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Ecological and evolutionary responses to landscape structure

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Ecological and Evolutionary Responses to Landscape Structure

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Summary

The aim of this thesis is to investigate the ecological and environmental dynamics of species that inhabit fragmented environments, using mathematical techniques that yield transparent predictions regarding the effects of habitat change.

Chapter 1 outlines the general problem and introduces some of the theoretical frameworks, in particular metapopulation theory, that have been developed to study fragmented ecosystems. The importance of studying evolutionary processes in conservation biology is discussed.

In chapter 2 mathematical techniques that have been used to model metapopulation dynamics are reviewed. The consequences of modelling space implicitly is investigated by comparing results with those from spatially explicit counterparts.

In chapter 3 a model of a single–species metapopulation inhabiting a landscape with heterogeneous patch structure is developed. The long–term ecological dynamics of the model are investigated and related to metapopulation persistence and viability. The model is then extended to include spatially limited dispersal.

In chapter 4 the ecological model is extended to investigate multi–species competition. Conditions for invasion and coexistence are derived and related to landscape structures. The limits of species diversity by competition is also discussed.

Chapters 5, 6 and 7 investigate the evolutionary dynamics of the model using an adaptive dynamics approach. In chapter 5 a limiting case is considered where some evolutionary properties of the single–species system can be derived analytically. Evolutionary branching (an ecological prerequisite for adaptive speciation) is defined and conditions for it to occur are discussed in terms of landscape structure. In chapter 6 both the evolution of habitat specialism and the evolution of dimorphic systems are investigated. In chapter 7 competitive interactions within habit patches are modelled and the consequences for single–species evolution is investigate.

Contents

Chapter 1

Introduction

Overview of Problem

Landscape structure has a major impact upon the ecology of inhabiting communities, the demography of a focal species and the genetic diversity of individuals. Predicting the impact that landscape change will have upon ecosystems 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 chronology of events spanning large time scales, and any change to the abiotic environment will upset the 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 among the conservationist's concern perhaps measures should be equally reserved for the protection of aspects that support 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*a*). 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.

1.1 Landscape Structure Induced by Habitat Loss

Landscape structure is one of the most important factors that determines the distribution and abundance of a species. It mediates the ecological interactions within and between species, setting the stage for the judgment of a species life–history characteristics (Gyllenberg et al. 2004). The homes of most species no longer comprise of expansive regions (although for some this was never the case), largely due the widespread deterioration of habitat attributed mainly to the progress of mankind. For example, around half of the world's original forests have disappeared and are still being destroyed (because of agricultural development; intensive harvesting of timber, wood for fuel and other forest products; overgrazing etc) at a rate that far exceeds any possible regrowth (as reported by the WWF). Alarmingly, forests (especially in equatorial zones) harbor much of the diversity found in the planets land–based species. A catastrophe on an equivalent scale is happening in marine ecosystems.

The effect of habitat loss is not only to reduce the total capacity of a landscape to support its inhabitants, but also to change the spatial distribution of the habitat that has further consequences for the remaining inhabitants (Forman 1995). These patterns generally include, after successive levels of loss:

- *Habitat perforation* as small areas of unsuitable habitat begin to punctuate a landscape.
- *Habitat fragmentation* when regions of suitable habitat become separated by the growing 'matrix' of unsuitable habitat. This results in the formation of a patchy landscape.
- *Patch shrinkage.*
- *Patch attrition* as the edges of patches become 'rounded off'.

Figure 1.1 stylizes this process.

The two major landscape factors that are believed to mediate ecological dynamics in fragmented enviroments are:

1. Patch structure (size, shape, quality etc).
2. Patch connectivity (i.e average distance to other patches).

The discipline of landscape ecology (Ingegnoli 2002) is concerned with classifying how landscapes are structured and how this structure evolves. The basic elements of the

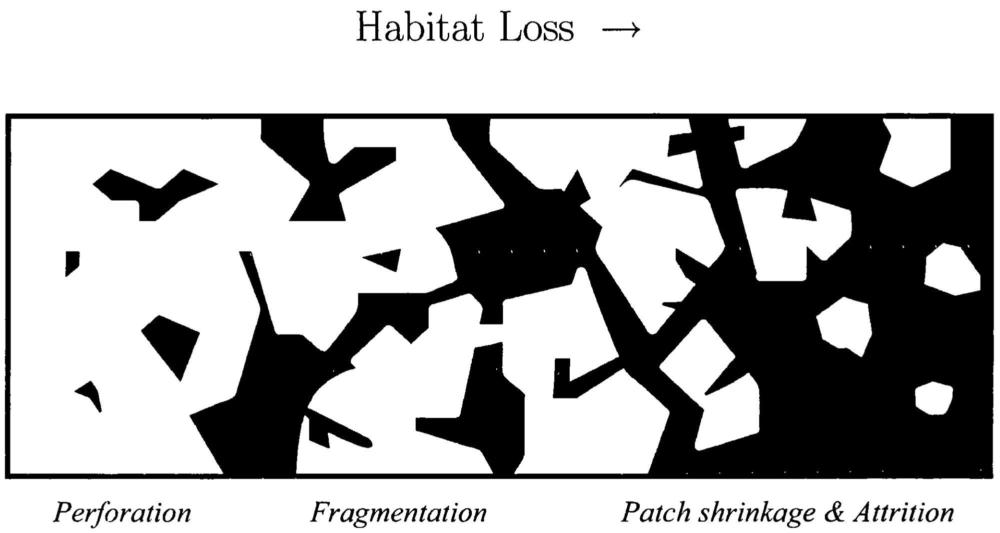


Figure 1-1: A caricature of how habitat loss can alter the spatial distribution of habitat.

landscape (Forman & Godron 1981) are generically identified as patches (that support local populations) and corridors (connecting patches). A central theme in landscape ecology is landscape connectivity, defined as the degree to which habitat distribution facilitates movement across the landscape (With et al. 1997). Once a landscape has fragmented into a patchy structure, further habitat loss will increase the isolation of patches, reducing connectivity. There is no unique way of quantifying the level of landscape connectivity since it relies on how the inhabitants interact with the patchy structure (With 2004) (see below). When landscapes are highly fragmented, measures are often patch based, relating the size and proximity of neighbouring patches.

1.2 Ecology Driven by Landscape Structure

The traditional approach in population ecology is to assume that the individuals of interest all share the same environment and that they interact equally among each other - populations are *panmictic*. These may be sensible assumptions when the spatial scale containing the population is small, minimizing both the distance between individuals, and the potential for habitat variation in the landscape. When we are interested in ecological systems that extend over large spatial scales, these assumptions will become unrealistic. Spatial ecology has developed to capture the spatial processes that affect population regulation (Tilman & Kareiva 1997).

Respecting spatial elements important when extensive and large–scale habitat fragmentation forces panmictic (well mixed) populations to subdivide, so that the interactions between individuals become restricted. Population subdivision is thought to play an important role in many processes including: the extinction or persistence of species; the size of viable populations; how communities of competing species (e.g. predators and prey) interact; the genetic differentiation among individuals; the spread of disease etc.

Variation in landscape structure is an obvious factor that effects spatial population structure but it is not a necessary requirement: localized interactions can be a consequence of other factors i.e. inherent restrictions on mobility in plants species, territorial animals, etc. The formation of spatial population structure in homogeneous landscapes has been illustrated with reaction–diffusion models (Britton 1986), individual–based models (Durrett & Levin 1994), etc. For a review see (Dieckmann et al. 2000).

It is important (especially in the context of investigating habitat loss) to try and decouple landscape structure from other factors that limit individual interactions, regulating spatial population dynamics.

1.3 The Metapopulation Paradigm

For a conservation perspective, models can be derived to estimate how prone a population is to extinction. When populations are small extinction risk can be great (i.e. through demographic stochasticity, inbreeding depressions, the existence of Allee effects, etc (Gabriel & Ferrière 2004)). If habitats are fragmented into small isolated patches, inhabiting populations will experience high extinction risks. Local extinctions will eventually cascade to regional–level extinction for any finite collection of extinction prone populations (Hanski 1999*a*). If patches are suitably isolated from each other a consideration of the regional configuration of the landscape is irrelevant and the expected time until regional extinction will only depend upon the distribution of extinction times in individual patches. However, patches may not be totally isolated if migration occurs between patches. Migration may prevent local extinction by boosting declining populations and also allow patches that are empty (following extinction) to become recolonized by dispersers. Regional extinction times will rely heavily upon regional configurations.

Such a collection of extinction-prone local populations, weakly connected by dispersal, has been dubbed a metapopulation (Levins 1969, Levins 1970). Metapopulation theory has become an important part of spatial ecology and a cornerstone of conservation theory due to the alarming fact that the spatial structure and dynamics of many species increasingly fit this description. Other approaches and theories that assume subpopulation structures or predict them as an emergent property (see above) abound the spatial ecology literature. One such theory is that of island biogeography, attributed to MacArthur & Wilson (1967). This theory is also concerned with patchy environments harbouring local populations. The theory attempts to explain the diversity found in small extinction–prone islands and archipelagos by assuming that diversity is sourced from a large mainland via migration. The the scenarios that support these assumption really form a subset of those that underpin metapopulation framework (Hanski 1999*a*), however a distinction has been made largely for historical reasons (the popularity of island biogeography overshadowed a slow maturing metapopulation theory that has only taken off in the last two decades).

1.4 Adaptation in Fragmented Landscapes

Since extinction and colonization are the driving forces of metapopulation dynamics it is crucial to understand the processes that affect them. Much of the attention naturally falls upon dispersal (Clobert et al. 2002). The positive benefits of dispersal, other than those outlined above, may also include: escaping imminent extinction, reducing kin competition, reducing inbreeding – each having an elevated effect when small populations become isolated. Negative consequences of dispersal are equally apparent when costs are associated with the failure to find and establish new local populations or the consequences of finding poor quality patches (i.e. in temporally constant environments (Hastings 1983)).

It is not only landscape structure that determines the efficiency of certain dispersal strategies; the ability of a species to select habitat, form viable populations and interact with other species given a certain dispersal behavior will also be factors. Life–history traits associated with dispersal, within-patch viability, etc, may be coupled with other traits that are not directly related to metapopulation dynamics. These couplings may be formed internally because of limits in a species' genetic and phenotypic architecture; or perhaps formed externally when different traits have conflicting consequences for population or metapopulation processes.

How life–history traits interact to determine success from the individual level to the metapopulation level is highly non–trivial and, furthermore, determining the evolution of such life–histories is a real challenge. Investigations require models that derive (meta)population dynamics mechanistically from the consideration of interactions at the individual level that are a direct consequence of life–history structure. This consideration of the individual within the population is of crucial importance when defining *invasion fitness* in metapopulations (Gyllenberg & Metz 2001). Determining invasion fitness tells us which life history strategies an invading individual require to have a positive probability of invading a metapopulation. Processes that bring ecological success to the metapopulation may actually penalize individuals who undertake them (e.g. dispersal may be hazardous whilst non-dispersers enjoy reduced local competition (Poethke & Hovestadt 2001, Poethke et al. 2003)).

Heterogeneity in 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 & Egas 2004). These elementary resources may have become segregated following habitat fragmentation. This can cause spatial variation in fitness if trait values that are optimal in one type of habitat patch type are suboptimal in another. This provokes the question 'What landscape conditions cause evolution to drive a species to specialize on a particular patch type?' and, furthermore, 'how will other life–history options (e.g. dispersal) mediate this process?' (Meszéna et al. 1997, Kisdi 2002, Parvinen & Egas 2004).

1.5 Adapting to Changing Environments

Conservation biology has largely been concerned with devising intervention strategies that *preserve* the current biotic state of an ecosystem (i.e. the diversity of species and the genetic diversity within species). The perspective is largely based on the principle that an ecosystem is the result of a long evolutionary history, intimately shaped by abiotic factors (i.e. non–living component of an ecosystem), and that abiotic or biotic change will, in all probability, leave the surviving members of the system disadvantaged. Conservation efforts usually focus on a limited subset of an ecosystem (often on species that have an aesthetic or emblematic appeal). Measures employed often have only short term success as the perturbed ecosystem is left in a state of disequilibrium, subsequently returning to previous state.

Ferrière et al. (2004*b*) argue that 'fostering ecological and evolutionary processes that are responsible for the generation and maintenance of biodiversity' may be more important trying to preserving current arrangements of an ecosystem. This position is supported by empirical research that shows that evolution can indeed occur on fast time–scales, resulting in the potential for adaptive responses to environmental change (Boag & Grant 1981, Losos et al. 387, Reznick et al. 2004, Hairston et al. 2005). Taking this alternative standpoint, it will be important to understand how quickly organisms can evolve and which features of a changing environment might drive selection. The processes of evolution is the key to the planets biodiversity. A key component of an *evolutionary conservation* approach should be predicting when landscape change might lead to an *increase* in diversity through natural selection (Dieckmann et al. 2004), or when evolution–driven extinction might occur (Parvinen 2005).

Chapter 2

Ecological Consequences of Habitat Loss: Insight From Simulations

2.1 Chapter Outline and Motivation

In this chapter we investigate how metapopulation processes that explicitly depend upon spatial structure are often crucially oversimplified in the implicitly–spatial classical models that comprise much of metapopulation theory. With an emphasis on the effects of spatially structured habitat destruction, we wish to show how explicitly spatial modelling can predict scenarios that have particular consequences for the persistence and viability of metapopulations. In particular we show how metapopulation recovery following dynamic habitat regeneration will in part depend upon spatial correlations between habitat patches.

The chapters that follow this one investigate the ecological and evolutionary consequences of habitat destruction for metapopulations. The modelling framework used is a generalization of the classic Levins model (Levins 1969, Levins 1970) chosen for the attractive property of analytic tractability, though at a cost that is exposed in this chapter.

2.2 Introduction

Much of metapopulation theory is based upon investigations of implicitly spatial models (Hanski 1999*a*) derived from the assumption that all habitat patches are equally connected, known as the mean–field assumption. This is equivalent to assuming that occupied patches produce dispersers that contribute to a hypothetical dispersal pool and that immigrants from this pool are distributed to patches chosen uniformly at random. Models of this kind have been useful for gaining insight into the consequences of averaged properties of landscapes. The classic model is the patch–occupancy model developed by Levins (1969) and generalized by Lande (1987) to incorporate a habitat loss parameter (see box 2.1).

The model in box 2.1 predicts that there is a threshold (Lande 1987, Bascompte & Sole 1996) amount of habitat $h_{crit} = \delta$, where $\delta = e/c$ is the extinction–colonization ratio, below which the metapopulation becomes extinct. This is illustrated in figure 2.2 and the celebrated result of the model: Local population extinctions only result in the global extinction of the metapopulation if the colonization process cannot compensate because of a shortage in habitat. The model also yields the useful observation, known as the Levins rule, that the fraction of empty yet habitable patches when a viable metapopulation is at equilibrium, $h - \hat{x}$, will equal δ. Since the parameter δ may be difficult to measure since it requires intimate knowledge of an organism's within-patch population dynamics as well as dispersal behaviour, this rule suggests that an alternative measurement at the metapopulation level can be used instead to ascertain the threshold value h_{crit}.

Box 2.1. **The Levins Metapopulation Model with Habitat Loss.**

The Levins model with habitat loss is a deterministic continuous–time ODE model that captures the basic extinction–colonization processes that drive metapopulation dynamics in an infinite landscape of habitable patches. The governing equation is of the form

$$\frac{dx}{dt} = cx(h - x) - ex \, . \tag{2.2.0.1}$$

Here x is the fraction of patches that are occupied and h is the fraction of patches that are habitable. Occupied patches go extinct at a rate e and empty and habitable patches become colonized at a rate cx.

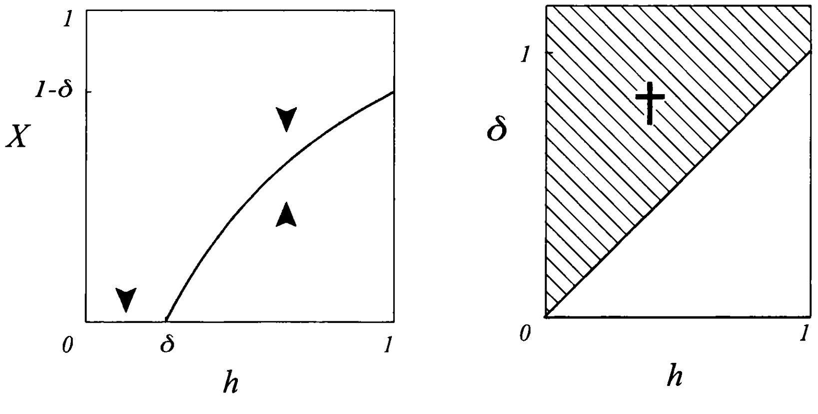
As well as simplifications in spatial structures there is also the assumption that all occupied patches are equal and thus explicit population dynamics within patches are ignored. This assumption incorporates the idea that the time scale of local population dynamics is much faster than that which governs extinction and colonization events, decoupling the population and metapopulation dynamics.

The long term dynamics of this simple system can be characterised by the *steady states*: Solving the steady state equation $\frac{dx}{dt} = 0$ yields two equilibrium metapopulation densities. The first is the extinction state $\hat{x} = 0$ (a necessary requirement of all *closed* ecological model). The second is

$$\hat{x} = h - \delta \, , \tag{2.2.0.2}$$

where the demographic parameter $\delta = \frac{e}{c}$. This is an ecologically realistic steady state only if $h > \delta$. It is trivial to show that the the extinction state is unstable if and only if the realistic non–trivial steady state exists, representing a viable metapopulation (see box 3.1 of chapter 3).

Thresholds are common in many population–based models. In epidemiology, the SIS model (named after the susceptible→infected→susceptible transition) with host immunity predicts that only a fraction of a population exposed to a disease need be vaccinated in order to prevent spread (Anderson & May 1991). The model actually shares the same structure as the Levins model but with an alternative description: Patches are equivalent to individuals of the host species, occupied patches are equivalent



(a) (b)

Figure 2-1: Predictions from the Levins model. Plot (a): How the fraction of habitable patches that are populated, $X = \hat{x}/h$, depends upon the fraction of habitat, h, and the extinction–colonization ratio δ. Arrows point towards the asymptotically stable steady states. Plot (b): The Levins model predicts that a metapopulation cannot persist if $h \leq \delta$ (as satisfied in the hatched region).

to infected hosts and the the spread rate of the disease and recovery rate of infected hosts are analogous to the colonization and extinction rates of the metapopulation. The threshold parameter is the fraction of vaccinated hosts and equivalent to the fraction of uninhabitable patches.

Although the Levins model predicts that there is a threshold amount of habitat required for a viable metapopulation (as do many other models eg. (Keymer et al. 2000)) we shall now argue that the predicted value of this threshold is not always robust when spatial factors are taken into consideration.

2.3 Explicitly Spatial Metapopulation Models

It is natural to hypothesise that the spatial location of patches and the spatial distribution of those that are occupied, can have significant consequences for metapopulation dynamics (Durrett & Levin 1994, Tilman & Kareiva 1997, Dieckmann et al. 2000). The colonization and extinction processes that drive metapopulation dynamics will depend upon the occupation state and the spatial location of all habitat patches within the landscape. The colonization process depends upon propagule production in occupied patches and how they then disperse to and colonize empty patches.

Hanski (1994*b*) distinguishes between models that incorporate realistic spatial structure and those that do not. Spatially realistic models include the spatially realistic Levins model (SRLM) (Ovaskainen & Hanski 2004) and the incidence function model (IFM) (Hanski 1994*a*), both formulated so that individual patches are parameterized according to spatial location and spatial extent, potentially according to those of a real patch network. Briefly, the SRLM model is a Markov process that models a finite collection of N patches that are either occupied or not. The rate at which an empty patch, indexed i, become colonized is,

$$\sum_{j}^{N} c_{ji} O_j \ ,$$

where $O_j = 1$ if patch j is occupied and 0 otherwise, and c_{ji} is the contribution that patch j makes to the colonization of patch i when occupied. Occupied patches are assumed to become extinct at rate e_i. c_{ji} can be parameterized according to particular assumptions about how the size of patches i and j, together with their distance apart, affects the colonization success of a particular organism. Similiarly, e_i can be parametrized according to how patch size is thought to affect extinction risk in local populations. Note that if all patches are assumed equal ($c_{ij} = c$ and $e_i = e$ for all i, j) the model reduces to a stochastic version of the Levins model (Ovaskainen & Hanski 2004), see box 2.2. The IFM is a more general version of the the SRLM in discrete time (mathematically a Markov chain) that is able to model such phenomena as the metapopulation rescue effects when patch extinction risk is reduced by immigration (resulting in a metapopulation–level Allee effect).

Spatially realistic models have been celebrated for their predictive power (Hanski & Ovaskainen 2000) and application to real metapopulations (Etienne et al. 2004), but to gain intuition into the basic consequences of incorporating space into models, a smaller step away from the implicitly spatial models is helpful. Lattice models are perhaps the simplest that include some notion of spatial interaction. The following sections of this chapter will introduce these models and show how they can help the ecologist to gain a basic intuition into the effects of space and the limitations of implicitly spatial models.

2.4 The Effects of Local Spatial Structure

2.4.1 Local Dispersal

The Levins model assumes that propagules can disperse to any patch within the landscape, but in nature dispersal is often a limited process depending upon landscape composition (Wiens 2002), organism physiology and behaviour (Murren et al. 2002, Stamps 2002), and many other factors. Long distance dispersal may be impossible for organisms with restricted movement or avoided if too costly. Costs may be associated with the investment of dispersal mechanism (e.g wing development), will be incurred when the time spent dispersing is taken from that spent investing in reproduction, feeding or any other vital processes. Dispersers, away from preferred environments, may also be at higher risk of factors such as decreased resource availability, higher risk of predation, etc. The costs and benefits of dispersal will be factored into the optimal dispersal behavior that will in turn determine the success that dispersers have in finding empty patches to colonize (Gandon & Michalakis 2002).

2.4.2 The Basic Contact Process with Habitat Loss

The basic contact process, as reviewed by Durrett & Levin (1994), on a finite square lattice in discrete time has been used to simulate stochastic metapopulation dynamics when dispersal is local and can be represented by a SRLM. Let each site on an $N = n^2$ finite lattice represent a habitat patch. Patches can be in one of three states: uninhabitable, habitable and empty or habitable and occupied with the value 0, 1, and 2 respectively. Before simulating the metapopulation dynamics, a fraction $(1 - h)$ of all patches randomly chosen, are made uninhabitable. Patches then remain habitable or uninhabitable for the entire duration of the simulation. With colonization rate c, extinction rate e and $\delta = e/c$, the simulation of the metapopulation process involves performing the following iteration procedure a certain number of times:

1. An occupied patch is chosen uniformly at random.
2. With probability $\frac{\delta}{1+\delta}$ the patch becomes extinct with the patch converted to state 1, otherwise a propagule is produced and 'sent' to one of the neighbouring patches (defined below) selected at random. If and only if this neighbouring patch is in state 1 it is converted to state 2, representing a successful colonization event.

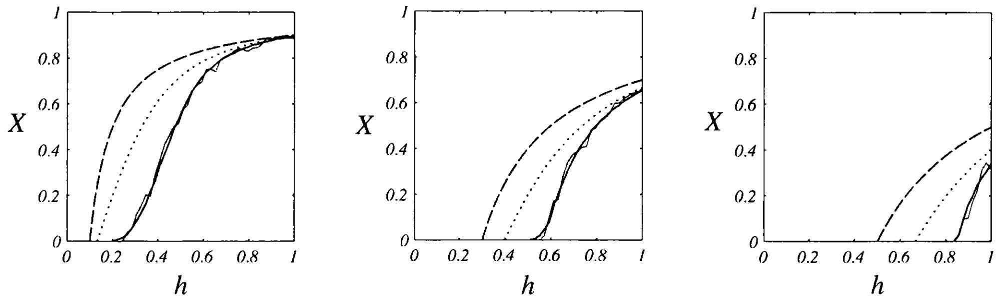
This process is repeated many times to simulate the long–term metapopulation dynamics.

The dispersal neighbourhood of each lattice patch is often chosen to be the four nearest neighbours (lattice patches directly above, below, to the left and to the right) known as the Neumann neighbourhood, or the eight nearest neighbours that include the diagonals and known as the Moore neighbourhood. Other dispersal neighbourhoods can be used to model greater dispersal ranges or to complement the geometry of different lattice structures (i.e the basic contact process can be simulated on a hexagonal lattice with the patch neighbourhood as the six nearest neighbours). For the simulations that follow, the Neumann neighbourhood has been used. The patches that lie on the edge of the lattice will have fewer neighbours as things stand, but we follow the common procedure of connecting the top and bottom row of the lattice, producing a tube, and connecting the ends of the tube together, producing a toric structure.

The time step represented by each iteration will depend upon the number of patches occupied; the expected time until a particular occupied patch either goes extinct or produces a propagule is $\Delta t = \frac{1}{e+c}$, since both the extinction and propagule production processes are modelled as Poisson processes. If there are N_2 occupied patches, the expected time until the first one either becomes extinct or produces a propagule is thus $\frac{1}{N_2(e+c)}$. This process of picking one patch at a time, referred to as the **asynchronous** approach, and will be used in this investigation.

An alternative approach often employed in lattice–based simulations is **synchronous** updating. The time step for each iteration of the simulation, $\Delta t \ll \frac{1}{e+c}$, is assumed to be small and constant. For each iteration of the simulation every occupied patch is processed with probability $(e+c)\Delta t$ according to step 2 of the asynchronous method. This approach requires both e and c to be explicitly defined whereas the asynchronous approach only requires that the ratio δ be given.

All realistic stochastic models of closed ecological systems will exhibit extinction in finite time because the probability that all patches become extinct, however small, will be non-zero. For every initial state the extinction state is an absorbing state that will eventually be reached with probability 1. Instead of determining whether the metapopulation becomes extinct, one can instead investigate the expected time to extinction and the behaviour of the system during the transient period. When the expected time is *suitably large* the metapopulation can be considered to be viable. For the basic contact process these measures will depend upon the initial occupation state of the metapopulation in addition to the fraction of habitable patches and the



(a) $\delta = 0.1$ (b) $\delta = 0.3$ (c) $\delta = 0.5$

Figure 2-2: Comparisons between the Levins model, the PA model and the lattice–based simulations of the basic contact process. h is the fraction of habitable patches and X is the fraction of habitable patches occupied. The solid curve shows the average fraction of habitable patches that where occupied after 50 simulations on a 50×50 lattice and the grey curve shows one realisation of the simulation. The dashed curve is occupation density predicted by the Levins model prediction and the dotted curve is occupation density predicted by the PA model (equation 2.4.3.11), presented in the following section.

extinction–colonization ratio. The limiting distribution of patch occupancy conditional upon non–extinction will converge on what is termed the *quasistationary* distribution in the Markov theory, with the mean of this distribution representing the expected size of a persisting metapopulation after the transient dynamics have settled (Ovaskainen & Hanski 2004).

Figure 2-2 shows the results of the following set of simulations on a 50×50 lattice over a range of h and for three instances of δ. The simulation was split into stages representing approximately equal periods of time. Each of these stages involved performing T iterations of the asynchronous approach above, where $T = N_2$ is the number of occupied patches at the the beginning of each stage. If at any time the number of occupied patches became zero the process was terminated. Otherwise the simulation was terminated after 1000 of these stages to allow for the transient dynamics to settle. The simulation was repeated 50 times for each parameter combination and the average was taken. The plots of figure 2-2 and 2-3 illustrates that the basic contact process exhibits threshold behaviour similar to the Levins model (and the pair–approximation (PA) model which is to be introduced in section 2.4.3), that is dependent upon both h and δ. The figures show however that the Levins model underestimates both the amount of habitat required for metapopulation persistence and the average number of

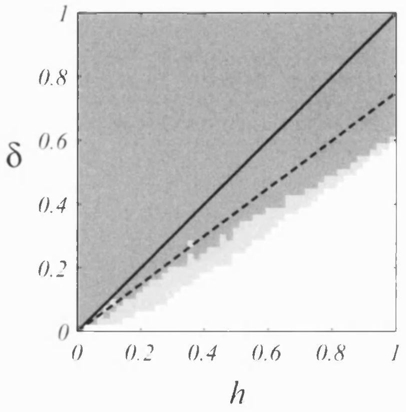


Figure 2-3: Stochastic extinction of the basic contact process on a 50 × 50 lattice. δ is the extinction–colonization ratio and h is the fraction of habitable patches, uniformly distributed on the lattice. 50 simulations were performed for every δ–h parameter combination: If parameters are in the white region the metapopulation still persisted after every simulation, the darker shaded region then the metapopulation went extinct for every simulation and in the intermediate pale shaded region some of the metpopulations persisted (see main text for a detailed description of the simulation). The solid line shows the optimistic prediction of the Levins type model: if parameters lie below this line the metapopulation is predicted to persistence. The dashed line shows the improved predictions of the PA model (equation 2.4.3.2 of section 2.4.3).

habitable patches that are occupied if viable. Figure 2-3 shows that threshold amount of habitat required for the probable persistence of the basic contact process (underpinning the grey region) is approximately proportional to δ, as predicted by the Levins model, but with a proportionality constant of about $\frac{5}{3}$ compared with 1 for the Levins model.

In box 2.2 we derive the Levins model by constructing a deterministic mean–field approximation of this stochastic process. The derivation confirms that it is the mean–field assumption of the Levins model that causes the observed discrepancy between it and simulations.

Box 2.2. **Deriving the Levins Model from a Stochastic Process.**

In order to derive an approximating differential equation model from the stochastic process defined at the beginning of section 2.4.2 we must embed it in real time t, so that $N_2(t)$ is the random variable giving the number of patches in state 2 at time t. Supposing that the N patches of a landscape are either in state 0, 1 or 2, representing uninhabitable, habitable and empty, and habitable and occupied, respectively. Fix δt small, in real time. Then

$$N_2(t+\delta t) = \begin{cases} N_2(t)+1 & \begin{array}{l}\text{if there is a single event in } (t, t+\delta t)\\ \text{and that event is an attempted}\\ \text{and successful colonization,}\end{array} \\ N_2(t)-1 & \begin{array}{l}\text{if there is a single event in } (t, t+\delta t)\\ \text{and that event is an extinction,}\end{array} \\ N_2(t) & \text{if there is no event in } (t, t+\delta t)\ . \end{cases} \qquad (2.4.2.1)$$

The probability of two or more events occurring in $(t, t+\delta t)$ is $O(\delta t^2)$.
We need to calculate the probability of the transition $N_2 \to N_2+1$ in $(t, t+\delta t)$. It depends on the value taken by by $N_2(t)$, so we shall find the conditional probability

$$p_c = \mathbb{P}\{N_2 \to N_2+1 \text{ in } (t, t+\delta t) | N_2(t) = n_2(t)\} = p_1 p_2\ , \qquad (2.4.2.2)$$

where

$$\begin{aligned} p_1 &= \mathbb{P}\{\text{single event in } (t, t+\delta t) \text{ which is an attempted colonization} \\ &\qquad |N_2(t) = n_2(t)\}\ , \end{aligned} \qquad (2.4.2.3)$$

and

$$p_2 = \mathbb{P}\{\text{colonization is successful} \mid \text{it is attempted and } N_2(t) = n_2(t)\}\ . \qquad (2.4.2.4)$$

Now $p_1 = \lambda_1 n_2(t)\delta t$, where λ_1 is the per patch rate of propagule production, and $p_2 = \lambda_2 \phi(n_2(t))$, where λ_2 is the probability that a dispersing propagule succesfully finds a patch and establishes a new population conditional on the probability that it is habitable and empty, $\phi(n_2(t))$.

Box 2.2 continued.

Similarly,

$$p_e = \mathbb{P}\{N_2 \rightarrow N_2 - 1 \text{ in } (t, t+\delta t) | N_2(t) = n_2(t)\} = e n_2(t)\delta t \ , \qquad (2.4.2.5)$$

and so

$$\mathbb{E}\{N_2(t+\delta t)|N_2(t) = n_2(t)\} = n_2(t) + c n_2(t)\phi(n_2(t))\delta t - e n_1(t)\delta t + O(\delta t^2) \ , \qquad (2.4.2.6)$$

where $c = \lambda_1 \lambda_2$.

The mean–field assumption consists of assuming that

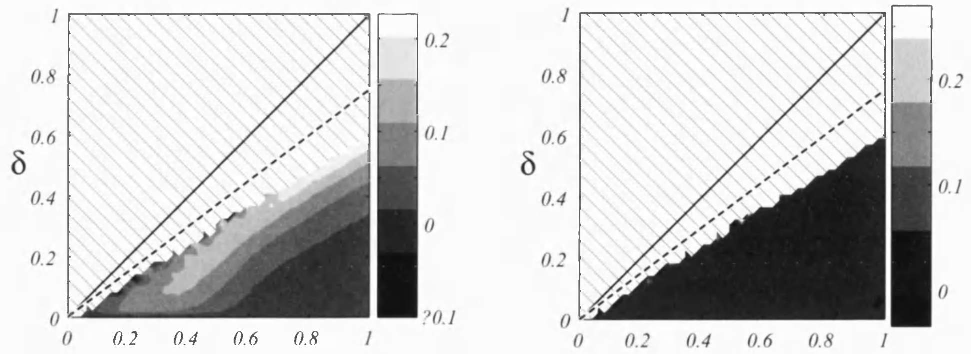
$$\phi(n_2(t)) = h - \frac{n_2(t)}{N} \ , \qquad (2.4.2.7)$$

the total fraction of empty and habitable patches. Taking the limit as $\delta t \rightarrow 0$, it follows that

$$\frac{dx}{dt} = cx(h-x) - ex \ , \qquad (2.4.2.8)$$

where $x = \frac{\mathbb{E}(N_2)}{N}$.

Since the number of patches in the simulations was assumed to be large and the basic rates e and c not explicitly given, the deviation of the mean-field model with the simulation must be a product of the assumption that ϕ, the probability that the a propagule lands in a habitable and empty patch, is given by $\phi = N_1^i/N = h - N_2^i/N$ (see box 2.2). ϕ, however, should ideally model the probability that the neighbour of an occupied patch is empty and habitable. This can be measured for a particular realisation of the basic contact process by counting the total number of neighbouring patch pairs that are in the ordered state with the first in state 1 and the second in state 2, N_{12}, and then dividing this by the total number patches that neighbour occupied patches, kN_2, where $k = 4$ is the neighbourhood size. We shall define $\rho_i = N_i/N$ to be the fraction of patches in the landscape in state i and $\rho_{ij} = N_{ij}/kN$ to be the fraction of neighbouring patch pairs in the ordered state i–j. Defining $\rho_{1/2} = \rho_{12}/\rho_2$ to be the realised conditional probability that the neighbour of an occupied patch is habitable



(a) $h - \hat{\rho}_1 - \hat{\rho}_{1/2}$

(b) $\hat{\rho}_{1/2} - \delta$

Figure 2-4: The plots of this figure illustrate how $\hat{\rho}_{1/2}$, the average fraction of patches neighboring occupied patches that are empty and habitable at quasistationary state, depend upon h and δ for the basic contact process. Plot (a) shows the difference between $h - \hat{\rho}_1$, the fraction of empty patches in the landscape, and $\hat{\rho}_{1/2}$ assumed to be zero in the Levins model. Plot (b) shows the difference between $\hat{\rho}_{1/2}$ and δ that is approximately zero when the metapopulation persists. No simulations persisted in the hatched region.

and empty.

The expected change in occupied patches, given by equation 2.4.2.6, is zero when $\hat{\phi} = \delta$. Plot (a) of figure 2-4 shows that, generally, $\hat{\rho}_{1/2} \approx \delta$ where $\hat{\rho}_{1/2}$ is the average value of $\rho_{1/2}$ at the end of the 50 simulations described above. Thus probability that the neighbour of an occupied patch is empty and habitable does drive the stochastic colonization processes. Note that parameter values near the probabilistic extinction boundary lead to substantial differences between $\hat{\rho}_{1/2}$ and δ. This is presumably from the fact that the number of occupied patches are in this case very low and stochastic noise plays a crucial role in determining $\hat{\rho}_{1/2}$.

When the metapopulation is at a non-zero quasistationary state the observation that $\hat{\rho}_{1/2} \approx \delta$ does not depend upon h, and thus offers no insight into whether the metapopulation should go extinct following a reduction of h by a particular amount. Predicting when ρ_2 becomes zero not only requires the modelling of the expected dynamics of N_2 but also the expected dynamics of N_{12}.

2.4.3 Modelling Local Dispersal

The dynamics of the basic contact process can be better approximated by explicitly modelling correlations between nearest neighbours. The pair–approximation (PA) method for modelling the basic contact process consists of a coupled pair of ODEs that model the states of neighbouring patch pairs a well as the global fraction of patch states (Matsuda et al. 1992, Sato & Iwasa 2000). It has been generalised to incorporate habitat loss by Ovaskainen et al. (2002) and Hiebeler (2004) as derived in box 2.3.

Defining $\kappa = \frac{k-1}{k}$, it is straightforward to show, as does Hiebeler (2004), that the metapopulation persists if and only if

$$q > \frac{\delta}{\kappa} \,, \tag{2.4.3.1}$$

reducing to the condition

$$h > \frac{4\delta}{3} \tag{2.4.3.2}$$

when the neighbourhood size $k = 4$ and habitat is distributed uniformly at random, $q = h$. Figure 2-3 illustrates that the PA model ,compared to the Levins model, is an improvement for predicting the persistence of the basic contact process.

If and only if the metapopulation persists, the fraction of habitable patches that are occupied at steady state, $0 < X \leq 1$, is given by

$$X = \frac{k}{2(k-1-\delta)} \left(\kappa(1-kq) - 2\delta - \kappa\sqrt{(kq-1)^2 + 4k(1-q)\delta} \right) \,, \tag{2.4.3.3}$$

reducing to

$$X = \frac{1}{6-2\delta} \left(3 + 12h - 8\delta - 3\sqrt{(4h-1)^2 + 16(1-h)\delta} \right) \,, \tag{2.4.3.4}$$

when $k = 4$ and $q = h$. Figures 2-2 and 2-3 illustrate the improved predictions made by the PA model.

Box 2.3. **The Pair Approximation Method** (Matsuda et al. 1992).

Let x_i be the fraction of patches in state $i = 0, 1, 2$, where $x_0 = 1 - h$ and $x_1 = h - x_2$. Also define x_{ij} to be the fraction of ordered neighbour pairs of patches with the first in state i and the second in state j. The dynamics of x_2 satisfy

$$\frac{dx_2}{dt} = cx_2\phi - ex_2, \tag{2.4.3.5}$$

as shown in box 2.2 where ϕ is the probability that a patch is in state 1 conditional on a neighbour patch being in state 2. Instead of assuming that $\phi = x_1$ we give it in the exact form

$$\phi = \frac{x_{12}}{x_2}\ , \tag{2.4.3.6}$$

that follows from the definition of conditional probability. Then

$$\frac{dx_2}{dt} = cx_{12} - ex_2\ . \tag{2.4.3.7}$$

To proceed, we shall model the dynamics of the x_{ij}. The number of ordered neighbouring patch pairs is nine (3×3), however the inherent symmetry given by $x_{ij} = x_{ji}$ reduces the potential number of independent pair variable to six. Defining $q = \frac{x_{11}+2x_{12}+x_{22}}{h}$ (the fraction of patches that neighbour habitable patches that are themselves habitable), with h and q held constant, the property that

$$\sum_j x_{ji} = x_i\ , \tag{2.4.3.8}$$

reduces the number of independent and sufficient state variables required to just three (Ovaskainen et al. 2002, Hiebeler 2004). We can choose x_2, x_{12} and x_{22}, with the dynamics of x_{12} and x_{22} derived as follows: x_{12} evolves according to

$$\frac{dx_{12}}{dt} = \underbrace{e(x_{22} - x_{12}) - \frac{c}{k}x_{12}}_{\text{Patch–pair interactions}} + \underbrace{\frac{(k-1)}{k}c\left(x_{11}\mathbb{P}\{2|11\} - x_{12}\mathbb{P}\{2|12\}\right)}_{\text{Triplet interactions}}\ . \tag{2.4.3.9}$$

Box 2.3 *continued.*

The first two terms model the extinction transitions and the third term models the rate at which the occupied patch of an empty–occupied pair colonizes the empty neighbour. This occurs at a rate $\frac{c}{k}$ since the total rate c is shared between each of the occupied patch's k neighbours. The final two terms represent the colonization of the empty patch of the neighbour pair by propagules originating from the other $k-1$ neighbours. This depends upon the probability that they are occupied, and is conditional on the pair state. Similiarly the equation for x_{22} is

$$\frac{dx_{22}}{dt} = -2ex_{22} + \frac{c}{k}(x_{12} + x_{21}) + \kappa c(x_{12} + x_{21})\mathbb{P}\{2|12\} \ , \quad (2.4.3.10)$$

where $\kappa = \frac{k-1}{k}$ The probabilities $\mathbb{P}\{i|jk\}$ can be formulated in terms of neighbouring triplets of patches in states i–j–k, x_{ijk}, as $\mathbb{P}\{i|jk\} = \frac{x_{ijk}}{x_{jk}}$. Modelling these requires the formulation of further dynamic equations and we can never arrive at a closed system (Sato & Iwasa 2000). Instead the fraction of triplets can be approximated in terms of pair fractions, the *pair approximation*, by assuming that $\mathbb{P}\{i|jk\} \approx \mathbb{P}\{i|j\}$ yielding

$$x_{ijk} \approx x_{ij}\frac{x_{jk}}{x_j} \ .$$

The system then becomes

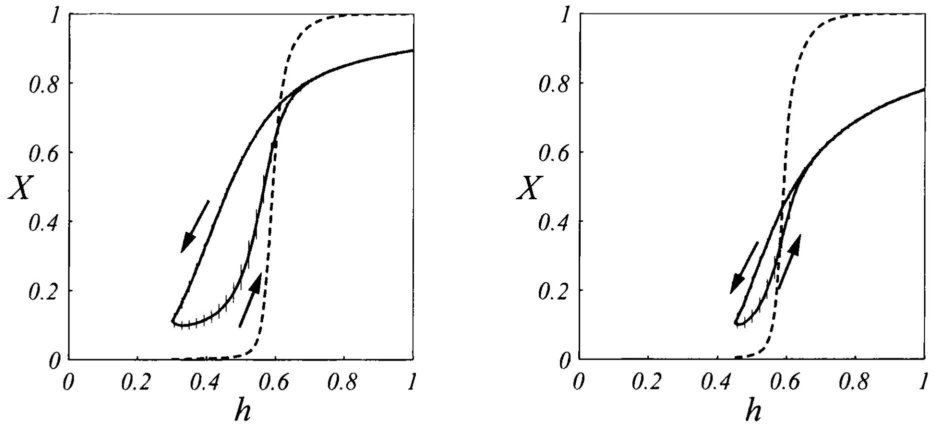
$$\begin{aligned}
\frac{dx_2}{dt} &= cx_{12} - ex_2 \ , & (2.4.3.11)\\
\frac{dx_{22}}{dt} &= -2ex_{22} + 2\frac{c}{k}x_{12} + 2\kappa c\frac{x_{12}^2}{h - x_2} \ , & (2.4.3.12)\\
\frac{dx_{12}}{dt} &= e(x_{22} - x_{12}) - \frac{c}{k}x_{12} + \kappa c(hq - 3x_{12} - x_{22})\frac{x_{12}}{h - x_2} \ , & \\
& & (2.4.3.13)
\end{aligned}$$

following from the symmetry condition, $x_{21} = x_{12}$, and the conservation of habitable pairs giving $x_{11} = hq - 2x_{12} - x_{22}$.

2.5 The Effects of Global Spatial Structure

The simulations presented in the last section began with all habitable patches initially occupied. Both the Levins model and the PA model predict that there exists a globally attracting steady state providing the metapopulation persists, suggesting that initial conditions are not important for the long term viability of a metapopulation. Ecological models abound in the literature where this is not the case e.g. if there is an Allee effect. Such models often assume that the per capita growth rate is not maximized when the population is low because positive effects of reduced inter-specific competition at low density are overshadowed by negative effects from other processes that occur at low density (e.g. limited mate choice). With the basic contact process there is no *deterministic* Allee effect (stochastic effects at very low density may result in extinction before the convergence to a quasistationary distribution) and one expects that a metapopulation that is initially at low density will recover to the density derived from the above initial conditions. An alternative way that small populations are kept low despite the capacity for populations to exist at greater density can be derived from landscape structures at large spatial scales. Tilman & Kareiva (1997, Chapter 1) presents a result from simulations like those in section 2.4.2 that illustrates this. The simulation is as follows. Initially all patches are habitable and a metapopulation with a suitably low value of δ is introduced and iterated until a non-zero quasi-steady state is reached. A small number of patches are then made uninhabitable (whether populated or not) and the dynamics are allowed again to settle. This last process is repeated further and to the point that still allows long–term persistence of the metapopulation. Then the process is reversed and habitat is restored in increments after transient effects have died away.

Figure 2-5 shows, in agreement with Tilman & Kareiva (1997, Chapter 1) that the equilibrium density depends not just upon the fraction of habitat but also on whether or not the landscape is going through a destructive or regenerative phase. This break in symmetry occurs when $h \approx 0.65$ and the difference becomes substantial when $h < 0.6$, independent of whether $\delta = 0.1$ or $\delta = 0.2$. The lag in population recovery can be explained in terms of global landscape connectivity.



(a) $\delta = 0.1$ (b) $\delta = 0.2$

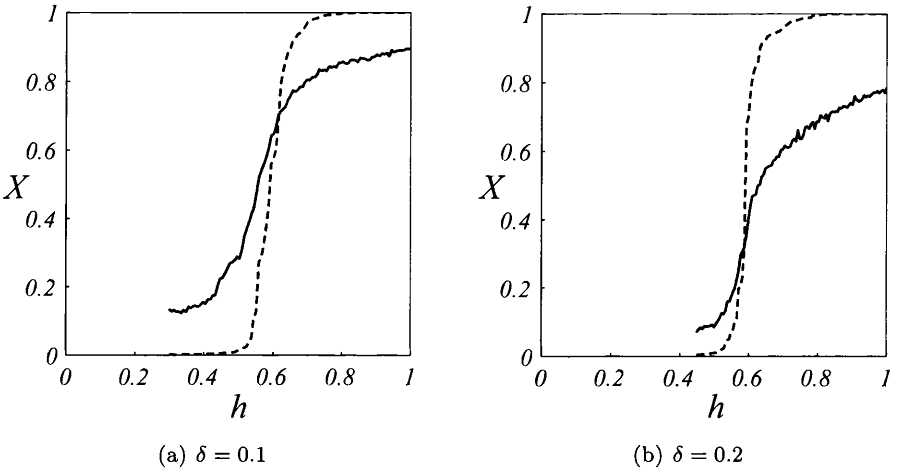
Figure 2-5: Metapopulation recovery following habitat regeneration. The solid curve gives the mean fraction of habitable patches that are occupied, X, after 100 simulations on a 100 × 100 lattice. The hatched regions are within one standard deviation of the mean occupation density. The arrows indicate that the curves represent occupation density whilst habitat is decreasing (arrows pointing left) or increasing (arrows pointing right). The dashed curve is the connectivity, ζ (defined below), averaged over the 100 simulations .

2.5.1 Landscape Connectivity and Percolation Theory

The effects of landscape connectivity are ignored in implicitly spatial models, when it is assumed that each patch is connected to all others. With explicitly spatial models, patch connectivity can vary greatly between different patches and landscape connectivity can vary greatly between different landscapes. Since the regeneration process of the simulations presented above work by changing small-scale structure it is not clear how the landscapes change at larger spatial scales. With increasing habitat, connected sets of patches will be generated, bringing together section of the landscape that were previously isolated. It is useful to have a simple measure of connectivity in order to compare the different regenerated landscapes. We define our measure of connectivity, ζ, to be the mean over every habitable site of the ratio of patch size to habitat size. More precisely, let Γ denote a landscape with N patches and let Γ_i be the i–th patch (the order of the indexing is not important). ζ is defined as

$$\zeta = \frac{1}{N - N_0} \sum_{i}^{N} \frac{P_i}{N - N_0 - 1} , \qquad (2.5.1.1)$$

where $N_0 = (1-h)N$ is the number of uninhabitable patches and $P_i = 0$ if Γ_i is uninhabitable, and equal to the number of habitable patches that are connected to patch i otherwise. Two patches, indexed i^1 and i^n, in the landscape are connected if there exists an ordered set of habitable patches $\{i^1, i^2, ..., i^{n-1}, i^n\}$ such that i^m is in the neighbourhood of i^{m-1} for $m = 2, 3.., n$. If patch i is habitable, $P_i + 1$ is thus the size of the connected cluster of habitat patches containing patch i. ζ is thus interpreted as the average fraction of all habitable patches in the landscape that a habitable patch is connected to.



(a) $\delta = 0.1$ (b) $\delta = 0.2$

Figure 2-6: Metapopulation recovery and the increase in landscape connectivity following habitat regeneration of a single simulation on a 100×100 lattice. The solid curve is the mean fraction of habitable patches that are occupied, X, and the dashed curve is the connectivity, ζ. Jumps in connectivity result in jumps in patch occupation.

The dependence that connectivity has upon the amount of habitat is illustrated in figure 2-6. When all patches are habitable every patch is connected to every other patch and so that $\zeta = 1$. Reducing the fraction of habitable patches to about 70% has very little affect on ζ since the 'holes' created do not isolate many patches. However, when habitat is reduced further to about 60% there is a dramatic decrease in ζ to almost 0. This threshold effect is an example of a *critical phenomenon*, the study of which comprises an important part of percolation theory (Stauffer 1985). One idea from percolation theory that is of interest here is the existence of a *percolating cluster*. In an infinite lattice a percolating cluster is defined as a cluster of infinite size. The theory states that if and only if the fraction of sites of the lattice exceeds the percolation threshold, $p_c \approx 0.6$ (assuming the Neumann neighbourhood), then a percolating cluster will *almost certainly* exist. The figures show that the measure of connectivity is suitably equivalent to the existence of percolating cluster in terms of the threshold value of $h \approx p_c$, for the finite landscapes considered.

The link between landscape connectivity and equilibrium metapopulation density following habitat regeneration is suggested in figure 2-5 and convincingly illustrated in figure 2-6 showing the results from a single simulation. The jumps in connectivity occur when two regions of connected habitat patches are joined. These often correspond to jumps in metapopulation density. If only one of these regions was initially occupied, after becoming connected the unoccupied patch will be colonised and the fraction of habitable patches that are occupied will be substantially increased. The reason some large regions of connected patches are unoccupied following severe habitat loss, is because the landscape will be composed of many small islands of connected regions with the populations of many going extinct.

2.6 Spatially Correlated Habitat

In the simulation described above, habitat was both removed and recovered uniformly at random, resulting in a characteristic landscape (see figure 2-9). If patches are destroyed or regenerated according to non–uniform random processes, the resultant landscapes generated can have properties with quite different consequences for declining or recovering metapopulations following habitat change.

Hiebeler (2000) introduced a lattice-based model of a metapopulation with non–uniform random habitat distribution. Simulating the basic contact process, he compared equilibrium metapopulation densities obtained with those on uniformly random landscapes. To construct landscapes with habitat distributes non-uniformly, he used an algorithm to create correlations between local pairs of habitable patches.

Box 2.4. **Determining Neighbour Pair Densities.**

Consider a random landscape on a torus consisting of N patches, each of which is either habitable (state 1), with probability $\mathbb{P}\{1\}$, or uninhabitable (state 0), with probability $\mathbb{P}\{0\} = 1 - \mathbb{P}\{1\}$.

In addition, let the state of any patch be independent of that of any other. Define an ordered neighbour pair of patches to be a patch together with one of its neighbours, so that if the neighbourhood size is k, there are kN ordered neighbour pairs in a lattice of N patches. The probability $\mathbb{P}\{i - j\}$ that an ordered neighbour pair of patches has patch 1 in state i and patch 2 in state j is given by $\mathbb{P}\{i-j\} = \mathbb{P}\{i\}\mathbb{P}\{j\}$, by the independence assumption. For N large, the fraction ρ_i of patches in state i in any given realisation will approximate to $\mathbb{P}\{i\}$, and the fraction ρ_{ij} of ordered neighbour pairs of patches in state $i - j$ to $\mathbb{P}\{i - j\} = \mathbb{P}\{i\}\mathbb{P}\{j\}$. We have, in the limit as $N \to \infty$, $\rho_{11} = \rho_1^2$, $\rho_{10} = \rho_{01} = \rho_1\rho_0 = \rho_1(1 - \rho_1)$ and $\rho_{00} = \rho_0^2 = (1 - \rho_1)^2$.

If the states of patches are not independent of each other we no longer have $\mathbb{P}\{i - j\} = \mathbb{P}\{i\}\mathbb{P}\{j\}$, but rather $\mathbb{P}\{i - j\} = \mathbb{P}\{i\}\mathbb{P}\{j/i\}$, where $\mathbb{P}\{j/i\}$ is the probability that the neighbour of a patch is in state j, conditional on the patch irself being in state i. For any realisation we have $\rho_0 + \rho_1 = 1$, $\rho_{10} + \rho_{11} = \rho_1$, $\rho_{00} + \rho_{01} = \rho_0$, and $\rho_{01} = \rho_{10}$, so that

$$\rho_{01} = \rho_{10} = \rho_1 - \rho_{11} \ , \qquad (2.6.0.2)$$

$$\rho_{00} = 1 - 2\rho_1 + \rho_{11} \ . \qquad (2.6.0.3)$$

Note that $\rho_{00} - {\rho_0}^2 = \rho_{11} - {\rho_1}^2$. The condition that $\rho_{00} \geq 0$ implies that $\rho_{11} \geq 2\rho_1 - 1$.

Alternatively we may write the realised conditional probabilities in terms of ρ_1 and $\rho_{1/1}$ as

$$\rho_{0/1} = 1 - \rho_{1/1} \ , \qquad (2.6.0.4)$$

$$\rho_{1/0} = \frac{\rho_1}{1-\rho_1}(1 - \rho_{1/1}) \ , \qquad (2.6.0.5)$$

$$\rho_{0/0} = \frac{1 - 2\rho_1 + \rho_1\rho_{1/1}}{1 - \rho_1} \ . \qquad (2.6.0.6)$$

The condition $\rho_{0/0} \geq 0$ implies that

$$\rho_{1/1} \geq 2 - \frac{1}{\rho_1} \ . \qquad (2.6.0.7)$$

To construct a landscape where $\rho_1 \approx h$ and $\rho_{1/1} \approx q \geq 2 - \frac{1}{h}$ (see bottom of box 2.4 for the reason behind this restriction), hereafter termed a $h - q$ landscape, the algorithm works as follows:

1. A realisation of a random landscape with a fraction $\rho_1 \approx h$ of habitable patches is generated by setting each patch habitable with probability h (ρ_1 will deviate from h since the lattice is finite), ρ_1 and ρ_{11} are calculated for this landscape.
2. A patch from the landscape is picked uniformly at random and the new values ρ'_1 and ρ'_{11} of ρ_1 and ρ_{11} are calculated when the state of the patch is changed. The change is kept if and only if $D = |\rho'_{11} - qh| + |\rho'_1 - h|$ has been reduced.
3. Step one and two are repeated until D is less than a predefined tolerance.

When $q > h$ so that $\rho_{1/1} = \frac{\rho_{11}}{\rho_1} > \rho_1$ (so $\rho_{11} > {\rho_1}^2$), the landscape will be referred to as aggregated since both $\rho_{11} > \rho_1^2$ and $\rho_{00} > \rho_0^2$ (see box 2.4). If $q < h$ (both $\rho_{11} < \rho_1^2$ and $\rho_{00} < \rho_0^2$) the landscape will be referred to as dispersed.

Simulations involved populating 50% of all habitable patches and iterating the basic contact process. Hiebeler (2000) claimed that the equilibrium fraction of habitable patches that are occupied depends more upon the habitat aggregation parameter, q, than the actual amount of available habitat, h. The simulation results were compared with the Levins and PA model with the PA model supporting this argument (note equation 2.4.3.1 and 2.4.3.3 are both independent of h). Ovaskainen et al. (2002) argue, however, that this interpretation of the results is erroneous because the degree of landscape aggregation is actually dependent upon the ratio $\frac{q}{h}$ and not just q.

2.7 Aggregated and Dispersed Habitat Regeneration

How might different regimes of habitat regeneration affect the observation of Tilman & Kareiva (1997, Chapter 1) regarding metapopulation recovery after habitat regeneration? In the investigation of Hiebeler (2000), q–h landscapes were generated before local populations were introduced and the basic contact process simulated. This procedure presumably restricts the impact that landscape connectivity at large spatial scales can have upon the long–term behaviour of a metapopulation since most of the habitable patch clusters that are large enough to harbour populated patches (i.e the expected time to cluster extinction is relatively large) will contain occupied patches. As the process of random habitat regeneration can severely alter this distribution of populated patches so might non–uniform random regeneration.

We investigate the consequences that non–uniform random habitat regeneration has upon the observation of Tilman & Kareiva (1997, Chapter 1) using an algorithm to regenerate habitat in either an aggregated or dispersed manner. The fraction of habitat, h_0, before regeneration is set below the percolation threshold ($h_0 << 0.6$) with the metapopulation parameter δ chosen so that the remaining metapopulation persisted. Habitat is then regenerated until all patches were made habitable, according to the algorithm described in the following section. The simulations are essentially identical to those of Tilman & Kareiva (1997, Chapter 1) except for the more general method of habitat regeneration.

The algorithm developed by Hiebeler (2000) to create the desired h–q landscapes involved the redistribution of habitable patches across the landscape. To model a strict increase in the fraction of habitat whereby habitable patches remain throughout the regeneration phase of the simulation, an alternative procedure for introducing auto-correlation in habitat state was devised. The purpose of our simulation is to see how the structure, imposed by the method of landscape regeneration, affects the increase in landscape connectivity and the increase in metapopulation density from that of a sparsely habitable initial landscape.

Our aim is to go from an initial h_0–q_0 landscape, randomly generated, to a final h_1–q_1 landscape, where $h_1 = 1$, after successive increments of habitat regeneration. Instead of predetermining q_1, however, we shall introduce an algorithm that regenerates patches according to a local aggregation process so that the evolution of q with h is an emerging property of this process.

Our algorithm regenerates habitat one patch at a time by converting an uninhabitable patch into a habitable and empty patch. The uninhabitable patch that is chosen depends upon how many habitable neighbours it has, the degree of non–uniformity in the random regeneration (aggregated or dispersed) that is required, and how many patches are currently habitable. The degree of aggregation/dispersion is controlled by the parameter $\psi(h) \in [0, 1]$: The algorithm works by choosing $n \sim Bin(k, \psi)$, (i.e. $n \in [0, k]$ is a random variable binomially distributed with mean $k\psi$ where $k = 4$ is the Neumann neighbourhood size) and picking an uninhabitable patch with n habitable neighbours at random. If none happen to exist then another value of n is picked according to the same distribution. Thus $\psi(h)$ is the *target* probability that the neighbour of the converted patch is also habitable.

The initial h_0–q_0 landscape will satisfy $q_0 \approx h_0$ when the destruction process is uniformly random. If $\psi(h) = h$ for all h, the landscape will be regenerated randomly with $q \approx h$. If, for a given $h - q$ landscape, $\psi(h) > \rho_{1/1}$, it is expected that a patch will be picked that increases the degree of habitat aggregation in the landscape. If $\psi(h) < \rho_{1/1}$, it is expected that a patch will be picked that increases the degree of habitat dispersion in the landscape.

We choose the following linear function for ψ

$$\psi(h) = \psi(h; h_0, \alpha) = \begin{cases} 1 - \frac{1-\alpha}{1-h_0}(1-h) & \text{if } > 0 \\ 0 & \text{otherwise ,} \end{cases} \tag{2.7.0.8}$$

where the parameter $\alpha \in (-\infty, 1]$ determines the degree of aggregation: If $\alpha = h_0$ then $\psi(h) = h$, and a random landscape will be generated since the distribution of habitable patches in the neighborhood of any patch of a random landscape is also binomial. If $\alpha' > \alpha$, then $\psi(h; \alpha', h_0) > \psi(h; \alpha, h_0)$ for all h, therefore if $\alpha > h_0$ an aggregated landscape will be generated, and if $\alpha < h_0$ a dispersed landscapes will be generated. Note that $\psi(h_0) = \alpha$ if and only if $\alpha \geq 0$, but a greater range of landscapes are regenerated if $\psi = 0$ for an initial range of h that corresponds to $\alpha < 0$. Figure 2-7 illustrates how $\psi(h)$ increases monotonically with α.

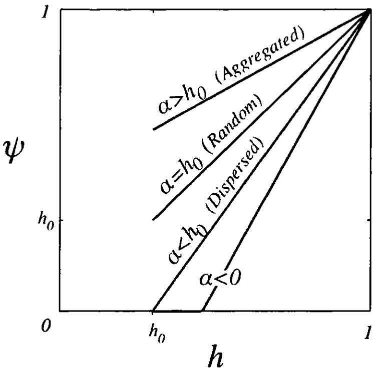
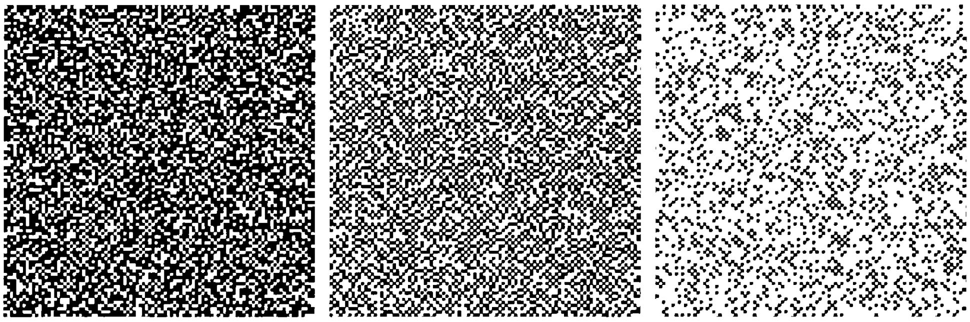


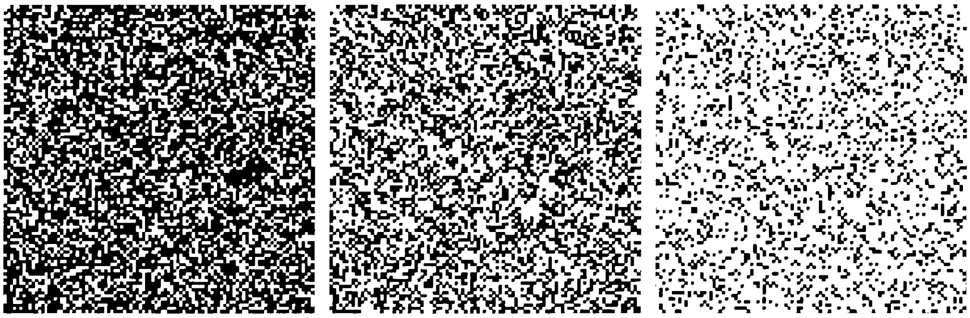
Figure 2-7: The target expected number of habitable neighbour patches of a regenerated patch, $\psi(h)$, is monotonically controlled by the aggregation parameter α (see equation 2.7.0.8).

Figures 2-8 to 2-11 illustrate 100 × 100 landscapes for $\alpha = 0,\ 0.3,\ 0.5$, and 0.8 with the initial fraction of habitat, $h_0 = 0.3$. This value of h_0 has been chosen because it is well below the percolation threshold yielding minimally connected landscapes (see plot (a) of figure 2-6).



(a) $h = 0.4$ (b) $h = 0.6$ (c) $h = 0.8$

Figure 2-8: Landscapes generated from $h = 0.3$ for $\alpha = 0$. Habitable patches are white. In this case $\psi < h$, generating the disperse landscape.



(a) $h = 0.4$ (b) $h = 0.6$ (c) $h = 0.8$

Figure 2-9: Landscapes generated from $h = 0.3$ for $\alpha = 0.3$. Habitable patches are white. In this case $\psi = h$ generating the random landscape.

The generation of dispersed landscapes (figure 2-8) initially results in the formation of regions with checkerboard patterns with habitable patches surrounded by uninhabitable patches. This pattern is a direct result of using the Neumann neighbourhood. The generation of aggregated landscapes results in the formation of large connected clusters of habitable patches (figures 2-10 and 2-11).

By comparing the plots of figure 2-12, we can see how the desired local structure, ψ, determined by α (plot (a)) drives the average value of the local habitat correlation,

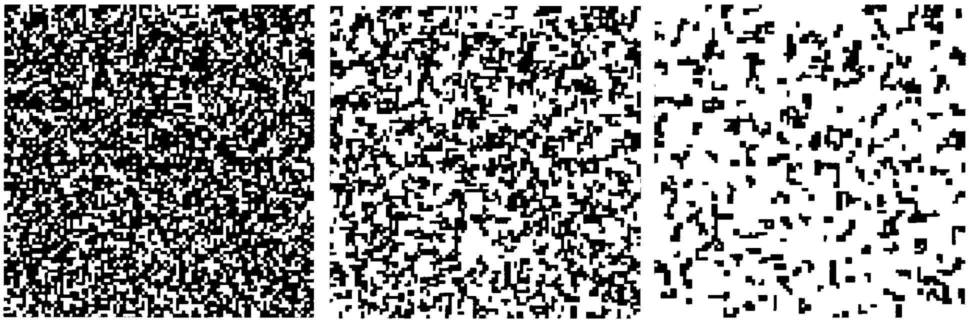

(a) $h = 0.4$ (b) $h = 0.6$ (c) $h = 0.8$

Figure 2-10: A Landscape generated when $\alpha = 0.5$ from a random $h = 0.3$ landscape. Habitable patches are white. In this case $\psi > h$, generating the aggregated landscape.

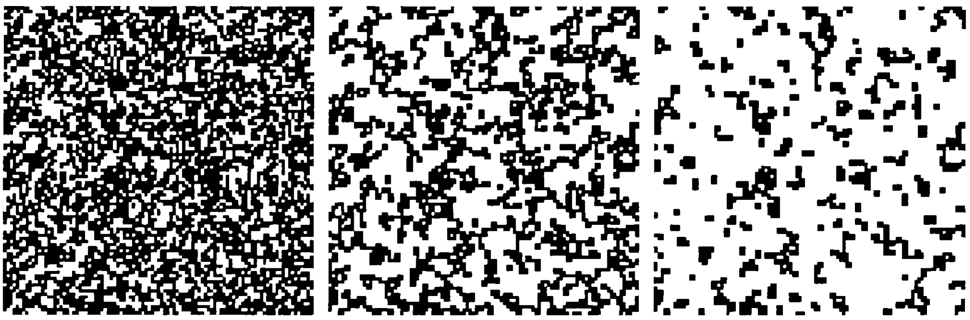
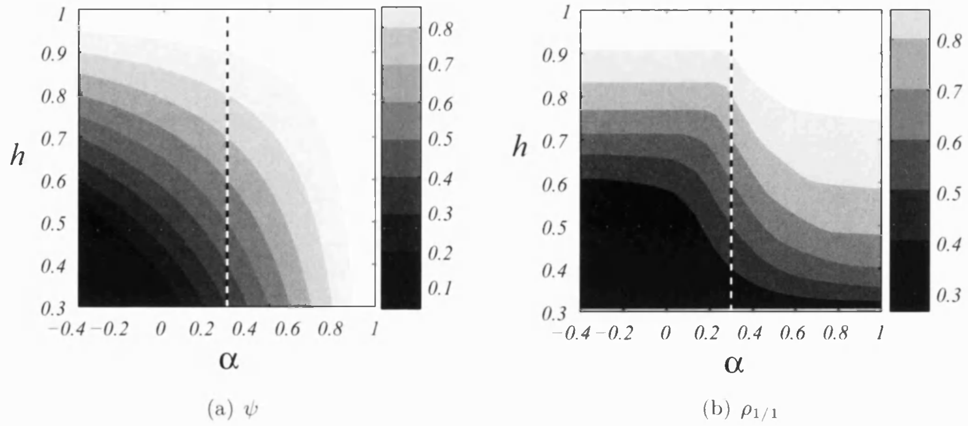

(a) $h = 0.4$ (b) $h = 0.6$ (c) $h = 0.8$

Figure 2-11: A Landscape generated when $\alpha = 0.8$ from a random $h = 0.3$ landscape. Habitable patches are white. In this case $\psi > h$, generating the aggregated landscape.

$\rho_{1/1}$ (plot (b)), when $h_0 = 0.3$. Not surprisingly, increasing α decreases the amount of habitat recovery required for $\rho_{11} \leq 1$ to exceed any particular value (recall that the restriction that $\rho_{11} > 2 - \frac{1}{\rho_1}$ derived in box 2.4 ensures that $\rho_{11} \to 1$ as $\rho_1 = h \to 1$, independent of α). The relationship between $\rho_{1/1}$ and α is not as smooth as that between ψ and α: When α is less than about h_0 and dispersed landscapes are generated, the consequences of decreasing α is most influential if α is close to h_0 (exceeding about 0) with the lower thresholds obtained by $\rho_{1/1} > h_0$ more sensitive to this change. This is presumably due the the restrictions that the randomly generated $h = h_0$ landscape have upon the generation of extremely dispersed landscapes. When α exceeds h_0 and aggregated landscape are generated, the largest consequences of varying α is once again obtained when α is closer to h_0, the generation of extreme aggregated landscapes is



(a) ψ

(b) $\rho_{1/1}$

Figure 2-12: Contour plots showing how α controls (a): ψ and (b): $\rho_{1/1}$, the probability that the neighbour of a habitable patch is habitable. $h_0 = 0.3$ with uniformly random landscapes correspond to $\alpha = 0.3$ (highlighted by the dashed line). The results were averaged over 100 simulations on a 100 × 100 lattice.

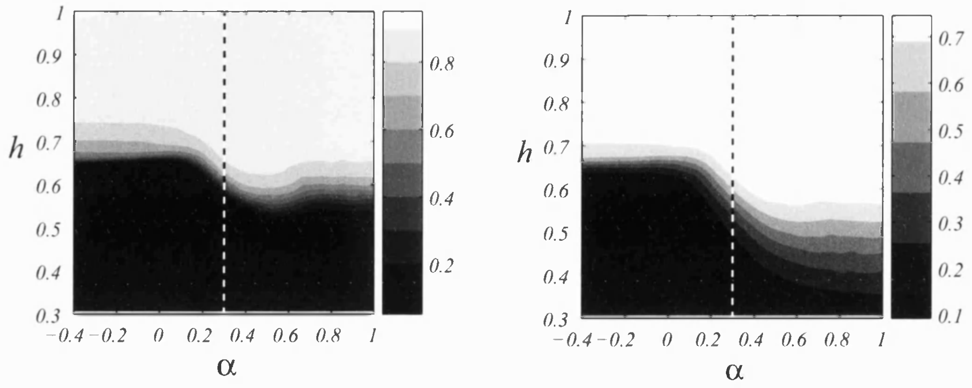
also limited by the initial structure.

It is natural to expect that degree of connectivity will also be influenced by the aggregation parameter α since the forming of connected habitat clusters will depend on how aggregated habitat is at different spatial scales and driven by the aggregation at the local scale. Connectivity, unlike local habitat correlation, does not quite depend monotonically upon α: Although a decrease in α below h_0 does increase the amount of habitat needed to reach any degree of connectivity, if α is increased above h_0 we can see that intermediate values of α generate landscapes that become connected after minimal habitat regeneration. This result, perhaps surprising when first encountered, has a straightforward explanation. Changes in connectivity depend principally upon two processes:

Cluster growth The incremental growth of connected clusters when patches neighbouring the boundary of the cluster become habitable.

Cluster conglomeration The sudden formation of large clusters when two small clusters become connected.

The degree of aggregation will influence the rate that these two processes occur as



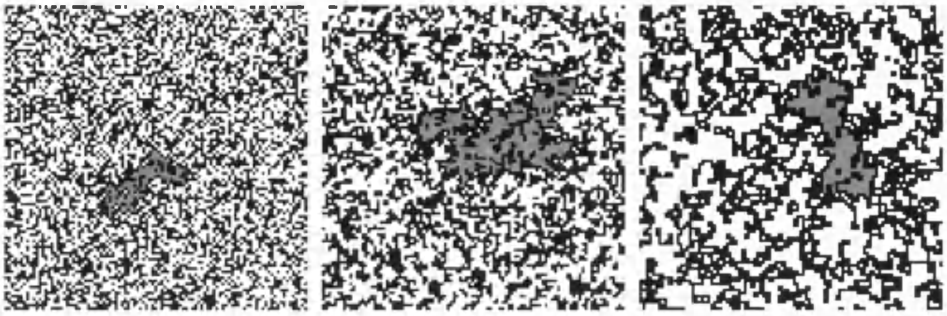
(a) ζ (b) X

Figure 2-13: Contour plots showing how α affects (a): connectivity, ζ, and (b): metapopulation recovery, X, when $\delta = 0.1$. $h_0 = 0.3$ with random landscapes correspond to $\alpha = 0.3$ (highlighted by the dashed line). The results where averaged over 100 simulations on a 100×100 lattice.

habitat is incrementally generated. Cluster growth depends directly on the aggregation strength, as previously observed.

Strong aggregation tends to create clusters that are spatially dense with few interior boundary patches. The clusters highlighted in figure 2-14 illustrate this well. The highlighted cluster in the strongly aggregated landscape (plot (c)) contains just two uninhabitable regions where as the clusters in the other landscapes have far more. Although the size of the strongly aggregated cluster is less than that highlighted for the moderately aggregated landscape of plot (b), at this stage of habitat generation when connectivity is low, the aggregated landscape does have the larger clusters. The reason that the connectivity is held low for the strongly aggregated landscape, following further habitat generation, is because cluster conglomeration is restricted. For clusters to join, corridors must be formed that span the uninhabitable regions. As these regions are themselves strongly aggregated, it will be aggregation strength that limits the construction of potential corridors. Plot (c) of figure 2-15 illustrates how the global connectivity has been restricted because large clusters exist have been kept separated. The moderately aggregated landscape on the other hand has reached a high state of global connectivity because corridors have been allowed to form.

In plot (b) of figure 2-13 the consequences of landscape aggregation for metapopulation recovery when $\delta = 0.1$ are given.Metapopulation recovery appears less sensitive



(a) $\alpha = 0.3$ (b) $\alpha = 0.5$ (c) $\alpha = 1.0$

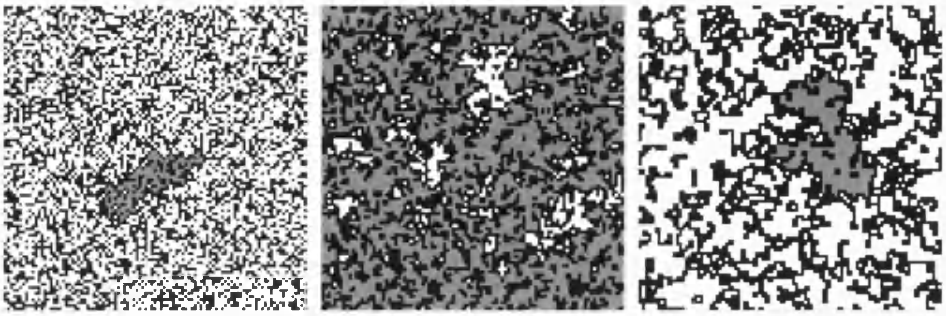
Figure 2-14: Examples of landscapes with $h = 0.51$ patches habitable. $h_0 = 0.3$ and so the landscape of plot (a) is random, (b) moderately aggregated, and (c) strongly aggregated. Black patches are uninhabitable and the shaded region identifies one of the connected cluster.

to the effect that intermediate aggregation has on connectivity change. The increases in X (the fraction of habitable patches that are occupied) do appear to coincide with those of ζ when α is less than about h_0, however there is an apparent discrepancy when α exceeds h_0. In this case increasing α will monotonically decrease the amount of habitat required for X to initially increase. As X approaches the maximum value the effect of increasing α does reduce.

2.8 Aggregated and Dispersed Habitat Destruction

To complete the investigation we also considered the non–uniformly random destruction of habitat and how this may affect the consequences of a particular regeneration regime. The establishment of habitat clusters that are connected by corridors (proposed above to be key in obtaining highly connected landscapes) may depend upon the structure of the initial landscape,'seeding' the regenerating landscape. The simulations designed to investigate these effects are identical to those in the previous section apart from the process of habitat destruction. We introduced a process of habitat destruction that was identical to the regeneration process: Patches were made uninhabitable depending upon the number of *uninhabitable* neighbours. The number of uninhabitable neighbours of the patch to be destroyed is $n \sim Bin(4, \mu)$, where

$$\mu(h;\beta) = \begin{cases} 1-(1-\beta)h & \text{if } >0 \\ 0 & \text{otherwise .} \end{cases} \qquad (2.8.0.9)$$



(a) $\alpha = 0.3$ (b) $\alpha = 0.5$ (c) $\alpha = 1.0$

Figure 2-15: Examples of landscapes with $h = 0.55$ patches habitable. $h_0 = 0.3$ and so the landscape of plot (a) is random, (b) moderately aggregated, and (c) strongly aggregated. Black patches are uninhabitable and the shaded region identifies one of the connected cluster.

The parameter $\beta \in (-\infty, 1]$ controls the aggregation of uninhabitable patches. $\mu(h) = 1 - h$ when $\beta = 0$, corresponding to the generation of random landscape. Destruction is aggregated when $\beta > 0$ and dispersed when $\beta < 0$.

Figure 2-16 illustrates how the destruction process affects the declining metapopulation when habitat is removed to $h = 0.4$ for the case when $\delta = 0.1$. Dispersed habitat destruction, resulting in heavily fragmented habitat clusters, has a particularly detrimental effect since the metapopulation actually goes extinct when β falls below about -0.1 (when habitat is reduced further to 30% extinction occurs for very slight levels of dispersion). The process is naturally far less detrimental when habitat is removed in an aggregated manner. Habitat clusters remain large when β exceeds about 0.3. Since, in this case, most clusters should remain inhabited, the only factor that impinges on the success of the metapopulation will come from the cluster edge effects (Forman 1995, Fahrig 2003) where occupied patches on the edge have decreased colonization success. The ratio of cluster–edge to cluster–area is perhaps a good measure of the strength of the edge effect (Forman 1995), and decreases with increased habitat aggregation.

When habitat patches are destroyed in a strongly aggregated manner (i.e. when β exceeds about 0.3 in this model) the form of habitat regeneration will be of less importance than when a landscape is highly fragmented and composed of clusters at high extinction risk. We shall therefore restrict our attention to the destruction regimes when $-0.2 \leq \beta \leq 0.3$.

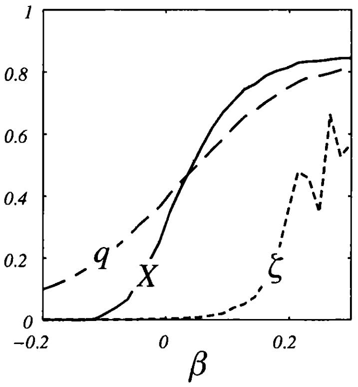
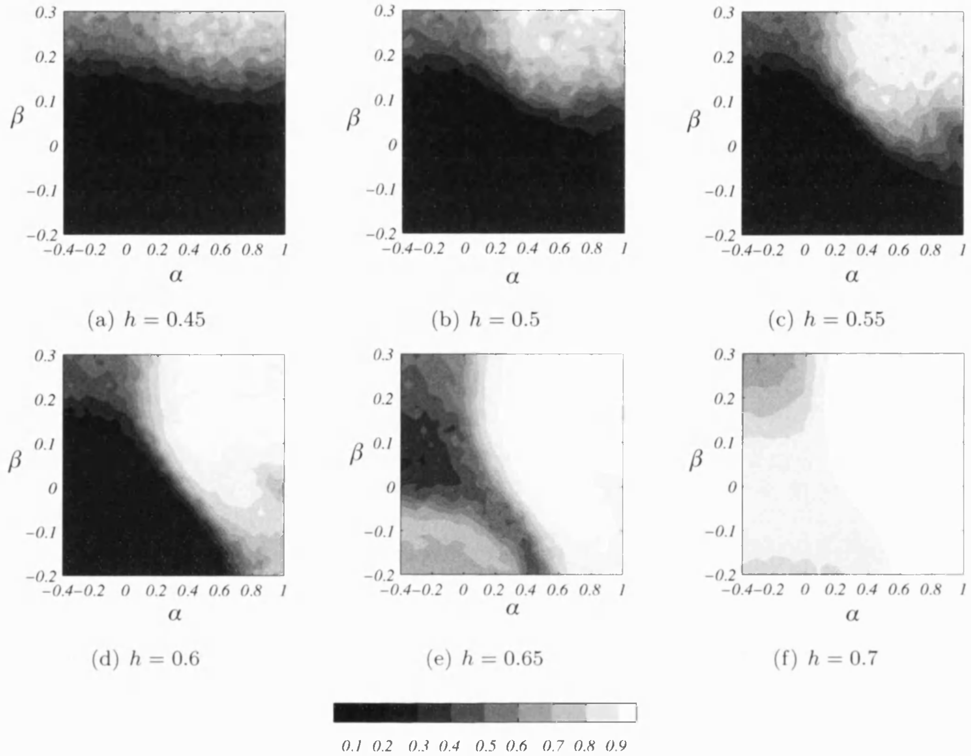


Figure 2-16: This plot shows how destroying the landscape with parameter β to $h = h_0 = 0.4$ affects the aggregation of habitat, q, the connectivity, ζ and the fraction of habitable patches that are occupied, X when $\delta = 0.1$. The results where averaged over 30 simulations on a 100×100 lattice.

Figure 2-17 illustrates how connectivity increases with h as dependent upon β and α. The intuitive idea that increasing either β or α will monotonically increase connectivity, ζ, for all levels of habitat h, which has already been dispelled for the case when $\beta = 0$, is unfounded, as clearly observed in plot (e). For only moderate increases in habitat (plots (a) and (b)) values of β in the approximate range $(0, 0.2)$ show that high values of α may retard the increasing of connectivity, presumably because of the arguments outlined for the $\beta = 0$ case. As habitat increases, the range of β in which this observation occurs increases and for lower values of β. When h becomes about 0.6, full landscape connectivity is generally obtained when both β and α are high, yet connectivity can be kept extremely low when they are both low. Interestingly, as h increases to about 0.65 (plot (e)) there is a dramatic change in connectivity when values of α and β are both very low. This also drastically increases the range of β that yields the intermediate α effect on maximising connectivity. There is a small range of β ($\beta < -0.1$) whereby increasing α initially decreases, then increases, and finally decreases connectivity.

In the final stages of habitat increase (plots (e) and(f)) another change in behaviour is observed for low α: maximal connectivity occurs for extreme values β when $h = 0.65$ yet for a single intermediate range when $h = 0.7$.

The recovering metapopulation density, X, is less sensitive to the changing patterns of connectivity caused by the different destruction and regeneration regimes (see

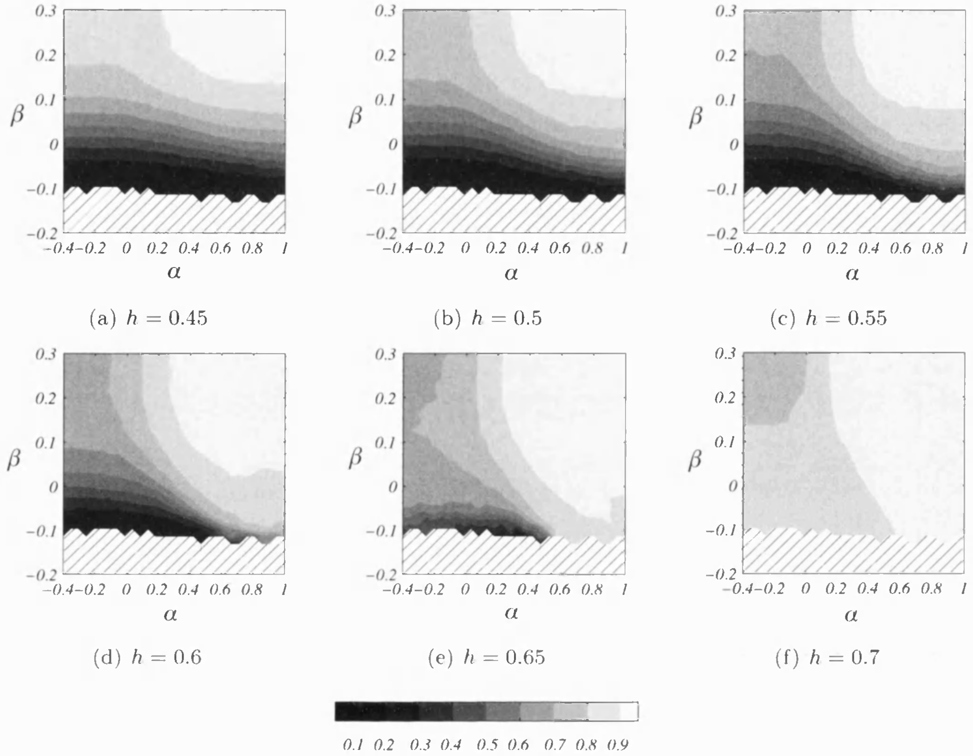


(a) $h = 0.45$ (b) $h = 0.5$ (c) $h = 0.55$

(d) $h = 0.6$ (e) $h = 0.65$ (f) $h = 0.7$

Figure 2-17: Contour plots showing how destroying landscape with parameter β and recreating with parameter α (see main text) affects the increase in connectivity, ζ, when the fraction of habitable patches, h, is increased from $h_0 = 0.4$, to 0.7. The results were averaged over 30 simulations on a 100×100 lattice. A randomly destroyed landscape corresponds to $\beta = 0$.

figure 2-18). Recovery generally increases monotonically with aggregation although, in the later stages of habitat generation and for low values of α, increased β leads to decreased values of X. This is because the large clusters of habitat formed from aggregated habitat loss are surrounded by large clusters of uninhabitable patches. With dispersed habitat regeneration, these clusters get filled with habitat but remain largely unoccupied, reducing the total fraction of habitable patches that are occupied. When habitat is initially dispersed, the process of dispersing the regenerated patches is heavily restricted and habitat clusters will be formed with the effect of boosting X.



(a) $h = 0.45$ (b) $h = 0.5$ (c) $h = 0.55$

(d) $h = 0.6$ (e) $h = 0.65$ (f) $h = 0.7$

Figure 2-18: Contour plots showing how destroying landscape with parameter β and recreating with parameter α (see main text) affects metapopulation recovery, X, when the fraction of habitable patches, h, is increased from $h_0 = 0.4$, to 0.7. The results were averaged over 30 simulations on a 100×100 lattice. In the hatched region the metapopulation became extinct. A landscape destroyed uniformly at random corresponds to $\beta = 0$.

2.9 Discussion

In this chapter we have highlighted some of the limitations of spatially implicit metapopulation models with a review of a spatially explicit counterpart – the basic contact process. There are two spatial processes that are captured in this model that were shown to make important contributions to metapopulation dynamics:

- Small–scale local dispersal. This is found to cause a crowding effect that reduces per–population colonization success, resulting in a reduction in the colonization–extinction ratio. The probability of metapopulation persistence and the size of viable metapopulations are both reduced by this effect.

- Reduced connectivity following extensive habitat loss. This causes the regional isolation of patches, heightening the negative effects of habitat loss. This effect also causes a non–unique relationship between the level of habitat loss and the size of a viable metapopulation: the viable history of a metapopulation is also important for determining the recovery of a metapopulation following habitat regeneration.

We also reviewed the use of the pair–approximation method consisting of an ODE system that models local correlations. Predictions of this model improve upon those of the mean–field Levins model, but are limited when parameter values in the basic contact process lead to low to viable metapopulations. Despite this, the method may give real insight into why explicitly spatial models behave differently from those models that treat space implicitly (Baalen 2000).

The results of this chapter concluded with an investigation into how non–uniform habitat destruction and regeneration affects metapopulation recovery. This was motivated by an observation of Tilman et al. (1997) regarding uniform habitat change. We first considered how regional connectivity increases in a landscape, with an initally uniform distribution of habitat, as a consequence of aggregated or disperse habitat regeneration. We found that:

- Increasing the degree of dispersion relative to uniform increased the fraction of regenerated habitat that was required for the landscape to become connected.
- Increasing the degree of aggregation relative to uniform had a non–monotonic effect: An intermediate degree of aggregation minimizes the amount of habitat required to increase connectivity.

The relationship between the level of aggregation of regenerated habitat and the recovery of the metapopulation was also significant. Dispersion was found to further increase the lag observed by Tilman et al. (1997) for the case of uniform regeneration. Increased aggregation generally corresponds to a decrease in the observed lag, although a small intermediate effect does exist, presumably corresponding to the one that is associated with connectivity.

Habitat regeneration when habitat had a non–uniform initial distribution was also investigated. Not surprisingly, increased aggregation in the destruction process minimized the decline in both connectivity and metapopulation density (i.e. fraction of habitable patches occupied). Only a small amount of dispersion led to the extinction of the metapopulation for the demographic parameters considered. When destruction is dispersed there is a small range of habitat regeneration where connectivity is minimized for intermediate levels of aggregation in the regeneration process (see plot (e) of figure 2-17). In general, metapopulation density either remains elevated or else recovery is facilitated when aggregation in both processes is increased (for a slight exception see plot (e) of figure 2-18).

The strength of these effects will depend upon both metapopulation demography (determined in this model by δ) and the fraction of patches that are destroyed before regeneration. We omitted a more comprehensive investigation into these parameters because of the time factors associated with running the simulations. The investigation could be extended to incorporate different neighborhood templates and different dispersal regimes that perhaps model the cost associated with - or restrictions on - long distance dispersal.

Although the intermediate effects outlined above are small, they do suggest that caution should be taken when making assumptions about how landscape alteration at certain scales affect processes and patterns that occur at other scales. When conservation issues factor into Landscape planning, it may be important to respect how patterns in the distribution of different landscape elements affect the ecology of the inhabitants.

Chapter 3

The Ecology of Metapopulations in Heterogeneous Landscapes

3.1 Chapter Outline and Motivation

In this chapter we develop a generalized Levins model (a system of coupled ODE's) to investigate how metapopulation dynamics are affected by heterogeneity in landscape features, including patch size and patch resource type, that are spatially distributed. The long–term behaviour of the model is analysed and translated into conditions for persistence and the size of viable metapopulations. The chapter concludes with a treatment of the spatial aggregation of occupied patches with a pair–approximation model.

The purpose of this chapter is not only to investigate how metapopulation ecology may depend upon features of a landscape, but also to develop a model that can be generalised to investigate metapopulation competition and evolution for the chapters that follow.

3.2 Introduction

The models in the previous chapter were devised to expose how the assumption of mean–field mixing in the dispersal process limits the credibility of the Levins model of metapopulation dynamics. For simplicity these models inherited the assumption that all inhabited patches are equal and with populations at quasistationary distribution. Even when mean–field dispersal is assumed, it is reasonable to imagine that variation in both of these factors across the landscape can have consequences for the colonization and extinction processes and lead to qualitative differences in the metapopulation dynamics predicted by models of homogeneous patch networks (Hanski 1999*a*, Ovaskainen & Hanski 2004). The variation in structure may also have a significant bearing upon the effects of habitat loss.

When modelling a particular fragmented landscape as a collection of uniform patches, the parameters that determine the metapopulation dynamics should be calibrated to approximate average values of occupied and empty patches (the *landscape dependence*) together with average properties of the target organisms (the *demographic dependence*). Table 3.1 suggests how the phenomenological incorporation of certain landscape features and the reaction of the organism should influence the tuning of the parameters e and c of the Levins model (introduced in the previous chapter).

Landscape Property	**Description**	**Demographic Reaction**	**Parameter Dependency**
Patch structure	Patch area, patch quality, patch resource type	Propagule production — Local pop. size — Patch extinction risk —	e & c e & c e
Landscape fragmentation	Patch isolation, landscape connectivity, Nearest neighbour distance	Dispersal risk — Migration success — Population rescue —	c c e

Table 3.1: Phenomenological parametrization of the Levins model from average landscape properties.

Box 3.1. Persistence and Viability in the Levins Model

The Levins model can be written in the form

$$\frac{dx}{dt} = cx(\hat{x} - x) \; , \qquad (3.2.0.1)$$

where $\hat{x} = h - \frac{e}{c}$ is the fraction of occupied patches at steady state if the metapopulation persists. Persistence can be determined by linearizing 3.2.0.1 about 0 yielding

$$\frac{dx}{dt} = \lambda x \; , \qquad (3.2.0.2)$$

where λ is the basic metapopulation growth rate given by

$$\lambda = c\hat{x} \; . \qquad (3.2.0.3)$$

The metapopulation persists if and only if $\lambda > 0$. The system linearized about $x = \hat{x}$ is

$$\frac{dx}{dt} = -\lambda(x - \hat{x}) \qquad (3.2.0.4)$$

and thus a viable steady metapopulation is always stable. Since λ and $\hat{x}$ are sign–equivalent the Levins model makes the simple prediction that persistence and viability are equivalent at the metapopulation scale.

Another quantity associated with persistence is the basic reproductive ratio, R_0. It is defined to be the expected number of patches a single occupied patch colonizes during its extant stage when introduced into an otherwise unoccupied landscape:

$$R_0 = \frac{ch}{e} \; . \qquad (3.2.0.5)$$

Persistence is equivalent to $R_0 > 1$ since the number of patches colonized before extinction must exceed 1 for the fraction of patches to increase. This statement follows mathematically from the observation that $\lambda = e(R_0 - 1)$.

Claim 1. Increasing $\hat{x}$ is equivalent to increasing R_0.

Proof. This follows from noting that

$$\nabla\hat{x} \cdot \nabla R_0 = \frac{c}{e} + \frac{h}{e} + \frac{e}{c^2} > 0 \; ,$$

where $\nabla = (\frac{\partial}{\partial h}, \frac{\partial}{\partial e}, \frac{\partial}{\partial c})$. □

Working with averaged properties, even when accurately used to calibrate parameters, may yield results that largely deviate from those of models that incorporate variation explicitly. If a property of a landscape is responded to in a non-linear way it may be strongly underrepresented when averaged. Hanski (1985) provides an example that makes this point well. He analysed a model that was identical to the Levins model except that occupied patches could be in two states of occupation representing small and large local populations. Modelling this local demographic variation required a relaxing of the assumption of a separation in the timescales of the dynamics of the local population and that of the metapopulation.

The model predictions were qualitatively different from those of the (appropriately averaged) Levins model (see box 3.1) because migrants from large populations could 'rescue' small populations from short–term extinction by increasing the rate that they increased to larger ones. In brief, the model exhibits a metapopulation–level *rescue effect* whereby the metapopulation cannot persist at low density yet can remain viable if the number of occupied patches initially exceeds a threshold amount. The rescue effect was first introduced by Brown & Kodrick-Brown (1977) in terms of a decreased risk of local population extinction with increased immigration rate. The rescue effect is comparable to the classic **Allee effect** when closed populations have non–maximal per capita growth rate at low density.

There are two major classes of metapopulation models that address the effects of heterogeneity in patch structure: The so–called *structured models* (Gyllenberg & Hanski 1992, Hanski & Gyllenberg 1993) that model the dynamics of local populations, and the spatially realist i.e. *stochastic patch occupation models* (SPOMs) (Ovaskainen & Hanski 2001, Ovaskainen & Hanski 2002, Ovaskainen & Hanski 2003), as reviewed by Ovaskainen & Hanski (2004), that model the salient properties of each patch explicitly.

The structured models, deterministic in continuous time, dispense with a time–separation assumption between local and global dynamics and model the explicit form of the local population dynamics. The metapopulation dynamics are underpinned by an implicitly spatial 'dispersal pool' immigration process, as with the Levins model, but with the contribution made to this pool by each occupied patch depending explicitly upon population size. Local rescue effects can occur when local demographic extinction is prevented by immigration, elevating the rescue effect to the metapopulation level (as with the finite dimensional model presented by Hanski (1985)) and yielding multiple stable equilibria (Hanski & Zhang 1993).

SPOMs are a natural counterpart to structured models in that they ignore variation in local population dynamics but explicitly account for spatial variation in patch size and patch isolation. They can be naturally modified to incorporate many other factors that are deemed relevant have been used to 'rank' patches of real patch networks in terms of their contribution to metapopulation persistence (Ovaskainen & Hanski 2003) and the total capacity of a landscape to prevent extinction (Hanski & Ovaskainen 2000).

From the modeller's point of view, both approaches lack analytic tractability when introducing spatial and structural realism (Gyllenberg et al. 2004). It can also be difficult to extract which key features of these models account for which phenomena, especially when the number of parameters required to define the system is very large (as with SPOMs). We proceed by constructing a generalised Levins model to investigate how the incorporation of minimal structure can alter some of the classic predictions.

3.3 A Generalized Levins Model

We extend the Levins model to include a discrete number of different habitat types. For N different types of patches, indexed by $i = 1, 2, ..., N$, let the fraction of type i be ρ_i where $\sum_i \rho_i = 1$, the fraction of i type patches that are habitable be $h_i \leq 1$ and the fraction of patches of i type patches that are populated be $x_i \leq h_i\rho_i$. The extinction and colonization processes that drive the metapopulation dynamics will depend upon patch type as follows: Let the extinction rate of a populated i type patch be $e_i > 0$ and the rate that propagules emigrate from j type patches and colonize i type patches be

$$c_{ji}x_j(h_i\rho_i - x_i) \ , \tag{3.3.0.6}$$

where $c_{ji} > 0$. The parameter values of e_i and c_{ji} can be chosen to model a particular patch structure. Before determining the structures we wish to model we shall investigate some properties of this generalized model.

The generalized Levins model is

$$\frac{dx_i}{dt} = \sum_j c_{ji}x_j(h_i\rho_i - x_i) - e_ix_i = \Omega^i(x_1, x_2, ..., x_N) \qquad i = 1, 2, ..., N \tag{3.3.0.7}$$

The patch occupancy variables x_i are restricted to the biologically realistic state space $[0, h_i\rho_i]$ since the set $\chi = [0, h_1\rho_1] \times [0, h_2\rho_2] \times ... \times [0, h_N\rho_N]$ is invariant. This follows because on the boundary $x_i = 0$ we have

$$\frac{dx_i}{dt}|_{x_i=0} = h_i\rho_i(\sum_{j\neq i} c_{ji}x_j) \geq 0 \ ,$$

and on the boundary $x_i = h_i\rho_i$

$$\frac{dx_i}{dt}|_{x_i=h_i\rho_i} = -e_ih_i\rho_i \leq 0 \ .$$

The ecological dynamics are characterized by the stability of the steady states of the system. It is convenient to adopt vector notation $\mathbf{x} = (x_1, x_2, ..., x_N)$.
$\hat{\mathbf{x}}$ is a steady states of equation 3.3.0.7 if $\Omega^1(\hat{\mathbf{x}}) = \Omega^2(\hat{\mathbf{x}}) = ... = \Omega_N(\hat{\mathbf{x}}) = 0$. The analysis proceeds by determining the linear stability of the system at the steady states.

The linearized system is in the form

$$\dot{\mathbf{x}}^T = J_R(\hat{\mathbf{x}})(\mathbf{x} - \hat{\mathbf{x}})^T \ , \tag{3.3.0.8}$$

where the elements of the Jacobian matrix $J_R(\hat{\mathbf{x}})$, satisfying $[J_R(\hat{\mathbf{x}})]_{ij} = \Omega^i_j(\hat{\mathbf{x}})$, where Ω^i_j is the partial derivative of Ω^i with respect to the jth argument.

The subscript R refers to the fact that the model describes the dynamics of a *resident* species. Although this notation is redundant when modelling a single species, the chapters that follow model metapopulation invasion and require a distinction between the resident types and invading types, and for continuity we shall adopt this notation now.

3.4 Two-Type Patch Models

Finding the eigenvalues of J_R requires solving the so-called characteristic equation consisting of a polynomial of degree N. For simplicity we will be considering models where $N = 2$ representing a two-type patch landscape. Since we are interested in comparing the predictions of structured and unstructured landscape models we expect the most basic introduction of structure to highlight any potential deviations. Equation 3.3.0.7 for $N = 2$ can be written

$$\frac{dx_1}{dt} = (c_{11}x_1 + c_{21}x_2)(h_1\rho_1 - x_1) - e_1x_1 = \Omega^1(x_1, x_2) \ , \tag{3.4.0.9}$$

$$\frac{dx_2}{dt} = (c_{12}x_1 + c_{22}x_2)(h_2\rho_2 - x_2) - e_2x_2 = \Omega^2(x_1, x_2) \ . \tag{3.4.0.10}$$

The Jacobian matrix of this system is

$$J_R(\hat{\mathbf{x}}) = \begin{pmatrix} c_{11}(h_1\rho_1 - 2\hat{x}_1) - c_{21}\hat{x}_2 - e_1 & c_{21}(h_1\rho_1 - \hat{x}_1) \\ c_{12}(h_2\rho_2 - \hat{x}_2) & c_{22}(h_2\rho_2 - 2\hat{x}_2) - c_{12}\hat{x}_1 - e_2 \end{pmatrix} , \quad (3.4.0.11)$$

with trace and determinant given by

$$trJ_R(\hat{\mathbf{x}}) = c_{11}(h_1\rho_1 - 2\hat{x}_1) + c_{22}(h_2\rho_2 - 2\hat{x}_2) - c_{12}\hat{x}_1 - c_{21}\hat{x}_2 - e_1 - e_2 , \quad (3.4.0.12)$$

$$\begin{aligned} detJ_R(\hat{\mathbf{x}}) = {} & (c_{11}(h_1\rho_1 - 2\hat{x}_1) - c_{21}\hat{x}_2 - e_1)(c_{22}(h_2\rho_2 - 2\hat{x}_2) - c_{12}\hat{x}_1 - e_2) \\ & -(c_{21}(h_1\rho_1 - \hat{x}_1))(c_{12}(h_2\rho_2 - \hat{x}_2)) . \quad (3.4.0.13) \end{aligned}$$

The Routh–Hurwitz criteria states that a steady state $\hat{\mathbf{x}}$ is asymptotically stable if $\mathrm{tr}J_R(\hat{\mathbf{x}}) < 0$ and $\det J_R(\hat{\mathbf{x}}) > 0$.

3.4.1 Extinction

The origin is always a steady state of a closed ecological model and represents the metapopulation extinction state. A metapopulation will go extinct if and only if the origin is asymptotically stable with respect to the dynamics in the positive quadrant. From the Routh–Hurwitz criteria the system is asymptotically stable if

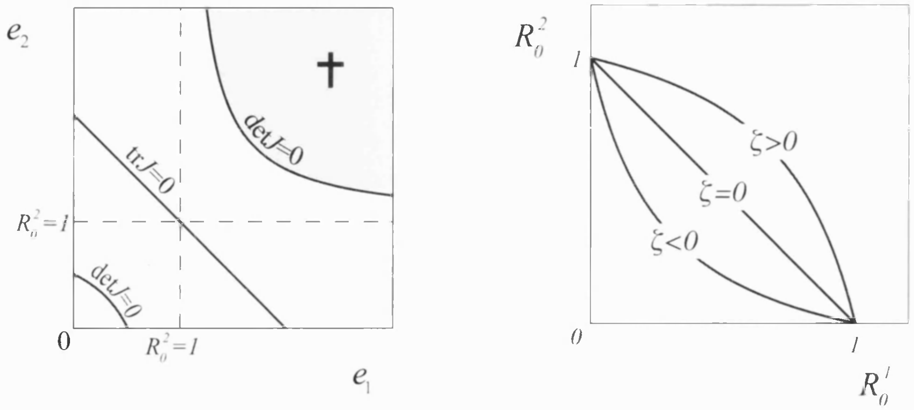
$$\mathrm{tr}J_R(0,0) = c_{11}h_1\rho_1 + c_{22}h_2\rho_2 - e_1 - e_2 < 0 , \quad (3.4.1.1)$$

and

$$\det J_R(0,0) = (e_1 - c_{11}h_1\rho_1)(e_2 - c_{22}h_2\rho_2) - c_{12}c_{21}h_1\rho_1h_2\rho_2 > 0 , \quad (3.4.1.2)$$

however the condition for asymptotic stability is slightly stronger than this when dynamics are restricted to the positive quadrant, as necessary for biological realsim. If either $\mathrm{tr}J_R(0,0)$ or $\det J_R(0,0) = 0$, then the linear system is neutrally stable, and asymptotic stability will depend upon the non–linear terms of the system. The system can be written as

$$\dot{\mathbf{x}}^T = J_R(\hat{\mathbf{0}})(\mathbf{x})^T - \mathbf{x}C\mathbf{x}^T , \quad (3.4.1.3)$$



(a) (b)

Figure 3-1: Parameter conditions for extinction. Plot (a): the shaded region in the e_1–e_2 parameter plane corresponds to extinction (3.4.1.4 and 3.4.1.5 both hold). The extinction region is bounded by a section of the curve det $J_R = 0$ whereby both $R_0^1 \leq 1$ and $R_0^2 \leq 1$, as defined by 3.4.1.6 and 3.4.1.7. Plot (b): The extinction regions in R_0^1–R_0^2 parameter space, dependent upon the values of c_{ij}, $i, j = 1, 2$, are bounded below the curves. For each curve the values of c_{ij}, $i, j = 1, 2$, are assumed constant (i.e R_0^i vary according to the parameters ρ,h_i and e_i only, and furthermore they are independent of c_{ij}) and on the curves $R_0^2 = \xi(R_0^1)$ as defined in 3.4.1.8. The plot illustrates how the degree of convexity of the extinction boundary is controlled by the $\zeta = \frac{c_{11}c_{22}-c_{12}c_{21}}{c_{11}c_{22}}$.

where the matrix C satisfies $[C]_{ij} = c_{ij} > 0$. Thus when $x_1 \geq 0$, $x_2 \geq 0$ and $\mathbf{x} \neq 0$, the non-linear terms will be strictly negative and thus $\mathbf{x} \to \mathbf{0}$.
Therefore the metapopulation goes extinct if and only if

$$\mathrm{tr} J_R(0,0) \leq 0 \ , \tag{3.4.1.4}$$

and

$$\det J_R(0,0) \geq 0 \ , \tag{3.4.1.5}$$

A graphical representation of the extinction region in $e_1 - e_2$ parameter space illustrated in plot (a) of figure 3-1. We see that there is hyperbolic relationship between e_1 and e_2 when $\det J_R = 0$ and furthermore the directrix of this hyperbola coincides with the solution curve of $\mathrm{tr} J(0,0) = 0$. This motivates an alternative condition for extinction:

$$R_0^1 = \frac{c_{11} h_1 \rho_1}{e_1} \leq 1 \ , \tag{3.4.1.6}$$

$$R_0^2 = \frac{c_{22}h_2\rho_2}{e_2} \le 1 \ , \tag{3.4.1.7}$$

and

$$R_0^2 \le \xi(R_0^1) := \frac{1 - R_0^1}{1 - \zeta R_0^1} \ , \tag{3.4.1.8}$$

where

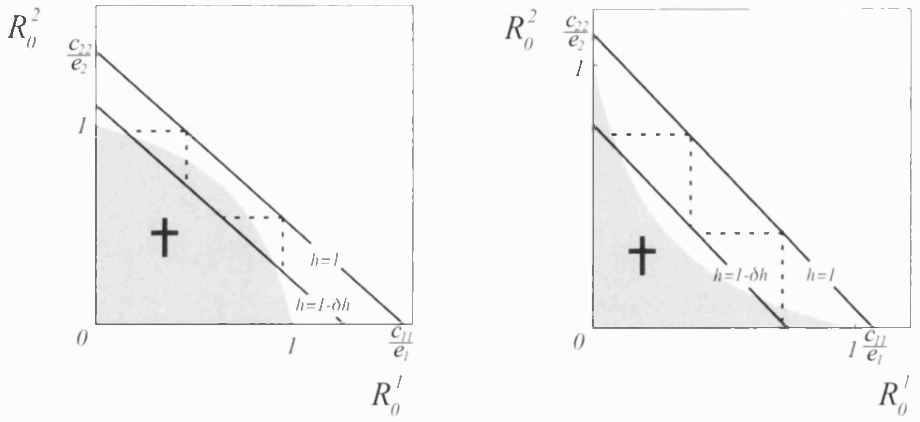
$$\zeta = \frac{c_{11}c_{22} - c_{12}c_{21}}{c_{11}c_{22}} \ . \tag{3.4.1.9}$$

3.4.1.8 is derived from a rearrangement of 3.4.1.5 and the equality of 3.4.1.6 and 3.4.1.6 give the equations of the asymptotes of the hyperbola in e_1–e_2 space that satisfies $\det J_R(0,0) = 0$. The quantity R_0^i has ecological meaning. R_0^i is the expected number of type i patches that are colonized by dispersers originating from a single populated type i patch in an otherwise empty landscape before extinction.

The quantity ζ determines the relative mixing between patch types of dispersers. Increasing this ζ correponds to increasing the likelihood that dispersers find patches of the same type as the natal patch. This quantity has important implications for persistence and the impact of patch–dependent habitat change as shown in figures 3-1 and figure 3-2. Plot (b) of figure illustrates 3-1 how the extinction boundary in R_0^1–R_0^2 depends upon ζ, assuming that c_{ij} $(i, j = 1, 2)$ is held constant for each value of ζ. Increasing ζ increases the degree of convexity of the boundary with convex boundaries corresponding to positive ζ. It is tempting to conclude that extinction is more likely when ζ is increased although this is generally erroneous. Since both R_0^i and ζ increase with c_{ii}, it may be that an increase in ζ is also coupled with the parameter combination (R_0^1, R_0^2) moving with the extinction region. The relative risk to the metapopulation corresponding to processes that alter the patch–type dependent colonization rates will thus not only rely on ζ, but also individual changes in magnitude.

Figure 3-2 relates the convexity parameter ζ to the consequences of habitat loss. The total fraction of habitable patches is $h = h_1\rho_1 + h_2\rho_2$. In the plot (a) and (b) it is assumed that the parameters h_i and e_i are held constant and that they are independent of c_{ij}. The constant h–curves are thus straight lines in the (R_0^1, R_0^2) plane: Moving along these curves i n the increasing R_0^1 direction is equivalent to keeping the number of habitable patches constant but converting type–2 patches to type–1.

Plot (a) corresponds to $\zeta > 0$. Prior to habitat loss ($h = 1$) the metapopulation can persist for all fractions of the two patch types since the curve lies outside extinction region. The consequences of removing a fraction δh of all patches (δh is about 0.2)



(a) $\zeta > 0$

(b) $\zeta < 0$

Figure 3-2: How the degree of convexity, ζ, mediates the affects of habitat loss (decreasing $h = h_1\rho_1 + h_2\rho_2$) on persistence, assuming that e_i and c_{ij} $(i, j = 1, 2)$ are constant. The shaded region corresponds to extinction as determined by 3.4.1.6 to 3.4.1.8. The dashed lines represent pure–type patch removal (horizontal lines corresponds to removing type–1 patches and vertical to type 2).

clearly depends upon the type of patches removed as well as the current fraction of both. The dashed curves indicate the extreme case when habitat is removed of a single type. Extinction is more likely when the patches of the more frequent type are removed. This effect is reversed when $\zeta < 0$ (plot (b)) where removing the infrequent patch types is more detrimental.

The differences in the relative patch suitability, c_{ii}/e_i, does not have a significant bearing on this result provided the difference is not too great the metapopulation can persist if $\rho = 1$ and $\rho = 0$ when $h = 1$. This means that destroying patches of the more suitable patch type will, in some cases, be the *least* detrimental for persistence when either $\zeta > 0$ or $\zeta < 0$, although not in the case $\zeta = 0$ (see figure 3-4 in section 3.5). Note that if both patch types are well represented in the landscape, destroying patches of purely one type is more detrimental when $\zeta > 0$ than a mixture, however a mixture is least detrimental if $\zeta < 0$. These results depend upon the the amount of habitat to be removed coupled with the relative slopes of the constant h–curve, and the extinction boundary within the 'cone' of possible destruction regimes bounded by the dashed curves stemming from the initial state.

The figure also shows that a mixture of habitat types sometimes lead to extinction despite viability when the landscapes are composed purely of one of *either* patch type (plot (a)) and visa versa (plot (b)).

3.4.2 Viability

If the origin is unstable then the invariance of $\chi = [0, h_1\rho_1] \times [0, h_2\rho_2]$ (the biologically realistic part of the state space) ensures that there will exist at least one steady state within the interior of χ.

Claim 2. An interior steady state is asymptotically stable.

Proof. For a non-trivial steady state

$$h_1\rho_1 - \hat{x}_1 = \frac{e_1\hat{x}_1}{c_{11}\hat{x}_1 + c_{21}\hat{x}_2} \,, \tag{3.4.2.1}$$

$$h_2\rho_2 - \hat{x}_2 = \frac{e_2\hat{x}_2}{c_{12}\hat{x}_1 + c_{22}\hat{x}_2} \,. \tag{3.4.2.2}$$

Hence

$$\begin{aligned} J_R(\hat{x}_1, \hat{x}_2) &= \begin{pmatrix} c_{11}(h_1\rho_1 - 2\hat{x}_1) - c_{21}\hat{x}_2 - e_1 & c_{21}(h_1\rho_1 - \hat{x}_1) \\ c_{12}(h_2\rho_2 - \hat{x}_2) & c_{22}(h_2\rho_2 - 2\hat{x}_2) - c_{12}\hat{x}_1 - e_2 \end{pmatrix} \\ &= \begin{pmatrix} -\frac{e_1c_{21}\hat{x}_2}{c_{11}\hat{x}_1 + c_{21}\hat{x}_2} - c_{11}\hat{x}_1 - c_{21}\hat{x}_2 & \frac{e_1c_{21}\hat{x}_1}{c_{11}\hat{x}_1 + c_{21}\hat{x}_2} \\ \frac{e_2c_{12}\hat{x}_2}{c_{12}\hat{x}_1 + c_{22}\hat{x}_2} & -\frac{e_2c_{12}\hat{x}_1}{c_{12}\hat{x}_1 + c_{22}\hat{x}_2} - c_{12}\hat{x}_1 - c_{22}\hat{x}_2 \end{pmatrix} . \end{aligned} \tag{3.4.2.3}$$

Then

$$\mathrm{tr}J_R = -\frac{e_1c_{21}\hat{x}_2}{c_{11}\hat{x}_1 + c_{21}\hat{x}_2} - c_{11}\hat{x}_1 - c_{21}\hat{x}_2 - \frac{e_2c_{12}\hat{x}_1}{c_{12}\hat{x}_1 + c_{22}\hat{x}_2} - c_{12}\hat{x}_1 - c_{22}\hat{x}_2 < 0 \,, \tag{3.4.2.4}$$

and

$$\begin{aligned} \det J_R &= \frac{e_1c_{21}\hat{x}_2}{c_{11}\hat{x}_1 + c_{21}\hat{x}_2}(c_{12}\hat{x}_1 + c_{22}\hat{x}_2) + \frac{e_2c_{12}\hat{x}_1}{c_{12}\hat{x}_1 + c_{22}\hat{x}_2}(c_{11}\hat{x}_1 + c_{21}\hat{x}_2) \\ &\quad +(c_{11}\hat{x}_1 + c_{21}\hat{x}_2)(c_{12}\hat{x}_1 + c_{22}\hat{x}_2) \\ &> 0 \,. \end{aligned} \tag{3.4.2.5}$$

Thus the Routh–Hurwitz criteria dictates that an interior steady state is asymptotically stable. □

By rearranging equations 3.4.2.1 and 3.4.2.2 we find that steady states satisfy

$$\hat{x}_1 = h_1\rho_1 - \frac{e_1 X}{c_{11}X + c_{21}} \; , \qquad (3.4.2.6)$$

$$\hat{x}_2 = h_2\rho_2 - \frac{e_2}{c_{12}X + c_{22}} \; , \qquad (3.4.2.7)$$

where $X = \dfrac{\hat{x}_1}{\hat{x}_2}$ is the patch type occupation ratio. Dividing equation 3.4.2.6 by equation 3.4.2.7 leads to the cubic equation

$$\begin{aligned} &c_{11}c_{12}h_2\rho_2X^3 + (c_{12}e_1 - c_{11}e_2 - c_{11}c_{12}h_1\rho_1 + (c_{11}c_{22} + c_{12}c_{21})h_2\rho_2)X^2 \\ &\quad (c_{22}e_1 - c_{21}e_2 - (c_{11}c_{22} + c_{12}c_{21})h_1\rho_1 + c_{21}c_{22}h_2\rho_2)X - c_{21}c_{22}h_1\rho_1 = 0 \; . \qquad (3.4.2.8) \end{aligned}$$

Claim 3. If the metapopulation persists there exists a unique *positive* solution $X = \hat{x}_1/\hat{x}_2$ of 3.4.2.8 such that $(\hat{x}_1, \hat{x}_2)$ lies in the interior of χ.

Proof. First note that equations 3.4.2.6 and 3.4.2.7 are both decreasing functions of X on $X > 0$ and thus $x_1 < h_1\rho_1$ and $x_2 < h_2\rho_2$ if $X > 0$.

The nullcines in the x_1–x_2 plane are those curves that satisfy either $\frac{dx_1}{dt} = 0$ or $\frac{dx_2}{dt} = 0$. The $\frac{dx_1}{dt} = 0$ nullclines intersect the $\frac{dx_2}{dt} = 0$ nullclines at steady states of the system. Define the function m_1 such that $x_2 = m_1(x_1)$ when $\frac{dx_1}{dt} = 0$ for $x_1 < h_1\rho_1$, and the function m_2 such that $x_1 = m_2(x_2)$ when $\frac{dx_2}{dt} = 0$ and $x_2 < h_2\rho_2$, then equation 3.4.2.1 yields

$$m_1(x_1) = \frac{x_1}{c_{21}}\left(\frac{e_1}{h_1\rho_1 - x_1} - c_{11}\right) \; , \qquad (3.4.2.9)$$

and equation 3.4.2.2 yields

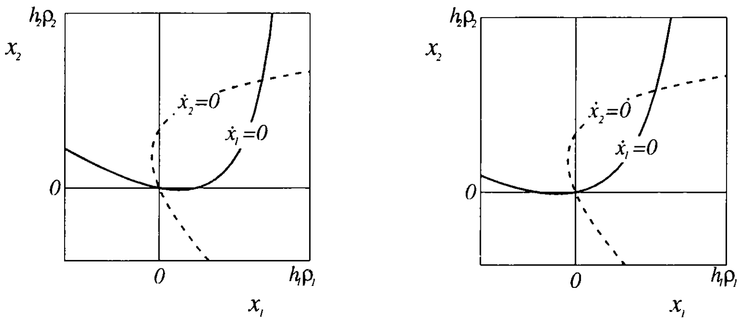
$$m_2(x_2) = \frac{x_2}{c_{12}}\left(\frac{e_2}{h_2\rho_2 - x_2} - c_{22}\right) \; . \qquad (3.4.2.10)$$

Note that $m_1(x_1) \to \infty$ as $x_1 \to -\infty$ and $x_1 \to h_1\rho_1$ and the curve intersects the x_1 axis at $x_1 = 0$ and $x_1 = h_1\rho_1 - e_1/c_{11}$.

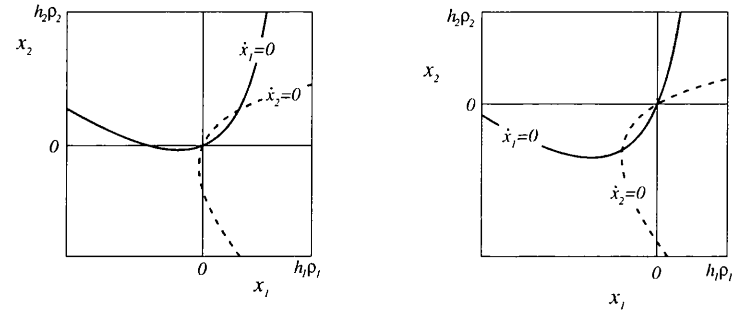
Now

$$\frac{d^2m_1}{dx_1{}^2} = \frac{2e_1h_1\rho_1}{c_{21}(h_1\rho_1 - x_1)^3} > 0 \; , \qquad (3.4.2.11)$$

on $x_1 < h_1\rho_1$ and it follows that m_1 is a monotonically increasing function when $max\{0, h_1\rho_1 - e_1/c_{11}\} < x_1 < h_1\rho_1$, and in particular when $x_1 > 0$ and $m_1(x_1) > 0$ (see the plots of figure 3-3). Due to the symmetry of the problem we deduce that m_2



(a) $R_0^1 > 1$ and $R_0^2 > 1$ (b) $R_0^2 > 1$



(c) $R_0^1 < 1$ and $R_0^2 < 1$ (d) $R_0^1 < 1$ and $R_0^2 < 1$

Figure 3-3: These plots indicate the nullcline curves satisfying $\frac{dx_1}{dt} = 0$ (the solid curve) and $\frac{dx_2}{dt} = 0$ (the dashed curve) when $R_0^i < 1$. These curves intersect at steady states. The metapopulation is not viable if and only if the gradient of the $\dot{x}_1 = 0$ nullcline at the origin is greater that of the $\dot{x}_2 = 0$ nulllcline and they are both positive, as in plot (d).

is also a monotonically increasing function when $x_2 > 0$ and $m_2(x_2) > 0$. From this we conclude that the nullclines can intersect at *most* once within the interior of χ.

Recall that the property that χ is invariant under the metapopulation dynamics stipulates that if the metapopulation persists then there exists at least one steady state within χ. We now show this is the unique steady state that satisfies $X > 0$. For there to exist another solution $X > 0$ of 3.4.2.8 it must satisfy $\hat{x}_1 < 0$ and $\hat{x}_2 < 0$. From equation 3.4.2.6 this implies that

$$0 > h_1\rho_1 - \frac{e_1 X}{c_{11}X + c_{21}} > h_1\rho_1 - \frac{e_1}{c_{11}} ,$$

i.e. that $R_0^1 < 1$. We also require $\hat{x}_2 < 0$ and thus, equivalently, $R_0^2 < 1$. Therefore for the case when either $R_0^1 > 1$ or $R_0^2 > 1$ we proved the claim. This is verified in plot (a) and plot (b) of figure 3-3.

The metapopulation can persist, however, if $R_0^1 < 1$ or $R_0^2 < 1$ provided that 3.4.1.2 is not satisfied (as in plot (c)). Plots (c) and (d) of figure 3-3 are plots of the nullcline curves when $R_0^1 < 1$ and $R_0^2 < 1$. Since the nullclines cross at the origin the monotonic nature of the gradients of the nullclines stipulates that the curves can cross at only one other place. From 3.4.2.11 we have that $\frac{dm_1}{dx_1}$, the gradient of the $\frac{dx_1}{dt} = 0$ nullcline, is monotonically increasing when $x_1 < h_1\rho_1$. Equivalenlty $\frac{dm_2}{dx_2}$ is monotonically increasing when $x_2 < h_2\rho_2$ and thus the gradient of the $\frac{dx_2}{dt} = 0$ nullcline, $1/\frac{dm_2}{dx_2}$, is monotonically decreasing with x_1. From these properties we deduce that the nullclines can only cross in the positive quadrant if and only if the gradients of these curves at the origin satisfy

$$\frac{dm_1}{dx_1}|_{x_1=0} < 1/\frac{dm_2}{dx_2}|_{x_2=0} , \tag{3.4.2.12}$$

as in plot (b). Upon evaluation, this condition becomes

$$\frac{e_1 - c_{11}h_1\rho_1}{c_{21}h_1\rho_1} < \frac{c_{12}h_2\rho_2}{e_2 - c_{22}h_2\rho_2} , \tag{3.4.2.13}$$

which is equivalent to the condition 3.4.1.2 (since both $R_0^1 < 1$ and $R_0^2 < 1$), i.e. that the metapopulation persists. This completes the proof. □

The last part of the proof also shows that there is no steady state in the interior of χ when the metapopulation does not persist.

The colonization and extinction rates will now be parameterized to model a variety of landscape structure scenarios.

3.5 Variation in Patch Structure

The qualities of a patch that ensure that it is habitable to a species can be somewhat varied when the niche base of the species is large. The quality of a habitat patch is not only measured by the size and abundance of the supporting resources, but also the types of resource represented within the patch. Patches can be composed of resources that are sufficient but not necessary for survival and breeding, and thus can be substituted by other patches. This type of heterogeneity can be modeled in much the same way to that of patch size or patch quality. Recognizing this structure may become important when we wish to consider the evolution of resource preferences (Tilman 1982). This is central to chapters that follow which are involved with the modelling of metapopulation competition and adaptive dynamics in structured landscapes.

We shall assume that patches are sorted into two classes. These classes could represent large and small patches, good quality and bad quality patches etc. Furthermore we assume that the variation in structure influences the rate that local populations produce immigrants and extinction risk. Populations inhabiting small or poor quality patches will generally have an increased extinction risk due to, among other things, demographic stochasticity and the synchrony in adverse environmental variation (Gabriel & Ferrière 2004). The influence of patch size on emigration may be less straightforward. Emigration rates may fall with local population size if dispersal is passive, however, dispersal behaviour may be mediated by patch suitability (Clobert et al. 2002, chapter 9). We shall assume, at this stage, that the type of patch encountered by a successful disperser does not depend upon natal patch type, but only on the relative frequencies of patches within the landscape.

Equations 3.4.0.9 and 3.4.0.10 can then be written in the form

$$\frac{dx_1}{dt} = (kc_1x_1 + kc_2x_2)(h_1\rho_1 - x_1) - e_1x_1 \qquad (3.5.0.14)$$

$$\frac{dx_2}{dt} = (c_1x_1 + c_2x_2)(h_2\rho_2 - x_2) - e_2x_2 \ , \qquad (3.5.0.15)$$

where x_1 and x_2 are the fraction of high and low quality patches, respectively, that are occupied. We assume that the extinction rates satisfy $e_1 < e_2$. The emigration rate of high quality patches, c_1, will be assumed greater than that of low quality patches, c_2. The parameter $k > 1$ models the relatively higher rate that high quality patches attract dispersers and support the foundation of new populations.

It is convenient to re-scale time to $t' = c_2t$, and to introduce $e_i' = \frac{e_i}{c_2}, i = 1, 2$ and $c = \frac{c_1}{c_2}$

$$\frac{dx_1}{dt'} = k(cx_1 + x_2)(h_1\rho_1 - x_1) - e_1'x_1 \ , \qquad (3.5.0.16)$$

$$\frac{dx_2}{dt'} = (cx_1 + x_2)(h_2\rho_2 - x_2) - e_2'x_2 \ . \qquad (3.5.0.17)$$

Dropping the prime notation for convenience, the system of equations in vector form is

$$\frac{d\mathbf{x}^T}{dt} = J_R\mathbf{x}^T - \mathbf{c}\cdot\mathbf{x}\begin{pmatrix} kx_1 \\ x_2 \end{pmatrix} = \Omega(\mathbf{x}) \ , \qquad (3.5.0.18)$$

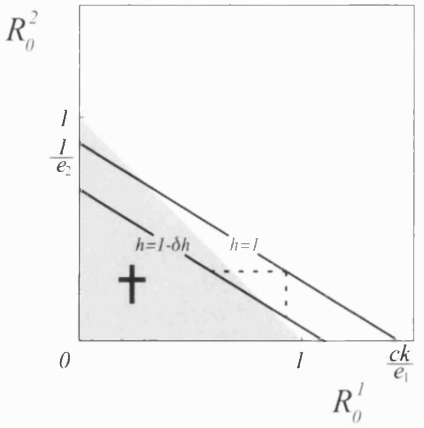


Figure 3-4: The shaded extinction region in R_0^1–R_0^2 parameter space for the model given by 3.5.0.18 for constant demographic parameters e_i and c_{ij}, $i, j = 1, 2$. $h = h_1\rho_1 + h_2\rho_2$ is the total fraction of habitable patches and constant along the solid lines. Type–1 patches are assumed to be more suitable than type–2 patches since $ck/e_1 > 1/e_2$ and furthermore, type–2 patches can not support a metapopulation in the absence of type–1 patches. Removing the type–1 patches is more detrimental than removing those type–2 as indicated by the dashed lines.

where $\mathbf{c} = (c, 1)$ and J_R as defined previously.

Extinction

In this model $c_{11}c_{22} - c_{12}c_{21} = 0$ reducing the three extinction conditions 3.4.1.6 to 3.4.1.8 to one:

$$R_0^1 + R_0^2 < 1 \; , \qquad (3.5.0.19)$$

where we recall that $R_0^i = \frac{c_{ii}h_i\rho_i}{e_i}$.

This condition can be reinterpreted in terms of the amount of habitable patches required for metapopulation to persist, as shown in figure 3-4. The total fraction of habitable patches, $h = h_1\rho_1 + h_2\rho_2$, is constant on the solid lines. The frequency of each patch type varies along the line: Extinction risk increasing intuitively as the frequency of type–1 patches decreases. Removing type–1 patches is also more detrimental to persistence as indicated by the dashed lines: In some cases removing fraction δh of patches of type–1 patches (i.e. moving horizontally in the parameter plane from the curve $h = 1$ to the curve $h = 1 - \delta h$) can lead to extinction whereas removing δh of type–2 patches (moving vertically) does not.

Viability

Since $c_{11}c_{22} = c_{12}c_{21}$ equation 3.4.2.8 reduces to a quadratic, simplifying the expression for the equilibrium fraction of occupied patches. A further observation can be made when the colonization of patches does not depend upon patch type, setting $k = 1$. Equation 3.5.0.18 then becomes

$$\frac{d\mathbf{x}^T}{dt} = (J_R - \mathbf{c}.\mathbf{x}I)\mathbf{x}^T \ . \tag{3.5.0.20}$$

Claim 4. The steady state $\hat{\mathbf{x}}$ is an eigenvector of J_R associated with the leading eigenvalue λ^+.

Proof. If $\mathbf{v}$ is a positive-valued eigenvector of J_R, with eigenvalue $\lambda^+ > 0$, then $\Omega(\mathbf{v}) = (\lambda^+ - \mathbf{c}.\mathbf{v})\mathbf{v}$. Since $\mathbf{c}.\mathbf{v} > 0$ we can re–scale $\mathbf{v}$ so that $\lambda^+ - \mathbf{c}.\mathbf{v} = 0$, so that $\mathbf{v}$ is the unique solution of $\Omega(\hat{\mathbf{v}}) = 0$, i.e. $\mathbf{v} = \hat{\mathbf{x}}$. ☐

$\mathbf{c} \cdot \hat{\mathbf{x}} = \lambda^+$ is a generalisation of equation 3.2.0.3 of box 3.1 but only holds if $c_{i1} = c_{i2}$, that is when the success of finding patch of a given type, and founding a new population, is only dependent upon the the relative frequency of that type of patch in the landscape. In this case the persistence condition can always be given in the linear form of equation 3.5.0.19.

3.6 Spatial Correlations in Landscape Structure

In section 3.5 we assumed that the composition of the dispersal neighborhood of each natal patch only depends upon the global parameters ρ_i, h_i and x_i, and not the habitat (or occupation) structure of the natal patch. This may be unreasonable when the distribution of patch types is spatially correlated. The distribution of uninhabitable patches following habitat loss may also have a spatial characteristic. Both of these properties may have consequences for the ecological dynamics of metapopulations not accounted for in section 3.5.

To model spatial patch type structure we now modify the colonization rates c_{ij}. Let i^σ denote an i-type patch in state $\sigma \in \{0, 1, 2\}$ where 0 represents uninhabitable patches, 1 habitable and empty, and 2 habitable and occupied. For convenience also let i^+ represent an i–type patch that is habitable (in state 1 or 2). If $\mathbb{P}\{i^\sigma/j^{\sigma'}\}$ is the conditional probability that a patch in the neighbourhood of an i–type patch in state

σ is of type j in state σ', then the we model the contribution that j-type patches make to the colonization of i-type patches by

$$k_{ji}x_j\mathbb{P}\{i^1/j^2\}\ . \tag{3.6.0.21}$$

k_{ji} combines the rate that occupied j type patches produce emigrants with the probability of surviving dispersal and the probability that an empty, habitable and type i patch, if found, becomes populated. We wish to write this in the form of equation 3.3.0.6 in order to determine c_{ij}. We continue to assume that the occupation state of a patch is independent of the occupation state of patches in the neighbourhood, the mean-field assumption. This is equivalent to assuming that

$$\mathbb{P}\{i^1/j^2\} = \mathbb{P}\{i^1/j^+\}\ , \tag{3.6.0.22}$$

and

$$\begin{aligned} \mathbb{P}\{i^1/j^+\} &= \mathbb{P}\{i^+/j^+\}\frac{\mathbb{P}\{i^1\}}{\mathbb{P}\{i^+\}} \\ &= \mathbb{P}\{i^+/j^+\}\frac{(h_i\rho_i - x_i)}{h_i\rho_i}\ . \end{aligned} \tag{3.6.0.23}$$

The final step in constructing the model requires distinguishing between both the spatial correlation in patch type and the spatial correlation in habitat.

3.6.1 Spatially Uniform Habitat Distribution

We shall first consider the case that the probability that a randomly choosen patch is habitable depends only upon the patch types of the neighbouring patches and not upon whether they are habitable.

This is modelled by assuming that

$$\mathbb{P}\{i^+/j^+\} = \mathbb{P}\{i^+/j\} = \mathbb{P}\{i/j\}\frac{\mathbb{P}\{i^+\}}{\mathbb{P}\{i\}} = \mathbb{P}\{i/j\}h_i\ ,$$

the colonization terms becoming

$$k_{ji}x_j\mathbb{P}\{i^1/j^2\} = k_{ji}x_j\mathbb{P}\{i/j\}\frac{(h_i\rho_i - x_i)}{\rho_i}\ . \tag{3.6.1.1}$$

Equating 3.3.0.6 with 3.6.1.1 with have

$$c_{ji} = k_{ji}\frac{\mathbb{P}\{i/j\}}{\rho_i} \ . \tag{3.6.1.2}$$

The quantities $\mathbb{P}\{i/j\}$ are not mutually independent as was demonstrated in the box 2.4 when representing a landscape by an infinite regular lattice with patches in one of two states. Thus, with $\rho = \rho_1$ and $q = \mathbb{P}\{1/1\}$, we find

$$\mathbb{P}\{2/1\} = 1 - q, \quad \mathbb{P}\{1/2\} = \frac{\rho(1-q)}{1-\rho} \ \text{and} \ \mathbb{P}\{2/2\} = \frac{1-2\rho+\rho q}{1-\rho} \ . \tag{3.6.1.3}$$

To keep the symmetry in the landscape variables transparent, it is convenient at times to retain the ρ_i notation and upon defining $q_i = \mathbb{P}\{i/i\}$ we have that

$$\mathbb{P}\{2/1\} = 1 - q_1 \ \text{and} \ \mathbb{P}\{1/2\} = 1 - q_2 \ .$$

Recall the condition that $0 \leq q_2 \leq 1$ enforces the constraint $q \geq 2 - \frac{1}{\rho}$. As with habitat state, we refer to patch types as aggregated when $q > \rho$ (since $\mathbb{P}\{i \ i\} > \rho_i^2$), dispersed when $q < \rho$, and uniformly distributed for the singular case $q = \rho$.

The model with spatially uniform habitat loss is

$$\begin{aligned} \frac{dx_1}{dt} &= (c_{11}x_1 + c_{21}x_2)(h_1\rho_1 - x_1) - e_1x_1 \ , && (3.6.1.4) \\ \frac{dx_2}{dt} &= (c_{12}x_1 + c_{22}x_2)(h_2\rho_2 - x_2) - e_2x_2 \ , && (3.6.1.5) \end{aligned}$$

where

$$\begin{aligned} c_{11} &= \frac{q_1}{\rho_1} \ , && (3.6.1.6) \\ c_{12} &= \frac{1-q_2}{1-\rho_2} = \frac{1-q_1}{1-\rho_1} = c_{21} \ , && (3.6.1.7) \\ c_{22} &= \frac{q_2}{\rho_2} \ . && (3.6.1.8) \end{aligned}$$

Extinction

To determine how the level of spatial aggregation or dispersion in patch type affects metapopulation persistence we shall de–couple q from the other parameters by considering how the quantities $\bar{R}_0^i = \frac{R_0^i}{c_{ii}} = \frac{h_i\rho_i}{e_i}$ affect persistence for a range of values of q.

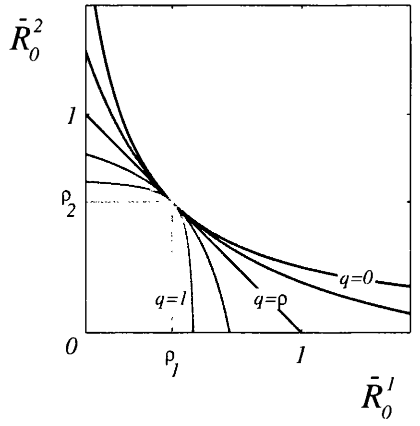


Figure 3-5: The extinction boundaries in $\bar{R}_0^1$-$\bar{R}_0^2$ parameter space for the model 3.6.1.5 when $\rho_1 = 0.4$ (and so q is only restricted to the range $0 \leq q \leq 1$). The extinction regions, for $q = 1, 0.8, 0.6, 0.4, 0.2, 0$, are bounded above by corresponding curve satisfying $\bar{R}_0^2 \leq \frac{\xi(c_{11}\bar{R}_0^1)}{c_{22}}$ (see 3.6.1.9 to 3.6.1.11). The point $(\bar{R}_0^1, \bar{R}_0^2) = (\rho_1, \rho_2)$ is the only such point that common to each extinction boundary, illustrating the monotonic dependency that the extinction boundary has upon the spatial aggregation parameter, q.

The extinction conditions, 3.4.1.6 to 3.4.1.8, in terms of $\bar{R}_0^1$ and $\bar{R}_0^2$ become

$$\bar{R}_0^1 \leq \frac{1}{c_{11}}, \tag{3.6.1.9}$$

$$\bar{R}_0^2 \leq \frac{1}{c_{22}}, \tag{3.6.1.10}$$

and

$$\bar{R}_0^2 \leq \frac{\xi(c_{11}\bar{R}_0^1)}{c_{22}}. \tag{3.6.1.11}$$

Figure 3-5 illustrates how extinction region in $\bar{R}_0^1$–$\bar{R}_0^2$ space, subject to ρ held constant, depends upon q. The level of spatial aggregation has a significant influence on the extinction region and hence the consequences of habitat loss and local extinction. The first observation of note is that increasing q reduces the extinction region. If $\bar{R}_0^2 = 0$ ($\bar{R}_0^1 = 0$) the metapopulation will only be able to inhabit type–1 (type–2) patches and the model can be reduced to the Levins model; we say that the metapopulation is endemic to type–1 (type–2) patches. If the metapopulation is endemic to type–i patches then $R_0 = R_0^i = \frac{h_i q_i}{e_i}$, an increasing function of q.

Another property of importance is the degree of convexity of the extinction boundary, determining how detrimental changing $\bar{R}_0^1$ or $\bar{R}_0^2$ is for persistence. Recall that the degree of convexity depends upon $\zeta = \frac{c_{11}c_{22} - c_{12}c_{21}}{c_{11}c_{22}} = \frac{q-\rho}{q(1-2\rho+\rho q)}$. The boundary is convex if $q < \rho$ and concave if $q > \rho$, as illustrated in figure 3-5. Since the extinction boundary is independent of q when $\bar{R}_0^1 = \rho$ and $\bar{R}_0^2 = 1-\rho$, the extinction region contracts as q increases. When $q > \rho$ decreasing either $\bar{R}_0^1$ or $\bar{R}_0^2$ only will have less impact, in general, than decreasing both. A reduction in $\bar{R}_0^i$ can be brought on by either a reduction in the fraction of habitable type i patches, $h_i\rho_i$, or by an increase in e_i, a reduction in patch i suitability. Therefore if a landscape is composed of aggregated elementary landscapes, protection efforts should be focused on single elementary landscapes. If $q < \rho$, this is no longer the case.

The effects of losing habitat depends not only on the aggregation of same-type patches but also on the present state of the landscape. These results suggest how sensitive a metapopulation can be to landscape configuration. 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 is also critical. If the initial loss in both patch types is relatively similar, reducing habitat in highly aggregated landscapes will be less detrimental to the metapopulation than if habitat loss is of one type. However, if the amounts of loss are initially quite different, losing habitat of the least abundant type minimizes the risk of extinction. For the case when $q < \rho$ the opposite behaviour is observed.

3.6.2 Aggregated and Dispersed Habitat Distribution

The process of habitat loss will seldom be spatially uniform (as discussed in the previous chapter). As in the case of patch type, the aggregated habitat loss can be included in this model. There are now sixteen ordered pairs of neighbouring patch states, $(2 \times 2)^2$, requiring sixteen equations to uniquely define the landscape. There are seven dependency relationships, one consisting from the property that

$$\sum_{i,j\ \sigma,\sigma'} \mathbb{P}\{i^{\sigma}\ j^{\sigma'}\} = 1 \ , \tag{3.6.2.1}$$

and six from the symmetry relationships

$$\mathbb{P}\{i^{\sigma}\ j^{\sigma'}\} = \mathbb{P}\{j^{\sigma'}\ i^{\sigma}\} \ , \tag{3.6.2.2}$$

reducing the number of parameters needed to nine. Two independent relationships conditions can be derived from

$$\mathbb{P}\{i\ j\} = \sum_{\sigma,\sigma'} \mathbb{P}\{i^{\sigma}\ j^{\sigma'}\}\ , \tag{3.6.2.3}$$

requiring the parameters ρ and q, reduces the number to seven and the condition that

$$\mathbb{P}\{i^{+}\} = \sum_{j,\sigma} \mathbb{P}\{i^{+}\ j^{\sigma}\}\ , \tag{3.6.2.4}$$

requiring the parameters h_1 and h_2, further reduce this to five. The final five require the definition of five parameters when describing the non–random distribution of habitable patches. For $i = 1, 2$ we choose the following parameters,

$$h_{ii} = \frac{\mathbb{P}\{i^{+}\ i^{+}\}}{\mathbb{P}\{i\ i\}}\ ,\quad h_{12} = \frac{\mathbb{P}\{1^{+}\ 2^{+}\}}{\mathbb{P}\{1\ 2\}}\ ,\quad d_{ii} = \frac{\mathbb{P}\{i^{+}\ i^{0}\}}{\mathbb{P}\{i\ i\}}\ , \tag{3.6.2.5}$$

subject to the following constraints:

$$h_{ii} \geq 0,\quad d_{ii} \geq 0,\quad h_{ii} + d_{ii} \leq 1,\quad 0 \leq h_{12} \leq 1\ . \tag{3.6.2.6}$$

The requirement that both $\mathbb{P}\{i^{+}\ i\} \leq \mathbb{P}\{i^{+}\}$ and $\mathbb{P}\{i^{+}\ j\} \leq \mathbb{P}\{i\ j\}$ yield the tighter constraint

$$\max\{0, 1 - \frac{1 - h_i}{q_i}\} \leq h_{ii} + d_{ii} \leq \min\{1, \frac{h_i}{q_i}\}\ . \tag{3.6.2.7}$$

Finally, the requirement that

$$0 \leq \mathbb{P}\{1^{+}\ 2^{0}\},\quad 0 \leq \mathbb{P}\{1^{0}\ 2^{+}\}\ , \tag{3.6.2.8}$$

and

$$\mathbb{P}\{1^{+}\ 2^{0}\} + \mathbb{P}\{1^{0}\ 2^{+}\} \leq \mathbb{P}\{1\ 2\} - \mathbb{P}\{1^{+}\ 2^{+}\}\ , \tag{3.6.2.9}$$

yields

$$\max\{0, \sum_{i} \frac{h_i - q_i(h_{ii} + d_{ii})}{(1 - q_i)} - 1\} \leq h_{12} \leq \min_{i} \frac{h_i - q_i(h_{ii} + d_{ii})}{(1 - q_i)}\ . \tag{3.6.2.10}$$

The probability tree structure of the diagram in figure 3-6 helps to make these conditions a bit clearer.

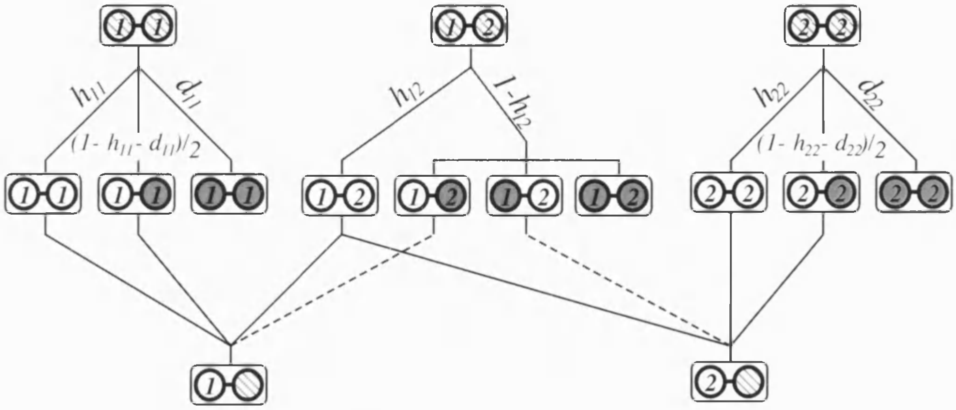


Figure 3-6: This tree diagram represents the conditional probability tree and verifies that the number of extra parameters required to determine the landscape with habitat loss locally correlated (as compared to a landscape with uniformly distributed habitat loss) is five (h_{11}, $h_2 2$, d_{11}, d_{22} and h_{12}). The patches are represented by white circles if habitable, shaded if uninhabitable and hatched when unspecified. The dashed branches indicate how the fraction of neighbouring patch pairs in the 1^+2^0 and 1^02^+ configuration can be determined from the fraction of 1^+-type and 2^+-type patches respectively.

From equations 3.6.0.21 and 3.6.0.23 we have

$$c_{ji} = \frac{k_{ji}\mathbb{P}(i^+j^+)}{h_i\rho_i h_j\rho_j} \ . \tag{3.6.2.11}$$

With $k_{ji} = 1$, equations 3.4.0.9 and 3.4.0.10 become

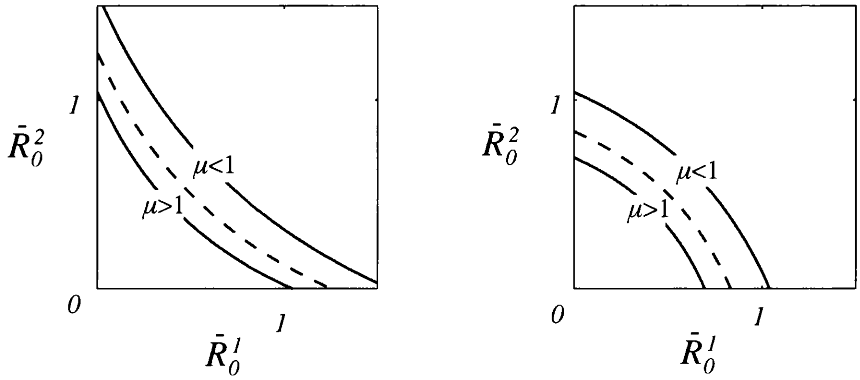
$$\frac{dx_1}{dt} = \left(\frac{h_{11}q_1}{h_1^2\rho_1}x_1 + \frac{h_{12}(1-q_1)}{h_1h_2(1-\rho_1)}x_2\right)(h_1\rho_1 - x_1) - e_1x_1 \ , \tag{3.6.2.12}$$

$$\frac{dx_2}{dt} = \left(\frac{h_{12}(1-q_2)}{h_1h_2(1-\rho_2)}x_1 + \frac{h_{22}q_2}{h_2^2\rho_2}x_2\right)(h_2\rho_2 - x_2) - e_2x_2 \ . \tag{3.6.2.13}$$

Note that d_{11} and d_{22} do not appear explicitly in the model equations, yet restrict the range of the parameters that do.

Extinction

Recall that the condition for persistence can be given in terms of the parameter $\bar{R}_0^i = \frac{\bar{R}_0^i}{c_{ii}} = \frac{h_i\rho_i}{e_i}$ (3.6.1.9 to 3.6.1.11). As with q (shown in the previous section), increasing h_{ii} will decrease the axis intercepts of the extinction boundary in the $\bar{R}_0^1$–$\bar{R}_0^2$ plane.



(a) $q = 0.4 < \rho$ (b) $q = 0.6 > \rho$

Figure 3-7: The extinction regions in $\bar{R}_0^1$–$\bar{R}_0^2$ parameter space. The solid curves indicate extinction boundaries for cases when $\mu \neq 1$ (see main text) with the dashed curve indicating $\mu = 1$ case. $\rho = 0.5$ in each plot.

The curvature of the boundary will now depend upon h_{11}, h_{12}, h_{22} as well as ρ and q since

$$\zeta = \frac{1}{h_{11}h_{22}q_1q_2}\left(h_{11}h_{22}q_1q_2 - h_{12}^2(1-q_1)(1-q_2)\right) , \qquad (3.6.2.14)$$

and thus ζ increases with h_{ii} and decrease with h_{12}.

3.6.3 Locally Correlated Patch–Type Independent Habitat Loss.

The assumption that all patches are equally connected to each other, regardless of patch type or habitat state, requires the explicit account of whether uninhabitable patches are of type 1 or type 2. For the following limiting case the five extra explicit parameters can be reduced to just one. Suppose that the distribution of habitable patches is independent of patch type yet locally correlated so that $h_2 = h_1 = h < 1$ and $\frac{\mathbb{P}\{i^+\ j^+\}}{\mathbb{P}\{i^+\}\mathbb{P}\{j^+\}}$ is independent of i and j. Letting $\mu = \frac{\mathbb{P}\{i^+\ j^+\}}{\mathbb{P}\{i^+\}\mathbb{P}\{j^+\}}$ for $i, j = 1, 2$, dividing equations 3.6.2.12 and 3.6.2.13 by μ yields

$$\frac{dx_1}{d\tau} = (h\rho_1 - x_1)\left(\frac{q_1}{\rho_1}x_1 + \frac{(1-q_1)}{(1-\rho_1)}x_2\right) - \frac{e_1}{\mu}x_1 \qquad (3.6.3.1)$$

$$\frac{dx_2}{d\tau} = (h\rho_2 - x_2)\left(\frac{(1-q_2)}{(1-\rho_2)}x_1 + \frac{q_2}{\rho_2}x_2\right) - \frac{e_2}{\mu}x_2 , \qquad (3.6.3.2)$$

where $\tau = \mu t$ and μ is constrained the consistency conditions above.

In this case the persistence boundary in ($\bar{R}_0^1$-$\bar{R}_0^2$) space is a projection of the $\mu = 1$

boundary: That is

$$\bar{R}_0^2 = \frac{\xi(\mu \bar{R}_0^1)}{\mu}, \tag{3.6.3.3}$$

where $\bar{R}_0^2 = \xi(\bar{R}_0^1)$ recall is the equation of the boundary when $\mu = 1$. Therefore increasing aggregation in habitable patches, μ, decreases the extinction region as illustrated in figure 3-7.

3.7 Relaxing the Mean–field Assumption

In the previous chapter we introduced the pair approximation (PA) method for modeling local correlations between dynamic patch states (see box 2.3). We shall now extend the model to incorporate two spatially correlated habitat types. The single patch–type PA model distinguished three patch states (uninhabitable, empty and habitable, occupied) and nine neighbouring pairs states, requiring three dynamic equations to supplement the six equations that were derived from symmetry conditions and the conservation of habitable and uninhabitable patches. We shall extend the model by assuming that all patches are habitable, yielding four patch states and thus sixteen pair states. We utilise the six symmetry equations together with the three landscape equations that describe the conservation of patch–types frequencies and spatial correlation, reducing the number of required dynamic equations to seven.

We begin with the equation for x_i^+, $i = 1, 2$:

$$\frac{dx_i^+}{dt} = x_i^+ \mathbb{P}\{i^0/1^+\} + x_2^+ \mathbb{P}\{i^0/2^+\} - e_i x_i^+ \ , \tag{3.7.0.4}$$

where the superscripts on the state variable x_i denote the occupation state and the dynamic variable $\mathbb{P}\{i^0/j^+\}$ is the probability that the neighbour of an occupied j–type patch is empty and of type i.

Using the definition of conditional probability we have that

$$\mathbb{P}\{i^0/j^+\} = \frac{x_{ij}^{+0}}{x_j^+} \ , \tag{3.7.0.5}$$

where x_{ij}^{+0} is the fraction of patch–pairs in the ordered state, the first type i and occupied and the second type j and empty. Thus equation 3.7.0.4 becomes

$$\frac{dx_i^+}{dt} = x_{1i}^{+0} + x_{2i}^{+0} - e_i x_i^+ \ . \tag{3.7.0.6}$$

The additional five equations will be chosen to track the dynamics of x_{11}^{++}, x_{11}^{+0}, x_{22}^{+0}, x_{22}^{+0} and x_{12}^{++} as follows: The dynamic of x_{ii}^{++} are governed by the equation

$$\frac{dx_{ii}^{++}}{dt} = \underbrace{\frac{1}{k}(x_{ii}^{+0} + x_{ii}^{0+})}_{\text{Pair Interaction}} -2e_i x_{ii}^{++} + \frac{k-1}{k}(x_{ii}^{+0} + x_{ii}^{0+}) \underbrace{(\mathbb{P}\{1^+/i^0\} + \mathbb{P}\{2^+/i^0\})}_{\text{Pair Approximation}} , \tag{3.7.0.7}$$

where the ordering of the superscripted occupation state corresponds to that of the subscripted habitat type. Recall that the pair approximation, employed here, is based upon the assumption that the neighbour of an empty i type patch, given that one neighbour is occupied and of type j, is $\mathbb{P}\{i^0/j^+\}$, i.e. that it is independent of the state of this single neighbour.

From the symmetry condition, $x_{ii}^{+0} = x_{ii}^{0+}$, and the conditional probability definition, this becomes

$$\frac{dx_{ii}^{++}}{dt} = \frac{2}{k} x_{ii}^{+0} - 2e_i x_{ii}^{++} + 2\kappa x_{ii}^{+0} \left(\frac{x_{1i}^{+0} + x_{2i}^{+0}}{x_i^0} \right) , \tag{3.7.0.8}$$

where $\kappa = \frac{k-1}{k}$. Applying the standard pair approximation method, the equations for x_{ii}^{+0} are

$$\frac{dx_{ii}^{+0}}{dt} = -\frac{x_{ii}^{+0}}{k} + e_i(x_{ii}^{++} - x_{ii}^{+0}) + \kappa(x_{ii}^{00} - x_{ii}^{+0}) \left(\frac{x_{1i}^{+0} + x_{2i}^{+0}}{x_i^0} \right) . \tag{3.7.0.9}$$

Finally the dynamics of x_{12}^{++} are governed by the equation

$$\begin{aligned} \frac{dx_{12}^{++}}{dt} = \frac{1}{k}(x_{12}^{0+} + x_{12}^{+0}) - (e_1 + e_2) x_{12}^{++} & \\ + \kappa x_{12}^{0+} \left(\frac{x_{11}^{+0} + x_{21}^{+0}}{x_1^0} \right) + \kappa x_{12}^{+0} \left(\frac{x_{12}^{+0} + x_{22}^{+0}}{x_2^0} \right) & . \end{aligned} \tag{3.7.0.10}$$

Equations 3.7.0.6, 3.7.0.8, 3.7.0.9 and 3.7.0.10 must now be given in terms of the landscape variables, $\rho_1 = \rho$, $\rho_2 = 1 - \rho$, $q_1 = q$ and $q_2 = \frac{1-2\rho+\rho q}{1-\rho}$, and the state variables x_1^+, x_2^+ x_{11}^{++}, x_{11}^{+0}, x_{22}^{+0}, x_{22}^{+0} and x_{12}^{++}: The conservation of singlet densities yields

$$x_1^0 = \rho_1 - x_1^+ , \tag{3.7.0.11}$$

$$x_2^0 = \rho_2 - x_2^+ . \tag{3.7.0.12}$$

The conservation in the densities of 11–type and 22–type neighbouring patch pairs yields

$$x_{11}^{00} = \rho_1 q_1 - x_{11}^{++} - 2x_{11}^{+0}\,, \tag{3.7.0.13}$$

$$x_{22}^{00} = \rho_2 q_2 - x_{22}^{++} - 2x_{22}^{+0}\,. \tag{3.7.0.14}$$

Since the neighbour of an occupied patch is in one of four states we also have

$$x_{12}^{0+} = x_2^{+} - x_{12}^{++} - x_{22}^{+0} - x_{22}^{++}\,, \tag{3.7.0.15}$$

$$x_{12}^{+0} = x_1^{+} - x_{12}^{++} - x_{11}^{+0} - x_{11}^{++}\,. \tag{3.7.0.16}$$

The system of equations can be written as

$$
\begin{aligned}
\frac{dx_1^+}{dt} &= x_{11}^{+0} + x_2^+ - x_{12}^{++} - x_{22}^{+0} - x_{22}^{++} - e_1 x_1^+ \ , \\
\frac{dx_{11}^{++}}{dt} &= \frac{2}{k} x_{11}^{+0} - 2e_1 x_{11}^{++} \\
&\quad + \frac{2(k-1)}{k} x_{11}^{+0} \left(\frac{x_{11}^{+0} + x_2^+ - x_{12}^{++} - x_{22}^{+0} - x_{22}^{++}}{\rho_1 - x_1^+} \right) \ , \\
\frac{dx_{11}^{+0}}{dt} &= -\frac{x_{11}^{+0}}{k} + e_1 (x_{11}^{++} - x_{11}^{+0}) \\
&\quad + \kappa(\rho_1 q_1 - x_{11}^{++} - 3x_{11}^{+0}) \left(\frac{x_{11}^{+0} + x_2^+ - x_{12}^{++} - x_{22}^{+0} - x_{22}^{++}}{\rho_1 - x_1^+} \right) \ , \\
\frac{dx_{12}^{++}}{dt} &= \frac{1}{k} (x_1^+ - x_{11}^{+0} - x_{11}^{++} - 2x_{12}^{++} + x_2^+ - x_{22}^{+0} - x_{22}^{++}) - (e_1 + e_2) x_{12}^{++} \\
&\quad + \kappa(x_2^+ - x_{12}^{++} - x_{22}^{+0} - x_{22}^{++}) \left(\frac{x_{11}^{+0} - x_{12}^{++} + x_2^+ - x_{22}^{+0} - x_{22}^{++}}{\rho_1 - x_1^+} \right) \\
&\quad + \kappa(x_1^+ - x_{12}^{++} - x_{11}^{+0} - x_{11}^{++}) \left(\frac{x_1^+ - x_{11}^{+0} - x_{11}^{++} + x_{22}^{+0} - x_{12}^{++}}{\rho_2 - x_2^+} \right) \ , \\
\frac{dx_2^+}{dt} &= x_{22}^{+0} + x_1^+ - x_{12}^{++} - x_{11}^{+0} - x_{11}^{++} - e_2 x_2^+ \ , \\
\frac{dx_{22}^{++}}{dt} &= \frac{2}{k} x_{22}^{+0} - 2e_2 x_{22}^{++} \\
&\quad + 2\kappa x_{22}^{+0} \left(\frac{x_{22}^{+0} + x_1^+ - x_{12}^{++} - x_{11}^{+0} - x_{11}^{++}}{\rho_2 - x_2^+} \right) \ , \\
\frac{dx_{22}^{+0}}{dt} &= -\frac{x_{22}^{+0}}{k} + e_2 (x_{22}^{++} - x_{22}^{+0}) \\
&\quad + \kappa(\rho_2 q_2 - x_{22}^{++} - 3x_{22}^{+0}) \left(\frac{x_{22}^{+0} + x_1^+ - x_{12}^{++} - x_{11}^{+0} - x_{11}^{++}}{\rho_2 - x_2^+} \right) \ .
\end{aligned}
\tag{3.7.0.17}
$$

This system of equations is difficult to analyze fully but we can obtain the persistence condition. Let $\mathbf{x}$ be the state vector $\mathbf{x} = (x_1^+, x_{11}^{++}, x_{11}^{+0}, x_{12}^{++}, x_2^+, x_{22}^{++}, x_{22}^{+0})$. Note the fraction of patches or pairs of patches represented by the state variables of 3.7.0.17, has at least one occupied state. The extinction state of the metapopulation is thus $\mathbf{x} = \mathbf{0}$, and a steady state. The stability of the extinction state can be determined in terms of the leading eigenvalues of the jacobian matrix of 3.7.0.17 evaluated at $\mathbf{0}$.

The jacobian matrix J_0 satisfies

$$J_0 = \begin{pmatrix} -e_1 & 0 & 1 & -1 & 1 & -1 & -1 \\ 0 & -2e_1 & \frac{2}{k} & 0 & 0 & 0 & 0 \\ 0 & e_1 & \kappa q_1 - \frac{1}{k} - e_1 & -\kappa q_1 & \kappa q_1 & -\kappa q_1 & -\kappa q_1 \\ \frac{1}{k} & -\frac{1}{k} & -\frac{1}{k} & -\frac{2}{k} - e_1 - e_2 & \frac{1}{k} & -\frac{1}{k} & -\frac{1}{k} \\ 1 & -1 & -1 & -1 & -e_2 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & -2e_2 & \frac{2}{k} \\ \kappa q_2 & -\kappa q_2 & -\kappa q_2 & -\kappa q_2 & 0 & e_2 & \kappa q_2 - \frac{1}{k} - e_2 \end{pmatrix}, \tag{3.7.0.18}$$

where $[J_0]_{ij}$ is the partial derivative with respect to the jth component of $\mathbf{x}$ of right hand–side of the i–th equation of 3.7.0.17, and evaluated at $\mathbf{0}$.

Claim 5. The extinction boundary satisfies

$$R_0^2 = \kappa\xi\left(\frac{R_0^1}{\kappa}\right), \tag{3.7.0.19}$$

where the function ξ gives the mean–field boundary as defined by equation 3.4.1.8.

We have only been able to verify this claim numerically, combined with the following argument: $\det(J_0) = 0$ when $R_0^2 = \kappa\xi(R_0^1/\kappa)$, and although we omit a presentation of this calculation, it can be computed symbolically (i.e. with *maple*). Thus 0 is an eigenvalue of the system linearized about the origin when 3.7.0.19 holds. Also, we claim, this is the eigenvalue with greatest real part when 3.7.0.19 holds. We can only verify this numerically in general, but it can be proved directly for two cases:

When $e_1 = e_2$ equation 3.7.0.19 reduces to $e_1 < \kappa$. In this case the system is identical to the two–state system with patches either occupied or empty, as analysed by Matsuda et al. (1992). The extinction conditions can be obtained from equation 2.4.3.1 by setting $e = e_1$ and $q = h = 1$.

The other case is the limiting case when e_2 (or equivalently e_1) tends to infinity. The persistence condition of the above system then becomes $e_1 < \kappa q_1$. Since the system in this case can be reduced to one of three state (Hiebeler 2004) with the type 2 patches representing uninhabitable patches, the model presented in box 2.3 of chapter 2 confirms this result (equation 2.4.3.1 with $e = e_1$ and $q = q_1$).

This result suggests that the extinction boundary (as in the case with locally correlated habitat loss) is a projection by the factor κ of the mean–field extinction boundary predicted by the generalized Levins model.

3.8 Discussion

In this chapter we have demonstrated how the Levins model can be extended to model heterogeneity in patch resource type. Restricting to two types of resource patch, we have shown that persistence depends upon the fraction of patches of each type that are habitable, the extinction risks corresponding to each patch type, and the distribution of patch types.

We have distinguished between aggregated and dispersed landscapes. In aggregated landscape the probability that dispersers encounter patches that are identical to their natal patch exceeds the probability that a patch picked uniformly at random from the landscape is of that type. For dispersed landscapes the opposite is true. The degree of aggregation/dispersion in real landscapes will depend upon landscape–ecological processes (Ingegnoli 2002): Landscapes that have been shaped by man (e.g. for agricultural purposes) may show characteristic distributions that have ecological consequences for inhabiting metapopulations. As habitats are destroyed the patterns of loss will also affect the negative impact upon residents. We have shown that the removing habitat that is predominantly of one type will be more detrimental if patch types are dispersed than if they are aggregated, whereas removing habitat in a more uniform manner will be more detrimental when landscapes are aggregated. This simple result has important implication for conservation and landscape planning.

Our results also suggest that increasing the degree of aggregation in the habitat destruction process decreases the detriment in terms of metapopulation persistence. This principle was discussed in chapter 2 and naturally extends to heterogeneous landscapes.

We have found that modelling the dynamics of spatial correlation in habitat occupation, using the pair–approximation method, is analytically difficult when there is diversity in patch types. We have verified without a rigorous proof that the persistence condition is a natural extension of the mean–field model: If the migration process is global (dispersers can reach all patches in the landscape with equal probability), or that the distribution of patch type is uniform, then the 'dyad heuristic' for persistence as described by Levin & Durrett (1996) will still hold. The dyad heuristic states that the expected number of patches colonized by an occupied neighbouring pair of patches (the colonisation rate of the pair will $C = 2c(k-1)/k$, and not $2c$, since only $k-1$ of the neighbours of each patch are empty) before the extinction of either patch (that occurs at rate $E = 2e$) in an otherwise empty landscape is

$$R_0^{pa} = \frac{C}{E} = \kappa R_0^{mf} \ ,$$

where $R_0^{mf} = c/e$ is the basic reproductive ratio predicted by mean–field theory. Persistence is then equivalent to $R_0^{pa} > 1$. With uniformly distributed habitat of two types we have verified that the persistence condition is also in the form

$$R_0^{pa} = \kappa R_0^{mf} > 1 \ ,$$

where $R_0^{mf} = R_0^1 + R_0^2$; the sum of the the patch type specific $R_0^i = \frac{\rho_i}{e_i}$ (since $h_i = 1$).

If patches are not uniformly distributed then R_0^{mf} is not a linear function of the patch type specific R_0^i. In this case we derived an alternative condition for persistence that was of the form $R_0^2 > \xi^{mf}(R_0^1)$. We have verified that scaling the R_0^i by κ, as in the case above, will still yield the PA persistence condition that

$$R_0^2 = \xi^{pa}(R_0^1) = \kappa \xi^{mf}\left(\frac{R_0^1}{\kappa}\right) > 1 \ .$$

We hypothesise that the result would extend to higher dimensional system (more than two patch types) so that if the mean–field persistence condition can be given in the form $R_0^{mf}(R_0^1, R_0^2, ..., R_0^m) > 1$ for m patches, then the pair–approximation model would yield the condition

$$R_0^{pa}(R_0^1, R_0^2, ..., R_0^m) = \kappa R_0^{mf}\left(\frac{R_0^1}{\kappa}, \frac{R_0^2}{\kappa}, ..., \frac{R_0^m}{\kappa}\right) > 1 \ .$$

Chapter 4

Metapopulation–Level Competition in Heterogeneous Landscapes

4.1 Chapter Outline

In this chapter we investigate metapopulation competition within heterogeneous landscapes. The model developed and analyzed is based upon the model presented in chapter 3. Of particular interest is finding conditions for competitive coexistence and we show that landscape structure strongly influences which species can coexist.

Determining the condition for an introduced species to invade a metapopulation that comprises of one or more resident species is key to investigating competition and characterising the evolution dynamics of the system (driven by competition between resident populations and *sufficiently similar* mutant populations introduced at low density) as modelled in the proceeding chapters.

4.2 Introduction

Patch networks may support metapopulations of more than one species. Interacting species may compete for habitat patches affecting both the extinction and colonization processes of each species (Hanski 1999*a*, chapter 7). Competition may occur at a local level when different species inhabit the same patch and at a global level for empty habitat patches. A competitive advantages at one of these scales may not necessarily translate as an advantage at the other and models that incorporate the dynamics at both of these two scales have been recently developed to investigate such phenomena (Gyllenberg & Metz 2001, Parvinen 2002).

Models of local competition abound the literature, extending the pioneering work of Lotka (1925) and Volterra (1926). These models usually satisfy the *competitive exclusion principle* (sometimes referred to as Gause's Law) that for a single population of two species, *limited identically by a common resource* and closed from immigration, one species will always have an advantage over the other leading to the extinction of the inferior competitor, thus preventing *coexistence.* Populations coexistence when their long term growth rates are simultaneously zero.

The competitive exclusion principle applies to any discrete number of resources as stated by Meszéna et al. (2006):

> 'The *structurally* stable coexistence of N species requires $M \geq N$, where M is the dimension of population regulation.'

The dimension of population regulation in this context refers to the number of different resource types regulating the population dynamics. A species is distinguished according to the utilisation of each resource and represented by an M–dimensional vector. The system of N species is structurally stable if and only if each species is contained within an M–dimensional open subset of the *species space* whereby each species of this subset can also coexist with the other $N-1$ species. The principle has also been demonstrated to apply to resource continua in terms of the *limiting similarity* of species (Meszéna et al. 2006).

When a local population is removed from isolation, an inferior species may be rescued from competitive exclusion. This can occur when the hierarchy of competitive ability varies between patches as a result of resource heterogeneity in the landscape. The resultant niche structure is thus a mechanism for harbouring species diversity (MacArthur & Levins 1967). This effect is particularly intuitive for cases when dispersal rates are low so that populations remain relatively closed. If dispersal is relatively high and differing competitor types frequently interact within patches, the effects of the relatively high local adaptation of competitive superiority may be overshadowed by a high influx of inferior competitor types (Holt 1995).

In the extreme case landscape heterogeneity can cause source–sink population structure (Pulliam 1988) whereby the populations of poor patches have negative intrinsic growth rate yet remain viable because of high immigration rates. This structure can prevent mutant competitor types that are more adapted to the poor patches from becoming established regionally. This is an example of a metapopulation level *priority effect* whereby the adaptive makeup of the initial populations can prevent other adaptive types from invading even though they may be more suitable at inhabiting the landscape.

Inferior species can also exploit inherent advantages of the dispersal process. At the metapopulation level, increased dispersal may well translate into a competitive advantage (Hamilton & May 1977). Even when habitat patches are uniform and one species is competitively superior (preventing local coexistence), an inferior competitor with superior colonization abilities can better exploit empty habitat patches. Regional coexistence may then be maintained via a competition–colonization trade–off. This mechanism has been termed fugitive coexistence by Hutchinson (1951) and later studied by Nee & May (1992), Hanski & Zhang (1993) and others.

Thus the success of an individual, and her descendants, not only depend upon local interactions within a patch, but also the ability to take advantage of other patches by dispersal (Poethke & Hovestadt 2001, Poethke et al. 2003, Parvinen 2002) as reviewed by Parvinen (2004). In a model developed by Brachet et al. (1999) the relationship between patch–type dependent dispersal and patch–type–adaptation was investigated in terms of metapopulation viability. They found that intermediate rates of dispersal may sometimes lead to extinction and that slight modifications in the fraction of patches of each type (or as they term elementary habitat) can have severe consequences for viability.

Investigating how a community of species, each with a particular suite of abilities, interacts at the metapopulation level may help to explain the levels of diversity found in real fragmented landscapes. This chapter will focus on how landscape structures, as modelled in chapter 3, affects the competitive interactions of species that differ only in terms of patch specialisation, modelled here via patch–type–specific extinction rates. In keeping with the Levins framework of assuming no population structure, we restrict interactions to the competition for empty patches only.

4.3 Modelling Metapopulation Competition in a Two Patch Landscape

Models of both metapopulation intra–specific (between same competitor types) and inter-specific (between distinct competitor types) competition are often analytically intractable when the dynamics within patches are coupled with the dynamics across patches. To address how landscape structure can affect competitive interactions between different populations we shall make assumptions to separate these two processes. Assume that the interspecific interactions of different competitor types (species or variants of a species), that compete for the same habitat patches, are limited to the competition for empty patches so that populated habitat patches only contain one type of individual at any time. This means that when a patch is occupied the established population does not allow the influx of any new dispersers. Such a scenario is known as *lottery competition* (Sale 1977).

Ecological scenarios where this assumption is well met include patchy landscapes where only one individual can occupy a given patch at any one time. Some plant systems provide an example of this; competition for light is heavily asymmetric between seedlings and adult plants, so that the probability of seed, dispersed from a neighbouring patch, developing in a populated patch can be very small, protecting the adult plant. In this chapter we focus on biological situations where there is a strong *founder effect*, when the chances of maturation are severely reduced for dispersers arriving in patches with established populations. With this assumption the explicit modelling of local population dynamics can be neglected and we can focus exclusively on how metapopulation level processes govern competitive ability (we investigate the consequences of relaxing this asumption in chapter 7).

Let competitor type n have extinction rate e_i^n in patch type i and let it colonize patch j from i at rate c_{ij}^n. We refer to the matrix $C^n = (c_{ij}^n)$ and vector $\mathbf{e}^n = (e_i^n)$ as the *strategy* of competitor n. The term strategy is motivated by the game theory literature where competing agents are distinguished by behavioural strategies. Then for two patch types and N competitor types the model is given by the $2N$ differential equations

$$\frac{dx_i^n}{dt} = \sum_j c_{ji}^n x_j^n (h_i\rho_i - \sum_m x_i^m) - e_i^n x_i^n =: \Omega_i^n(x_1^1, x_2^1, ..., x_1^N, x_2^N) \ , \tag{4.3.0.1}$$

for $i = 1, 2$ and $n = 1, ..., N$, where x_i^n is the fraction of all patches that are of type i and occupied by competitor type n. Defining $\mathbf{x} = (x_1^1, x_2^1, ..., x_1^N, x_2^N)^T$, $\Omega = (\Omega_1^1, \Omega_2^1, ..., \Omega_1^N, \Omega_2^N)^T$, this may be written

$$\frac{d\mathbf{x}}{dt} = \Omega(\mathbf{x}) \ . \tag{4.3.0.2}$$

We shall begin by assuming the general form of c_{ji} given in chapter 3 by equation 3.6.2.11:

$$c_{ji}^n = \frac{k_{ji}^n \mathbb{P}(i^+ j^+)}{h_i\rho_i h_j\rho_j} \ .$$

The component k_{ji}^n is the only part that can vary between competitor types, assuming that the dispersal neighbourhood is fixed.

With two patch types and two competitor types we write $\mathbf{x} = (x_1, x_2, x_1', x_2')^T$, and the system consists of the following four equations:

$$\begin{aligned}
\frac{dx_1}{dt} &= (c_{11}x_1 + c_{21}x_2)(h_1\rho_1 - x_1 - x_1') - e_1 x_1 \ , && (4.3.0.3)\\
\frac{dx_2}{dt} &= (c_{12}x_1 + c_{22}x_2)(h_2\rho_2 - x_2 - x_2') - e_2 x_2 \ , && (4.3.0.4)\\
\frac{dx_1'}{dt} &= (c_{11}'x_1' + c_{21}'x_2')(h_1\rho_1 - x_1 - x_1') - e_1' x_1' \ , && (4.3.0.5)\\
\frac{dx_2'}{dt} &= (c_{12}'x_1' + c_{22}'x_2')(h_2\rho_2 - x_2 - x_2') - e_2' x_2' \ , && (4.3.0.6)
\end{aligned}$$

where primed variables correspond to the second competitor type. The study of competition will begin by addressing the central (evolutionary) question: What are the conditions for an initially rare competitor to invade a single-resident (monomorphic) metapopulation? As with the analysis of the monomorphic ecology, we proceed using definitions and techniques from dynamic systems theory.

4.4 Invasion of a Monomorphic Metapopulation

Suppose a viable monomorphic resident, with extinction rates e_i and colonization rates c_{ij}, is at the (stable) non-trivial steady state $(\hat{x}_1, \hat{x}_2)$ as determined by equations

3.4.2.6, 3.4.2.7 and 3.4.2.8 of chapter 3. A competitor with extinctions rates e_i' and colonization rates c_{ij}' will invade a resident at equilibrium if and only if the monomorphic steady state $\hat{\mathbf{x}} = (\hat{x}_1, \hat{x}_2, 0, 0)^T$, representing the resident at dynamic equilibrium in the absence of the competitor, is unstable.

Invasion is determined by the linear stability of the system given by equations 4.3.0.3 to 4.3.0.6. The system linearized about the state $\mathbf{x}_0$ can be written as

$$\dot{\mathbf{x}} = J(\mathbf{x}_0)(\mathbf{x} - \mathbf{x}_0)^T ,$$

where the 4 × 4 Jacobian matrix , $J(\mathbf{x}_0)$, is given by

$$[J(\mathbf{x}_0)]_{mn} = \frac{\partial \Omega_m(\mathbf{x}_0)}{\partial x_n} , \tag{4.4.0.7}$$

and where Ω_m is the mth component of Ω and x_n is the nth component of $\mathbf{x}$. Evaluating J at the monomorphic steady state $\hat{\mathbf{x}} = (\hat{x}_1, \hat{x}_2, 0, 0)^T$ gives

$$J = \begin{pmatrix} J_R & \star \\ \mathbf{0} & J_M \end{pmatrix} , \tag{4.4.0.8}$$

where J_R is as defined by equation 3.4.2.3, $\star$ represents a 2 × 2 matrix with inconsequential entries, and

$$J_M(e_1', e_2', e_1, e_2) = \begin{pmatrix} c_{11}'(h_1\rho_1 - \hat{x}_1) - e_1' & c_{21}'(h_1\rho_1 - \hat{x}_1) \\ c_{12}'(h_2\rho_2 - \hat{x}_2) & c_{22}'(h_2\rho_2 - \hat{x}_2) - e_2' \end{pmatrix} . \tag{4.4.0.9}$$

Since $\hat{x}_1 = \hat{x}_1(e_1, e_2)$ and $\hat{x}_2 = \hat{x}_2(e_1, e_2)$ (see equations 3.4.2.6, 3.4.2.7 and 3.4.2.8), we have $J_M = J_M(e_1', e_2', e_1, e_2)$. The trace and determinant of J_M are given by

$$\mathrm{tr} J_M(e_1', e_2', e_1, e_2) = c_{11}'(h_1\rho_1 - \hat{x}_1) - e_1' + c_{22}'(h_2\rho_2 - \hat{x}_2) - e_2' , \tag{4.4.0.10}$$

and

$$\begin{aligned} \det J_M(e_1', e_2', e_1, e_2) = {} & e_1'e_2' - e_1'c_{22}'(h_2\rho_2 - \hat{x}_2) - e_2'c_{11}'(h_1\rho_1 - \hat{x}_1) \\ & + (c_{11}'c_{22}' - c_{12}'c_{21}')(h_1\rho_1 - \hat{x}_1)(h_2\rho_2 - \hat{x}_2) , \end{aligned} \tag{4.4.0.11}$$

or with $X = \dfrac{\hat{x}_1}{\hat{x}_2}$,

$$\mathrm{tr} J_M(e'_1, e'_2, e_1, e_2) = \frac{c'_{11} e_1 X}{c_{11} X + c_{21}} - e'_1 + \frac{c'_{22} e_2}{c_{12} X + c_{22}} - e'_2 \ , \tag{4.4.0.12}$$

and

$$\begin{aligned} \det J_M(e'_1, e'_2, e_1, e_2) = e'_1 e'_2 &- \frac{e'_1 c'_{22} e_2}{c'_{12} X + c'_{22}} - \frac{e'_2 c'_{11} e_1 X}{c'_{11} X + c'_{21}} \\ &+ \frac{(c'_{11} c'_{22} - c'_{12} c'_{21}) e_1 e_2 X}{(c'_{11} X + c'_{21})(c'_{12} X + c_{22'})} \ . \end{aligned} \tag{4.4.0.13}$$

Recall that J_R has stable eigenvalues since $(\hat{x}_1, \hat{x}_2)^T$ is a stable steady state of the monomorphic system, and thus stability will be determined by J_M.

Applying the Routh-Hurwitz criteria, we can deduce that the steady state $\hat{\mathbf{x}}$ is asymptotically stable, so that invasion does not occur, if and only if $\mathrm{tr} J_M < 0$ and $\det J_M > 0$.

If the invader is identical to the resident, that is $e'_i = e_i$ and $c'_{ij} = c_{ij}$, then equation 4.4.0.12 gives

$$\mathrm{tr} J_M = -\frac{e_1 c_{21}}{c_{11} X + c_{21}} - \frac{e_2 c_{12} X}{c_{12} X + c_{22}} < 0 \ , \tag{4.4.0.14}$$

and from equation 4.4.0.13 gives

$$\det J_M = 0 \ . \tag{4.4.0.15}$$

Thus a competitor that is identical to the resident is invasively neutral as expected. Since $\mathrm{tr} J_M$ is a continuous function of the invader parameters, $\mathrm{tr} J_M < 0$ when the invader parameters are sufficiently close to the resident ($\mathbf{e}' \approx \mathbf{e}$ and $C' \approx C$). Thus the invasion of *similar* competitor types can be determined exclusively from $\det J_M$, a quantity that is sign–opposite to the maximal intrinsic growth rate of an invading strategy *close* to the resident strategy. In section 4.4.1 it is shown that this property is true for all invading strategies if there is variation in extinction rates only.

We can now determine, for a given viable strategy S:

- Which strategies S' can invade S?

- Which resident strategies S' can be invaded by S?

4.4.1 Strategy–Independent Colonization

For the remainder of this chapter we shall focus the investigation on how landscape structure mediates competition between strategies that differ in terms of patch type specialisation, determined by the extinction rates, only. By fixing colonization rates ($k'_{ji} = k_{ji} = 1$ for $i, j = 1, 2$) we assume that all strategies have the same dispersal behaviour, so that the factors that influence the expected extinction times of local populations do not influence the colonization process. This reduces strategy space to the two–dimensional plane of extinction rates and allows for a geometric analysis. This model will be referred to as model **M1**.

A strategy S will be represented by (e_1, e_2), the ordered pair of extinction rates. Consider a fixed strategy S. A strategy S', with corresponding extinction rates (e'_1, e'_2), can *invade* S if and only if either $\det J_M(e'_1, e'_2, e_1, e_2) < 0$ or $\mathrm{tr} J_M(e'_1, e'_2, e_1, e_2) > 0$ (or both). Define the curve $e'_2 = \mu(e'_1; e_1, e_2)$ to be the curve in (e'_1, e'_2) space in which $\det J_M = 0$, i.e.

$$\det J_M(e'_1, \mu(e'_1; e_1, e_2), e_1, e_2) = 0 \ . \tag{4.4.1.1}$$

This may be rearranged to give

$$\mu(e'_1; e_1, e_2) = c_{22}(h_2\rho_2 - \hat{x}_2) + \frac{c_{12}c_{21}(h_1\rho_1 - \hat{x}_1)(h_2\rho_2 - \hat{x}_2)}{e'_1 - c_{11}(h_1\rho_1 - \hat{x}_1)} \ . \tag{4.4.1.2}$$

This is the equation of a hyperbola and the directrix of this hyperbola coincides with $\mathrm{tr} J_M = 0$. On the branch of the hyperbola that satisfies $\mathrm{tr} J_M < 0$,

$$e'_1 > c_{11}(h_1\rho_1 - \hat{x}_1) \ , \tag{4.4.1.3}$$

therefore the curve $e'_2 = \mu(e'_1; e_1, e_2)$ for $e'_1 > c_{11}(h_1\rho_1 - \hat{x}_1)$ is the set of neutrally invasive strategies that bound the strategies that can and cannot invade S.

Similarly, the strategies that can be *invaded* by S are bounded by a branch of the curve in in (e'_1, e'_2) space with equation $e'_2 = \gamma(e'_1; e_1, e_2)$ defined implicitly by

$$\det J_M(e_1, e_2, e'_1, \gamma(e'_1; e_1, e_2)) = 0 \ . \tag{4.4.1.4}$$

Unfortunately deriving the explicit form of γ is generally difficult since it involves inverting the expressions $\hat{x}'_1$ and $\hat{x}'_2$ which we recall are in general the roots of cubic equations in terms of e'_1 and e'_2. We shall prove general a general property of all invasion curves, and then consider some limiting cases.

Claim 6. The invasion curves are tangential when evaluated at the resident strategy;

$$\frac{d\mu}{de'_1}(e_1; e_1, e_2) = \frac{d\gamma}{de'_1}(e_1; e_1, e_2) \ . \tag{4.4.1.5}$$

Proof. For convenience we shall use the notation $\Delta(e'_1, e'_2, e_1, e_2) = -\det J_M(e'_1, e'_2, e_1, e_2)$ (the minus sign is introduced so that positive invasion fitness corresponds to positive Δ) and let Δ_i be the partial derivative of Δ with respect to the ith argument. Define $D(e_1, e_2) = \Delta(e_1, e_2, e_1, e_2)$. Then $D(e_1, e_2) = 0$, by equation 4.4.0.15, so $\frac{\partial D}{\partial e_1} = \frac{\partial D}{\partial e_2} = 0$, i.e.

$$\Delta_1(e_1, e_2, e_1, e_2) + \Delta_3(e_1, e_2, e_1, e_2) = 0 \ , \tag{4.4.1.6}$$

$$\Delta_2(e_1, e_2, e_1, e_2) + \Delta_4(e_1, e_2, e_1, e_2) = 0 \ . \tag{4.4.1.7}$$

Now, from 4.4.1.1

$$\Delta(e'_1, \mu(e'_1; e_1, e_2), e_1, e_2) = 0 \ , \tag{4.4.1.8}$$

and from 4.4.1.4

$$\Delta(e_1, e_2, e'_1, \gamma(e'_1; e_1, e_2)) = 0 \ . \tag{4.4.1.9}$$

Differentiating equations 4.4.1.8 and 4.4.1.9 with respect to e'_1 gives

$$\Delta_1(e'_1, \mu(e'_1; e_1, e_2), e_1, e_2) + \frac{d\mu(e'_1; e_1, e_2)}{de'_1}\Delta_2(e'_1, \mu(e'_1; e_1, e_2), e_1, e_2) = 0 \ , \tag{4.4.1.10}$$

and

$$\Delta_3(e_1, e_2, e'_1, \gamma(e'_1; e_1, e_2)) + \frac{d\gamma(e'_1; e_1, e_2)}{de'_1}\Delta_4(e_1, e_2, e'_1, \gamma(e'_1; e_1, e_2)) = 0 \ . \tag{4.4.1.11}$$

Evaluating these equations at $e'_1 = e_1$ and using equations 4.4.1.6 and 4.4.1.7 yields the required result. □

Note that this proof does not require the explicit form of Δ. If Δ is any well defined fitness function for two competitor types with two–dimensional strategies it must satisfy equation 4.4.0.15 and so this property of the invasion curves, as defined above, is quite general (Bowers et al. 2005).

The Invasion Curves of Strategies Endemic to Patches of a Single Type

It is fairly straightforward to derive an expression explicitly for both μ and γ for the strategy $(e,\infty) := \lim_{e_2\to\infty}(e,e_2)$, that persists in the absence of competition when $e < c_{11}h_1\rho_1$. This strategy is endemic to type–1 patches since it is unable to establish populations in type–2 patches.

Claim 7.

$$\mu^1(e_1';e) \;:=\; \lim_{e_2\to\infty}\mu(e_1';e,e_2) \;=\; c_{22}h_2\rho_2 + \frac{c_{12}c_{21}h_2\rho_2 e}{c_{11}(e_1'-e)} \tag{4.4.1.12}$$

Proof. The persistence condition given by the inequalities 3.4.1.6 to 3.4.1.8 becomes $e < c_{11}h_1\rho_1$. Trivially then

$$\hat{x}_1(e,\infty) \;=\; \lim_{e_2\to\infty}\hat{x}_1(e,e_2) \;=\; h_1\rho_1 - \frac{e}{c_{11}} \ ,$$

and

$$\hat{x}_2(e,\infty) \;=\; \lim_{e_2\to\infty}\hat{x}_2(e,e_2) \;=\; 0 \ .$$

Substituting $\hat{x}_1$ and $\hat{x}_2$ into equation 4.4.1.2 yields 4.4.1.12 and completes the proof. □

Claim 8.

$$\gamma^1(e_1';e) \;:=\; \lim_{e_2\to\infty}\gamma(e_1';e,e_2) \;=\; \mu^1(e_1';e) - (c_{11}h_1\rho_1 - e)\left(\frac{c_{12}}{c_{11}} + \frac{c_{22}}{c_{21}}(\frac{e_1'}{e} - 1)\right) \tag{4.4.1.13}$$

Proof. From equation 4.4.0.11,

$$\lim_{e_2\to\infty}\det J_M(e,e_2,e_1',\gamma(e_1';e,e_2)) \;=\; 0$$

requires that

$$c_{11}(h_1\rho_1 - \hat{x}_1') \;=\; e \ ,$$

or equivalently that

$$\hat{x}_1' = \; h_1\rho_1 - \frac{e}{c_{11}} \ .$$

Also equation 3.4.2.1 may be rearranged to give

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

Finally, equation 3.4.2.2 yields

$$\begin{aligned} e_2' &= (h_2\rho_2 - \hat{x}_2')(c_{12}\frac{\hat{x}_1'}{\hat{x}_2'} + c_{22}) \\ &= c_{22}h_2\rho_2 + \frac{c_{12}c_{21}h_2\rho_2 e}{c_{11}(e_1' - e)} - (c_{11}h_1\rho_1 - e)\left(\frac{c_{12}}{c_{11}} + \frac{c_{22}}{c_{21}}(\frac{e_1'}{e} - 1)\right) , \end{aligned}$$

as required. □

We observe that $\mu^1 > \gamma^1$ whenever $e_1' > e$, thus a coexisting strategy (e_1', e_2') will exist for any $e_1' > e$ provided that e_2' is bounded. However, if $e_1' < e$ the endemic competitor is unable to invade, forbidding coexistence. If two strategies S and S' that are endemic to the same patch type compete, the strategy S invades strategy S' if and only if strategy S' cannot invade strategy S. Thus competition for a single patch type always results in the competitive exclusion of all but one strategy. Trivially, persistent strategies that are endemic to different patch types will always coexist since $\mu^1 \to c_{22}h_2\rho_2$ and $\gamma^1 \to -\infty$ as $e_1' \to \infty$.

The invasion curves for strategies endemic to type–2 patches are derived in an equivalent way to the type–1 case. Consider the endemic strategy $(\infty, e) := \lim_{e_1\to\infty}(e_1, e)$. On the μ curve, where $e_2' = \lim_{e_1\to\infty}\mu(e_1'; e_1, e) = \mu(e_1'; \infty, e)$, we define the curve μ^2 such that

$$\mu^2(e_2'; e) = \mu^2(\mu(e_1'; \infty, e), e) = e_1' \ . \tag{4.4.1.14}$$

Then

$$\mu^2(e_2'; e) = c_{11}h_1\rho_1 + \frac{c_{12}c_{21}h_1\rho_1 e}{c_{22}(e_2' - e)} , \tag{4.4.1.15}$$

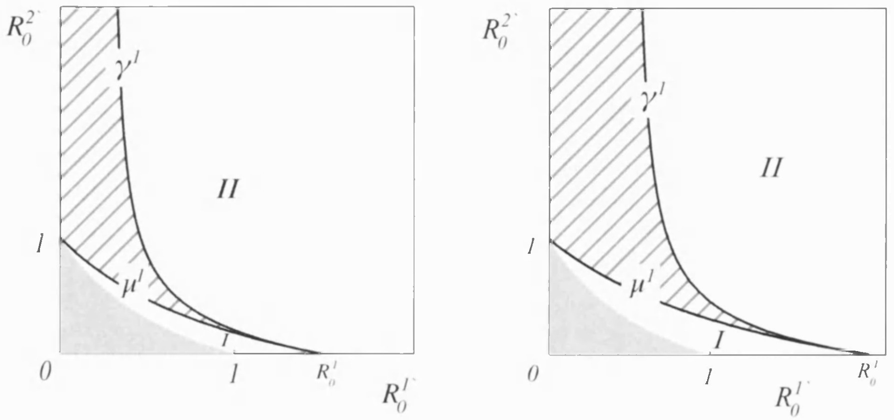
following from equation 4.4.1.12 with the indices 1 and 2 swapped around. Equivalently on the γ curve, where $e_2' = \lim_{e_1\to\infty}\gamma(e_1'; e_1, e) = \gamma(e_1'; \infty, e)$, we define the curve γ^2 such that

$$\gamma^2(e_2'; e) = \gamma^2(\mu(e_1'; \infty, e), e) = e_1' \ . \tag{4.4.1.16}$$

Then

$$\gamma^2(e_2'; e) \ = \ \mu^2(e_2'; e) - (c_{22}h_2\rho_2 - e)\left(\frac{c_{21}}{c_{22}} + \frac{c_{11}}{c_{12}}(\frac{e_2'}{e} - 1)\right) , \tag{4.4.1.17}$$

following from equation 4.4.1.13 with the indices 1 and 2 swapped around. Recall that a strategy can be defined in terms of the quantities R_0^1 and R_0^2 where $R_0^i = c_{ii}h_i\rho_i/e_i$.



(a) $R_0^1 = 1.5$ (b) $R_0^1 = 2$

Figure 4-1: The invasion regions of a patch type 1 endemic competitor in the $(R_0^{1'}, R_0^{2'})$ plane when $\rho_1 = 0.5$, $q = 0.4$ $(c_{11}c_{22} < c_{12}c_{21})$ and $h_1 = h_2 = 1$. The curve labeled μ^1, with equation given by 4.4.1.18, bounds region I: those strategies that cannot invade the strategy $(R_0^1, 0)$. The curve labeled γ^1, with equation given by 4.4.1.19, bounds region II: those strategies that are invaded by the strategy $(R_0^1, 0)$. Both curves bound the hatched region of mutual invasion that leads to coexistence. Strategies in the shaded region are non-viable.

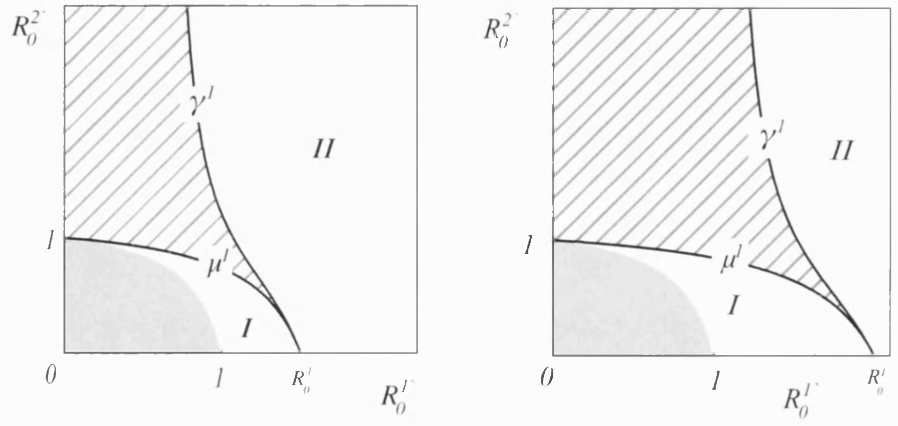
Thus the the type–1 endemic strategy (e, ∞) can be represented by $(R_0^1, 0) = (\frac{c_{11}h_1\rho_1}{e}, 0)$ and plots of figures 4-1 and 4-2 show the μ^1 and γ^1 invasion curves in the $(R_0^{1'}, R_0^{2'})$ plane for this strategy. The μ^1 curve is given by

$$R_0^{2'} = \frac{c_{22}h_2\rho_2}{\mu^1(\frac{c_{11}h_1\rho_1}{R_0^{1'}}; \frac{c_{11}h_1\rho_1}{R_0^1})}, \qquad (4.4.1.18)$$

and the γ^1 curve is given by

$$R_0^{2'} = \frac{c_{22}h_2\rho_2}{\gamma^1(\frac{c_{11}h_1\rho_1}{R_0^{1'}}; \frac{c_{11}h_1\rho_1}{R_0^1})}. \qquad (4.4.1.19)$$

Any strategy with $(R_0^{1'}, R_0^{2'})$ below the γ^1-curve can be invaded by the strategy $(R_0^1, 0)$ and any strategy $(R_0^{1'}, R_0^{2'})$ above the μ^1-curve can invade the strategy $(R_0^1, 0)$. In figure 4-1 $c_{11}c_{22} < c_{12}c_{21}$, a property of landscapes with spatially dispersed habitat types in



(a) $R_0^1 = 1.5$

(b) $R_0^1 = 2$

Figure 4-2: The invasion regions of a patch type 1 endemic competitor in the $(R_0^{1'}, R_0^{2'})$ plane when $\rho_1 = 0.5$, $q = 0.7$ $(c_{11}c_{22} > c_{12}c_{21})$ and $h_1 = h_2 = 1$. The curve labeled μ^1, with equation given by 4.4.1.18, bounds region I: those strategies that cannot invade the strategy $(R_0^1, 0)$. The curve labeled γ^1, with equation given by 4.4.1.19, bounds region II: those strategies that are invaded by the strategy $(R_0^1, 0)$. Both curves bound the hatched region of mutual invasion that leads to coexistence. Strategies in the shaded region are non-viable.

the model of uniform habitat loss. Figure 4-2 illustrates the case when $c_{11}c_{22} > c_{12}c_{21}$, as for aggregated habitat types. Endemic strategies coexist with an increasing range of strategies if landscape aggregation is increased. This makes intuitive sense because aggregation in elementary landscapes leads to a separation in strategies that thrive in different patches and thus reduces between–strategy (inter–species) competition. This property of $c_{11}c_{22} - c_{12}c_{21}$ holds for non-endemic resident strategies too.

Claim 9. The quantity $\zeta = \frac{c_{11}c_{22} - c_{12}c_{21}}{c_{11}c_{22}}$ determines convexity of the μ curve in the $(R_0^{1'}, R_0^{2'})$ plane.

Proof. On the μ curve of the monomorphic resident strategy (R_0^1, R_0^2)

$$R_0^{2'} = \frac{c_{22}h_2\rho_2}{\mu\left(\frac{c_{11}h_1\rho_1}{R_0^{1'}}; \frac{c_{11}h_1\rho_1}{R_0^1}, \frac{c_{22}h_2\rho_2}{R_0^2}\right)} . \tag{4.4.1.20}$$

Since μ satisfies 4.4.1.2, 4.4.1.20 can be rearranged to yield

$$\left(\frac{R_0^{1'}}{h_1\rho_1} - \frac{1}{\zeta\xi_1}\right)\left(\frac{R_0^{2'}}{h_2\rho_2} - \frac{1}{\zeta\xi_2}\right) = \frac{c_{12}c_{21}}{c_{11}c_{22}\zeta^2\xi_1\xi_2} \; , \tag{4.4.1.21}$$

where $\xi_i(R_0^1, R_0^2) = h_i\rho_i - \hat{x}_i > 0$, the fraction of type i patches that are empty and habitable when the resident strategy is at steady state. Now the degree of convexity of the hyperbolic μ curve depends upon where the asymptotes intersect the $R_0^{1'} = 0$ and $R_0^{2'} = 0$ axis. If $\zeta < 0$ they both intersect at negative values and the μ curve is convex. If $\zeta > 0$ they both intersect at positive values and the μ curve is concave. □

4.5 Dimorphic Metapopulation Dynamics

A pair of strategies in a state of coexistence will be described as a dimorphic coalition.

Claim 10. The dynamics of a dimorphic coalition will always equilibrate to an asymptotically stable steady state

Proof. Replacing the prime with a 2 superscript to denote the second strategy and assuming distinct coexisting strategies ($e_i^2 \neq e_i^1$), equations 4.3.0.3 to 4.3.0.6 evaluated at steady state yield

$$\begin{aligned} h_1\rho_1 - \hat{x}_1^1 - \hat{x}_1^2 &= \frac{e_1^1 X^1}{c_{11}X^1 + c_{21}} = \frac{e_1^2 X^2}{c_{11}X^2 + c_{21}} \; , && (4.5.0.22) \\ h_2\rho_2 - \hat{x}_2^1 - \hat{x}_2^2 &= \frac{e_2^1}{c_{12}X^1 + c_{22}} = \frac{e_2^2}{c_{12}X^2 + c_{22}} \; , && (4.5.0.23) \end{aligned}$$

where $X^i(e_1^1, e_2^1, e_1^2, e_2^2) = \dfrac{\hat{x}_1^i}{\hat{x}_2^i}$ is the patch type occupation ratio of competitor i. From 4.5.0.23 we have that

$$X^2 = \frac{e_2^2}{e_2^1}X^1 + \frac{c_{22}}{c_{12}}\left(\frac{e_2^2}{e_2^1} - 1\right) \neq X^1$$

for $e_2^2 \neq e_2^1$, and substituting this into 4.5.0.22 yields

$$(E_1^1 - 1){X^1}^2 + \left(\frac{c_{22}}{c_{12}}(E_1^1 - 1)(1 - E_2^1) + \frac{c_{21}}{c_{11}}(E_1^1 E_2^1 - 1)\right) X^1 + \frac{c_{22}c_{21}}{c_{12}c_{11}}(E_2^1 - 1) = 0 \; , \tag{4.5.0.24}$$

where $E_i^1 = \dfrac{e_i^1}{e_i^2} \neq 1$.

Coexisting strategies must satisfy $(1-E_1^1)(1-E_2^1) < 0$: $sign\{1-E_i^1\}$ is a measure of how specialized competitor 1 is relative to competitor 2 in type i patches and a strategy that is inferior in both patch types, satisfying $(1-E_1^1)(1-E_2^1) > 0$, cannot invade and hence cannot coexist. From this it follows that the sign of the product of the ${X^1}^2$ coefficient and the constant coefficient of equation 4.5.0.24 is negative. Therefore equation 4.5.0.24 has a unique positive root. This implies that there is a unique steady coalition, since 4.5.0.22 and 4.5.0.23 rearrange to

$$X^1\hat{x}_2^1 + X^2\hat{x}_2^2 = h_1\rho_1 - \frac{e_1^1 X^1}{c_{11}X^1 + c_{21}} \tag{4.5.0.25}$$

$$\hat{x}_2^1 + \hat{x}_2^2 = h_2\rho_2 - \frac{e_2^1}{c_{12}X^1 + c_{22}}\,, \tag{4.5.0.26}$$

since $\hat{x}_1^i = X^i\hat{x}_2^i$. □

It is worth outlining that X^1 (and equivalently X^2) is a solution of a quadratic equations as opposed to a cubic equation in the monomorphic metapopulation case. Furthermore, in contrast to the monomorphic case, the coefficients do not depend explicitly upon the fraction of destroyed habitat (providing that the amount of habitat loss does not prevent strategies from coexisting).

4.6 Invasion of a Dimorphic Coalition

If a third competitor type is introduced into the system, invasion will depend upon the strategy type of both the introduced and the coalition strategies. In the monomorphic case an invader may coexist with a resident strategy due to the existence of asymptotically stable dimorphic steady state, however this is not permitted in the dimorphic case. This follows from an application of the *competitive exclusion principle*, that the number of resources (in this model there are two patch types) is an upper limit for the number of possible coexisting competitor types (Tilman 1982). Then if a strategy can invade the dimorphic metapopulation, at least one of the two residents will go extinct, which we prove below for this model.

The model 4.3.0.1 for three competitor types with equal colonization rates ($c_{ij}^n = c_{ij}$)

is

$$
\begin{aligned}
\frac{dx_1^1}{dt} &= (c_{11}x_1^1 + c_{21}x_2^1)(h_1\rho_1 - x_1^1 - x_1^2 - x_1') - e_1^1 x_1^1 \ , && (4.6.0.27)\\
\frac{dx_2^1}{dt} &= (c_{12}x_1^1 + c_{22}x_2^1)(h_2\rho_2 - x_2^1 - x_2^2 - x_2') - e_2^1 x_2^1 \ , && (4.6.0.28)\\
\frac{dx_1^2}{dt} &= (c_{11}x_1^2 + c_{21}x_2^2)(h_1\rho_1 - x_1^1 - x_1^2 - x_1') - e_1^2 x_1^2 \ , && (4.6.0.29)\\
\frac{dx_2^2}{dt} &= (c_{12}x_1^2 + c_{22}x_2^2)(h_2\rho_2 - x_2^1 - x_2^2 - x_2') - e_2^2 x_2^2 \ , && (4.6.0.30)\\
\frac{dx_1'}{dt} &= (c_{11}x_1' + c_{21}x_2')(h_1\rho_1 - x_1^1 - x_1^2 - x_1') - e_1' x_1' \ , && (4.6.0.31)\\
\frac{dx_2'}{dt} &= (c_{12}x_1' + c_{22}x_2')(h_2\rho_2 - x_2^1 - x_2^2 - x_2') - e_2' {x_2}' \ , && (4.6.0.32)
\end{aligned}
$$

where the variables for the ith resident have an i superscript. Here we define $\mathbf{x} = (x_1^1, x_2^1, x_1^1, x_2^2, x_1', x_2')$. As with the case for a single resident, the mutant fitness is determined by the Jacobian matrix J satisfying

$$[J(\mathbf{x}_0)]_{ij} = \Omega_j^i(\mathbf{x}_0) \ ,$$

where $\mathbf{x}_0 = (\hat{x}_1^1, \hat{x}_2^1, \hat{x}_1^2, \hat{x}_2^2, 0, 0)$ represents the dimorphic steady state. This has the form, similar to the monomorphic case,

$$J = \begin{pmatrix} J_R & \star \\ \mathbf{0} & J_M \end{pmatrix} \ , \qquad (4.6.0.33)$$

where J_R is the 4×4 Jacobian matrix of the dimorphic system, linearized about $(\hat{x}_1^1, \hat{x}_2^1, \hat{x}_1^2, \hat{x}_2^2)$, $\star$ represents a 4×2 matrix with inconsequential entries, and J_M is the matrix

$$J_M = \begin{pmatrix} c_{11}(h_1\rho_1 - \hat{x}_1^1 - \hat{x}_1^2) - e_1' & c_{21}(h_1\rho_1 - \hat{x}_1^1 - \hat{x}_1^2) \\ c_{12}(h_2\rho_2 - \hat{x}_2^1 - \hat{x}_2^2) & c_{22}(h_2\rho_2 - \hat{x}_2^1 - \hat{x}_2^2) - e_2' \end{pmatrix} . \qquad (4.6.0.34)$$

Since $\hat{x}_i^j = \hat{x}_i^j(e_1^1, e_2^1, e_1^2, e_2^2)$, for $i, j = 1, 2$, we have $J_M = J_M(e_1', e_2', e_1^1, e_2^1, e_1^2, e_2^2)$. The trace and determinant of J_M are given by

$$\mathrm{tr} J_M = c_{11}(h_1\rho_1 - \hat{x}_1^1 - \hat{x}_1^2) - e_1' + c_{22}(h_2\rho_2 - \hat{x}_2^1 - \hat{x}_2^2) - e_2' \ , \qquad (4.6.0.35)$$

and

$$\det J_M = e'_1 e'_2 - e'_1 c_{22}(h_2\rho_2 - \hat{x}^1_2 - \hat{x}^2_2) - e'_2 c_{11}(h_1\rho_1 - \hat{x}^1_1 - \hat{x}^2_1)$$
$$+(c_{11}c_{22} - c_{12}c_{21})(h_1\rho_1 - \hat{x}^1_1 - \hat{x}^2_1)(h_2\rho_2 - \hat{x}^1_2 - \hat{x}^2_2) \ , \qquad (4.6.0.36)$$

or equivalently, from equations 4.5.0.23 and 4.5.0.22,

$$\mathrm{tr} J_M = \frac{e^i_1 c_{11} X^i}{c_{11}X^i + c_{21}} - e'_1 + \frac{c_{22} e^i_2}{c_{12}X^i + c_{22}} - e'_2 \ , \qquad (4.6.0.37)$$

and determinant given by

$$\det J_M = e'_1 e'_2 - \frac{e'_1 e^i_2 c_{22}}{c_{12}X^i + c_{22}} - \frac{e'_2 e^i_1 c_{11} X^i}{c_{11}X^i + c_{21}}$$
$$+ \frac{e^i_1 e^i_2 (c_{11}c_{22} - c_{12}c_{21}) X^i}{(c_{11}X^i + c_{21})(c_{12}X^i + c_{22})} \ , \qquad (4.6.0.38)$$

for $i = 1, 2$.

The unique steady state $(\hat{x}^1_1, \hat{x}^1_2, \hat{x}^2_1, \hat{x}^2_2)$ of the dimorphic system is stable since we have assumed that the two strategies of the coalition coexist. Therefore J_R has stable eigenvalues and invasion will depend upon J_M only. Invasion does not occur if and only if $\mathrm{tr}J_M < 0$ and $\det J_M > 0$. As in the monomorphic case, we define the curve $e'_2 = \mu(e'_1; e^1_1, e^1_2, e^2_1, e^2_2)$ to be the curve in which $\det J_M = 0$, i.e

$$\det J_M(e'_1, \mu(e'_1; e^1_1, e^1_2, e^2_1, e^2_2), e^1_1, e^1_2, e^2_1, e^2_2) = 0 \ . \qquad (4.6.0.39)$$

This may be rearranged to give

$$\mu(e'_1; e^1_1, e^1_2, e^2_1, e^2_2) \ = \ c_{22}(h_2\rho_2 - \hat{x}^1_2 - \hat{x}^2_2) + \frac{c_{12}c_{21}(h_1\rho_1 - \hat{x}^1_1 - \hat{x}^2_1)(h_2\rho_2 - \hat{x}^1_2 - \hat{x}^2_2)}{e'_1 - c_{11}(h_1\rho_1 - \hat{x}^1_1 - \hat{x}^2_1)} \ , \qquad (4.6.0.40)$$

and is again a hyperbola with directrix coinciding with the $\mathrm{tr}J_M = 0$ curve, and hence the extinction rates of invaders on the invasion boundary satisfy $\det J_M = 0$ and $\mathrm{tr}J_M < 0$. Trivially both resident strategies lie on the invasion boundary curve. Similarly, strategies that form a coalition with strategy 2 which can be *invaded* by strategy 1 are bounded by a branch of the curve $e'_2 = \gamma(e'_1; e^1_1, e^1_2, e^2_1, e^2_2)$ in which

$\det J_M = 0$, i.e.

$$\det J_M(e_1^1, e_2^1, e_1', \gamma(e_1'; e_1^1, e_2^1, e_1^2, e_2^2), e_1^2, e_2^2) = 0 \ . \tag{4.6.0.41}$$

The following claim is analogous to claim 9 regarding the monomorphic case.

Claim 11. The quantity ζ determines convexity of the μ curve in the $(R_0^{1'}, R_0^{2'})$ plane.

Proof. On the μ curve of the dimorphic resident coalition $(R_0^1, R_0^2, \tilde{R}_0^1, \tilde{R}_0^2)$

$$R_0^{2'} = \frac{c_{22}h_2\rho_2}{\mu(\frac{c_{11}h_1\rho_1}{R_0^{1'}}; \frac{c_{11}h_1\rho_1}{R_0^1}, \frac{c_{22}h_2\rho_2}{R_0^2}, \frac{c_{11}h_1\rho_1}{\tilde{R}_0^1}, \frac{c_{22}h_2\rho_2}{\tilde{R}_0^2})} \ . \tag{4.6.0.42}$$

Equation 4.6.0.42 with μ satisfying 4.6.0.40 can be rearranged to yield

$$\left(\frac{R_0^{1'}}{h_1\rho_1} - \frac{1}{\zeta\xi_1}\right)\left(\frac{R_0^{2'}}{h_2\rho_2} - \frac{1}{\zeta\xi_2}\right) = \frac{c_{12}c_{21}}{c_{11}c_{22}\zeta^2\xi_1\xi_2} \ , \tag{4.6.0.43}$$

where $\xi_i = \xi_i(R_0^1, R_0^2, \tilde{R}_0^1, \tilde{R}_0^2) > 0$ is the fraction of type i patches that are empty and habitable when the resident coalition is at steady state. This exactly the same equation as the monomorphic case except for the difference in ξ_i. As in the monomorphic case the degree of convexity of the hyperbola μ curve depends upon where the asymptotes intersect the $R_0^{1'} = 0$ and $R_0^{2'} = 0$ axis. Thus if $\zeta < 0$ the μ curve is convex and if $\zeta > 0$ then the μ curve is concave. □

Claim 12. There do not exist any structurally stable trimorphic steady states.

Proof. A non–trivial trimorphic steady state of the system 4.6.0.27 to 4.6.0.32 satisfies

$$h_1\rho_1 - \hat{x}_1^1 - \hat{x}_1^2 - \hat{x}_1^3 = \frac{e_1^1 X^1}{c_{11}X^1 + c_{21}} = \frac{e_1^2 X^2}{c_{11}X^2 + c_{21}} = \frac{e_1^3 X^3}{c_{11}X^3 + c_{21}} \ , \tag{4.6.0.44}$$

$$h_2\rho_2 - \hat{x}_2^1 - \hat{x}_2^2 - \hat{x}_2^3 = \frac{e_2^1}{c_{12}X^1 + c_{22}} = \frac{e_2^2}{c_{12}X^2 + c_{22}} = \frac{e_2^3}{c_{12}X^3 + c_{22}} \ , \tag{4.6.0.45}$$

where $X^i = \frac{\hat{x}_1^i}{\hat{x}_2^i}$ is the patch type occupation ratio of competitor $i = 1, 2, 3$. Since there are six equations for three occupation ratios X^1, X^2 and X^3, the system is over–determined. Even in the presence of the third competitor, X^1 will still satisfy equation 4.5.0.24 since it is independent of e_1^3 and e_2^3. It follows from a rearrangement of 4.6.0.44 and 4.6.0.45 that for consistency in the system it is required that e_1^3 and e_2^3 satisfy $e_2^3 = \mu(e_1^3; e_1^1, e_2^1, e_1^2, e_2^2)$, and hence (e_1^3, e_2^3) is invasively neutral. For structural stability, recall, an open subset of (e_1^3, e_2^3) (in the two–dimensional extinction rate space) of invading strategies must exist. Since the condition $e_2^3 = \mu(e_1^3)$ represents only a one–dimensional manifold, structural stability is forbidden. □

4.6.1 Invasion of Endemic Coalitions

Let S^1 and S^2 represent two viable strategies that are endemic to type–1 and type–2 patches, respectively, with extinction rates (e, ∞) and (∞, f). Recall that these strategies are viable provided $e < c_{11}h_1\rho_1$ and $f < c_{22}h_2\rho_2$, and in the previous section it was shown that such strategies can coexist. Let

$$\mu(e_1'; e, \infty, \infty, f) = \lim_{e_2^1 \to \infty} \{ \lim_{e_1^2 \to \infty} \mu(e_1'; e, e_2^1, e_1^2, f) \} \ ,$$

$$\gamma(e_1'; e, \infty, \infty, f) = \lim_{e_2^1 \to \infty} \{ \lim_{e_1^2 \to \infty} \gamma(e_1'; e, e_2^1, e_1^2, f) \} \ ,$$

$$\gamma(e_1'; \infty, f, e, \infty) = \lim_{e_1^1 \to \infty} \{ \lim_{e_2^2 \to \infty} \gamma(e_1'; e_1^1, f, e, e_2^2) \} \ .$$

Claim 13. The invasion curves of the endemic coalition (e, ∞, ∞, f) satisfy

$$\mu(e_1'; e, \infty, \infty, f) = \gamma(e_1'; e, \infty, \infty, f) = \gamma(e_1'; \infty, f, e, \infty) = f + \frac{c_{12}c_{21}ef}{c_{11}c_{22}(e_1' - e)} \tag{4.6.1.1}$$

Proof. Since the two strategies occupy different patch types, the fraction of occupied patches at steady state $(\hat{x}_1^1, \hat{x}_2^1, \hat{x}_1^2, \hat{x}_2^2)$ for the coalition (e, ∞, ∞, f) satisfy

$$\hat{x}_1^1 = \lim_{e_2^1 \to \infty} \{ \lim_{e_1^2 \to \infty} \hat{x}_1^1(e, e_2^1, e_1^2, f) \} = h_1\rho_1 - \frac{e}{c_{11}} \ , \tag{4.6.1.2}$$

$$\hat{x}_2^1 = \lim_{e_2^1 \to \infty} \{ \lim_{e_1^2 \to \infty} \hat{x}_2^1(e, e_2^1, e_1^2, f) \} = 0 \ , \tag{4.6.1.3}$$

$$\hat{x}_1^2 = \lim_{e_2^1 \to \infty} \{ \lim_{e_1^2 \to \infty} \hat{x}_1^2(e, e_2^1, e_1^2, f) \} = 0 \ , \tag{4.6.1.4}$$

$$\hat{x}_2^2 = \lim_{e_2^1 \to \infty} \{ \lim_{e_1^2 \to \infty} \hat{x}_2^2(e, e_2^1, e_1^2, f) \} = h_2\rho_2 - \frac{f}{c_{22}} \ , \tag{4.6.1.5}$$

Then equation 4.6.0.40 becomes

$$\mu(e_1'; e, \infty, \infty, f) = f + \frac{c_{12}c_{21}ef}{c_{11}c_{22}(e_1' - e)} \ . \tag{4.6.1.6}$$

Now, when $e_2' = \gamma(e_1'; e, \infty, \infty, f)$, equation 4.6.0.38 requires that

$$\lim_{e_2^1 \to \infty} \det J_M(e, e_2^1, e_1', e_2', \infty, f) \ = \ 0 \ ,$$

that leads to

$$\frac{c_{11}e_1'X'}{c_{11}X' + c_{21}} = e \ , \tag{4.6.1.7}$$

or

$$X' = \frac{ec_{21}}{c_{11}(e_1' - e)} \ , \tag{4.6.1.8}$$

where $X' = \dfrac{\hat{x}_1'}{\hat{x}_2'}$.

Since the invasion curve passes through both strategies of the coalition, we also have that

$$\det J_M(\infty, f, e_1', e_2', \infty, f) = 0 \ ,$$

leading to

$$\frac{c_{22}e_2'}{c_{12}X' + c_{22}} = f \ , \tag{4.6.1.9}$$

or, following from equation 4.6.1.8

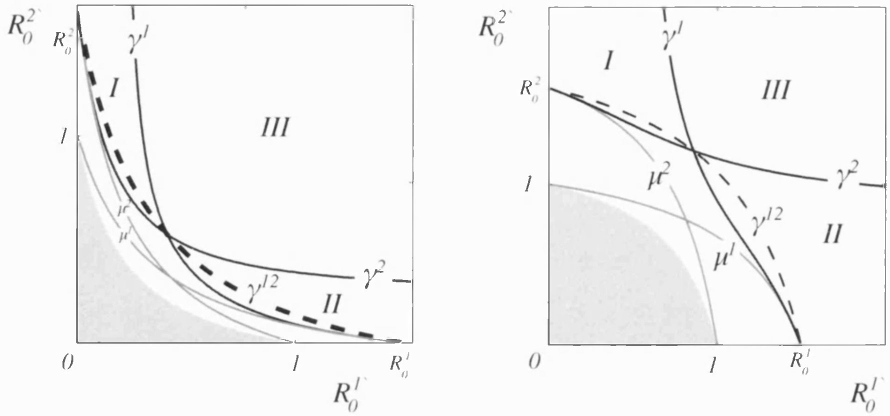
$$\begin{aligned} e_2' &= \frac{f(c_{12}X' + c_{22})}{c_{22}} \\ &= f + \frac{c_{12}c_{21}ef}{c_{11}c_{22}(e_1' - e)} \\ &= \mu(e_1'; e, \infty, \infty, f) \ . \end{aligned} \tag{4.6.1.10}$$

Finally, from the symmetry of the problem we can also deduce that

$$\begin{aligned} \gamma(e_1'; \infty, f, e, \infty) &= \mu(e_1'; \infty, f, e, \infty) \\ &= \mu(e_1'; e, \infty, \infty, f) \ . \end{aligned} \tag{4.6.1.11}$$

□

If S^i denotes a strategy endemic to patch type i, the strategy S^1 can invade a



(a) $\rho = 0.5$ and $q = 0.3$ (b) $\rho = 0.4$ and $q = 0.6$

Figure 4-3: The invasion regions of an endemic coalition in the ($R_0^{1'}$,$R_0^{2'}$) plane for $h_1 = h_2 = 1$, $R_0^1 = 1.5$, and $R_0^2 = 1.6$. The dashed curve labeled γ divides those strategies that can invade the S^1–S^2 coalition, and those strategies that, if able to form coalitions with S^1 or S^2, can be invaded by S^2 or S^1 respectively. The solid curves labeled γ^1 and γ^2 bound the strategies that the endemic strategies $S^1 = (R_0^1, 0)$ and $S^2 = (0, R_0^2)$ respectively, that can and cannot invade. The γ_1 curve satisfies equation 4.4.1.19 and the γ_2 curve satisfies 4.6.1.12. Invader strategies in region *I* (bounded by γ and γ^1) expel S^2 forming a coalition with S^1. Invader strategies in region *II* (bounded by γ and γ^2) expel S^1 forming a coalition with S^2. Invader strategies in region *III* (bounded by γ^1 and γ^2) expel both S^1 and S^2. Strategies in the shaded region are non-viable.

coalition when strategy S^2 is present if and only if, S^2 can invade a coalition when strategy S^1 is present.

The plots of figure 4-3 illustrate the dimorphic invasion curves in the ($R_0^{1'}$, $R_0^{2'}$) plane for the endemic coalition, with strategies $S^1 = (R_0^1, 0)$ and $S^2 = (0, R_0^2)$, for the case $c_{11}c_{22} > c_{12}c_{21}$ in plot (a) and $c_{11}c_{22} < c_{12}c_{21}$ in plot (b).

In the monomorphic case, following successful invasion, only two outcomes were possible. The invader can either expel the resident or else coexist in a dimorphic coalition. In the dimorphic case there are now three scenarios. Coexistence with the resident coalition, we recall, is never possible and verified here for the case of an endemic coalition since the γ curve coincides with the μ curve. The three possible scenarios are:

1. S^2 is expelled and the invader forms a coalition with S^1

2. S^1 is expelled and the invader forms a coalition with S^2

3. Both S^1 and S^2 are expelled and the dimorphism collapses to the invader monomorphism.

The monomorphic γ curves, γ^1 for S^1 and γ^2 for S^2, together with the dimorphic γ curve will determine whic of these outcomes of scenarios is realised. Recall that the strategies on the γ^1 curve satisfies 4.4.1.19. On the γ^2 curve strategies satisfy

$$R_0^{1'} = \frac{c_{11}h_1\rho_1}{\gamma^2(\frac{c_{22}h_2\rho_2}{R_0^{2'}}; \frac{c_{22}h_2\rho_2}{R_0^2})} \; . \tag{4.6.1.12}$$

Note that in figure 4-3 the γ^1 curve intersects the γ^2 curve at a unique point that lies on the γ curve. This is always the case for endemic coalitions. The value $e^* > e$ that satisfies $\gamma(e^*; e, \infty, \infty, f) = \gamma^1(e^*; e)$ is

$$e^* = e(1 + \frac{c_{21}(c_{22}h_2\rho_2 - f)}{c_{22}(c_{11}h_1\rho_1 - e)}) \; , \tag{4.6.1.13}$$

also satisfying $e^* = \gamma^2(\gamma(e^*; e, \infty, \infty, f), f)$. It is a trivial matter to show that

$$\lim_{e_2^1 \to \infty} \left\{ \lim_{e_1^2 \to \infty} \frac{d\gamma(e; e, e_2^1, e_1^2, f)}{de_1'} \right\} > \lim_{e_1^1 \to \infty} \frac{d\gamma^1(e; e, e_1^1)}{de_1'} \; ,$$

therefore in the $(R_0^{1'}, R_0^{2'})$ plane the γ curve lies above the γ^1 if and only if $R_0^{1'} > R_0^{1*} := \frac{c_{11}h_1\rho_1}{e^*}$. These two properties ensure that strategies that can invade endemic coalitions lie within three distinct regions of the $(R_0^{1'}, R_0^{2'})$ plane (i.e. region *I*, *II* and *III* in figure 4-3) corresponding to the three invasion scenarios listed above:

I $R_0^{2'}$ lies under the γ^1 curve and above the γ^2 curve. The strategy S^2 will be unable to coexist with the invader and driven to extinction and the invader will coexist with strategy S^1.

II $R_0^{2'}$ lies under the γ^2 curve and above the γ^1 curve. The strategy S^1 will be unable to coexist with the invader and driven to extinction and the invader will coexist with strategy S^2.

III $R_0^{2'}$ lies above the γ^1 curve and above the γ^2 curve. Neither S^1 or S^2 can coexist and hence the invader will exist in a monomorphic state.

4.7 Discussion

In this chapter a model of metapopulation competition for empty habitat patches was presented and analyzed for the case when only extinction rates differ between competitor types. The polymorphic model is naturally extended from the monomorphic model when it is assumed that occupied patches are immune from invasion (a priority effect). We have confirmed the competitive exclusion principle by proving that the number of distinct competitor types that can stably coexist (i.e. each competitor type of a stable polymorphism has *positive* invasion fitness when rare in an environment consisting of textbfall other competitor types at steady state) to the number of resource types, in this case two corresponding to each patch type.

Understanding invasion is key to classifying the competitive interactions between species. In the monomorphic case it is shown that every persistent strategy, $S = (R_0^1, R_0^2)$, has associated to it two curves through $R_0^{1'}$–$R_0^{2'}$ invasion space; one bounding strategies that can and cannot invade S (the μ curve), and another bounding strategies that can and cannot be invaded by S (the γ curve). We conjecture that these curves only intersect when $S' = S$ and do so tangentially. This is proved for the case when S satisfies $R_0^2 = 0$ or $R_0^1 = 0$, but it was found to be true in general following from numerical verification not explicitly presented. If this were not the case an asymptotically unstable dimorphic steady state would exist representing a bistable situation of mutual un–invadability causing a metapopulation level priority effect, potentially reducing species richness.

The properties of the invasion curves yield three qualitatively distinct competitive outcomes that may occur between a strategy S', introduced at low density into a monomorphic metapopulation, at equilibrium, with resident strategy S:

1. S' cannot invade S.
2. S' is competitively superior to S, so that S' invades S but S cannot invade S'.
3. S' and S can mutually invade.

The third case of mutual invasion is necessary for the coexistence of a dimorphic coalition. The invasion outcomes of dimorphic coalition are also restricted. Trimorphic coexistence is not permitted in this model, nor we believe, is the mutual un–invadability of two strategies that both form a coalition with a third strategy, as shown explicitly when two strategies are endemic. There are three distinct outcomes between the strategy S', and the coalition of strategies S^1 and S^2:

1. S' cannot invade, leaving the coalition unaffected.
2. S' can invade, ousting one of the coalition strategies.
3. S' can invade, ousting both of the coalition strategies.

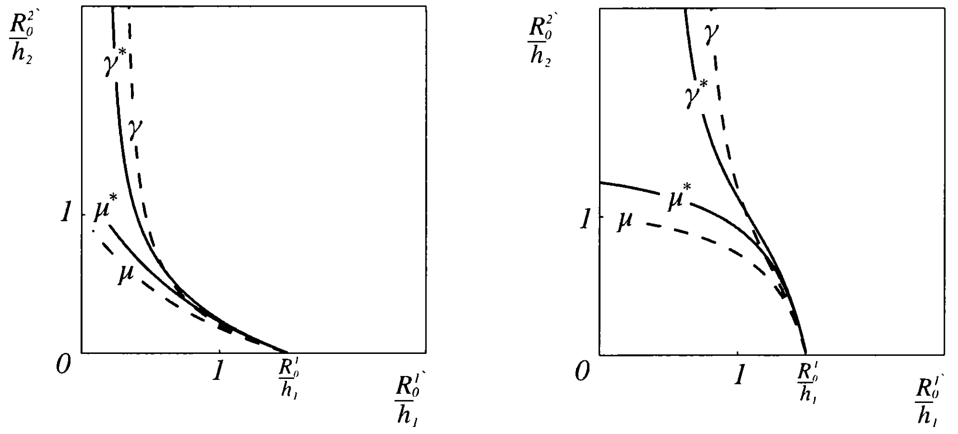
Of particular interest is how landscape structure can affect competitive interactions. A measure of landscape structure in the model that has a qualitative impact on invasion is ζ. For the model of aggregated patch type model with uniform habitat loss, given by equations 3.6.1.5 to 3.6.1.8, $\zeta = \frac{q-\rho}{q(1-2\rho+\rho q)}$ and therefore equal in sign to the measure of landscape aggregation, $q - \rho$. The convexity of monomorphic and dimorphic μ curves were shown to depend upon ζ (see claims 9 and 11) and are thus convex when $q < \rho$ and concave when $q > \rho$, with the region of invading strategies decreasing with increased aggregation. This means that strategies that are relatively specialized to one patch type (R_0^1 and R_0^2 are suitably different) experience increased competitive abilities when $q - \rho$ is increased. This makes intuitive sense since colonizers within landscapes with strongly aggregated patch types will have an increased probability of finding empty patches that are identical in type to the natal patch, and so a specialist will perceive a network consisting of mainly favorable patches. The number of specialists that inhabit unfavourable patches will be kept relatively low because the colonization output from these patches will be less.

Habitat removal can also have an impact upon competition between strategies, but only when competition is between two strategies. The invasion curve of a dimorphic coalition (where we conjecture that $\gamma = \mu$) in the $(R_0^{1'}, R_0^{2'})$ plane satisfies equation 4.6.0.43:

$$\left(\frac{R_0^{1'}}{h_1\rho_1} - \frac{1}{\zeta\xi_1}\right)\left(\frac{R_0^{2'}}{h_2\rho_2} - \frac{1}{\zeta\xi_2}\right) = \frac{c_{12}c_{21}}{c_{11}c_{22}\zeta^2\xi_1\xi_2}\ .$$

However this equation is independent of the fraction of habitable patches, h_1 and h_2, since $\frac{R_0^{i'}}{h_i} = \frac{c_{ii}\rho_i}{e_i'}$, $\xi_1 = \frac{e_1X_1}{c_{11}X_1+c_{21}}$ and $\xi_2 = \frac{e_2}{c_{12}X_1+c_{22}}$ are all independent of h_1 and h_2, as shown in section 4.5.

The invasion curves of monomorphic residents are affected by levels of habitat loss since the monomorphic resident fraction X is the solution of equation 3.4.2.8 of chapter **??** that depends upon h_1 and h_2. Figure 4-4 shows how the invasion curves in the $(\frac{R_0^{1'}}{h_1}, \frac{R_0^{1'}}{h_1})$ strategy plane for endemic residents can depend upon habitat loss. Note that considering the curves in the $(\frac{R_0^{1'}}{h_1}, \frac{R_0^{1'}}{h_1})$ strategy plane allows for an easy comparison. The comparison is made for two landscapes; one, corresponding to the $*$



(a) $q = 0.4$ (b) $q = 0.7$

Figure 4-4: The invasion regions of a patch type 1 endemic competitor in the $(\frac{R_0^{1'}}{h_1}, \frac{R_0^{2'}}{h_2})$ plane when $\rho_1 = 0.5$, $\frac{R_0^1}{h_1} = 1.5$, (a) $q = 0.4$ ($\zeta < 0$) and (b) $q = 0.7$ ($\zeta > 0$). The solid $*$ curves represent the invasion curves when $h_1 = h_2 = 0.8$ and are compared to the case when $h_1 = h_2 = 1$ for the dashed curves. On the curves μ and μ^* $\frac{c_{22}h_2\rho_2}{R_0^{2'}} = e_2' = \mu^1(e_1'; e) = \mu^1(\frac{c_{11}h_1\rho_1}{R_0^{1'}}; \frac{c_{11}h_1\rho_1}{R_0^1})$ (μ^1 as defined by equation 4.4.1.12), and on the curves γ and γ^* $\frac{c_{22}h_2\rho_2}{R_0^{2'}} = e_2' = \gamma^1(e_1'; e) = \gamma^1(\frac{c_{11}h_1\rho_1}{R_0^{1'}}; \frac{c_{11}h_1\rho_1}{R_0^1})$ (γ^1 as defined by equation 4.4.1.13).

labels, with 80% of all patches uniformly removed ($h_1^* = 0.8$ and $h_2^* = 0.8$) relative to one with no habitat removed ($h_1 = h_2 = 1$).

h_1^* and h_2^* affect the the invasion curves in the following ways. Equation 4.4.1.12 does not depend upon h_1 and so decreasing h_1^* does not alter μ^*. The slope of μ^* at the endemic strategy, however, increases as h_2^* decreases which we recall is equal to the slope of the γ^* at the endemic strategy. Decreasing h_1^* only ($h_2^* = h_2$) leads to a drop in the γ^* curve away from the endemic strategy. This explains the slight difference in gradients between the two γ and curves and why they cross.

For endemic strategies at least, removing habitat contracts the set strategies that can coexist although can also allow some strategies to form coalitions that, pre–habitat change, could not (represented by strategies both below the γ^* curve and above the γ curve).

The model analysed provides a simple explanation of how landscape structure may strengthen or weaken patch–type specialists (i.e. individuals that form populations with large variations in patch–type specific extinction rates). It cannot, however, be used to investigate the success of certain dispersal strategies (as have Brachet et al. (1999), Parvinen & Egas (2004) and others) since the dispersal process has not been modelled to explicitly affect the dynamics of local populations. The model provides a good starting point for an investigation into the evolution of specialisation in heterogeneous landscapes where the dispersal process is not modelled by the traditional dispersal pool; an assumption that is central to most implicitly spatial models of metacommunity dynamics.

Chapter 5

Generalist Evolution in Heterogeneous Landscapes

5.1 Chapter Outline

In this chapter we model the evolution of traits that determine patch–type generalism as a response to landscape composition. As an extension of the previous chapter, we model the introduction of phenotypic variation in the metapopulation. We find conditions for the evolution of patch–type generalists in symmetric landscapes and conclude the chapter with an investigation into patch–type–dependent dispersal. We discuss the potential for evolutionary branching, an ecological prerequisite of adaptive speciation, investigated further in the following chapter. The work in this chapter appears in the December 2006 edition of the journal *Evolutionary Ecology Research.*

5.2 Introduction

In the previous chapter we investigated the competitive outcomes of dimorphic and trimorphic metapopulation with a particular focus upon extreme specialist strategies (i.e. strategies that are endemic to one patch type). The origin of different competitors was not explicitly accounted for: One explanation could be that the landscape is not totally isolated from another landscape that supports a different metapopulation that provides an infrequent source of novel competitor types. This explanation requires no extra assumptions than those given in the previous chapter. An alternative source of competitor types can come from within the system. The reproductive process employed by the organism will naturally produce novel mutations at the genotypic level that will translate to the phenotypic level in terms of competitive variation. The production of new competitor types together with selection via metapopulation competition combine to define an evolving system.

As landscapes become increasingly fragmented the evolutionary change of the inhabitants will depend heavily upon the resultant metapopulation structure (Ronce & Olivieri 2004). Following habitat loss and fragmentation, high dispersal rates may be increasingly costly as patches become isolated (Murrell et al. 2002, Hiebeler 2004) yet at the same time beneficial as patch sizes reduce, increasing local extinction rates.

In the model of the previous chapter, competition was driven by the structure of the fragmented landscape; however, other constraints on adaptation may have a strong influence on evolutionary dynamics. The degree of phenotypic plasticity, for example, will govern how much variation there can be within a species. A key component of life history theory (Stearns 1999) is the covariance between those phenotypic traits that determine fitness and constrain adaptive change. Evolution can only proceed in the 'direction' of the selective pressure if the mutants of this type can be derived from the mutation process.

If the distribution of heterogeneity in patch quality is also altered by habitat loss other landscape–driven changes in selective pressure may occur. A model of two connected populations occupying different habitat patches was considered by Meszéna et al. (1997) and Kisdi (2002) to investigate, among other things, the evolution of patch generalists or specialists. Meszéna et al. (1997) investigated how the interplay between patch difference and phenotypic sensitivity can influence the evolution of patch specialisation and they identified a potential mechanism for *parapatric* speciation (different species live in different habitats yet with no migratory barrier) via evolutionary branching (see below).

The parallel evolution of dispersal rates with patch specialisation was investigated by Kisdi (2002). A strong joint dependency between dispersal and specialisation was found for a range of environmental conditions and an array of other complicated evolutionary dynamics. These including the successional evolution of a dimorphism in dispersal, followed by a dimorphism in habitat specialisation, and finally the evolution of low dispersal rates in both subpopulations. Parvinen & Egas (2004) considered an infinite metapopulation model, structured by local population size and with a similar consideration of patch type variation. With an inclusion of local population extinction, the evolution of specialisation was investigated for a range of dispersal abilities paralleling some of the qualitative results of the two-patch studies.

The size-structured model considered by Parvinen & Egas (2004) assumed well-mixed dispersal (a dispersal pool), thus limiting the potential effects that non–uniform distributions of landscape heterogeneity can have. We can now address this issue to some extent with the models developed in previous chapters.

5.3 Modelling Evolutionary Dynamics

The analysis of equations 4.3.0.3 to 4.3.0.6 in chapter 4 lead to a classification of the competition dynamics, but to study the metapopulation in an evolutionary context requires a few extra assumptions. Different competitors will now represent the different phenotypes of a single species and the evolution of this species will be investigated. To do this the model is extended to characterize the levels of diversity of phenotypes within the species and how this diversity is generated in the system, as required to model the process of evolution by natural selection.

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 (since we assume 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). Physiological constraints can be due to a multitude of processes:

- Trade-offs can exist between traits when the physiological development associated with one trait causes a depletion in a shared internal resource that is critical to the development of other traits.

- Regions in trait space may be out of bounds because of physical limitations in species morphology.
- The interdependency of traits might be determined by a common physiological property i.e. increasing body size may increase reproductive output while increasing predation risk.

In an unconstrained system the fitness gradient will define the possible adaptive pathways through trait space.

We shall begin by assuming 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 shown to intricately link the ecological dynamics to the evolutionary dynamics.

5.4 An Introduction to Adaptive Dynamics

The theory of adaptive dynamics (Geritz et al. 1998) has gained great popularity during the last decade for many reasons. The framework was devised to model the evolution of continuous traits driven by *frequency–dependent* selection (Dieckmann et al. 2004, chapter 4) Frequency–dependent selection occurs when individual fitness depends upon the phenotypic composition of the resident populations, as does the model presented in chapter 4. The framework is particularly suited to models with complex ecological dynamics derived mechanistically from properties of the individuals. The analysis determines the long term course of evolution and can predict such phenomena as evolutionary branching – a necessary component of sympatric speciation (described in detail below). The analysis will be restricted to clonal species so as to remain analytically tractable as in chapter 4.

A model of adaptive dynamics can be formulated from an ecological model that is supplemented with:

- A description of phenotypic variation.
- Sufficient limitations on the mutation process.
- A measure of mutant fitness that uniquely depends upon the set of competing phenotype strategies.

Phenotypic Variation

We shall assume that the phenotype space can be parameterized by a single continuous variable. Initially we assume that phenotypic variation will be in patch extinction rates only and that the one–dimensional phenotype space is parameterized by the extinction rate in type 1 patches together with the trade–off function, f.

Introduction of Mutants

It will be assumed that the phenotype of a mutant strategy is similar to at least one of the resident phenotypes. The assumption is that the individual physiology that determines the probability of local population extinction is a continuous trait and small mutation at the genotype level will map to small changes at the phenotype level. Mutant individuals are derived from the resident populations and it will be assumed that at least one local population within the landscape is purely of the mutant type. Furthermore mutants occur infrequently so that the resident, perhaps following previous invasion events, are at ecological equilibrium.

Invasion Fitness

Invasion fitness is the exponential growth rate of a rare mutant strategy in the environment set by a given resident population (Metz et al. 1992). The resident dynamics are assumed to have settled to either a point or periodic attractor so that invasion fitness is uniquely determined by the mutant and resident strategies. The adaptive dynamics of a one–dimensional trait does not depend upon the magnitude of the invasion fitness but just the sign. In chapter 4 we showed that the sign of invasion fitness was equal to $sign\{-\det J_M\}$, where J_M was defined for both monomorphic and dimorphic resident metapopulations. With the extinction rate in type 1 patches defining each phenotypic strategy, the monomorphic invasion function Δ^1 can be defined as a function of the mutant extinction rate e' and the resident extinction rate e

$$\Delta^1(e', e) = -\det J_M(e', f(e'), e, f(e)) \; , \tag{5.4.0.1}$$

or for a dimorphic resident coalition, with extinction rates e^1 and e^2, we define

$$\Delta^2(e', e^1, e^2) = -\det J_M(e', f(e'), e^1, f(e^1), e^2, f(e^2)) \; . \tag{5.4.0.2}$$

Directional Selection

The theory of adaptive dynamics states that the evolutionary behaviour of a monomorphic (meta)population under the above assumptions is determined by the partial derivatives of Δ^1 with respect to the resident and mutant extinction rates. For convenience we shall drop the 1 superscript.

Monomorphic evolution is characterized by a sequence of evolutionary steps. Each step involves the introduction of mutant (with strategies constrained according to a particular model of phenotypic variation) that invades and ousts the current resident. The conditions for such a step to occur can be given, for a resident with strategy e and mutant with strategy e', in terms of the selection gradient: Defining Δ_i to be the partial derivative of Δ with respect to the ith argument, the selection gradient, D, is defined as

$$D(e) = \Delta_1(e, e) \ . \tag{5.4.0.3}$$

If non-zero, the sign of the selection gradient determines the direction of selection. This follows since the fitness of a mutant strategy in the neighbourhood of (but distinct from) a resident strategy can be Taylor expanded to give

$$\begin{aligned} \Delta(e', e) &= \Delta(e, e) + \Delta_1(e, e)(e' - e) + O((e' - e)^2) \\ &= D(e)(e' - e) + O((e' - e)^2) \ , \end{aligned} \tag{5.4.0.4}$$

since $\Delta(e, e) = 0$ from equation 4.4.0.15 of chapter 4.

- If $D(e) > 0$ then mutants can invade the resident metapopulation if $e' > e$, and cannot invade if $e' < e$.
- If $D(e) < 0$ then mutants can invade the resident metapopulation if $e' < e$, and cannot invade if $e' > e$.

Note also that

$$\begin{aligned} \Delta(e, e') &= \Delta(e', e') - \Delta_1(e', e')(e' - e) + O((e' - e)^2) \\ &= -(\Delta_1(e, e) + O(e' - e))(e' - e) + O((e' - e)^2) \\ &= -D(e)(e' - e) + O((e' - e)^2) \ , \end{aligned} \tag{5.4.0.5}$$

and thus if the resident and mutant are sufficiently close, an invading mutant strategy cannot itself be invaded by the resident strategy. Thus directed selection in which a successfully invading mutant ousts the resident strategy will always occur if $D(e) \neq 0$, assuming closeness of the mutant. Note that this is intuitively true for the model presented in the previous chapter since a dimorphic coexistence is only possible when invasion is mutual between strategies. However, even in ecological models where this is not so, the statement still holds under quite general conditions, as shown by Geritz (2005).

5.4.1 Singular Strategies and their Evolutionary Properties

A strategy e^* satisfying

$$D(e^*) = 0 \ , \tag{5.4.1.1}$$

where directional selection vanishes, is called an *evolutionarily singular strategy* (Geritz et al. 1998). The existence of these strategies will be intimately linked to both ecological interactions and the species–specific tradeoff relationship. The adaptive dynamics framework involves two major properties of singular strategies that are based upon the quadratic approximation of the fitness function, with respect to both the mutant and resident variables. Firstly, a singular strategy, e^*, is an *evolutionarily stable* strategy (ES) if it cannot be invaded by mutants (Smith 1982). An expansion of the mutant fitness with respect to the mutant variable about a singular strategy yields

$$\Delta(e', e^*) = \Delta_{11}(e^*, e^*)(e' - e^*)^2 + O((e' - e^*)^3) \ , \tag{5.4.1.2}$$

where $\Delta_{ij}(e', e)$ is the partial derivative of Δ_i with respect to the jth argument. Thus the strategy e^* is ES if

$$\Delta_{11}(e^*, e^*) < 0 \ . \tag{5.4.1.3}$$

Alternatively, if $\Delta_{11}(e^*, e^*) > 0$, then all mutants in the locality can invade the singular strategy.

Secondly, a singular strategy, e^*, is *convergence stable* (CS) if a strategy, e', local to e^* can be invaded by mutants even closer to e^*; that is if e^* is a an attractor of directional selection (Eshel 1983). This is equivalent to both $D(e') > 0$ for $e' < e^*$ and $D(e') < 0$ if $e' > e^*$, e' close to e^*. Since the gradient changes sign from positive to negative, e^* is CS if and only if

$$\frac{dD(e^*)}{de} = \Delta_{11}(e^*, e^*) + \Delta_{12}(e^*, e^*) < 0 \ . \tag{5.4.1.4}$$

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.

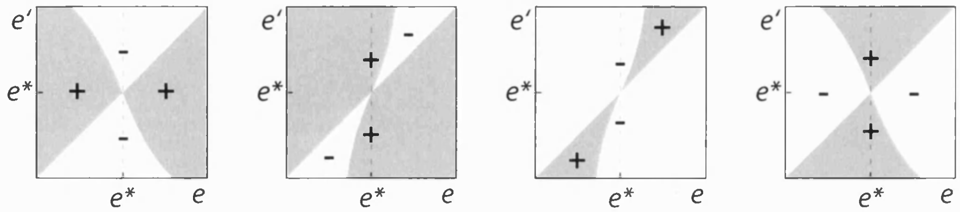
These two properties of singular strategies have a simple geometric interpretation in terms of the invasion fitness function, and in particular the plots of the sign of the invasion fitness function known as *pairwise invasibility plots* (PIPs) (Matsuda 1985). The plots of figure 5-1 represent examples of pairwise invasibility plots of a fictitious continuous invasion fitness function. Each plot depicts a single singular strategy with a unique ES/CS classification.

The points in the (e, e') plane are shaded if a mutant with strategy e' can invade a resident with strategy e. On the boundary of the shaded regions of PIPs the fitness function is zero and these curves will termed zero–clines. Since the invasion fitness of a mutant that is identical to a resident is zero, the line $e' = e$ is always a zero–cline of any PIP. Away from a singular strategy selection recall that selection is directional. If the strategy e is non-singular then the direction of selection at e depends on the sign change of invasion fitness on the vertical that passes through (e, e): Selection is for strategies e', with $e' > e$ (e' close to e) if and only the shaded region is directly above (e, e).

At the singular strategies (e^* in the plots of figure 5-1) the direction of selection reverses as indicated by the order of the sign change switching for resident strategies either side of e^*. For this to occur it is necessary that a second boundary curve must pass through the point (e^*, e^*). The singular strategy is CS if selection is directed towards it, that is, if strategies directly to the left of the singular strategy have the shaded region directly above, as depicted in plots (a) and (b).

The sign of the fitness function in the locality of and on the vertical line passing through the singular strategy determines whether the strategy is ES: The singular strategy is ES if and only if this region is not shaded as depicted in plots (a) and (c). Note that the slope of the non–trivial zero–cline passing through a singular strategy, together with the CS property, can also be used to determine the ES property. A singular strategy is ES if and only if the slope is negative and the strategy is CS, or the slope is positive and the strategy is not CS. The slope of the non–trivial zero–cline at e^* also yields other properties of singular strategies as shown by Geritz et al. (1998); however these properties are not of interest in this study and thus an explanation is omitted.

Pairwise invasibility plots may show more than one singular strategy and the graph-



(a) ES & CS (b) non–ES & CS (c) ES & non–CS (d) non–ES & non–CS

Figure 5-1: Pairwise invasibility plots depicting the four classifications of singular strategies for a fictitious fitness function. The points in the (e, e') plane are shaded grey if and only if a mutant with strategy e' can invade a resident with strategy e. On the boundary of the shaded regions the fitness function is zero. The strategy e^* is a singular strategy.

ical analysis of each strategy can be performed for each. The ES and CS properties lead to four classifications of singular strategies as shown in table 5.1.

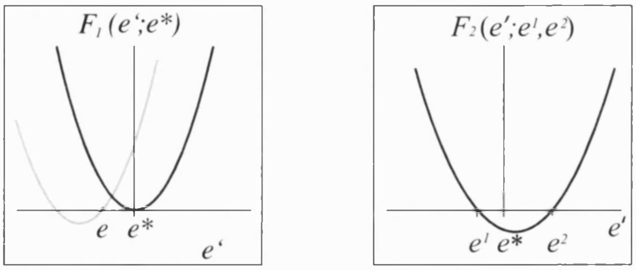
	ES	non-ES
CS	*Evolutionary Stable Attractor* Plot (a)	*Evolutionary Unstable Attractor* Plot (b)
non-CS	*Evolutionary Stable Repeller* Plot (c)	*Evolutionary Unstable Repeller* Plot (d)

Table 5.1: A basic classification of singular strategies. The plots refer to figure 5-1.

5.4.2 Evolutionary Branching

The CS and non-ES singular strategy is an evolutionarily unstable attractor and is termed an evolutionary branching point (Geritz et al. 1998). Evolution is directed to such a strategy however the evolution process does not stop there since it is evolutionarily unstable. From plot (b) we see that strategies in the proximity and either side of such a singular strategy can mutually invade, which we recall is the condition for coexistence in the model presented in chapter 4, and true in general when mutants are close to the resident strategy (Geritz 2005).

The term branching refers to the branching of the resident strategy space since evolution drives the diversification of a monomorphic metapopulation to a dimorphic



(a) (b)

Figure 5-2: The plots of the monomorphic (a) and dimorphic (b) invasion fitness functions, F_1 and F_2 respectively. Plot (a): The singular strategy e^* is CS since resident strategies nearby (e.g. the resident strategy e with corresponding mutant fitness $F_1(e';e)$) are invaded by strategies that are *closer* to e^*. The strategy e^* is not ES since all neighbouring strategies can invade. Plot (b): The resident coalition, (e^1, e^2), is in the locality of the singular strategy, e^*. The dimorphic fitness function, F_2 is necessarily zero when $e' = e^1$ and $e' = e^2$, and by continuity will approximately inherit the curvature of F_1. Strategies can invade the coalition if and only they lie in a locality outside of the set $[e_1, e_2]$ and thus the dimorphism is protected.

one. Furthermore the dimorphism is protected since *locally* evolution will drive the divergence of the dimorphic coalition. This follows from the continuity of the fitness function: Plot (a) of figure 5-2 shows a typical plot of the invasion fitness function of a mutant strategy e' set by a non-ES singular resident e^*, $F_1(e';e^*)$ (i.e. $F_1(e';e^*) = \Delta_1(e', e^*)$ where e^* is a singular and ES).

The dimorphic coalition (e^1, e^2), such that $e^1 \leq e^* \leq e^2$, corresponds to an invasion fitness function $F_2(e';e^1,e^2)$ (e.g. $F_2(e';e^1,e^2) = \Delta_2(e', e^1, e^2)$). When e^1 and e^2 are in the locality of e^*, continuity will ensure that the dimorphic function is a perturbation of the monomorphic function and inherits the positive curvature in the neighbourhood of the non-ES singular strategy. $F_2(e^1;e^1,e^2) = F_2(e^2;e^1,e^2) = 0$, therefore the invasion fitness of mutants that lie between e^1 and e^2 will be negative and thus selection will be for mutants that form a more diverse coalition. Away from the locality of the singular strategy, dimorphic evolution depend upon the full form of F_2.

5.5 The Adaptive Dynamics of Model M1

We shall first investigate evolution for the ecological model **M1** which we recall was given by equations 4.3.0.3 to 4.3.0.6 in chapter 4 together with the assumption that colonization was strategy– and patch–type independent (i.e. that all strategies populating j–type patches produce propagules that colonize empty i–type patches at the rate $k_{ji} = 1$). With the trade-off function f, equation 4.4.0.13 of chapter 4 gives

$$\begin{aligned}\Delta(e', e) = -\det J_M(e', f(e'), e, f(e)) = \frac{e' c_{22} f(e)}{c_{12}X + c_{22}} + \frac{f(e') c_{11} e X}{c_{11}X + c_{21} - e' f(e')} \\ - \frac{(c_{11}c_{22} - c_{12}c_{21}) e f(e) X}{(c_{11}X + c_{21})(c_{12}X + c_{22})} .\end{aligned} \tag{5.5.0.1}$$

The selection gradient is then

$$D(e) \;=\; -\frac{e f'(e) c_{21}}{c_{11}X(e) + c_{21}} - \frac{f(e) c_{12} X(e)}{c_{12}X(e) + c_{22}} , \tag{5.5.0.2}$$

adopting the prime notation for differentiation. The singular strategy condition is traditionally given, in terms of the first derivative of the trade-off function, as

$$f'(e^*) = -\frac{f(e^*) X^* (c_{11}X^* + c_{21})}{e^* (c_{12}X^* + c_{22})} , \tag{5.5.0.3}$$

where $X^* = X(e^*)$. It is worth pointing out that this property is satisfied *everywhere* by the μ and γ curves presented in the previous chapter (i.e. differentiating μ in equation 4.4.1.2 can be rearranged to give 5.5 and furthermore, $\frac{d\mu}{de} = \frac{d\gamma}{de}$). Bowers et al. (2005) developed a geometric theory of adaptive dynamics based upon this property, de–coupling competition dynamics with trade–off structure.

The conditions for a singular strategy to be ES is

$$f''(e^*) > -2 f'(e^*) \frac{(c_{11}X^* + c_{21})}{c_{21} e^*} , \tag{5.5.0.4}$$

following from an evaluation and trivial rearrangement of 5.4.1.3. The singular strategy equation 5.5 reduces this to

$$f''(e^*) > \frac{2 f(e^*) X^* (c_{11}X^* + c_{21})^2}{c_{21} e^{*2} (c_{12}X^* + c_{22})} . \tag{5.5.0.5}$$

A singular strategy is CS if

$$f''(e^*) > \frac{f(e^*)(c_{11}X^* + c_{21})}{e(c_{12}X^* + c_{22})} \cdots$$
$$\left(\frac{X^*(c_{11}X^{*2} + 2c_{12}X^* + c_{22})}{e^*(c_{12}X^* + c_{22})} - \left(\frac{c_{11}X^*}{c_{11}X^* + c_{21}} + \frac{c_{22}}{c_{12}X^* + c_{22}} \right) \frac{dX^*}{de} \right) , \quad (5.5.0.6)$$

where $\frac{dX^*}{de} = \frac{d\hat{X}(e^*)}{de}$, following from an evaluation and rearrangement of 5.4.1.4.

Since the occupation ratio X will depend upon f also, solving the singular strategy equation is generally difficult and must usually be done numerically. Alternatively trade–off functions can be considered that are singular for certain extinction strategies when the landscape is in a particular configuration.

5.5.1 Singular Generalist Strategies in Symmetric Landscapes

Singular strategies can only occur within regions of strategy space where the trade–off function has negative gradient since the right hand side of equation 5.5.0.5 is always negative. This is intuitive since the selection gradient is negative when f' is positive since selection will act to lower both patch extinction rates. From a biological point of view, describing f as a trade–off function implies that f' is negative so that adapting to one type of patch results in a corresponding maladaption to the other with the local net benefit reflected in the selection gradient.

The generalist strategy is defined to be the strategy such that $e_2 = f(e_1) = e_1$, and will be denoted e_G. All other strategies will be referred to as specialist: A type 1 specialist satisfies $e_1 < e_2$ and a type 2 specialist satisfies $e_2 < e_1$. If the landscape is equally composed of both patch types ($\rho_1 = \rho_2 = \frac{1}{2}$) that are equally habitable ($h_1 = h_2 = h$) the landscape will be referred to as symmetric. For such a case the generalist strategy is viable if and only if $e_G < h$, and then $X(e_G) = 1$ follows trivially from equation 3.4.2.8 since $c_{11} = c_{22}$. We shall consider the class of trade–off functions that lead to singular generalists when the landscape is symmetric. To assume otherwise would implicitly introduce a species bias towards one patch type, and so this assumption is a good place to begin.

From equation 5.5 with landscape symmetry, the generalist is singular if

$$f'(e_G) = -1 \ . \quad (5.5.1.1)$$

Defining $f''_G = f''(e_G)$, the ES condition on the trade-off function when the landscape is symmetric is

$$f''_G > \frac{2}{(1-q)e_G} =: f''_{ES} \,, \tag{5.5.1.2}$$

following directly from equation 5.5.0.4.

Claim 14. The CS condition for a singular generalist in a symmetric landscape is

$$\begin{aligned} f''_G &> f''_{ES} - \frac{2q(h-e_G)}{e_G(1-q)(h+(1-2q)e_G)} \\ &= \frac{2(h+e_G)}{(h+e_G(1-2q))e_G} =: f''_{CS} \,. \end{aligned} \tag{5.5.1.3}$$

Proof. With $X(e_G) = 1$, $c_{11} = c_{22} = 2q$ and $c_{12} = c_{21} = 2(1-q)$ equation 5.5.0.6 becomes

$$\begin{aligned} f''_G &> \frac{2}{e_G} - 2q\frac{dX(e_G)}{de} \\ &= f''_{ES} - 2q(\frac{1}{e_G(1-q)} + \frac{dX(e_G)}{de}) \,. \end{aligned} \tag{5.5.1.4}$$

Now $\frac{dX(e_G)}{de}$ is derived as follows. Recall equation 3.4.2.8, that $X(e)$ satisfies

$$\begin{aligned} &c_{11}c_{12}h_2\rho_2X^3 + (c_{12}e - c_{11}f(e) - c_{11}c_{12}h_1\rho_1 + (c_{11}c_{22} + c_{12}c_{21})h_2\rho_2)X^2 \\ &\quad (c_{22}e - c_{21}f(e) - (c_{11}c_{22} + c_{12}c_{21})h_1\rho_1 + c_{21}c_{22}h_2\rho_2)X - c_{21}c_{22}h_1\rho_1 = 0 \,, \end{aligned} \tag{5.5.1.5}$$

which for the symmetric case simplifies to

$$\begin{aligned} &c_{11}c_{12}h_1X^3 + (2c_{12}e - 2c_{11}f(e) + (c_{11}^2 + c_{12}^2 - c_{11}c_{12})h)X^2 \\ &\qquad (2c_{11}e - 2c_{12}f(e) - (c_{11}^2 + c_{12}^2 - c_{11}c_{12})h)X - c_{11}c_{12}h = 0 \,. \end{aligned} \tag{5.5.1.6}$$

Differentiating this yields

$$\begin{aligned} &[\, 3c_{11}c_{12}hX^2 + 2(2c_{12}e - 2c_{11}f(e) + (c_{11}^2 + c_{12}^2 - c_{11}c_{12})h)X \\ &\qquad + (2c_{11}e - 2c_{12}f(e) - (c_{11}^2 + c_{12}^2 - c_{11}c_{12})h) \,]\, \frac{dX}{de} \\ &\qquad\qquad + (2c_{12} - 2c_{11}f'(e))X^2 + (2c_{11} - 2c_{12}f'(e)X = 0 \,. \end{aligned} \tag{5.5.1.7}$$

Evaluating this at $e = e_G$ and rearranging gives us

$$\begin{aligned} \frac{dX(e_G)}{de} &= -\frac{4(c_{11}+c_{21})}{(c_{12}+c_{11})^2 h + 2(c_{12}-c_{11})e_G} \\ &= -\frac{2}{h+(1-2q)e_G} \; . \end{aligned} \qquad (5.5.1.8)$$

Then substituting this into equation 5.5.1.4 provides the required result. □

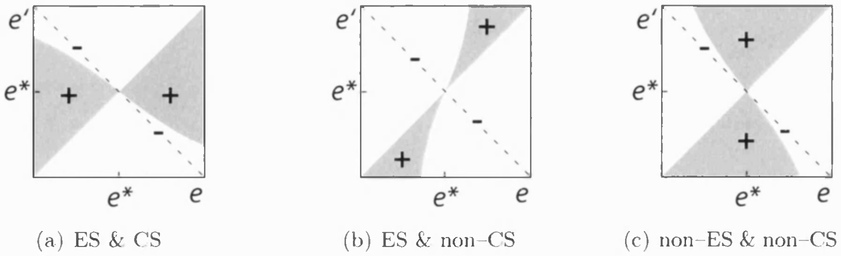
Note that increasing f''_G always increases the likelihood of the generalist becoming both ES and CS. This makes intuitive sense since increasing f''_G will increase the relative cost incurred through from the maladaption to one patch type (from an increase in the extinction rate in that patch type) when a mutant arrives that is more adapted to the other patch type (a decreased extinction rate in this patch type), and thus the relative success of the generalist increases with f''_G.

The ES condition is stronger than the CS condition since

$$f''_{ES} - f''_{CS} = \frac{2q(h-e_G)}{e_G(1-q)(h+(1-2q)e_G)} > 0 \; ,$$

when $h > e_G$ (the condition that the generalist persists). This ensures that the generalist is never an evolutionarily stable repeller. This result holds for all singular strategies of this model. For a singular strategy to be an evolutionarily stable repeller it must have a pairwise invasion plot of a form similar to that illustrated in plot (c) of figure 5-1, that is, the region directly above the singular strategy must show negative invasion fitness (for ES singular strategies) and the non–trivial zero–cline must have a positive gradient (for the evolutionary repulsion of ES singular strategies). It follows that the line, passing through (e^*, e^*) with gradient -1 will be locally contained within a region of negative invasion. Then if (e^1, e^2) lies on this line in the region of negative in invasion the strategy e_1 and e_2 are mutually uninvadable. However, in chapter 4 it was verified that mutual un–invadability was not possible in this particular model. Note that some evolutionarily unstable repellers and evolutionarily stable attractors are also not possible in this model, as illustrated in figure 5-3.

The other three evolutionary scenarios, outlined in table 5.1, are all possible for certain parameter combinations. The plots of figure 5-4 illustrate how the classification of a singular generalist depends upon h, q e_G, and f''_G parameter values. In all plots the ES–curve satisfies$f''_G = f''_{ES}$ and the CS–curve $f''_G = f''_{CS}$. If parameters lie above the CS–curve in region I or region II the generalist is CS. If parameters lie above the



(a) ES & CS (b) ES & non–CS (c) non–ES & non–CS

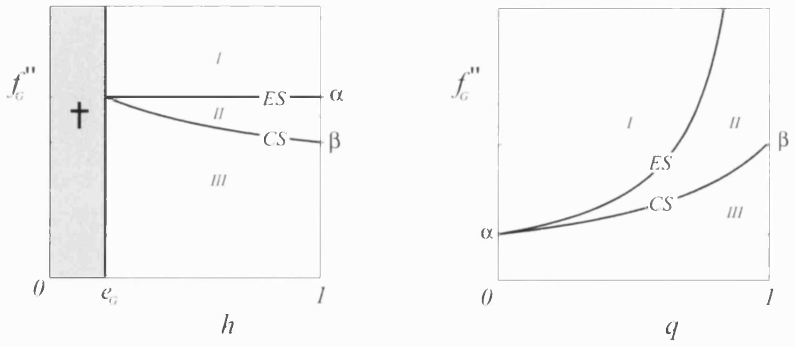
Figure 5-3: Pairwise invasibility plots showing strategies in the neighbourhood of a singular strategy, e^*,that are mutually uninvadable. The points in the (e, e') plane are shaded grey if and only if a mutant with strategy e' can invade a resident with strategy e. Mutually uninvadability can occur if the dashed diagonal is in the unshaded region of negative invasion fitness.

ES–curve the generalist is ES. Therefore if parameters lie in region I the generalist is an evolutionarily stable attractors, in region III a branching point, and in region II an evolutionarily unstable repeller.

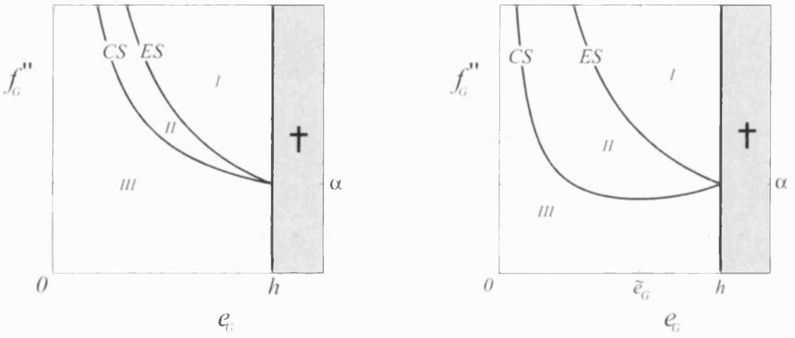
Some general results are apparent. In plot (b) we see that increasing the degree of patch type aggregation, q, contracts the ES region, expanding both the regions of branching and evolutionary repulsion. The biological explanation of this is quite intuitive. When aggregation is high dispersers are more likely to arrive in patches that are similar in type 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 to 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 habitat uniformly from both patch types does not alter the ES behavior of the generalist however it does contract the CS region (see plot (a) of figure 5-4), thus decreasing the range of branching strategies. Habitat loss is often regarded as a mechanism for reducing biodiversity. Here is an example of how evolutionary branching, a process that can increase biodiversity, can also be constricted by habitat loss.

Increasing e_G always expands both the ES and CS regions yet contracts the branching region II (this is not obvious from plots (c) and (d) though true). If the generalist



(a) $q \neq 0$ (b)



(c) $q = 0.5$ (d) $q = 0.8$

Figure 5-4: The evolutionary classification of a singular generalist strategy in a symmetric landscape. The plots show how the ES and CS classification depends upon f''_G and h (plot (a)), q (plot (b)), and e_G (when $q < \frac{2}{3}$ in plot (c) and $q > \frac{2}{3}$ in plot (d)). If parameters lie in region *I*, bounded by the ES–curve, the generalist is an evolutionarily stable attractor. If parameters lie in region *II*, bounded by the ES–curve and CS–curve, the generalist is an evolutionarily unstable attractor (a branching point). If parameters lie in region *III*, bounded by the CS–curve, the generalist is an evolutionarily unstable repeller. When $f''_G = \alpha$ the ES and CS curves intersect: in plot (a) $\alpha = 2/((1-q)e_G)$, in plot (b) $\alpha = 2/e_G$ and in plots (c) and (d) $\alpha = 2/(h(1-q))$. In plot (a) $\beta = 2/e_G + 4q/(1+(1-2q)e_G)$ and in plot (b) $\beta = 2/e_G + 4/(h - e_G)$. If parameters lie in the shaded region the generalist cannot persist.

resident metapopulation is fragile, any attempts to specialize may be penalized. Increasing e_G does not always change the CS behaviour of the generalist in a monotonic way as illustrated in plot (*d*). Only an intermediate range of e_G will result in the convergence stability of the generalist. This range exists and can only exist when f''_{CS} increases with e_G at $e_G = h$ which happens if and only if $q > \frac{2}{3}$. In this case the value of f''_G on the CS–curve is a minimum when

$$e_G = \tilde{e}_G = h(\sqrt{\frac{2q}{2q-1}} - 1) , \tag{5.5.1.9}$$

and thus the range of f''_G leading to this non–monotonic change with e_G is

$$\frac{2}{\tilde{e}_G} + \frac{4q}{h + (1-2q)\tilde{e}_G} < f''_G < \frac{2}{h(1-q)} . \tag{5.5.1.10}$$

5.6 Model M2: Patch Type Dependent Emigration

We shall now consider the generalization of model **M1** to investigate the assumption that the dispersal process is dependent upon patch type and the consequences for the evolutionary properties of a singular generalist.

The ecological model analyzed so far in this chapter has assumed that patch-type specialisation (modelled through local extinction rate) does not influence the rate that local populations produce dispersing propagules. There are good arguments for why this assumption may be too restrictive for some ecological situations. In many cases:

1. Propagule production will depend upon the state of the local populations (size, spatial extent etc) which in turn will depend upon the degree of patch specialisation of the individuals in the population.

2. Dispersal behavior, as a mechanism for promoting metapopulation level viability, will depend upon local population state.

The first point stems from the observation that a healthy local population will be expected to produce more dispersers than a relatively unhealthy one if per capita propagule production is identical within both populations. The second point is raised when we appreciate that the role of dispersal (at the local population level at least), is to counteract the consequences of local extinction and may strongly depend upon the state of the local population; a product of the degree of specialisation. The 'decision' to disperse (i.e an increased investment in propagule production at the population level) may be influenced by local cues that arise from the degree of patch specialisation.

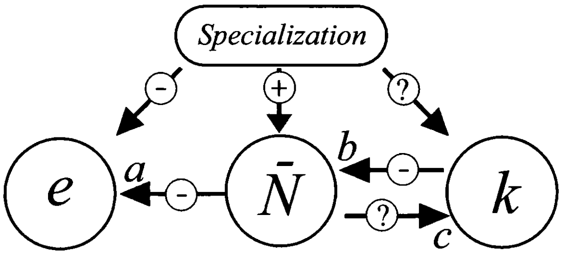


Figure 5-5: A schematic representation of how the propagule production rate, k, and the extinction rate, e, may inter-depend through the mediation of the equilibrium population size, $\bar{N}$. Arrows indicate the direction of influence. The sign on the arrow represents the nature of the influence (i.e. a positive influences is indicated by a '+').

The diagram 5-5 illustrates the influence relationships between propagule production rate, k, extinction rate, e, and equilibrium population state $\bar{N}$. The arrows show the direction of influence with the plus sign, for example, indicating a net positive effect. The variable $\bar{N}$ implicit in the model equations may represent a measure of the population state, perhaps equilibrium population size, that depends upon both the degree of specialisation and the metapopulation–level parameters e (patch specific extinction rate) and k (patch specific emigration rate). The causal relationships, labeled a, b and c represent:

a Increased specialisation, via population size, reduces extinction risk (as presently modelled.)

b Increased propagule production may decrease local population size following dispersal.

c Increasing population size may have a positive (see point 1 above) or negative (point 2) affect upon emigration.

A metapopulation model that incorporates these processes explicitly would require an explicit description of local population dynamics, as dependent upon the life history traits of individuals and in particular the dispersal traits. The model developed so far is not equipped to deal with this description but a modification offers some insight into these mechanisms.

Relationship (a) has been built into the model already through the extinction trade-off relationship. Relationship (b) will be disregarded since the time scale that dictates local population dynamics will still be assumed much faster than the time scale of metapopulation dynamics.

To incorporate relationship (c) we shall model the emigration component of the colonization parameter k_{ji}. Recall that k_{ji} incorporates propagule production rate in type j patches and the colonization success rate in type i patches. Then as a function of the population state in patch j only:

$$k_{ji} = k_i(\bar{N}_j).$$

Assuming that the population state determines the extinction rate so that $e_j = e(\bar{N}_j)$, that is population state is a perfect indicator of extinction risk. Furthermore, we shall assume that for a suitably large subset of strategies (including the generalist strategy) this relationship is invertible,

$$\bar{N}_j = \bar{N}(e_j) \ ,$$

so that the emigration rate can be given as a function of the extinction rate,

$$k_{ji} = k_i(e_j) \ . \tag{5.6.0.11}$$

For complicated emigration responses this monotonic nature may be too simple.

Let us further assume that the establishment of local populations is not patch–type dependent so that $k_1(e) = k_2(e)$ for all e. Furthermore, without loss of generality, we may assume that $k(e_G) = 1$.

The colonization rates for the nth competitor then become

$$c^n_{ji} = \frac{k(e^n_j)\mathbb{P}(i/j)}{\rho_i} \ . \tag{5.6.0.12}$$

The model equation for competitor n with N competitor types is thus

$$\begin{aligned} \frac{dx^n_1}{dt} &= (c^n_{11}x^n_1 + c^n_{21}x^n_2)(h_1\rho_1 - \sum_{m=1}^{N} x^m_1) - e^n_1 x^n_1 \\ \frac{dx^n_2}{dt} &= (c^n_{12}x^n_1 + c^n_{22}x^n_2)(h_2\rho_2 - \sum_{m=1}^{N} x^m_2) - e^n_2 x^n_2 \ . \end{aligned} \tag{5.6.0.13}$$

With the trade–off $e^n_2 = f(e^n_1)$ the strategy space remains 1–dimensional: i.e. $l_{ji} = \frac{\mathbb{P}(i/j)}{\rho_i}$

colonization rates are in the form

$$c_{ji}(e_j^n) = k(e_j^n) l_{ji} \, .$$

This model will be referred to as model **M2**. Recall that monomorphic invasion is dependent solely upon $\det J_M$ (see equation 4.4.0.13 of chapter 4). The monomorphic invasion function $\Delta(e', e) = -\det J_M(e', e)$, for the mutant strategy e' when the strategy e is resident, becomes

$$\begin{aligned} \Delta(e', e) = f(e')k(e')l_{11}\frac{eX(e)}{c_{11}(e)X(e) + c_{21}(e)} &+ e'k(f(e'))l_{22}\frac{f(e)}{c_{12}(e)X(e) + c_{22}(e)} \\ &- e'f(e') \\ + k(e')k(f(e'))(l_{12}l_{21} - l_{11}l_{22}) &\frac{ef(e)X(e)}{(c_{11}(e)X(e) + c_{21}(e))(c_{12}(e)X(e) + c_{22}(e))} \, , \end{aligned} \tag{5.6.0.14}$$

where $X(e) = \frac{\hat{x}_1(e)}{\hat{x}_2(e)}$, the steady patch occupation ratio of the monomorphic resident. The selection gradient, again defined as $D(e) = \Delta_1(e, e)$, is

$$\begin{aligned} D(e) = \frac{d}{de}\{f(e)k(e)\}l_{11}&\frac{eX(e)}{c_{11}(e)X(e) + c_{21}(e)} \\ &+ \frac{d}{de}\{ek(f(e))\}l_{22}\frac{f(e)}{c_{12}(e)X(e) + c_{22}(e)} \\ &- f(e) - ef'(e) \\ &+ \frac{d}{de}\{k(e)k(f(e))\}(l_{12}l_{21} - l_{11}l_{22})\ldots \\ &\ldots\frac{ef(e)X(e)}{(c_{11}(e)X(e) + c_{21}(e))(c_{12}(e)X(e) + c_{22}(e))} \, . \end{aligned} \tag{5.6.0.15}$$

The definition of singular strategies and the ES and CS conditions still hold from the previous section i.e. e^* is a singular strategy if $D(e^*) = 0$.

e^* is ES if $\Delta_{11}(e^*, e^*) < 0$ where

$$\begin{aligned}\Delta_{11}(e^*,e^*) = {} & \\ & \frac{d^2}{de^2}\left\{f(e)k(e)\right\}\big|_{e=e^*} l_{11}\frac{e^*X^*}{c^*_{11}X^* + c^*_{21}X^*} \\ & + \frac{d^2}{de^2}\left\{ek(f(e))\right\}\big|_{e=e^*} l_{22}\frac{f(e^*)}{c^*_{12}X^* + c^*_{22}} \\ & - 2f'(e^*) - e^*f''(e^*) \\ + \frac{d^2}{de^2} & \left\{k(e)k(f(e))\right\}\big|_{e=e^*}(l_{12}l_{21} - l_{11}l_{22})\frac{e^*f(e^*)X^*}{(c^*_{11}X^* + c^*_{21})(c^*_{12}X^* + c^*_{22})}\ ,\end{aligned} \tag{5.6.0.16}$$

$X^* = X(e^*)$ and $c^*_{ij} = c_{ij}(e^*)$.

e^* is CS if $\Delta_{11}(e^*, e^*) + \Delta_{12}(e^*, e^*) < 0$ where

$$\begin{aligned}\Delta_{12}(e^*,e^*) = {} & \{X^*(c^*_{11}X^* + c^*_{21}) - e^*X^*(f'(e^*)k'(f(e^*))l_{21} + k'(e^*)l_{11}X^*)\}A \\ & + \{f'(e^*)(c^*_{12}X^* + c^*_{22}) - f(e^*)(k'(e^*)l_{12}X^* + f'(e^*)k'(f(e^*))l_{22})\}B \\ & + \{(f(e^*) + e^*f'(e^*))X^*(c^*_{11}X^* + c^*_{21})(c_{12*}X^* + c^*_{22}) \\ & + e^*f(e^*))X^*(k'(e^*)l_{12}X^* + f'(e^*)k'(f(e^*))l_{22})(c^*_{11}X^* + c^*_{21}) \\ & + e^*f(e^*)X^*(k'(e^*)l_{11}X^* + f'(e^*)k'(f(e^*))l_{21})(c^*_{12}X^* + c^*_{22})\}C \\ & + [e^*c^*_{21}A - f(e^*)c^*_{12}B + e^*f(e^*)((c^*_{11}X^* + c^*_{21})(c^*_{12}X^* + c^*_{22}) \\ & + c^*_{11}(c^*_{12}X^* + c^*_{22}) + c^*_{12}X^*(c^*_{11}X^* + c^*_{21}))C]\frac{dX^*}{de}\ ,\end{aligned} \tag{5.6.0.17}$$

and where

$$A = \frac{\frac{d^2}{de^2}\left\{f(e)k(e)\right\}\big|_{e=e^*} l_{11}}{(c^*_{11}X^* + c^*_{21})^2}\ , \tag{5.6.0.18}$$

$$B = \frac{\frac{d^2}{de^2}\left\{ek(f(e))\right\}\big|_{e=e^*} l_{22}}{(c^*_{12}X^* + c^*_{22})^2}\ , \tag{5.6.0.19}$$

and

$$C = \frac{\frac{d^2}{de^2}\left\{k(e)k(f(e))\right\}\big|_{e=e^*}(l_{12}l_{21} - l_{11}l_{22})}{(c^*_{11}X^* + c^*_{21})(c^*_{12}X^* + c^*_{22})}\ . \tag{5.6.0.20}$$

These inelegant conditions simplify for the case of a singular generalist in a symmetric landscape.

5.6.1 Singular Generalist Strategies in Symmetric Landscapes

We again resort to considering the evolutionary behaviour of a generalist strategy, e_G such that $e_G = f(e_G)$, that is singular when the landscape has the symmetry $h_1 = h_2 = h$ and $\rho = \frac{1}{2}$. Since $k(e_G) = 1$, for $D(e_G, e_G) = 0$ the extinction trade-off function must again satisfy $f'(e_G) = -1$. Landscape symmetry also leads to the persistence condition $e < h$, and $X(e_G) = 1$. Let $k'_G = k'(e_G)$ and $k''_G = k''(e_G)$.

From the ES condition 5.6.0.16

$$\Delta_{11}(e_G, e_G) = 2 - 4qe_Gk'_G - 2(1-2q)e_G^2{k'_G}^2 + 2(1-q)e_G^2k''_G - (1-q)e_G(1-e_Gk'_G)f''_G \,. \tag{5.6.1.1}$$

This may be rearranged to give the ES condition for a singular generalist as

$$(1-e_Gk'_G)f''_G \; > \; \frac{2}{(1-q)e_G}(1-e_Gk'_G)\left(1+(1-2q)e_Gk'_G\right) + 2e_Gk''_G \,, \tag{5.6.1.2}$$

or with f''_{ES} as previously defined

$$(1-e_Gk'_G)f''_G \; > \; f''_{ES}(1-e_Gk'_G)\left(1+(1-2q)e_Gk'_G\right) + 2e_Gk''_G \,. \tag{5.6.1.3}$$

Claim 15. The CS condition for a singular generalist is

$$(1-e_Gk'_G)f''_G \; > \; f''_{CS}(1-e_Gk'_G)\left(1+(1-2q)e_Gk'_G\right) + 2e_Gk''_G \,. \tag{5.6.1.4}$$

Proof. With landscape and trade–off symmetry equation 5.6.0.18 gives $A = -q(1 - k'_Ge_G)/2$, equation 5.6.0.19 gives $B = -A$ and 5.6.0.20 gives $C = 0$. This simplifies equation 5.6.0.17 evaluated at for at generalist strategy to

$$\Delta_{12}(e_G, e_G) \; = \; -2q(1-k'_Ge_G)(1+(1-2q)e_Gk'_G + (1-q)e_G\frac{dX(e_G)}{de}) \,. \tag{5.6.1.5}$$

Landscape symmetry reduces equation 3.4.2.8 of chapter 3 to

$$\begin{aligned} &c_{11}(e)c_{12}(e)hX^3 \\ &\quad + (2c_{12}(e)e - 2c_{11}(e)f(e) + (c_{11}(e)c_{22}(e) + c_{12}(e)c_{21}(e) - c_{11}(e)c_{12}(e))h)X^2 \\ &\quad\; (2c_{22}(e)e - 2c_{21}(e)f(e) - (c_{11}(e)c_{22}(e) + c_{12}(e)c_{21}(e) - c_{21}(e)c_{22}(e))h)X \\ &\hspace{20em} - c_{22}(e)c_{21}(e)h = 0 \,. \end{aligned} \tag{5.6.1.6}$$

Differentiating this expression leads to

$$\begin{aligned}
&[3c_{11}(e)c_{12}(e)hX^2 \\
&\quad + 2(2c_{12}(e)e - 2c_{11}(e)f(e) + (c_{11}(e)c_{22}(e) + c_{12}(e)c_{21}(e) - c_{11}(e)c_{12}(e))h)X \\
&\quad (2c_{22}(e)e - 2c_{21}(e)f(e) - (c_{11}(e)c_{22}(e) + c_{12}(e)c_{21}(e) - c_{21}(e)c_{22}(e))h)]\frac{dX(e)}{de} \\
&\qquad + 2k(e)k'(e)l_{11}l_{12}hX^3 \\
&\qquad + [2c_{12} - 2c_{11}f'(e) + 2ek'(e)l_{12} - 2f(e)k'(e)l_{11} \\
&\qquad + (k'(e)l_{11}c_{22} + f'(e)k'(f(e))l_{22}c_{11})h \\
&\qquad + (k'(e)l_{12}c_{21} + f'(e)k'(f(e))l_{21}c_{12})h - k'(e)(l_{11}c_{12} + l_{12}c_{11})h]X^2 \\
&\qquad + [2c_{22} - 2c_{21}f'(e) + 2ef'(e)k'(f(e))l_{22} - 2f(e)f'(e)k'(f(e))l_{21} \\
&\qquad - (k'(e)l_{11}c_{22} + f'(e)k'(f(e))l_{22}c_{11})h \\
&\qquad - (k'(e)l_{12}c_{21} + f'(e)k'(f(e))l_{21}c_{12})h + f'(e)k'(f(e))(l_{21}c_{22} + l_{22}c_{21})h]X \\
&\qquad - (f'(e)k'(f(e))l_{21}c_{22} + f'(e)k'(f(e))l_{22}c_{21})h = 0\ . \qquad (5.6.1.7)
\end{aligned}$$

Then evaluating at e_G and rearranging yields

$$\begin{aligned}
\frac{dX(e_G)}{de} &= -\frac{4(c_{11} + c_{21}) + 4(c_{12} - c_{11})e_G k'_G}{(c_{12} + c_{11})^2 h + 2(c_{12} - c_{11})e_G} \\
&= -\frac{2 + 2(1-2q)e_G k'_G}{h + (1-2q)e_G}\ . \qquad (5.6.1.8)
\end{aligned}$$

Then 5.6.1.5 gives

$$\begin{aligned}
\Delta_{12}(e_G, e_G) &= -2q(1 - k'_G e_G)\left(1 + (1-2q)e_G k'_G - (1-q)e_G \frac{2 + 2(1-2q)e_G k'_G}{h + (1-2q)e_G}\right) \\
&= \frac{-2q(h - e_G)}{h + (1-2q)e_G}(1 - e_G k'_G)\left(1 + (1-2q)e_G k'_G\right) \\
&= (1-q)e_G(f''_{CS} - f''_{ES})(1 - e_G k'_G)\left(1 + (1-2q)e_G k'_G\right)\ . \qquad (5.6.1.9)
\end{aligned}$$

The CS condition $\Delta_{11}(e_G, e_G) + \Delta_{12}(e_G, e_G) < 0$ may be rearranged to

$$(1 - e_G k'_G)f''_G \quad > \quad f''_{ES}(1 - e_G k'_G)\left(1 + (1-2q)e_G k'_G\right) + 2e_G k''_G + \frac{\Delta_{12}(e_G, e_G)}{(1-q)e_G}\ , \qquad (5.6.1.10)$$

thus giving the required result. □

In terms of f''_G the ES condition is

$$\begin{aligned} f''_G &> f''_{ES}\left(1+(1-2q)e_Gk'_G\right)+\frac{2e_Gk''_G}{(1-e_Gk'_G)} \quad \text{if} \quad k'_G<\frac{1}{e_G} \\ f''_G &< f''_{ES}\left(1+(1-2q)e_Gk'_G\right)+\frac{2e_Gk''_G}{(1-e_Gk'_G)} \quad \text{if} \quad k'_G>\frac{1}{e_G}\,, \end{aligned} \tag{5.6.1.11}$$

and the CS conditions is

$$\begin{aligned} f''_G &> f''_{CS}\left(1+(1-2q)e_Gk'_G\right)+\frac{2e_Gk''_G}{(1-e_Gk'_G)} \quad \text{if} \quad k'_G<\frac{1}{e_G} \\ f''_G &< f''_{CS}\left(1+(1-2q)e_Gk'_G\right)+\frac{2e_Gk''_G}{(1-e_Gk'_G)} \quad \text{if} \quad k'_G>\frac{1}{e_G}\,. \end{aligned} \tag{5.6.1.12}$$

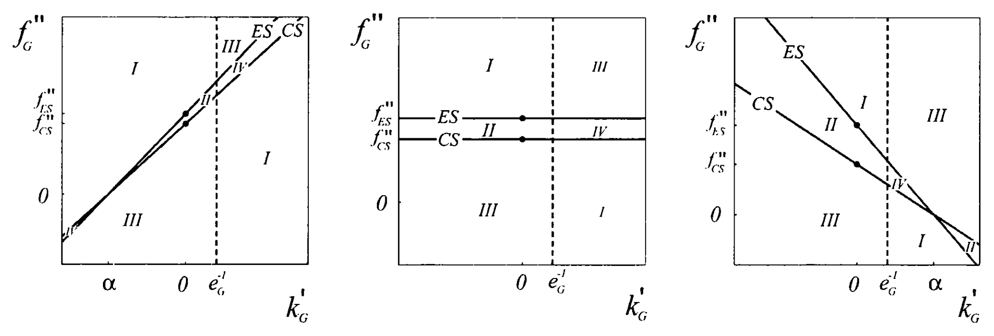
These conditions in terms of k'_G and k''_G are illustrated in figures 5-6, 5-7 and 5-8. Each plot indicates the evolutionary classification of the generalist in terms of the extinction rate trade-off parameter f''_G and the emigration rate parameter k'_G for constant values of k''_G. In every plot $e_G = 0.5$ and $h = 1$, although the values do not change the results in a qualitative way. In each plot the ES–curves indicate equality of 5.6.1.11 and the CS–curves indicate equality of 5.6.1.12. Region I represents evolutionarily stable attractors, III evolutionarily unstable repellers. The regions bounded by the ES– and CS–curves represent evolutionarily unstable attractors if $k'_G < \frac{1}{e_G}$ (region II) and evolutionarily stable repellers if $k'_G > \frac{1}{e_G}$ (region IV).

For the singular case when $k''_G = 0$ (figure 5-6) the ES–curves and CS–curves are lines with gradients $f''_{ES}(1-2q)e_G$ and $f''_{CS}(1-2q)e_G$ respectively. Thus the effect of increasing k'_G will depend upon whether the landscape is aggregated ($q > \frac{1}{2}$) or not. When $q > \frac{1}{2}$ increasing k'_G, for $k'_G < \frac{1}{e_G}$, results in the monotonic transition from unstable repellers to unstable attractors to stable attractors. If $q < \frac{1}{2}$ the transition order is reversed. This means that specialisation through monomorphic evolution is more likely to occur if either

1. Emigration rates are greater within favoured patches and the landscape is aggregated.

2. Emigration rates are greater within un–favoured patches and the landscape is disperse.

When landscapes are aggregated, propagules that come from favoured populated patches are more likely to find favoured patches. If k'_G is decreased the emigration



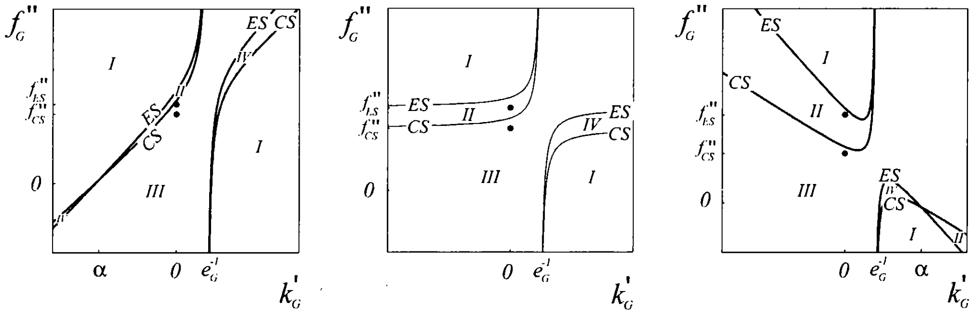
(a) $q = 0.3$ (b) $q = 0.5$ (c) $q = 0.7$

Figure 5-6: The evolutionary classification of a singular generalist strategy in a symmetric landscape when $k''_G = 0$. The plots show how the ES and CS classification depends upon f''_G and k'_G when $h = 1$ and $e_G = 0.5$. The ES–curve and the CS–curve together with the dashed line $k'_G = \frac{1}{e_G}$ bounds the regions *I–IV* of different evolutionary classification: *I* Evolutionarily stable attractor. *II* Evolutionarily unstable attractor (a branching point). *III* Evolutionarily unstable repeller. *IV* Evolutionarily stable repeller. The ES–curve crosses the CS–curve when $k'_G = \alpha = \frac{1}{(2q-1)e_G}$. f''_{ES} and f''_{CS} were defined by 5.5.1.2 and 5.5.1.3.

rate from favoured patches to favoured patches will also increase, amplifying the effects of landscape aggregation. The decreasing emigration rates from un-favoured patches will have a negative impact, however the net gain in terms of patch occupation will be positive. If the landscape is dispersed the opposite consequences of decreasing k'_G comes from an equivalent argument. The ecological benefits will naturally correspond to a competitive advantage that drives the evolution of specialism.

If k'_G exceeds $\frac{1}{e_G}$ (and $k'_G < \frac{1}{(2q-1)e_G}$ if $q > \frac{1}{2}$) the classification transitions of the generalist with increasing f''_G is different. Recall that $R_0^1 = \frac{c_{11}h_1\rho_1}{e_1} = \frac{k(e_1)qh}{e_1}$ is the number of type 1 patches colonized by a single occupied type 1 patch before extinction when the landscape is empty. Now $k(e_1) = 1 + k'_G(e_1 - e_G) + O((e_1 - e_G)^2)$ so that $R_0^1 \approx (\frac{1-e_Gk'_G}{e_1} + k'_G)qh$ and thus R_0^1, when $e_1 - e_G$ is small, is an increasing function of e_1 if $k'_G > \frac{1}{e_G}$ so that any ecological benefits from the adaptation to type 1 patches by decreasing e_1 are exceeded by the cost associated with a decline in propagule production and thus the colonizing of type 1 patches. Therefore it is not unreasonable that the evolutionary mechanisms that yield a net advantage for specializing should be different if $k'_G > \frac{1}{e_G}$ as opposed to when $k'_G < \frac{1}{e_G}$. When $k'_G > \frac{1}{e_G}$ the generalist can be a evolutionary stable repeller; a classification that not possible in the constant colonization model.

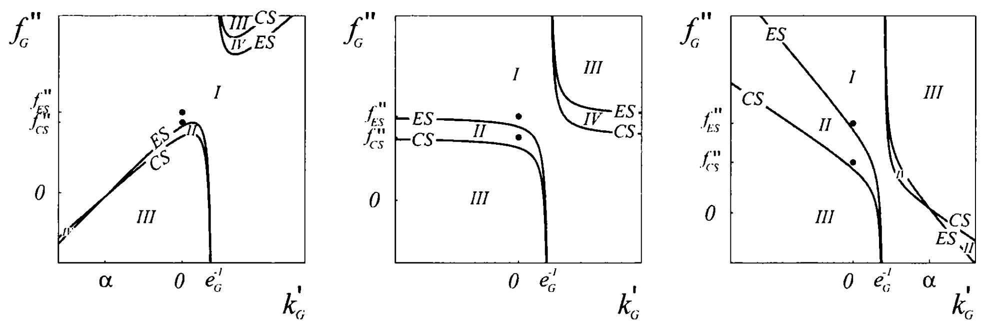
If $q > \frac{1}{2}$ and $k'_G > \frac{1}{(2q-1)e_G}$, then classification transitions with increasing f''_G will change again since the ES–curve drops below the CS–curve and the intermediate region becomes a branching region. If $q < \frac{1}{2}$ and $k'_G < \frac{1}{(2q-1)e_G}$ the intermediate region, following the crossing of the ES and CS–curves, will give evolutionarily stable repellers. In both case the transitions all occur when $f''_G < 0$, however if $k''_G < 0$ and $q > \frac{1}{2}$, or if $k''_G > 0$ and $q < \frac{1}{2}$, the transitions can occur for positive values of f''_G, provided k'_G is close to $\frac{1}{(2q-1)e_G}$. This follows from the fact that the left–hand side of 5.6.1.11 and 5.6.1.12 are equal to $-\frac{(2q-1)e_G k''_G}{1-q}$ when $k'_G = \frac{1}{(2q-1)e_G}$ which is positive for these cases. This result is not obvious in plot (a) of figure 5-7 or plot (c) of figure 5-8.



(a) $q = 0.3$ (b) $q = 0.5$ (c) $q = 0.7$

Figure 5-7: The evolutionary classification of a singular generalist strategy in a symmetric landscape when $k''_G = 1 > 0$. The plots show how the ES and CS classification depends upon f''_G and k'_G when $h = 1$ and $e_G = 0.5$. The ES–curve and the CS–curve bound the regions *I*–*IV* of different evolutionary classification: *I* Evolutionarily stable attractor. *II* Evolutionarily unstable attractor (a branching point). *III* Evolutionarily unstable repeller. *IV* Evolutionarily stable repeller. The ES–curve crosses the CS–curve when $k'_G = \alpha = \frac{1}{(2q-1)e_G}$. f''_{ES} and f''_{CS} were defined by 5.5.1.2 and 5.5.1.3.

When $k''_G \neq 0$ the transitions orders with increasing f''_G do not change however the values of f''_G when they occur can be quite different. The most striking result is perhaps the monotonic nature of the ES–curves and CS–curves with respect to k'_G that was observed in figure 5-6, can break down if $k''_G \neq 0$. When $q > \frac{1}{2}$ and $k''_G > 0$, and when f''_G is suitably large (above about f_{ES}), increasing k'_G can lead result in four transitions: An evolutionary unstable repeller can become an attractor and then evolutionarily stable, yet the further increase of $k'_G < 1/e_G$ will lead to evolutionary instability and a repellor. This is illustrated in plot (c) of figure 5-7 when $k''_G = 1$. A



(a) $q = 0.3$ (b) $q = 0.5$ (c) $q = 0.7$

Figure 5-8: The evolutionary classification of a singular generalist strategy in a symmetric landscape when $k''_G = -1 < 0$. The plots show how the ES and CS classification depends upon f''_G and k'_G when $h = 1$ and $e_G = 0.5$. The ES–curve and the CS–curve bound the regions *I*–*IV* of different evolutionary classification: *I* Evolutionarily stable attractor. *II* Evolutionarily unstable attractor (a branching point). *III* Evolutionarily unstable repeller. *IV* Evolutionarily stable repeller. The ES–curve crosses the CS–curve when $k'_G = \alpha = \frac{1}{(2q-1)e_G}$. f''_{ES} and f''_{CS} were defined by 5.5.1.2 and 5.5.1.3.

similar result is illustrated in plot (a) of 5-8 when $k'' = -1$. The transition is from an evolutionarily stable attractor, to an evolutionarily unstable attractor and then to an evolutionarily unstable repeller, and back again. It is also possible for all four classifications to be obtained by changing k'_G. This occurs if $k''_G > 0$ and $q < \frac{1}{2}$ (plot (a) of 5-7) and alternatively if $k''_G < 0$ and $q > \frac{1}{2}$ (plot (c) of 5-8).

5.7 Discussion

In this chapter a model of metapopulation evolution was presented when competition is for *empty* habitat patches only. In this case the selective pressures acting upon individuals, driving evolution, are assumed to be equivalent to the pressures that act upon local pure–type populations. An adaptive dynamics approach was taken in the analysis of the model. This involved the determination and classification of *evolutionarily singular strategies* of the evolving trait space. One type of singular strategy of particular interest is the branching strategy; despite the inherent property that every strategy has an open neighbourhood of coexisting strategies within the full two–dimensional (e_1, e_2) parameter space (verified in the previous chapter), the trade–off relationship restricts this property to branching strategies *only* (Meszéna et al. 2006). This limits the potential for maximising biodiversity (as limited by resource and community structure) through evolution. In this chapter we investigated how landscape structures affect the evolution process and, consequentially, biodiversity.

In general the conditions for evolutionary branching and other singular scenarios are algebraically complicated and do not provide a good aid for developing intuition. However, for certain landscape parameter values and classes of trade–off relationships, we have shown that these conditions can be reduced to a simple pair of inequalities. In particular we considered the evolutionary properties of the generalist strategy that is singular when both the landscape and trade–off relationship are symmetric. Both of these assumptions may be well approximated in real landscapes, resulting in qualitatively similar adaptive outcomes with regards to singular strategies that are only marginally specialized ($e_1^* \approx e_2^*$).

Two ecological models were considered, **M1** and **M2**, both being instances of the generalized Levins model that was introduced in chapter 3. The model **M1** assumes that colonization is patch–type independent with the model **M2** constructed to relax this by assuming that emigration depends upon patch–type and consequently strategy type.

Patch–type *Independent* Emigration

Each of the landscape and meta–demographic parameters, q (controlling the spatial correlation in patch–type), h (the fraction of patches habitable), e_G (the generalist extinction rate) and f_G'' (the trade–off strength at the generalist strategy) have a unique input into the determination of the generalist. In summary:

- Increasing q destabilises the generalist strategy when high correlations between same type patches promotes specialisation; via either evolutionary branching or monomorphic specialisation (although this may result in branching as discussed in the following chapter).

- Decreasing h has no affect upon the ES stability of the generalist however it may lead to monomorphic specialism.

- Increasing trade–off strength is qualitatively similar to decreasing q: As the cost of specializing increases, monomorphic generalism (locally at least) may become adaptive.

- Increasing e_G has perhaps the most surprising consequences. The general effect is the same as increasing f''_G, although extinction may occur before any evolutionary transition. In particular the generalist can become ES. This challenges the intuitive idea that increasing e_G is equivalent to decreasing h, as is the case with the ecological dynamics whereby the generalist persists if and only if $\frac{h}{e} > 1$. Another point of interest is the non–monotonic effect that e_G can have upon the CS classification (see plot (d) of figure 5-4).

The result illustrated in plot (b) of figure 5-4 is similar to those found by Meszéna et al. (1997) and Kisdi (2002) in two–population models, and by Parvinen & Egas (2004) in a structured metapopulation model. Meszéna et al. (1997) compared the joint effect of patch difference and dispersal rates that compare intuitively here with trade–off *weakness* (promoting specialisation) and decreased aggregation (promoting patch type mixing), respectively.

Patch–type *Dependent* Emigration

It is likely that the rate of propagule production correlates with the degree of patch specialisation. We demonstrated how only two parameters are needed to fully classifying the evolutionary consequences of variable emigration in the locality of the generalist strategy; k'_G (the strength of the specialisation effect) and k''_G (the degree of non–linearity of this effect). When $k'_G < 0$ emigration rates *increase* with patch specialism. This may happen if population sizes increase with patch suitability, producing more dispersers. When $k'_G > 0$ emigration rates *decrease* with patch specialism. This could perhaps model a case when *increasing* emigration rate, cued by patch type, increases extinction risk, or perhaps a case when poor patches cue dispersal behaviour so as to rescue populations inhabiting poor patches.

In summary:

- Generalism is more likely to be adaptive when either dispersal is positively correlated $k'_G < 0$ with patch adaptation and the landscape is dispersed, when weakly dependent dispersal is negatively correlated with patch adaptation and the landscape is aggregated, or when strongly dependent dispersal is negatively correlated and the landscape is dispersed.

- The effects of changing k'_G if the landscape is aggregated ($q > \frac{1}{2}$) can be very different to when the landscape is dispersed. In particular the classification transition as k'_G increases (ES and CS → non–ES and CS → non–ES to non–CS), observed for dispersed landscapes, is reversed when the landscape is aggregated.

- Extreme values of k'_G (negative if the landscape is dispersed, positive if the landscape is aggregated) can allow a ES generalist to become non–CS (known as a 'garden of Eden' strategy). This permits local strategies to be mutually non–invadable, exhibiting a metapopulation–level priority effect.
- Non–linear emigration only has noticeable affect for intermediate values of k'_G with greatest deviation when $k'_G \approx \frac{1}{e_G}$.

Increasing e_G increases the effects of patch–type dependent emigration but, arguably, moderate patch–type dependent emigration would have limited consequences upon the classification of the generalist. In the following chapter we investigate the evolution of specialism with the model **M1**, thus assuming no patch–type dependent emigration. To include more complicated emigration would require a full model of the patch specialism–patch emigration relationship, and perhaps even the modelling of independent traits as did Kisdi (2002) and Parvinen & Egas (2004).

Chapter 6

Specialist and Dimorphic Evolution in Heterogeneous Landscapes

6.1 Chapter Outline

In this chapter we model phenotypic variation explicitly and study the evolution of specialisation, evolutionary branching and dimorphic evolution. We find that landscape composition and trade–off strength can cause an array of interesting phenomena: Evolution can act to optimize for persistence locally (evolutionary rescue) yet sometimes limit persistence in a global sense (evolutionary trapping). The evolution of dimorphisms, we shall show, often terminates in a *symmetric* coalition, even when the landscape is not. The reverse of this situation is also shown to be possible when we give an example of the evolutionarily stable attraction of an asymmetric *near*–generalist–specialist dimorphism.

6.2 Introduction

Species coexistence in the context of resource usage is naturally related to patch–type specialisation (Brown & Pavlovic 1992, Kisdi 2002) as illustrated in chapter 4. The more specialised the competitors are the less they interact at the metapopulation level. If specialising to a particular patch is risky, evolutionary pressures for generalism may conspire against specialist dimorphisms. Clearly, landscape and trade–off structure will both play important parts in the co–evolution of variants of a species (and differing species), as was illustrated in the case of the generalist evolution in the previous chapter. We wish to investigate and delineate these processes and expose any exceptions.

An important question to ask is 'when will monomorphic evolution lead to evolutionary branching and coexistence?' and 'when are potential dimorphisms, that harbour important varieties, unobtainable via monomorphic evolution?'. Egas et al. (2004), investigating a model of two coupled populations, found that evolution tends to restrict coexistence (in particular that between specialist and generalists) and related the findings to trade–off strength. Our results, with a focus broadened to include landscape structure, back their arguments.

An important graphical tool that we employ in this chapter are the so called 'ecology–evolution–environment' diagrams, or E^3 diagrams (Dieckmann & Ferrière 2004). Akin to the diagrams of classic bifurcation theory that represent the value and stability of fixed points of a dynamic system in relation to a bifurcation parameter, E^3 diagrams relate an *evolving* variable (i.e. a phenotypic trait) with an environmental variable (i.e. habitat quality), but with added complexities; fixed traits (singular strategies) are ES–classified, and any non–persisting region of trait space are exposed (the *ecological* component). In short, these plots capture the salient details of a PIP for a continuous range of a particular system parameter. These plots are useful for pinpointing interesting phenomena, such as evolutionary rescue and evolutionary trapping (as discussed in the main text).

Since the analysis of the evolutionary dynamics was restricted to the generalist in the previous chapter (for the special case when the landscape is symmetric) only a local description of the trade–off relationship was required. To model specialisation however, evolutionary branching and dimorphic evolution the trade-off function must be described in full.

6.3 Modelling Trade-off Relationships

We shall restrict our investigation to the model **M1**. The analysis of Δ (given by equation 5.5.0.1 of chapter 5), our measure of local mutant fitness, is hampered by the difficulty of working with the expression for resident metapopulation density which we recall is the unique positive root of the cubic equation 3.4.2.8 in chapter 3. Some results relating to phenotypic specialisation, where selection is for the decreasing of 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 $e : \tau \mapsto e(\tau) > 0$ where

$$e_1 = e(\tau) \ , \tag{6.3.0.1}$$

$$e_2 = e(-\tau) \ . \tag{6.3.0.2}$$

τ represents a phenotypic strategy and $\tau = 0$ is the generalist strategy ($e_G = e_1(0) = e_2(0)$). We shall assume that the phenotype with strategy $\tau = 1$ is the one most adapted to type–1 patches, and so e takes a minimum value at $\tau = 1$. It follows that e_2 thus takes a minimum value when $\tau = -1$. The strategies $\tau = 1$ and $\tau = -1$ will be referred to as the extreme patch–type specialists. We shall further assume that e has no other turning points so that $e(\tau)$ increases with $|\tau - 1|$. This will ensure that the strategy set $[-1, 1]$ is evolutionary attracting: If $\tau > 1$ e_1 and e_2 both increase with τ hence local selection will be for decreasing values of τ. Equivalently if $\tau < -1$ local selection is for increasing values of τ. The evolutionary dynamics of interest will thus take place in this finite range of phenotype space. Figure 6-1 illustrates an example trade–off with the properties outlined above.

In section 5.5 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 may not possible to find the explicit form of f if $e(\tau)$ is not explicitly invertible, however it can be implicitly defined as $f(e(\tau)) = e(-\tau)$. Using the chain rule we have that

$$f'(e(\tau)) = -\frac{de(-\tau)}{d\tau} / \frac{de(\tau)}{d\tau} \ , \tag{6.3.0.3}$$

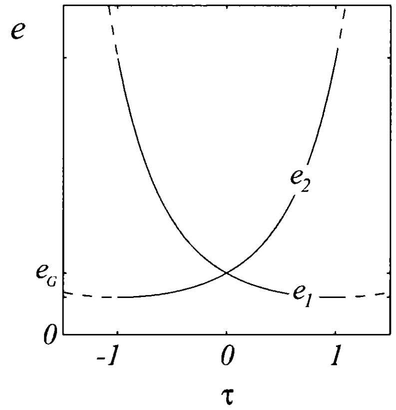


Figure 6-1: The patch type extinction rates e_1 and e_2 as functions of the phenotype strategies, τ, for the Gaussian trade-off (presented below) when $e_G = 0.5$ and $\beta = 0.5$. Trivially, selection acts to decrease $|\tau|$ when $|\tau| > 1$, since both patch type extinction rates will be decreased.

and

$$f''(e(\tau)) = \left(\frac{de(-\tau)}{d\tau}\frac{d^2e(\tau)}{d\tau^2} + \frac{de(\tau)}{d\tau}\frac{d^2e(-\tau)}{d\tau^2}\right) / \left(\frac{de(\tau)}{d\tau}\right)^3 . \qquad (6.3.0.4)$$

Therefore all of the adaptive dynamics definitions of the previous chapter can be used to investigate the evolutionary behaviour subject to the particular extinction rate $e(\tau)$.

The symmetry in the trade-off yields the property that $f'_G = f'(e(0)) = -1$. In chapter 5 (see equation 5.5.1.1) it was shown that this is the condition for the generalist to be singular when the landscape is symmetric (equal fractions of the two patches, $\rho = \frac{1}{2}$, that are equally habitable, $h_1 = h_2$).

The extreme specialists, $\tau = 1$ and $\tau = -1$, are never singular strategies: Recall that the condition for τ^* to be a singular strategy (see equation 5.5.1.1 of chapter 5) is

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

where $e^* = e(\tau^*)$.

Now $f'(e(-1)) = 0$ since e_2 is a minimum when $\tau = 1$. $\tau = -1$ cannot be singular the right-hand side of the singular condition is never zero ($X^* > 0$ and $f(e(\tau)) = e_2(\tau) > 0$).

6.3.1 An Example Trade-off: Gaussian Patch Preference

The two patch types may be composed of different types of resources or perhaps different quantities of an identical resource. Resource quantity is perhaps best modelled as a continuous variable and could represent anything from the concentration of a chemical the size of a seed or average altitude. The 1–dimensional variation between the phenotype of the species could correspond to preference for a given resource quantity; that is τ is a measure of the the resource type and the strategy τ refers to the phenotype with a preference for resource level τ. Discrete landscape composition may still be maintained even when the resource can be considered continuous. An example of such a organism and resource could be a species of bird consuming seeds. Even though seed size is a continuous quantity the target species may consume from two different plants with seeds that have distinctly differing mean sizes. If the plants are spatially patchy and patches are comprised of one plant species, then the model may be a fairly faithful representation of this situation. Beak size could be one of the adaptive traits that corresponds to seed size variation.

Consider $\xi(\tau';\tau) = \frac{1}{E(\tau;\tau')}$, where $E(\tau;\tau')$ is defined to be the extinction rate that the phenotype with preference for resource level τ experiences in patches of resource τ', and in particular $E(\tau;1) = e_1(\tau)$ and $E(\tau;-1) = e_2(\tau)$. ξ is the expected extinction time of a type τ population in a type τ' patch and a measure of patch preference. A natural trade-off relationship corresponds to Gaussian distributed extinction times: For the phenotype with patch preference τ we assume that the level of adaptation to resource level τ' depends upon $|\tau' - \tau|$ so that

$$\xi(\tau';\tau) = \alpha \exp(-\beta(\tau - \tau')^2) \ , \tag{6.3.1.1}$$

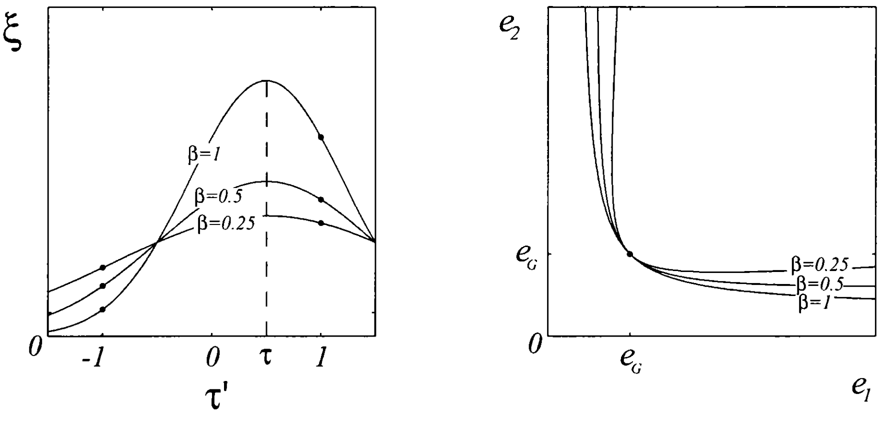
where α (> 0 for positive extinction) and β (> 0 for the adaptation to be maximized at $\tau' = \tau$) are species constants.

From this we derive

$$e(\tau) = e_1(\tau) = \frac{1}{\xi(1;\tau)} = \frac{\exp(\beta(\tau - 1)^2)}{\alpha} \ . \tag{6.3.1.2}$$

Since $e(0) = e_G$ we have that $\alpha = \frac{\exp(\beta)}{e_G}$ and thus

$$e(\tau) = e_G \exp(\beta(\tau^2 - 2\tau)) \ . \tag{6.3.1.3}$$



(a) (b)

Figure 6-2: The Gaussian trade–off. Plot (a) shows how expected extinction time, ξ, depends upon phenotypic resource preference, τ, and patch resource type τ', for three different trade-off strengths, $\beta = 0.25, 0.5, 1$. Type 1 patches correspond to resource $\tau = 1$ and type 2 patches correspond to resource level $\tau = -1$. Plot (b) illustrates how patch type 1 and 2 extinction rates, e_1 and e_2, depend upon phenotype habitat preference τ, for three different trade-off strengths, $\beta = 0.25, 0.5, 1$. $e_G = 0.5$ for each plot.

The parameter β is a measure of how different specialist phenotypes of the species perceives type–1 patches and type–2 patches. Increasing β increases the difference characterizing more sensitive species. This is illustrated in figure 6-2.

Meszéna et al. (1997) and Kisdi (2002) consider trade-off functions for patch adaptation that explicitly model patch difference. The evolutionary properties of the singular generalist in a symmetric landscape ($\rho = \frac{1}{2}$ and $h_1 = h_2 = h$) can now be given in terms of β: Evaluating 6.3.0.4 yields

$$f_G'' = \frac{1+2\beta}{\beta e_G} , \tag{6.3.1.4}$$

and thus

$$\beta = \frac{1}{e_G f_G'' - 2} . \tag{6.3.1.5}$$

Since $\beta > 0$ we have that $f_G'' > \frac{2}{e_G}$. Increasing β decreases f_G'' and thus the strength of the trade–off function.

Now recall that the generalist is ES when the landscape is symmetric if

$$f''_G > f''_{ES} = \frac{2}{(1-q)e_G} > \frac{2}{e_G} \ ,$$

(see equation 5.5.1.2 of chapter 5) and in terms of β this condition is

$$\beta < \frac{1-q}{2q} =: \beta_{ES} \ . \tag{6.3.1.6}$$

The generalist is CS when the landscape is symmetric if

$$f''_G > f''_{CS} = \frac{2(h+e_G)}{(h+e_G(1-2q))e_G} > \frac{2}{e_G} \ ,$$

(see equation 5.5.1.3 of chapter 5) and in terms of β this condition is

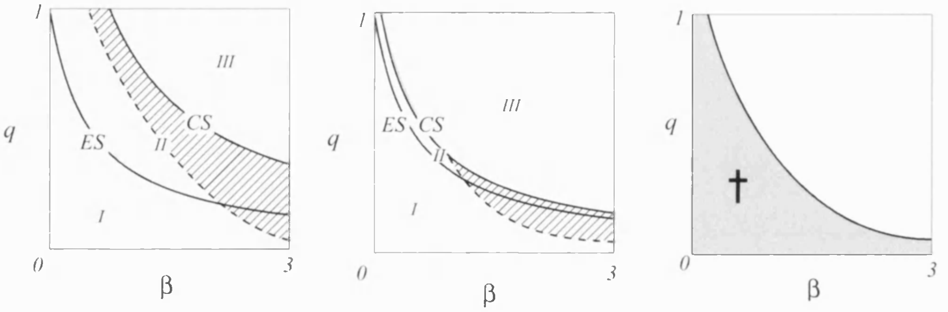
$$\beta < \frac{h+(1-2q)e_G}{4qe_G} =: \beta_{CS} \ . \tag{6.3.1.7}$$

6.4 Specialisation and Dimorphic Evolution in Symmetric Landscapes

The trade–off function e can be expressed in the form $e(\tau) = e_G\bar{e}(\tau)$, where $\bar{e}$ does not depend upon e_G. This means that the evolutionary dynamics that take place in $[-1,1]^N$ strategy space, where N is the number of resident types, with the landscape parameters ρ, q, h_1, h_2, and occupation state variables x_1^n and x_2^n (for strategy $n = 1, 2, ..., N$), will be equivalent to those of a 'tilde' system where $\tilde{\rho} = \rho$, $\tilde{q} = q$, $\tilde{h}_1 = 1$, $\tilde{h}_2 = \frac{h_2}{h_1}$, $\tilde{x}_1^n = \frac{x_1^n}{h_1}$ and $\tilde{x}_2^n = \frac{x_2^n}{h_1}$. This follows from a simple rescaling of time in the competition equation 4.3.0.1 ($\tilde{t} = \frac{t}{h_1}$). Therefore, when the landscape is symmetric, it is sufficient only to investigate the model with $h_1 = h_2 = 1$. Habitat loss may still be modelled by increasing e_G.

The evolutionary dynamics away from the generalist will be determined by finding the singular strategies, $\tau^* \neq 0$, which we recall are solutions of $D(e(\tau^*)) = 0$ (see equation 5.4.1.1 of the previous chapter), and classifying such strategies. Away from the generalist this must be done numerically. A treatment of dimorphic resident fitness, Δ^2, will also be carried out to determine dimorphic evolution following branching or from dimorphic initial conditions.

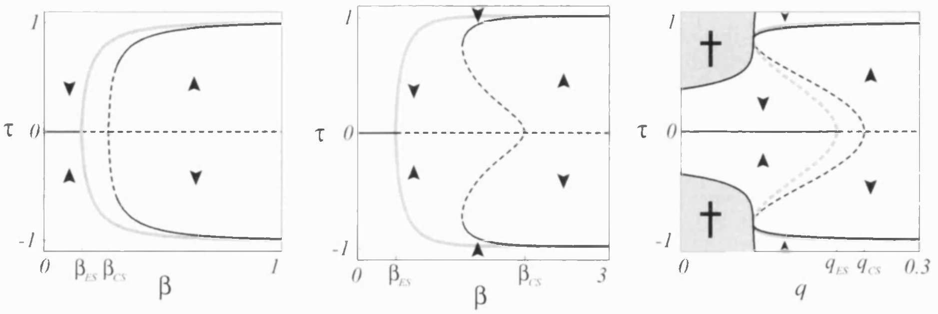
The evolutionary dynamics will depend upon the parameters q, e_G and β. To investigate this 3–dimensional parameter space it is again useful to consider parameter planes like those of the previous chapter. The plots of figures 6-3, 6-5 and 6-6 illustrate how the classification of the singular generalist and specialist singular strategies depend upon landscape aggregation, trade–off strength and the generalist extinction rate.



(a) $e_G = 0.25$ (b) $e_G = 0.75$ (c) $e_G = 1.25$

Figure 6-3: The evolutionary classification of the generalist and specialist singular strategies in symmetric landscapes, dependent upon β and q, for $e_G = 0.25, 0.75, 1.25$. On the ES–curve $\beta = \beta_{ES}$ and on the CS–curve $\beta = \beta_{CS}$. These curves bound the regions I, II, and III that determine the classification of the generalist: Region I corresponds to an evolutionary stable attractor. Region II corresponds to an evolutionary unstable attractor (a branching point). Region III corresponds to an evolutionary unstable repeller. If parameters lie in region III there exists two specialist strategies that are evolutionary stable attractors unless within the slight shaded region of plot (b) where they are evolutionary unstable attractors. There will exist four non specialist singular strategies when parameters are within the hashed region. Two are evolutionary unstable repeller and two are evolutionary stable attractors. In plot (c) the generalist cannot persist ($e_G > 1$) however specialist can if parameters lie outside of the shaded region and there will then exist two evolutionary stable attractors.

Specialist singular strategies come in pairs: the symmetry in both the trade-off function and the landscape means that $-\tau^*$ is a singular strategy whenever τ^* is, and with identical evolutionary properties. In each figure the behaviour of the generalist is determined by the ES–curve where $\beta = \beta_{ES}$ and the CS–curve where $\beta = \beta_{CS}$. When the generalist is an evolutionary repeller at least two new singular strategies will be present in the trait space, representing more specialized phenotypes. At least two will be CS following from the fact that the set $[-1, 1]$ of trait space is evolutionary attracting and the selection gradient, $D(e(\tau))$, is continuous. The figures show that only two non–specialist singular strategies exist when the generalist is divergent. They tend to be ES, though for small ranges of parameter values they are non–ES and hence



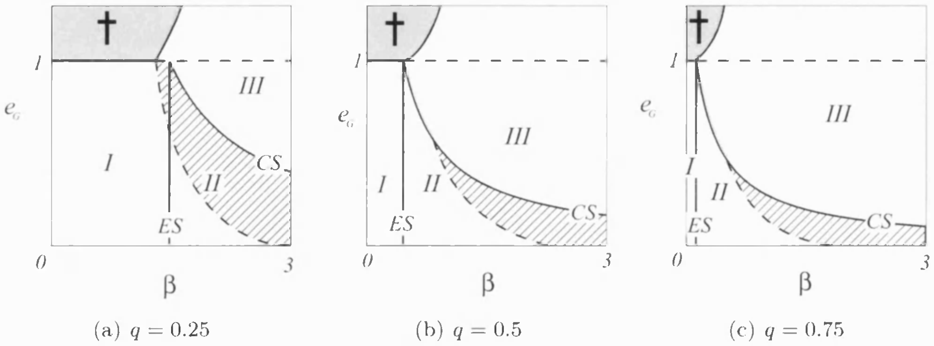
(a) $q = 0.75$ and $e_G = 0.75$ (b) $q = 0.5$ and $e_G = 0.25$ (c) $\beta = 2.0$ and $e_G = 0.75$

Figure 6-4: Bifurcation plots of the evolutionarily singular strategies and singular coalitions for the bifurcation parameter β (plot (a) and (b)) and q (plot (c)). The black curves show the mononomorphic singular strategies. These curves bound regions with positive directional selection (labeled with an arrow pointing upwards) and negative directional selection (labeled with an arrow pointing downwards). Arrows point towards CS singular strategies. The curve is solid if the singular strategy is ES. The grey curve indicates one strategy, τ^*, of the evolutionarily singular coalition $(\tau^*, -\tau^*)$ as defined by equations 6.4.2.1 and 6.4.2.2 of section 6.4.1. The curve is solid if the singular coalition is ES. (see equation 6.4.3.3 for the dimorphic ES condition). The shaded regions labeled with a 'cross' indicate strategies that cannot persist. If $q < q_{ES}$ the generalist is ES, and If $q < q_{CS}$ the generalist is CS.

branching strategies (for an example see the E^3 diagram plot (a) of figure 6-4).

Even when the generalist strategy is an evolutionarily stable attractor specialist singular strategies can exist. The hatched regions of the figures indicate the existence of two pairs of specialists, one pair evolutionarily unstable repellers and the other pair evolutionarily stable attractors. The necessity of the repeller–attractor pair follows again from the evolutionary attraction of $[-1, 1]$. Plot (b) and (c) of figure 6-4 illustrate how the specialist strategies, when the generalist remains attracting, come to existence at a saddle–node bifurcation.

If specialists only occur when the generalist is repelling, they come as a single attracting pair and come into existence following a pitchfork bifurcation. This is illustrated in plot (a) of figure 6-4 when the bifurcation parameter is the trade–off weakness, β. This behaviour is qualitatively similar to that found by Meszéna et al. (1997) for the case of two connected populations inhabiting differing patches. The branching nature of the generalist is inherited by the specialist when β is in the locality of the critical value β_{CS}. The specialists eventually becomes ES with increasing β. If specialists can exist when the generalist is attracting, the repelling specialist are annihilated at a reverse pitchfork bifurcation at $\beta = \beta_{CS}$, as illustrated in plots (b) and (c).

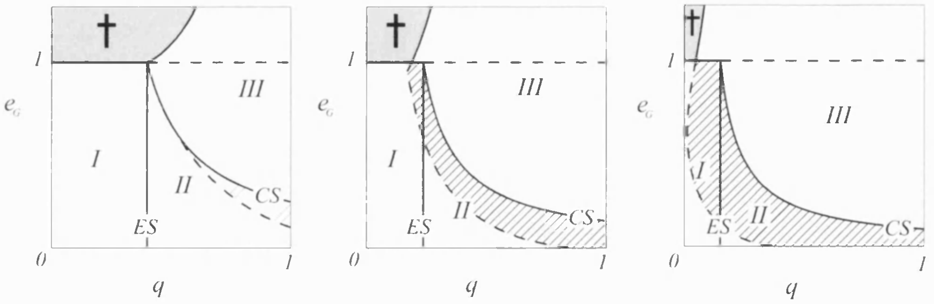


(a) $q = 0.25$ (b) $q = 0.5$ (c) $q = 0.75$

Figure 6-5: The evolutionary classification of the generalist and specialist singular strategies in symmetric landscapes, dependent upon β and e_G, for $q = 0.25, 0.5, 0.75$.When $e_G \geq 1$ the generalist no longer persists and no strategy persists in the shaded region labeled with a 'cross'. On the ES–curve $\beta = \beta_{ES}$ and on the CS–curve $\beta = \beta_{CS}$. These curves and the extinction region bound the regions I, II, and III that determine the classification of the generalist: Region I corresponds to an evolutionarily stable attractor. Region II corresponds to an evolutionarily unstable attractor (a branching point). Region III, when $e_G < 1$, corresponds to an evolutionarily unstable repeller. When parameters lie in region III there exists two specialist singular strategies that are evolutionarily stable attractors (unless within the slight shaded region hugging the the CS–curve of plots (b) and (c) where they are evolutionarily unstable attractors). When parameters are within the hashed region there will exist four specialist singular strategies: Two are evolutionarily unstable repellers and two are evolutionarily stable attractors.

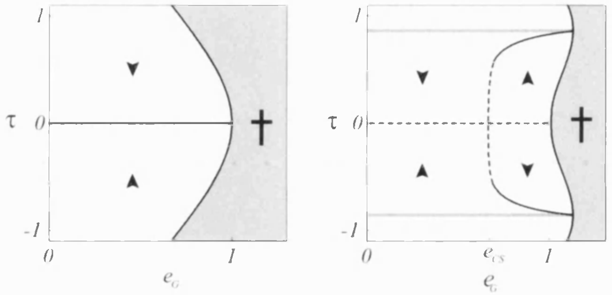
Evolutionary Consequences of Trade-off Strength and Landscape Aggregation

Increasing trade–off strength (decreasing β) has a qualitatively similar effect to decreasing aggregation: generalists tend to become monomorphic–adaptive as CS singular specialists either converge with repelling specialists and are annihilated, or when they converge upon the generalist. However specialism is not necessarily reduced, since the generalist may be non-ES and promote branching to dimorphisms composed of strategies that are more specialized than the monomorphic specialists (see figure 6-8).



(a) $\beta = 0.75$ (b) $\beta = 1.5$ (c) $\beta = 2.5$

Figure 6-6: The evolutionary classification of the generalist and specialist singular strategies in symmetric landscapes, dependent upon q and e_G, for $\beta = 0.75$, 1.5 and 2.5. Refer to the caption of figure 6-3 for details.

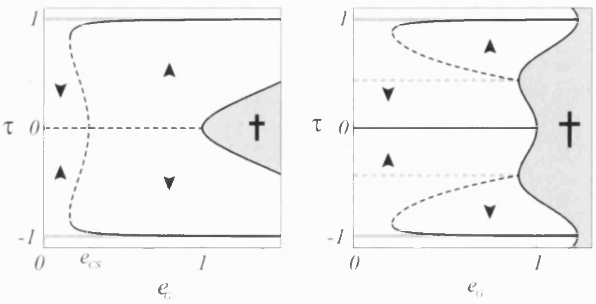


(a) $\beta = 0.75$ and $q = 0.25$ (b) $\beta = 0.75$ and $q = 0.5$

Figure 6-7: Bifurcation plots of the evolutionarily singular strategies and singular coalitions for the bifurcation parameter e_G. See the caption of figure 6-4 for details. Plot (b) is an example of evolutionary rescue: The evolutionarily attracting singular generalist is more sensitive to landscape degradation (increasing e_G is equivalent to decreasing h_1), than the evolutionarily attracting singular specialists. In plot (b) $\beta = \beta_{CS}$ when $e_G = e_{CS}$.

Evolutionary Consequences of Uniform Habitat Loss

Following excessive habitat reduction, which we recall is equivalent to increasing e_G, no phenotypic variant of the species can persist. However for more moderate levels of habitat loss some strategies may remain viable when the generalist cannot (i.e. when $e_G \geq 1$). In this case a pair of CS specialist singular strategy must exist. If this was not the case the evolving resident strategy would converge upon the extinction boundary



(a) $\beta = 1$ and $q = 0.75$ (b) $\beta = 2.5$ and $q = 0.1$

Figure 6-8: Bifurcation plots of the evolutionarily singular strategies and singular coalitions for the bifurcation parameter e_G. See the caption of figure 6-4 for details. Both plots show evolutionary rescue and plot (b) also exhibits evolutionary trapping. In plot (a) $\beta = \beta_{CS}$ when $e_G = e_{CS}$.

resulting in what is termed *evolutionary suicide.* However Gyllenberg & Parvinen (2001) proved that whenever equilibrium (meta)population density is a continuous function of an evolving phenotypic trait, as is the case in this model, evolution cannot lead to extinction.

If the generalist is initially ES it will remain so, following patch-type independent habitat loss, until the generalist goes extinct as e_G reaches unity. Plot (a) of figure 6-7 is an example of when evolutionary behaviour is not affected by habitat loss. The ES generalist in this case is the only singular strategy. The generalist is also ES in Plot (b) of figure 6-8. In this case the low value of q and high value of β yields some interesting results. For moderate to high values of e_G the CS generalist is also accompanied by a pair of CS specialists. The phenotypic domain of attraction of the CS specialists increases with e_G and when the generalist, following the non-CS specialists, becomes non-viable there is a range of e_G that allows the specialist phenotypes to persist.

If the generalist is not ES, removing habitat results in a characteristic sequence of stages:

1. The generalist is CS and non-ES.
2. The generalist becomes non-CS and *at least* one pair of CS singular specialist exist.
3. If specialist are initially branching points they become ES.
4. The generalist strategy becomes non-viable.

5. All phenotypic variants become non-viable.

This sequence is observed in both figures 6-7 and 6-8. In the penultimate stage when the generalist strategy is no longer viable the species can persist in a dimorphic state (two distinct coexisting resident phenotypes) or as a single resident partial to either patch type. If the evolutionary process 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 & Ferrière 2004, Chapter 11). Adapting to the environment can sometimes be detrimental to the metapopulation. Even though the metapopulation cannot evolve to extinction it can evolve to a region of phenotype space that is not globally optimum. Plot (b) of figure 6-8 illustrates this point well. If the phenotype of the metapopulation is initially in the domain of attraction of the generalist, the benefits of evolutionary rescue are limited compared to the specialist. The evolutionary process therefore can trap the metapopulation to a generalist attractor that will go extinct whilst other phenotypes may persist. This phenomena where by the fate of an evolving (meta)population is sensitive to initial resident type has been termed *evolutionary trapping* (Dieckmann & Ferrière 2004).

Figures 6-4 and 6-7 also show information regarding dimorphic evolution. The study of dimorphic evolution will require a few more definitions.

6.4.1 Evolutionary Singular Coalitions

Following evolutionary branching of the monomorphic system, two residents with differing trait values will coexist, and even in the absence of branching strategies this may be true. The evolution of the emergent dimorphic system requires the extension of the system to include three phenotypes: a mutant with strategy τ' and corresponding extinction rates $e' = e(\tau')$ in type 1 patches and $f(e(\tau'))$ in type 2 patches, and two residents with strategies τ^1 and $\tau^2 \neq \tau^1$ with extinction rates equivalently defined. The evolutionary dynamics will depend upon $\Delta^2(e', e^1, e^2)$ (see equation 5.4.0.2 of the previous chapter) where

$$\Delta^2(e', e^1, e^2) = \frac{e'f(e^1)c_{22}}{c_{12}X^1 + c_{22}} + \frac{f(e')e^1c_{11}X^1}{c_{11}X^1 + c_{21}} - e'f(e') + \frac{e^1f(e^1)(c_{12}c_{21} - c_{11}c_{22})X^1}{(c_{11}X^1 + c_{21})(c_{12}X^1 + c_{22})}, \tag{6.4.1.1}$$

and $X^1(e^1, e^2) = \dfrac{\hat{x}_1^1(e^1, e^2)}{\hat{x}_1^2(e^1, e^2)}$, satisfying equation 4.5.0.24 of chapter 4.

In the dimorphic case mutant fitness will depend upon the resident strategy the mutant is derived from. Defining

$$D^1(e^1, e^2) = \Delta_1^2(e^1, e^1, e^2) \ , \tag{6.4.1.2}$$

and

$$D^2(e^1, e^2) = \Delta_1^2(e^2, e^1, e^2) \ , \tag{6.4.1.3}$$

where Δ_i^2 is the partial derivative of Δ^2 with respect to the ith variable:

- If $D^i(e^1, e^2) > 0$ then mutant strategies τ' close to strategy τ^i can invade the coalition if $e' > e^i$, and cannot invade if $e' < e^i$.
- If $D^i(e^1, e^2) < 0$ then mutant strategies τ' close to strategy τ^i can invade the coalition if $e' < e^i$, and cannot invade if $e' > e^i$.

Note that this result does not require that the trade–off function be symmetric. The dimorphic coalition (τ^{1*}, τ^{2*}) is an *evolutionarily singular coalition*, as defined by Geritz et al. (1998), if and only if

$$D^1(e^{1*}, e^{2*}) = D^2(e^{1*}, e^{2*}) = 0 \ , \tag{6.4.1.4}$$

where $e^{i*} = e(\tau^{i*})$. This definition extends naturally from the monomorphic case where directional selection vanishes.

6.4.2 Singular Coalitions for Symmetric Trade-offs

Claim 16. When $\rho = 0.5$ and the trade-off function is symmetric, a symmetric coalition $(\tau^*, -\tau^*)$, $\tau^* \neq 0$, is a singular coalition if

$$f'(e(\tau^*)) = -X^{*2} \ , \tag{6.4.2.1}$$

where

$$(X^*)^2 + \frac{q}{1-q}\left(1 - \frac{f(e(\tau^*))}{e(\tau^*)}\right) X^* - \frac{f(e(\tau^*))}{e(\tau^*)} = 0 \ . \tag{6.4.2.2}$$

Proof. Partially differentiating equation 6.4.1.1 yields

$$D^i(e^1, e^2) = \frac{f(e^1)c_{22}}{c_{12}X^1 + c_{22}} + \frac{f'(e^i)e^1 c_{11}X^1}{c_{11}X^1 + c_{21}} - f(e^i) - e^i f'(e^i) \ . \tag{6.4.2.3}$$

Now rearranging $D^1(e^1, e^2) = 0$ gives

$$\begin{aligned} f'(e_1) &= -\frac{f(e_1)X^1(c_{11}X^1 + c_{21})}{e_1 c_{21}(c_{12}X^1 + c_{22})} \\ &= -\frac{X^1 f(e_1)(qX^1 + 1 - q)}{e_1((1-q)X^1 + q)} \ . \end{aligned} \tag{6.4.2.4}$$

Recall, from equation 4.5.0.24 of chapter 4, that X^1 satisfies

$$(E_1^1 - 1)(X^1)^2 + \left(\frac{c_{22}}{c_{12}}(E_1^1 - 1)(1 - E_2^1) + \frac{c_{21}}{c_{11}}(E_1^1 E_2^1 - 1)\right) X^1 + \frac{c_{22}c_{21}}{c_{12}c_{11}}(E_2^1 - 1) = 0 \ , \tag{6.4.2.5}$$

where $E_i^1 = \frac{e_i^1}{e_i^2} \neq 1$. When the trade–off is symmetric, a symmetric coalition will satisfies $e^2 = f(e^1)$ and $e^1 = f(e^2)$, reducing this to

$$(X^1)^2 + \frac{q}{1-q}(1 - \frac{f(e^1)}{e^1})X^1 - \frac{f(e^1)}{e^1} = 0 \ . \tag{6.4.2.6}$$

This can be rearranged to give

$$X^1 = \frac{f(e_1)(qX^1 + 1 - q)}{e_1((1-q)X^1 + q)} \ , \tag{6.4.2.7}$$

hence, from equation 6.4.2.4, we have the result that $D^1(e^1, e^2) = 0$ if $f'(e^1) = -{X^1}^2$.

We also require that $D^2(e^1, e^2) = 0$: Now Δ satisfies $\Delta(e', e^2, e^1) = \Delta(e', e^1, e^2)$ (the order of the coalition is not important), and therefore $D^2(e^1, e^2) = D^1(e^2, e^1)$. $D^1(e^2, e^1) = 0$ then follows, trivially, by swapping the coalition indices and applying the previous argument. ☐

Note that it was not assumed that $h_1 = h_2$ when deriving the singular coalition condition. This means that a coalition will remain symmetric even when the numbers of habitable patches of each patch type are not equal in the landscape. Habitat loss will only affect a singular coalition if it drives one or both of the strategies extinct. This happens if either one the strategies cannot persist in a monomorphic state but the stronger condition is when the coalition $(\tau^*, -\tau^*)$ is not stable; that is when either

$\Delta(e(-\tau^*), e(\tau^*)) \leq 0$ or $\Delta(e(\tau^*), e(-\tau^*)) \leq 0$, where τ^* satisfies $f'(\tau^*) = -X^{*2}$. See the following section for more detail.

Figures 6-7 and 6-8 illustrates how the singular coalition curves terminate at certain critical points on the extinction boundary in the (e_G, τ) plane.

Claim 17. Suppose $\rho = 0.5$, then symmetric singular coalition curves collide with the extinction boundary in the (e_G, τ) plane given by $e_G = \phi(\tau)$ at the points $(\tau^*, \phi(\tau^*))$ that satisfy $\frac{d\phi(\tau^*)}{d\tau} = 0$.

Proof. Since $\rho = 0.5$, the extinction boundary $e_G = \phi(\tau)$ implicitly satisfies

$$F(\tau, \phi(\tau)) = 0 \ , \tag{6.4.2.8}$$

where

$$F(\tau, e_G) = f(e(-\tau; e_G)) - \frac{2q - 1 - qe(\tau; e_G)}{q - e(\tau; e_G)} \ , \tag{6.4.2.9}$$

is derived from a rearrangement of $\det J_R$ of equation 3.4.1.2 of chapter 3 for $e_1 = e(\tau; e_G)$ and $e_2 = f(e(\tau; e_G))$.

Now on $e_G = \phi(\tau)$ we have that $\frac{dF}{d\tau} = \frac{\partial F}{\partial \tau} + \frac{d\phi}{d\tau}\frac{\partial F}{\partial \phi} = 0$. Thus the condition that $\frac{d\phi}{d\tau} = 0$ yields $\frac{\partial F}{\partial \tau} = 0$ which can be rearranged to give

$$f'(e(\tau)) = -\left(\frac{1-q}{e(\tau) - q}\right)^2 . \tag{6.4.2.10}$$

However, it is a trivial matter to show that if τ satisfies $F(\tau, e_G) = 0$ then $X = \frac{1-q}{e(\tau)-q}$ since this satisfies 6.4.2.2.

Therefore if τ^* satisfies $\frac{d\phi(\tau^*)}{d\tau} = 0$ then $f'(e(\tau^*)) = -X^{*2}$ so that τ^* indeed satisfies the symmetric singular coalition condition. ☐

6.4.3 Classifying Evolutionarily Singular Coalitions

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 (τ^{1*}, τ^{2*}) is ES if

$$\Delta^2_{11}(e_1(\tau^{1*}), e_1(\tau^{1*}), e_1(\tau^{2*})) < 0 \ , \tag{6.4.3.1}$$

and

$$\Delta^2_{11}(e_1(\tau^{2*}), e_1(\tau^{1*}), e_1(\tau^{2*})) < 0 \ . \tag{6.4.3.2}$$

The ES Condition of Symmetric Singular Coalitions for Symmetric Trade-offs and Landscapes with $\rho = \frac{1}{2}$

Claim 18. A symmetric singular coalition $(\tau^*, -\tau^*)$ is ES when the trade-off is symmetric and $\rho = 0.5$ if

$$f''(e_1(\tau^*)) > \frac{2X^{*2}}{e_1(\tau^*)}\left(\frac{qX^*}{(1-q)} + 1\right) . \tag{6.4.3.3}$$

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

$$\Delta^2(e(-\tau'), e(-\tau^1), e(-\tau^2)) = \Delta^2(e(\tau'), e(\tau^1), e(\tau^2)) . \tag{6.4.3.4}$$

From this we deduce, since $\Delta^2(e(\tau'), e(\tau^1), e(\tau^2)) = \Delta^2(e(\tau'), e(\tau^2), e(\tau^1))$, that

$$-\frac{de(-\tau)}{d\tau}\Delta^2_1(e(-\tau), e(\tau), e(-\tau)) = \frac{de(\tau)}{d\tau}\Delta^2_1(e(\tau), e(\tau), e(-\tau)) , \tag{6.4.3.5}$$

and

$$\begin{aligned} &\frac{de(-\tau)}{d\tau}^2 \Delta^2_{11}(e(-\tau), e(\tau), e(-\tau)) - \frac{d^2e(-\tau)}{d\tau^2}\Delta^2_1(e(-\tau), e(\tau), e(-\tau)) \\ &\quad = \frac{de(\tau)}{d\tau}^2 \Delta^2_{11}(e(\tau), e(\tau), e(-\tau)) + \frac{d^2e(\tau)}{d\tau^2}\Delta^2_1(e(\tau), e(\tau), e(-\tau)) , \end{aligned} \tag{6.4.3.6}$$

which at a singular coalition, $(\tau^*, -\tau^*)$, reduces to

$$\Delta^2_{11}(e(-\tau^*), e(\tau^*), e(-\tau^*)) = \frac{1}{f'(e(\tau^*))^2}\Delta^2_{11}(e(\tau^*), e(\tau^*), e(-\tau^*)) , \tag{6.4.3.7}$$

applying equation 6.4.1.4 and equation 6.3.0.3.

Then

$$sign\{\Delta^2_{11}(e(-\tau^*), e(\tau^*), e(-\tau^*))\} = sign\{\Delta^2_{11}(e(\tau^*), e(\tau^*), e(-\tau^*))\} , \tag{6.4.3.8}$$

and the ES condition for a symmetric coalition is thus equivalent to

$$\Delta^2_{11}(e(\tau^*), e(\tau^*), e(-\tau^*)) < 0 .$$

In terms of the trade-off function this can be written

$$f''(e(\tau^*)) > -\frac{2f'(e(\tau^*))}{e(\tau^*)}\left(\frac{qX^*}{1-q}+1\right) , \tag{6.4.3.9}$$

since Δ^2 satisfies 6.4.1.1. With $f'(e(\tau^*)) = -X^{*2}$ from the singular strategy condition 6.4.2.1 we obtain the required result. ☐

Deriving the condition for convergence stability is not as straightforward for the dimorphic case (Geritz et al. 1998). The condition that both $D_1^1(e^{1*}, e^{2*}) < 0$ and $D_2^2(e^{1*}, e^{2*}) < 0$ is neither necessary or sufficient: This is equivalent to the fact that the stability of a generic dynamic system, $\dot{\mathbf{x}} = F(\mathbf{x})$, $\mathbf{x} = (x_1, x_2)$, $F = (f^1, f^2)$, at a fixed point $\mathbf{x}_0$ cannot be solely determined by $\frac{\partial f^1(\mathbf{x}_0)}{\partial x_1}$ and $\frac{\partial f^2(\mathbf{x}_0)}{\partial x_2}$, the diagonal entries of the Jacobian matrix. CS stability is thus determined by the matrix

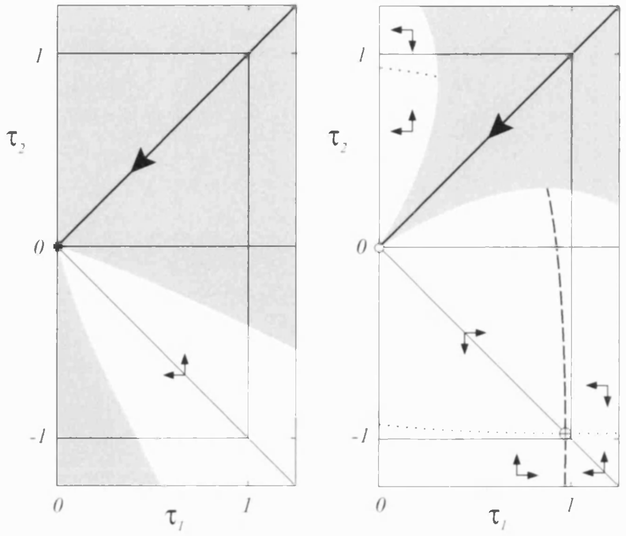
$$\begin{pmatrix} D_1^1(e^{1*}, e^{2*}) & D_2^1(e^{1*}, e^{2*}) \\ D_1^2(e^{1*}, e^{2*}) & D_2^2(e^{1*}, e^{2*}) \end{pmatrix} . \tag{6.4.3.10}$$

Since we are proceeding with a graphical analysis, we shall omit a treatment of the CS condition, and instead call upon the following properties of the CS strategies of *this* model:

- If a singular coalition is not ES then it is not CS. Otherwise further branching would lead to a protected trimorphism, not permitted in this model.
- If a singular coalition is situated within an invariant box of the dimorphic evolutionary dynamics (determined by $sign\{D_1^1\}$ on the vertical edges and $sign\{D_2^2\}$ on the horizontal edges), the coalition is CS.

Figures 6-9 and 6-10 illustrate an example of the evolutionary dynamics of the monomorphic and dimorphic system for four values of β when $q = 0.5$ and $e_G = 0.25$ (parameter values are the same as plot (b) of 6-4). The axis represent the trait values of a coalition. Symmetry in the landscape and trade–off function means that it is sufficient to assume that one of the trait value τ^1 is positive. When $\tau^2 = \tau^1$ the dimorphism collapses to the monomorphic case.

If the coalition (τ^1, τ^2) is not stable the point (τ^1, τ^2) is in the shaded region. This occurs if either one, or both of the strategies cannot persist in isolation, or they are not mutually invasive (either $\Delta(e(-\tau^*), e(\tau^*)) \leq 0$ or $\Delta(e(\tau^*), e(-\tau^*)) \leq 0$). The shaded regions thus correspond to the PIP plots as discussed in the previous chapter. If the

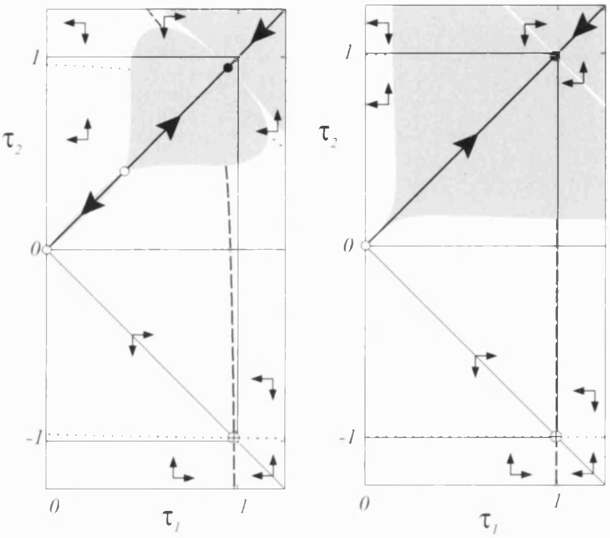


(a) $\beta = 0.25$ (b) $\beta = 1$

Figure 6-9: Monomorphic and dimorphic evolution dynamics. The plots show regions of the coalition strategy plane, (τ^1, τ^2), that correspond to the sign of $D^1(e(\tau^1), e(\tau^2))$ and the sign of $D^2((\tau^1), e(\tau^2))$ (see main text). These regions are bounded by curves that satisfy $D^1 = 0$ (dashed), $D^2 = 0$ (dotted) and the boundary of the shaded region. The shaded region indicates non-viable coalitions where, either one or both of the strategies cannot persist, or they cannot form a coalition (the condition for this is given in chapter 4 in terms of the monomorphic invasion function Δ^1). The arrow pairs point to mutant strategies that can invade the coalition. Evolutionary singular coalitions occur when the $D^1 = 0$ curve and the $D^2 = 0$ curve intersect. For the evolutionary classification of singular coalitions see the main text. Monomorphic evolution occurs on the line $\tau^2 = \tau^1$ (i.e. only one distinct resident strategy). The arrow head indicates directional selection, pointing towards singular strategies that are represented by black circles if ES and white if non-ES. $q = 0.5$ and $e_G = 0.25$ in each plot, corresponding to plot (b) of figure 6-4.

point (τ^1, τ^2) or (τ^2, τ^1) is in the negative sign region of the corresponding PIP plot then both (τ^1, τ^2) and (τ^2, τ^1) are in shaded regions of the coalition dynamics plots.

The selection gradient is determined by the arrow heads that point to CS singular strategies. ES singular strategies are denoted by black circles. The generalist in plot (b) and (c) is a branching point whereby evolution drives the system dimorphic. Stable coalitions will evolve according Δ^2 as discussed above. These figures are akin to the standard phase planes that are analyzed for deterministic dynamical systems: The



(a) $\beta = 1.5$ (b) $\beta = 3$

Figure 6-10: See the caption of figure 6-9.

coupled arrows indicate the vector field (D_1, D_2) and the dashed and dotted curves indicating when D_1 and D_2 change sign. The vector field, however, does not uniquely define the evolutionary pathways through coalition space. Since the mutation process is inherently random and furthermore mutations should be assumed *small but finite*, the vector field will only indicate the quadrant that the evolutionary pathway is directed. Determining the expected direction would require further assumptions about the mutation process. Because of this the outcomes of some evolutionary process, starting from certain initial coalitions, can be ambiguous. This will be discussed in more detail later.

For the majority of stable coalitions, the evolution process terminates unambiguously at either a CS monomorphism or CS dimorphism. In plot (a) of figure 6-9 the only CS evolutionary singularity is the monomorphic resident. In this plot the shaded region approximates a cone as $(\tau^1, \tau^2) \to (0, 0)$ and the random component of the mutation process allows an evolutionary trajectory to collide with this region. If this happens one of the coalition strategies will be driven extinct, depending on which side of the cone the trajectory leaves. Evolution then follows the monomorphic route to the generalist.

In plot (b) of figure 6-9 the generalist is a branching point and a globally CS

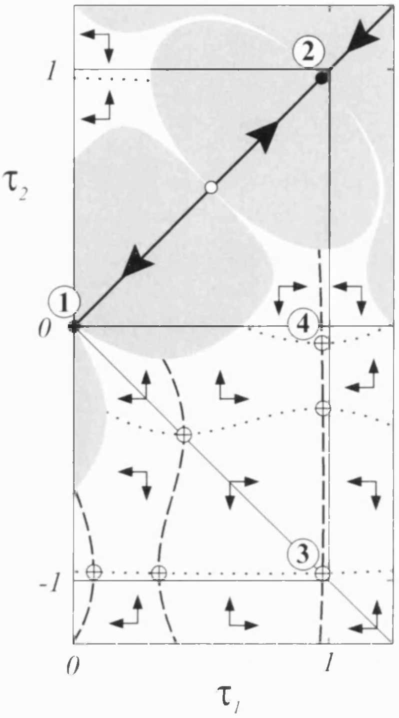


Figure 6-11: Monomorphic and dimorphic evolutionary dynamics. See the caption of figure ?? for explanation. For these parameter values ($\beta = 2$, $q = 0.15$ and $e_G = 0.75$) evolutionary branching does not occur however some coalitions are ecologically stable and the subsequent dimorphic evolution will depend upon the initial trait values of the coalition. There are four qualitatively distinct evolutionary stable attractors of the system labelled **1**, **2**, **3** and **4**: **1** is the monomorphic generalist $\tau^* = 0$. **2** is a monomorphic specialist $\tau \approx 1$. **3** is the specialist coalition $(\tau^{1*}, \tau^{2*}) \approx (1, -1)$. **4** is the specialist–generalist coalition $(\tau^{1*}, \tau^{2*}) \approx (1, 0)$.

strategy in terms of monomorphic evolution. The branching nature of the generalist means that it is an evolutionary repeller of the dimorphic system. The zero–clines of directional selection (the curves where either $D^1 = 0$ or $D^2 = 0$) indicate that the singular specialist coalition $\tau^*, -\tau^*$, $\tau^* \approx 1$, is CS since an invariant box can be constructed around the strategy. It then follows that the coalition is also ES.

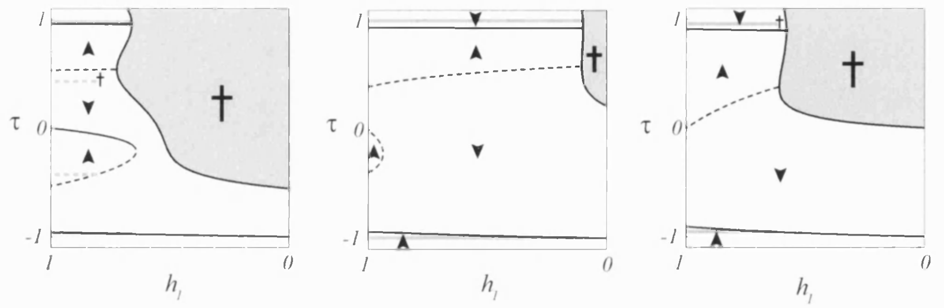
In plot (a) of figure 6-10 the generalist is again a branching strategy, but not a global attractor of the monomorphic system. If initial trait values lie in the attracting domain of the generalist evolution will drive the metapopulation dimorphic and evolution will terminate at a CS coalition similar to that of plot (b) of figure 6-9. If, however a monomorphic system is in the attractor of one of the two CS and ES specialist singular strategies, evolution will terminate there. It is also possible for the dimorphic system to collapse to a monomorphic for certain initial conditions. Coalitions exist, of the form (τ^1, τ^2) such that $\tau^1 > 1$ and $\tau^2 > 0$ above the curve $D^2 = 0$, where selection is driven towards the shaded region. This leads to the dimorphic collapse and monomorphic evolution towards the specialist. There also exists a region in coalition space where $\tau^1 > 1$ and $\tau^2 > 0$ that is below the curve $D^2 = 0$ where the outcome is undetermined. In this region selection in the τ^1 direction is towards the extinction boundary yet selection in the τ^2 is away from the extinction boundary. Initial conditions, the relative strengths of selection D^1 and D^2, and the mutation process will all determine the probability that system remains dimorphic or collapses to a monomorphic one.

In plot (b) of figure 6-10 the generalist is repelling and thus the CS coalition cannot be reached from monomorphic initial conditions. Coalition do exist that are arbitrarily close to $(0,0)$ and that are within attracting domain of the CS coalition $(\tau^*, -\tau^*)$, $\tau^* \approx 1$.

In figures 6-9 and 6-10 there is only ever at most one singular coalition and it is always symmetric, CS and ES. In plot (c) of figure 6-4 and plot(b) figure 6-8 it is shown that a non-ES symmetric dimorphism can exist that is necessarily evolutionarily repelling. Figure 6-11 shows the dimorphic evolutionary dynamics for a case when parameter values correspond to an instance of plot (c) of figure 6-4. In this case the CS and non–CS symmetric singular coalitions are complimented by two other non–symmetric singular coalitions. One of these is CS and of the form (τ^{1*}, τ^{2*}) where $\tau^{1*} \approx 1$, $\tau^{2*} \approx 0$ and $sign\{\tau^{1*}\} \neq sign\{\tau^{2*}\}$. This approximately corresponds to generalist–specialist pair.

6.5 Some Evolutionary Consequences of 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 uneffected (e.g. logging a particular tree species). We conclude the results section of this chapter with a few examples of how asymmetric habitat loss can shape the adaptive responses of the metapopulation. We shall assume, without loss of generality, that patches are removed from type 1 patches only, i.e.



(a) $\beta = 2.0$, $q = 0.15$ and $e_G = 0.75$ (b) $\beta = 1.5$, $q = 0.5$ and $e_G = 0.25$ (c) $\beta = 0.5$, $q = 0.75$ and $e_G = 0.75$

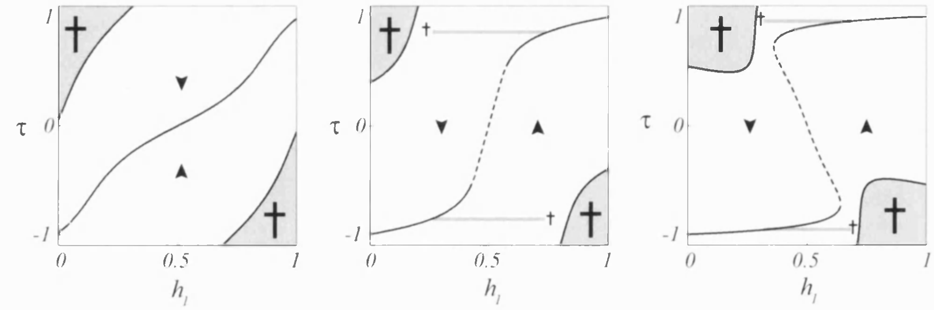
Figure 6-12: Bifurcation plots of the evolutionarily singular strategies and singular coalitions for the bifurcation parameter h_1 when $h_2 = 1$. See the caption of figure 6-4 for details.

$h_2 = 1$. We will also continue to assume that $\rho = 0.5$.

It is a trivial matter to show that when type 1 patches are destroyed ($h_1 < 1$) that $D(e_G) > 0$ and thus the generalist can be invaded by mutants that favour the more abundant type 2 patches. In this case a CS singular strategy that is relatively more specialized to type 2 patches ($\tau^* < 0$) will exist. Singular strategies, however, can still exist that favour type 1 patches ($\tau^* > 0$), as illustrated in figure 6-12 for certain ranges of parameter values.

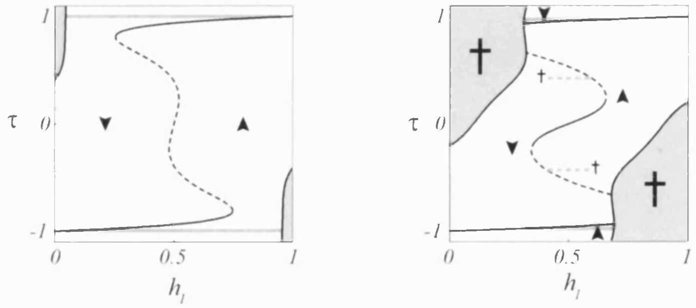
Each plot of figure 6-12 demonstrates both evolutionary rescue and trapping. Evolutionary trapping can occur because phenotype space is segregated by an evolutionary repeller or by a region of non–viable traits. The metapopulation can be saved from evolutionary trapping if the metapopulation is dimorphic. In each plot a specialized CS coalition can harbour type–2 specialists that survive episodes of habitat loss even when the type–1 specialist is driven to extinction. Sometimes the inferior coalist may become extinct, despite being viable when monomorphic (plot (c)). This appears to happens when the superior coalist collides with a monomorphic singular strategy.

Habitat loss appears always to be detrimental for biodiversity, either by causing the collapse of singular coalitions, or by destroying branching strategies (plot (b)) as was the case when habitat loss is uniform (e.g. plot (b) of figure 6-7). Even when habitat loss is kept at a constant value, removing habitat asymmetrically also appears to have detriment for the evolution of biodiversity. Figure 6-13 and figure 6-14 illustrate how branching generalists are perturbed in phenotype space following asymmetric habitat change, and either become ES (plot (b) of figure 6-13) or are annihilated (plot (a) of



(a) $\beta = 0.75$, $q = 0.25$ and $e_G = 0.25$ (b) $\beta = 0.75$, $q = 0.5$ and $e_G = 0.25$ (c) $\beta = 0.5$, $q = 0.75$ and $e_G = 0.375$

Figure 6-13: Bifurcation plots of the evolutionarily singular strategies and singular coalitions for the bifurcation parameter h_1 when $h_1 + h_2 = 1$. See the caption of figure 6-4 for details.



(a) $\beta = 1.5$, $q = 0.5$ and $e_G = 0.125$

(b) $\beta = 2.0$, $q = 0.15$ and $e_G = 0.375$

Figure 6-14: Bifurcation plots of the evolutionary singular strategies and singular coalitions for the bifurcation parameter h_1 when $h_1 + h_2 = 1$. See the caption of figure 6-4 for details.

figure 6-14).

6.6 Discussion

In this chapter we studied the evolution of patch specialisation and evolutionary branching, as have Meszéna et al. (1997), Kisdi (2002) and Parvinen & Egas (2004), as a response to trade-off strength, habitat abundance and basic dispersal.

We found that 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 specialisation. Removing habitat and decreasing the trade-off strength has a similar effect, as demonstrated by Kisdi (2002) and Parvinen & 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 to the benefits of specialising to the other type. The evolution of monomorphic specialists drives the spatial aggregation of the metapopulation, resulting in asymmetric patch usage that may further promote specialisation.

For the case of habitat loss the causal link is perhaps less obvious. Removing patches will lower the success of dispersers with perhaps 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 the 'risk spreading' ability, already restricted with landscape change. Spatial aggregation may be sufficient, but is not necessary for specialisation. Parameter instances can be found that drive specialisation for negatively correlated landscape arrangements. Since no single parameter of this model solely dictates the evolution of specialisation, predicting the likelihood in a real setting should be treated with caution.

Evolutionary branching, a necessary requirement for adaptive speciation in sexual systems, is influenced by the same factors that are responsible for specialisation. The classic transitions of a generalist singular strategy from evolutionary unbeatable, to evolutionary branching, and then to evolutionary repelling is not shared by monomorphic specialists. CS specialist were generally found to be ES, although, for slight parameter regions CS specialists that bifurcate from the generalist (plot(b) of figure 6-7) will inherit the non–ES property. The ES nature of a singular strategy is a local property of the trade–off function. It is very easy to find classes of trade–off functions that can switch this property with the monotonic variation of landscape or trade–off parameters. We have shown (Hancock & Britton 2006) that the branching nature of CS specialists can peform a 'non–ES → ES → non–ES' transition as a response to both landscape aggregation and asymmetric habitat loss.

Evolutionary branching leads to the coexistence of a dimorphic coalition. The trait values of each member of the coalition will diverge away from the generalist. For the case when both patch types were equally represented in the landscape ($\rho = \frac{1}{2}$), following the evolutionary branching of a monomorphic system, the evolving coalition will always converge upon a symmetric and ES singularity. Surprisingly we found that the CS singular coalition remains symmetric if patches of one type are destroyed, provided the coalition is still viable.

Strategies may coexist despite the lack of branching singular strategies. For such a case we found that a non–symmetric CS singular coalition could exist in the form of a generalist–specialist dimorphism. We did not find any CS singular coalitions of this type whenever a monomorphic singular strategy were branching, leading us to conclude that evolution restricts the coexistence of generalist–specialist pairs, as did Egas et al. (2004).

We concluded the chapter by investigating the effects of asymmetric habitat loss upon monomorphic evolution. The map from trait space to population viability, $\hat{\mathbf{x}} : \tau \mapsto \hat{\mathbf{x}}(\tau)$ in our model is continuous and thus strategies on the extinction boundaries of phenotype space are always evolutionarily repelling (Gyllenberg & Parvinen 2001). When evolutionary change happens on a time–scale similiar to that of habitat destruction, evolution can rescue a metapopulation from extinction, depending critically upon the relative rates of evolutionary and habitat change (Dieckmann & Ferrière 2004). Evolution trapping can also occur if a repelling singular strategy exists that closes off a portion of phenotype space that would otherwise ensure viability following extensive habitat loss.

The realisation of these two processes can be quite delicate, as illustrated in figure 6-15 (see plot (c) of figure 6-13 for parameter values). The grey curves in the plot are hypothetical (the rates of habitat change, mutation and the strength of selection have not been explicitly modelled), depicting the evolution of three metapopulations as habitat is reduced from type–1 patches. If mutation rates or ecological interactions are too slow the metapopulation will not adapt and go extinct (curve I), if these rates too fast the metapopulation may get trapped (curve II). In this example, intermediate rates of adaptation can allow the metapopulation to escape the domain of attraction of the endangered CS strategy, but also evolve away from the extinction region.

The results in this chapter discredit the commonly held position that habitat loss should always result in a reduction in biodiversity: figures 6-5 and 6-6 both illustrate how uniform habitat loss can lead to an increase in diversity via evolutionary branching. Interestingly though, we did not find an example where asymmetric habitat loss brought

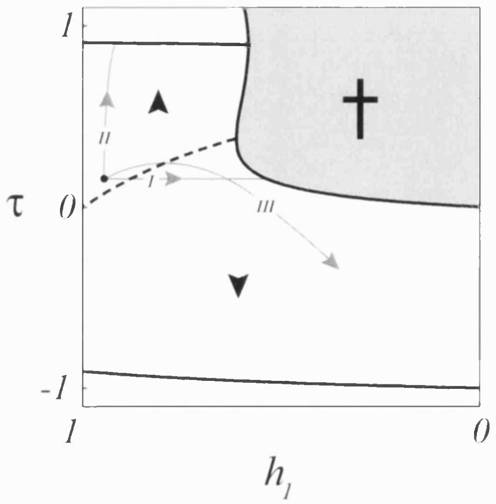


Figure 6-15: The potential for rescue can depend critically upon the relative rates of adaptation and habitat change. The grey curves represent the evolution of three metapopulations, with identical initial conditions, but different adaptive rates: (*I*) evolves slowly relative to habitat change; (*II*) evolves fast relative to habitat change, and (*III*) evolves at an intermediate rate.

upon branching. However this is not a general result. We (Hancock & Britton 2006) have shown, using a different trade-off relationship, that asymmetric habitat loss can indeed lead to the evolutionary branching of specialist singular strategies. Whilst this result offers a ray of hope regarding the habitat-biodiversity relationship, it highlights how subtle the process can be, not only a response to ecological and environmental factors, but also the constraints upon phenotypic adaptation.

Chapter 7

Evolutionary Consequences of Patch Invasion

7.1 Chapter Outline

In this chapter we investigate how competition within local populations may affect the general evolutionary trends outlined in the previous two chapters. We do this by expanding the present model to incorporate patch invasion. We compare invasion processes that do and do not depend upon how adapted an invader and resident are to the particular patch type. We find that patch–dependent local invasion increases the range of landscape and demographic parameters that result in specialisation (relative to no patch invasion), whereas independent invasion decreases the range.

We use a simple model for the within–patch dynamics, however the procedure lends itself to the substitution of more realisitic models, parameterized by stochastic local dynamics.

7.2 Introduction

Without local competition evolution will favour individuals that form local populations that are 'successful' at the metapopulation level. In this scenario, the local populations are the *basic entity* of the metapopulation, and analogous to an individual in ordinary populations (Gyllenberg et al. 2004). When local populations are prone to invasion, the ability to compete must also play a role in the evolution of adaptive traits at the population and metapopulation level.

Modelling metapopulations that incorporate patch invasion should be treated with caution. Hanski (1999*b*) expanded the Levins model to include two species (following Levins & Culver (1971), Slatkin (1974) and others) where patches (equal with regard to habitat type) could be simultaneously occupied by both species. The model predicted that a mutant at low density (at the metapopulation level) had *positive* invasion fitness when identical to the resident resulting in stable coexistence. This challenges the theory of competitive exclusion (see chapter 4) that exists at the population level and has lead some to argue that principle of competitive exclusion only applies to certain ecological scenarios. However the result, as exposed by Hanski (1999*a*)(chapter 7), hinges critically upon the fact that the assumption of a distinct time–scales between the local population dynamics and the metapopulation dynamics has been relaxed by allowing mixed patch populations. The result stems from disregarding the explicit structure of these mixed patches that should depend upon regional trends (i.e if a competitor type is more common at the metapopulation level it could be more common on average in mixed patches).

Models that relax the assumption of separate time–scales have been used successfully for modelling metapopulation evolution when local dynamics have been modelled explicitly: Structured metapopulation models (Gyllenberg & Parvinen 2001, Parvinen 2002, Gyllenberg et al. 2004) incorporate how the immigration rate of a particular competitor type affects the population dynamics within a patch, and thus the subsequent emigration of each competitor. The feedback between demographic and metademographic processes results in an emergent trade–off between individual behaviour at these different scales.

As discussed in previous chapters, the analysis of structured metapopulations relies upon the assumption that emigrants contribute to a 'dispersal pool', members of which get distributed uniformly to each patch. To model how spatial landscape structure effects an evolving metapopulation that consists of invasion–prone local populations, we shall extend our generalised Levins model to include within–patch competition.

7.3 Modelling Within–Patch Competition Dynamics

We shall extend the model of the previous chapters to include within-patch invasion. We shall continue to assume that the time scale of the patch dynamics is much faster than that of the metapopulation dynamics. Therefore we assume that populated patches remain monomorphic. This could be due to genetic drift or competitive exclusion: Let γ_i^{nm} be the probability that a propagule of competitor type n, arriving at a patch of type i and populated by competitor type m, invades, ousts the resident and establishes a new population. We extend the model of chapter 4 given by equation 4.3.0.1 to

$$\begin{aligned}\frac{dx_i^n}{dt} &= \sum_j c_{ji}^n x_j^n (h_i \rho_i - \sum_m x_i^m) - e_i^n x_i^n \\ &+ \underbrace{\sum_j c_{ji}^n x_j^n \sum_m \gamma_i^{nm} x_i^m}_{\text{Invasion rate of type } i \text{ patches}} - \underbrace{\sum_m \sum_j c_{ji}^m \gamma_i^{mn} x_j^m x_i^n}_{\text{Exclusion rate in type } i \text{ patches}} \\ &=: \tilde{\Omega}_i^n (x_1^1, x_2^1, ..., x_1^N, x_2^N) \ . \qquad (7.3.0.1)\end{aligned}$$

We shall use a 'tilde' to denote functions that relate to the extended system (functions and matrices without will refer to those defined in previous chapters). If only one competitor type is present then it is trivial to show that the metapopulation dynamics are identical to those of the previous model. With two patch types and a dimorphic metapopulation the within–patch competition term for competitor type $n = 1, 2$ in patch type $i = 1, 2$ is thus

$$+ (c_{1i}^n x_1^n + c_{2i}^n x_2^n) \gamma_i^{nm} x_i^m - (c_{1i}^m x_1^n + c_{2i}^m x_2^m) \gamma_i^{mn} x_i^n \ , \qquad (7.3.0.2)$$

where $m \neq n$.

Let the occupation states of a resident type be (x_1, x_2) and the occupation states of mutant type be (x_1', x_2'). Let γ_i' be the probability that the mutant type invades an i type patch populated by the resident type and γ_i be the probability that the resident type invades an i type patch populated by the mutant type.

Following the analysis of chapter 4 it is straightforward to show that invasion of the rare mutant competitor is dependent upon the sub–matrix, $\tilde{J}_M$, of the Jacobian matrix defined by equations 4.4.0.9 and 4.4.0.7 respectively, where $\mathbf{x} = (x_1, x_2, x'_1, x'_2)$ is the system state vector and $\hat{\mathbf{x}} = (\hat{x}_1, \hat{x}_2, 0, 0)$ is the steady state of the resident with no mutant. Then

$$\tilde{J}_M = J_M + \begin{pmatrix} (\gamma'_1 - \gamma_1)c_{11}\hat{x}_1 - \gamma_1 c_{21}\hat{x}_2 & \gamma'_1 c_{21}\hat{x}_1 \\ \gamma'_2 c_{12}\hat{x}_2 & (\gamma'_2 - \gamma_2)c_{22}\hat{x}_2 - \gamma_2 c_{12}\hat{x}_1 \end{pmatrix} . \quad (7.3.0.3)$$

Note that $\mathrm{tr}\tilde{J}_M \leq \mathrm{tr}J_M$ when the mutant is identical to the resident (i.e. $e'_i = e_i$ and $\gamma'_i = \gamma_i$), and thus invasion will depend upon

$$\begin{aligned} \tilde{\Delta}(e'_1, e'_2, e_1, e_2) &= -\det \tilde{J}_M(e'_1, e'_2, e_1, e_2) \\ &= \Delta(e'_1, e'_2, e_1, e_2) \\ &\quad +(e'_1 - \frac{c_{11}e_1X}{c_{11}X + c_{21}})((\gamma'_2 - \gamma_2)c_{22}\hat{x}_2 - \gamma_2 c_{12}\hat{x}_1) + \frac{c_{12}c_{21}e_1X\hat{x}_2}{c_{11}X + c_{21}}\gamma'_2 \\ &\quad +(e'_2 - \frac{c_{22}e_2}{c_{12}X + c_{22}})((\gamma'_1 - \gamma_1)c_{11}\hat{x}_1 - \gamma_1 c_{21}\hat{x}_2) + \frac{c_{12}c_{21}e_2\hat{x}_1}{c_{12}X + c_{22}}\gamma'_1 \\ &\quad c_{12}c_{21}\hat{x}_1\hat{x}_2(\gamma'_1\gamma'_2 - \gamma_1\gamma_2) - c_{11}c_{22}\hat{x}_1\hat{x}_2(\gamma'_1 - \gamma_1)(\gamma'_2 - \gamma_2) \\ &\quad +c_{11}c_{12}\hat{x}_1^2\gamma_2(\gamma'_1 - \gamma_1) + c_{21}c_{22}\hat{x}_2^2\gamma_1(\gamma'_2 - \gamma_2) , \end{aligned} \quad (7.3.0.4)$$

when the mutant competitor is sufficiently similiar to the resident ($e'_i \approx e_i$ and $\gamma'_i \approx \gamma_i$).

It is easy to show that $\tilde{\Delta} = 0$ when the mutant is identical to the resident. Recall that this is a crucial property in a model of adaptive dynamics and was lacking in the two–species model presented by Hanski (1999*a*). His example model was chosen as an argument for taking caution when expanding monomorphic metapopulation models to capture species competition: the model predicted, for all resident metapopulation, that the growth rate of a low density mutant that was identical to the resident was strictly positive, violating the competitive exclusion principle.

We shall restrict the analysis of the model to that of monomorphic evolution and proceed in a manner that parallels the previous chapter by assuming the following:

- Dispersal is independent of competitor type ($c^n_{ij} = c_{ij}$ for all n).
- Extinction rates are correlated according to a trade–off relationship $e^n_1 = e_1(\tau^n)$ and $e^n_2 = e_2(\tau^n)$, or equivalently $e^n_2 = f(e^n_1)$.

To restrict the dimension of the effective trait space we shall also make an assumption about the within–patch competition terms. It is reasonable to assume that the competitive ability of an attempting invader depends upon how relatively adapted both the invader and the patch resident (the resident of a patch need not be the regional resident) are to the particular patch type. Although other factors could be conceived that cause variation in competitive ability (e.g. traits that are directly involved in competition) we shall restrict the competition to depend exclusively on patch adaptation, and thus upon the extinction rates of an invader and the patch resident. If e_i^m is the extinction rate of the patch invader when established in type i patches and e_i^r is the corresponding extinction rate of the patch resident, then we shall assume that the invasion probability is of the form

$$\gamma_i^{mr} = \gamma(e_i^m, e_i^r) \ , \tag{7.3.0.5}$$

i.e. that it does not depend explicitly upon patch type. Therefore we have that

$$\gamma_1' = \gamma(e_1', e_1), \quad \gamma_1 = \gamma(e_1, e_1'), \quad \gamma_2' = \gamma(e_2, e_2'), \quad \gamma_2' = \gamma(e_2, e_2') \ . \tag{7.3.0.6}$$

With the trade–off relationship given by equation 6.3.1.3 in chapter 6 we can now write $\tilde{\Delta} = \tilde{\Delta}(e_1', e_1) = \tilde{\Delta}(e_1(\tau'), e_1(\tau))$ and we can proceed with the standard analyse of the adaptive dynamics theory as in the previous chapters.

The selection gradient at the resident strategy $(e_1, e_2) = (e, f(e))$ will depend upon $\frac{\partial\gamma(e',e)}{\partial e'}|_{e'=e}$ and $\frac{\partial\gamma(e,e')}{\partial e'}|_{e'=e}$. Furthermore, the ES and CS classifications of singular strategies will depend upon $\Delta_{11}(e,e)$ and thus $\frac{\partial^2\gamma(e',e)}{\partial e'^2}|_{e'=e}$ and $\frac{\partial^2\gamma(e,e')}{\partial e'^2}|_{e'=e}$. These derivatives will depend upon the particular model of within–patch competition.

7.4 A Simple Model of Within–Patch Competition

To model the competitive dynamics within patches we can call upon a vast body of work. We shall distinguise between three senarios:

- **Lottery competition**– This is the basic scenario, as modelled in the previous chapters, where patch populations cannot be invaded because of a priority/founder effect. This is modelled by setting $\gamma = 0$.
- **Competition in large patches**– When patches can support large populations, infiltrating propagules will not be able invade and oust the resident if they are competitively inferior (less adapted to the patch) and modelled by setting $\gamma(e^m, e^r) = 0$ if $e^m > e^r$

- **Stochastic invasion of inferior types**– If patch populations are small then equal or even inferior competitors may have a non–zero probability of ousting a population of superior residents.

We shall consider the following 'toy' model of within–patch competition that can exhibit all the the above scenarios. Assume that patches can support N individuals regardless of how specialised they are. We imagine that each individual occupies one of N sites. Assume that a single mutant, arriving at a populated patch, has probability μ of ousting one indivdual to occupy one of the sites. Now assume that the birth–death dynamics of the mutant population consists of a directed random walk that occurs with constant probability $p(e^m, e^r)$ (no frequency dependence), terminating when either the mutant population dies out or ousts the resident: That is, if $1 < n < N$ is the number of sites occupied by mutants, then

$$n' = \begin{cases} n & \text{if } n = 0 \text{ or } N \\ n+1 & \text{with probability } p \\ n-1 & \text{with probability } 1-p \ , \end{cases} \tag{7.4.0.7}$$

where n' is the number of mutants following one competitive event.

This basic Markovian process has been used to illustrate the 'Gambler's ruin' principle (Feller 1968). The probability δ that $n = N$ as the number of events $t \rightarrow \infty$, conditional on $n^0 = 1$, is

$$\delta = \frac{1 - \frac{1-p}{p}}{1 - (\frac{1-p}{p})^N} \ . \tag{7.4.0.8}$$

The final requirement is to model how p depends upon the relative patch specialisation of the mutant and the resident. Let

$$p(e^m, e^r) = \frac{e^r}{e^m + e^r} \ , \tag{7.4.0.9}$$

so that 7.4.0.8 reduces to the form

$$\delta\left(\frac{e^m}{e^r}\right) = \frac{1 - \frac{e^m}{e^r}}{1 - (\frac{e^m}{e^r})^N} \ . \tag{7.4.0.10}$$

Thus we assume that the probability that a mutant successfully invades after arriving at a patch with extinction rate e^m and occupied by a resident with extinction

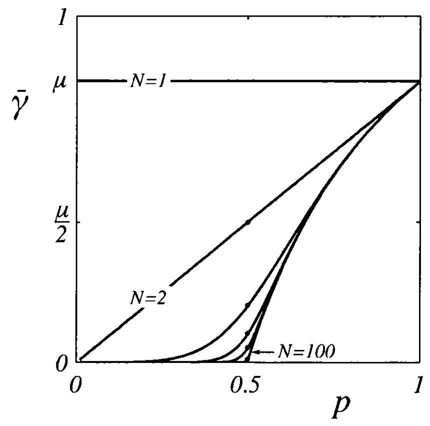


Figure 7-1: The probability of mutant invasion, $\bar{\gamma}$, depends upon the relative probability that a resident individual is replaced by a mutant individual, $p = \frac{e^r}{e^m+e^r}$, the equilibrium population size N and the probability of patch infiltration μ. $\bar{\gamma}$ monotonically decreases with increasing N: $N = 2, 5, 10, 20, 100$.

rate e^r is

$$\gamma(e^m, e^r) = \bar{\gamma}\left(\frac{e^m}{e^r}\right) = \mu\delta\left(\frac{e^m}{e^r}\right) . \tag{7.4.0.11}$$

This crude model of local competition serves as a very simple example of incorporating some notion of within–patch competition and could be easily replaced by more sophisticated models. Figure 7-1 illustrates how the infiltration parameter, μ, and the patch population size, N, affect invasion probability. When $N = 1$ the population consist of a single individual and invasion occurs with probability μ, independent of invader and resident patch adaptation. As N gets large invasion is increasingly difficult for competitor types and increasingly dependent upon patch adaptation. In the limit as $N \to \infty$ $\gamma(e^m, e^r) = 0$ if $e^m \geq e^r$ and only superior competitors can invader.

Before returning to the adaptive dynamics analysis we shall first determine some necessary partial derivatives of γ (see equation 7.4.0.23 below). We first note that δ cannot be evaluated at $e^m = e^r$ directly, however, applying L'Hôpital's rule, we have that

$$\lim_{e^m \to e^r} \delta\left(\frac{e^m}{e^r}\right) = \lim_{e^m \to e^r} \frac{1}{N(\frac{e^m}{e^r})^{N-1}} = \frac{1}{N} , \tag{7.4.0.12}$$

and thus $\gamma(e^r, e^r) = \bar{\gamma}(1) = \frac{\mu}{N}$.

In an equivalent manner we calculate that

$$\bar{\gamma}'(1) = -\frac{\mu(N-1)}{2N} , \tag{7.4.0.13}$$

and

$$\bar{\gamma}''(1) = \frac{\mu(N-1)(N+1)}{6N} , \tag{7.4.0.14}$$

where the primes in this context represents differentiation. We then have

$$\frac{\partial \gamma_1'}{\partial e'}|_{e'=e} = \frac{\partial \gamma(e',e)}{\partial e'}|_{e'=e} = \frac{\bar{\gamma}'(1)}{e} , \tag{7.4.0.15}$$

and

$$\frac{\partial^2 \gamma_1'}{\partial e'^2}|_{e'=e} = \frac{\partial^2 \gamma(e',e)}{\partial e'^2}|_{e'=e} = \frac{\bar{\gamma}''(1)}{e^2} . \tag{7.4.0.16}$$

After equivalent calculations we also have

$$\frac{\partial \gamma_1}{\partial e'}|_{e'=e} = -\frac{\bar{\gamma}'(1)}{e} , \tag{7.4.0.17}$$

$$\frac{\partial \gamma_2'}{\partial e'}|_{e'=e} = \frac{f'(e)\bar{\gamma}'(1)}{f(e)} , \tag{7.4.0.18}$$

$$\frac{\partial \gamma_2}{\partial e'}|_{e'=e} = -\frac{f'(e)\bar{\gamma}'(1)}{f(e)} , \tag{7.4.0.19}$$

and

$$\frac{\partial^2 \gamma_1}{\partial e'^2}|_{e'=e} = \frac{2\bar{\gamma}'(1) + \bar{\gamma}''(1)}{e^2} , \tag{7.4.0.20}$$

$$\frac{\partial^2 \gamma_2'}{\partial e'^2}|_{e'=e} = \frac{f''(e)\bar{\gamma}'(1)}{f(e)} + \frac{f'(e)^2\bar{\gamma}''(1)}{f(e)^2} , \tag{7.4.0.21}$$

$$\frac{\partial^2 \gamma_2}{\partial e'^2}|_{e'=e} = \frac{(2f'(e)^2 - f''(e))\bar{\gamma}'(1) + f'(e)^2\bar{\gamma}''(1)}{f(e)^2} . \tag{7.4.0.22}$$

We can now calculate the selection gradient $\tilde{D}(e) = \frac{\partial \tilde{\Delta}(e,e)}{\partial e'}$ which yields

$$\begin{aligned}\tilde{D}(e) = D(e) - (c_{12}\hat{x}_1 + f'(e)c_{21}\hat{x}_2)\bar{\gamma}(1) \\ + 2\frac{f'(e)ec_{21}}{f(e)(c_{11}X + c_{21})}(c_{12}\hat{x}_1 + c_{22}\hat{x}_2)\bar{\gamma}'(1) \\ + 2\frac{f(e)c_{12}}{e(c_{12}X + c_{22})}(c_{11}\hat{x}_1 + c_{21}\hat{x}_2)\bar{\gamma}'(1) \\ + 2\left(\frac{c_{11}c_{12}\hat{x}_1^2}{e} + c_{12}c_{21}\hat{x}_1\hat{x}_2(\frac{1}{e} + \frac{f'(e)}{f(e)}) + \frac{f'(e)c_{21}c_{22}\hat{x}_2^2}{f(e)}\right)\bar{\gamma}(1)\bar{\gamma}'(1)\ . \quad (7.4.0.23)\end{aligned}$$

Note that, trivially, $\tilde{D}(e_G) = 0$ when the landscape is symmetric ($\rho = \frac{1}{2}$ and $h_1 = h_2 = h$) and the generalist strategy is singular ($f'(e_G) = -1$).

We shall omit a presentation of both the ES and CS conditions since the general forms of these offer no direct insight into the effects of within–patch invasion. Instead we shall present the ES and CS conditions for a singular generalist strategy in a symmetric landscape.

7.5 Singular Generalists in Symmetric Landscapes

As we did in chapter 5, we can derive formulae for the ES and CS condition with relative ease. We shall omit a presentation of the derivations, but they proceed along similar lines to those of chapter 5. The ES condition, $\tilde{\Delta}_{11}(e_G, e_G) < 0$ (equation 5.4.1.3 of chapter 5), in terms of f''_G is

$$\begin{aligned}\left\{1 + \frac{(h-e_G)}{e_G}\left(\bar{\gamma}(1) - 2\bar{\gamma}'(1)\left(1 + \frac{(h-e_G)}{e_G}\bar{\gamma}(1)\right)\right)\right\} f''_G \\ > f''_{ES}\left\{1 - 2\frac{(h-e_G)}{e_G}\bar{\gamma}'(1)\left(2 + \frac{(h-e_G)}{e_G}\left((1-q)\bar{\gamma}(1) - 2q\bar{\gamma}'(1)\right)\right)\right\}\ , \quad (7.5.0.24)\end{aligned}$$

where $f''_G > f''_{ES} = \frac{2}{(1-q)e_G}$ was the ES condition found in section 5.5.1 of chapter 5 in the absence of within–patch invasion.

For the model 7.4.0.11 of invasion this becomes

$$f''_G > f''_{ES}\left\{1 + \frac{(h-e_G)}{e_G}\frac{\mu(N-2)}{\alpha}\left(1 + q\frac{(h-e_G)}{e_G}\frac{\mu(N-1)}{N}\right)\right\} =: \tilde{f}''_{ES}\ , \quad (7.5.0.25)$$

where $\alpha = N + \mu\frac{(h-e_G)}{e_G}(N + \frac{(h-e_G)}{e_G}\frac{\mu(N-1)}{N}) > 0$.

From equation 7.3.0.4 it is clear that the derivation of the CS condition, $\frac{d\tilde{D}(e_G)}{de} < 0$, will require both $\frac{d\hat{x}_1(e_G)}{de}$ and $\frac{d\hat{x}_2(e_G)}{de}$. Since the monomorphic ecology is not altered by the competition terms we can use results of previous chapters: From equations 3.4.2.6 and 3.4.2.7 of chapter 3 we have that

$$\frac{d\hat{x}_1(e_G)}{de} = -\frac{d\hat{x}_2(e_G)}{de} = \frac{(h-e_G)}{4}\frac{dX(e_G)}{de} \tag{7.5.0.26}$$

where $\frac{dX(e_G)}{de} = -\frac{2}{h+(1-2q)e_G}$, as given in section 5.5.1 of chapter 5 . The CS condition, $\frac{d\tilde{D}(e_G)}{de} < 0$ (equation 5.4.1.4 of chapter 5), in terms of f''_G is

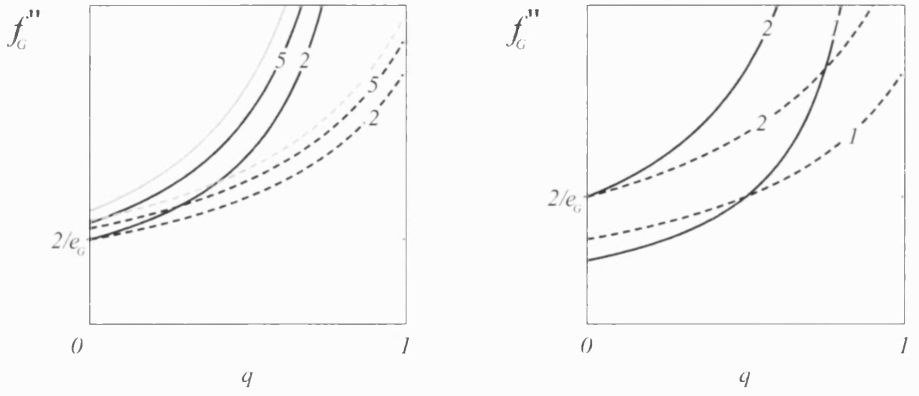
$$\begin{aligned}&\left\{1 - \frac{(h-e_G)}{e_G}\left(-\bar{\gamma}(1) + 2\frac{(h-e_G)}{e_G}\bar{\gamma}(1)\bar{\gamma}'(1) + 2\bar{\gamma}'(1)^2\right)\right\} f''_G \\ &> f''_{CS}\left\{1 + \frac{(h-e_G)}{h+e_G}\bar{\gamma}(1) - 2\frac{(h-e_G)}{e_G}\left((1+\frac{h}{h+e_G})\bar{\gamma}'(1) + \frac{(h-e_G)}{e_G}\bar{\gamma}(1)\bar{\gamma}'(1)\right)\right\} ,\end{aligned} \tag{7.5.0.27}$$

where $f''_G > f''_{CS} = \frac{2(h+e_G)}{(h+(1-2q)e_G)e_G}$ was the CS condition found in section 5.5.1 of chapter 5 in the absence of within–patch competition. Note that both the ES and CS condition do not depend upon $\bar{\gamma}''(1)$. For the model 7.4.0.11 of invasion this becomes

$$f''_G > f''_{CS}\left\{1 + \frac{(h-e_G)h}{e_G(h+e_G)}\frac{\mu(N-2)}{\alpha}\right\} =: \tilde{f}''_{CS} \; . \tag{7.5.0.28}$$

Note that competition has no effect upon generalist evolution when $N = 2$. In this case the competitive advantage of specialising to one patch is equally matched by the competitive disadvantage in the poorer patches since the invasion probability is linear when $N = 2$. It is straightforward to show that $\tilde{f}''_{ES}$ and $\tilde{f}''_{CS}$ increase with N, as illustrated in figure 7-2. This suggests that within–patch competition promotes patch specialisation, either through branching or monomorphic repulsion. From plot (a) we see how the effects of competition are limited as N gets large. Even when local populations are small (e.g. when $N = 5$) competition still has a significant effect.

Setting $N = 1$ models patch–independent patch invasion. In this case (plot (b)) the regions that promote specialisation are restricted. Furthermore, when the landscape is dispersed, the generalist strategy can become ES and non–CS. Therefore, if local patches can only support single and fragile individuals there can exist a metapopulation–level priority effect (the existence of pairs of strategies, each of which cannot be invaded by the other at the metapopulation level). Recall that this was shown to be possible in



(a) $\mu = 1$

(b) $\mu = 0.5$

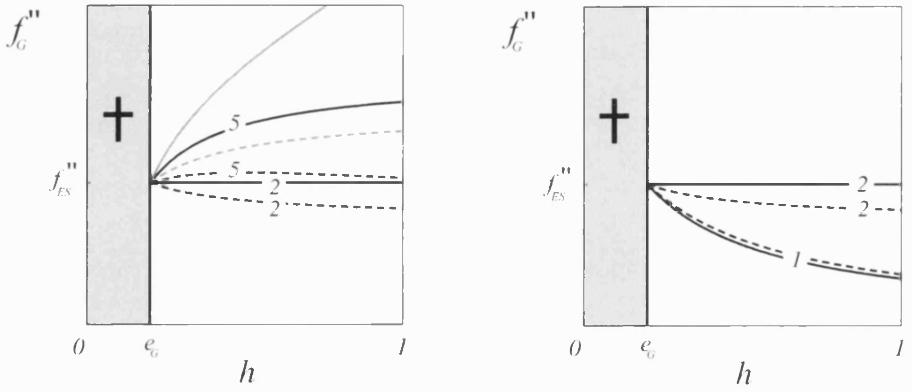
Figure 7-2: The classification of the generalist with competition and as a response to trade–off strength, f''_G, and patch–type aggregation, q. Solid curves bound the ES region and the dashed curve bounds the CS region. The shaded curves of plot (a) represent the limit curves as $N \to \infty$. The $N = 2$ –curves coincide with the basic model. $e_G = 0.5$ and $h = 1$.

the model of patch–dependent dispersal presented in chapter 5, although for extreme parameter values.

Within–patch competition can also have interesting consequences when habitat is removed (see figure 7-3 when the landscape is dispersed). With patch competition the ES condition becomes explicitly dependent upon the fraction of habitat, h. With increasing patch size (plot (a)) the ES condition becomes restricted and in this case decreasing habitat can, for certain trade–off strengths, turn the generalist strategy evolutionarily stable. However, if patch takeover is strategy independent (plot (b)), the reverse may happen with habitat loss. This result also holds when the landscape is aggregated.

The potential for branching can be quite complicated. When $N = 1$ the ES condition coincides with the CS condition ($\tilde{f}''_{ES} = \tilde{f}''_{CS}$) when $q = \frac{\mu}{1+\mu}$, thus if $q \leq \frac{\mu}{1+\mu}$ the generalist is never a branching strategy, as indicated in plot (b). When $N > 2$ the potential for branching increases. This is true for both aggregated and dispersed landscapes. The CS curves when $N = 5$ is not monotonic, mirroring the the observation of chapter 5 as a response to varying e_G when $q > \frac{2}{3}$.

We shall assume that the extinction rates vary according to the trade–off relationship defined in the previous chapter (equation 6.3.1.3). As in the previous model,



(a) $N \geq 2$ and $\mu = 1$

(b) $N \leq 2$ and $\mu = 0.5$

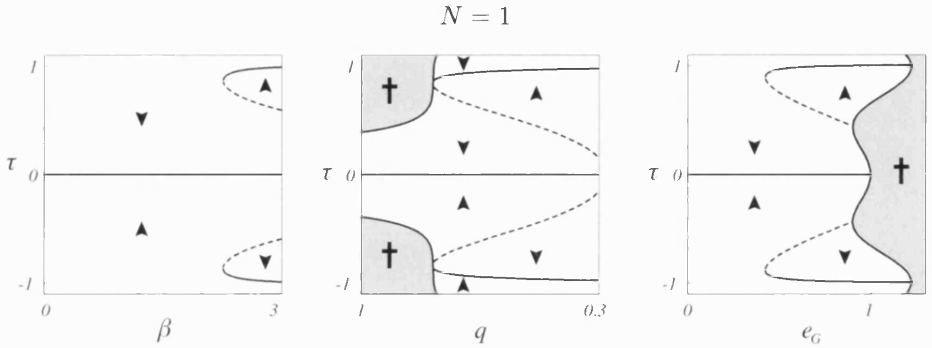
Figure 7-3: The classification of the generalist with competition and as a response to trade–off strength, f''_G, and the fraction of patches habitable, h. Solid curves bound the ES region and the dashed curve bounds the CS region. The shaded curves of plot (a) represent the limit curves as $N \to \infty$. The $N = 2$ curves coincide with the basic model. $e_G = 0.2$ and $q = 0.25$.

increasing e_G is trivially equivalent to decreasing both by h_1 and h_2 equally. Recall that $f''_G = \frac{1+2\beta}{\beta e_G} \geq \frac{2}{e_G}$. When $N = 1$ $\tilde{f}''_{ES} > \frac{2}{e_G}$ if and only if $q \leq \frac{\mu}{1+\mu}$ and $h \geq 2e$ and in this case values of β exist whereby the generalist can become a 'Garden of Eden' strategy.

7.6 Specialist Evolution

We will restrict our investigation to the evolution of monomorphic specialisation and not consider the evolutionary dynamics of a dimorphic system. We shall do this by comparing the numerical results of the previous chapter to those obtained by including within–patch competition. Figure 7-4 illustrates some of the general consequences of within–patch competition when the landscape is symmetric.

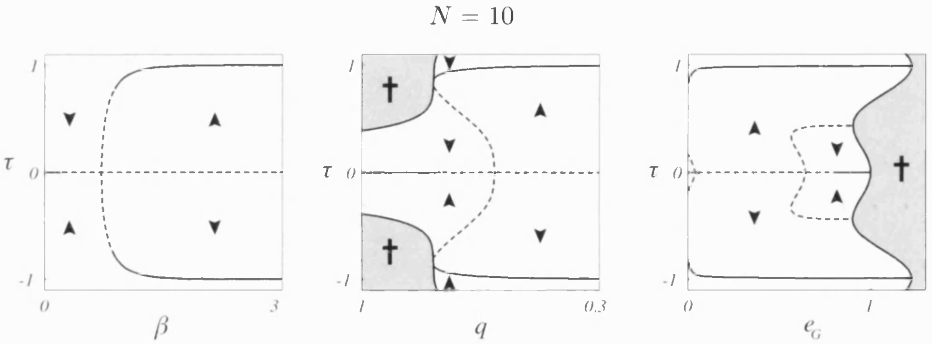
With increasing N, the regions of parameter values that lead to the existence of CS specialists increase, together with their domain of attraction. This is particularly obvious when comparing plots (a) and (d). Over the range $0 < \beta < 3$ the generalist goes from being ES everywhere when $N = 1$ to being ES for only a small range when $N = 10$. The specialist only exists for values of β exceeding about 2.5 when $N = 1$. When $N = 10$ the specialist exists when β exceeds about 1. In plot (f) we observe



(a) $q = 0.5$ and $e_G = 0.25$

(b) $\beta = 2$ and $e_G = 0.75$

(c) $\beta = 2.5$ and $q = 0.1$



(d) $q = 0.5$ and $e_G = 0.25$

(e) $\beta = 2$ and $e_G = 0.75$

(f) $\beta = 2.5$ and $q = 0.1$

Figure 7-4: Bifurcation plots of the evolutionarily singular strategies depend upon the strength of within-patch competition. For the top row plots $N = 1$ (patch-type independent invasion) and for the bottom row plots $N = 10$. Plot columns share the same parameters. $\mu = 0.5$ for each plot. Arrows point towards CS singular strategy curves. Solid curves correspond to ES singular strategies. The shaded region indicates non-persisting strategies. A plot for each parameter combination is given in the chapter 6 for the case when $\mu = 0$ (or equivalently $N = 2$): The left column of plots compares to plot (b) of figure 6-4, the middle column compares to plot (c) of figure 6-4, the right column compares to plot (b) of figure 6-8.

that there can exist seven singular strategies, four of which are CS. We did not find parameter values that led to this scenario when patches were immune to invasion.

7.7 Discussion

In this chapter we model the situation when local populations can be invaded. We present a simple model of patch invasion that depends upon the capacity of a patch to support a population, the rate that propagules engage in competition, and competitive advantages attained from patch specialization.

In summary we found that

- Specialists become more adaptive when the competitive advantage within their favoured patches increases.
- Generalists are more adaptive when competition does not depend upon patch type; as compared to situations when there is no patch competition, or when competition is patch–dependent.

With large N the expected time until competitive exclusion for some competitor types can be very long, calling into question the assumption that local population dynamics and metapopulation dynamics occur at distinct time–scales. We found, however, that the evolutionary behaviour when N exceeded about 25 was very close to the limiting case when $N \to \infty$.

Patch invasion rates could be derived from more complicated models of within–patch competition. The selection gradient (equation 7.4.0.23) depends upon $\bar{\gamma}(1)$ and $\bar{\gamma}'(1)$ provided that $\gamma^{mr} = \bar{\gamma}(e^m/e^r)$, a function of the ratio of extinction rates. More realistic stochastic models of competition that also depend upon the ratio e^m/e^r could be substituted for the example we have considered. Even if an expression for the invasion probability cannot be derived analytically for a particular model, $\bar{\gamma}(e^m/e^r)$ and $\bar{\gamma}'(e^m/e^r)$ could be approximated at $e^m = e^r$ from simulations, and then substituted into equation 7.4.0.23. An approximation of the ES and CS conditions could also be derived in this way (requiring an approximation of $\bar{\gamma}''(1)$ too).

Striving for further realism, the local population dynamics of one or two phenotypes could be modelled explicitly, parameterized by the degree of patch adaptation of each type. The extinction rates of the resident and invader, e^r and e^m, together with the invasion probability, γ^{mr}, could be derived from this model and substituted into the full model by modifiy γ and perhaps the trade–off function, f. Incorporating trade–offs between competitive ability, extinction risk and dispersal rates may offer insight into any emergent trade-offs between adaptations that benefit individuals at the patch level and adaptations that benefit individuals at the metapopulation level.

Chapter 8

Summary and Discussion

In this thesis I have investigated the role that fragmented landscape structure plays in the ecology and evolution of metapopulations.

The models investigated in the majority of this thesis are variants of the implicitly spatial Levins model. Since the dynamics of metapopulations are inherently spatial, I began the thesis in chapter 2 by comparing the predictions of the Levins model with a spatially explicitly counterpart; the basic contact process on a lattice. This helped in clarifying the consequences of limiting the spatial extent of metapopulation processes.

The chapter, following previous investigations in the literature, led us to conclude that:

- Local dispersal leads to a crowding effect that decreases the size of a viable metapopulation as compared to the predictions of the Levins model.
- The global distribution of habitat destruction has an important role in determining the size of a viable metapopulation; a result that is not captured in the Levins model.

Following an exposition into the use of the pair–approximation method for capturing local spatial structure, I investigated how dynamic habitat change can effect a metapopulation after extending a result of Tilman & Kareiva (1997) by considering spatially correlated habitat destruction and regeneration. In summary:

- Spatially correlated habitat destruction and habitat regeneration can affect landscape patterns at large–scale (i.e. landscape connectivity) in a non–trivial way. Intermediate aggregation in the regeneration process can minimize the amount of habitat required for landscape connectivity.

- Metapopulation recovery depends heavily upon the patterns of habitat destruction and regeneration.

These observations suggest that landscape planning and conservation efforts could benefit greatly from the careful consideration of the distribution of habitat.

In chapter 3 I introduced a generalized the Levins model that includes different patch types to model heterogeneous landscape structure. I assumed that the distribution of patch types can be non–uniform, resulting in a patch–type–dependent dispersal process. Landscapes were referred to as aggregated when patches of one type were spatially clustered, or otherwise dispersed. Non–uniform and aggregated habitat destruction was also investigated. In summary:

- Increasing the degree of aggregation of same patch types increases the chances of persistence by reducing the range of parameters that lead to extinction.
- The effects of asymmetric habitat destruction depended upon the degree of patch–type aggregation; aggregated landscapes were more likely to remain able to support a metapopulation if habitat was removed predominately of the least favoured patch type. Removing habitat of the favoured patch type was found to be less detrimental when landscapes were dispersed.

I also considered a pair–approximation model to capture local correlations in patch occupation. The results obtained have led me to hypothesise that the qualitative results found with the Levins–type model will extend to explicitly spatial models. These results emphasise the importance of considering the distribution of habitat types, together with the habitat preference of the inhabitants, when planning landscape change that attempts to protect or boost a current biotic range.

In chapter 4 I investigate how landscape structure mediates the competitive interactions between two and three competitor types. The model is a natural extension of the single species version in chapter 3, with competition for empty patches only. I assume that competitors vary in terms of how adapted they are to different patch types, modelled by variations in patch–type–specific extinction rates; a particular combination of extinction rates defined a strategy. I analysed explicitly the competitive interactions of endemic strategies (strategies that only resides in one type of patch) and related these interactions to landscape structure. in summary:

- Aggregated landscapes increase the range of strategies that can coexist with an endemic strategy.

- Given any two strategies (one of which is endemic), at least one strategy is able to invade the other.
- Habitat change restricts the range of strategies that can coexist with a given endemic strategy, although it can allow some new strategies to exist.

Through numerical calculations (not presented in the chapter) I found that these results also apply to pairs of strategies when when neither is endemic. I also investigated the invasion of dimorphic coalitions. I showed that trimorphic systems were structurally unstable, and thus highly unlikely to form in real situations, as predicted by the competitive exclusion principle. I found that dimorphic invasion could result in the exclusion of one or both strategies of an endemic coalition and that landscape aggregation increased the likelihood that the a dimorphism is preserved following successful invasion.

The study of competition provides a foundation for modelling the adaptive change of a metapopulation. Chapters 5, 6 and 7 investigated the effects that landscape composition has upon metapopulation evolution, adopting techniques from the theory of adaptive dynamics. In chapter 5 I show that the evolution of habitat specialisation can become complicated when a trade–off exists that inhibits the joint specialisation to both path types. In this case the species can be characterised by a one–dimensional family of phenotypic strategies and described by a trade–off function. When both the landscape and the trade–off were symmetric, I was able to obtain formulae that transparently related the effects of model parameters to the evolutionary properties of the patch–type generalist. In summary:

- Decreasing landscapes aggregation promotes the evolution of patch–type generalists.
- Increasing the trade–off strength (i.e. increasing the costs incurred when specializing to a particular patch type) and removing habitat has the same effect as decreasing landscapes aggregation.
- Evolutionary branching, leading to the evolution of a dimorphic system, tends to occur for intermediate levels of landscape aggregation, habitat loss and trade–off strength.
- The generalist is evolutionarily repelling, so monomorphic specialists evolve ,when parameter take opposite values to those promoting generalist evolution. The evo-

lution of a particular patch–type specialist will depend upon the initial configuration of the species, as shown in chapter 6.

I also investigated the consequences of patch–type–specific emigration. I found that the evolutionary consequences of emigration depended critically upon landscape aggregation. The evolution of a generalist is more likely to occur when either landscapes are aggregated and emigration rates are relatively low in the patches favoured by specialists; or when landscapes are dispersed and emigration rates are relatively high in patches favoured by specialists.

In chapter 6 I investigated the evolution of dimorphic metapopulations. I found, under restricted conditions, that a generalist–specialist coalition could be an evolutionary attractor, although this was not obtainable via monomorphic evolution. I found that asymmetric habitat destruction did *not* result in the evolution of a dimorphism that was composed of asymmetric specialist. Both symmetric and asymmetric habitat loss could fragment regions of trait space that allowed persistence. When this happens the process of evolution does not optimize in a global sense and thus harmful for the metapopulation.

In chapter 7 I show how the Levins–type model can be extended to investigate competition within patches when retaining the assumption of time–scale separation between population and metapopulation ecology. With a simple yet explicit model of patch competition, I investigated consequences for an evolving system in comparison with the case when local populations are immune from invasion. In summary:

- When competitive ability is enhanced by patch adaptation evolution tends to favour patch specialists.
- When competitive ability is not affected by patch specialisation evolution tends to favour generalists.

8.1 Potential Directions for Future Work

The conclusions of this thesis hinge upon some major modelling assumptions, and in particular:

1. Fast local population dynamics.
2. Mean–field dispersal.

The results obtained suggest possible links between landscape structure and metapopulation ecology and evolution that may or may not hold when these assumptions are relaxed.

Assumption one above is relaxed in models that allow dispersal processes to interact explicitly with population dynamics. The analysis of such models is helped by assuming that the dispersal process is not affected by the distribution of any heterogeneity in the landscape (the assumption of a 'dispersal pool' migration process), as demonstrated by Parvinen & Egas (2004). To my knowledge, structured models with more complicated dispersal have not been developed that are analytically tractable.

With heterogeneity in the distribution of patch occupation state, one should expect to find characteristic spatial correlations of such states, as shown in chapter 2 for two state (occupied and empty) cases. There has been a lot of interest recently into how local dispersal (Ferrière & Galliard 2001, Doebeli & Dieckmann 2004), and local competition (Mágori et al. 2005), may affect invasion fitness. When heterogeneous landscapes are spatially structured, a further impact upon invasion fitness will be present. Devising models that incorporate such processes and expose their contributions to ecological and evolutionary trends. In this thesis adaptation has been restricted to traits that effect patch specialisation only. Since dispersal has been shown, implicitly, to be a strong mediator in the evolution of patch adaptation, driving metapopulation dynamics and to some extent defining the scale at which local landscape correlations are measured, the co–evolution dispersal must be considered in more unified theory. Again, models that neglect local population dynamics are not suitable candidates for such extensions.

The results of the chapter 7 regarding evolution mediated by patch competition could be verified with other models. The local growth functions that are used in size–structured metapopulation models could incorporate parameters that determine competition strength. These parameters could be positively correlated with patch specialisation so as to investigate the conclusions of chapter 7. Alternatively a trade–off between local competition and local specialisation could be modelled. This could be incorporated quite naturally into the Levins–type model of chapter 7.

The work in this thesis adds to a growing body of work that attempts to marry ecological, environmental and evolutionary processes into a holistic synthesis of ecosystem dynamics in changing environments. The models presented here yield transparent predictions, sometimes in the form of simple formulae (often lacking in the literature), regarding how spatial landscape structures influence the ecology and evolution of inhabitants. Determining the robustness of these predictions should perhaps be the next step in the development of this theory. In particular, can we expect more realistic ecological models that also include the structures of this system (e.g. dispersers exposed to spatially correlated heterogeneity in habit) to yield qualitatively similar results?

Bibliography

Anderson, R. M. & May, R. M. (1991), *Infectious diseases of humans. Dynamics and control.*, Oxford University Press.

Baalen, M. V. (2000), *The Geometry of Ecological Interactions: Simplifying Spatial Complexity.*, Cambridge University Press, chapter 19, pp. 359–387.

Bascompte, J. & Sole, R. V. (1996), 'Habitat fragmentation and extinction thresholds in spatially explicit models.', *The Journal of Animal Ecology* **65**, 465–473.

Boag, P. T. & Grant, P. R. (1981), 'Intense natural-selection in a population of darwin finches (geospizinae) in the galapagos', *Science* **214**(4516), 82–85.

Bowers, R. G., Hoyle, A., White, A. & Boots, M. (2005), 'The geometric theory of adaptive evolution: Trade–off and invasion plots.', **233**, 363–377.

Brachet, S., Olivieri, I., Godelle, B., Klein, E., Frascaria-Lacoste, N. & Gouyon, P.-H. (1999), 'Dispersal and metapopulation viability in a heterogeneous landscape.', *Journal of Theoretical Ecology* **198**, 479–495.

Britton, N. F. (1986), *Reaction-Diffusion Equations and Their Applications to Biology.*, Academic Press, New York.

Brown, J. H. & Kodrick-Brown, A. (1977), 'Turnover rates in insular biogeography: Effect of immigrationon extinction.', *Ecology* **58**, 445–449.

Brown, J. H. & Pavlovic, N. B. (1992), 'Evolution in heterogeneous environments: Effects of migration on habitat specialization.', *Evolutionary Ecology* **6**, 360–382.

Clobert, J., E.Danchin, Dhondt, A. & Nichols, J., eds (2002), *Dispersal.*, Oxford university Press.

Dieckmann, U. & Ferrière, R. (2004), *Evolutionary Conservation Biology.*, Cambridge University Press, chapter 11, pp. 222–223.

Dieckmann, U., Law, R. & Metz, J., eds (2000), *The Geometry of Ecological Interactions: Simplifying Spatial Complexity.*, Cambridge University Press.

Dieckmann, U., M.Doebeli, Metz, J. & Tautz, D., eds (2004), *Adaptive Speciation.*, Cambridge university Press.

Doebeli, M. & Dieckmann, U. (2004), *Adaptive Speciation.*, Cambridge University Press, chapter 7, pp. 140–167.

Durrett, R. & Levin, S. (1994), 'The importance of being discrete (and spatial).', *Theoretical Population Biology* **46**, 363–394.

Egas, M., Dieckmann, U. & Sabelis, M. W. (2004), 'Evolution restricts the coexistence of specialists and generalists: The role of trade–off strength.', *The American Naturalist* **163**, 518–531.

Eshel, I. (1983), 'Evolutionary and continuous stability.', *Journal ofTheoretical Biology* **103**, 99–111.

Etienne, R. S., ter Braak, C. J. F. & Vos, C. C. (2004), *Ecology, genetics and Evolution of Metapopulations.*, Elsevier Academic Press, chapter 5, pp. 105–132.

Fahrig, L. (2003), 'Effects of habitat fragmentation on biodiversity.', *The Annual Review of Ecology, Evolution, and Systematics* **34**, 487–515.

Feller, W. (1968), *An Introduction to Probability Theory and Its Application.*, Wiley: New York.

Ferrière, R. (2000), 'Adaptive responses to environmental threats: Evolutionary suicide, insurance, and rescue.', *Options* pp. 12–16.

Ferrière, R., Dieckmann, U. & Couvet, D. (2004*a*), *Evolutionary Conservation Biology.*, Cambridge University Press, chapter 1, pp. 1–9.

Ferrière, R., Dieckmann, U. & Couvet, D., eds (2004*b*), *Evolutionary Conservation Biology.*, Cambridge University Press.

Ferrière, R. & Galliard, J.-F. L. (2001), *Dispersal.*, Oxford University Press, chapter 5, pp. 57–79.

Forman, R. T. T. (1995), 'Some general principles of landscape and regional ecology.', *Landscape Ecology* **10**, 133–142.

Forman, R. T. T. & Godron, M. (1981), 'Patches and structural components for a landscape ecology.', *Bioscience* **31**, 733–740.

Gabriel, W. & Ferrière, R. (2004), *Evolutionary Conservation Biology.*, Cambridge University Press, chapter 2, pp. 19–40.

Gandon, S. & Michalakis, Y. (2002), *Multiple Causes of the Evolution of Dispersal.*, Oxford university Press.

Geritz, S. (2005), 'Resident–invader dynamics and the coexistence of similar strategies.', *Journal of Mathematical Biology* **50**, 67–82.

Geritz, S., Kisdi, É., Meszena, G. & Metz, J. (1998), 'Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree.', *Evolutionary Ecology* **12**, 35–57.

Gyllenberg, M. & Hanski, I. (1992), 'Single-species metapopulation dynamics: A structured model.', *Theoretical Population Biology* **72**, 35–61.

Gyllenberg, M., Hanski, I. & Metz, J. A. J. (2004), *Evolutionary Conservation Biology.*, Cambridge University Press, chapter 4, pp. 59–79.

Gyllenberg, M. & Metz, J. (2001), 'On fitness in structered metapopulations.', *Journal of Mathematical Biology* **43**, 545–560.

Gyllenberg, M. & Parvinen, K. (2001), 'Necessary and sufficient conditions for evolutionary suicide.', *Bulletin of Mathematical Biology* **63**, 981–993.

Hairston, N. G., Ellner, S. P., Yoshida, M. A. G. T. & Fox, J. A. (2005), 'Rapid evolution and the convergence of ecological and evolutionary time', *Ecology Letters* **8**(10), 1114–1127.

Hamilton, W. D. & May, R. M. (1977), 'Dispersal in stable habitats.', *Nature* **269**, 578–581.

Hancock, P. J. F. & Britton, N. F. (2006), 'Adaptive responses to spatial aggregation and habitat destruction in heterogeneous landscapes.', *Evolutionary Ecology Research* **8**, 1349–1376.

Hanski, I. (1985), 'Single–species spatial dynamics may contribute to long–term rarity and commonness.', *Ecology* **66**, 335–343.

Hanski, I. (1994*a*), 'A practical model of metapopulation dynamics.', *Journal of Animal Ecology* **63**, 151–162.

Hanski, I. (1994*b*), 'Spatial scale, patchiness and population dynamics on land.', *Philosophical Transactions of the Royal Society, London B* **343**, 19–25.

Hanski, I. (1999*a*), *Metapopulation Ecology.*, Oxford University Press.

Hanski, I. (1999*b*), *Metapopulation Ecology.*, Oxford University Press, chapter 7, pp. 117–119.

Hanski, I. & Gyllenberg, M. (1993), 'Two general metapopulation models and the core species hypothesis.', *Amateur Naturalist* **142**, 17–41.

Hanski, I. & Ovaskainen, O. (2000), 'The metapopulation capacity of a fragmented landscape.', *Nature* **404**, 755–758.

Hanski, I. & Zhang, D.-Y. (1993), 'Migration, metapopulation dynamics and fugitive co–existence.', *Journal of Theoretical Biology* **163**, 491–504.

Hastings, A. (1983), 'Can spatial variation alone lead to selection for dispersal.', *Theoretical Population Biology* **24**, 244–251.

Hiebeler, D. (2000), 'Populations on fragmented landscapes with spatially structured heterogeneities: Landscape generation and local dispersal.', *Ecology* **81**(6), 1629–1641.

Hiebeler, D. (2004), 'Competition between near and far dispersers in spatially structured habitats.', *Theoretical Population Biology* **66**, 205–218.

Holt, R. D. (1995), 'Demographic constraints in evolution: Towards unifying the evolutionary theories of senescence abd the niche conservatism.', *Evolutionary Ecology* **10**, 1–11.

Hutchinson, G. E. (1951), 'Copepodology for the ornithologist.', *Ecology* **32**, 571–577.

Ingegnoli, V. (2002), *Landscape Ecology: A Widening Foundation.*, Springer.

Keymer, J. E., Marquet, P. A., Velasco-Hernandez, J. X. & Levin, S. A. (2000), 'Extinction thresholds and metapopulation persistence in dynamic landscapes.', *The American Naturalist* **156**(5), 478–494.

Kisdi, É. (2002), 'Dispersal: Risk spreading versus local adaptation.', *The American Naturalist* **159**(6), 579–596.

Lande, R. (1987), 'Extnction thresholds in demographic models of territorial populations.', *The American Naturalist* **130**, 624–635.

Levin, S. A. & Durrett, R. (1996), 'From individuals to epidemics.', *Philosophical Transactions: Biological Sciences* **2**, 1615–1621.

Levins, R. (1969), 'Some demographic and genetic consequences of environmental heterogeneity for biological control.', *Bull. Entomol. Soc. Amer.* **15**, 237–240.

Levins, R. (1970), 'Extinction.', *Lect. notes Math* **351**, 75–107.

Levins, R. & Culver, D. (1971), 'Regional coexistence of species and competition between rare species.', *Proceedings of the National Academy of Science USA* **68**, 1246–1248.

Losos, J. B., Warheit, K. I. & Schoener, T. W. (387), 'Adaptive differentiation following experimental island colonization in anolis lizards.', *Nature* pp. 70–73.

Lotka, A. J. (1925), *Elements of Physical Biology.*, Williams and Wilkins.

MacArthur, R. H. & Wilson, E. O. (1967), *The Theory of Island Biogeography*, Princeton University Press.

MacArthur, R. & Levins, R. (1967), 'The limiting similarity, convergence and divergence of coexisting species.', *American naturalist* **101(921)**, 377–385.

Mágori, K., Szabá, P., Mizera, F. & Meszéna, G. (2005), 'Adaptive dynamics on a lattice: Role of spatiality in competion, co–existence and evolutionary branching.', *Evolutionary Ecology Research* **7**, 1–21.

Matsuda, H. (1985), 'Evolutionary stable strategies for predator switching.', *Journal of Theoretical Biology* **115**, 351–366.

Matsuda, H. N., Ogita, A. & ad K Sato, A. S. (1992), 'Statistical mechanics of population: The lattice lotka–volterra model.', *Progress in Theoretical Physics* **88**, 1035–1049.

Meszéna, G., Czibula, I. & Geritz, S. (1997), 'Adaptive dynamics in a 2-patch environment: A toy model for allopatric and parapatric speciation.', *Journal of Biological Systems* **5**, 265–284.

Meszéna, G., Gyllenberg, M., Pásztor, L. & Metz, J. A. J. (2006), 'Competitive exclusion and limiting similarity: A unified theory.', *Theoretical Population Biology* **69**(1), 68–87.

Metz, J., Nisbet, R. & Geritz, S. (1992), 'How should we define fitness for general ecological scenarios?', *Trends in Ecology and Evolution* **7**, 198–202.

Murrell, D. J., travis, J. M. J. & Dytham, C. (2002), 'The evolution of dispersal distance in spatially–structured populations.', *OIKOS* **97**, 229–236.

Murren, C. J., Julliard, R., Schlichting, C. D. & Clobert, J. (2002), *Dispersal, Individual Phenotypa, and Phenotypic Plasticity.*, Oxford university Press.

Nee, S. & May, R. M. (1992), 'Dynamics of metapopulations: Habitat destruction and competitive coexistence.', *Journal of Animal Ecology* **61**, 37–40.

Ovaskainen, O. & Hanski, I. (2001), 'Spatially structured metapopulation models: Global and local assessmen of metapopulation capacity.', *Theoretical Population Biology* **60**, 281–302.

Ovaskainen, O. & Hanski, I. (2002), 'Transient dynamics in metapopulation response to perturbation.', *Theoretical Population Biology* **61**, 285–295.

Ovaskainen, O. & Hanski, I. (2003), 'How much does an individual habitat fragment contribute to metapopulation dynamics and persistence?', *Theoretical Population Biology* **64**, 481–495.

Ovaskainen, O. & Hanski, I. (2004), *Ecology, genetics and Evolution of Metapopulations.*, Elsevier Academic Press, chapter 4, pp. 73–103.

Ovaskainen, O., Sato, K., Bascompte, J. & Hanski, I. (2002), 'Metapopulation models for extinction thresholds in spatially correlated landscapes.', *Journal of Theoretical Biology* **215**, 95–108.

Parvinen, K. (2002), 'Evolutionary branching of dispersal strategies in structured metapopulations.', *Journal of Mathematical Biology* **45**, 106–124.

Parvinen, K. (2004), *Evolutionary Conservation Biology.*, Cambridge University Press.

Parvinen, K. (2005), 'Evolutionary suicide.', *Acta biotheoretica* **52**(3), 241–264.

Parvinen, K. & Egas, M. (2004), 'Dispersal and the evolution of specialisation in a two-habitat type metapopulation.', *Theoretical Population Biology* **66**, 633–248.

Poethke, H. & Hovestadt, T. (2001), 'Evolution of density- and patch-size-dependent dispersal rates.', *Proceedings of the Royal Society of London B* **269**, 637–645.

Poethke, H., Hovestadt, T. & Mitesser, O. (2003), 'Local extinction and the evolution of dispersal: Causes and correlations.', *Proceedings of the Royal Society of London B* **161**(4), 631–640.

Pulliam, H. R. (1988), 'Sources, sinks, and population regulation.', *American Naturalist* **132**, 652–661.

Reznick, U., Rodd, H. & Nunney, L. (2004), *Evolutionary Conservation Biology.*, Cambridge University Press, chapter 6, pp. 101–118.

Ronce, O. & Olivieri, I. (2004), *Life History Evolution in Metapopulations.*, Elsevier Academic Press.

Sale, P. F. (1977), 'Maintenance of high diversity in coral reef fish communities.', *American Naturalist* **111**, 337–359.

Sato, K. & Iwasa, Y. (2000), *The Geometry of Ecological Interactions: Simplifying Spatial Complexity.*, Cambridge University Press.

Slatkin, M. (1974), 'Competition and regional coexistence.', *Ecology* **55**, 128–134.

Smith, J. M. (1982), *Evolution and the Theory of Games.*, Cambridge University Press.

Stamps, J. A. (2002), *Habitat Selection by Dispersers: Integrating Proximate and Ultimate Approaches.*, Oxford university Press.

Stauffer, D. (1985), *Introduction to Percolation Theory.*, Taylor and Francis.

Stearns, S. C. (1999), *The Evolution of Life History Traits.*, Oxford University Press.

Tilman, D. (1982), *Resource Competition and Community Structure.*, Princeton University Press.

Tilman, D. & Kareiva, P., eds (1997), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions.*, Princeton University Press.

Tilman, D., Lehman, C. L. & Kareiva, P., eds (1997), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions.*, Princeton University Press, chapter 1, pp. 6–14.

Volterra, V. (1926), 'Variations and fluctuations of the numbers of individuals of animal species living together.', *J. Cons. Perm. Int. Ent. Mer.* **3**, 3–51.

Wiens, J. A. (2002), *The Landscape Context of Dispersal.*, Oxford university Press.

With, K. A. (2004), *Ecology, genetics and Evolution of Metapopulations.*, Elsevier Academic Press, chapter 2, pp. 23–44.

With, K. A., h Gardner, R. & Turner, M. G. (1997), 'Landscape connectivity and population distribution in heterogeneous environments.', *Oikos* **78**, 151–169.