the trait axis into 99 equal intervals, or bins, with x_i the midpoint of the i-th bin. Ω was set equal to 2500. Finally (5.2) was modified to the extent that at each birth event the newborn was put only with probability $1-\theta$ in the bin of its parent, and with probability $\theta/2$ in either of the adjacent bins. The mutation probability θ was set equal to 0.003; the value of the "competition strength" is the same as that from figure 7, $\alpha = 2$.

The rightmost pane of figure 10 shows the results from approximating the full individual-based model by the large number limit

$$\frac{dn(x_i)}{dt} = \left[1-\theta - \frac{\sum_j a(x_i,x_j)n(x_j)}{k(x_i)}\right] n(x_i) + \tfrac{1}{2}\,\theta\left[n(x_{i-1}) + n(x_{i+1})\right], \qquad i = 1,\ldots,99. \tag{5.4}$$

(Note that (5.4) formally turns into (4.1) when we let $\theta \to 0$.) The dark area corresponds to $n(x_i,t) > 0.005$.

5.2. *The Adaptive Dynamics formulation of the same population models*

The leftmost pane of figure 10 shows the result of a simulation of the adaptive dynamics type. This figure is comparable to the middle pane of figure 7, except that we (i) assumed that the rate at which mutants were produced by type x_i was proportional to the system size times the equilibrium density $\tilde{n}(x_i)$ of that population, calculated from (4.1), (ii) we set the probability that a mutant got established equal to

$$\left[1-\mu(y,\tilde{E})\right]_+, \qquad \tilde{E} = \{(x_1,\tilde{n}(x_1)),\ldots,(x_{99},\tilde{n}(x_{99}))\}. \tag{5.5}$$

These assumptions are based on the following arguments: (i) If mutants appear sufficiently rarely then the population dynamics has time to reach equilibrium before the appearance of the next mutant. (ii) Mutants appear as single individuals. As long as N(y) is small, and Ω large, (a) it still makes sense to count the mutants in integer numbers, (b) the mutants contribute only negligibly to E as perceived by the individuals (i.e., through the functions $\mu(x,E(t))$). Therefore the mutant population initially grows according to a linear birth and death process with per capita birth and death rates

$$\lambda = \lambda(y,\tilde{E}) = 1, \qquad \mu = \mu(y,\tilde{E}) = \frac{\sum_j a(y,x_j)\tilde{n}(x_j)}{k(y)}. \tag{5.6}$$

The sample path of such a process hits zero in finite time with probability $\min\{1,\mu/\lambda\}$, and with probability $(1-\mu/\lambda)_+$ eventually grows exponentially at rate $\rho = \lambda-\mu$. Only mutants which get into the exponential growth regime eventually get established, with a time to establishment which scales as $\log(\Omega)/\rho$.

Remark: The stochastic process $\{n(x_i)\}$ cannot equilibrate in the strict sense since "everybody dead" is an absorbing state. However, (i) the average time to extinction scales exponentially in Ω, (ii) when $\theta = 0$ the functionals $n(x_i,t)$ converge in distribution to the solution of (4.1) for any bounded time, and (iii) an interior fixed point of (4.1) attracts the full interior of the positive cone. (i) to (iii) combine into the statement that for $\theta = 0$ (a) the convergence to quasi-equilibrium (i.e., convergence to equilibrium of the process that results from a conditioning on non-extinction) is much faster than extinction, (b) the distribution of $n(x_i)$ at quasi-equilibrium weakly converges to a point mass at $\tilde{n}(x_i)$ for $\Omega \to \infty$.

5.3. *A comparison of the results from the three different formulations*

All three simulations in figure 10 show the same branching pattern. The most obvious difference is in the overall speed of the three processes: The large number limit is about 15 times, and the adaptive dynamics approximation about 3 times as fast as the real thing. We believe that latter difference is largely due to the demographic noise resulting from the smallness of Ω (necessitated by the limited computer speed at our disposal): The realised instantaneous fitnesses for the full model fluctuated considerably over short time spans, and their moving time averages were much flatter functions of y than the $s_C(\cdot)$ calculated from the adaptive dynamics approximation. (The latter effect also resulted in a much decreased propensity for further branching in simulations at higher values of α.) The increased speed of the large number limit is due to the presence of all possible types immediately after t = 0, even when the differential equation is started up with all but one $n(x_i)$ equal to zero. These types may be present in extremely low densities, corresponding to a number much lower than 1 for any realistic value of Ω, but they can make up for this lack in numbers by their rapid reproduction. (In simulations for smaller values of α this even resulted in the growth of a secondary peak, seemingly out of the blue, opposite to the primary peak, followed by a movement of the two peaks towards each other ending in their merger into a single peak around the EUS.)

5.4. *The justification of any general theory of Adaptive Dynamics*

Generalising from the previous example we argue that adaptive dynamics type models should be seen as limits, for the system size Ω going to infinity, of stochastic individual-based models in which (i) the influences of individuals on E scale as $1/\Omega$, (ii) the initial numbers of individuals are proportional to Ω, (iii) the mutation probabilities per birth event scale as θ, where $\Omega\theta \to 0$ when $\Omega \to \infty$, while (iv) we look on a time scale $T = \Omega\theta t$, t the old time scale, and (v) concentrate on following the trait values which are represented by numbers of individuals that are not $o(\Omega)$.

(i) and (ii) should guarantee that the population dynamical influences on E becomes free from demographic fluctuations on the t-scale, and (iii) should guarantee that that limiting population dynamics is not influenced by the occurrence of mutations. Finally (iv) guarantees that (a) the average number of mutations per unit of T-time remains bounded and bounded away from zero, provided the original process had mutation rates which were so bounded, (b) the E dynamics converges to its attractor infinitely quickly in T-time, provided that the limiting E dynamics in t-time has the right convergence properties, and (c) only time averaged properties in t-time E dynamics matter in T-time (but we should be careful to do our averaging right!).

It is in the light of this interpretation that we should judge the list of assumptions in the next section.

6. Prolegomena to a general theory of Adaptive Dynamics

6.1. *Some notational conventions*

Adaptive Dynamics are stochastic processes with piece-wise constant sample functions mapping $\mathbb{R}_+$ to finite subsets of a compact and simply connected trait space $\mathbb{X} \subset \mathbb{R}^k$, with elements X, $X_1,\ldots,X_n$,Y, satisfying certain special assumptions which we shall outline below.

For notational purposes it is useful to introduce

$$\mathcal{X} := \bigcup_{n=0}^{\infty} \mathbb{X}^n, \tag{6.1}$$

where

$$\mathbb{X}^0 := \{V\}, \quad V \text{ the "virgin world".} \tag{6.2}$$

The elements of $\mathcal{X}$ will generically be denoted as $C = (X_1,\ldots,X_n)$. The connection between $\mathcal{X}$ and the finite subsets of $\mathbb{X}$ is made through the map

$$\text{Set: } C \mapsto \text{Set}(C) := \{X_1,\ldots,X_n\}, \qquad \text{Set}(V) := \varnothing, \tag{6.3}$$

and the equivalence relation

$$(X_1,\ldots,X_n) \sim (X_1,\ldots,X_m) \;:\Leftrightarrow\; \{X_1,\ldots,X_n\} = \{X_1,\ldots,X_m\}. \tag{6.4}$$

The equivalence class of C can be written as $\text{Set}^{-1}(\text{Set (C)})$.

For later use we moreover define

$$C/\{1_1,\ldots,i_m\} := (X_1,\ldots,X_{i1-1},X_{i1+1},\ldots,X_{im-1},X_{im+1},\ldots, X_n\}. \tag{6.5}$$

6.2. *Fitness and protected polymorphisms*

6.2.1. Preliminaries about the fitness s

Each process is "governed" by a function

$$s: \mathbb{P} \times \mathbb{X} \to \mathbb{R} : (P,Y) \mapsto s_P(Y), \tag{6.6}$$

where

$$\mathbb{P} \subset \mathbb{X} \quad \text{is the set of "protected polymorphisms".} \tag{6.7}$$

The elements of $\mathbb{P}$ will generically be denoted as P. A recursive definition of $\mathbb{P}$, itself involving s, will be given in the next subsection. For the time being we only note that ($\mathbb{P}$,s) and ~ should be compatible, in the sense that

P0: $\mathrm{Set}^{-1(}\mathrm{Set}(\mathbb{P}\,) = \mathbb{P}$,

S0: $s_{P'}(Y) = s_P(Y)$ whenever $P' \sim P$.

Moreover s satisfies the selective neutrality of residents condition:

S1: $s_P(X_i) = 0$ for all $X_i \in \mathrm{Set}(P)$.

6.2.2. Delineating the protected polymorphisms, first go

A taxonomically oriented theory of adaptive dynamics requires that we can decide whether $C \in \mathbb{P}$ by a consideration of all expressions $s_{C'}(X)$, with $\mathrm{Set}(C') \subset \mathrm{Set}(C)$, and $X \in \mathrm{Set}(C)\backslash\mathrm{Set}(C')$. A rather straightforward generalisation of the constructions from sections 3 and 4 leads to the tentative definition

P1a: $\mathbb{P}_0 := \{V\}$,

$$\mathbb{P}_n := \Big\{ C \in \mathbb{X}^n \;\Big|\; \begin{array}{l} \text{for all P such that (1) } \mathrm{Set}(P) \subset \mathrm{Set}(C), \text{ and} \\ \qquad\qquad\qquad\qquad \text{(2) } P \in \mathbb{P}_{n-k} \text{ for some } k > 0, \\ \quad \text{there is at least one } X \in \mathrm{Set}(C)\backslash\mathrm{Set}(P) \\ \qquad\qquad \text{for which } s_P(X) > 0 \end{array} \Big\},$$

P1b: $P_{<n} := \bigcup_{j=0}^{n-1} P_j$,

$$\mathbb{D}_n := \big\{ C \in \mathbb{X}^n \;\big|\; \mathrm{Set}(C) \in \mathrm{Set}(\mathbb{P}_{<n}) \big\},$$

$$\mathbb{A}_n := \mathbb{P}_n \cup \mathbb{D}_n,$$

$$\boldsymbol{P} := \bigcup_{n=0}^{\infty} A_n.$$

Figure 11 exemplifies the meaning of **P1a**: The three numbered corners of the triangle symbolise three trait values X_1, X_2, and X_3. Vertices midway between two corners, say i and j, symbolise combinations of two trait values, $C = (X_i, X_j)$. The vertex at the centre represents the combination of all three trait values, $C = (X_1, X_2, X_3)$. Vertices corresponding to trait combinations $P \in \mathbb{P}$ have been encircled. An outgoing arrow from such an encircled vertex pointing to the i-th corner signifies that $s_P(X_i) > 0$, and an ingoing arrow that $s_P(X_i) < 0$. The arrows attached to the three corner vertices tell us that (X_1, X_2) is the only protected dimorphism (up to equivalence) that can be made out of $\{X_1, X_2, X_3\}$. We consider (X_1, X_2, X_3) a protected polymorphism since all four encircled non-centre vertices have at least one outgoing arrow attached to them.

P1a is a direct adaptation to the clonal case of a definition appearing in various places in the population genetical literature (see e.g. Eshel, 1995). But this definition is not without problems, as we shall see in the next subsection. However, before we deal with these problems we first go a little further into the population dynamical intuition underlying **P1a**, or rather figure 11.

At the community dynamical level the vertices in figure 11 should be interpreted as representing a community with one, two or three types present out of $\{X_1, X_2, X_3\}$.

Explanatory remark: The state space of a single X_i population necessarily is a positive cone. Negative population densities don't exist. The state space of a community comprising a combination $C = (X_1, \ldots, X_n)$ of n types necessarily is a product of n of these positive cones times the state space of the remainder of the community. When the state of the X_i population is zero we say that X_i has been deleted from the community. The faces of the community state space defined by the deletion one or more of the X_1, …, X_n, are community dynamically invariant. We call an attractor of a community global when it attracts for almost all initial conditions for which the states of all its ingredient populations are essentially non-zero (meaning that there is a positive mass of individuals which are still able to reproduce effectively). An internal global attractor of a k-type sub-community (a) globally attracts inside the face of the community state space which results from deleting the remaining n-k types, (b) puts no community mass on the faces of the state space of the sub-community.

The fact that the three corner vertices are encircled tells us that the faces of the community state space corresponding to the three single-type sub-communities are supposed to have internal global attractors. The arrows attached to these vertices tell us that each of these internal attractors is externally unstable in the (X_1, X_2, X_3) community. The same arrows also tell us that only one of the three possible two type communities can ever have an internal global attractor. For believers in a bounded noisy world the arrow pattern also strongly suggest that it indeed has such an attractor. (But few general theorems to this effect have been proved as yet; see e.g. Ellner (1984) and Chesson and Ellner (1989).) The total arrow pattern does not point to any structure in the combined faces of the community state space with the potential to attract all community mass from the interior. By a leap of faith we take this as an indication that the three type community should have an internal attractor.

6.2.3. Some flies in the ointment, and two optional axioms

Figure 12 shows, in a notation comparable to that of figure 11, three possible sign configurations of s on subsets of $\{X_1, \ldots, X_4\}$ which according to **P1a** should make $(X_1, \ldots, X_4)$ into an element of $\mathbb{P}_4$. The left and right configurations are unproblematical, but the middle configuration contains a "heteroclinic loop". Any community dynamical model underlying this sign configuration necessarily sports a heteroclinic loop in the standard sense of the word.

It is possible to construct community dynamical models with heteroclinic loops, or, more generally, heteroclinc networks, which attract with respect to the interior of the positive cone. **P1a** fails to exclude that an underlying population dynamics possesses an attracting heteroclinic network. Therefore "space of protected polymorphisms" is somewhat of a misnomer for a $\mathbb{P}$ which just satisfies **P1**. (NB: There is no inherent contradiction in the existence of a combination ($\mathbb{P}$,s) satisfying **P1**, and of a corresponding formal adaptive dynamics, which makes no community dynamical sense.)

There are three ways in which we can proceed:
(i) We just ignore the complication. Although it is impossible to interpret the resulting mathematical theory fully in terms of individual-based processes, there is no immediate reason that it contains internal inconsistencies. Of course we should be somewhat careful how we interpret any ensuing theorems. But none of our results so far seems to be particularly vulnerable to interpretational problems caused by the ensuing semantic gap.
(ii) We modify **P1a** by including some additional conditions which should exclude from (include in) $\mathbb{P}_n$ any $(X_1,\dots,X_n)$ supporting attracting (repelling) heteroclynic networks of an underlying community dynamics. This strategy will only fit in our taxonomically oriented approach when it is generally possible to distinguish unequivocally between attracting and non-attracting heteroclinic networks solely in terms of our function s. Since all results so far known about the (non-)attractivity of heteroclinic networks in (differential equation models for) community dynamics are phrased in terms of that s (Brannath, 1994; Hofbauer, 1994) there is some hope that such an approach may become feasible in the future.
(iii) We just exclude any s which happens to produce heteroclinic loops from our consideration by adding an axiom to that account:

P2: No $P \in \mathbb{P}$ supports a heteroclinic loop.

Unfortunately we don't have easy ways for checking **P2** for a given function s. Moreover, so far we never made explicit use of **P2** in deriving results. Therefore strategies (i) and (iii) essentially amount to the same.

P2 is but one way of singling out a special subclass of adaptive dynamics. A still smaller subclass is determined by

P3: $P \in \mathbb{P}$ implies that $P/\{i\} \in \mathbb{P}$ for all $i = 1,\dots, \#\mathrm{Set}(P)$.

The rightmost diagram of figure 12 provides an illustration. **P3** trivially implies **P2**. Moreover it excludes all adaptive dynamics with sign configurations of s for which the existence of a good internal attractor of any underlying community dynamics may be contentious. (But we wish to point out here that we have devised community models not satisfying **P3** that behaved perfectly well adaptive-dynamically.)

The following proposition, given without proof, provides a somewhat more easily checkable sufficient condition for **P3**: s satisfies **P3** if (i) for every P there is at least one i such that $P/\{i\} \in \mathbb{P}$, and (ii) $s_P(Y) > 0 \Rightarrow S_{P/\{i1,\dots,ik\}}(Y) > 0$ for all pairs $P, P/\{i_1,\dots,i_k\} \in \mathbb{P}$.

6.3. *Smoothness of s*

The two main reasons to develop any high level theory, i.e., a theory which is not immediately tied to a particular class of models, are that (i) such a theory may point at results which risk to go unnoticed under the clutter of detail inherent in the analysis of special models, (ii) it is only through those means that we can bring out the robust properties of larger classes of models. Both (i) and (ii) hold water only if the ensuing results are sufficiently unexpected. Adaptive dynamics starts to get interesting when we may assume that s is sufficiently smooth. But there is a snag: It is rather hard to find what kind of smoothness conditions are condoned by our requirement that the theory can be tied to at least some classes of community dynamical models. Below we give our present insights in this matter, but this clearly is a topic in need of greater scrutiny.

6.3.1. Smoothness of s away from the diagonal planes of $\mathbb{X}^n$

Away from the diagonal planes of $\mathbb{X}^n$ it is relatively harmless to assume fairly unrestricted smoothness of s. This smoothness may be flouted for some specific community dynamical models, but the models that remain form a sufficiently large class. Moreover, when smoothness is flouted we often can produce the complete picture by gluing together the results for a number of regions inside which smoothness holds fine. An example of a useful smoothness assumption is

S2a: s can be continuously extended to (closure$\mathbb{P}_n$)×$\mathbb{X}$, n = 1, 2, … ,

and for all P ∈ (closure$\mathbb{P}_n$)\$\mathbb{E}_\delta$, $\mathbb{E}_\delta$ the δ-neighbourhood of the diagonal planes of $\mathbb{X}^n$, this extension satisfies, for both Q ∈ $\mathbb{R}^{nk}$ and V ∈ $\mathbb{R}^k$ small,

$$s_{P+Q}(Y+V) \;=\; s_P(Y) \;+\; Ds_P(Y)\,(Q,V) \;+\; {}^1\!/\!{}_2\,(Q,V)^T\,D^2s_P(Y)\,(Q,V)$$

$$+\;\; R(P,Y;Q,V),$$

with the remainder term

$$R(P,Y;Q,V) \;=\; O(|(Q,V|^3)$$

uniformly in (P,Y) on (closure$\mathbb{P}_n$)\$\mathbb{E}_\delta$,

where D^i denotes the i-th derivative of s with respect to (P,Y). The reason for removing $\mathbb{E}_\delta$ is disclosed in the next subsection

6.3.2. Smoothness of s on closure$\mathbb{P}_n$

Figure 13 illustrates the problems that we run into when we try to extend **S 2** to the intersection of closure$\mathbb{P}_n$ and the diagonal planes of $\mathbb{X}^n$. The left hand diagram shows the isocline pattern for two members of a family of hypothetical unstructured two-type communities. In community A the two types differ, and there is a single, stable, internal equilibrium; community B consists of two exactly equal types, so that the two isoclines become a straight line connecting the two equivalent single species equilibria. The right hand diagram once more shows the position of these equilibria, but now accompanied by two pairs of paths traced by the equilibrium when we move along smooth curves in closure$\mathbb{P}_2$. The two curves passing through the parameter vector of community A map into two paths which intersect at the position of the single A equilibrium. However, there is no reason at all why the paths corresponding to the curves passing through the parameter vector of community B, should intersect.

Remark: We drew the latter paths as staying on one side of the line of B equilibria, instead of crossing that line, since this happens to be the generic pattern for Lotka-Volterra models. (Remember that the places where closure$\mathbb{P}_2$ intersects the diagonal of $\mathbb{X}^2$ are strongly constrained; it is this constraint which is at the heart of an otherwise maybe rather unexpected result.) We haven't yet tried to prove that this pattern extends to general ODE community models though. The same Lotka-Volterra models also provide immediate counter examples against the existence of a derivative of s on (closure$\mathbb{P}_n$)×$\mathbb{X}$.

The upshot is that community dynamical considerations may condone assuming that s has smooth directional derivatives in closure$\mathbb{P}_n$, but not that it has smooth derivatives. Since these considerations only apply to the P-component of (P,Y) we conjecture that any overall smoothness assumptions on s should take the following format

S2b: s can be continuously extended to (closure$\mathbb{P}_n$)×$\mathbb{X}$, n = 1, 2, … ,

and this extension satisfies, for V ∈ $\mathbb{R}^k$ small,

$$s_P(Y+V) \;=\; s_P(Y) \;+\; B(P,Y)\,V \;+\; V^T\,C(P,Y)\,V \;+\; O(|V|^3)$$

with B and C continuous in (P,Y), and, for Q ∈ $\mathbb{C}$(P) (see below), |Q| = 1,

$$\begin{aligned} s_{P+\varepsilon Q}(Y) &= s_P(Y) + \varepsilon\, a_1(P,Y;Q) + \varepsilon^2\, a_2(P,Y;Q) + O(\varepsilon^3), \\ B(P+\varepsilon Q,Y) &= B(P,Y) + \varepsilon\, B_1(P,Y;Q) + O(\varepsilon^2), \\ C(P+\varepsilon Q,Y) &= C(P,Y) + O(\varepsilon), \end{aligned}$$

with $a_1(P,Y;Q)$, $a_2(P,Y;Q)$, $B_1(P,Y;Q)$ homogeneous in Q, and continuous in P, Y, and Q, and the various order estimates uniform on $\mathbb{P}_n$,

where

$$\mathbb{C}(P) := \text{closure}\Big\{ Q \in \mathbb{R}^{nk} \;\Big|\; P+\varepsilon Q \in \mathbb{P}_n \text{ for all sufficiently small } \varepsilon \Big\}. \qquad (6.8)$$

Remark: S2b almost implies **S2a**. (The proof follows the lines of the proof of theorem 12.11 in Apostol (1974).) The exceptions are the corners of $\mathbb{P}_n$ (the set of points of non-smoothness of $\partial\mathbb{P}_n$), not only the corners where $\mathbb{P}_n$ touches a diagonal plane of $\mathbb{X}^n$.

6.3.3. Extending **S 0**, and some consequences

Below we shall no longer distinguish between s and its extension to closure$\mathbb{P}$. However, before we can do this we first have to assume explicitly that our old

S0: $s_{P'}(Y) = s_P(Y)$ whenever $P' \sim P$,

also holds good for that extension.

By applying **S 1** to **S2b** we find that, for small $Q = (U_1,\dots,U_n)$ and V,

$$s_{P+Q}(X_i+V) = {}_iB(P)\,(V-U_i) + {}_iB_1(P,Q)\,(V-U_i)$$
$$- U_i^T\, {}_iC_{22}(P)\, U_i + V^T\, {}_iC_{22}(P)\, V + O(|(Q,V)|^3), \qquad (6.9)$$

with

$${}_iB(P) := B(P,X_i), \quad {}_iB_1(P,Q) := B_1(P,X_i;Q), \quad {}_iC_{22}(P) := C(P, X_i\,). \qquad (6.10)$$

S 1 and **S2a** tell us that away from the diagonal planes of $\mathbb{X}^n$ (6.9) may be replaced by the stronger

$$s_{P+Q}(X_i+V) = {}_iB(P)\,(V-U_i) + \sum_{j=1}^{n} U_j^T\; {}_iB_{1,j}(P)\,(V-U_i)$$
$$- U_i^T\, {}_iC_{22}(P)\, U_i + V^T\, {}_iC_{22}(P)\, V + O(|(Q,V)|^3), \qquad (6.11)$$
$$= {}_iB(P)\,(V-U_i) + \sum_{\substack{j\neq i\\ j=1}}^{n} U_j^T\; {}_iB_{1,j}(P)\,(V-U_i)$$
$$+ U_i^T\, {}_iC_{11}(P)\, U_i + 2\, U_i^T\, {}_iC_{12}(P)\, V + V^T\, {}_iC_{22}(P)\, V + O(|(Q,V)|^3),$$

with

$${}_iC_{11}(P) := -{}^1\!/_2({}_iB_{1i}(P)+{}_iB_{1i}^T(P)) - {}_iC_{22}(P), \qquad {}_iC_{12}(P) := {}^1\!/_2\; {}_iB_{1i}(P), \qquad (6.12)$$

so that

$${}_iC_{11}(P) + {}_iC_{12}(P) + {}_iC_{12}{}^T(P) + {}_iC_{22}(P) \;=\; 0. \qquad (6.13)$$

Formulas (6.9), (6.11), and (6.13) are the real workhorses.

S 2 may also be used together with **S 0** and **S 1** to justify the assumption made in section 3 for 1-dimensional $\mathbb{X}$, that $s|_{\mathbb{P}_2\times\mathbb{X}}$ unrestrictedly allows a second order Taylor formula. **S2a** already tells that this is the case away from the diagonal. For $P = (x^*,x^*)$ we use an elegant argument due to Christiansen & Loeschcke (1987). The first formula of **S2b** says that $s_{P+Q}(x_i+v)$ consists of a quadratic in v plus a third order correction term, with the leading term of the quadratic equal to ${}_ic_{22}(P)v^2$, and the other coefficients also depending on $Q = (u_1,u_2)$. The equality of the components of P in combination with **S0** tell us that ${}_1c_{22}(P) = {}_2c_{22}(P)$, so that we can drop the i. The equality of the components of P combines with **S 1** to tell us that this quadratic should be zero when either $v = u_1$ or $v = u_2$. But for a single variable, and only for a single variable, this implies that the quadratic equals $c_{22}(P)(v-u_1)(v-u_2)$.

6.3.3. Consistency conditions connecting s on different $\mathbb{P}_n$.

Figure 14 shows the $\mathbb{A}_2$'s, with the stagnation sets drawn in, for a sequence of parameter values measuring the steepness of competition between differently sized seedlings, of a family of models for the competition among plants differing evolutionarily only in the sizes of the seeds which they produce. On the part of the boundary of where x_2 goes extinct the (x_1,x_2)-community reduces to a pure x_1 community. Therefore the x_1-stagnation set should intersect this boundary exactly at the values of x_1 where the monomorphic x_1-dynamics has a singular point. Moreover the local colour of the stagnation set should match the type of that singular point. A slightly more involved graphical argument shows that the x_2-stagnation sets should intersect the x_1-extinction boundary at the local extrema of that boundary in the x_1-direction. Local convexity of $\mathbb{P}_2$ around such an an extremum, call it $(x_1°,x_2°)$, implies that ${}_2c_{22}(x_1°,x_2°) > 0$, local concavity that ${}_2c_{22}(x_1°,x_2°) < 0$. Figure 14 also shows that these rules considerably constrain how $\mathbb{P}_2$ can transform when we change process parameters.

The previous observations form the motivation for the introduction of two assumptions, of increasing strength, which tell how $s|_{\mathbb{P}_n\times\mathbb{X}}$ connects to some of the $s|_{\mathbb{P}_m\times\mathbb{X}}$, $m<n$. But before we can state these assumptions we first need to introduce some additional notation: Let $J \subset \{1,\dots,n\}$, $0 \leq \#J \leq n-1$, and let $i \in \{1,\dots,n\}$, $i \notin J$. With this convention we define the smooth boundary components

$$\partial_{i;J}\mathbb{P}_n \;:=\; \Big\{ C \in \mathbb{X}^n \;\Big|\; \begin{array}{l} (1)\ (a)\ \ C/\{i\}\cup J \in \mathbb{P}_{n-\#(\{i\}\cup J)} \\ \qquad\ (b)\ \ s_{C/\{i\}\cup J}(X_i) = 0 \\ \qquad\ (c)\ \ s_{C/\{i\}\cup J}(X_j) < 0 \ \text{ for all } j \in J, \\ (2)\ \text{for any } P \text{ such that} \\ \qquad\ (a)\ \ \mathrm{Set}(P) \subset \mathrm{Set}(C) \\ \qquad\ (b)\ \ \mathrm{Set}(P) \neq \mathrm{Set}(C) \\ \qquad\ (c)\ \ \mathrm{Set}(P) \neq \mathrm{Set}(C/\{i\}\cup J), \text{ and} \\ \qquad\ (d)\ \ P \in \mathbb{P}_{n-h} \text{ for some } h > 0, \\ \quad \text{there is at least one } X \in \mathrm{Set}(C)\backslash\mathrm{Set}(P) \\ \qquad\qquad \text{for which } \ s_P(X) > 0 \end{array} \Big\}, \qquad (6.14)$$

together with the corners

$$\partial_{i1,\dots,ik;J1,\dots,Jk}\mathbb{P}_n := (\text{closure}\partial_{i1;J1}\mathbb{P}_n)\cap\dots\cap(\text{closure}\partial_{ik;Jk}\mathbb{P}_n), \tag{6.15}$$

with the convention that when $\#J = 0$ we just write $\partial_i\mathbb{P}_n$ instead of $\partial_{i;J}\mathbb{P}_n$. (Of course many of these boundary components may be empty!)

For completeness we moreover introduce the boundary components, for $J \subset \{1,\dots,n\}$, $1 \le \#J \le n$,

$$\Delta_J\mathbb{P}_n := \Big\{ C\in\mathbb{X}^n \;\Big|\; \begin{array}{l} (1)\ (a)\ \ C/J\in\partial\mathbb{P}_{n-\#J} \\ \qquad (b)\ \ s_{C/J}(X_j) < 0 \text{ for all } j\in J, \\ (2) \text{ for any } P \text{ such that} \\ \qquad (a)\ \ \text{Set}(P)\subset\text{Set}(C) \\ \qquad (b)\ \ \text{Set}(P)\neq\text{Set}(C), \text{ and} \\ \qquad (c)\ \ \text{Set}(P)\neq\text{Set}(C/J) \\ \qquad (d)\ \ P\in\mathbb{P}_{n-h} \text{ for some } h>0, \\ \quad \text{there is at least one } X\in\text{Set}(C)\backslash\text{Set}(P) \\ \qquad\qquad\qquad \text{for which } s_P(X)>0 \end{array}\Big\}. \tag{6.16}$$

and

$$\delta_i\mathbb{P}_n := \Big\{ P=(X_1,\dots,X_n)\in\mathbb{P}_n \;\Big|\; X_i\in\partial\mathbb{X} \Big\}. \tag{6.17}$$

To simplify the discussion we shall below sometimes invoke the transversality condition

$\mathbf{T}_{<\mathbf{n}}$: the graph of $s|\mathbb{P}_{<n}\times\mathbb{X}$ is transversal to the graph of the nul-function on $\mathbb{P}_{<n}\times\mathbb{X}$.

From the definition of $\mathbb{P}_n$ and the continuity of s it immediately follows that, whenever $\mathbf{T}_{<\mathbf{n}}$,

$$\partial\mathbb{P}_n = \bigcup_{1\le i\le n,\, J\subset\{1,\dots,n\},\, 0\le\#J\le n-1} \text{closure}\partial_{i;J}\mathbb{P}_n \;\cup \bigcup_{J\subset\{1,\dots,n\},\, 1\le\#J\le n} \text{closure}\Delta_J\mathbb{P}_n \;\cup \bigcup_{0\le i\le n} \delta_i\mathbb{P}_n. \tag{6.18}$$

We start with an assumption about the behaviour of s near the smooth boundary components:

S3: $\quad s_P(Y) = s_{P/\{i\}\cup J}(Y) \quad$ for all $\ P\in\partial_{i;J}\mathbb{P}_n$.

S 3 may be thought of as expressing the community level assumption that the attractors of the community dynamics depend smoothly on the parameters differentiating the constituting species.

S 3 nicely does away with the $\Delta_J\mathbb{P}_n$ in the sense that, whenever $\mathbf{T}_{<\mathbf{n}}$,

$$\partial\mathbb{P}_n = \bigcup_{1\le i\le n,\, J\subset\{1,\dots,n\},\, 0\le\#J\le n-1} \text{closure}\partial_{i;J}\mathbb{P}_n \;\cup \bigcup_{0\le i\le n} \delta_i\mathbb{P}_n. \tag{6.19}$$

(The proof goes by induction on n.)

Next we observe that the combination of **S 2** and **S 3** implies that

$$s_P(Y) = s_{P/\{i1\}\cup J1}(Y) = \dots = s_{P/\{ik\}\cup Jk}(Y) \quad \text{whenever } P\in\partial_{i1,\dots,ik;J1,\dots,Jk}\mathbb{P}_n, \tag{6.20}$$

i.e., in the corners the full functions $s_{P/\{i_j\}\cup J_j}(\cdot)$, $j = 1,\dots,k$, should coincide. This would be rather a coincidence, except when it so happens that the we are basically dealing with an invasion rate into one and the same P', such that $\mathrm{set}(P') \subset \bigcap_j \mathrm{Set}(P/\{i_j\}\cup J_j)$. (The points $P/\{i_j\}\cup J_j$, $P \in \partial_{i_1,\dots,i_k;J_1,\dots,J_k}\mathbb{P}_n$, then should be also boundary points of $\mathbb{P}_{n-\#(\{i_j\}\cup J_j)}$.) This observation suggests that we may without great loss of community dynamical generality assume:

S4: $$s_P(Y) = s_{P/\{i_1,\dots,i_k\}\cup J_1\cup\dots\cup J_k}(Y) \quad \text{for all} \quad P \in \partial_{i_1,\dots,i_k;J_1,\dots,J_k}\mathbb{P}_n.$$

S 4 trivially implies **S 3**, but not vice versa.

S 4 has two immediate consequences. The first is, not unexpectedly,

$$(\partial_{i_1,\dots,i_k;J_1,\dots,J_k}\mathbb{P}_n)/\{i_1,\dots,i_{j-1},i_{j+1},\dots,i_k\}\cup J_1\cup\dots\cup J_k \subset \partial\mathbb{P}_{n-\#(\{i_1,\dots,i_k\}\cup J_1\cup\dots\cup J_k)+1}. \tag{6.21}$$

The second one is slightly more involved. Therefore we will only give an example: For figures 6, 7, 8 and 14, **S 4** together with **S 1** implies that near to the outer corners of $\mathbb{P}_2$ the adaptive movement is away from the corner.

6.4. *The trait substitution process*

An adaptive dynamics is governed by its s not only through its sample functions being maps from $\mathbb{R}_+$ to $\mathrm{set}\mathbb{P}$; s also governs the mechanics of the trait substitution process.

A trait substitution, i.e., a jump in the sample function, is generated by the composition of three processes:

(1) The production of a mutant $Y = X_i+V$ from an $X_i \in \mathrm{Set}(P)$.

Mutations result from rare copying errors of the genetic material during individual reproduction events. A mutation gets expressed as a step in the trait vector of the mutant relative to that of its parent only through the action of the developmental process on the individual mutated genotype.

(2) The establishment of that mutant.

When $s_P(Y) \le 0$ the mutant will fail to establish and the sample function continues smoothly, when $s_P(Y) > 0$ there is a chance that the mutant gets established.

(3) The production of a new value of the sample function.

The establishment of a mutant leads to a shake-up of the community in which one or more of the $X_i \in \mathrm{Set}(P)$ may be lost.

Only the end result of these three processes is visible at the level of the sample function, as the positions and types of jumps.

6.4.1. The production of mutants

Since the production of mutants contains a large intra-individual component we have but few a priori considerations to base our assumptions on. The list of assumptions below tries to strike a compromise between being biologically as weak as possible and yet being mathematically sufficiently useful. It is only at the intra-individual level that we strived for weakness. Where we could strengthen the assumptions by bringing in a community dynamical argument we have done so.

From the present jump moment till the next one, mutations in X_i may be assumed to occur in a Poisson process with rate λ_i.

Basic biological considerations tell us that λ_i (a) may depend on the history of the line of descent leading to X_i, and (b) depends on P. (a) is due to the fact that the map from genotype to any simple phenotypic representation necessarily is very many to one, so that there is no good reason to expect that on the phenotypic level the mutation process is Markovian, (b) to the fact that at the community dynamical level P determines the average birth rate into the X_i-population. We shall make only the weak assumption that the mutation probabilities per birth event are bounded away from both 0 and ∞. If we make the same sort of continuity assumptions on the attractors of the community dynamics as before, we end up with the overall assumption:

M1: $$0 < {}_{-}\lambda_i(P) \leq \lambda_i \leq {}_{+}\lambda_i(P),$$

with

(i) ${}_{\pm}\lambda_i$ continuous in all points $P \in \mathrm{closure}\mathbb{P}_n$, with the exception of P for which $X_j = X_i$ for some $j \neq i$,

(ii) for $P = (X_1,\ldots,X_n) \to C = (X'_1,\ldots,X'_n) \in \partial_{i;J}\mathbb{P}_n$, $\#\mathrm{Set}(C) = n$,

$${}_{\pm}\lambda_i(P) = O(|X_h - X'_h|) \qquad \text{for } h \in [i] \cup J,$$

$${}_{\pm}\lambda_i(P) \to {}_{\pm}\lambda_i(C/[i] \cup J) \qquad \text{for } h \notin [i] \cup J,$$

(iii) for $P = (X_1,\ldots,X_n) \to C = (X'_1,\ldots,X'_n)$ with $X'_j = X'_i$, $j > i$,

$${}_{\pm}\lambda_i(P) + {}_{\pm}\lambda_j(P) \to {}_{\pm}\lambda_i(C/\{j\}).$$

Of course, special adaptive dynamics may satisfy stronger assumptions, e.g. the Markovian dependence of λ_i on P.

Biology also tells that the distribution of the mutational steps $V = Y - X_i$ may well depend on the history of the line of descent leading to X_i. Therefore we only make an overall non-degeneracy assumption:

M2: The mutational steps are continuously distributed, with the possible exception of a concentration of mass on

$$\mathbb{B}(X_i) := \{V \mid Y = V + X_i \in \partial\mathbb{X}\};$$

the latter mass is continuously distributed on $\mathbb{B}(X_i)$.

M2b: Let f temporarily denote the density of Y in $\{V \mid Y = V + X_i \in \mathbb{X}\}$, and g the density of Y in $\mathbb{B}(X_i)$. Both f and g are uniformly continuous on the closures of their domains and there exists a single constant $c > 0$ such that $f(0) > c$, and, when $X_i \in \partial\mathbb{X}$, $g(0) > c$.

M2b guarantees that mutations effectively occur in all directions.

To make the smoothness assumptions on s pay, other than by providing some constraints on the possible shapes of $\mathbb{P}$, we have to assume that the mutational steps are uniformly small:

M3: There exists an ε such that

$$\mathcal{P}\{|V| > \varepsilon\} = 0.$$

6.4.2. The establishment of a mutant

To get established, the mutant population has to grow from a single individual to a number of individuals which is of the order of the system size Ω (compare the discussion in section 5). The initial phase of this growth process is dominated by stochastic demographic fluctuations. In the limit of infinite Ω the probability of establishment should equal that of the stochastic branching process where Y type individuals reproduce in the environment E(P).

The estimates for the establishment probability of particular branching processes with low growth rates (Haldane 1927; Kendall, 1948, 1949; Eshel, 1981, 1984; Hoppe 1992a, b; Athreya 1992, 1993; Pollak 1992; Haccou & Iwasa, in prep) all have an initial term which is linear in the growth rate. Therefore it seems safe to assume that

B: The probability $\pi_P(Y)$ that a Y mutant successfully invades a P community is zero when $s_P(Y) < 0$, and when $s_P(Y) \geq 0$ we can bound $\pi_P(Y)$ by

$$\alpha\, s_P(Y) + o(s_P(Y)) \leq \pi_P(Y) \leq \beta\, s_P(Y),$$

with α, $\beta > 0$, and the order term uniform on $\mathbb{P}$.

Remark: We slightly oversimplified the argument above. On the community dynamical time scale both the birth rate of Y mutants and the probability that a mutant gets established are time dependent, except in the special cases that the community attractor is a deterministic equilibrium. Therefore the two processes, production of mutants by X_i and the establishment of a mutant, cannot be treated separately. The correct argument runs as follows: Let $\lambda'_i(t)$ denote the production rate of mutants from X_i, and $\pi'_P(Y)(t)$ the probability that a Y mutant gets established. Then

$$\lambda_i = \lim_{t\to\infty} t^{-1} \int_0^t \lambda_i'(\tau)\, d\tau, \qquad \pi_P(Y) = \lambda_i^{-1} \lim_{t\to\infty} t^{-1} \int_0^t \lambda_i'(\tau)\, \pi_P'(Y)(\tau)\, d\tau.$$

When moreover'

$$a(t)\, s_P(Y) + o(s_P(Y)) \leq \pi'_P(Y)(t) \leq b(t)\, s_P(Y),$$

with the order term uniform in t, then **B** holds good with α and β the corresponding time averages of a(t) and b(t). With these definitions the only visible effect on the evolutionary time scale of a complicated community dynamics is a dependence of $\pi_P(Y)$ on the parent of Y, which we didn't make explicit in our notation. When **M3** is in operation this dependence is necessarily slight, and it should be possible to make the estimate **B** independent of the parent of Y.

6.4.3. The production of the post-jump value of the sample function

The establishment of a mutant leads to a shake-up of the community in which one or more of the $X_i \in$ Set(P) may be lost. The following assumption about the types that are kept around is directly in line with the arguments underlying **P1**.

K: The new value of the sample function is chosen at random,
with probabilities which depend only on P and Y,
from among all P' such that

(i) $P' \in \mathbb{P}$,

(ii) $\mathrm{Set}(P') \subset \mathrm{Set}(P) \cup \{Y\}$,

(iii) for all $X \in (\mathrm{Set}(P) \cup \{Y\}) \setminus \mathrm{Set}(P')$

$$s_{P'}(X) \leq 0.$$

Figure 15 provides an illustration.

Remark: On the community dynamical level **K** only holds water as long as any heteroclinic loops are repelling. When the theory gets modified to cope in an acceptable manner with such loops, as we hope that will be possible in the future, the natural assumption is that P' also may be any trait combination that occurs in a vertex of an attracting heteroclinic loop.

7. One research strategy and some conclusions

The assumptions made in the previous section aren't the only possible ones. We listed them to make explicit our own preconceptions and to get a discussion started about possible useful and/or justifiable alternatives. Moreover, it is possible to explore their consequences in a number of different directions. One useful direction is the development of a bifurcation theory for EUSes. In this section we discuss, without proofs, a number of heuristically derived macro-evolutionary results, as an example of one other direction that could be taken.

We emphasise that it is as yet unclear how robust the results below are with respect to relaxing our basic time scale argument.

7.1. *The research strategy*

The results below were derived by adhering to the following research strategy

1. Let the scale of the mutational steps, as measured by their maximum seize ε, go to zero, and simultaneously rescale time so that the process doesn't freeze (which choice of scale is appropriate depends on the phenomenon that is considered).

2 a.Forget about features of the sample path that can only be seen at a resolution of $O(\varepsilon^{1/2})$.
  b.Forget about events that only occur, in interestingly long stretches of the sample path, with probability $o(1)$.
  c.Concentrate on phenomena that are stable under slight changes of s.

Remark: 2a also provides an exegesis of some of the verbiage in sections 3 and 4: "Small" should be interpreted as "$O(\varepsilon^{1/2})$ but not $o(\varepsilon^{1/2})$", "very small" as "$o(\varepsilon^{1/2})$", and "visible" as "not very small".

7.2. *Overall environment constant on the evolutionary time scale*

We start our discussion on the assumption that on the evolutionary time scale(s) the environment can be considered constant, i.e., the environmental fluctuations are fully restricted to the community dynamical time scale. In that case we should distinguish two time scales, each relevant to a particular type of evolutionary phenomena:

1. Both the number of steps needed to cover a fixed distance in any $\mathbb{P}_n$, n = 1, 2,… , and the time needed for one step, scale as ε^{-1} (remember axiom **B**). Therefore starting from some point $P \in \mathbb{P}_n$, the time needed for convergence to an attractor in $\mathbb{P}_m$, $m \leq n$, and time pattern of the movement on a non-point attractor in $\mathbb{P}_m$, scales as ε^{-2}. We shall label the corresponding evolutionary time scale fast.
2. Branching, however, takes a time which scales as ε^{-3}, since s is locally quadratic in $Y\text{-}X_i$ near a branching point of X_i. We shall label the corresponding evolutionary time scale slow.

If the mutation process is Markovian the movement on the fast evolutionary time scale can, but for the jumps to a lower degree of polymorphism, be approximated by an ODE (Dieckmann & Law, 1995).

Branching only occurs on the slow time scale after the fast process has come to rest at a point attractor of the adaptive dynamics in $\mathbb{P}_m$ which allows for the branching of, say, h, $1 < h \leq m$, lines of descent. Even for $\varepsilon \to 0$ the number of lines that branch may stay stochastic: Simulation results suggest that, due to the peculiar geometry of $\mathbb{P}$, the fast evolution of those branches that happen to have taken a relatively larger lead, inhibits the branching of the remaining lines of descent.

The previous considerations may be translated into the following predictions about macro-evolutionary patterns that derive from our model assumptions: If there are no long term environmental changes due to external perturbations, the natural overall behaviour of an adaptive dynamics will often show a number of alternations between short periods of fast change in the species in the community, and long periods of stasis of the community as a whole. The time scale of these phases is set by the production rate of mutational variation. "Speciation" is initiated only during static phases; the eventual divergence of the nascent species starts the next fast phase. This alternation goes on till the process gets trapped in a non-equilibrium attractor of the adaptive dynamics, or in a fully attractive evolutionarily unbeatable combination of strategies.

As a final point we mention once more that in higher dimensional trait spaces polytomies (in which one line of descent gives rise to more than two branches during a single slow phase) shouldn't be unusual, the higher the dimension of the trait space the higher the degree of polytomy.

7.3. *Changing physical environments*

As a final topic we consider the consequences of overall environmental fluctuations on the evolutionary time scale, say due to climate change.

Again we have to consider two time scales, but now of the environmental fluctuations. If the overall environment fluctuates on the fast evolutionary time scale the fluctuations will inhibit branching, by the same geometric mechanism by which progressive evolution of other lines of descent inhibited branching. (This may be seen as a, tongue in cheek, explanation for the low species diversity in the North, where the ice ages provided precisely this type of fluctuations.)

The second possibility is that the overall environment only fluctuates on the time scale of the static phases or even slower (the usual time scale of the geological record!). The typical patterns seen on that scale derive from the stable bifurcations of attractors of the adaptive dynamics. As this subject has hardly been broached, our conclusions all derive from a few immediate graphical arguments. Two stably occurring types of hard bifurcations are (i) saddle node type bifurcations and (ii) bifurcations in which an evolutionary point attractor located in, say, $\mathbb{P}_n$ transforms into a branching point. Intriguingly the latter type of bifurcation need not be of the pitchfork type in $\mathbb{P}_{n+1}$: The constraints on the places where the stagnation sets touch the boundary of $\mathbb{P}_{n+1}$ make that it is possible that an evolutionary point attractor located in $\mathbb{P}_n$ stably transforms into a branching point without making contact with evolutionarily singular points in $\mathbb{P}_{n+1}$. The result of such a bifurcation on the longest time scale is seen as the occurrence out of the blue, of an abrupt branching event, followed by fast progressive evolution of the novel "species".

In the parlance of paleontologists the patterns resulting from hard bifurcations of point attractors are called punctuated equilibria, (i) within a line of descent or (ii) with speciation.

One punctuation event may lead to more in its wake, as the fast evolution of one line of descent reverberates through the species assemblage, potentially resulting in extinctions and/or further branching events. We therefore may expect that the overall effect of a continually changing environment has the look of quasi-stasis interspersed with clusters of fast events, consisting of both extinctions and speciations.

8. Concluding remarks

In this section we place our main results in a larger biological context; in the final subsection we indicate some potentially fruitful further lines of research

8.1 *Branching*

The prediction and characterisation of branching events may well be considered the most interesting result from our attempt at classifying the various possible evolutionarily singular points. However, as was clearly put forward by Christiansen (1991), it is also the result which is the least robust against the introduction of a realistic diploid genetics (no obligate self-fertilisation or absolute assortative mating). To keep our other results obtained so far intact under realistic diploid genetics we have to assume that heterozygotes have phenotypes lying in between those of the two corresponding homozygotes. But this same assumption forces us to deal with the potential of a continual stream of intermediate types where the sample path of a clonal model would start branching. Branching can only be rescued by assuming some newly developing or preexisting mechanism which impedes the mating between two individuals from the diverging strains. Interestingly the few working ecological models for speciation through the development of some mating barrier, indeed seem to be organised around an evolutionarily singular point of the branching type (e.g. Seger, 1985). Moreover, there recently has been a spate of publications (e.g. Henry, 1994) about so-called cryptic speciation, i.e., the development of mating barriers (based on special mate recognition systems, compare Paterson, 1993) which are not yet reflected in the divergence of some readily observable traits. Our hunch is that the crypsis will be lifted when, and more often than not only when, the community dynamically relevant trait values of those species come to lie in the neighbourhood of a branching point.

Remark: Only populations which are sufficiently strongly coupled by migration allow a representation by a single fitness function s. The existence of such a representation formed the basis for all our considerations. Therefore allopatric speciation, in which two populations become migratorily uncoupled before the onset of divergence, falls outside the range of our formalism. Only the so-called sympatric and parapatric speciation modes fall squarely within its range (compare Meszéna, in prep). However, past opinion was that the latter modes of speciation were at best rare, compared to the allopatric one. However, recently more and more field evidence is coming available for the frequent occurrence of rapid speciation in populations which are not divided up by any clear physical barriers to migratory exchange (e.g. Meyer, 1993.) And better still, in a number of instances such events have occurred in a repeatable manner, following the immigration of a founder species into separate lakes or islands (Schluter & Nagel, 1995; Losos, 1995).

8.2. *On the non-commutativity of limits*

The results from the previous section were based on three subsequent limiting arguments, (i) the approximation of an individual-based stochastic community model by a deterministic one, combined with (ii) the assumption of rarity of mutations, together allowing the transition from the framework of community dynamos to that of adaptive dynamics, and (iii) the assumption of uniform smallness of the mutational steps, allowing the deduction of the macro-evolutionary conclusions in section 7. Both intuition and figure 10 suggest that we cannot be too sure that these three arguments are all the way compatible.

The community dynamical time needed for a substitution of one type by another, say X_i by Y, scales as $\log(\Omega)/[s_P(Y)-s_{(P,Y)/\{i\}}(X_i)]$, Ω the system size. The denominator of this expression goes to zero when the size of the mutational steps, ε, goes to zero. Therefore the limits $\varepsilon \to 0$, and $\Omega \to \infty$ together with $\Omega\theta \to 0$, θ the mutation probability per birth event, don't commute. Depending on the route we follow in $(\Omega,\theta,\varepsilon)$-space to $(\infty,0,0)$ we get a different limit process. To get the results described in the previous section for the fast phase we should have that $\Omega\theta\log(\Omega)/\varepsilon \to 0$. The results for the slow phases may be only expected to hold good when $\Omega\theta\log(\Omega)/\varepsilon^2 \to 0$. In other words, those results can only have biological relevance if in reality $\Omega\theta\log(\Omega)/\varepsilon$, respectively $\Omega\theta\log(\Omega)/\varepsilon^2$, are sufficiently small.

As a final point we mention that at very small distances from an evolutionary point attractor the framework breaks down all the way. As soon as evolution has come sufficiently near to such an attractor new mutants are selectively almost neutral, so that on this scale the scene will be effectively dominated by demographic stochastic fluctuations.

8.3. *Some directions for further research*

We see at least two immediate directions for further progress. First of all the underpinning and/or modification of our present assumptions, as far as these are based on community dynamical arguments, should be further explored. Two immediate research problems are (i) the exploration of the continuity assumption **S2**, for example by elaborating the bifurcation patterns of community equilibria in some appropriately chosen general ODE framework, (ii) the modification of our assumptions **P1a** and **K** to account for the occurrence of attracting heteroclinic networks. The second, and ultimately most interesting, topic is the development of a bifurcation theory for Evolutionarily Singular Strategies (but to get started we need a better insight in the potential for generalising assumption **S2b**).

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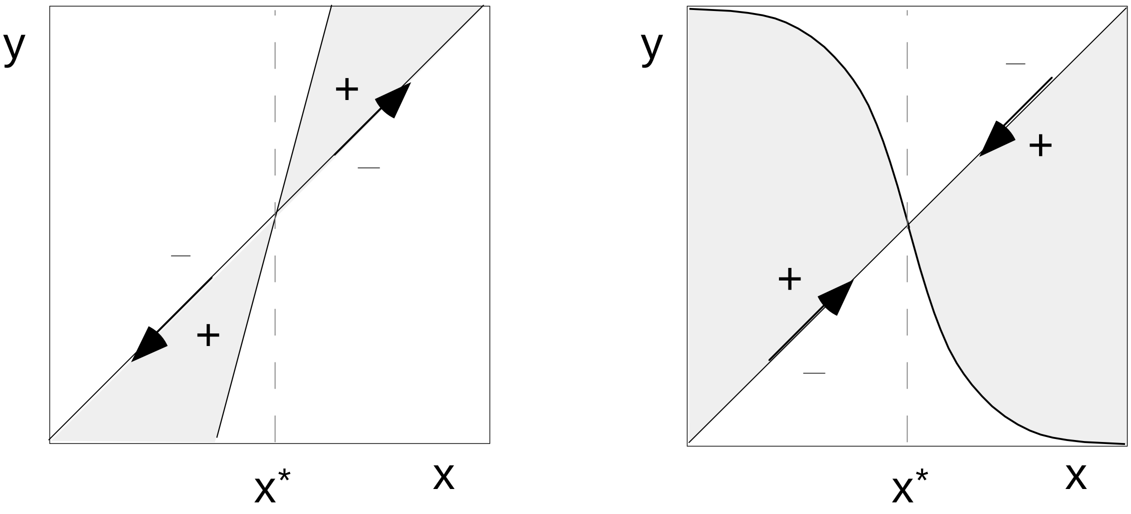

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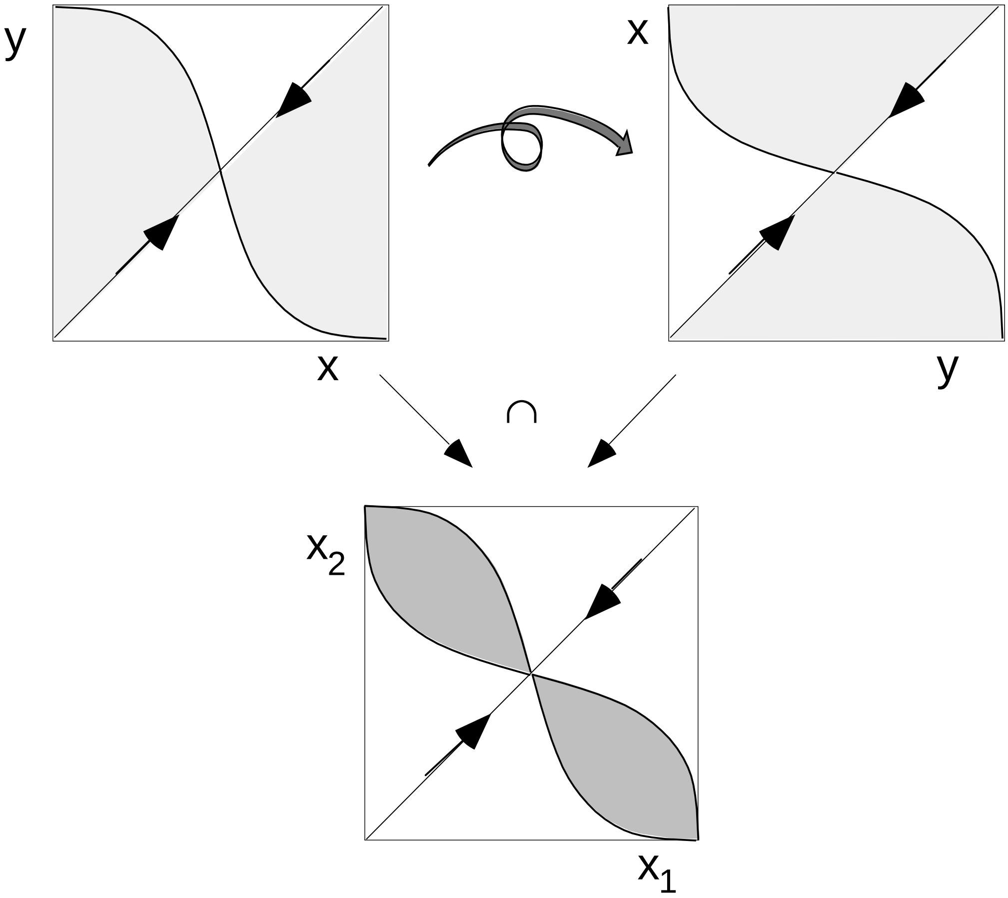

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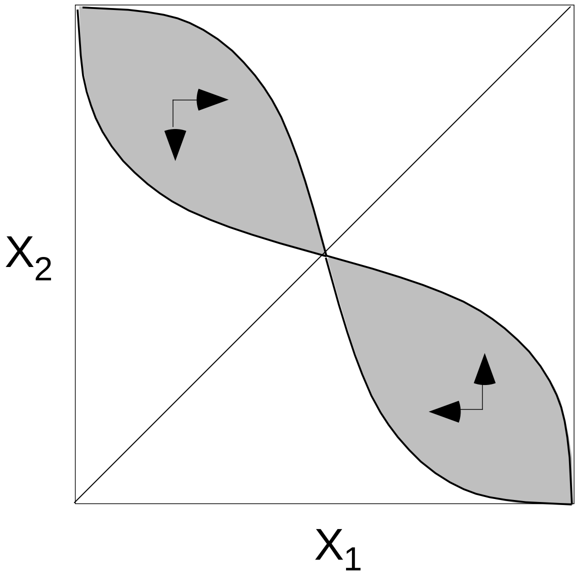

X_2
X_1

Fig. 3

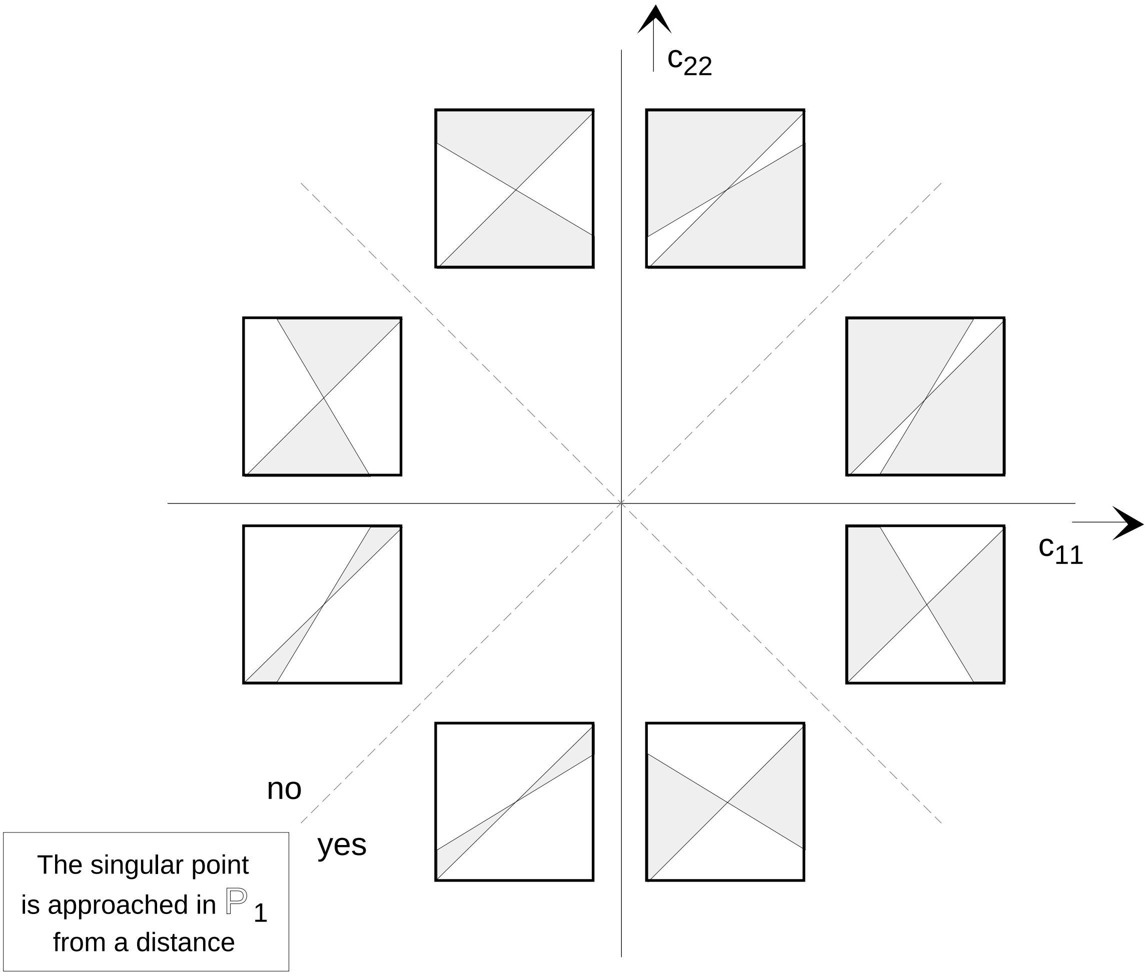

c_{22}
c_{11}
no
yes
The singular point is approached in $\mathbb{P}_1$ from a distance

Fig. 4

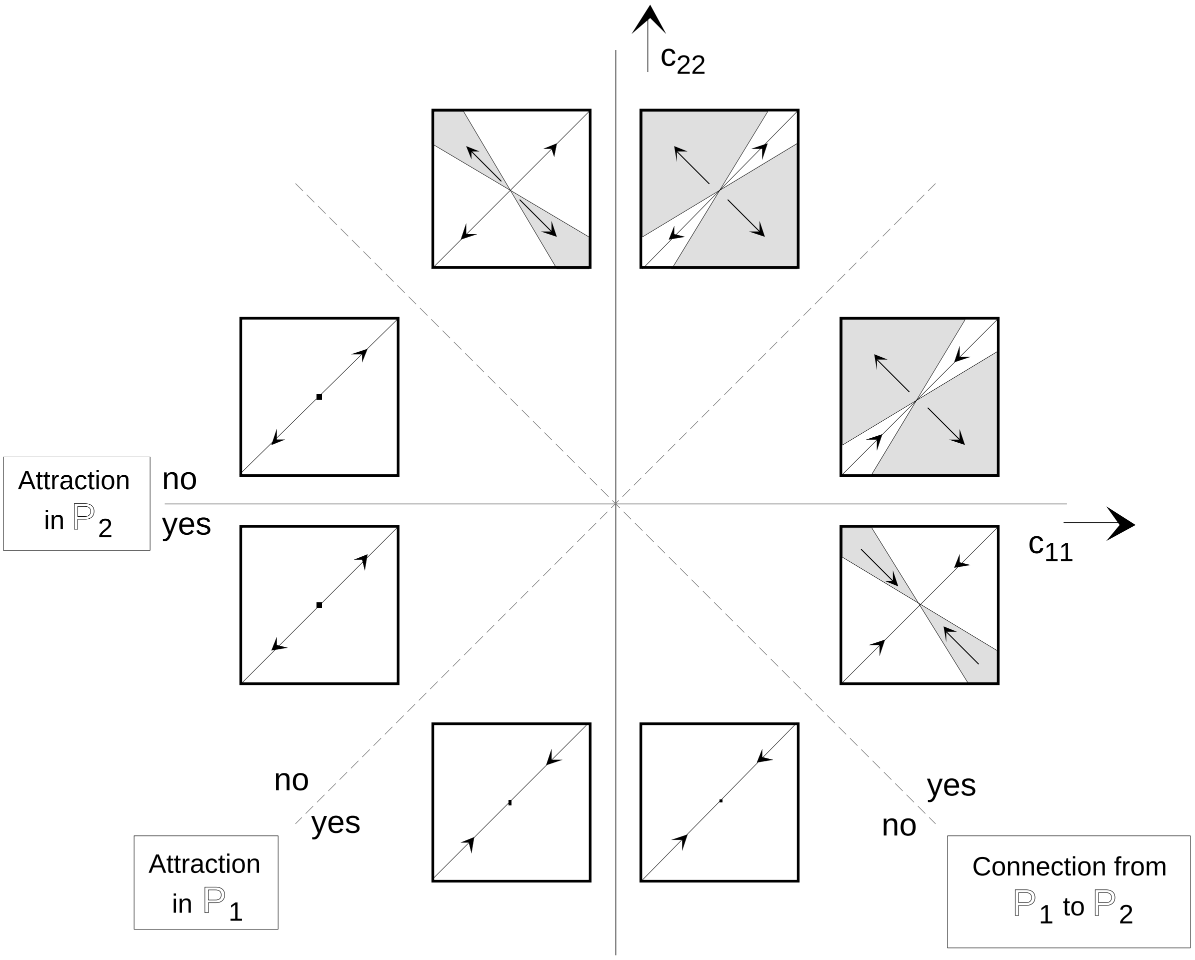
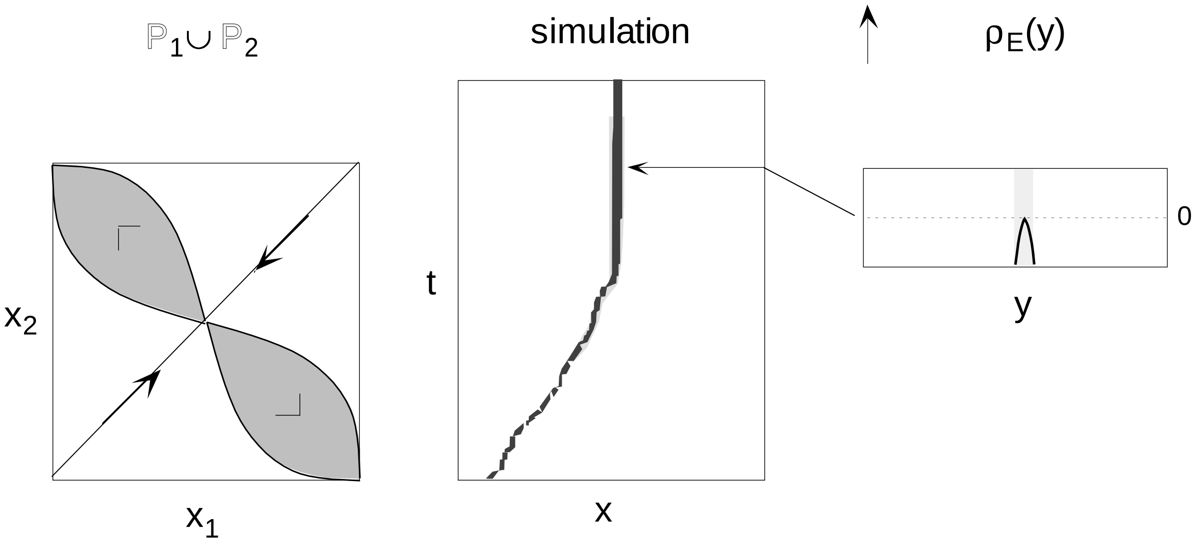

c22
Attraction in ℙ2
no
yes
c11
no
yes
Attraction in ℙ1
yes
no
Connection from ℙ1 to ℙ2

Fig. 5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simulation
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0
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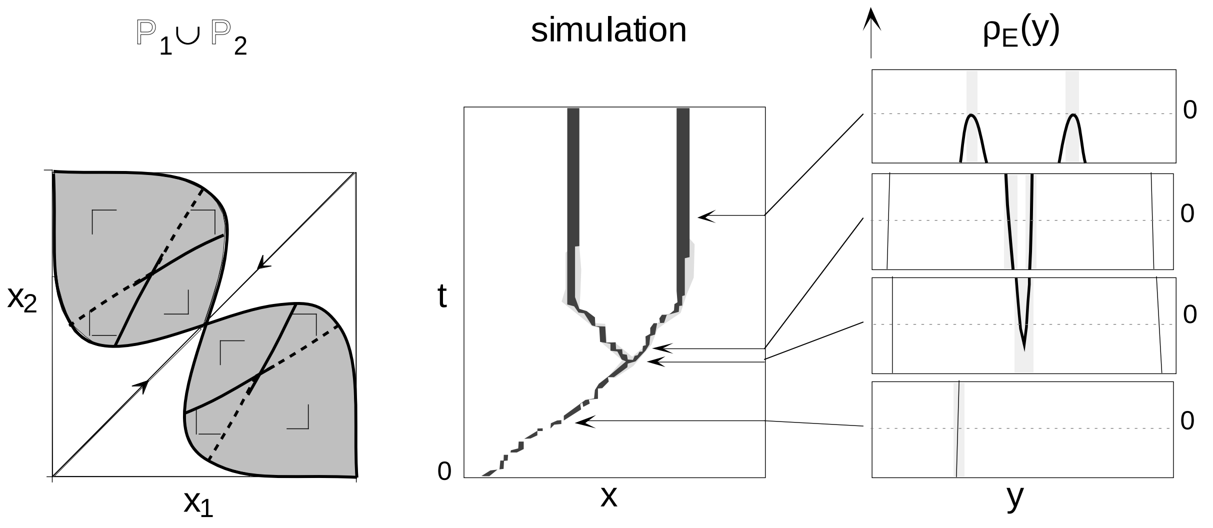
Fig. 6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x2
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simulation
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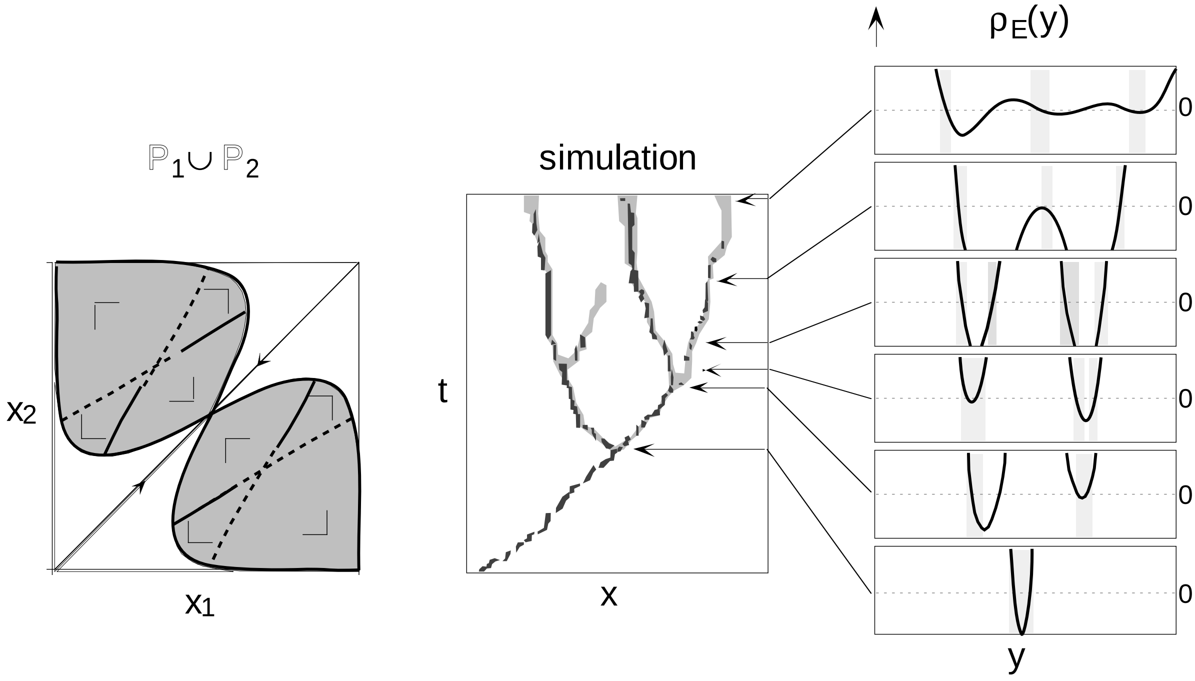
y

Fig. 7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x2
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simulation
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ρE(y)
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y

Fig. 8

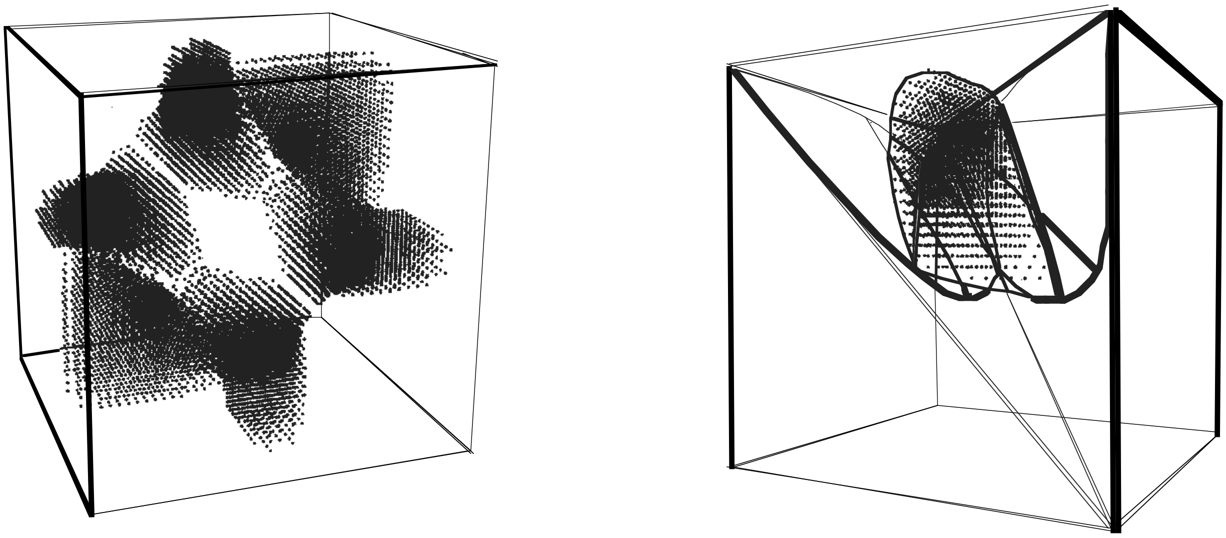
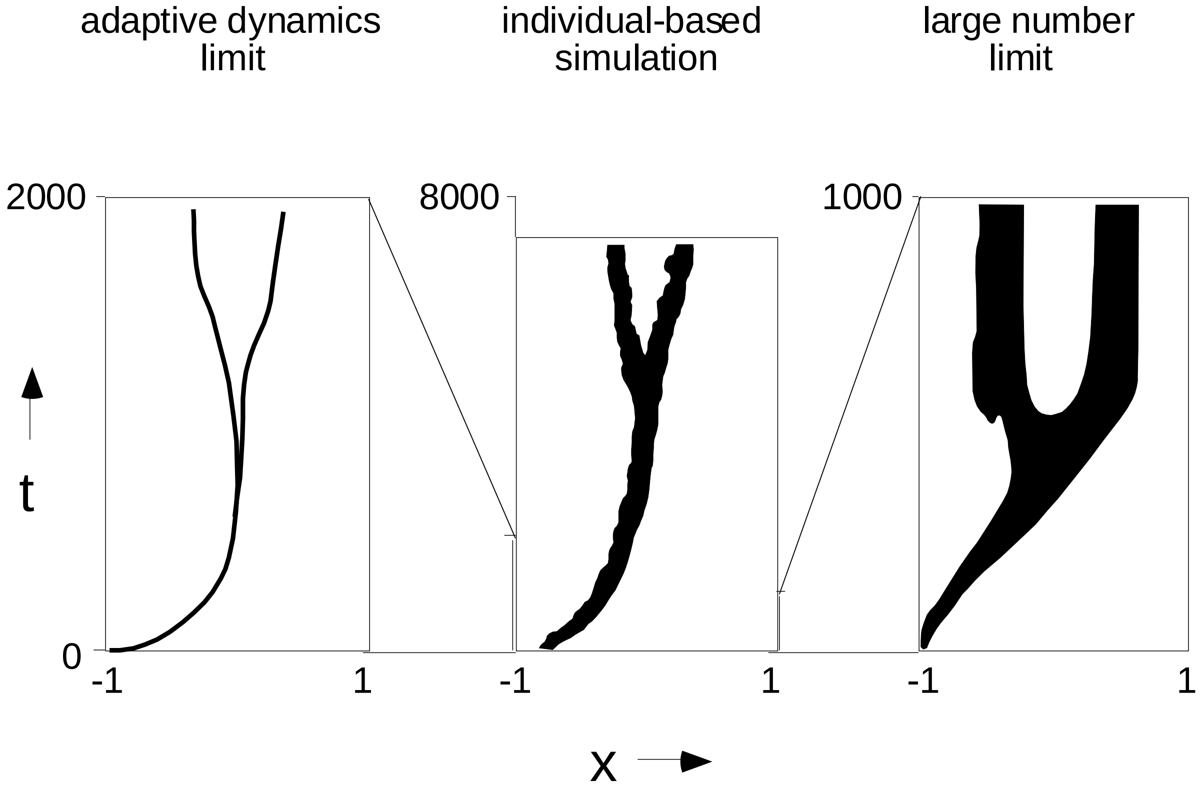


Fig. 9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individual-based simulation
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t
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Fig. 10

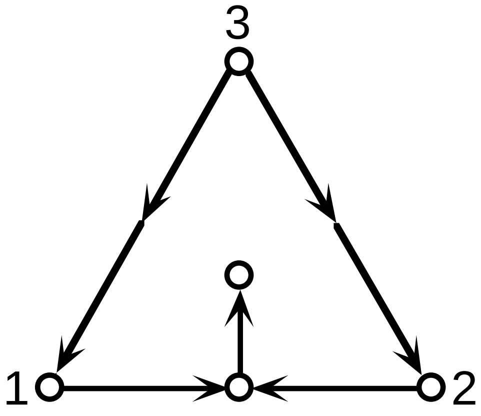
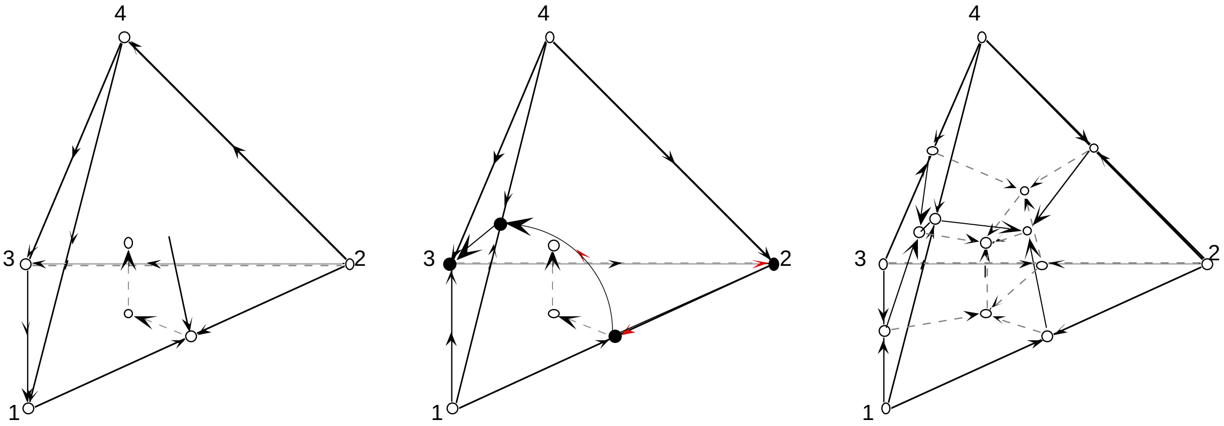


Fig. 11



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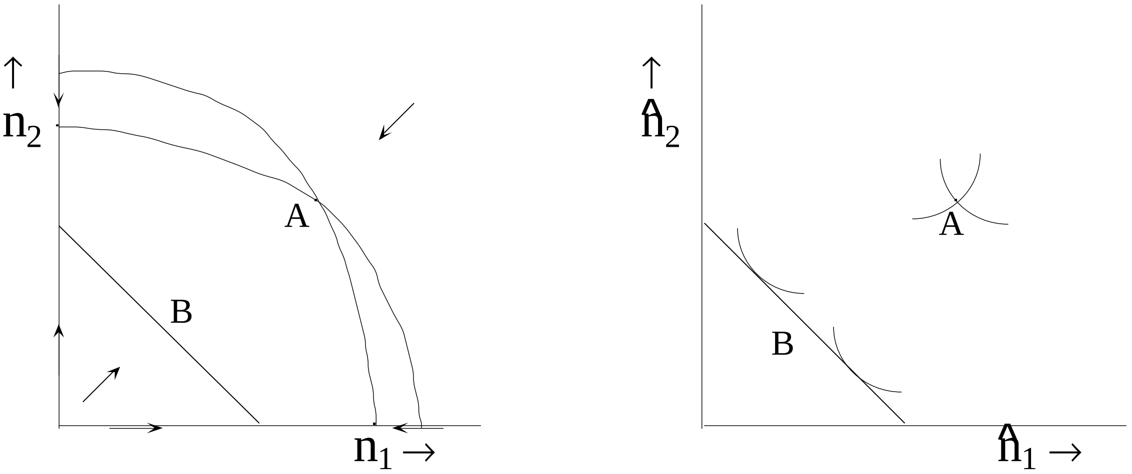
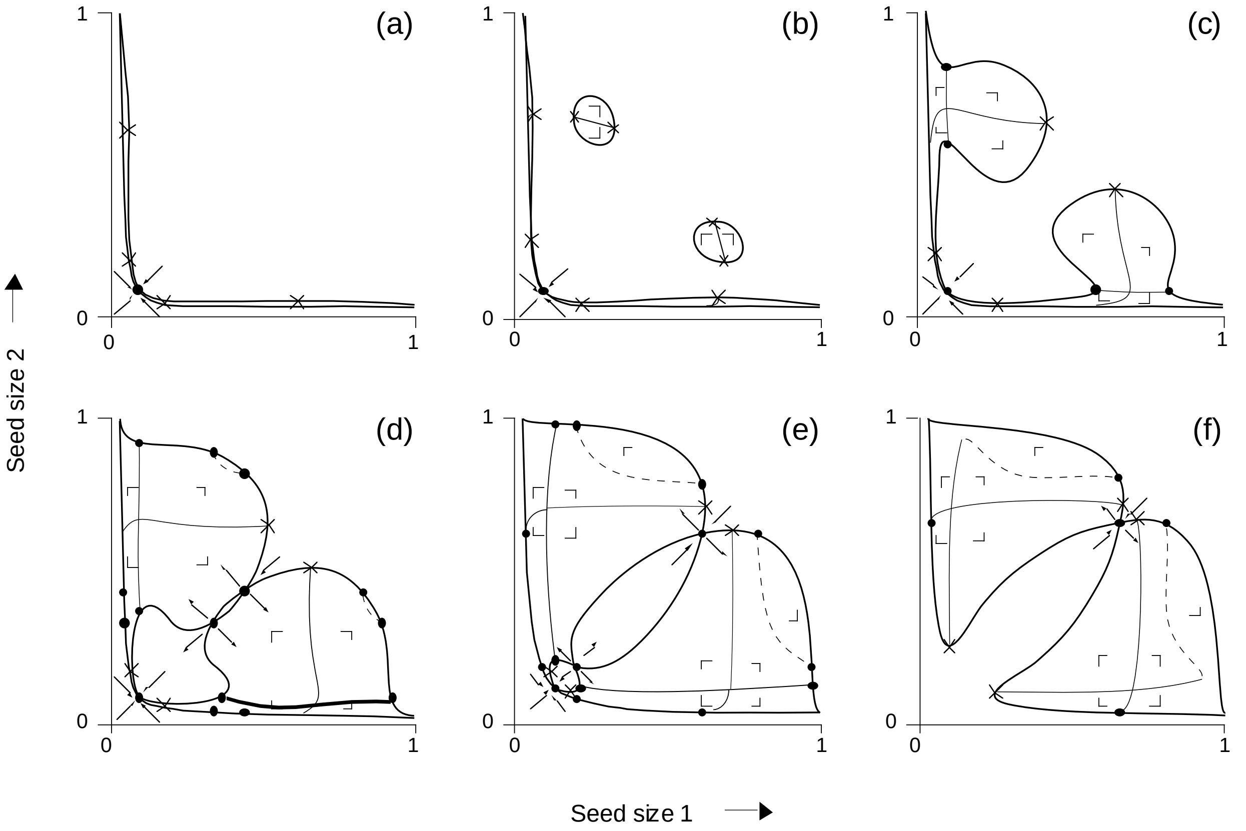


Fig 13



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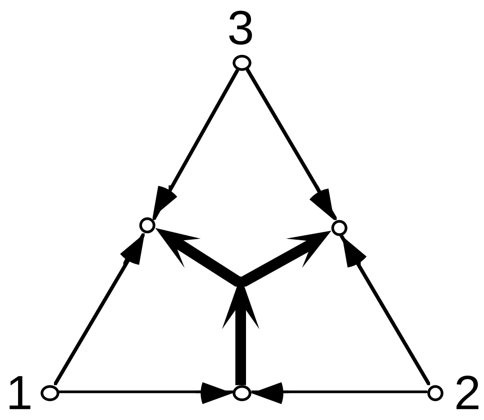

Fig. 15