Evolutionary Ecology Research, 2006, **8**: 1349–1376

Adaptive responses to spatial aggregation and habitat destruction in heterogeneous landscapes

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ABSTRACT

Question: How does the spatial aggregation of landscape structure affect the ecological and evolutionary dynamics of metapopulations?

Mathematical methods: Analytical and numerical analysis of a generalized Levins type metapopulation model using procedures developed in adaptive dynamics theory.

Key assumptions: Landscapes are composed of patches of two types that are spatially aggregated with constant autocorrelation. Patch type determines population extinction rates but not the ability to establish new populations. Local populations are genetically identical.

Predictions: Niche switching following habitat disturbance is critically dependent upon landscape composition as well as phenotypic plasticity. Landscape configurations can result in evolutionary trapping. Increasing the degree of spatial aggregation can lead to a decline in evolutionary attractors, corresponding to a potential reduction in biodiversity.

Conclusions: The results are at odds with the commonly held opinion that aggregating spatial heterogeneity is a mechanism for promoting and sustaining biodiversity. Metapopulation models developed to investigate adaptive responses to landscape degradation would benefit if spatial variation in habitat structure, and not just population structure, is incorporated.

Keywords: adaptive dynamics, evolutionary branching, evolution of specialization, heterogeneous landscape, metapopulation, spatial aggregation.

INTRODUCTION

Landscape alteration has a major impact upon the ecology of communities, the demography of a focal species, and the genetic diversity of individuals. Predicting this impact is an important conservation goal. The diversity in landscape structure can be inferred from the diversity of the inhabitants; the spatial arrangement of habitat is a catalyst for the ecological dynamics. Classical conservation approaches focus upon protecting the elements of landscapes that preserve the current biotic arrangement. The consensus has been that evolutionary processes shaping these arrangements are largely dependent upon the

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chronology of events spanning large time scales, and any change to the abiotic environment will upset this delicate balance of biodiversity. But how delicate are these systems and what aspects of them are we trying to protect? When the degree of biodiversity is the conservationist's concern, perhaps measures should be equally reserved for the protection of aspects that support the evolutionary processes. Evidence increasingly suggests that adaptations through natural selection can occur on relatively fast time scales following abrupt changes to the environment (Ferrière, 2000; Ferrière *et al.*, 2004). Although a species may be maladapted to a modified landscape, evolutionary rescue may take place before deterministic extinction occurs; the species may adapt to take advantage of the changed structure.

Habitat reduction affects many spatial landscape patterns, each having a consequence for the remaining inhabitants (Forman, 1995). These patterns include, after successive levels of loss, habitat perforation, fragmentation, dissection, patch shrinkage, and attrition. After large-scale habitat removal, landscapes characteristically are highly fragmented and the consequence for inhabitants may be severe. As a result, populations are expected to be left fragmented and weakly connected and this will play an important role in species persistence, individual home range size and dispersal abilities, gene flow, and speciation. Such a collection of extinction-prone local populations, weakly connected by dispersal, has been dubbed a 'metapopulation' (Levins, 1970). The prevalence of metapopulation study is in part due to the alarming fact that the spatial structure and dynamics of many species increasingly fit this description due to the land reform activities of man (Hanski, 1999).

Dispersal and extinction are the driving processes of metapopulation dynamics. Populations are kept small by limited patch sizes, becoming prone to extinction through environmental and demographic variation. With high rates of local extinction, dispersal is an essential process for maintaining a viable metapopulation, allowing empty patches to be recolonized following an extinction event. Dispersal may, among other things, play a positive role in reducing kin competition and inbreeding that come into effect when small populations become isolated. Negative consequences of dispersal are equally apparent, with costs associated with the failure to find and establish new local populations. The landscape structure will highlight some of these benefits and costs and be essential in determining the efficiency of dispersal strategies. The life-history traits associated with dispersal and those that maximize within-patch viability may be coupled together or coupled with other life-history traits not directly related to metapopulation dynamics. Therefore, predicting the consequence of certain traits in maximizing the fecundity of individuals, or the establishment of new local populations, is highly non-trivial. When studying the fine-tuning of life-history traits through evolution by natural selection, the assumptions about and ecological consequence of these traits will be important. Evolution of life-history traits in metapopulations is a challenge for the modeller. Since many metapopulation models have the local population as the smallest biological unit, modelling of evolutionary processes that depend upon the selection of individuals is problematic. Processes that bring ecological success to the metapopulation, like increased dispersal, may actually penalize individuals who undertake them [dispersal may be hazardous, while non-dispersers enjoy reduced local competition (Poethke and Hovestadt, 2001; Poethke *et al.*, 2003)]. This consideration of the individual within the population is thus of crucial importance when defining invasion fitness in metapopulations (Gyllenberg and Metz, 2001). The measure of invasion fitness tells us which life-history strategies an invading individual must possess to have a positive probability of invading a metapopulation.

When invasion potential is naturally derived from an ecological model, it can be studied under the adaptive dynamics framework (Geritz *et al.*, 1998). The framework gives a rich insight into the evolutionary dynamics of populations/metapopulations and a synthesis of adaptive speciation via evolutionary branching is naturally derived. The framework has been applied to study the evolution of dispersal in metapopulations by Doebeli and Ruxton (1997) and Kisdi (2002) (for a review, see Parvinen, 2004). The role of spatial and temporal variability in habit quality, stochastic local demography, and direct costs of dispersal all have an influence on the adaptive levels of dispersal and evolutionary branching of low and high dispersal strategies.

Heterogeneity in the landscape composition may have strong implications for the evolution of dispersal and other traits. Landscapes are typically composed of an array of elementary resources with characteristic spatial arrangements (Brachet *et al.*, 1999; Parvinen and Egas, 2004). These elementary resources may become segregated following habitat destruction. This may leave local populations exposed to a reduced resource base and a new set of pressures. A model of two connected populations that occupy different habitat patches has been considered by both Meszena *et al.* (1997) and Kisdi (2002) to investigate the evolution of patch specialization. A patch specialist in a two-patch environment is a phenotypic variant well adapted to one habitat type, yet minimally adapted to the other, in contrast to patch generalists who are moderately adapted to both types. Meszena *et al.* (1997) investigated how patch differences and fixed rates of inter-patch dispersal can influence the evolution of patch specialization and identified a potential mechanism for parapatric speciation. The parallel evolution of dispersal rates with patch specialization was investigated with the model presented by Kisdi (2002). A strong joint dependency between dispersal and specialization was found for a range of environmental conditions and complicated evolutionary dynamics. These included the successional evolution of a dimorphism in dispersal, followed by a dimorphism in habitat specialization, and finally the evolution of low dispersal rates in both subpopulations.

Parvinen and Egas (2004) considered a metapopulation model that was structured by local population size with a similar consideration of elementary resources. With the inclusion of local population extinction, the evolution of specialization was investigated for a range of dispersal abilities. The size-structured model considered by Parvinen and Egas (2004) assumed a well-mixed dispersal pool, implying a limited description of the heterogeneity in landscape. The distribution of the resources in real landscapes will depend upon geographic and biographical factors, often attributed to human landscape reform.

In this paper, we address this with a simple description of elementary resource aggregation in a generalized Levins model. We investigate the impact that spatial aggregation and habitat destruction have upon the evolution of patch specialization, adaptive speciation, and the evolution of dimorphic populations. We find that spatial aggregation and asymmetric habitat removal have strong, and often counterintuitive, consequences on the adaptive evolution of metapopulations: interestingly, we find that high-level spatial aggregation, promoting disjointed subpopulations, is not a necessary condition for adaptive speciation, and indeed sometimes inhibits it. Habitat reduction is shown to sometimes promote adaptive speciation, contrary to the commonly held belief that biodiversity will always decline.

The model is particularly suited to the case when patches only accommodate single individuals, since patch populations are assumed to be genetically pure. This assumption is reasonable when organisms have strong founder effects, like seed-dispersing plants that are regionally patchy. The results are qualitatively similar to those of Parvinen and Egas (2004) for uniformly distributed patches, leading us to conjecture that a structured model with aggregated elementary resources may share many of the results we have uncovered. Harding and McNamara (2002) suggest that the shortcomings of the Levins model may not be solely down to the neglect of individuality, but also to the dynamic described at the population scale. Some of the classic results from structured metapopulation models, namely the rescue effect, can be recovered in an unstructured model with a reworking of the colonization and extinction processes. Whether such an argument could ever reasonably be applied to evolutionary processes is unclear.

THE MODEL

The foundation metapopulation model

The model to be considered in this paper is a generalization of the classic Levins metapopulation model (Levins, 1969, 1970) modified by Lande (1987) to include the process of habitat loss. In the classic Levins model, the fraction of occupied patches, x, of an infinite set of identical habitat patches is modelled in continuous time. Occupied patches become extinct at the same rate in each patch, while empty patches are colonized at a rate proportional to the fraction of occupied patches. Some patches are permanently removed from the network to model the level of habitat loss. The time evolution of x is determined by

$$\frac{\mathrm{d}x}{\mathrm{d}t} = cx(h - x) - ex.$$

Here e is the extinction rate, c is the colonization rate per occupied patch, and h is the fraction of patches that are habitable. These three parameters determine metapopulation persistence and viability. A metapopulation persists if the extinction state $x = 0$ is unstable, resulting in the parameter condition

$$R_0 = \frac{hc}{e} > 1.$$

R_0 is the expected number of patches that are colonized by a single occupied patch in an otherwise unoccupied landscape before extinction and is known as the *basic reproductive ratio*. If $R_0 > 1$, a single stable attractor of the metapopulation dynamics will exist, given by

$$\hat{x} = h - \frac{e}{c} = h\left(1 - \frac{1}{R_0}\right).$$

In practice, by measuring the fraction of empty yet habitable patches of a metapopulation at equilibrium, we obtain an estimate for e/c, the minimum fraction of habitat needed for persistence.

The single-species model with two patch types

The habitat patch is the basic unit of the landscapes in the Levins model and is assumed to be uniform in every respect except occupation state. In reality the size, shape, and quality of the patches, together with the spatial arrangement, will influence everything from the local demography to the metapopulation dynamics. To appreciate the implications of patch variation, we introduce it into the model. Variation could be in any of the patch qualities mentioned above but the focus here is on elementary resource type: patches will be purely composed of one of two elementary resources. How the species utilizes each resource will have an impact upon the local extinction and demographic processes, with consequences for emigration as well. This structure is thus critical to the ecological and evolutionary dynamics.

In our initial model, we assume that there is no spatial correlation between patch types. The model is given by

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = k(x_1 + x_2)\,(h_1\rho_1 - x_1) - e_1x_1, \tag{1}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = k(x_1 + x_2)\,(h_2\rho_2 - x_2) - e_2x_2. \tag{2}$$

Here ρ_i is the proportion of all patches of type i ($\rho_1 + \rho_2 = 1$), and h_i is the fraction of type i patches that are habitable. The dynamic variables $x_i \le h_i\rho_i$ is the fraction of all patches that are of type i and populated. Occupied patches of type i go extinct at the rate e_i.

We have assumed that patch type does not affect colonization, i.e. that neither propagule production nor foundation success depends on patch type. Thus populated patches produce emigrants that populate empty habitable patches at a per capita rate k. This depends upon the mean-field assumption that the probability that an arbitrarily chosen propagule from a type j patch attempts to colonize a patch that is habitable, type i and empty is proportional to the fraction of habitable type i empty patches in the landscape, leading to a colonization term $kx_j(h_i\rho_i - x_i)$.

In our full model, we include the effect of spatial correlation between patch types, by defining $\mathbb{P}\{i/j\}$ to be the probability that a randomly chosen patch in the neighbourhood of a given patch of type j is of type i, while retaining the mean-field assumption that the probability that a patch of type i in the neighbourhood is habitable and empty is equal to the fraction of type i patches that are both habitable and empty, $(h_i\rho_i - x_i)/\rho_i$. The equations become

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = kx_1\mathbb{P}\{1/1\}\,\frac{h_1\rho_1 - x_1}{\rho_1} + kx_2\mathbb{P}\{1/2\}\,\frac{h_1\rho_1 - x_1}{\rho_1} - e_1x_1, \tag{3}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = kx_1\mathbb{P}\{2/1\}\,\frac{h_2\rho_2 - x_2}{\rho_2} + kx_2\mathbb{P}\{2/2\}\,\frac{h_2\rho_2 - x_2}{\rho_2} - e_2x_2, \tag{4}$$

or, with $c_{ji} = k\,\dfrac{\mathbb{P}\{i/j\}}{\rho_i}$,

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = (c_{11}x_1 + c_{21}x_2)\,(h_1\rho_1 - x_1) - e_1x_1, \tag{5}$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = (c_{12}x_1 + c_{22}x_2)\,(h_2\rho_2 - x_2) - e_2x_2. \tag{6}$$

The quantities $\mathbb{P}\{i/j\}$ represent the spatial correlations between patch types. They are not independent. Since all patches are either of type 1 or type 2 we have

$$\mathbb{P}\{2/i\} = 1 - \mathbb{P}\{1/i\}. \tag{7}$$

Defining $\mathbb{P}\{i\,j\}$ to be the probability that an ordered pair of neighbouring patches are of type i and type j respectively, then, by symmetry, $\mathbb{P}\{i\,j\} = \mathbb{P}\{j\,i\}$, and so

$$\mathbb{P}\{i/j\} = \mathbb{P}\{j/i\}\,\frac{\rho_1}{\rho_j}. \tag{8}$$

Combining equations (7) and (8) yields

$$\mathbb{P}\{j/j\} = 1 - \frac{\rho_i}{\rho_j}(1 - \mathbb{P}\{i/i\}). \tag{9}$$

Thus the landscape is uniquely defined by the two parameters $\rho := \rho_1$ and $q := \mathbb{P}\{1/1\}$. The condition that $0 \leq \mathbb{P}\{2/2\} \leq 1$ leads to the constraint that $q \geq 2 - 1/\rho$. If $q > \rho$, then $\mathbb{P}\{i\,i\} > \rho_i^2$ and in such a situation the elementary landscapes will be referred to as aggregated.

Without loss of generality, we set $k = 1$ because a trivial re-scaling of time allows for the absorption of k into the patch extinction rates. Thus we have

$$c_{11} = \frac{q}{\rho} \qquad c_{12} = c_{21} = \frac{1-q}{1-\rho} \qquad c_{22} = \frac{1 - 2\rho + \rho q}{(1-\rho)^2}. \tag{10}$$

SINGLE-SPECIES ECOLOGICAL DYNAMICS

The ecological dynamics are characterized by the stability of the steady states of the system giving conditions for metapopulation persistence and viability. It is useful to adopt the vector notation $\mathbf{x} := (x_1, x_2)$. $\hat{\mathbf{x}}$ is a steady state if $\dot{\mathbf{x}}|_{\mathbf{x}=\hat{\mathbf{x}}} = 0$, and of ecological interest if $\hat{\mathbf{x}} \in [0, h_1\rho_1] \times [0, h_2\rho_2] =: \chi$.

Persistence

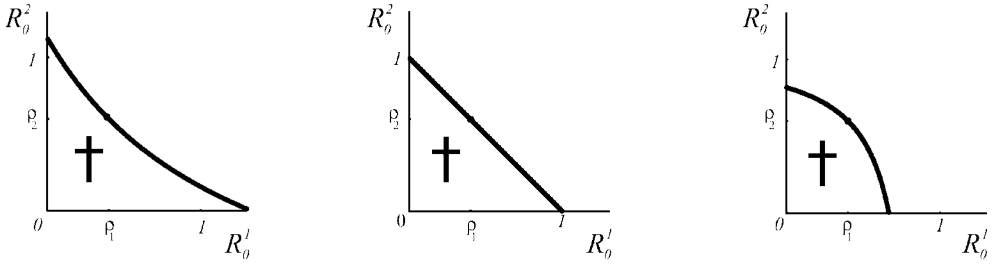
The origin (0, 0) is the steady state representing metapopulation extinction and the metapopulation persists if and only if the origin is unstable. The conditions for stability at the origin are derived in Appendix 1 and, defining $R_0^i := (h_i\rho_i)/e_i$, are equivalent to

$$R_0^1 \leq \frac{1}{c_{11}}, \tag{11}$$

$$R_0^2 \leq \frac{1}{c_{22}}, \tag{12}$$

$$c_{11}R_0^1 + c_{22}R_0^2 + R_0^1R_0^2(c_{12}c_{21} - c_{11}c_{22}) \leq 1. \tag{13}$$

The quantity R_0^i has ecological meaning. R_0^i is the expected number of type i patches colonized by dispersers from a single type i patch in an otherwise unoccupied landscape before extinction, provided that the elementary landscapes have a random spatial distribution ($q = \rho$). This quantity is analogous to the basic reproductive ratio, R_0.



(a) $q = 0.3$ (b) $q = 0.4$ (c) $q = 0.6$

Fig. 1. The extinction regions in R_0^1–R_0^2 parameter space ($R_0^i = h_i\rho_i/e_i$) for the model equations (5) and (6) when $\rho_1 = 0.4$. The extinction region, labelled with a cross, is bounded above by the curve satisfying equality (13) subject to (11) and (12). The point (ρ_1, ρ_2), represented by a circle, is always on the boundary of extinction regions.

The persistence condition in this form is useful because it isolates the effect that the landscape parameter q has on extinction, as shown in Fig. 1. The curve in the (R_0^1–R_0^2) plane that satisfies equality (13), subject to (11) and (12), is a hyperbola that bounds the extinction region from above. The curvature of the hyperbola depends upon $sign\{c_{11}c_{22} - c_{12}c_{21}\} = sign\{q - \rho\}$: If $q > \rho$ the boundary is concave, if $q < \rho$ then convex. For the degenerate case when $q = \rho$ the curve is a line. Note that the point $(R_0^1, R_0^2) = (\rho_1, \rho_2)$ lies on the boundary for all values of q, and thus the extinction region contracts as q increases, assuming a constant value for ρ.

Decreasing R_0^i, either by reducing the fraction of habitable i type patches or increasing the extinction rates of i type populations, relates to habitat deterioration. The curvature of the extinction boundary will dictate how detrimental relative amounts of patch-type-specific habitat loss can be, when assuming constant extinction rates. When predicting metapopulation extinction risk, it is not enough to just know the dispersal behaviour, proneness to local extinction, or the frequency of patch types; knowledge of spatial distributions of patches is also crucial.

Viability

The stability boundary for the extinction state (0, 0) was shown in the previous subsection to be one branch of the hyperbola $c_{11}R_0^1 + c_{22}R_0^2 + R_0^1R_0^2(c_{12}c_{21} - c_{11}c_{22}) = 1$. As the stability boundary is crossed, there is a transcritical bifurcation to a non-trivial steady state $(\hat{x}_1, \hat{x}_2)$ in the interior of χ. This steady state is globally asymptotically stable when it exists in the interior of χ and the metapopulation is therefore viable whenever it persists. In this case, $\hat{x}_1$ is the unique root of

$$\begin{aligned} &c_{11}\zeta\hat{x}_1^3 + (\zeta + c_{11}c_{22}e_1 - c_{11}c_{21}e_2 + \zeta(c_{21}h_2\rho_2 - 2c_{11}h_1\rho_1))\hat{x}_1^2 + (c_{22}e_1^2 - c_{21}e_1e_2 + \\ &\quad (c_{22}c_{21}h_2\rho_2 - h_1\rho_1(c_{12}c_{21} + 2\zeta))e_1 + 2c_{11}c_{21}h_1\rho_1e_2 + h_1\rho_1\zeta(c_{11}h_1\rho_1 - 2c_{21}h_2\rho_2))\hat{x}_1 \\ &\qquad + c_{21}h_1\rho_1e_1e_2 - c_{22}c_{21}\,h_1\rho_1h_2\rho_2e_1 - c_{11}c_{21}h_1^2\rho_1^2e_2 + c_{21}\zeta h_1^2\rho_1^2h_2\rho_2 = 0, \end{aligned} \quad (14)$$

in $(0, h_1\rho_1)$, where $\zeta = c_{11}c_{22} - c_{21}c_{12}$, and $\hat{x}_2$ is given by

$$\hat{x}_2 = \frac{e_1\hat{x}_1}{c_{21}(h_1\rho_1 - \hat{x}_1)} - \frac{c_{11}\hat{x}_1}{c_{21}}. \quad (15)$$

The uniqueness of $\hat{x}_1$ is easily verified from an inspection of the x_1 and x_2 nullclines, the curves in (x_1, x_2) space satisfying $\mathrm{d}x_1/\mathrm{d}t = 0$ and $\mathrm{d}x_2/\mathrm{d}t = 0$ respectively, that trivially cross at most once within χ.

MULTIPLE PHENOTYPES AND EVOLUTIONARY DYNAMICS

The model extends naturally to incorporate competition between different species or phenotypes if we make the assumption that local populations are pure: any dispersers arriving in an occupied patch are unable to establish a subpopulation and leave the resident unaffected. This assumption is not unreasonable in many systems, such as those with strong founder effects where the chances of maturation are severely reduced for dispersers arriving in patches with established populations. In plant systems, for example, whereby competition for light is heavily asymmetric between seedlings and adult plants, the probability of seed, dispersed from a neighbouring patch, developing in a populated patch could be very small.

The implication of this assumption is that competition at the metapopulation level is for empty patches only. Patch colonization success is dependent upon the metapopulation traits of individuals, and not traits that will affect within-patch competition. We make this assumption to focus on the effects of large-scale landscape structure on patch type specialization, and to keep the model analytically tractable.

For N different competitors, tracking the density of all patches that are of type i populated by competitor j, the model extends to

$$\frac{\mathrm{d}x_i^j}{\mathrm{d}t} = (c_{1i}x_1^j + c_{2i}x_2^j)\left(h_i\rho_i - \sum_{n=1}^{N} x_i^n\right) - e_i^j x_i^j, \tag{16}$$

where $(h_i\rho_i - \sum_{n=1}^{N} x_i^n)$ is the fraction of habitable i type patches, less those that are occupied. e_i^j is the extinction rate that competitor j experiences in i type patches, and it is these rates that distinguish the different competitors.

These equations now describe all the ecological dynamics but to study the metapopulation in an evolutionary context will require a few extra assumptions. Different competitors can now represent the different phenotypes of a single species. An account of how diverse the phenotypes of the species can be, together with an explanation of how they are introduced into the system, is needed.

The classic Levins model predicts that persistence and fitness, defined as the invasion exponent of a rare mutant population, are both dependent upon the ratio of extinction and colonization rates (assuming no within-patch competition). Any mutant population with a reduction in the ratio of these two rates will invade a resident population. In reality, phenotypic variation will be subject to constraining factors and different phenotypic traits that influence these rates are likely to be strongly correlated (Stearns, 1999). In this model we assume that phenotypic variation affects only the patch extinction rates and that these are constrained according to a trade-off relationship: if a phenotypic variant has an extinction rate e_1 in type 1 patches, a unique extinction rate $e_2 = f(e_1)$ is experienced in type 2 patches. The function f will be referred to as the trade-off function and will be intricately linked to both the ecological and the evolutionary dynamics.

Of particular interest will be the patch type *generalist* and the *extreme specialists*. The generalist phenotype experiences the (generalist) extinction rate e_G, satisfying $e_G = f(e_G)$, in both patch types. Non-generalists will be referred to as *specialist* phenotypes. A phenotype is a type 1 specialist if $e_1 < e_2 = f(e_1)$ or a type 2 specialist if $e_1 > e_2 = f(e_1)$. Extreme specialists are phenotypic variants with extinction rates that correspond to the minimum values that e_1 and $f(e_1)$ can take.

Mutant phenotypes are assumed to be similar to at least one of the resident phenotypes and are introduced into the system in a discrete temporal manner after the resident system has reached dynamic equilibrium. If the mutant deterministically replaces one or more of the phenotypes, or co-exists with the resident phenotypes, an evolutionary event has occurred. These assumptions allow the evolutionary process to be modelled using the adaptive dynamic framework (Geritz *et al.*, 1998).

Invasion of a monomorphic metapopulation

Modelling the evolutionary process requires a derivation of an invasion condition. We will assume that, at any given time, there is a single resident phenotype with extinction rates e_1 and e_2 and patch occupation densities x_1 and x_2. The invading phenotype's extinction rates and patch occupation densities will be labelled with a prime. The system extends from equation (16) to

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = (c_{11}x_1 + c_{21}x_2)\,(h_1\rho_1 - x_1 - x'_1) - e_1x_1,$$

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = (c_{12}x_1 + c_{22}x_2)\,(h_2\rho_2 - x_2 - x'_2) - e_2x_2,$$

$$\frac{\mathrm{d}x'_1}{\mathrm{d}t} = (c_{11}x'_1 + c_{21}x'_2)\,(h_1\rho_1 - x_1 - x'_1) - e'_1x'_1,$$

$$\frac{\mathrm{d}x'_2}{\mathrm{d}t} = (c_{12}x'_1 + c_{22}x'_2)\,(h_2\rho_2 - x_2 - x'_2) - e'_2x'_2. \tag{17}$$

Biologically realistic states must satisfy x_i, $x'_i \geq 0$ and $x_i + x'_i \leq h_i\rho_i$. The set of all such states is invariant under (17) since, for $j \neq i$, $\mathrm{d}x_i/\mathrm{d}t = (h_i\rho_i - x'_i)c_{ji}x_j \geq 0$ when $x_i = 0$, and $\mathrm{d}x_i/\mathrm{d}t + \mathrm{d}x'_i/\mathrm{d}t = -e_ix_i - e'_ix'_i < 0$ when $x_i + x'_i = h_i\rho_i$.

Since the resident phenotype is at dynamic equilibrium before the introduction of the mutant, invasion occurs if the steady state ($\hat{x}_1(e_1,e_2)$, $\hat{x}_2(e_1,e_2)$, 0, 0) is unstable. This is equivalent to either $trJ_M > 0$ or $detJ_M < 0$, as derived in Appendix 2, where

$$trJ_M(e'_1, e'_2, e_1, e_2) = \frac{(e_1 - e'_1)c_{11}\hat{X} - e'_1c_{21}}{c_{11}\hat{X} + c_{21}} + \frac{(e_2 - e'_2)c_{22} - e'_2c_{12}\hat{X}}{c_{12}\hat{X} + c_{22}}, \tag{18}$$

$$detJ_M(e'_1, e'_2, e_1, e_2) = e'_1e'_2 - \frac{e'_1e_2c_{22}}{c_{12}\hat{X} + c_{22}} - \frac{e'_2e_1c_{11}\hat{X}}{c_{11}\hat{X} + c_{21}} + \frac{e_1e_2(c_{11}c_{22} - c_{12}c_{21})\hat{X}}{(c_{11}\hat{X} + c_{21})\,(c_{12}\hat{X} + c_{22})} \tag{19}$$

and $\hat{X} = \hat{x}_1/\hat{x}_2$.

Singular strategies: conditions on the trade-off constraint

We assume that the mutant phenotypes are *closely* derived from existing resident strains and constrained by a trade-off relation. These assumptions mean that the adaptive behaviour is dependent solely on $\Delta(e', e) := -detJ_M(e', f(e'), e, f(e))$ as shown in Appendix 2. The expression Δ defines the mutant fitness at low density and compares to intrinsic mutant growth rate (Mathias *et al.*, 2001) or the log of the basic reproductive ratio R_{mut} (Gyllenberg and Parvinen, 2001), which are all sign equivalent. In Appendix 2, we show that $detJ_M(e_1, e_2, e_1, e_2) = 0$, and thus $\Delta(e_1, e_1) = 0$ verifying that a mutant that is phenotypically identical to the resident has neutral invasion fitness.

The adaptive outcomes of a monomorphic metapopulation are determined by the partial derivatives of Δ with respect to the resident and mutant extinction rates. If $\frac{\partial\Delta(e,e)}{\partial e'} \neq 0$, selection is directed according to $sign\,\frac{\partial\Delta(e,e)}{\partial e'}$. A strategy e^* satisfying $\frac{\partial\Delta(e^*, e^*)}{\partial e'} = 0$, whereby directional selection vanishes, is called an *evolutionarily singular strategy*. Singular strategies are potentially the end of the evolution process and the focus of the adaptive dynamics analysis of monomorphic (meta)populations.

The adaptive dynamics framework involves two major classifications of singular strategies: First, a singular strategy, e^*, is *evolutionarily stable* (ES) if it is locally un-invadable. It is ES if there exists an open set of strategies, $\xi \ni e^*$, such that $\Delta(e', e^*)\,|_{e' \in \xi / e^*} < 0$. Second, a singular strategy, e^*, is *convergence stable* (CS) if it is locally an evolutionary attractor. It is CS if there exists an open set, $\xi \ni e^*$, where the direction of invasion satisfies $sign\left(\left.\frac{\partial\Delta}{\partial e'}\right|_{e'=e}\right) = sign(e^* - e)$ for all $e \in \xi$. The boundary of the attraction domain of a CS singular strategy will either consist of a non-CS singular strategy, a strategy on the boundary of phenotype space, or a strategy on the threshold of persistence.

The local ES and CS properties of a singular strategy are determined by the expressions in Table 1 involving the second partial derivatives. A CS and non-ES singular strategy is named a branching strategy because such a situation promotes the evolution to a dimorphic (meta) population as strategies in the locality of a branching strategy are mutually invasive (Geritz *et al.*, 1998).

Table 1. Basic classification of singular strategies

	$\frac{\partial^2\Delta^*}{\partial e'^2} < 0$	$\frac{\partial^2\Delta^*}{\partial e'^2} > 0$
$\frac{\partial^2\Delta^*}{\partial e'^2} + \frac{\partial^2\Delta^*}{\partial e \partial e'} < 0$	ES ✓ CS ✓ *Evolutionary unbeatable*	ES × CS ✓ *Evolutionary branching*
$\frac{\partial^2\Delta^*}{\partial e'^2} + \frac{\partial^2\Delta^*}{\partial e \partial e'} > 0$	ES ✓ CS × *Garden of Eden*	ES × CS × *Evolutionary repeller*

The evolutionary dynamics are dependent upon both the intrinsic species properties, characterized by the trade-off function, and the landscape properties described by the landscape parameters. The selection gradient is

$$\frac{\partial\Delta(e,\, e)}{\partial e'} = -\frac{ef'(e)c_{21}}{c_{11}\hat{X}(e) + c_{21}} - \frac{f(e)c_{21}\hat{X}(e)}{c_{12}\hat{X}(e) + c_{22}}, \tag{20}$$

adopting the prime notation for differentiation. The condition on the trade-off function f at a singular strategy is thus

$$f'(e^*) = -\frac{f(e^*)X^*(c_{11}X^* + c_{21})}{e^*(c_{12}X^* + c_{22})}, \tag{21}$$

where $X^* = \hat{X}(e^*)$. Similarly, we can find conditions for the evolutionary classification of the these singular strategies. A singular strategy is ES if

$$f''(e^*) > -\,2f'(e^*)\,\frac{(c_{11}X^* + c_{21})}{c_{21}e^*}, \tag{22}$$

which, using equation (21), is

$$f''(e^*) > \frac{2f(e^*)X^*(c_{11}X^* + c_{21})^2}{c_{21}e^{*2}\,(c_{12}X^* + c_{22})}\,. \tag{23}$$

A singular strategy is CS if

$$f''(e^*) > \frac{f(e^*)(c_{11}X^* + c_{21})}{e(c_{12}X^* + c_{22})}\left(\frac{X^*(c_{11}X^{*2} + 2c_{12}X^* + c_{22})}{e^*(c_{12}X^* + c_{22})} - \left(\frac{c_{11}X^*}{c_{11}X^* + c_{21}} + \frac{c_{22}}{c_{12}X^* + c_{22}}\right)\frac{\mathrm{d}X^*}{\mathrm{d}e}\right), \tag{24}$$

where $\mathrm{d}X^*/\mathrm{d}e = \mathrm{d}\hat{X}(e^*)/\mathrm{d}e$.

An example trade-off function

The analysis of Δ, our measure of local mutant fitness, is hampered by the difficulty of working with the expression for resident metapopulation density, which we recall is a root of the cubic equation (14). Some results relating to phenotypic specialization, where selection is for a decrease of the particular extinction rate, and the evolutionary behaviour of the generalist strategy $e_1 = e_2 = e_G$ can be obtained but an example trade-off must be realized for further analysis. We are then limited to calculating the resident metapopulation densities numerically.

For simplicity, we consider a suitably smooth trade-off relationship such that the trade-off curve is reflectively symmetric about the line $e_2 = e_1$ in the e_1–e_2 plane. The symmetric trade-off relationship can be defined by the parametric function $e : t \mapsto e(t)$ where

$$e_1 = e(t), \tag{25}$$

$$e_2 = e(-t). \tag{26}$$

t (not to be confused with time) represents a phenotypic strategy and $t = 0$ is the generalist strategy ($e_G = e_1(0) = e_2(0)$).

We choose

$$e(t) = e_G \exp(\tau t^2) + 2e_G \tau \exp(\tau)t, \tag{27}$$

where τ is a constant of the species and restricted to $\tau < 0.5$ to maintain strictly positive extinction rates, and $\tau > 0$ to ensure that $e(t) \to \infty$ as $t \to \pm\infty$, but our results do not depend on this choice.

The strategy set $(-1, 1)$ is evolutionary attracting. This follows since $e(t)$ and $e(-t)$ are both monotonically increasing when $|t| > 1$ and thus decreasing $|t|$ reduces both extinction rates, and furthermore, the selection gradient (20) is negative when $t = 1$ and unbounded and positive when $t = -1$. The strategies $t = -1$ and $t = 1$ represent extreme specialists of the species since e_1 is a minimum when $t = -1$ and e_2 is a minimum when $t = 1$.

The trade-off curve for three instances of τ are plotted in Fig. 2. The parameter τ is a measure of trade-off weakness since increasing τ decreases the cost of specializing; that is, the relative decrease in the extinction rate in the adapted patch is less than the increase in the maladapted patch. This property determines how different the species perceives the two patch types to be since increasing the trade-off parameter will increase the difference between patches. Meszena *et al.* (1997) and Kisdi (2002) consider trade-off functions for patch adaptation that explicitly model patch difference.

In the previous subsection, the evolutionary properties of a strategy were presented in terms of the trade-off function f and in particular $f'(e)$ and $f''(e)$. It is not possible to find the explicit form of f since $e(t)$ is not explicitly invertible; however, it can be implicitly defined as

$$f(e(t)) = e(-t).$$

Using the chain rule we have that

$$f'(e(t)) = -\frac{\mathrm{d}e(-t)}{\mathrm{d}t} \Big/ \frac{\mathrm{d}e(t)}{\mathrm{d}t},$$

and

$$f''(e(t)) = \left(\frac{\mathrm{d}e(-t)}{\mathrm{d}t}\frac{\mathrm{d}^2e(t)}{\mathrm{d}t^2} + \frac{\mathrm{d}e(t)}{\mathrm{d}t}\frac{\mathrm{d}^2e(-t)}{\mathrm{d}t^2}\right) \Big/ \left(\frac{\mathrm{d}e(t)}{\mathrm{d}t}\right)^3. \tag{28}$$

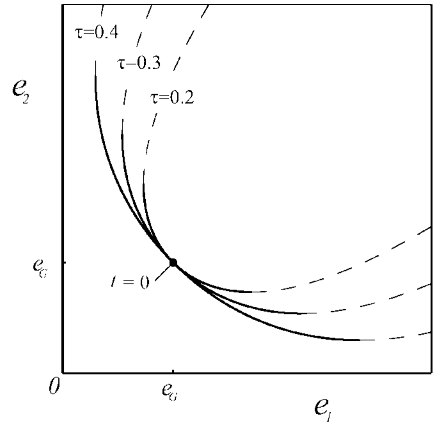


Fig. 2. The trade-off curve for different values of the trade-off parameter, τ. Singular strategies can only lie on the solid region of the trade-off curve where $f' \leq 0$ exclusively.

The symmetry in the trade-off yields the property that the generalist strategy is a singular strategy if the landscape is symmetric; that is, if there are equal fractions of the two patches ($\rho = \frac{1}{2}$) that are equally habitable ($h_1 = h_2$). This follows since, in this case, $\hat{x}_1(e_G) = \hat{x}_2(e_G)$ and the right-hand side of the singular strategy condition (21) becomes equal to $-1 = f'(e_G)$ for the symmetric trade-off.

Defining $f''_G = f''(e_G)$, we have $f''_G = 1/e_G\tau \exp(2\tau)$, a decreasing function of τ that will determine the ES and CS properties of the singular generalist.

RESULTS

The parameter Δ is crucial in establishing how the landscape- and species-specific parameters ρ, q, h_1, h_2, e_G, and τ determine the location and classification of singular strategies $t^* \in [-1, 1]$. For the remainder of the investigation, we assume that $\rho = \frac{1}{2}$ so that the generalist is singular when habitat loss is independent of patch type. This will mean that any breakdown in landscape symmetry will be a consequence of asymmetric habitat removal only. We determine the evolutionary properties of the generalist strategy below.

It is trivial to show that, with a rescaling of time, that the evolutionary dynamics of the system with symmetric habitat loss is equivalent to a *tilde* system with $\tilde{h}_1 = 1$, $\tilde{h}_2 = h_2/h_1$, $\tilde{x}_i(t) = x_i(t)/h_1$, and $\tilde{e}_G = e_G/h_1$, since the trade-off is in the form $\tilde{e}(t) = e(t)/h_1$.

Note that when $\tilde{e}_1 = \tilde{e}_2$, the ecological dynamics of the generalist strategy degenerate to the classic Levins model with

$$R_0 = \frac{1}{\tilde{e}_G} = \frac{h_1}{e_G}.$$

A reduction in R_0 can represent the destruction of habitat patches or a deterioration in average patch quality.

Metapopulation evolution in symmetric landscapes

Unbiased habitat degradation ($h := h_1/h_2 = 1$) preserves an element of symmetry in the model and in this case we calculate the evolutionary classification of the singular generalist explicitly (see Appendix 3). The singular generalist strategy is ES if

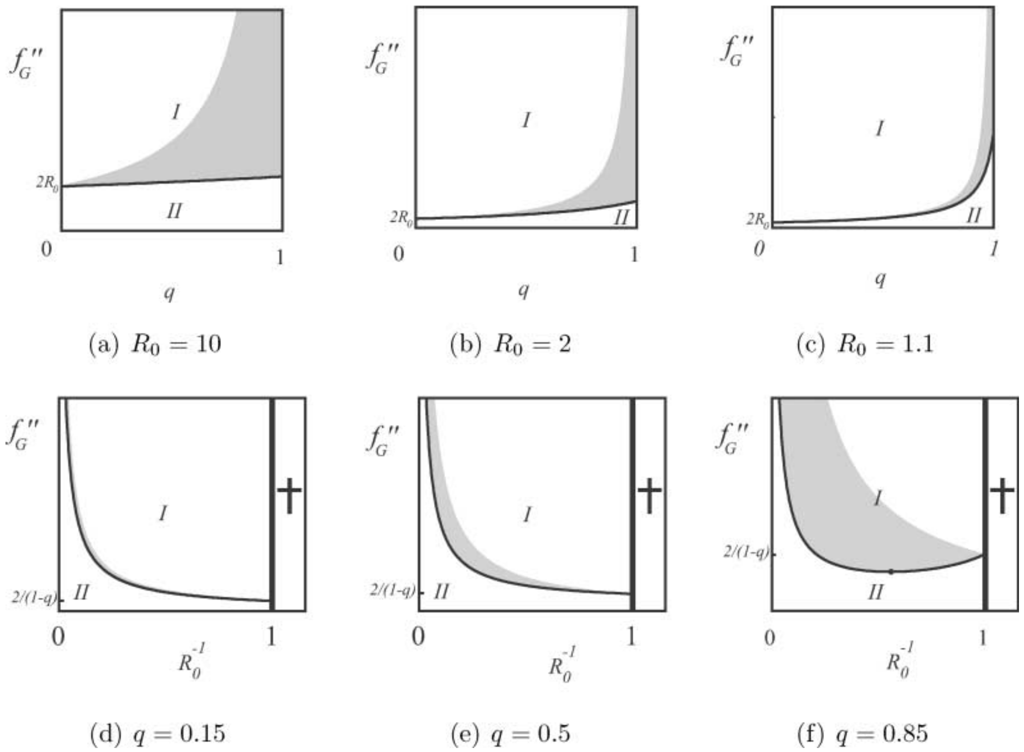
$$f''_G > \frac{2R_0}{1-q}, \tag{29}$$

and is CS if

$$f''_G > \frac{2R_0(1+R_0)}{1+R_0-2q}. \tag{30}$$

The ES condition is stronger than the CS conditions, ensuring that the generalist is never a 'Garden of Eden' strategy. The other three scenarios, outlined in Table 1, are all feasible.

The plots of Fig. 3 illustrate how the classification of a singular generalist depends upon different regions of parameter space. When parameters lie in region *I*, bounded below by the solid curve, the generalist is a CS singular strategy. The shaded region of *I* represents the CS strategies that are not ES, the condition for evolutionary branching. In region *II*, the generalist singular strategy is not CS and, therefore, an evolutionary repeller.



(a) $R_0 = 10$ (b) $R_0 = 2$ (c) $R_0 = 1.1$

(d) $q = 0.15$ (e) $q = 0.5$ (f) $q = 0.85$

Fig. 3. The evolutionary properties of a singular generalist strategy. The thin solid curve bounds regions of parameter space that lead to CS (I) and non-CS (II) generalists. Within the shaded region, the generalist is non-ES and hence an evolutionary branching point. The generalist cannot persist if $R_0 \leq 1$.

Some general results are apparent. Increasing q always contracts the ES region, expanding both the regions of branching and evolutionary repulsion. The biological explanation of this is quite simple. When q is high, dispersers are more likely to arrive in patches that are similar to the natal patch. It therefore pays to specialize to some degree on same-type patches. From an evolutionary perspective, this leads to partial habitat specializers emerging, through branching, or the monomorphic evolution away from the generalist. Increasing q locally segregates the landscapes and the mechanism for speciation may be considered allopatric. However, this is not the only branching mechanism; branching does occur for low q albeit under a restricted range of conditions. In this case, different strains of the metapopulation will be well mixed across the landscape, competing directly for empty habitat patches. How to sensibly uncouple these two mechanisms for branching is not clear.

Decreasing R_0 expands the ES region and contracts the branching region. If the generalist resident metapopulation is fragile, any attempts to specialize may be penalized. Interestingly, decreasing R_0 does not always have a monotonic effect on the CS condition, as illustrated in Fig. 3f. Only an intermediate range of R_0 will result in the convergence stability of the generalist. This range only exists if the right-hand side of (30) is a decreasing function of R_0 when $R_0 = 1$; a condition that is equivalent to $q > \frac{2}{3}$. The minimum value of f''_G on the CS boundary curve occurs when

$$R_0 = \tilde{R}_0 = 2q - 1 + \sqrt{2q}\,\sqrt{2q - 1}, \tag{31}$$

and so an intermediate range of R_0 will exist if and only if

$$q > \tfrac{2}{3}, \tag{32}$$

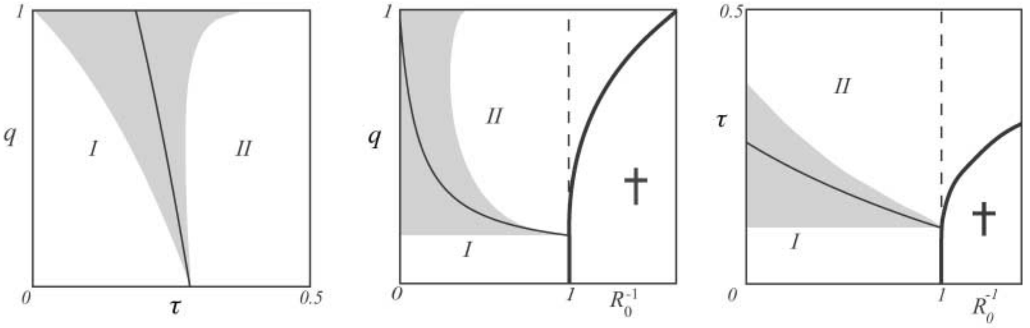
and

$$\frac{2\tilde{R}_0(1 + \tilde{R}_0)}{1 + \tilde{R}_0 - 2q} < f''_G < \frac{2}{1 - q}. \tag{33}$$

When the generalist is not CS at least two new singular strategies will be present in the trait space, representing more specialized phenotypes, and at least two will be CS. We illustrate this with the example trade-off presented earlier. The symmetry in both the trade-off function and the landscape means that if t^* is a singular strategy, then $-t^*$ is, and with the same evolutionary properties. The evolutionary classifications of the singular specialists were found numerically and the plots of Figs. 4 and 5 show how the classification of these strategies can depend upon q, R_0, and τ. The continuity of the trade-off ensures that specialist singular strategies in the locality of the generalist CS bifurcation curve always inherit branching status. This is well illustrated in the plots of Fig. 5. The shaded grey region indicates the strategies that do not satisfy (22) and hence singular strategies in this region are non-ES.

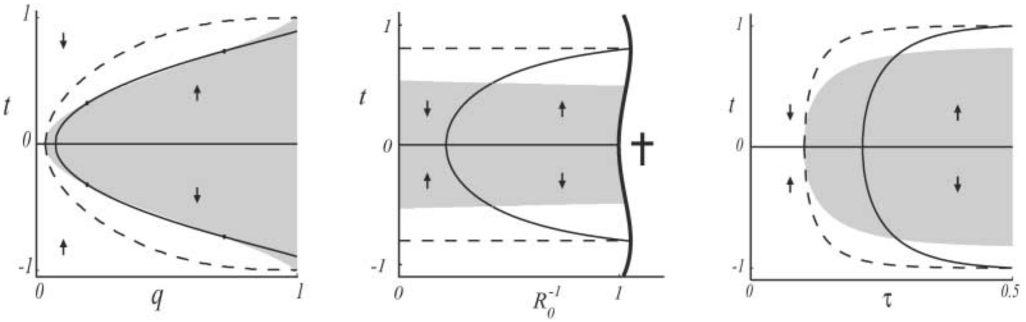
Away from the locality of the generalist, the determination of the location and classification of singular strategies is intricately dependent upon this particular choice of trade-off function. In Fig. 5c we observe how increasing τ ultimately causes these emerging singular strategies to become ES and evolution terminates in a monomorphic resident phenotype. This behaviour is qualitatively similar to that found by Meszena *et al.* (1997) for the case of two populations.

This sequence of behaviour is not always observed. When the generalist is repelling, increasing q can change an ES singular strategy to non-ES and vice versa as illustrated in



(a) $R_0 = 3.3$ (b) $\tau = 0.25$ (c) $q = 0.75$

Fig. 4. The classification of both generalist and specialist singular strategies. The thin solid curve bounds regions of parameter space that lead to CS (I) and non-CS (II) generalists. In the shaded region, the CS strategies are non-ES and hence evolutionary branching points.



(a) $\tau = 0.2775$ and $R_0 = 3.3$ (b) $q = 0.5$ and $\tau = 0.25$ (c) $q = 0.75$ and $R_0 = 3.3$

Fig. 5. The trait value and classification of singular strategies. The solid thin black curves indicate the monomorphic singular strategies. The dashed curve represents one strategy of a dimorphic singular coalition. Monomorphic singular strategies that lie within the shaded region are non-ES. The arrows indicate directional selection and point towards CS singular strategies.

Fig. 4b. This happens only for small intermediate ranges of R_0 and τ but the result may be more robust with alternative trade-off relationships. This suggests that the potential for evolutionary branching is a local property that depends upon a balance between the trade-off strength constraining adaptation and the spatial arrangement of patches that affect the relative advantage of specialist resource utilization. This highlights the potential difficulty in making concrete predictions about how habitat composition facilitates evolutionary branching.

Following excessive habitat reduction (decreasing R_0), no phenotypic variant of the species can persist, but for relatively moderate loss persistence is maintained and changes in evolutionary behaviour can be observed (Fig. 5b,c). When $R_0 \leq 1$, the generalist cannot persist, though some strategies may remain viable. For such a case a CS non-generalist singular strategy must exist. If this was not the case the evolving resident strategy would converge upon the extinction boundary resulting in evolutionary suicide; however, this is not permitted in a system whereby the viable population density is a continuous function of the evolving phenotypic trait as shown by Gyllenberg and Parvinen (2001). If a generalist is ES, a persistent generalist after habitat reduction ($R_0 > 1$) will remain ES. Otherwise, removing habitat results in a strictly ordered sequence of stages:

1. The generalist is CS and non-ES.
2. The generalist becomes non-CS and two strategies, CS and non-ES, bifurcate from the generalist.
3. The non-generalist strategies become ES.
4. The generalist strategy becomes non-viable.
5. Finally, all phenotypic variants become non-viable.

In the penultimate stage when the generalist strategy is no longer viable, the species could persist in a dimorphic state (two distinct co-existing resident phenotypes) or as a single resident phenotype partial to one patch type. If the adaptation rate is relatively faster than the rate at which habitat is removed, it is predicted that evolution may rescue the species from extinction. Evolutionary rescue of this kind is discussed in Dieckmann and Ferrière

(2004, Chapter 11). We also note that removing habitat eventually converts all evolutionary branching strategies to evolutionary attractors that are ES.

Following evolutionary branching, two residents with differing trait values will co-exist. The evolution of the emergent dimorphic system requires the extension of the system (equations 16 with $j = 3$) to include three competitors – two representing a dimorphic coalition and an invading mutant as in Appendix 4. The two resident phenotypes are represented by two resident strategies t^1 and t^2.

With $X^1(t_1, t_2) = \dfrac{\hat{x}_1^1(e(t^1), e(t^2))}{\hat{x}_1^2(e(t^1), e(t^2))}$, we show in Appendix 4 that the measure of the fitness of a mutant with strategy t' is

$$\Delta(e(t'), e(t^1), e(t^2)) =$$

$$\frac{e(t')e(-t^1)c_{22}}{c_{12}X^1 + c_{22}} + \frac{e(-t')e(t^1)c_{11}X^1}{c_{11}X^1 + c_{21}} - e(t')e(-t') + \frac{e(t^1)e(-t^1)(c_{12}c_{21} - c_{11}c_{22})X^1}{(c_{11}X^1 + c_{21})\,(c_{12}X^1 + c_{22})}, \qquad (34)$$

derived in an equivalent way as the monomorphic case. Evolution of the dimorphic system is characterized by *evolutionary singular coalitions* as defined and classified by Geritz *et al.* (1998). An evolutionary singular coalition, (t_1^*, t_2^*), satisfies

$$\frac{\partial \Delta}{\partial e_1'}(e_1(t_1^*), e_1(t_1^*), e_1(t_2^*)) = \frac{\partial \Delta}{\partial e_1'}(e_1(t_2^*), e_1(t_1^*), e_1(t_2^*)) = 0, \qquad (35)$$

extending naturally from the monomorphic case whereby directional selection vanishes.

When the landscape and trade-off function are both symmetric, a symmetric dimorphic coalition $(t^*, -t^*)$ is a singular coalition if

$$f'(e_1(t^*)) = -\,X^1(t^*, -t^*)^2, \qquad (36)$$

where

$$X^1(t^*, -t^*) = \frac{qe_2(t^*)}{2(1-q)e_1(t^*)}\left(1 - \frac{e_1(t^*)}{e_2(t^*)} + \sqrt{\left(1 - \frac{e_1(t^*)}{e_2(t^*)}\right)^2 + \frac{4(1-q)^2 e_1(t^*)}{q^2 e_2(t^*))}}\right), \qquad (37)$$

as derived in Appendix 5.

Determining the evolutionary properties of dimorphic singular coalitions is less straightforward than that of the monomorphic case. A singular coalition is ES if no mutant, derived from either resident, can invade the coalition. A dimorphic singular coalition (t^{1*}, t^{2*}) is ES if

$$\frac{\partial^2 \Delta}{\partial e_1'^2}(e_1(t'), e_1(t^{1*}), e_1(t^{2*})) < 0, \qquad (38)$$

when both $t' = t^{1*}$ and $t' = t^{2*}$. When the landscape is symmetric, a symmetric singular coalition $(t^*, -t^*)$ is ES if

$$f''(e_1(t^*)) > -\frac{2f'(e_1(t^*))}{e_1(t^*)}\left(\frac{qX^1(t^*, -t^*)}{(1-q)} + 1\right), \qquad (39)$$

as derived in Appendix 5. In the symmetric case, the dimorphic ES condition is analogous to that of the monomorphic case (22), since the formulae are identical if, in the monomorphic case, X represents the ratio of the monomorphic patch occupation densities. The dimorphic ES condition is stronger than the monomorphic ES condition because the monomorphic ratio is greater than the dimorphic ratio and the right-hand side of (A43) is an increasing function of X. From this it follows that all the dimorphic singular coalitions depicted in Fig. 5 are ES since they lie outside of the shaded region.

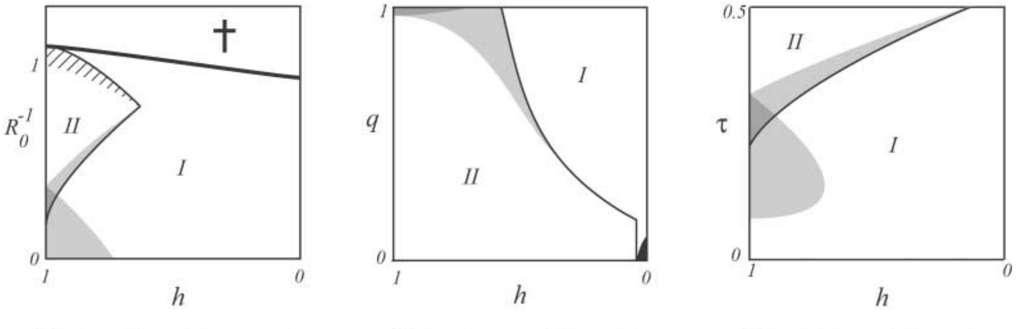
Deriving the condition for convergence stability is not straightforward for the dimorphic case but we claim, without a proof, that if a single symmetric dimorphism ($t^* \neq 0$) exists, then it will be CS. Furthermore, we also claim that no other dimorphic singular coalitions exist for the example trade-off. Since the only singular coalition is symmetric, and therefore ES, evolution can only terminate with at most two phenotypic varieties. This is not, however, a consequence of this particular trade-off function or the symmetry in the landscape. Applying the competitive exclusion principle, that the number of resources, in this case two, is an upper limit on the number of possible co-existing phenotypes (Tilman, 1982), excludes the possibility of further evolutionary branching to a trimorphic state. Note that a singular dimorphism can exist in the absence of monomorphic branching strategies; however, evolution will terminate in a dimorphism only if the system is initially dimorphic and within the domain of evolutionary attraction.

Asymmetric habitat loss

The mechanism of patch destruction may be more detrimental to one of the patch types. Anthropogenic landscape change is often focused on a particular resource and may leave other habitats relatively unaffected. The invasion of another species that favours one of the habitat types could, under certain conditions, be considered as a form of habitat loss provided the ecology of this species occurs at a suitably slow time scale and the interspecific interactions are well modelled by this assumption. We conclude the Results section with a few examples of how asymmetric habitat loss can shape the adaptive responses of the metapopulation, dependent upon the parameter investigated in the previous subsection.

It is a trivial matter to show that if there is more habitat removed of type 1 ($h < 1$), then $\left.\frac{\partial \Delta}{\partial t'}\right|_{t'=t=0} > 0$ and thus a generalist can be invaded locally by phenotypic variants that favour the more abundant type 2 patches. In this case, a CS singular strategy that is relatively more specialized to type 2 patches ($t_2^* > 0$) must exist. Singular strategies, however, can still exist that favour type 1 patches ($t_1^* < 0$), as illustrated in Fig. 6 for certain ranges of parameter values.

The potential for evolutionary branching can increase or decrease following habitat reduction. Habitat loss, reducing either R_0 or h, can only result in a type 2 CS specialist making a non-ES to ES transition, and hence a loss branching. However, as shown in all three plots of Fig. 6, it is possible for a type 1 CS specialist to go from ES to non-ES. This happens for an intermediate range of R_0 (Fig. 6a) and upper ranges of q (Fig. 6b) and τ (Fig. 6c). This occurs when the type 1 CS specialist is lost through a saddle node bifurcation in the parameter h. If h_c is the critical value of h such that two CS strategies exist exclusively for $h > h_c$, then the geometric nature of this bifurcation means that there must exist a neighbourhood (h_c, h') where the type 1 CS specialist is non-ES and hence a branching strategy. We omit the proof which relies upon the continuity of the trade-off function. The range of h that leads to branching can be very slight for low values of q. In such a case,



(a) $q = 0.6$ and $\tau = 0.25$ (b) $\tau = 0.4$ and $R_0 = 5$ (c) $q = 0.8$ and $R_0 = 5$

Fig. 6. The classification of singular strategies when habitat loss is asymmetric ($h_1 < h_2$). The thin curve intersects region *I*, with one CS singular strategy ($t_1^* < 0$) present, and region *II*, with two CS singular strategies ($t_1^* < 0$ and $t_2^* > 0$). The two CS strategies in the striped region of plot (a) are separated in trait space by non-viable phenotypes. Within the dark shaded region both CS strategies are branching strategies, and in the pale shaded region only one is a branching strategy: t_1^* in region *I* and t_2^* in region *II*. No phenotypic variant is viable in the region outside of the thick curve.

reducing h by only a small amount could cause the singular resident metapopulation to make an adaptive switch from a type 1 to a type 2 specialist.

In Fig. 6b we see how decreasing the spatial aggregation parameter q can also lead to such a saddle node bifurcation. This suggests that increasing spatial aggregation can sometimes decrease biodiversity, if such diversity is to be obtained through evolutionary branching. The ecological reason for this is perhaps as follows: When q is small, the colonizers of type 1 patches have, more often than not, come from type 2 patches. The relative advantage that type 2 specialists have for persisting in type 2 patches is traded off against the disadvantage that type 2 specialist colonizers have in being less likely to find habitable patches. Increasing q will reduce this disadvantage for type 2 specialists and as a consequence the type 1 specialist is out-competed regionally.

Figure 6a shows an example of evolutionary trapping as described by Dieckmann and Ferrière (2004, Chapter 11). If, following habitat loss, parameters cross the upper boundary of region *II*, the type 1 CS specialist becomes non-viable following the non-CS singular strategy. If, before an episode of habitat reduction, evolution resulted in the type 1 evolutionary unbeatable CS specialist, further habitat reduction may lead to extinction of the species despite some phenotypic strain, including the type 2 CS specialist, remaining viable.

DISCUSSION

In this paper, we investigated how simple landscape structures can play a role in the ecological and evolutionary dynamics of metapopulations. We consider a landscape consisting of two elementary landscape types, building upon the structures considered by Brachet *et al.* (1999) and Parvinen and Egas (2004), and including a notion of spatial aggregation of same-type patches. We studied the evolution of patch specialization and evolutionary branching, as have Kisdi (2002) and Parvinen and Egas (2004), as a response to trade-off strength, habitat abundance, and basic dispersal rate.

Extreme specialism (maximizing preference for a particular patch type) can never actually occur, but specialists can evolve that are arbitrarily close. For landscapes equally represented by both patch types and with uniform patch destruction, we found that increasing the spatial aggregation of same-type patches increases the degree of specialization. Removing habitat and decreasing the trade-off strength has a similar effect, as demonstrated by Kisdi (2002) and Parvinen and Egas (2004).

The explanation is intuitive for the patch aggregation and trade-off cases. Aggregating same-type patches means that dispersers are more likely to find patches that are identical to their natal patch. It will therefore pay for the establishing population to be marginally adapted to the same patch. Weakening the trade-off strength will mean that the cost of becoming maladapted to one patch type is relatively small compared with the benefits of specializing to the other type. The evolution of specialists drives the spatial aggregation of the metapopulation, resulting in asymmetric patch usage that may further promote specialization.

For the case of habitat loss, the causal link is perhaps less obvious. Removing patches will lower the success of dispersers with the success of a strategy being increasingly based upon local population survival rather than colonization ability. Specialists may then be selected because the benefits of minimal extinction rates outweigh the reduction in risk-spreading ability, already restricted with landscape change. Spatial aggregation may be sufficient, but is not necessary for specialization. Parameter instances can be found that drive specialization for negatively correlated landscape arrangements. No single parameter alone dictates the evolution of specialization.

Evolutionary branching, a necessary requirement for adaptive speciation in sexual systems, is influenced by the same factors that are responsible for specialization. The evolutionary classification of the generalist strategy in the model hints at causes for adaptive speciation. The classic transitions of a generalist singular strategy from evolutionary unbeatable to evolutionary branching and then to evolutionary repelling were shown to be driven by the three processes referred to above. This strict transitional order, however, need not be preserved when habitat is removed uniformly from both habitat types, as it is possible for a non-ES generalist to go from being evolutionary repelling to evolutionary branching and then back to repelling when habitat is removed uniformly.

Evolutionary branching is a surprising consequence of habit destruction and our results suggest that it is perhaps more common when the destruction targets one particular patch type. The usual assumption that habitat loss should cause a reduction in biodiversity is erroneous and caution must be taken in using regional biodiversity as a measure of landscape suitability or metapopulation viability.

The results also suggest that the evolutionary properties of singular specialists can also be unpredictable. Increasing the level of spatial aggregation in the landscape could convert evolutionary branching singular specialist to evolutionary unbeatable and then back to evolutionary branching. Determining whether adaptive speciation via evolutionary branching is possible for a particular landscape configuration may be difficult.

When the landscape was symmetric, an evolutionary unbeatable singular dimorphic coalition existed whenever the singular generalist was non-ES. The degree of specialism of each member of the dimorphic singular coalition was shown to increase with landscape aggregation and decrease with trade-off strength; the explanation applied to the monomorphic case still holding.

It was shown that increasing the aggregation of same-type patches across the landscape could, in some cases, lead to a reduction in CS monomorphic singular strategies and eliminate branching strategies. This result goes against what intuition may suggest are the consequences of increased aggregation in a symmetric landscape. The inclusion of spatial aggregation in this model breaks down the uniform dispersal assumption, often employed to simplify the dynamics of the metapopulation.

To include spatial aggregation of habitat in an analytically tractable model, we made the simplifying assumption that there was no within-patch competition between different strains. In reality, colonizers will sometimes invade populations comprised of different phenotypic strains, either deterministically because of competitive advantage, or stochastically due to small local populations. Structured metapopulation models have been devised to address this issue (Gyllenberg and Metz, 2001; Parvinen and Egas, 2004), but in doing so simplified the dispersal processes that we wished to include. Many of the results here are evident in structured models and it is certainly plausible that including spatial aggregation would have similar effects if incorporated into models that respect within-patch competition. Questions regarding the evolution of dispersal would also benefit from such a treatment of landscape structure. Dispersal is not always such a passive process and dispersal behaviours that take advantage of particular landscape structures may be expected to evolve. A deep investigation into random dispersal in structured metapopulations would be a valuable and necessary endeavour in the understanding of the ecology and evolution of metapopulation as a consequence of, and an influence upon, dispersal in heterogeneous fragmented habitats.

ACKNOWLEDGEMENTS

P.H. wishes to thank Éva Kisdi for her help during early drafts of the manuscript, and Michael Doebeli for valuable comments. This work was funded by the EPSRC.

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APPENDIX 1: STABILITY OF THE MONOMORPHIC STEADY STATES

The stability of the steady states $(\hat{x}_1, \hat{x}_2)$ of the monomorphic system (5) and (6) is determined by the Jacobian matrix

$$J_R(\hat{x}_1, \hat{x}_2) = \begin{pmatrix} (c_{11}(h_1\rho_1 - 2\hat{x}_1) - c_{21}\hat{x}_2 - e_1 & c_{21}(h_1\rho_1 - \hat{x}_1) \\ c_{12}(h_2\rho_2 - \hat{x}_2) & c_{22}(h_2\rho_2 - 2\hat{x}_2) - c_{12}\hat{x}_1 - e_2 \end{pmatrix}, \tag{A1}$$

with trace and determinant given by

$$trJ_R(\hat{x}_1, \hat{x}_2) = c_{11}(h_1\rho_1 - 2\hat{x}_1) + c_{22}(h_2\rho_2 - 2\hat{x}_2) - c_{12}\hat{x}_1 - c_{21}\hat{x}_2 - e_1 - e_2, \tag{A2}$$

$$detJ_R(\hat{x}_1, \hat{x}_2) = (c_{11}(h_1\rho_1 - 2\hat{x}_1) - c_{21}\hat{x}_2 - \mathrm{e}_1)\,(c_{22}(h_2\rho_2 - 2\hat{x}_2) - c_{12}\hat{x}_1 - e_2) - (c_{21}(h_1\rho_1 - \hat{x}_1))\,(c_{12}(h_2\rho_2 - \hat{x}_2)). \tag{A3}$$

The Routh-Hurwitz criteria states that $(\hat{x}_1, \hat{x}_2)$ is stable if and only if $trJ_R < 0$ and $det\ J_R > 0$. Defining $R_0^i = h_i\rho_i/e_i \geq 0$, at the origin (0, 0) these conditions reduce to

$$trJ_R(0, 0) = e_1(c_{11}R_0^1 - 1) + e_2(c_{22}R_0^2 - 1) < 0, \tag{A4}$$

$$detJ_R(0, 0) = (c_{11}R_0^1 - 1)\,(c_{22}R_0^2 - 1) - c_{12}c_{21}\,R_0^1R_0^2, \tag{A5}$$

and it is easy to see that for stability we require both $c_{11}R_0^1 - 1 < 0$ and $c_{22}R_0^2 - 1 < 0$ and the determinant condition (A5).

APPENDIX 2: CONDITION FOR MUTANT INVASION

Mutant invasion is determined by the linear stability of the system given by equation (17). Linearizing about $(\hat{x}_1, \hat{x}_2, 0{,}0)$ we obtain

$$J = \begin{pmatrix} J_R & \bigstar \\ 0 & J_M \end{pmatrix}, \tag{A6}$$

where J_R is as defined in Appendix 1, $\bigstar$ represents a 2×2 matrix with inconsequential entries, and

$$J_M = \begin{pmatrix} c_{11}(h_1\rho_1 - \hat{x}_1) - e'_1 & c_{21}(h_1\rho_1 - \hat{x}_1) \\ c_{12}(h_2\rho_2 - \hat{x}_2) & c_{22}(h_2\rho_2 - \hat{x}_2) - e'_2 \end{pmatrix}, \tag{A7}$$

with trace and determinant given by

$$trJ_M(e'_1, e'_2, e_1, e_2) = c_{11}(h_1\rho_1 - \hat{x}_1) - e'_1 + c_{22}(h_2\rho_2 - \hat{x}_2) - e'_2, \tag{A8}$$

$$\begin{aligned} detJ_M(e'_1, e'_2, e_1, e_2) = {} & e'_1e'_2 - e'_1c_{22}(h_2\rho_2 - \hat{x}_2) - e'_2c_{11}(h_1\rho_1 - \hat{x}_1) \\ & + (c_{11}c_{22} - c_{12}c_{21})(h_1\rho_1 - \hat{x}_1)(h_2\rho_2 - \hat{x}_2). \end{aligned} \tag{A9}$$

Using the Routh-Hurwitz criteria, we deduce that a mutant phenotype cannot invade if $trJ_M \leq 0$ and $detJ_M \geq 0$. Using the monomorphic steady-state condition that

$$h_i\rho_i - \hat{x}_i = \frac{e_i\hat{x}_i}{c_{ii}\hat{x}_i + c_{ji}\hat{x}_j},$$

$j \neq i$, then

$$trJ_M = \frac{(e_1 - e'_1)c_{11}\hat{x}_1 - e'_1c_{21}\hat{x}_2}{c_{11}\hat{x}_1 + c_{21}\hat{x}_2} + \frac{(e_2 - e'_2)c_{22}\hat{x}_2 - e'_2c_{12}\hat{x}_1}{c_{12}\hat{x}_1 + c_{22}\hat{x}_2}, \tag{A10}$$

and

$$\begin{aligned} det\,J_M &= e'_1e'_2 - \frac{e'_1e_2c_{22}\hat{x}_2}{c_{12}\hat{x}_1 + c_{22}\hat{x}_2} - \frac{e'_2e_1c_{11}\hat{x}_1}{c_{11}\hat{x}_1 + c_{21}\hat{x}_2} + \frac{e_1e_2(c_{11}c_{22} - c_{12}c_{21})\hat{x}_1\hat{x}_2}{(c_{11}\hat{x}_1 + c_{21}\hat{x}_2)(c_{12}\hat{x}_1 + c_{22}\hat{x}_2)} \\ &= \frac{(e'_1e'_2 - e_1e'_2)c_{11}\hat{x}_1}{c_{11}\hat{x}_1 + c_{21}\hat{x}_2} + \frac{(e'_1e'_2 - e'_1e_2)c_{22}\hat{x}_2}{c_{12}\hat{x}_1 + c_{22}\hat{x}_2} + \frac{(e_1e_2 - e'_1e'_2)(c_{11}c_{22} - c_{12}c_{21})\hat{x}_1\hat{x}_2}{(c_{11}\hat{x}_1 + c_{21}\hat{x}_2)(c_{12}\hat{x}_1 + c_{22}\hat{x}_2)}. \end{aligned} \tag{A11}$$

Note that if $e'_1 = e_1$ and $e'_2 = e_2$, then $detJ_M = 0$ and $trJ_M < 0$ and so a mutant that is identical to the resident has neutral invasion potential. Since $trJ_M < 0$ when $e'_1 = e_1$ and $e'_2 = e_2$, continuity ensures that $trJ_M(e'_1, e'_2, e_1, e_2) < 0$ when the mutant is sufficiently similar to the resident, and in this case invasion will be dependent upon $detJ_M(e'_1, e'_2, e_1, e_2)$ only.

APPENDIX 3: EVOLUTIONARY CLASSIFICATION OF THE SINGULAR GENERALIST STRATEGY

The ES condition for a singular generalist

When $h_1 = h_2 = 1$, the condition for the singular generalist strategy ($e_1 = e_2 = e_G$) to be ES is

$$f''(e_G) > \frac{2\rho_1}{\rho_2(1-q)e_G}. \tag{A12}$$

Proof. The resident generalist satisfies

$$\hat{x}_1(e_G) = \rho_i(1 - e_G) \tag{A13}$$

when $h_1 = h_2 = 1$, and therefore $\hat{X}_G = \hat{X}(e_G) = \rho_1/\rho_2$. The ES condition (23) then reduces to

$$f''(e_G) > \frac{2\rho_1}{\rho_2(1-q)e_G},$$

as required.

The CS condition for a singular generalist

When $h_1 = h_2 = 1$, the condition for the singular generalist strategy ($e_1 = e_2 = e_G$) to be CS is

$$f''(e_G) > \frac{\rho_1(1+e_G)}{\rho_2((\rho_1 - q)e_G + \rho_2)e_G}. \tag{A14}$$

Proof. For a singular strategy to be CS we require

$$f''(e^*) > \frac{f(e^*)(c_{11}X^* + c_{21})}{e(c_{12}X^* + c_{22})}\left(\frac{X^*(c_{11}X^{*2} + 2c_{12}X^* + c_{22})}{e^*(c_{12}X^* + c_{22})} - \left(\frac{c_{11}X^*}{c_{11}X^* + c_{21}} + \frac{c_{22}}{c_{12}X^* + c_{22}}\right)\frac{\mathrm{d}\hat{X}(e^*)}{\mathrm{d}e}\right).$$

Now $\hat{X}(e_G) = \rho_1/\rho_2$ following from equation (A13), and a singular generalist satisfies $f'_G = -\rho_1/\rho_2$, and so the CS condition for the generalist is

$$f''(e_G) > \frac{\rho_1}{\rho_2^2 e_G} + \frac{(\rho_1 - \rho_2 - q)}{\rho_2}\frac{\mathrm{d}\hat{X}(e_G)}{\mathrm{d}e}. \tag{A15}$$

Now $\mathrm{d}\hat{X}(e_G)/\mathrm{d}e$ can be derived as follows: The steady-state equations

$$\hat{x}_1 = h_1\rho_1 - \frac{e_1\hat{X}}{c_{11}\hat{X} + c_{21}},$$

and

$$\hat{x}_2 = h_2\rho_2 - \frac{e_2}{c_{12}\hat{X} + c_{22}},$$

are combined and rearranged to get

$$c_{11}c_{12}h_2\rho_2\hat{X}^3 + (c_{12}e_1 - c_{11}e_2 - c_{11}c_{12}h_1\rho_1 + (c_{11}c_{22} + c_{12}c_{21})h_2\rho_2)\hat{X}^2$$

$$(c_{22}e_1 - c_{21}e_2 - (c_{11}c_{22} + c_{12}c_{21})h_1\rho_1 + c_{21}c_{22}h_2\rho_2)\hat{X} - c_{12}c_{22}h_1\rho_1 = 0. \quad \text{(A16)}$$

This expression can be differentiated and evaluating at $e_1 = e_2 = e_G$ with $h_1 = h_2 = 1$ to get

$$\frac{\mathrm{d}\hat{X}(e_G)}{\mathrm{d}e} = -\frac{\rho_1}{\rho_2((\rho_1 - q)e_G + \rho_2)}. \quad \text{(A17)}$$

Then, substituting this into equation (A15), we have

$$f''(e_G) > \frac{\rho_1(1 + e_G)}{\rho_2((\rho_1 - q)e_G + \rho_2)e_G}.$$

APPENDIX 4: THE SYMMETRIC SINGULAR DIMORPHISM FOR A SYMMETRIC TRADE-OFF AND LANDSCAPE

With three competing phenotypes the dynamics are

$$\frac{\mathrm{d}x_1^1}{\mathrm{d}t} = (c_{11}x_1^1 + c_{21}x_2^1)(h_1\rho_1 - x_1^1 - x_1^2 - x_1') - e_1^1x_1^1, \quad \text{(A18)}$$

$$\frac{\mathrm{d}x_2^1}{\mathrm{d}t} = (c_{12}x_1^1 + c_{22}x_2^1)(h_2\rho_2 - x_2^1 - x_2^2 - x_2') - e_2^1x_2^1, \quad \text{(A19)}$$

$$\frac{\mathrm{d}x_1^2}{\mathrm{d}t} = (c_{11}x_1^2 + c_{21}x_2^2)(h_1\rho_1 - x_1^1 - x_1^2 - x_1') - e_1^2x_1^2, \quad \text{(A20)}$$

$$\frac{\mathrm{d}x_2^2}{\mathrm{d}t} = (c_{12}x_1^2 + c_{22}x_2^2)(h_2\rho_2 - x_2^1 - x_2^2 - x_2') - e_2^2x_2^2, \quad \text{(A21)}$$

$$\frac{\mathrm{d}x_1'}{\mathrm{d}t} = (c_{11}x_1' + c_{21}x_2')(h_1\rho_1 - x_1^1 - x_1^2 - x_1') - e_1'x_1', \quad \text{(A22)}$$

$$\frac{\mathrm{d}x_2'}{\mathrm{d}t} = (c_{12}x_1' + c_{22}x_2')(h_2\rho_2 - x_2^1 - x_2^2 - x_2') - e_2'x_2'. \quad \text{(A23)}$$

As with the case for a single resident, the mutant fitness is determined by the leading eigenvalue of the 2 × 2 Jacobian matrix

$$J_M = \begin{pmatrix} c_{11}(h_1\rho_1 - \hat{x}_1^1 - \hat{x}_1^2) - e_1' & c_{21}(h_1\rho_1 - \hat{x}_1^1 - \hat{x}_1^2) \\ c_{12}(h_2\rho_2 - \hat{x}_2^1 - \hat{x}_2^2) & c_{22}(h_2\rho_2 - \hat{x}_2^1 - \hat{x}_2^2 - e_2' \end{pmatrix}.$$

The sign of the determinant will determine the sign of the leading eigenvalue. Defining $X^1 = \hat{x}_1^1/\hat{x}_2^1$, a rearrangement of the first two equations of (A23) at steady state, when the mutant is absent, gives

$$h_1\rho_1 - \hat{x}_1^1 - \hat{x}_1^2 = \frac{e_1^1 X^1}{c_{11}X^1 + c_{21}}, \tag{A24}$$

$$h_2\rho_2 - \hat{x}_2^1 - \hat{x}_2^2 = \frac{e_2^1}{c_{12}X^1 + c_{22}}, \tag{A25}$$

then

$$\Delta(e'_1, e_1^1, e_1^2) := -\,detJ_M = \frac{e'_1 e_2^1 c_{22}}{c_{12}X^1 + c_{22}} + \frac{e'_2 e_1^1 c_{11}X^1}{c_{11}X^1 + c_{21}} - e'_1 e'_2 + \frac{e_1^1 e_2^1 (c_{12}c_{21} - c_{11}c_{22})X^1}{(c_{11}X^1 + c_{21})(c_{12}X^1 + c_{22})}. \tag{A26}$$

With a trade-off, the dimorphic residents are defined by the extinction rates in the first patch, (e_1^1, e_1^2).

(e_1^1, e_1^2) represents a singular coalition if

$$\left.\frac{\partial\Delta}{\partial e'_1}\right|_{e' = e_1^1} = \left.\frac{\partial\Delta}{\partial e'_1}\right|_{e' = e_1^2} = 0. \tag{A27}$$

Claim 1. Suppose $\rho = 0.5$, $h_1 = h_2 = 1$, and the trade-off function f is symmetric. The condition on f for the symmetric dimorphic resident strategy $((e_1^1, e_2^1) = e_1^1, f(e_1^1))$, $e_1^1, > e_G$, to be a singular coalition is:

$$f'(e_1^1) = -X^{1^2}, \tag{A28}$$

where

$$X^1 = \frac{qf(e_1^1)}{2(1-q)e_1^1}\left(1 - \frac{e_1^1}{f(e_1^1)} + \sqrt{\left(1 - \frac{e_1^1}{f(e_1^1)}\right)^2 + \frac{4(1-q)^2 e_1^1}{q^2 f(e_1^1)}}\right). \tag{A29}$$

Proof. Symmetry in the trade-off will impose that at a symmetric singular dimorphism

$$e_1^2 = e_2^1 = f(e_1^1), \tag{A30}$$

$$e_2^2 = f(e_1^2) = e_1^1. \tag{A31}$$

With the symmetry in the landscape as well the symmetric singular dimorphism will satisfy

$$\hat{x}_2^2 = \hat{x}_1^1, \tag{A32}$$

$$\hat{x}_1^2 = \hat{x}_2^1. \tag{A33}$$

Differentiating the expression equation (A26) gives and dropping the redundant superscript ^{1} we get

$$\left.\frac{\partial\Delta}{\partial e'}\right|_{e' = e_1} = \frac{f(e_1)c_{22}}{c_{12}X^1 + c_{22}} + \frac{f'(e_1)e_1c_{11}X^1}{c_{11}X^1 + c_{21}} - f(e_1) + e_1 f'(e_1). \tag{A34}$$

At the singular dimorphism, this is equal to zero and a rearrangement gives

$$f'(e_1) = -\frac{f(e_1)c_{12}X^1(c_{11}X^1 + c_{21})}{e_1c_{21}(c_{12}X^1 + c_{22})}. \tag{A35}$$

Note that rearranging (A24) and (A25) at steady state and applying conditions from (A31) and (A33) yields

$$\frac{e_1 X^1}{c_{11}X^1 + c_{21}} = \frac{f(e_1)}{c_{21}X^1 + c_{11}}, \tag{A36}$$

or, equivalently,

$$\frac{f(e_1)(c_{11}X^1 + c_{21})}{e_1(c_{21}X^1 + c_{11})} = X^1. \tag{A37}$$

Symmetry in the landscape means that $c_{11} = c_{22} = 2q$ and $c_{12} = c_{21} = 2(1-q)$, then (A37) yields

$$f'(e_1) = -{X^1}^2, \tag{A38}$$

and also that

$$\frac{e_1}{e_2}\,{X^1}^2 + \frac{q}{1-q}\left(\frac{e_1}{e_2} - 1\right)X^1 - 1 = 0. \tag{A39}$$

Since we have assumed $e_1 > f(e_1)$, we have

$$X^1 = \frac{qf(e_1)}{2(1-q)e_1}\left(1 - \frac{e_1}{f(e_1)} + \sqrt{\left(1 - \frac{e_1}{f(e_1)}\right)^2 + \frac{4(1-q)^2 e_1}{q^2 f(e_1)}}\right). \tag{A40}$$

The condition is thus explicitly given in terms of the resident's metapopulation extinction rates. For (e_1, e_2) to be singular we also require that $\left.\frac{\partial \Delta}{\partial e'}\right|_{e' = e_2} = 0$, but this is already satisfied when $\left.\frac{\partial \Delta}{\partial e'}\right|_{e' = e_1} = 0$, again because of the symmetries in the problem.

APPENDIX 5: THE ES CONDITION FOR A SYMMETRIC SINGULAR DIMORPHISM WHEN THE LANDSCAPE AND TRADE-OFF ARE SYMMETRIC

Claim 2. A symmetric singular dimorphism $(e_1(t^*), e_1(-t^*))$ is ES when the trade-off and landscape are symmetric if

$$f''(e_1(t^*)) > \frac{2{X^1}^2}{e_1(t^*)}\left(\frac{qX^1}{(1-q)} + 1\right), \tag{A41}$$

X^1 defined by equation (A40).

Proof. Symmetry in the landscape and the trade-off dictates that

$$\Delta(e(-t'), e(-t^1), e(-t^2)) = \Delta(e(t'), e(t^1), e(t^2)),$$

where Δ is given in (A26). From this we deduce, since $\Delta(e(t'), e(t^1), e(t^2)) = \Delta(e(t'), e(t^2), e(t^1))$, that

$$-\frac{\mathrm{d}e(-t)}{\mathrm{d}t}\,\frac{\partial\Delta}{\partial e'_1}(e(-t), e(t), e(-t)) = \frac{\mathrm{d}e(t)}{\mathrm{d}t}\,\frac{\partial\Delta}{\partial e'}(e(t), e(t), e(-t))$$

and

$$\left(\frac{\mathrm{d}e(-t)}{\mathrm{d}t}\right)^2\frac{\partial^2\Delta}{\partial {e'}_1^2}(e(-t), e(t), e(-t)) - \frac{\mathrm{d}^2e(-t)}{\mathrm{d}t^2}\,\frac{\partial\Delta}{\partial e'_1}(e(-t), e(t), e(-t)) =$$
$$\left(\frac{\mathrm{d}e(t)}{\mathrm{d}t}\right)^2\frac{\partial^2\Delta}{\partial e'^2}(e(t), e(t), e(-t)) + \frac{\mathrm{d}^2e(t)}{\mathrm{d}t^2}\,\frac{\partial\Delta}{\partial e'}(e(t), e(t), e(-t)), \qquad \text{(A42)}$$

which at a singular coalition reduces to

$$\frac{\partial^2\Delta}{\partial {e'}_1^2}(e(-t), e(t), e(-t)) = \frac{1}{f'(e(t))^2}\,\frac{\partial^2\Delta}{\partial {e'}_1^2}(e(t), e(t), e(-t)).$$

Then the ES condition (38) is equivalent to

$$\frac{\partial^2\Delta}{\partial {e'}_1^2}(e_1(t^*), e_1(t^*), e_1(-t^*)) < 0,$$

which in terms of the trade-off function can be written as

$$f''(e_1(t^*)) > -\frac{2f'(e_1(t^*))}{e_1(t^*)}\left(\frac{qX^1}{1-q}+1\right), \qquad \text{(A43)}$$

X^1 defined by equation (A40). The singular strategy condition (36) reduces this to

$$f''(e_1(t^*)) > \frac{2{X^1}^2}{e_1(t^*)}\left(\frac{qX^1}{1-q}+1\right). \qquad \text{(A44)}$$