The evolution of dispersal and seed size in plant communities

Simon A. Levin* and Helene C. Muller-Landau

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA

ABSTRACT

Uniting frameworks used by Hamilton and May (1977), Levin *et al.* (1984) and Ezoe (1998), we show that the problem of the evolution of seed size – or of any other single dispersal-determining trait – can, under certain conditions, be understood as a constrained optimization problem. We find a function, F, whose maxima represent convergence stable strategies – evolutionary attractors towards which selection will drive populations (given sufficient diversity of types, either initially or generated through mutation). This function has a nice interpretation as the product of competitive ability and fecundity (both squared) and a functional describing the spread of the dispersal kernel. Using ideas pioneered by Dan Cohen and the theory of adaptive dynamics, we explore the consequences for the evolution of dispersal and seed size in populations, focusing on examples in metapopulations, with some comments on more general spatial models.

Keywords: adaptive dynamics, evolutionarily stable strategy, seed dispersal, seed size.

INTRODUCTION

The study of biodiversity is the study of how species co-exist – that is, of how life-history adaptations arise and become established, and how they facilitate persistence and co-existence. Few have contributed more in the way of original insights into this problem than Dan Cohen, and this paper is inspired by all he has brought to the subject.

A consistent theme in life-history theory, and especially in Dan Cohen's work, is the role of temporal and spatial heterogeneity in the environment, and the interplay between life-history adaptations and the perceived level of variability faced by organisms and their progeny. Dispersal and dormancy, in particular, are complementary ways of averaging over variability, changing the scale of variation and replacing the unknowable with the knowable (Cohen and Levin, 1987). In this paper, we focus primarily on dispersal; dormancy and diapause are treated in Cohen (1996) and Ellner (1985, 1987), among other sources.

Seed dispersal is a critical element of a plant's life history, fundamental in determining spatial patterns, population growth rates, rates of species advances following climatic or

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* Author to whom all correspondence should be addressed. e-mail: slevin@eno.princeton.edu

other environmental changes, and the very survival of the species. Dispersal strategies are highly variable both within and among plant communities, with greatly differing numbers and types of seeds being produced, and highly diverse patterns of spread (Willson, 1992). Typical dispersal distances vary among plant communities and life forms: short dispersal is common among plants on isolated islands (Carlquist, 1965) and among shade-tolerant trees, while long dispersal is typical of specialists on ephemeral habitats (e.g. light-demanding pioneer trees) and of epiphytes. It is therefore fundamental to understand why dispersal varies with community and species characteristics, why a particular array of strategies is found within a given plant community and, more basically, why plant species should disperse seeds at all.

The main tools for theoretical analysis of dispersal are game-theoretic; typically, one seeks strategies that will emerge from a competitive dynamic, and resist subsequent invasion by other strategies (Maynard Smith and Price, 1973; Maynard Smith, 1982). Most early models were couched exclusively in a metapopulation framework, treating large assemblages of subpopulations connected by a global pool of dispersers (Hamilton and May, 1977). These studies generally sought (and found) a single winning strategy for the fraction of offspring dispersed globally under any given set of conditions; under some conditions, however, evolutionarily stable assemblages of mixed dispersal strategies emerged (Cohen and Murray, 1981; Ludwig and Levin, 1991). Selection upon traits governing dispersal strategies is, of course, influenced by trade-offs with other aspects of fitness as well. Indeed, such trade-offs provided the starting points for Dan Cohen's early investigations of a suite of life-history traits (Cohen, 1966, 1968). Recent work (Geritz *et al.*, 1988, 1999; Ezoe, 1998) has focused upon the evolution of traits influencing both dispersal and other characters, such as competition. When trade-offs exist, so that advantages in one trait are compensated by disadvantages in another, there is increased scope for co-existence of multiple types. Very recently, spatially explicit models have been used to study the evolution of dispersal distances themselves; in these, additional phenomena such as self-organized clustering have the potential to become important influences upon selection for dispersal (Ezoe, 1998; Bolker and Pacala, 1999).

In this paper, we first review past work on the adaptive dynamics of dispersal, focusing in particular on work by Dan Cohen. In that context, we introduce and prove a general condition for finding local winning strategies for dispersal, or for a dispersal-determining trait. Through specific examples in metapopulations, we also show that the ESS (evolutionarily stable strategy) concept may be problematical, and that the power of modern adaptive dynamic methods can help to clarify the situation. Finally, we consider how such problems become more complex when explicit space is incorporated, due to increased self-organized heterogeneity.

SELECTION FOR DISPERSAL

Dispersal arises evolutionarily for a variety of reasons. Most crucially, one must view the evolution of dispersal within a competitive framework: dispersal may evolve even if it is costly, provided that it allows dispersers to win sites from non-dispersers. For example, Hamilton and May (1977) showed that, for an annual species, dispersal will be selected even in a stable environment, and even if there is a cost to dispersal. The intrinsic advantage held by dispersers is enhanced in this model because they experience reduced competition among close relatives, especially sibs. Variability in space and time brings

further advantages to dispersers, as dispersal enables the discovery of the best sites for growth and reproduction, and facilitates capitalization on the benefits of bet-hedging in an uncertain environment (Levin *et al.*, 1984). Environmental variation resulting in differential site quality may be abiotic or biotic, exogenous or endogenous. Density dependence of various forms may play a role in creating such heterogeneity – for example, the presence of parent plants themselves may make a site less favourable, due to resource competition or disease risk, thereby favouring genotypes that disperse their offspring elsewhere (Gillett, 1962; Janzen, 1970; Connell, 1971). Finally, dispersal can reduce the risk of inbreeding, and thereby facilitate escape from deleterious genetic effects (Shields, 1987).

In their fundamental 1977 paper, Hamilton and May used a simple model to illustrate powerfully the general advantages of dispersal, showing that dispersal of an annual's seeds must always be selected for in a constant environment. They cast the problem within a game-theoretic framework (Maynard Smith and Price, 1973; Maynard Smith, 1982) to find what they refer to as the 'unbeatable' strategy – 'unbeatable in the sense that [a type having any other strategy] will have a diminishing frequency in any mixture'. Thus, this strategy meets the criteria for what had been defined as a global *evolutionarily stable strategy* (ESS) for dispersal, a strategy that cannot be invaded by any other strategy (Maynard Smith and Price, 1973), and for what was later defined as a global *neighbourhood invader strategy* (NIS), a strategy that can invade any other strategy (Apaloo, 1997). Hamilton and May (1977) found that, in a metapopulation context, this type would disperse a fraction

$$D = \frac{1}{2-s} \tag{1}$$

of its seeds into a common (global) pool, where s is the probability a dispersed seed will find a potentially favourable habitat. If $s = 1$ (no cost to dispersal), this formula predicts that the parent plant should disperse all of its seeds. Remarkably, even as s tends towards zero, the plant should still disperse half of its seeds broadly, thereby investing half its energy in the high-risk, high-payoff strategy of long-distance dispersal.

In extensions of this work, Comins *et al.* (1980) demonstrated how this advantage depends upon the variance in types possible within and among sites. That is, as the number of adults per site increases, the variance in frequencies among sites decreases, reducing the advantages to moving from one site to another. At the same time, the variance in frequencies within sites increases, reducing sib–sib competition and thereby the role of kin selection in favouring dispersal. Thus, an increase in adults per site leads to an ESS of lower dispersal, an effect also observed by Levin *et al.* (1984). As the number of adults per site goes to infinity in the models with stable habitats (those treated by Hamilton and May, 1977; Comins *et al.*, 1980), the ESS dispersal fraction goes to zero.

The introduction of environmental variability leads to increases in the ESS dispersal fraction, because of the additional advantage of dispersal as a means of averaging over uncertainty. Perhaps the simplest formulation of environmental variability is random extinction of all individuals on particular sites, a situation treated in Comins *et al.* (1980) as well as in Levin *et al.* (1984). Comins *et al.* (1980) demonstrated that the dispersal rate increases as the probability of a site becoming extinct increases, due to the resulting increase in the probability of a dispersing individual colonizing an empty site. If X is the probability of site extinction, then in the limit as the number of adults per site goes to infinity, the ESS dispersal fraction is

$$D = \frac{X}{1 - (1 - X)s} \tag{2}$$

The results obtained by Comins *et al.* (1980) do not reduce in the limit to Hamilton and May's conclusion that some dispersal is always selected, even when the habitat is entirely stable, because in this formulation there are multiple individuals per site (whereas Hamilton and May considered a single individual per site).

Levin *et al.* (1984) explored environmental variation more broadly, allowing for un-correlated patterns of fluctuation in total yield (Cohen and Levin, 1991, extended this to correlated environments). In their work, environments were locally unpredictable, with yield at a given site in a given year determined by a probability distribution (which was identical across sites and constant in time). They showed that, for arbitrary distributions of environmental quality (total yield), the evolutionarily stable dispersal fraction will depend, among other things, on the normalized harmonic mean of the distribution. In particular, if the harmonic mean is positive (zero probability of a zero yield year), then there will be a threshold value of *s* below which the ESS is to disperse nothing. It is easy to understand this: If there is a positive probability of a zero year, it always pays to buy some insurance by dispersing, to ensure survival. However, this is not essential if the probability of a zero year is zero. Because these models treat local population size as continuous, they in effect treat the number of individuals per site as infinite. Thus, again the results do not reduce in the limit to Hamilton and May's conclusion that some dispersal is always selected even when the habitat is entirely stable.

Levin *et al.* (1984) also explored the interplay between dispersal and dormancy in variable environments (see also Cohen and Levin, 1987; Ellner, 1987). Dispersal and dormancy are alternative solutions to dealing with uncertainty. Not surprisingly, the evolution of either decreases the selection pressure for the evolution of the other. This leads to the prediction of a negative correlation between the appearance of these traits (Cohen and Levin, 1987), which is in line with what is found in natural populations (Werner, 1979).

Differences among species and among communities in the types of environmental variation experienced, as well as in the spatial structure of the populations themselves (number of adults per site), are thus expected to lead to selection for different dispersal strategies. Parallel results have been obtained in studies that explicitly modelled genetics, using either gene frequencies or means and variations in characters within the population, rather than using a phenotypically based game-theoretic approach (reviewed in Johnson and Gaines, 1990).

Spatial and temporal correlations in environmental conditions can further change selection pressures on dispersal, both qualitatively and quantitatively. Cohen and Levin (1991) found that, in spatially and temporally correlated environments, there need not be a single ESS at all – co-existence of multiple dispersal types is possible. In some instances, they were able to find what they called an *evolutionarily compatible strategy* (ECS), a type that cannot resist invasion, but can invade and co-exist with any nearby strategy (Cohen and Levin, 1991). Hence, it is an NIS that is not an ESS. Some of these ECSs were also found to be *convergence stable* – that is, their near neighbours can invade those slightly further away (Eshel, 1983; Christiansen, 1991) in the same direction. They are hence what Geritz *et al.* (1997) prefer to call 'evolutionary branch points'.

Ludwig and Levin (1991) carried this two-strategy reasoning a step further, showing how the existence of multiple such strategies requires the generalization of the notion of the ESS

to one of evolutionarily stable coalitions of types. Mathias and co-workers (A. Mathias, E. Kisdi and I. Olivieri, unpublished manuscript) determined the precise membership of this coalition for a particular formulation of the model of Cohen and Levin (1991), demonstrating that the evolutionarily stable state is a coalition of two types, which is arrived at evolutionarily first by convergence upon the ECS, and then divergence from there. Sasaki and Ellner (1995) considered the general case of temporal variation, and demonstrated that the distribution of types within an ESS will in general be discrete, rather than continuous, for any stationary distribution of environmental conditions (and thus optimal phenotypes) with bounded support. Rather than being a nuisance, this phenomenon of evolutionarily stable coalitions should be viewed as the beginnings of the theory of the evolution of community properties. Communities are not, after all, composed of single species, or of multiple species all sharing the same dispersal strategy; hence explanations must be found for how species with different dispersal strategies manage to co-exist.

THE INFLUENCES OF TRADE-OFFS

Selection upon dispersal traits is influenced not only by environmental conditions, but also by organismal characters. Particularly important are trade-offs with other adaptations, such as the number of seeds produced, seedling competitive ability, and resistance to natural enemies; trade-offs also involve details such as the distribution of dispersal distances and survival during and after dispersal. These functions may be jointly determined by a smaller subset of morphological or physiological characteristics that enforce constraints, thereby imposing correlations between traits and dictating trade-offs. Theoretical studies of dispersal have incorporated such trade-offs by treating the evolution not of dispersal alone, but of a trait (such as seed size) that jointly determines dispersal and one or more other characteristics.

In one of the first studies to take such trade-offs into account, Cohen and Motro (1989) considered the effects of changing the amount invested in dispersal structures upon fecundity and upon the dispersal fraction, simultaneously (again in a metapopulation context). Cohen and Motro (1989) assumed that, as the amount invested in dispersal structures increases, the dispersal rate increases and the number of seeds produced decreases. They give the equation for the ESS dispersal rate under these general conditions. For the particular case in which the dispersal fraction is proportional to the investment in dispersal structures, the dispersal rate is an increasing function of the efficiency with which investment in dispersal is converted into dispersal rates, converging on the result of Hamilton and May (1977) as the efficiency increases (and thus the cost of dispersal structures declines to zero).

Other authors have considered selection upon seed size, which directly influences not only dispersal strategies but also establishment success and competitive ability. Smaller seeds, or really diaspores (the units dispersed), may be able to travel further (Augspurger, 1986), and may allow for the sampling of more sites, due to a trade-off between size and number of seeds produced (Westoby *et al.*, 1996). However, smaller seeds also typically have higher mortality rates and lower probabilities of successful establishment, due to less protection from pests and lower stored reserves (Westoby *et al.*, 1992). The work discussed so far, although generally couched in terms of the fraction of seeds dispersed, in reality deals with the fraction of energy committed to dispersal. It remains to determine how that energy is packaged. That is, what are the number and size distribution of seeds, which in turn will

determine such features as dispersal distance and competitive ability? A plant may choose to put its dispersal energy into a few large, well-protected seeds, or it may adopt a shotgun approach of producing huge numbers of seeds involving very little energy each, or it may assume an intermediate strategy. Indeed, there is no reason that all seeds must be the same size, and seed dimorphism or polymorphism is one way in which mixed strategies may be explored (Venable, 1985).

Geritz *et al.* (1988) examined selection on seed size in a metapopulation. Seed production is assumed to be a decreasing function of seed size, while seedling competitive ability is an increasing function of size. Their metapopulation model differs from many of those previously discussed in two respects: all sites are destroyed every year (or, equivalently, plants are annual) and seed rain is stochastic (specifically Poisson) rather than deterministic (but see Comins *et al.*, 1980). Because all sites are destroyed every year, there is nothing different about the circumstances faced by seeds that 'stay home' and those that disperse. In a complementary manner, the home site is assumed to be identical to other sites in the expected number of arriving seeds, although the stochastic nature of dispersal will lead to realized variation. Competitive ability is quantified by a parameter c_i. That is, the probability that a seed of type i wins a site is

$$\frac{c_i n_i}{\sum_j c_j n_j}$$

where n_i is the number of seeds of type i landing on the site. Geritz *et al.* (1988) showed that, for strong competitive dominance (such that types with larger seeds always or almost always win) and a strong trade-off between seed number and competitive ability, selection will always be for the largest seed size possible. All strategies can be invaded and outcompeted by types with slightly larger seed sizes. However, the largest possible seed size is itself not a global ESS – species with sufficiently smaller seeds, and thus higher fecundity, will always be able to invade and co-exist.

Geritz (1995) extended this work, showing that there is a continuous distribution of seed sizes that is evolutionarily stable – that is, a type producing seeds of varying sizes as specified by this probability distribution cannot be displaced by any other type. Therefore, a coalition of types with the same overall probability distribution of seed sizes would also be evolutionarily stable, at least neutrally so, although Geritz (1995) did not discuss this possibility. Such a neutrally stable coalition would, of course, be fragile; temporal variance in the environment would generally tip the balance in favour of a bet-hedger (Sasaki and Ellner, 1995). However, where additional bet-hedging through the production of multiple diverse phenotypes is costly, we might expect a coalition of types to emerge instead.

This trade-off has also been incorporated into some models investigating the co-existence of species in ecological time. Tilman (1994), Lehman and Tilman (1997) and Kinzig *et al.* (1999) examined competitive dynamics of species that vary according to a strict trade-off between seed production and competitive ability, in a metapopulation model in which sites are opened up only by the deaths of their inhabitants, and in which seed rain is deterministic. These studies have shown that this trade-off, with extreme competitive asymmetry (larger seeds always win), makes stable co-existence of a potentially infinite number of types possible. However, this co-existence is stable only under the assumption of no variation in, and hence no selection upon, seed size within species; the introduction of such variation leads each species to evolve towards larger seed sizes in a runaway process,

and facilitates invasion by types with sufficiently smaller seeds. Since larger seed sizes come at the expense of lower fecundity and smaller population sizes, selection shifts species towards vanishingly small population sizes, vulnerable to stochastic extinction. Thus, the addition to such a model of within-species variation and selection, combined with demographic stochasticity, results in cascades of extinctions and invasions (Kinzig et al., 1999).

The evolutionary dynamics of seed size when there are trade-offs between seed production, seedling survival and competitive ability are treated in Geritz et al. (1999), for various degrees of competitive asymmetry – or, equivalently, for varying strengths of the trade-offs. They expand upon the model of Geritz et al. (1988), adding pre-competitive seedling mortality that is an increasing function of seed size. Unlike Tilman (1994), Lehman and Tilman (1997) and Kinzig et al. (1999), they consider not only completely asymmetric seedling competition, but rather a range of differing degrees of competitive asymmetry. Using methods from the theory of adaptive dynamics developed by Metz et al. (1996) and Geritz et al. (1997), they find not only evolutionarily stable strategies (ESSs), but also evolutionary branching points – types that are evolutionary attractors but not ESSs. With these methods, they show how selection will proceed for different degrees of competitive asymmetry and different trade-off strengths. In particular, they show that, as competitive asymmetry increases, more seed sizes can stably co-exist (Geritz et al., 1999).

A trade-off between seed production and seedling competitive ability can thus lead to stable co-existence of types with different seed sizes (Geritz, 1995; Geritz et al., 1999). This is in accord with the tremendous within-community variation in seed size observed in natural communities, typically at least a 10^5-fold range of seed mass among species (Westoby et al., 1992). Trade-offs with other characters make it possible for alternative dispersal strategies to attain equal fitnesses within communities, and thereby to co-exist. In the next section, we derive a general condition for identifying convergence stable dispersal strategies. The condition applies not only to the metapopulation models treated so far, but also to spatially explicit models.

A GENERAL CONDITION FOR FINDING EVOLUTIONARY ATTRACTORS

As in the papers just discussed, we will focus on the example of seed size (of an annual plant) as the variable under selection, interpreting dispersal ability and competitive ability as being determined by seed size. We treat the environment in a spatially explicit manner, and assume that it is composed of a large, but finite, number N of sites, each of which can support a single adult plant. Following Ezoe (1998), we assume that an individual plant genotype produces seeds of a single size (weight) w, and let $n(w)$ be the number of such seeds produced and $c(w)$ their relative competitive advantage. This means that the probability of a seed of size w winning a site upon which it lands is proportional to $c(w)$. Furthermore, we define the function $P = c(w)n(w)$, here termed the *potency*, essentially a measure of potential competitive performance. We assume that the habitat is convex and so large that we can ignore boundary effects; one could instead treat it as periodic – that is, as if it were the surface of a torus. With this simplification, we furthermore assume that seed numbers are large enough that stochastic effects can be ignored, and that dispersal from a site is unaffected by site properties. Thus the probability of dispersing a given distance is a property of seed size alone, not of location. We formalize this by defining (after Ezoe)

$\delta(w, \boldsymbol{x})$ to be the probability a seed is dispersed $\boldsymbol{x}$ from its source, where $\boldsymbol{x}$ is a vector. We will assume isotropy, and furthermore allow $\boldsymbol{x} = 0$ to characterize non-dispersing seeds.

Now, let a particular genotype u be established in the population and occupy all of the sites. Introduce a mutant v, which displaces the resident at exactly one site. In the next generation, the number of sites occupied by the invader v will increase by

$$r(v|u) = \sum_{\boldsymbol{x}} \frac{P(v)\delta(v,\boldsymbol{x})}{P(v)\delta(v,\boldsymbol{x}) + P(u)(1 - \delta(u,\boldsymbol{x}))} - 1 \tag{3}$$

which we interpret as the fitness of the invader (it is the per capita growth rate when the type is rare (Metz *et al.*, 1992)). Note that $r(u|u) = 0$ for all u. At least initially, v can invade u if $r(v|u) > 0$, but cannot if $r(v|u) < 0$. This simple characterization does not tell the whole story, however. Because of clustering, a type that can invade initially might inhibit its own further spread and, indeed, might disappear entirely due to the stochastic nature of establishment. Similarly, it is possible that a type whose expectation is less than 0 might still be able to spread once it (stochastically) establishes a beachhead. Our approach, therefore, was simply to begin from the naive initial spread projection, and then use simulations to verify that the putative winner in competition indeed triumphs.

Within this framework, the natural candidate for an ESS is a type w^* for which $r(v|w^*) < 0$ for all other types v, at least for v close to w^*. Although, as we shall see, things are not so simple, we begin (following Ezoe) by setting $\partial r(v|u)/\partial v = 0$ at $v = u = w^*$. (We will later need to distinguish among critical points, and to consider candidate strategies that are on the boundaries of the region.) From (3), after some algebraic manipulation, we then obtain the condition

$$\sum_{\boldsymbol{x}} \left[\frac{\partial}{\partial w^*} (P(w^*)\delta(w^*,\boldsymbol{x})) \right] (1 - \delta(w^*,\boldsymbol{x})) = 0; \tag{4}$$

or, equivalently, that the first derivative of the quantity

$$F = P^2(w) \left[1 - \sum_{\boldsymbol{x}} (\delta(w,\boldsymbol{x}))^2 \right] \tag{5}$$

vanishes at $w = w^*$ (see Appendix 1). Thus, a candidate internal ESS must be a critical point of F. Note that F is composed of two components: the square of the potency P and a functional describing the degree of spread of the dispersal kernel. It is reasonable to conjecture that large values of either are favourable, and that an ESS should maximize the product, subject to the constraints imposed by their common dependence on w.

In general, from (3), we obtain that the first derivative of r with respect to v is given by

$$\left. \frac{\partial r}{\partial v} \right|_{v=u=w^*} = \frac{F'(w^*)}{2[P(w^*)]^2} \tag{6}$$

where the prime denotes a derivative. (The proof follows the lines of Appendix 1.) Note that, because $r(w|w) \equiv 0$, this ensures that any type for which $F' < 0$ can be invaded from its left, and any type for which $F' > 0$ can be invaded from its right. Therefore, boundary maxima that are not critical points are automatically convergence stable ESSs – that is, continuously stable strategies *sensu* Eshel (1983). More generally, because $r(w|w) \equiv 0$, it also follows that along the line $v = u$, the directional derivative

$$\frac{\partial r}{\partial v} + \frac{\partial r}{\partial u} = 0, \tag{7}$$

so that

$$\left.\frac{\partial r}{\partial u}\right|_{v=u=w^*} = -\frac{F'(w^*)}{2[P(w^*)]^2} \tag{8}$$

Taking the directional derivatives of (6) and (8) along the line $u = v$, we obtain the two equations

$$\frac{\partial^2 r}{\partial v^2} + \frac{\partial^2 r}{\partial v \partial u} = \frac{\mathrm{d}}{\mathrm{d}u}\left[\frac{F'(u)}{2[P(u)]^2}\right] = -\frac{\partial^2 r}{\partial v \partial u} - \frac{\partial^2 r}{\partial u^2} \tag{9}$$

Note that, since $F'(w^*) = 0$, the middle term in (9) becomes $F''(w^*)/2[P(w^*)]^2$ at a critical point of F. Note also (Ludwig and Levin, 1991) that the mixed partial derivative is the negative of the average of the two pure second derivatives along $u = v$, and hence that (9) can be expressed in terms of those pure derivatives alone (see (10) below).

Interpretation of the character of the critical point clearly depends upon the shape of the function F. The criterion for identifying strategies that are convergence stable is exactly that the left-hand-side of (9) is less than zero (Eshel, 1983), or equivalently (Ludwig and Levin, 1991) that

$$\frac{\partial^2 r}{\partial v^2} - \frac{\partial^2 r}{\partial u^2} = \frac{\mathrm{d}}{\mathrm{d}u}\left[\frac{F'(u)}{[P(u)]^2}\right] < 0 \tag{10}$$

and hence that $F''(u) < 0$, since $F' = 0$ at a critical point (Fig. 1). We thus see that convergence stability depends on the relative magnitude of the two pure second derivatives (Ludwig and Levin, 1991; Geritz *et al.*, 1997). Therefore, maxima of F, whether they are critical points or on the boundary, are automatically convergence stable; they are, in essence, evolutionary attractors. Indeed, we will show that the maxima are the only convergence stable strategies.

In general, the properties of the internal critical points of F can be determined through examination of the two pure second derivatives (Fig. 1). An ESS is a type w^* for which $\partial^2 r/\partial v^2 < 0$ at $v = u = w^*$; that is, a type for which $r(v|w^*)$ is maximized at $v = w^*$ (we here ignore the marginal case of zero second derivative). An NIS, defined as a type that can invade any nearby type, is a type for which $\partial^2 r/\partial u^2 > 0$ – that is, a type for which $r(w^*|u)$ is minimized as a function of u at $u = w^*$. Any type that is both an ESS and NIS, termed an ESNIS (after Apaloo, 1977), is automatically convergence stable; hence, the only candidates are the maxima of F (this is also apparent from equation 9). Such maxima, however, need not be ESNISs. A convergence stable strategy that fails to be an ESNIS by virtue of failing to be an ESS may, as mentioned earlier, actually represent an evolutionary branch point, leading to disruptive selection regimes (Geritz *et al.*, 1997). This phenomenon does not occur in the specific metapopulation examples we treat in this paper, but can occur in other metapopulation examples (Cohen and Levin, 1991; Geritz *et al.*, 1999). Alternatively, a convergence stable strategy that fails to be an ESNIS by virtue of failing to be an NIS will, by (10), still be an ESS, since $\partial^2 r/\partial u^2 < 0$ (again, we ignore the borderline case). Thus, it will be a continuously stable strategy or CSS (Eshel, 1983) – that is, a convergence stable ESS – and evolution should drive the distribution towards it even though it cannot invade its neighbours from low densities.
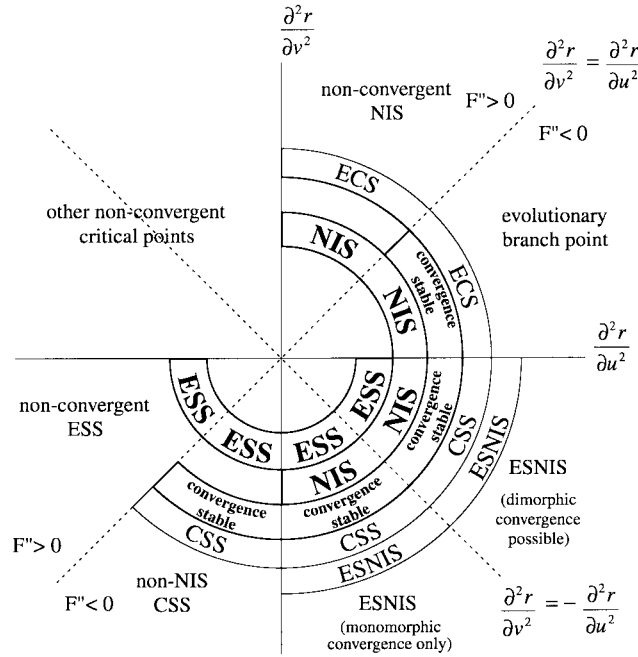
Fig. 1. Classifications of the properties of critical points of the fitness function, r, in terms of their pure second partial derivatives with respect to the type of the resident, u, and of the invader, v. ESS = evolutionarily stable strategy; NIS = neighbourhood invader strategy; CSS = continuously stable strategy; ECS = evolutionarily compatible strategy; ESNIS = evolutionarily stable neighbourhood invader strategy. Note that the points to the right and below the line where the two derivatives are equal (convergence stable points) are ones for which the function F has a maximum.

The minima and inflection points of F are also relevant, primarily because they can serve to separate distinct regions of behaviour: The minima can in some circumstances be ESSs or NISs (as in the examples that follow), but can never be both; in fact, they can never be convergence stable, and hence will not emerge from realistic adaptive dynamics. Inflection points also can never be convergence stable, but are always either ESSs or NISs (never both).

These abstract concepts define the range of potential behaviours, and allow for the possibility of multiple ESSs. In the next sections, we explore these further through specific examples that exhibit some of the phenomena that can occur.

ADAPTIVE DYNAMICS IN METAPOPULATIONS

To illustrate the general principles derived so far, consider a metapopulation of an essentially infinite number of patches connected by dispersal through a global pool. Each site is assumed to be able to support a single adult plant; local interactions, therefore, are restricted to competition among seeds for individual sites. Individuals can vary in type, i, characterized by potency P_i and in the fraction z_i of seeds that remain at the natal site. Note that, in general, we expect larger z to correspond to larger seed sizes. According to the

calculations of the last section, a convergence stable strategy corresponds to a value of w for which the function

$$F = P^2(1 - z^2) \qquad (11)$$

is maximized, at least locally.

We can demonstrate that, to a first approximation, selection must move a population towards higher values of F, provided that all types are restricted to a small neighbourhood of the maximum. We shall see later that this result need not be true if sufficiently broad initial distributions are considered. (It is not an exact result even for the Hamilton–May example; it is always possible to choose sufficiently skewed initial distributions such that the mean value of F initially decreases, and the population moves away from the ESNIS.) Assume that w^* is a (strict) local maximum of F and that, initially, the landscape is populated by a distribution of n types ($i = 1, 2, \ldots n$) in an ε-neighbourhood of w^*, with frequencies q_i. All sites are occupied, so $\Sigma\, q_i = 1$. Assume furthermore that w^* is initially present at some level; without loss of generality, we associate w^* with type 1, so that $q_1 > 0$ initially.

In each generation, sites will flip from one state to another; the net expected transformation from j to i will be

$$q_i q_j \left[\frac{P_i(1 - z_i)}{P_j z_j + H} - \frac{P_j(1 - z_j)}{P_i z_i + H} \right] \qquad (12)$$

where

$$H = \sum_k q_k P_k (1 - z_k)$$

The expression above represents the difference between the gain of type j sites by i, and the loss of i sites to j. Henceforth, we will assume $i = 1$, and compute the net exchange of sites held by the putative convergence stable strategy and sites of type j. Note that, as long as the functions P and z are continuous in w, each term $P_k(1 - z_k)$ can be approximated to order ε by the expression

$$\frac{1}{2}\,(P_1(1 - z_1) + P_j(1 - z_j)) \qquad (13)$$

and hence so can the weighted sum H. Thus, to order ε^2 the net expected transformation from j to 1 will be (from equation 12, after algebraic manipulation)

$$\frac{q_1 q_j (F(w_1) - F(w_j))}{2(P_1 z_1 + H)(P_j z_j + H)} \qquad (14)$$

Since $w_1 = w^*$ is a strict local maximum of F, and if we assume ε is chosen small enough so that F is a strict maximum on the ε-neighbourhood of w^*, it follows that there will be a net flow from sites of type j to sites of type 1, except possibly for types j in an order ε^2 neighbourhood of w^*. It is then clear from this heuristic proof that, for sufficiently small ε, the system will evolve to an arbitrarily small neighbourhood of w^*, the local maximum of F, whether or not w^* is an NIS. The reasoning here is deterministic, of course, and the stochastic model will show some deviation from its predictions.

In general, under realistic biological assumptions, we might expect the function F to

have a unique maximum, which will represent the CSS (towards which the population will evolve). The Hamilton–May model is an example of this. This need not always be the case, however, and multiple stable states are possible (see metapopulation example 3). Thus, a local maximum that is not a global maximum may become established, and resist invasion by the global maximum. Moreover, the arguments in the previous section show that it is possible, in general, for there to be convergence stable strategies that are not ESSs, but instead are evolutionary branching points, which can be re-invaded by other types (Geritz *et al.*, 1997). We now examine whether such behaviour is possible for a particular class of metapopulation models, in which we assume that there is a one-to-one correspondence between z, the fraction of seeds that stay home, and P, the potency of seeds (fecundity $\times$ competitive ability). We can therefore reparameterize in terms of z, so that we write $P = P(z)$.

Assume that the type $z = x$ is established in the population, and that $z = y$ is introduced at low density. The fitness of the invader y – that is, the per capita increase in the number of sites it occupies per generation – is then

$$r(y|x) = \frac{yP(y)}{yP(y) + (1 - x)P(x)} + \frac{(1 - y)P(y)}{P(x)} - 1 \tag{15}$$

For y to be able to invade, this per capita rate of increase must be greater than 0, which occurs precisely if

$$P^2(y)[1 - y^2] - P^2(x)[1 - x^2] > [P(y)(1 - y) - P(x)(1 - x)]^2 \tag{16}$$

(See Appendix 2. Note that this implies that mutual invadability is impossible. Similarly, one can easily rule out, by repeated application of (16), loops in which say A can invade B, B can invade C, and C can invade A.) Let φ be the difference between the two sides in (16), so that

$$\varphi(y|x) = P^2(y)[1 - y^2] - P^2(x)[1 - x^2] - [P(y)(1 - y) - P(x)(1 - x)]^2 =$$
$$F(y) - F(x) - [P(y)(1 - y) - P(x)(1 - x)]^2 \tag{17}$$

Then y can invade x if, and only if, $\varphi(y|x) > 0$.

It is clear from this that a necessary condition for y to invade x is that its F value is larger; that is,

$$F(y) > F(x) \tag{18}$$

Thus, maxima of F cannot be invaded; they are ESSs. This means that, for this class of metapopulation models, there exist no evolutionary branching points – all convergence stable strategies are ESSs as well, and thus they are CSSs. This occurs because, for critical points in these systems,

$$\left.\frac{\partial^2 r}{\partial x^2}\right|_{y=x} + \left.\frac{\partial^2 r}{\partial y^2}\right|_{y=x} = \frac{-4[(1 - x)P'(x) - P(x)]^2}{P(x)^2} \tag{19}$$

(see Appendix 3). Since this quantity is never positive, it follows from (10) that maxima of F must be ESSs, and may be NISs (if $\partial^2 r > \partial y^2$ is sufficiently large). From (10) and (19) it also follows that minima cannot be NISs but may be ESSs, and that all inflection points are ESSs. (In general, all critical points in these metapopulations are on the left side of the line $\partial^2 r/\partial v^2 = \partial^2 r/\partial u^2$ in Fig. 1.)

Because the function F is defined only for $0 \leq z \leq 1$, we also need to check the boundaries, $z = 0$ and $z = 1$, in our search for CSSs. These may be local maxima (or minima) on the

interval [0,1] even though they are not critical points of F. Thus they can also be local or even global CSSs, ESSs and/or NISs. (A global ESS cannot be invaded by any other type, nearby or otherwise. Similarly, a global NIS can invade any other type, and a global CSS is a global ESS such that types nearer to it can always invade types further from it in the same direction.) When they are not critical points, the status of boundary points cannot be evaluated in the usual way by looking at the second derivatives. In general, to determine the stability properties of a boundary point that is not a critical point, we must examine the function F, and consider the invasion criterion $\varphi > 0$ for invasion of or by nearby types. As mentioned earlier, boundary maxima are always convergence stable ESSs (CSSs); they may or may not be NISs, depending on the sign of the invasion criterion for invasion of nearby types. Specifically, substitution into (17) shows that $z = 1$ is never an NIS, while $z = 0$ is an NIS if, and only if, it is a local maximum of $P(z)$ (see Appendix 4). Boundary minima can be ESSs if, and only if, they are critical points and satisfy the usual ESS conditions.

Although it is possible for there to be multiple peaks in F, and thus multiple local CSSs, only transient co-existence of pairs of types is possible for this class of metapopulation model in general. (The situation is less clear when many types are involved.) We can see this by considering head-to-head competition between just two types, x and y. Type y will increase in frequency provided

$$F(y) - F(x) > (1 - 2q)[P(y)(1 - y) - P(x)(1 - x)]^2 \qquad (20)$$

where q is the proportion of sites occupied by y (see Appendix 5). Note the positive frequency dependence here: The more abundant y is (i.e. the higher the value of q is), the more likely it is that the conditions for y to invade will be satisfied. (When $q \sim 0$, (20) is simply the invasion criterion (16).) If $F(y) = F(x)$, then the more abundant type will increase in frequency. If $F(y) \neq F(x)$ but $|F(y) - F(x)|$ is sufficiently small relative to the square of the bracketed terms, there will be a value of q (which will be less than $1/2$ if $F(y) > F(x)$) that represents a threshold q_{cr} for y. If y is more abundant than this value, it will take over the population; if it is not that frequent, x will win even though its F value might be smaller. (Thus, competition between two types can actually lead to a decrease in the average value of F in the populations.) For $F(y) - F(x)$ sufficiently large relative to the square of the bracketed term, y will always win. In particular, this must always be the case for y sufficiently close to x.
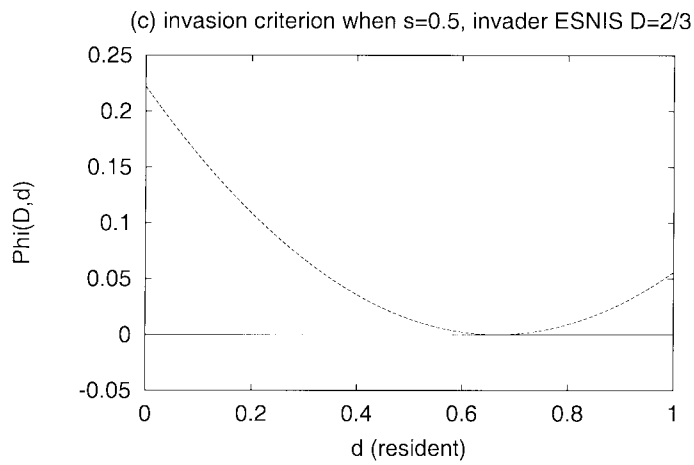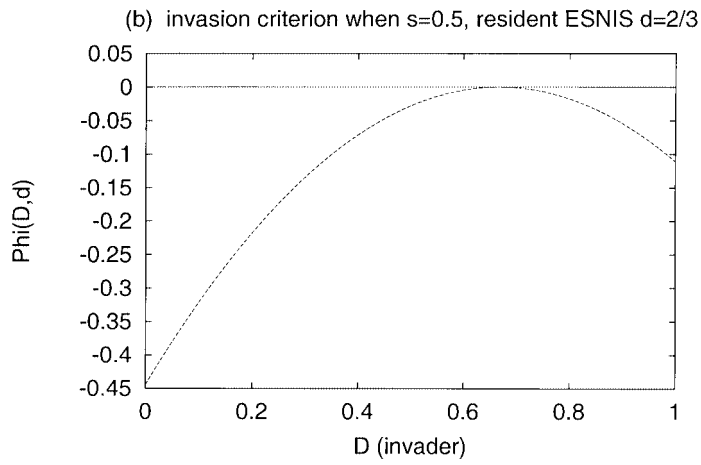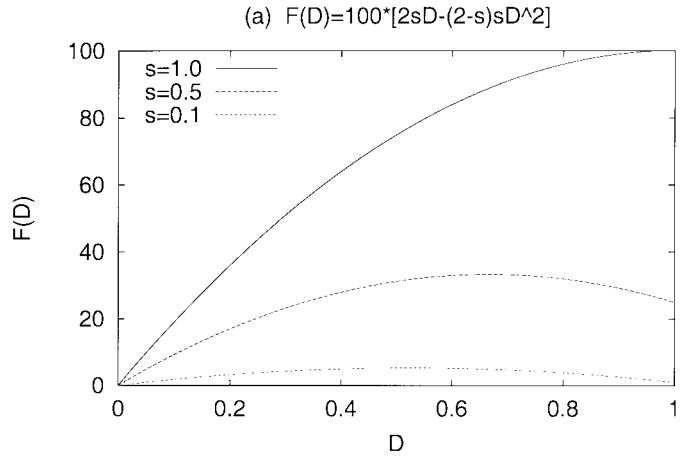
In general, we expect that seed number n will decrease with seed weight as a consequence of resource allocation, and competitiveness c will increase. Thus the potency P, the product of n and c, may increase or decrease. We consider three simple examples that explore the consequences.

Metapopulation example 1

Our first example is that due to Hamilton and May (1977), described earlier. In this case, where D is the fraction of seeds dispersed, s is the survival rate of dispersed seeds and m is the number of seeds produced, we have $P = m[Ds + (1 - D)]$ and $z = m(1 - D)/P$. (Note that z is the fraction of *surviving* seeds that stay home.) Thus,

$$F = m^2[Ds + (1 - D)]^2 - m^2[1 - D]^2$$

$$= sm^2D[2 - (2 - s)D] \qquad (21)$$

(Fig. 2a), which has a unique maximum at

(a) F(D)=100*[2sD-(2-s)sD^2]

F(D)

s=1.0
s=0.5
s=0.1

D

(b) invasion criterion when s=0.5, resident ESNIS d=2/3

Phi(D,d)

D (invader)

(c) invasion criterion when s=0.5, invader ESNIS D=2/3

Phi(D,d)

d (resident)

(d) invasion criterion when s=0.5, resident d=0.5
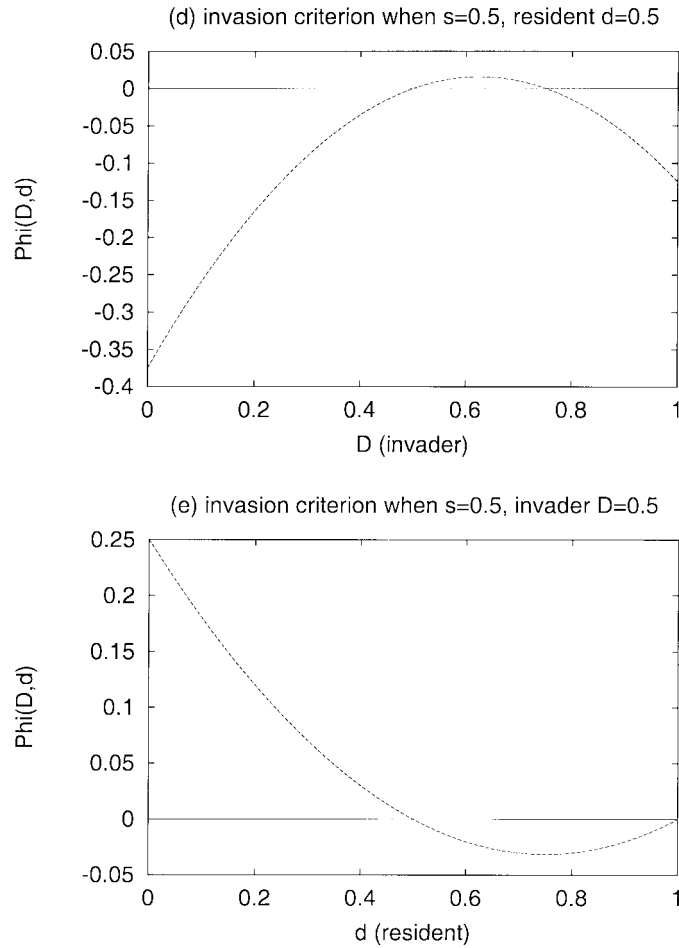

(e) invasion criterion when s=0.5, invader D=0.5

Fig. 2. For metapopulation example 1, due to Hamilton and May (1977), the function F has a single maximum, or ESNIS, for all values of the survival probability, s (a). The invasion criterion, φ, for a resident at this value, shows that it is able to resist invasion from any other type (b); the invasion criterion for an invader at the ESNIS shows that it is able to invade any other type as well (c). Other types are invasible from types closer than themselves to the maximum and on the same side, but not necessarily by superior types on the opposite side (d). Similarly, they can invade types farther away on the same side, but may not be able to invade inferior types on the other side of the maximum (e).

$$D = \frac{1}{2-s} \tag{22}$$

It is easy to see that this strategy is an ESNIS, and hence convergence stable, as Hamilton and May (1977) basically argue. Indeed, for this example, it may be shown that the invasion criterion is quadratic in both D (the dispersal fraction of the invader) and d (the dispersal fraction of the resident), with $\varphi_{DD} < 0 < \varphi_{dd}$:

$$\varphi = 2s(D-d)(1-d+sd-D) \tag{23}$$

Hence it follows that the ESNIS cannot be invaded by any other type (Fig. 2b) but can invade any other type (Fig. 2c).

In this example, a type can always invade other types having lower values of F that are on the same side of the maximum. However, it may or may not be able to invade types having lower values of F that are on the other side of the maximum – that is, inferior types that are very different. For example, if $s = 1/2$, then the type $D = 0.5$ can be invaded by types with higher F on the same side of the maximum (in this case, $D = 2/3$), and some of the types with higher F on the other side of the maximum, but not by all (Fig. 2d). Similarly, it can invade types lower than it on the same side of the maximum, but none that are on the other side of the maximum (Fig. 2e). Nevertheless, if variation is originally present or generated in the neighbourhood of this type, then natural selection will gradually move the population towards the ESNIS.

Metapopulation example 2

For our second example, suppose that z and P both increase with seed weight, and are related by the trade-off

$$P = \frac{1}{1 - hz^2} \tag{24}$$

for $0 < h < 1$ (Fig. 3a). Then it follows that

$$F(z) = \frac{1 - z^2}{(1 - hz^2)^2} \tag{25}$$

(Fig. 3b).

For $h < 1/2$, there is a single global maximum of F, and hence a CSS, at $z = 0$ (Figs 3b,c). However, it is not an NIS; it is unable to invade any other type, even though it is an evolutionary attractor. We can see this by examining the invasion criterion $\varphi > 0$ (see equation 17). For this example, we have

$$\varphi(y|x) = \frac{1 - y^2}{(1 - hy^2)^2} - \frac{1 - x^2}{(1 - hx^2)^2} - \left[\frac{1 - y}{1 - hy^2} - \frac{1 - x}{1 - hx^2}\right]^2 \tag{26}$$

We substitute for the invader by setting $y = 0$ to obtain

$$\varphi(0|x) = \frac{2hx^2(x - 1)}{(1 - hx^2)^2} \tag{27}$$

(Fig. 3d), which is negative for all residents x in [0,1].

As h increases beyond 1/2, $z = 0$ becomes a local minimum, and an interior maximum (hence, a CSS) emerges. Application of $\varphi > 0$, however, shows that, for $h < 3/4$, neither this maximum nor any other type can invade $z = 0$; hence, $z = 0$ remains a global ESS even though it is no longer an evolutionary attractor (Fig. 3c). Whether it will survive a competitive dynamic depends on how abundant it is and what other types are in the initial mix. For $3/4 < h < 1$, $z = 0$ is still a local ESS, but is invadable by an intermediate range of types; that range expands as h tends to 1 (Fig. 3c).

For $1/2 < h < 1$, there is also an interior maximum at

$$z = \sqrt{2 - 1/h} \qquad (28)$$

(Fig. 3b), perforce necessarily a CSS (Fig. 3e). To see whether it is an NIS, we examine the invasion condition (26), taking as invader y the type given by (28). The internal maximum will be an NIS if, and only if, $\varphi(y|x)$ achieves a local minimum, as a function of x, at $x = y = \sqrt{2 - 1/h}$; that is, if the second derivative $\varphi_{xx} > 0$ there. Applying this criterion to (28), we find that $\varphi_{xx} > 0$ at $y = \sqrt{2 - 1/h}$ if, and only if,

$$17h^3 - 19h^2 + 7h - 1 > 0 \qquad (29)$$

Thus, $\sqrt{2 - 1/h}$ is not an ESNIS for $h = 1/2$, but becomes one as h is increased beyond about 0.5867 (Fig. 3f).

In summary, the picture for this simple example is rather complicated, which illustrates the complexity of the more general problem. Note that the value of h is a measure of the relative sensitivity of competitive ability to weight, compared with dispersal. For low h, the competition curve is relatively flat compared with that for dispersal, meaning that increasing weight reduces dispersal without a substantial gain in competitive ability. Under such conditions, high seed weights are a disadvantage and low seed weights, which result in dispersal of all seeds away from the parent, are selected. Thus, for $h < 1/2$, we find that $z = 0$ is the only critical point; it is a CSS (convergence stable and an ESS), but not an NIS. As h is increased, the balance shifts towards higher seed weights because the competitive response is enhanced. For $h > 1/2$, $z = 0$ is a minimum, and there is an internal maximum given by (28). The internal CSS, present for h between 0.5 and 1, represents a trade-off between the highest seed weights, which are disadvantageous due to their inhibition of dispersal, and the lowest ones, which have very poor competitive ability. Between $h = 1/2$ and about 0.59, both critical points are global ESSs, although only the maximum is convergence stable, and neither is an NIS. Between about 0.59 and 0.75, $z = 0$ is a global ESS, and $z = \sqrt{2 - 1/h}$ is an ESNIS (and hence convergence stable). In general, between 0.50 and 0.75, the outcome of competition will be determined by initial conditions. From 0.75 to 1, $z = 0$ is only a local ESS, and loses that property in the limit as h approaches 1, while $z = \sqrt{2 - 1/h}$ remains an ESNIS throughout.

Instructive as this example is, it does not alter the conclusions of the last section. Even when the minimum is an ESS, it is not convergence stable; thus, evolution does not proceed towards it. Since such a type can never become established, the fact that it can resist invasion is essentially irrelevant. Similarly, even in the parameter range when the maximum is not an NIS, evolution is ultimately towards higher F, and thus towards the maximum (which is convergence stable); indeed, evolution proceeds to an arbitrarily small neighbourhood of the maximum. Given an initial continuous distribution of types surrounding the maximum, selection will eliminate the types with the lowest F, contracting the distribution towards the maximum.

Metapopulation example 3

A more complex relationship between seed weight and potency is reflected in the function

$$P(z) = (z - a)^2 + b \qquad (30)$$

where a and b are positive (see Fig. 4a).(Note that if a were zero, this potency function would be similar in behaviour to that from example 1, at least for small z.) For $0 < a < 1$, this
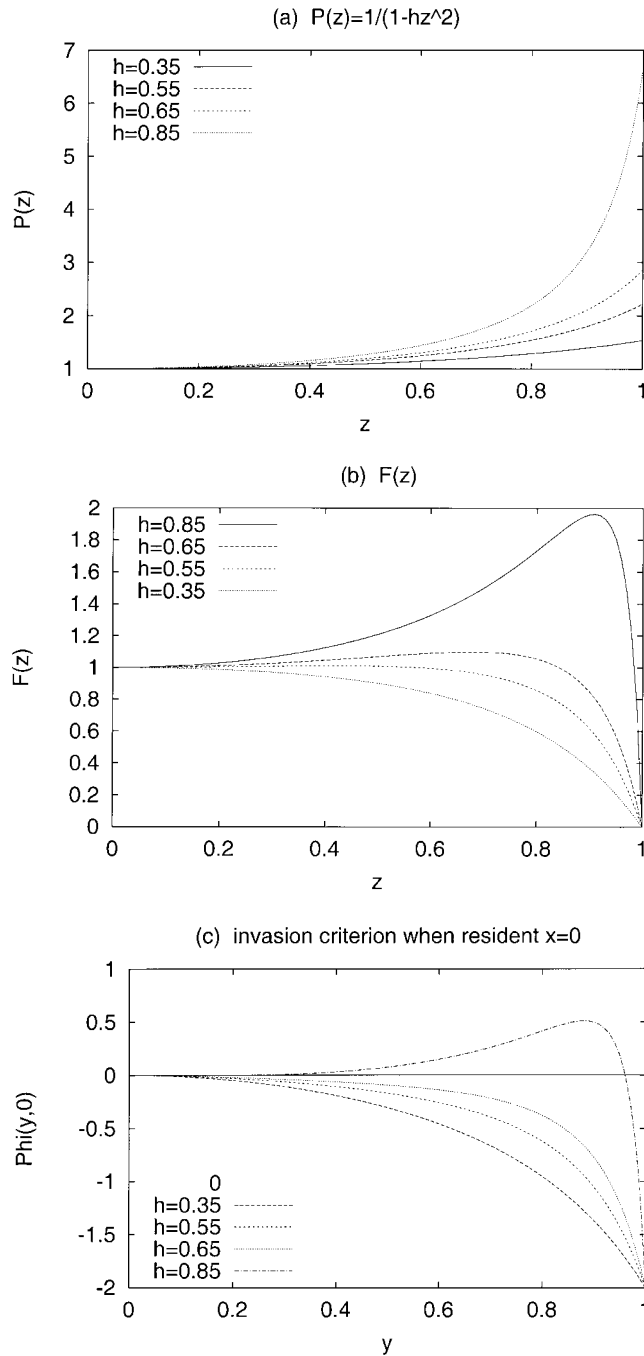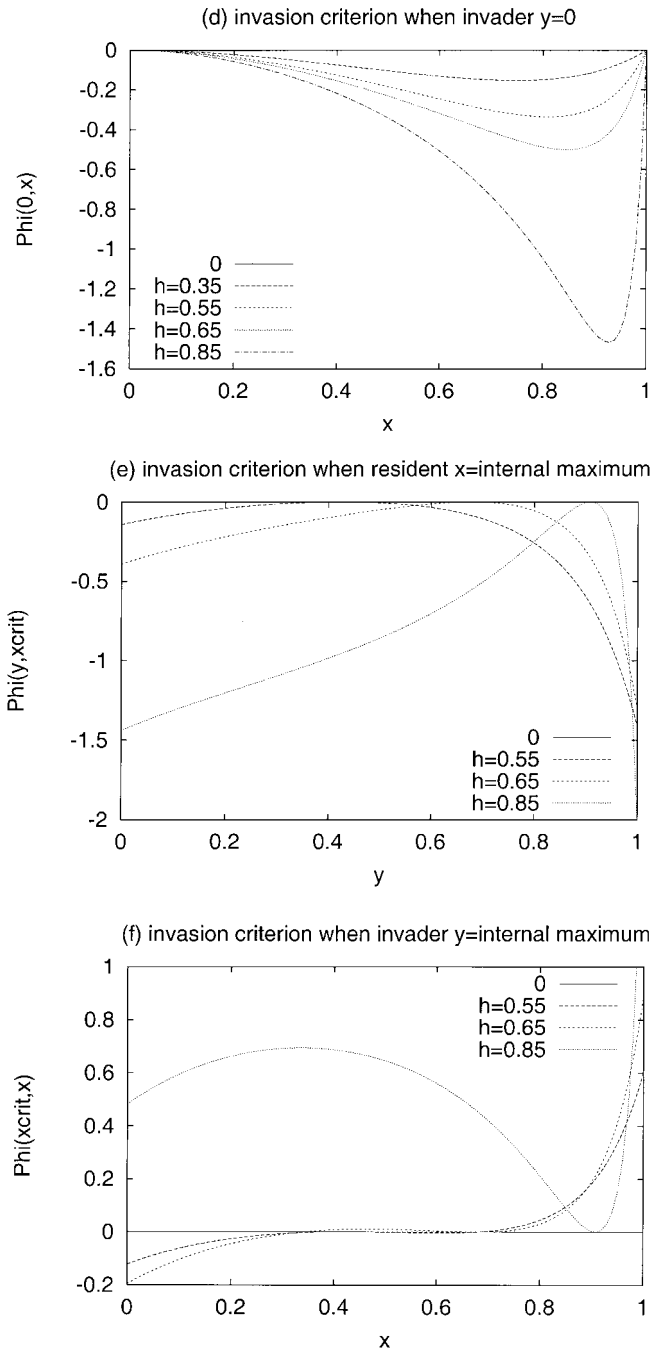
(a) P(z)=1/(1-hz^2)

(b) F(z)

(c) invasion criterion when resident x=0

Fig. 3. For metapopulation example 2, potency increases monotonically with the fraction of seeds staying home, z, for all $0 < h < 1$ (a). Depending on the value of the parameter h, the function F may be strictly decreasing ($h < 1/2$) or unimodal ($h > 1/2$) (b). The invasion criterion, φ, for a resident at $z = 0$, shows that this is always an ESS (c); the invasion criterion for an invader at $z = 0$ shows that

(d) invasion criterion when invader y=0

(e) invasion criterion when resident x=internal maximum

(f) invasion criterion when invader y=internal maximum

this is never an NIS (d). For the internal maximum $\sqrt{2 - 1/h}$, the invasion criterion for a resident there shows that it is always an ESS (e); the invasion criterion for an invader there shows that it is not an ESS for h less than approximately 0.59, becomes a local NIS for $0.59 < h < 0.75$, and is a global NIS for $h > 0.75$ (f).
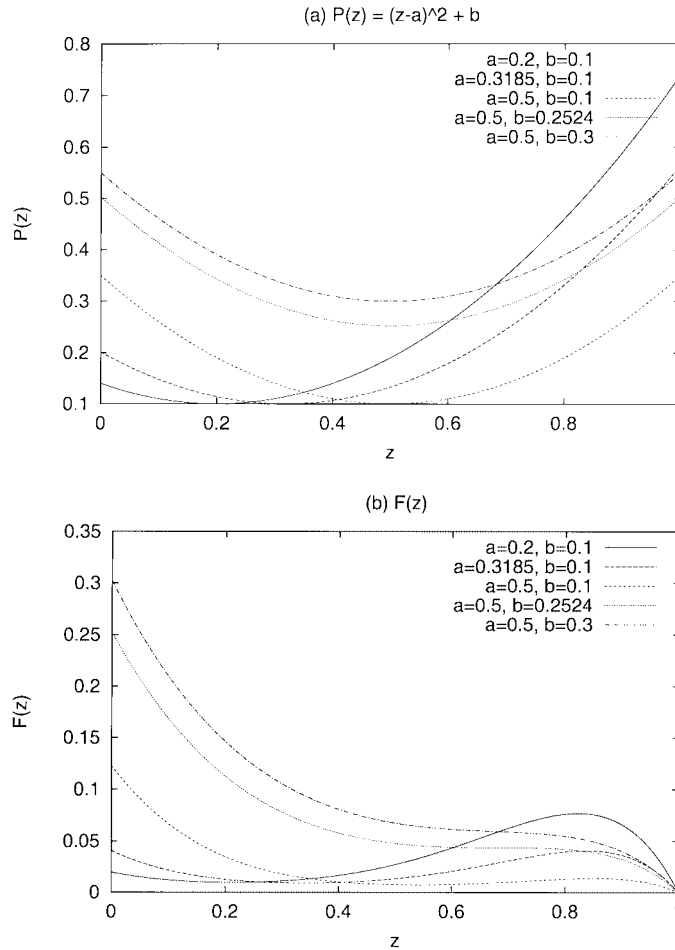
Fig. 4. For metapopulation example 3, potency $P = (z - a)^2 + b$ is a parabola with minimum of b at $z = a$ (a). Thus, on the interval [0,1], the function F may be strictly decreasing, decreasing with an inflection point, or decreasing and then increasing and decreasing again, depending on the values of parameters a and b (b).

suggests that potency at first decreases with weight, and then increases. The result is that multiple ESNISs may co-exist. Specifically, in this case, F becomes

$$F(z) = (1 - z^2)((z - a)^2 + b)^2 \tag{31}$$

(see Fig. 4b). For $a > 1$ or large b, this function has a single maximum at $z = 0$. For small b and $a > 1$, however, there is also a minimum close to $z = a$, and a second maximum at a point intermediate between this minimum and 1 (Fig. 3b). When the minimum and internal maximum first appear, the minimum is an ESS and the internal maximum is not an NIS; even so, points between the two will be invadable from the right, and so selection will move types in that region towards the convergence stable internal maximum. As b decreases, the minimum ceases to be an ESS and the internal maximum becomes an NIS.

The existence of two maxima means that there are two local CSSs. For fixed small b and small a, the interior maximum is a global ESNIS; as a increases, eventually that property transfers to the maximum at $z = 0$. For intermediate a and b such that the maxima are similar in F values, there is a region in which both are global ESSs and local NISs. In general, whenever there are two peaks, there is the potential for bistability. Distributions of types that start on one side of the minimum will be moved by selection towards the peak on that side. If both maxima are global ESSs, the resulting population at a maximum will be uninvadable by types from the other maximum, even if the other has a higher F value. (Note that to determine whether a type is a global ESS, we must use the invasion condition (16) and not rely on second derivatives, which only tell the story locally.) Should the initial distribution include types on both sides of the minimum, the peak to which selection eventually converges will depend on the relative frequencies of types on either side of the minimum and on their F values, as well as upon stochastic effects. It is even possible that there will be a transient bimodal distribution; however, because of the positive frequency dependence in this system, selection will eliminate types on one side of the minimum, leading to simple convergence on the other side. The complexity of such situations illustrates the care that must be taken in the evaluation of adaptive strategies.

EXTENSIONS TO EXPLICIT SPACE

Extensions of these ideas beyond the metapopulation are complicated by the build-up of correlations. An arbitrary plant of type j, dispersing a proportion of its seeds $\delta_j(x)$ to a particular site removed by x from their source, will have an expected yield $v = P_j \delta_j(x)$ divided by an appropriate weighted average V of $P\delta$, with that average taken over space and plant type and representing the total input of seeds into that site. Computation of that average is complicated by at least two factors: stochasticity, and the degree to which the underlying probability distribution for seed rain there deviates from a random sample of the whole population, due to the local (and thus spatially clumped) nature of seed dispersal in many systems. The expected conditional fitness of a seed is the expectation of v/V; this can be approximated by $v/E(V|j)$, where $E(V|j)$ is the expected value of V given j, with an error that depends on the spread in the distribution of $P\delta$. We here assume homogeneity in intrinsic conditions, so that the only spatial information is associated with clustering. We again invoke the assumption that the spread in the distribution of genotypes in the population is small, and estimate the conditional fitness as $v/E(V|j)$.

It remains to estimate $E(V|j)$. To a first approximation, we may make the mean-field approximation

$$E(V|j) = E(V) \tag{32}$$

That is, the conditional expectation is independent of the identity of the seed that we know has dispersed to the site. This is a very poor estimate, however; a better approximation is achieved by taking into account that the identity of a certain proportion of the seeds $(n_i \delta_i(x)$, with potency $P_i)$ is known, and that the others may be estimated by the properties of the average plant in the population:

$$\bar{w} = \sum q_i w_i \tag{33}$$

This is, of course, a crude approximation, relying again on the fact that the distribution of seed types is tight, in order to replace the average of $P\delta$ by $P\delta$ of the average. Furthermore, it

ignores the effect of clustering – that is, that the other seeds landing on the site are more likely to be similar to i than would be a randomly selected sample from the population.

With these assumptions, we may express the conditional fitness as

$$\frac{P_i \delta_i(\boldsymbol{x})}{P_i \delta_i(\boldsymbol{x}) + \bar{P}(1 - \bar{\delta}(\boldsymbol{x}))} - 1 \tag{34}$$

where $\bar{P}$ and $\bar{\delta}$ are used to refer to functions of the average type $\bar{w}$. Averaging over $\boldsymbol{x}$, we obtain the fitness $r(i|.)$ of type i. Following Ezoe's method, we differentiate this fitness as a function of seed type w_i to obtain expression (6) with the resident type w^* replaced by $\bar{w}$. Thus, a Taylor expansion of r about $\bar{w}$ yields the expression

$$f(i|.) = \frac{1 + (w - \bar{w})F'(\bar{w})}{2(P(\bar{w}))^2} \tag{35}$$

plus higher-order terms, where F is defined as in (5).

Now, set

$$A = \sum q_i F(w_i), \tag{36}$$

the average value of F in the population. The value of A in the next generation is then

$$A_{\text{new}} = \sum q_i F(w_i) r(i|.) \tag{37}$$

which by the approximation equals

$$A + \frac{\sum q_i F(w_i)(w - \bar{w})F'(\bar{w})}{2(P(\bar{w}))^2} \tag{38}$$

plus higher-order terms.

Finally, expand $F(w_i)$ in a Taylor expansion about $\bar{w}$. The first-order terms will drop out, by definition of the mean, leaving the approximation

$$A_{\text{new}} \approx A + \frac{1}{2}[P(\bar{w})]^2[F'(\bar{w})]^2\sigma^2 \tag{39}$$

where σ is the standard deviation of seed weight in the population. Thus, under these conditions, A can be viewed as a population mean fitness, in that the mean value of F increases monotonically, at a rate proportional to the variance in seed size. This is analogous to Fisher's Fundamental Theorem of Natural Selection, both in the statement of the result and in the strong assumptions that underlie its validity. Nonetheless, it provides a null hypothesis, expected to be valid when selection for dispersal distance is strong and when population heterogeneity is small.

The dynamics of seed size evolution in spatially explicit environments, however, are much more complicated than this simple result might suggest. The assumption of small variance in phenotypic characters means that this result may not hold when there is multimodality – that is, when discrete types co-exist – a ubiquitous feature of real communities. The assumption of no clustering means that, if selection for dispersal is weak and clustering does develop, this approximation will underestimate the advantages of dispersal (which would result from decreased kin competition), and may thus predict a seed size larger than that of the true evolutionary winner. Durrett and Levin (1994, 1998) explore the complexities of

competition–dispersal trade-offs in spatially extended environments, showing (among other things) that we should expect the possibility of bistability (the existence of multiple evolutionary attractors) to disappear when the metapopulation examples are replaced by spatially explicit analogues over effectively infinite regions. In a sequel to this paper, we will explore these differences.

DISCUSSION

Uniting frameworks used by Hamilton and May (1977), Levin *et al.* (1984) and Ezoe (1998), we show that the problem of the evolution of seed size – or of any other single dispersal-determining trait – can, under certain conditions, be understood as a constrained optimization problem. The function F, which defines the quantity to be optimized, has a nice interpretation as the product of competitive ability and fecundity (both squared), and a functional describing the spread of the dispersal kernel (equation 5). Maxima of this function are continuously stable strategies – evolutionary attractors towards which selection will drive populations (given sufficient diversity of types, either initially or generated through mutation).

This appealing simplification, however, is not without its complexities. Although we have confirmed that maximization of F allows us to replicate easily the results obtained by Hamilton and May (1977) and Ezoe (1998), it remains an open question whether it can be applied with equal validity, and ease, to the more complicated cases considered by Levin *et al.* (1984), Ludwig and Levin (1991), Geritz *et al.* (1999) and others. We already know that, in some cases, the convergence stable strategies identified by maximization are not themselves evolutionarily stable strategies (ESSs) – that is, they are invadable by other types; they are branching points, rather than endpoints, of the evolutionary process.

Thus, it is crucial that the framework we introduce here be elaborated further to allow incorporation of spatial and temporal heterogeneity in the environment, and of populations that are very heterogeneous, even multimorphic, in the trait under selection. The spatio-temporal structure of real environments dramatically expands the scope for co-existence, as Cohen and Levin (1987) and Ludwig and Levin (1991) have shown. Co-existence is not a curious complication, as many studies of ESSs suggest, but is a fact of life in natural communities. Because co-existence of many different strategies within communities is ubiquitous for seed size and dispersal, these multiple types should be considered in examining evolution of single types. The nascent subject of adaptive dynamics provides a promising, and necessary, approach to these (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998).

It has long been appreciated that locally inferior competitors can be sustained in spatially variable environments through their capacity to survive as fugitives (Horn and MacArthur, 1972), and that the evolution of community properties in part involves the spacing of types along gradients of ability to exploit different stages of succession (Watt, 1947; Levin and Paine, 1974; Whittaker and Levin, 1977). Even when simple theories might predict the asymptotic elimination of types, changing environmental conditions (Hutchinson, 1959) or simply immigration from source areas (Shmida and Ellner, 1984) may allow those types new beachheads before they are eliminated regionally. Those source areas may be external to the areas under consideration, or they may be internal – slow extinctions of types in areas in which they are disadvantaged may be offset by increases of those types in refuge areas. All of these issues have been explored in separate investigations by a diversity of authors, but the time is ripe to unite them in a comprehensive theory of community organization.

The challenge before us is to build theories of the adaptive dynamics of communities, and how community organization emerges from the individualistic evolution of its component species, across diverse scales of space and time. In this paper, we have only scratched the surface.

ACKNOWLEDGEMENTS

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APPENDIX 1: CONDITION THAT $F' = 0$ AT AN ESS

Condition (14) may be rewritten

$$0 = \sum_x P'\delta(1-\delta) + \sum_x P\delta'(1-\delta) \tag{A1}$$

where the primes indicate derivatives with respect to w^*. Multiplying by $2P$ and using the fact that P does not depend upon x, we rewrite (A1) as

$$0 = 2PP'\left(\sum_x \delta(1-\delta)\right) + P^2\left(2\sum_x \delta'(1-\delta)\right) \tag{A2}$$

Since $\sum_x \delta = 1$, and hence $\sum_x \delta' = 0$, (A2) may be rewritten

$$0 = (P^2)'\left(1 - \sum_x \delta^2\right) + P^2\left(1 - \sum_x \delta^2\right)' \tag{A3}$$

$$= F'$$

as claimed.

APPENDIX 2: CONDITION (16)

Rewriting (15), we obtain that for y to be able to invade, we require

$$r(y|x) = -\frac{(1-x)P(x)}{yP(y) + (1-x)P(x)} + \frac{(1-y)P(y)}{P(x)} > 0 \tag{A4}$$

Equivalently,

$$y(1-y)[P(y)]^2 - (1-x)[P(x)]^2 + P(y)P(x)(1-y)(1-x) > 0 \tag{A5}$$

Multiplying all terms by 2 and then substituting

$$2P(y)P(x)(1-y)(1-x) = [P(y)]^2(1-y)^2 + [P(x)]^2(1-x)^2 - [P(x)(1-x) - P(y)(1-y)]^2 \tag{A6}$$

(16) we obtain at once.

APPENDIX 3: CONDITION (19)

For these metapopulation cases, we can rewrite (15) as

$$r(y|x) = \frac{\varphi(y|x)}{B(y,x)} \tag{A7}$$

where we define

$$B(y,x) = P(x)[yP(y) + (1-x)P(x)] \tag{A8}$$

Then differentiation shows that at critical points, with $x = y = z^*$, the derivatives of $r(y|x)$ are simply the derivatives of $\varphi(y|x)$ divided by $B(y,x)$. (Recall that, at the critical points, the first derivatives of r with respect to x and to y are both zero.) Since $B(y,x)$ is always positive, this means that we need only examine the derivatives of $\varphi(y|x)$ to evaluate stability conditions. From (17), it is clear that

$$\left.\frac{\partial^2 \varphi}{\partial x^2}\right|_{y=x} = -F''(x) - 2[P'(x) \cdot (1-x) - P(x)]^2$$

$$\left.\frac{\partial^2 \varphi}{\partial y^2}\right|_{y=x} = +F''(x) - 2[P'(x) \cdot (1-x) - P(x)]^2 \tag{A9}$$

Since $B(x,x) = P^2(x)$, (19) follows immediately upon summation.

APPENDIX 4: BOUNDARY EQUILIBRIA AS NISs

In a metapopulation, the criterion for a type y to be able to invade an established type x is given by (17). In the special case that the invader $y = 0$, we obtain

$$\varphi(y|x) = P^2(y) - P^2(x)[1-x^2] - [P(y) - P(x)(1-x)]^2$$

$$= 2P(x)(1-x)[P(y) - P(x)] \tag{A10}$$

Thus $y = 0$ is a local NIS if, and only if, it is a local maximum of P. Similarly, substitution of $y = 1$ into (17) shows that $y = 1$ can never be an NIS.

APPENDIX 5: CONDITION (20)

Let there be two types, y and x, with frequencies q and $1 - q$. Then

$$H = qP(y)(1-y) + (1-q)P(x)(1-x)$$

$$= \frac{1-y}{2}P(y) + \frac{1-x}{2}P(x) - \left(\frac{1}{2} - q\right)[P(y)(1-y) - P(x)(1-x)] \tag{A11}$$

With this substitution, (20) follows at once from (12) upon cross-multiplication.