Evolution at shifting range margins

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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapter 2 contains work from a jointly authored publication:

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Author contributions are as follows: ECE and SJC jointly designed the model. ECE carried out simulations of the model, calculated the invasion speeds and wrote the initial drafts of the manuscript. SJC gave guidance on the calculations in particular how to calculate when each invasion speed occurs and edited the final version of the manuscript.

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Abstract

The speed at which biological range expansions occur has important consequences for species experiencing climate change, and for invasions by exotic organisms. There is growing empirical and theoretical evidence that during range expansions there is selection for increased dispersal, and that this can result in faster rates of spread. However, few models consider whether increased dispersal comes at a cost.

In this thesis I investigated how two different trade-offs between dispersal and other traits affected the rates of range expansions. The first modelled a direct trade-off between dispersal and reproduction, and the second incorporated a trade-off so that adaptation to an environmental gradient came at a cost to dispersal.

The first trade-off was investigated by modelling a population that consisted of two dispersal phenotypes, one that has a higher population growth rate and one that has a higher dispersal rate. Using a simple deterministic model it was found that when there was a big trade-off between the morphs in terms of these traits, anomalous invasion speeds were observed whereby a population consisting of both phenotypes invades at a speed faster than either single phenotype. It was found that these anomalous invasion speeds were robust to demographic stochasticty. Adding a shifting climate to the model revealed that a trade-off between dispersal and establishment ability can help a species to keep up with climate change.

The second trade-off was investigated using a quantitative trait model, which revealed that a trade-off between dispersal and adaptation can result in the formation of range margins. Introducing a shifting environment allowed a species to expand its range at a speed determined by the steepness of the gradient and the size of the trade-off.

These models reveal that trade-offs can alter range shifting dynamics, the consequences of which for predicting rates of range expansions were discussed.

In loving memory of my grandfather Alan Charles Elliott

1930–2013

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1. Introduction

1.1 Introduction: The importance of shifting range margins

Two of the most important threats to biodiversity are climate change and invasions by exotic species. During the past century, mean global surface temperatures have increased by 0.6°C (IPCC, 2007). These temperatures are predicted to continue increasing, with a 1.8°C best estimate of warming at the end of the 21st century under a low scenario, and a best estimate of 4°C for the high scenario (IPCC, 2007). A changing climate may lead to what was formerly suitable habitat for a species becoming unsuitable. This poses a challenge for many species; species will need to either adapt to the new conditions, or shift with the conditions to which they are currently adapted.

1.1.1 Evidence of species shifting their ranges with climate change

There is lots of empirical evidence that species are shifting their ranges to higher latitudes and/or altitudes in response to recent warming (Chen et al., 2011; Hickling et al., 2006; Parmesan and Yohe, 2003; Root et al., 2003). It has been estimated using a meta-analysis that the distributions of species have shifted to higher latitudes at a median rate of 16.9 km per decade, and to higher elevations at a median rate of 11.0 m per decade (Chen et al., 2011). However, this response was found to vary greatly within taxonomic groups and between individuals (Chen et al., 2011; Moritz and Agudo, 2013), and has also been found to vary over time (Mair et al., 2012).

Not all species are able to respond to climate change by shifting their range, and even if they can they may not be able to track it at the same rate as the shifting climate. Evidence from British butterflies shows that many species are not keeping up with climate change (Menendez et al., 2006; Warren et al., 2001). Also, even if species are able to expand their range with climate change this does not necessarily mean that the species will increase in abundance. For example, in response to recent climate warming, the northern range margin of the small skipper butterfly, *Thymelicus sylvestris*, has shifted northwards, but this has been accompanied by a decrease in distribution area and abundance (Mair et al., 2012). There are numerous factors that affect whether a species is able to respond, many of which will interact with one another. Some of the main factors are discussed below.

Dispersal ability

Higher dispersal ability will mean a species is more likely to be able to track climate change, and so escape the adverse direct and indirect effects of increased temperatures (Watkinson and Gill, 2002) . For example, it has been found that faster northern range shifts are observed in more mobile butterflies living in forest edges in Finland (Pöyry et al., 2009). In Britain, it has also been found that sedentary butterfly species tend to lag behind climate more than mobile species (Warren et al., 2001; Wilson et al., 2009). There is also growing evidence of evolutionary changes in dispersal in response to climate change (see Le Galliard et al., 2012, for a review), which will be discussed in more detail later in the Introduction.

Habitat fragmentation

Species may not be able to expand their ranges if they have to pass through areas of unsuitable habitat (Thomas et al., 2001), and this may result in species being unable to keep pace with climate change (Travis, 2003). For example, in Britain, the expansion rate of the silver-spotted skipper butterfly, *Hesperia comma*, is being controlled by habitat fragmentation (Wilson et al., 2009). There is also some evidence that species expanding their range have been found to disproportionately expand into protected areas, where habitat may be less fragmented (Thomas et al., 2012). This highlights the importance of having suitable habitat available for species to be able to expand into in response to climate change.

Species interactions

A single species may be limited or prevented from expanding its range as a result of interactions with other species (Berg et al., 2010). If interacting species have different dispersal rates the spatial association of two species may be interrupted (Callaway et al., 2004). For example, Kinlan and Gaines (2003) have shown that plants disperse over smaller distances than their herbivores; so although the herbivorous insects are able to track shifts in temperature, the plant hosts lag behind constraining the insects' expansion.

However, novel species interactions may help species to expand their ranges. For example, the brown argus butterfly, *Aricia agestis*, has spread northwards in Britain 2.3 times faster than the average global expansion rate of species (Pateman et al., 2012). This

rapid expansion has occurred as a result of warmer conditions enabling this butterfly to use a new larval host plant in Britain (Pateman et al., 2012). This suggests that a change in interactions between species may in some cases facilitate range expansions.

1.1.2 Evidence of species responding to climate change *in situ*

Species that are unable to shift with the climate will need to respond to the new conditions in their current location in order to survive. Populations can do this either by adjusting to the new conditions by means of phenotypic plasticity, or by adapting to the new conditions by means of genetic changes through evolution (see Gienapp et al., 2008, for a review of the current evidence for each response). There is lots of evidence of plastic responses to climate change. For example, there is evidence that the timing of phenological events, such as bird nesting, first flowering and frog breeding has become earlier in response to increased temperatures (reviewed in Parmesan and Yohe, 2003). However, it is unlikely that species facing continued directional climate change will be able to survive by plastic responses alone in the long term (Gienapp et al., 2008).

There is limited evidence that some species have adapted by means of genetic changes to the conditions that have arisen as a result of climate warming. One of the few studies where genetic responses to increased temperatures have been observed is in the Canadian red squirrel, *Tamiasciurus hudsonicus*. In this squirrel, advanced parturition dates as a result of warmer springs have been shown to be a genetic response, resulting in earlier breeding (Réale et al., 2003). Experimental evidence from yeast populations suggests that rapid evolution can help populations to survive environmental change (Bell and Gonzalez, 2009). However, further studies using genetic data are needed to be able to predict whether species will be able to survive climate change by adapting to new conditions.

1.1.3 Evidence of species extinctions as a result of climate change

If a species fails to adapt or to shift with the changing climate then it may become extinct. Predictions about future extinctions as a result of climate change vary, with one study estimating that between 18 and 35% of terrestrial species could become extinct by 2050, depending on the level of warming (Thomas et al., 2004). It is uncertain whether extinctions will ultimately reach this level, but there is evidence that species are becoming locally extinct at their lower latitude range margins. Range contractions have been observed in montane butterfly species as they have failed to adapt to increased

temperatures at their lower elevation range margins (Franco et al., 2006; Wilson et al., 2005).

There is also some evidence that species have already become extinct as a result of climate change. For example, 67% of harlequin frogs in the tropics have gone missing and presumed extinct in recent years as a result of increased night time temperatures spreading fungal pathogens (Pounds et al., 2006). Indeed, in a review of how climate change causes extinctions Cahill et al. (2012) found that changing species interactions as a result of climate change are an important cause of extinctions.

1.1.4 Evidence of invasions by exotic species

Native species are also being threatened by the invasion of their ranges by exotic species. Exotic species have been introduced accidentally or deliberately throughout the world, and when these species spread and become pests (Ziska et al., 2011), this has economic impacts and important consequences for biodiversity (Gurevitch and Padilla, 2004; Sakai et al., 2001). For example, the introduction of the cane toad, *Bufo marinus*, into Australia to control sugar cane pests was unsuccessful, and instead the cane toad has caused declines in native species (Urban et al., 2008).

Climate change will also have an impact on invasive species (Hellmann et al., 2008). One impact is that climate change is enabling exotic species to further expand their ranges into areas in which they would not historically survive (Walther et al., 2009). For example, warmer winter temperatures have enabled the spread of the introduced hemp palm, *Trachycarpus fortunei*, into southern Switzerland (Walther et al., 2007). Invasive species also often have high dispersal (Hellmann et al., 2008), and so in species where population dynamics are affected by temperature, climate change could increase rates of dispersal (Walther et al., 2009). For example, in an invasive thistle, *Carduus nutans*, in North America, climate warming has been shown to result in increased plant height, which means there are increased seed dispersal distances (Zhang et al., 2011). If climate change results in increased dispersal in invasive species then this could result in increased rates of spread, potentially threatening a greater number of native species.

From the evidence reviewed above, it can be seen that predicting whether species will be able to shift with the changing climate, and whether they keep up with the rate of change, will be important in helping to conserve species. Predicting the rate at which invasive

species spread will also be important in helping to control the impact that exotic species may have on native species. The focus of this introduction, therefore, will be to review the scientific literature relating to what is currently known about shifting range margins.

In the following sections I will first briefly review different types of mathematical models and methods that have been used in population ecology, in order to give some background to the types of models used to make the predictions that will be discussed in the remaining sections. Theoretical work investigating factors that create limits to species' ranges will then be discussed; it is important to understand why a species has a range margin as this may influence its potential to expand its range. I will then give a detailed review of theoretical and empirical work investigating the evolution of a species' range. Particular emphasis will be given to how dispersal affects species' range shifting, as dispersal directly influences a species' ability to expand its range. Finally, I will discuss how evolution of dispersal may trade-off with other life-history traits, which leads into an outline of the questions that will be investigated in this thesis.

1.2 Mathematical models and methods

Mathematical models have a long history of use in ecology. They are used to analyse and quantitatively describe biological systems and processes of interest. They have the power to make predictions and can help in our understanding of why a phenomenon is occurring. Models are important where it is difficult to obtain empirical data, in which case they can help us to gain a general understanding. Below I will summarise some of the different types of models used in theoretical ecology, with emphasis on differences that are relevant to models that will be developed in this thesis. I will also introduce mathematical methods that will be used in this thesis.

1.2.1 Deterministic versus stochastic models

The simplest types of models used in ecology are deterministic models. These make the assumption that the future condition of a system can be predicted by its present condition (Gurney and Nisbet, 1998). These models tend to be based on a small number of simple assumptions, so are analytically tractable (Okubo, 2000), and are often used because they are elegant and give simple predictions. However, this comes at the cost of biological realism, as in these models infinite population sizes are assumed and random demographic events and fluctuations in the environment are ignored. Instead it is assumed that on

average a greater proportion of individuals in a population follow a deterministic path (Okubo, 2000).

Stochastic models incorporate some randomness, so that probabilities are used to predict the future condition of a system. Randomness can either be incorporated through environmental or demographic stochasticity. Demographic stochasticity is introduced by modelling population dynamics as random processes, and environmental stochasticity by allowing variation in the environment. Stochastic models are based on more realistic assumptions than deterministic models, and so tend to be more complex.

Deterministic models are population based and so do not explicitly model individuals. Whilst stochastic models can also be population based, increasingly, individual based models (IBMs) are used. These models use specific rules for the interactions between individuals and with the environment (McKane and Newman, 2004), and so can take into account differences between individuals. Despite the simplification of deterministic models, these are useful as a starting point for understanding ecological processes upon which more complex stochastic models with greater realism can be built.

1.2.2 Modelling population dynamics

Mathematical ecology is based on the study of population dynamics. Population change over time is given by the numbers of births minus deaths plus migration. Population models relate these numbers to the population size. If these rates are modelled as being density-independent then the per capita growth rate is constant and populations experience exponential growth. However, these rates are likely to depend on the current population density. The simplest model that introduces density-dependent population dynamics is the logistic equation (Verhulst, 1838). This assumes that the environment has a carrying capacity K, which is determined by the availability of resources. This leads to the rate of change of the population size N being given by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{1.1}$$

where r is the per capita growth rate at low density. Solving this equation describes whether populations will die out or approach carrying capacity given a particular starting population density.

More complex models take into account interactions between populations, for example, different species competing for resources, predator-prey interactions and populations of

the same species linked by dispersal. The simplest two-species model is given by the Lotka-Volterra model. This models the control of population growth by two species competing for a resource, or by interactions between a predator and its prey. If populations of a species live in patches with dispersal between them, then these may be described as metapopulation models (Levins, 1970). Patches in the landscape can become extinct and be recolonised by dispersal of individuals. These kinds of models have often been used to understand the evolution of dispersal, which will be discussed later in this Introduction.

The models described so far are continuous in time and are represented by differential equations. These assume that population dynamics occur continuously in time and space. Models may also be discrete in time, for example, representing a species that has discrete generations, so that in each time step population dynamics occur in discrete steps. If these models are deterministic then they may be represented by difference equations.

Since these early models, many developments have been made to incorporate other aspects of population dynamics, such as modelling age structured populations, more complex interactions between different populations and introducing demographic stochasticity.

1.2.3 Spatially-explicit models

The models discussed up to this point are not spatially explicit, however, biological parameters may vary in space and individuals interact and disperse locally. This means population density can vary in space, and so models with explicit space dependence are needed. Space can be modelled as being either continuous or discrete. Continuous models can incorporate environmental clines, whereas in discrete models there may be patches of landscape.

The simplest method for modelling dispersal through a landscape is by random diffusion. In continuous time deterministic models this leads to reaction-diffusion equations. In these types of equations dispersal is modelled as an emigration rate, which only encompasses one aspect of the dispersal process, which will be discussed in more detail later in the Introduction.

More complex types of dispersal can be modelled using dispersal kernels. A dispersal kernel describes the distribution of locations after dispersal relative to the starting point using a probability density function, and can take many forms (review, see Nathan et al., 2012). Dispersal kernels can take into account more complex dispersal, for example,

allowing long and short distance dispersal events to occur which cannot be modelled using a single rate. Models can also incorporate more realistic dispersal strategies, by modelling dispersal as being density dependent or condition-dependent (Bowler and Benton, 2005).

1.2.4 Calculating wavespeeds of spatially-explicit models

The focus of this thesis will be on calculating range expansion speeds, and so I will now introduce some methods used to calculate wavespeeds. The earliest work looking at predicting the rate of range expansions was by Fisher (1937) and Skellam (1951), who incorporated random dispersal into the logistic equation. This results in the following equation

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN\left(1 - \frac{N}{K}\right), \tag{1.2}$$

where r and K are defined as in Eqn. (1.1) and D is the diffusion coefficient. The invasion speed of this equation can be determined by looking for a travelling wave solution. A travelling wave is defined as a wave that travels without changing its shape (Murray, 1993). The speed c of this travelling wave can then be calculated by introducing the new variable $z = x - ct$, and looking for a wave moving to the right of the form

$$N(x,t) = U(x - ct) = U(z). \tag{1.3}$$

The partial differential equation (Eqn. (1.2)) can then be transformed into an ordinary differential equation

$$-cU' = DU'' + rU\left(1 - \frac{U}{K}\right),$$

where prime means differentiation with respect to z. This can be rewritten as

$$U' = V,$$

$$V' = -cV - rU\left(1 - \frac{U}{K}\right).$$

This system has two steady states for (U, V), one at $(K, 0)$ and the other at $(0, 0)$. In order for a travelling wave moving to the right to exist, it is required that

$$\lim_{z\to-\infty}(U,V) \to (K,0),$$

$$\lim_{z\to+\infty}(U,V) \to (0,0).$$

Using a linear stability analysis (see Appendix 1 of Murray, 1993) the eigenvalues λ of the steady states can then be found. The eigenvalues of $(K, 0)$ are

$$\lambda_{\pm} = \frac{-c \pm \sqrt{c^2 + 4Dr}}{2},$$

which means that $(K, 0)$ is a saddle point; and the eigenvalues of $(0, 0)$ are

$$\lambda_{\pm} = \frac{-c \pm \sqrt{c^2 - 4Dr}}{2}.$$

If $c^2 < 4Dr$ then $(0, 0)$ is a stable spiral, and so around the origin U oscillates. If $c^2 > 4Dr$ then the origin is a stable node. For travelling wave solutions to occur between the two steady states it is therefore required that $c \geq 2\sqrt{Dr}$. Hence, the speed of invasion has been shown to depend upon a species' dispersal ability and population growth rate.

It is then fairly straightforward to prove that $c \geq 2\sqrt{Dr}$ is a necessary condition for a travelling wave to exist, by looking for a heteroclinic connection between the two steady states. However, for more complex systems of reaction-diffusion equations it is more difficult to find heteroclinic connections, and hence show that there must be a travelling wave solution. Therefore, in this thesis an alternative method, called the method of front propagation (van Saarloos, 2003), will be used to calculate wavespeeds.

The front propagation method involves calculating the linear spreading velocity v^*, which is the velocity at which arbitrarily small linear perturbations about the unstable state grow and spread, according to the equations obtained by linearising the full model about the unstable steady state (van Saarloos, 2003). This method can be used to determine the long time behaviour of the front which propagates to the right into the unstable steady state. It is therefore preferable to the method described above where an Ansatz of the form $N(x, t) = U(x - ct)$ is made, because that method gives a continuous family of front solutions (van Saarloos, 2003). Fig. 1.1 shows an example of how a typical initial condition grows and spreads in time according to the equations linearised about the unstable steady state (for example, the linearised Fisher equation given in Eqn. (1.4) below). The linear spreading speed is then defined as the asymptotic speed of the point $x_C(t)$:

$$v^* \equiv \lim_{t \to \infty} \frac{\mathrm{d}x_C(t)}{\mathrm{d}t}$$

I will now use the example of Eqn. (1.2) to explain how the front propagation method works (this is based on the explanation given in van Saarloos (2003)). Linearising

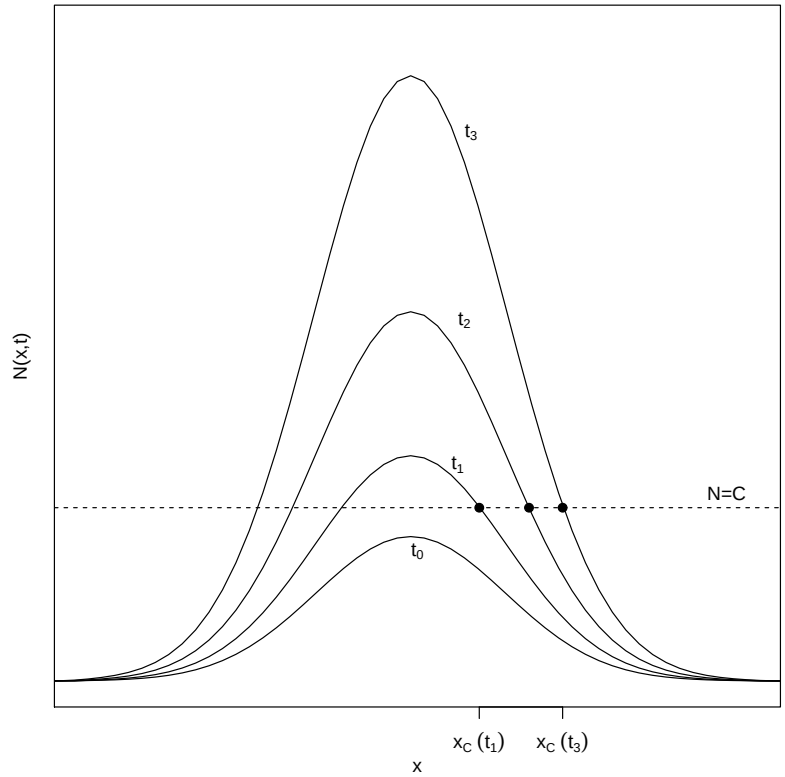

Figure 1.1: Growth and spread of a population N according to Eqn. (1.4). The curves show the initial condition $N(x, t_0)$ and how the population spreads at successive times. The asymptotic spreading speed v^* to the right is defined as the asymptotic speed of the positions $x_C(t)$, where $N(x, t)$ reaches the dashed line $N = C$ (shown as the points on this graph). This figure is adapted from Fig. 2 in van Saarloos (2003).

Eqn. (1.2) about the unstable steady state $N = 0$ gives

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN. \tag{1.4}$$

Linearising about the unstable state means that Fourier modes grow for a range of spatial wavenumbers k. This means taking a spatial Fourier transform, so that

$$\tilde{N}(k,t) = \int_{-\infty}^{\infty} N(x,t)\mathrm{e}^{-ikx}\mathrm{d}x,$$

and substituting in the Ansatz

$$\tilde{N}(k,t) = \bar{N}(k)\mathrm{e}^{-i\omega(k)t},$$

gives the dispersion relation $\omega(k)$ of Fourier modes of Eqn. (1.4), where $\bar{N}(k)$ is the Fourier transform of the initial condition $N(x, t = 0)$.

It is then possible to write $N(x,t)$ for $t > 0$ as the inverse Fourier transform

$$N(x,t) = \frac{1}{2\pi}\int_{-\infty}^{\infty} \bar{N}(k)\mathrm{e}^{ikx-i\omega(k)t}\mathrm{d}k. \tag{1.5}$$

Assuming that the asymptotic spreading speed v^* is finite implies that to look in the frame $\zeta = x - v^*t$, the right flank is seen neither to grow nor decay exponentially. Then to determine v^*, the inverse Fourier formula Eqn. (1.5), needs to be written in this frame

$$N(\zeta,t) = \frac{1}{2\pi}\int_{-\infty}^{\infty} \bar{N}(k)\mathrm{e}^{ik\zeta-i[\omega(k)-kv^*]t}\mathrm{d}k. \tag{1.6}$$

v^* can then be determined by analysing when Eqn. (1.6) neither leads to exponential growth nor decay in the limit where ζ is finite and $t \to \infty$. It is not possible to just evaluate the integral by closing the contour in the upper half of the k-plane, because the large-k behaviour of the exponent is dominated by the large-k behaviour of $\omega(k)$. However, the large time limit means that a saddle-point approximation can be performed, where the k-contour can be deformed to go through the point in the complex k plane where the term between square brackets in Eqn. (1.6) varies least with k. The integral is then dominated by the contribution from the region near this point, and so the saddle point k^* is given by

$$\left.\frac{\mathrm{d}[\omega(k) - v^*k]}{\mathrm{d}k}\right|_{k^*} = 0 \quad \Rightarrow \quad v^* = \left.\frac{\mathrm{d}\omega(k)}{\mathrm{d}k}\right|_{k^*}. \tag{1.7}$$

These equations have solutions in both the upper and lower half of the complex k-plane. Here, I am interested in the right flank, and so look for solutions in the upper half of the plane which correspond to the asymptotic decay towards large x in Eqn. (1.6). If the k-contour is deformed into the complex plane to go through the saddle point in the upper half plane, then the dominant term of the integral is the exponential factor in Eqn. (1.6) evaluated at the saddle point, so $\mathrm{e}^{i[\omega(k^*)-v^*k^*]t}$. The requirement that this term neither grows nor decays exponentially gives that

$$\Im\omega(k^*) - v^*\Im k^* = 0 \quad \Rightarrow \quad v^* = \frac{\Im\omega(k^*)}{\Im k^*}, \tag{1.8}$$

where $\Im$ denotes the imaginary part.

Returning to the example of the Fisher equation, substituting into Eqn. (1.4) the Fourier mode $N_0\mathrm{e}^{ikx-i\omega(k)t}$, where N_0 is the initial condition, gives

$$-i\omega(k)N_0\mathrm{e}^{ikx-i\omega(k)t} = -Dk^2N_0\mathrm{e}^{ikx-i\omega(k)t} + rN_0\mathrm{e}^{ikx-i\omega(k)t}.$$

The Fourier mode cancels throughout, giving $\omega(k)$ to be

$$\omega(k) = i(r - Dk^2).$$

v^* can then be calculated using Eqns. (1.7) and (1.8). First k^* needs to be calculated, this can be done by letting $k^* = x + iy$, where x and y are real numbers to be determined. This gives that

$$\omega(k^*) = i(r - Dx^2 + Dy^2 - 2iDxy),$$

and using Eqn. (1.7)

$$v^* = \left.\frac{\mathrm{d}\omega(k)}{\mathrm{d}k}\right|_{k^*} = -2iD(x + iy).$$

Substituting these into Eqn. (1.8) gives

$$r - Dx^2 - Dy^2 + 2iDxy = 0.$$

Both the imaginary and real parts must equal zero, which gives that $x = 0$ and $y = \sqrt{\frac{r}{D}}$. This gives that $k^* = i\sqrt{\frac{r}{D}}$ and that the linear spreading speed is given by $v^* = 2\sqrt{rD}$. For the Fisher equation, the speed at which perturbations about the unstable steady state grow and spread is therefore found to be $2\sqrt{rD}$.

1.2.5 Statistical models

The models described above are mechanistic models and explicitly take into account demographic processes. In predicting the response of species to climate change species distribution models can also be used. These models look at the relationship between a species' current distribution and climate, and use this to predict a species' future distribution under different climate change scenarios. This approach has limitations, although recent advances have begun to incorporate population dynamics and dispersal (for a discussion of these see Travis and Dytham, 2012). However, as these types of models will not be used in this thesis they will not be discussed further.

1.3 Limits to species' ranges

All species globally exist in a limited area, known as a species' 'range'. In the short term populations cannot become established beyond their range because they have negative growth rates in these new habitats (Bridle and Vines, 2007). However, over long timescales species have adapted to unfavourable conditions. For range margins to form it must therefore be that something is preventing adaptation at the range edge. There are two different explanations for why adaptation fails: (i) adaptation and hence range expansions may be prevented because locally beneficial alleles at the range edge may be limited by Allee effects, genetic drift and a low rate of mutation into these populations; and (ii) continual immigration of locally deleterious alleles into populations at the range edge can swamp locally adapted alleles and so prevent expansion, which is termed gene swamping (reviewed in Bridle and Vines, 2007; Sexton et al., 2009). Examples of theoretical models that have investigated these explanations for the prevention of adaptation at range margins will be discussed below (see Table 1.1 for a summary).

Quantitative trait models have been used to investigate whether gene flow from central to edge populations can result in populations failing to adapt (reviewed in Lenormand, 2002). These models incorporate population ecology and genetics by following changes in the mean of a quantitative trait along a cline, and looking at how range margins are formed along this gradient. The environment changes as a linear function of space and/or time, and so there is an optimum value of the trait at each point along the gradient which maximises survival and reproduction. Using these models it has been shown that at the centre of a species' range the equilibrium for a trait mean is close to its optimum, but further out towards the range edge the mean increasingly departs from the optimum

(García-Ramos and Kirkpatrick, 1997). When gene flow from regions of high to low density occurs, adaptation at the periphery is then hampered (Kirkpatrick and Barton, 1997).

In this case one of two scenarios may evolve. If the trait mean matches the optimum for the entire range then the population is adapted everywhere, and so can expand without limit. However, if the environmental gradient is steep then gene swamping of maladapted phenotypes prevents the trait mean from matching the optimum, and so the species has a limited range (Kirkpatrick and Barton, 1997). Competition with other species has been found to increase this effect as competition reduces population densities at the range edge, thus increasing gene swamping from central populations, which can sharpen range edges (Case and Taper, 2000). Other biotic interactions, such as between predators and prey, can also result in the formation of range margins. If predators are effective dispersers then this can increase the effect of gene flow limiting the prey species' range (Holt et al., 2011).

The form of density dependence used in these models has been found to influence the formation of range margins. If density dependence is strong at high densities then this can reduce the effects of gene swamping (Filin et al., 2008), so that steeper gradients are needed to prevent uniform adaptation than found by Kirkpatrick and Barton (1997) who assume logistic density dependence. However, taking into account demographic stochasticity suggests that the local carrying capacity can have an effect on adaptation at range margins (Bridle et al., 2010), with smaller ranges predicted than those predicted using deterministic models (Kirkpatrick and Barton, 1997).

In these models genetic variance is assumed to be fixed across the entire range, whereas in reality mutation, migration and selection will mean it evolves (Bridle and Vines, 2007). If genetic variance is allowed to evolve then gene flow to peripheral populations is predicted to cause an increase in genetic variance, and so outweigh the effect of gene swamping (Barton, 2001). This allows the species to adapt to a wider range, and so predicts a contrasting effect, that gene flow can rescue peripheral populations. Genetic drift also increases gene flow, which can lower differences in fitness across the range, and so result in higher total fitness (Alleaume-Benharira et al., 2006). Positive effects of immigration on local adaptation are also found if species experience Allee effects as a result of low population densities at the range edge (Holt et al., 2004; Kanarek and Webb, 2010). These models therefore suggest that gene flow can facilitate adaptation and not hinder it, with the amount of genetic variance predicted to be important in determining whether adaptation

Table 1.1: Summary of theoretical studies investigating limits to species' ranges

Type of model				Assumptions		Main conclusion of study	Reference
Deterministic /stochastic	Type of trait	Spatial variation		Genetic variance	Population growth		
		Habitat	Environment				
Deterministic	Quantitative	Continuous	Cline	Fixed	Negative density-dependence	Trait mean close to optimum at centre of range, and departs from this as move to range edge.	[1]
			Fixed in time			Strong density dependence means steeper gradients are needed for gene flow to prevent adaptation.	[2]
						Gene flow from central populations can prevent adaptation at the periphery.	[3]
			Varies in time				[4]
				Not fixed		Gene flow to peripheral populations causes an increase in genetic variance, which allows adaptation at range edges.	[4]
			Fixed in time				[5]
Stochastic		Patches	Fixed in time				[6]
	Diploid	Continuous	Cline	Not fixed		Local carrying capacity affects	[7]

Type of model				Assumptions		Main conclusion of study	Reference
Deterministic /stochastic	Type of trait	Spatial variation Habitat	Environment	Genetic variance	Population growth		
	bi-allelic loci		Fixed in time			adaptation at range margins.	
Deterministic	Haploid variation	Two patches	Source and sink Fixed in time		Allee effects	Immigration to peripheral populations can increase adaptation if they	[8]
	Quantitative	Continuous	Cline	Fixed		are experiencing Allee effects.	[9]
			Fixed in time		Negative density-dependence	Competitive interactions increase the effects of gene flow sharpening range edges.	[10]
						Predators can increase the effects of gene flow on limiting prey species' range.	[11]
		Not spatially explicit	Two niches fixed in time and space		Resource dependent	Competition for limited resources results in stable range limits even without gene flow.	[12]

References: [1] García-Ramos and Kirkpatrick (1997); [2] Filin et al. (2008); [3] Kirkpatrick and Barton (1997); [4] Polechova et al. (2009); [5] Barton (2001); [6] Alleaume-Benharira et al. (2006); [7] Bridle et al. (2010); [8] Holt et al. (2004); [9] Kanarek and Webb (2010); [10] Case and Taper (2000); [11] Holt et al. (2011); [12] Price and Kirkpatrick (2009).

occurs at range margins (Bridle et al., 2010; Kanarek and Webb, 2010).

Apart from a failure to adapt to unfavourable conditions, range margins may also be formed as a result of obstacles preventing further dispersal, abrupt changes in the environment or by interactions with other species (Gaston, 2003). Competition between species is considered to be a common process that sets range limits (reviewed in Case et al., 2005). If species compete for limited resources then it is predicted that range limits can be evolutionarily stable in time, even if there is no gene flow disrupting adaptation (Price and Kirkpatrick, 2009).

1.3.1 Empirical evidence of limits to species' ranges

Many of the theories behind why species have range limits have also been investigated empirically. Sexton et al. (2009) reviewed empirical evidence for the different causes of range limits and determined how much support there is from current studies for each cause. They found that 23 out of 26 studies provided support for the role of competition in setting rage limits. This support has come from correlative approaches, mechanistic models and experimental manipulations. For example, transplantation experiments have shown that in the absence of competition from the barnacle *Semibalanus balanoides* another barnacle *Chthamalus fragilis* can exist beyond its northern range limit (Wethey, 2002). This suggests that competition between these barnacles is setting the range limit of *C. fragilis*.

There is less empirical evidence supporting the theory that a failure to adapt results in species having range limits. However, recent technological and analytical advances have meant that these theories are now easier to test, and so evidence is starting to accumulate. For example, Bridle et al. (2009) have found that the effects of gene flow on local adaptation in rainforest *Drosopila* can depend on the steepness of the environmental gradient. The swamping effect of gene flow preventing evolution of cold tolerances was found to occur along a steep altitudinal gradient. However, along a shallower gradient gene flow may have facilitated local adaptation. This study provides evidence to show that under some conditions gene swamping may prevent adaptation at range margins, supporting the predictions of theoretical models (e.g. Bridle et al., 2010; Kirkpatrick and Barton, 1997).

1.4 Evolution of a species' range

1.4.1 The speed of range expansions

If marginal conditions change, for example as a result of climate change, then species' ranges may be able to evolve. Models have shown that the rate of climate change can have an effect on whether species can respond by expanding their range. If the climate changes at a slow enough rate, it is predicted that a species is able to persist and shift its range along the climate gradient (Pease et al., 1989). However, if the rate of environmental change is too fast then the species will become extinct. In a continuously changing environment another model found that the mean phenotype evolves to lag behind the optimum, as the optimum changes with climate. The magnitude of this lag determines whether or not a species becomes extinct (Bürger and Lynch, 1995). There have been many developments since these early models that also predict there will be a time lag between the climate shifting and the population shifting (e.g. Mustin et al., 2009). However, if species have larger amounts of genetic variation then they are predicted to survive greater rates of environmental change (Duputié et al., 2012; Pease et al., 1989; Polechova et al., 2009)

Adaptation to the environment, as previously discussed, has an impact on range expansions (reviewed in Shaw and Etterson, 2012). If range expansions are occurring along environmental gradients then the steeper the gradient, the slower the rate of expansion because there is more maladaptation in the advancing wave front (García-Ramos and Rodríguez, 2002). Climate change may lead to reductions in the steepness of temperature gradients, as temperatures are increasing more towards the poles (Walther et al., 2002). In this case there may be moderate increases in the speed of expansion as faster invasion speeds are observed on shallower gradients (García-Ramos and Rodríguez, 2002).

The size of a species' range may also affect its ability to respond, as results from stochastic simulations predict that species with broader ranges are more likely to be susceptible to extinction as a result of climate change (Atkins and Travis, 2010). This is because if individuals continue to persist in an area despite their optimum climatic conditions having shifted, they can block locally adapted genotypes and prevent them from expanding their range. If maladapted individuals have higher rates of mortality this weakens the blocking effect (Atkins and Travis, 2010).

Interactions with both the environment and other species can have an effect on whether

species are able to respond to climate change by expanding their range. Investigations of different patterns of habitat loss on range expansions predict that even if a species survives a period of climate change, the spatial structure of the landscape may mean that it has a new smaller range (McInerny et al., 2007). This is because the arrangement of the landscape in the new climate window may mean that available habitat is not accessible, and so the species can only inhabit part of the landscape. The spatial arrangement of the landscape that benefits static and dynamic range margins may also be different, as it has been predicted that the spatial arrangement that maximises the speed of range expansions is different from the arrangement that maximises species persistence in a static landscape (Hodgson et al., 2012)

Range expansions into areas occupied by a competitor have been found to occur more slowly (Burton et al., 2010), with the type of competition occurring between species having an effect on the evolution of a species' range. For example, if dispersal increases with population density, a species experiencing contest competition is less likely to persist than a species experiencing scramble competition (Best et al., 2007). Rates of climate change can also have differing effects on species that are mutualists and competitors. A slower rate of climate change favours the persistence of mutualists, whereas with higher rates, competitors out-compete the mutualists and prevent their range from expanding (Brooker et al., 2007). During climate change the nature of species interactions may also be affected. For example, a lack of suitable host plants beyond herbivorous species' current ranges may restrict range expansions, or the release of natural enemies may promote range expansions as interacting species shift at different rates (Hellmann et al., 2012).

1.4.2 Changing genetic compositions of expanding populations

During range expansions the genetic compositions of populations may change (review see Excoffier et al., 2009), which may either facilitate or hinder range shifting. A low rate of mutation into edge populations, which limits the presence of locally beneficial alleles for adaptation, has been proposed as a mechanism for forming range margins. During range expansions a theory emerging from the literature is that 'mutation surfing' can occur (Klopfstein et al., 2006). This is where mutations arising on the edge of a range expansion can sometimes 'surf' on the wave of advance (Edmonds et al., 2004). This occurs because occasionally new mutations increase in frequency and spread with the invasion wave, potentially over long distances, and become fixed in the population.

It is predicted that if neutral (Klopfstein et al., 2006) or beneficial (Hallatschek and Nelson, 2010) mutations surf then beneficial alleles can become fixed at the invasion front, which can increase the rate of evolutionary adaptation of an expanding population. However, other studies have found that non-neutral mutations can also surf leading to high frequencies of deleterious mutations at the range edge. This can mean that instead of increased evolution there is increased mutational load during a range expansion (Hallatschek and Nelson, 2010; Travis et al., 2007).

Other models also suggest that mutations can have an impact on range expansions. In a spatially continuous environment it is predicted that individual mutations that successfully establish often lead to substantial increases in range because they increase adaptation at the range front (Behrman and Kirkpatrick, 2011). Mutations that become established in shallow gradients were found to result in larger range expansions than those that become established in steep gradients. However, if the environment is also changing in time, then there is a limit to the rate of change that allows beneficial mutations to become established (Kirkpatrick and Peischl, 2013). Only below this limit are beneficial mutations able to aid adaptation to a changing environment. Beneficial mutations may therefore result in increased range expansions if they can become established, but deleterious mutations may prevent range expansions.

1.5 Evolution of dispersal

Dispersal is a key trait that will determine whether species' ranges can evolve, and so will be discussed in more detail now. First, the causes of dispersal evolution will briefly be discussed, followed by a review of the current theoretical and empirical evidence for the evolution of dispersal during range expansions.

Dispersal is any movement of individuals or propagules which has the potential to allow gene flow across space (Ronce, 2007). This encompasses both natal and breeding dispersal. There are three stages that make up dispersal movement: (i) emigration, (ii) a transient stage and (iii) immigration. Dispersal is important because it enables species to be able to persist and evolve (Clobert et al., 2001). Dispersal may evolve when the cost of movement is smaller than the fitness benefit from moving to a new patch (Bowler and Benton, 2005). The costs of dispersal can be either energetic, time, risk or opportunity costs and can occur during any (or all) of the different stages of dispersal movement (review see Bonte et al., 2012).

1.5.1 Scenarios under which dispersal evolves

The scenarios under which dispersal evolves have been divided into three main categories (Ronce et al., 2001):

- **Spatial heterogeneity in habitat quality.** If habitat quality differs in space then dispersal enables individuals to arrive or depart from different locations. A species can then choose to become established in a habitat where they may have a higher fitness, a process referred to as habitat selection.
- **Temporal heterogeneity in habitat quality.** If habitat quality fluctuates over time then dispersal can evolve to escape local extinctions, and may be viewed as a bet-hedging strategy. This is because dispersal distributes offspring from the same parents over different conditions, so increasing the variance in expected fitness.
- **Local competition.** By dispersing from its natal patch an individual can reduce the strength of competition in the patch. If this occurs dispersal can be thought of as an altruistic trait and its evolution understood using kin selection theory.

Spatial heterogeneity in habitat quality: Different models disagree in whether spatial heterogeneity is required for evolution of dispersal. A simple two patch model predicts that if there are differences in habitat quality, then dispersal will be selected for (McPeek and Holt, 1992). However, inclusion of demographic stochasticity predicts that dispersal can evolve even if there is no spatial variation (Cadet et al., 2003; Travis and Dytham, 1998). Demographic stochasticity has been found to select for intermediate rates of dispersal (Travis and Dytham, 1998). High dispersal is selected against because after dispersal high dispersers are more likely to be in a patch that is above its equilibrium density. Low dispersal is also selected against because these dispersers are less efficient at recolonising patches where they have become extinct.

Patterns of habitat availability affect the rate of dispersal that evolves. Reducing the amount of available habitat results in lower rates of dispersal evolving (Travis and Dytham, 1999). For example, in a fragmented landscape, dispersal propensity of the bog fritillary butterfly, *Boloria eunomia*, was found to be one order of magnitude lower than in a continuous landscape (Schtickzelle et al., 2006). However, if in a fragmented landscape individuals can distinguish between suitable and unsuitable habitat patches, then a higher rate of dispersal evolves (Heino and Hanski, 2001). There can also be differences in the dispersal strategy that evolves at different points in a species' range, with lower mean

dispersal distances often found at the range margin than at the range core (Gros et al., 2006).

Temporal heterogeneity in habitat quality: Models predict that dispersal will be favoured in habitats that are temporally heterogenous (Travis and Dytham, 1999), because if a resource is moving species need to be able to track it. Metapopulation models that investigate evolutionary stable strategies find that when local extinctions occur because of environmental and demographic stochasticity, dispersal is selected for (Comins, 1982; Comins et al., 1980; Levin et al., 1984; Olivieri et al., 1995). It has also been shown using an experimental microcosm that dispersive mutants of *Caenorhabditis elegans* increase in frequency when there are increased rates of patch destruction (Friedenberg, 2003). There are, however, contrasting predictions as incorporation of within-patch dynamics into a metapopulation model suggests that increasing extinction rates may not always lead to the evolution of increased dispersal rates (Ronce et al., 2000).

Local competition: Competitive interactions between relatives have been found to favour positive dispersal rates even if the environment is temporally and spatially constant (Comins, 1982; Comins et al., 1980). It has been demonstrated that there is a threshold population density for which staying and leaving are equally profitable, but above this threshold everybody should leave (Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002). A generalisation of this model predicts that if there is enough variability in patch types and enough temporal variation as a result of catastrophes, then evolutionary branching of dispersal strategies will occur (Parvinen, 2002). It has been found that offspring increase their dispersal rate in response to the presence of kin in some species. For example, the decision to disperse in response to potential kin competition has been found to occur in lizards (Le Galliard et al., 2003) and fig wasps (Moore et al., 2006).

However, models have not always found kin selection to lead to evolution of dispersal. For example, dispersal rates may decrease rather than increase as a result of kin selection occurring between dispersers that have originated from the same population (Gandon and Michalakis, 1999). Also, if population sizes are small or there is a low deme size, dispersal rate has been found to decrease (Gandon and Rousset, 1999; Travis and Dytham, 1998). If populations experience Allee effects this may result in the dispersal rate evolving to be too low for metapopulations to be able to persist (Rousset and Ronce, 2004). Also, one study suggests that it may in fact be competition with unrelated individuals, rather than the more generally accepted explanation of kin competition, that explains the evolution of dispersal (Jansen and Vitalis, 2007). This has been found to be the case in feral horses,

where although dispersal from the natal group is affected by kin competition, dispersal from the natal area is affected by the size of non-kin groups (Kaseda et al., 1997).

1.5.2 Evolution of dispersal during range expansions

There is increasing empirical and theoretical evidence that during range expansions evolution of dispersal occurs, as there is selection pressure for increased dispersal during invasions and range expansions. It has been found that faster rates of spread can occur if dispersal evolves during an invasion, with the cost of dispersal determining the rate of expansion that evolves (Travis and Dytham, 2002). The extent to which dispersal evolves during range expansions, and how this results in increased rates of spread, has been found to depend on different factors. Increased levels of evolution have been found to occur if there are no competitors present (Burton et al., 2010; Kubisch et al., 2013), if escape from natural enemies occurs (Phillips et al., 2010b), if Allee effects are absent (Travis and Dytham, 2002), if there is a greater quantity of habitat available (Hughes et al., 2007) and if there are faster rates of climate change (Boeye et al., 2013).

Modelling different dispersal behaviours can also lead to species' range expansions occurring at different rates. Faster range expansions have been found to occur when dispersal is density dependent (Travis et al., 2009), because dispersal evolves to occur at lower population densities during a range expansion than if dispersal is density-independent. Including more complexity in models so that there is evolution of a dispersal kernel, rather than just of an emigration rate, also results in faster range expansions (Boeye et al., 2013; Phillips et al., 2008; Travis et al., 2010), as does temporal variability of dispersal (Ellner and Schreiber, 2012). This is because fluctuations in the mean dispersal distance generate occasional long distance dispersal events, which result in faster speeds than if the mean dispersal distance was constant over time.

Dispersal behaviour may also evolve during a range expansion. It has been shown that selection favours individual disperser behaviour that increases the rate of range expansion for the population, rather than selecting for behaviour that minimises disperser mortality (Bartoń et al., 2012). Evolution of straighter dispersal trajectories has also been found to result in faster range expansions (Bartoń et al., 2012; Phillips et al., 2008). There is evidence that the increased rates of spread found to be occurring during the invasion of cane toads in Australia (Phillips et al., 2006, 2010a) is partly a result of this change in behaviour (Phillips et al., 2008). Lindström et al. (2013) have quantified this effect and predict that displacement of toads at the invasion front can be twice as far as toads at the

same site a few years later, which is a result of these toads spending longer time dispersing and having longer, more directed movements when dispersing.

Increasing empirical evidence supports these predictions that evolutionary adaptations related to dispersal ability are occurring in species that are expanding their ranges as a result of climate change (review see Hill et al., 2011). For example, traits related to increased flight ability have been found in more recently colonised sites of the speckled wood butterfly, *Pararge aegeria*. These sites were found to have populations with larger adults, greater thorax mass and broader thorax shape (Hill et al., 1999a; Hughes et al., 2003, 2007). The cane toad has also been found to have evolution of traits related to dispersal at the front of its range expansion. As well as the toads travelling in straighter lines at the range front (Phillips et al., 2008), these toads have also been found to have longer legs (Phillips et al., 2006) so disperse over longer distances.

1.5.3 Evolution of dispersal along environmental gradients

Most studies discussed so far have looked at range expansions in a homogenous environment. However, most species' ranges are structured across gradients (Bridges et al., 2007). On a static gradient it has been shown that different dispersal strategies evolve at different positions along a species' range (Dytham, 2009). Increased dispersal distances are found to evolve at the range margin if there is increased habitat turnover, reduced birth rate and reduced habitat quality, whereas reduced dispersal distances are found if there are increased costs to dispersal (Dytham, 2009). When a shifting environment is introduced then for all types of gradient there is always increased dispersal during range expansions (Kubisch et al., 2010).

Climate change is expected to result in increased environmental stochasticity, which along gradients of dispersal mortality is predicted to result in evolution of increased dispersal (Kubisch et al., 2011). In this case greater range expansions are found to occur if dispersal is density dependent. However, sometimes evolution of increased dispersal can lead to the range overshooting what will be its final position when the environmental conditions have stabilised, which is a result of selection favouring lower dispersal at stable range margins (Kubisch et al., 2010).

If a species expands its range for some time along a homogenous environment before encountering an environmental gradient, then the evolution of increased dispersal can slow adaptation to the gradient, which may hamper (and even stop) range shifting

(Phillips, 2012). Increased dispersal means that there are more maladapted genes from the homogenous conditions preventing adaptation to the environmental gradient. The extent to which the gradient acts as a barrier depends upon when the environmental gradient is encountered during the range expansion. The earlier during range shifting the gradient is encountered, the less prone to stopping the expansion will be (Phillips, 2012). This is in contrast to the case where instead of encountering a gradient during a range expansion, a species encounters an area of unsuitable habitat. In this case evolution of increased dispersal at the range edge can help a species to overcome this barrier and continue expansion (Travis et al., 2010). When encountering gaps in the landscape more rapid climate change can result in greater dispersal distances evolving, which can again aid range expansions (Boeye et al., 2013).

1.6 Trade-offs between dispersal and other traits

There is evidence, then, that during range expansions there is often selection for evolution of increased dispersal and that this can lead to increased rates of spread. However, not all theoretical studies that look at the evolution of dispersal consider whether increased dispersal will lead to trade-offs in other traits despite lots of empirical evidence for their existence (review see Bonte et al., 2012).

A common trade-off is that more dispersive individuals have reduced fecundity. For example, extreme trade-offs occur in wing polymorphic insects, where one morph is capable of flight and the other is flightless (review see Zera and Denno, 1997). In these insects the morph capable of flight has large functional flight muscles, whereas the flightless morph has small non-functional flight muscles but has much bigger ovaries (Zera and Harshman, 2001). During range expansions it has been found that increased frequencies of the long winged morphs of four species of wing-dimorphic bush crickets were found in recently colonised sites at the range margin (Simmons and Thomas, 2004). However, the impact that these extreme trade-offs between dispersal and reproduction may have on the rate of range expansions is unknown, and so this is a question that I will explore in this thesis.

There is also evidence that the evolution of increased dispersal during range expansions can cause trade-offs. For example, populations at the expanding range margin of the speckled wood butterfly were found to invest more in dispersal at the cost of reduced investment in reproduction (Hughes et al., 2003). This trade-off between dispersal and

reproductive rate is the most common assumption made in theoretical models (Phillips et al., 2010b). However, there are many other costs associated with increased dispersal (Bonte et al., 2012).

One of the few theoretical studies that investigates trade-offs with other traits during range expansions predicts that increased dispersal at the range front results in decreased investment in competitive ability rather than reduced fecundity (Burton et al., 2010). It has also been suggested that increased dispersal and reproduction may be able to trade-off with other traits not related to fitness at the invasion front, such as defence against natural enemies (Phillips et al., 2010b). Further research is therefore needed to understand how evolution of increased dispersal ability during range expansions may result in trade-offs with other traits. In particular, little is known about how trade-offs may affect range expansions along environmental gradients, and so this will also be investigated in this thesis.

1.7 Outline of thesis

This thesis uses both deterministic and stochastic population-based models to investigate how interactions between dispersal evolution and other traits can influence the formation of range margins and the rates of range expansions.

Chapter 2 uses a deterministic model to look at the invasion of a species that consists of two morphs that exhibit dispersal polymorphism. This study shows that if there are trade-offs in the establishment and dispersal abilities of the two morphs then the presence of both phenotypes can result in faster range expansions than if a single phenotype were present in the population, a phenomenon known as 'anomalous invasion speeds'. Surprisingly, these speeds were found to persist when the mutation rate between morphs is vanishingly small.

Chapter 3 uses a stochastic model to determine whether the anomalous invasion speeds found in Chapter 2 are observed in a model that incorporates demographic stochasticity. Simulations of this model suggest that anomalous speeds are still found to occur in stochastic models. In this case, anomalous speeds occur when the carrying capacity of the population is high, the mutation rate between morphs is high or the individual morphs have similar invasion speeds.

Chapter 4 is an extension of the model in Chapter 3 to explicitly model a shifting climate. This model is used to investigate whether dispersal polymorphism helps or hinders a

species' ability to keep up with climate change. The results suggest that if there is a trade-off between dispersal and establishment then this helps a species to keep up with climate change, but if one morph is superior either in terms of establishment or dispersal then being polymorphic can stop a species keeping up with the rate of climate change.

Chapter 5 uses a quantitative trait model to investigate whether a trade-off between dispersal and adaptation to an environmental gradient can result in the formation of range margins. The results suggest that this trade-off can lead to the formation of range margins with the size of the range determined by the steepness of the environmental gradient, the cost of the trade-off, the size of the phenotypic variance and the strength of stabilising selection. When a shifting gradient was introduced into the model species were then able to expand their ranges.

Chapter 6 is a summary of the results found in this thesis with a discussion of questions for future research that the findings of this work have highlighted. The wider context of this research is discussed with reference to the pressing questions that need to be answered in predicting species' responses to climate change.

2. Dispersal polymorphism and the speed of biological invasions

2.1 Introduction

There is evidence that species are expanding their range as a result of climate change and due to accidental or deliberate introductions of exotic organisms (Hickling et al., 2006; Parmesan and Yohe, 2003; Root et al., 2003; Sakai et al., 2001). The speed at which a species is able to expand its range has important implications for conservation management. Whether a species can shift its range at the same rate as the climate shifts, or whether, and by how much, it lags behind will be important in determining how likely a species is in surviving a period of climate change (Chen et al., 2011; Mustin et al., 2009). The rate of spread of exotic species as a result of introductions can also be important, especially if these species become pests (Ziska et al., 2011).

The speed of a species' invasion depends upon its dispersal ability and population growth rate, which are affected by a number of demographic and environmental parameters. Many theoretical models have investigated species' invasion speeds under different conditions, beginning with the work of Fisher (1937). Developments since Fisher have found that many factors including Allee effects, timing of reproduction and dispersal in the life cycle, and environmental heterogeneity can influence the speed of invasion (reviewed in Hastings et al., 2005). Adaptation to local conditions has also been found to influence the rate of spread. García-Ramos and Rodríguez (2002) found that in a spatially heterogeneous environment the rate of local adaptation can be the key limiting factor to spread, with faster range expansions occurring when the environmental gradient is shallower.

During invasions there is a selection pressure for increased dispersal. The effect that the evolution of dispersal rate has on the speed of invasion has been investigated using an individual-based model (IBM) by Travis and Dytham (2002). They found that if dispersal evolves during an invasion then there is a faster rate of spread, with the rate that evolves determined by the cost of dispersal. Other studies have also revealed that during range expansions there is evolution towards increased dispersal resulting in faster rates of spread. The extent to which increased dispersal evolves can depend on different

factors, with increased levels of evolution if there are no competitors present (Burton et al., 2010), if Allee effects are absent (Travis and Dytham, 2002), and if there is a greater quantity of habitat available (Hughes et al., 2007). It has also been shown that the rate at which species expand their range can be affected by the way that dispersal is modelled. Faster range expansions occur when density-dependent strategies are allowed to evolve (Travis et al., 2009), when a dispersal kernel rather than just an emigration rate is evolving (Travis et al., 2010), and when there is temporal variability in dispersal (Ellner and Schreiber, 2012).

There is also increasing empirical evidence from species that are expanding their range of evolutionary adaptations related to dispersal ability in individuals in more recently colonised areas (review see Hill et al., 2011). For example, more recently colonised sites of the speckled wood butterfly, *Pararge aegeria*, contain populations with larger adults, greater thorax mass and broader thorax shape (Hill et al., 1999a; Hughes et al., 2003, 2007). All of these traits are related to flight ability, and so mean that these individuals are more dispersive and hence may invade faster.

There is both increasing empirical and theoretical evidence that during range expansions individual dispersal phenotypes can evolve, and that the speed of range expansions can also evolve. It has been shown that during a range expansion selection favours individual behaviour that increases the rate of expansion for the population, rather than selecting for behaviour that minimises disperser mortality (Bartoń et al., 2012). Most other studies, however, consider individual dispersal evolution and it is not known what the effect of a population being polymorphic has for the speed of a range expansion. To investigate this I use a simple spatially-explicit deterministic model which describes the invasion of a species into a landscape previously unoccupied by the species. The species is modelled using Lotka-Volterra dynamics, with mutation between two morphs of a species which differ in their dispersal and establishment abilities. The parameters used in the model are varied to investigate whether having two dispersal phenotypes in a population affects the invasion speed.

2.2 Model

A spatially-explicit general Lotka-Volterra model is used, which assumes that individuals disperse and reproduce randomly during the lifetime of the individual. Time is assumed to be continuous and the landscape to be spatially and temporally homogenous. In this

model there are two phenotypes that differ in their dispersal ability. There is:

- an establisher morph, e, that after establishment has a higher growth rate but is a poorer disperser; and
- a disperser morph, d, that has a lower growth rate after establishment but is a better disperser.

This model describes the spatio-temporal dynamics for the population density of each of these morphs. Population density of the species is denoted by n_i with subscript $i \in \{e, d\}$ representing density of each morph. Morph i has dispersal rate D_i and growth rate r_i. A general set of Lotka-Volterra equations are used, so m_{ee} and m_{dd} represent competition between morphs of the same type, and m_{ed} and m_{de} competition between the different morphs. There is mutation between morphs at birth so that a fraction of offspring of each morph are of the other type. The morphs have different mutation rates, which are represented by μ_e and μ_d respectively. Thus the equations are given by:

$$\frac{\partial n_e}{\partial t} = D_e \frac{\partial^2 n_e}{\partial x^2} + r_e n_e (1 - m_{ee} n_e - m_{ed} n_d) + \mu_d n_d - \mu_e n_e, \tag{2.1}$$

$$\frac{\partial n_d}{\partial t} = D_d \frac{\partial^2 n_d}{\partial x^2} + r_d n_d (1 - m_{de} n_e - m_{dd} n_d) + \mu_e n_e - \mu_d n_d. \tag{2.2}$$

The first term on the right hand side of each equation describes the random dispersal of each morph. The second term describes the population growth of each morph, and the third and fourth term describe the mutation of morphs into each other, i.e. the fraction of offspring of either phenotype that is of the other type.

I am interested in the case where there is a cost to being a better disperser. I have investigated this by imposing the condition $D_d > D_e$ and $r_d < r_e$. This implies that d the disperser morph is better at dispersing, but has a cost in terms of being a poorer establisher and hence has a lower growth rate after establishment, and that e the establisher morph is a poorer disperser but has a higher growth rate after establishment. The scenario where one morph is both a better disperser and establisher was also investigated but as this morph is then always dominant, and so less interesting biologically, this case will not be discussed further.

This model was analysed using both analytical techniques and numerical simulations. First the invasion of each morph present on its own in the landscape was investigated, and then the case where mutation between morphs allows coexistence. I am interested in the

biologically relevant case where the mutation rate is small, for which scenario analytical solutions were found.

Analytical results for the underlying partial differential equations were obtained by first finding the equilibrium population density of each morph and then using the method of front propagation to calculate the invasion speed (van Saarloos, 2003). The equations were then solved numerically by approximating the spatial derivatives by finite differences, so that the partial differential equations become a set of coupled ordinary equations, and then carrying out simulations in R (R Development Core Team, 2011) using the deSolve function (Soetaert et al., 2010). These simulations produced a travelling wave at the invasion front which rapidly approached a constant speed as the invasion progressed. The invasion speed was estimated by calculating the distance that the density profiles at different times need to be displaced in order to lie on top of each other.

2.3 Results

2.3.1 Calculation of invasion speed

First the case where each morph is present in the landscape on its own was investigated. In this case the system of equations (2.1) and (2.2) reduces to $\frac{\partial n_i}{\partial t} = D_i \frac{\partial^2 n_i}{\partial x^2} + r_i n_i \left(1 - \frac{n_i}{K_i}\right)$ where $K_i = \frac{1}{m_{ii}}$ is the carrying capacity of morph i. I looked for travelling wave solutions and found that the invasion speed, v_i, is determined by the species' growth rate and dispersal ability: $v_i = 2\sqrt{r_i D_i}$, so that the invasion is faster when either the growth rate or dispersal ability is increased, as was originally found by Fisher (1937).

I then investigated the case where both morphs were present in the landscape and there is mutation between them. In this case the front propagation method of van Saarloos (2003) was used to calculate the invasion speed. An explanation for why this method was used instead of the method of looking for travelling wave solutions is given in Appendix A. The general system of Lotka-Volterra equations has two steady states, an unstable extinction state $(n_e, n_d) = (0, 0)$ and a stable coexistence state which I will denote by (n_e^*, n_d^*). The front propagation method involves linearising the equations about the unstable steady state, which gives:

$$\frac{\partial n_e}{\partial t} = D_e \frac{\partial^2 n_e}{\partial x^2} + (r_e - \mu_e) n_e + \mu_d n_d, \tag{2.3}$$

$$\frac{\partial n_d}{\partial t} = D_d \frac{\partial^2 n_d}{\partial x^2} + (r_d - \mu_d) n_d + \mu_e n_e. \tag{2.4}$$

Note that these equations only depend upon the morphs' population growth rates, dispersal abilities and mutation rates and not on the competition coefficients. Here it is assumed that the speed calculated using the linear system (2.3) and (2.4) also applies to the nonlinear system (2.1) and (2.2). This linear speed is known to be a lower bound of the invasion speed but it is not always exact (Weinberger et al., 2002). In the numerical simulations section I will therefore check that the results obtained based on this linear conjecture are valid.

Using these linearised equations, then following van Saarloos (2003), I substitute $\begin{pmatrix} n_e \\ n_d \end{pmatrix} \propto \exp(-i\omega(k)t + ikx)$ where $\omega(k)$ is the dispersion relation of Fourier modes of the linearised equations (2.3), (2.4) and k is the spatial wavenumbers. This gives the equations:

$$[i\omega(k) - k^2 D_e + r_e - \mu_e]n_e + \mu_d n_d = 0, \tag{2.5}$$

$$\mu_e n_e + [i\omega(k) - k^2 D_d + r_d - \mu_d]n_d = 0. \tag{2.6}$$

After algebraic manipulation this leads to an eigenvalue problem, with solutions

$$\omega(k) = \frac{i}{2}[r_e + r_d - \mu_e - \mu_d - k^2(D_e + D_d) \pm R], \tag{2.7}$$

where $R^2 = [k^2(D_d - D_e) + r_e - r_d - \mu_e + \mu_d]^2 + 4\mu_e\mu_d$. This gives that

$$\frac{d\omega}{dk} = -ik(D_e + D_d) \pm \frac{ik(D_d - D_e)[k^2(D_d - D_e) + r_e - r_d - \mu_e + \mu_d]}{R}.$$

The wave speed can then be calculated by finding k^*, where k^* is the linear spreading point (van Saarloos, 2003), such that

$$\frac{d\omega(k^*)}{dk^*} = \frac{\Im\omega(k^*)}{\Im k^*}, \tag{2.8}$$

where $\Im$ denotes the imaginary part. These equations represent a biological invasion so n_e and n_d cannot be negative, and so it can be deduced that k^* is purely imaginary. I can then make the assumption that $k^* = iq$ and substituting into (2.8) gives

$$R^2[r_e + r_d - \mu_e - \mu_d - q^2(D_e + D_d)]^2 = [q^4(D_d - D_e)^2 - (r_e - r_d - \mu_e + \mu_d)^2 - 4\mu_e\mu_d]^2. \tag{2.9}$$

The wavespeed is obtained by finding the real solution q to Eqn. (2.9) that corresponds to the largest speed $v = \frac{\Im\omega(iq)}{q}$ (van Saarloos, 2003). As Eqn. (2.9) is a quartic equation in

q^2, it can only easily be solved numerically. Simple analytical results can be obtained in the biologically interesting limit of weak mutation between the morphs. Taking the limit $\mu_e \to 0$ and $\mu_d \to 0$ in Eqn. (2.9) gives

$$\begin{aligned}&[r_e - r_d - q^2(D_d - D_e)][r_e + r_d - q^2(D_e + D_d)] = \\ &\pm[r_e - r_d - q^2(D_d - D_e)][r_e - r_d + q^2(D_d - D_e)].\end{aligned} \tag{2.10}$$

This gives three values for q^2: $q^2 = \frac{r_e - r_d}{D_d - D_e}$, $q^2 = \frac{r_d}{D_d}$ and $q^2 = \frac{r_e}{D_e}$ which after substitution into Eqn. (2.8) in the limit that $\mu_e \to 0$ and $\mu_d \to 0$ gives three values for the wavespeed:

$$v_e = 2\sqrt{r_e D_e}, \tag{2.11}$$

$$v_d = 2\sqrt{r_d D_d}, \tag{2.12}$$

$$v_p = \frac{|r_e D_d - r_d D_e|}{\sqrt{(r_e - r_d)(D_d - D_e)}}. \tag{2.13}$$

v_e is the speed at which the establisher invades in isolation, v_d is the speed of the disperser and v_p is a third wavespeed that is dependent on both morphs' establishment and dispersal abilities. For a finite but small mutation rate, it is expected that the invasion speed would equal one of the above values plus a small correction proportional to some power of the mutation rate.

The conditions under which each invasion speed is expected to occur were then investigated. These conditions were determined by assuming that the mutation rates are small but not necessarily the same, and so I substitute $\mu_e = e\mu$ and $\mu_d = d\mu$, where e and d are positive. I then substitute $q^2 = \frac{r_e - r_d}{D_d - D_e} + \epsilon$ into (2.9), where ϵ is small when the mutation rate is small. Taking the the limit $\mu \to 0$, gives that $\frac{\epsilon}{\mu} \to g$, where

$$\left([g(D_d - D_e) + e - d]^2 + 4ed\right) \frac{(r_d D_d - r_e D_e)^2}{(D_d - D_e)^2} = (r_e - r_d)^2 \left(g(D_d - D_e) + e - d\right)^2,$$

$$\Rightarrow \frac{4ed}{\left(g(D_d - D_e) + e - d\right)^2} = \frac{(r_e - r_d)^2 (D_d - D_e)^2}{(r_d D_d - r_e D_e)^2} - 1.$$

Since e and d are both positive, g will be real if and only if

$$(r_e - r_d)^2 (D_d - D_e)^2 \geq (r_d D_d - r_e D_e)^2.$$

This condition is satisfied in the positive quadrant of $\left(\frac{r_e}{r_d}, \frac{D_d}{D_e}\right)$ space that is bounded by

the curves

$$\frac{D_d}{D_e} = 2 - \frac{r_d}{r_e}, \tag{2.14}$$

and

$$\frac{D_e}{D_d} = 2 - \frac{r_e}{r_d}. \tag{2.15}$$

Below the curve (2.14) the invasion proceeds at the speed of the monomorphic establisher v_e and above curve (2.15) the invasion proceeds at the monomorphic disperser speed v_d. The third speed v_p occurs between each of these curves. As long as these conditions are satisfied the speed v_p is always faster than v_e and v_d. The parameter regions where each of these speeds occurs can be seen in Fig. 2.1.

The faster invasion speed occurs when the difference of both traits between morphs is roughly greater than a factor of two, and for the parameter regions shown can be up to twice as fast as the single phenotypes invasion speeds (Fig. 2.1). Polymorphic invasion speeds could be more than twice as fast as either monomorphic speed if the morphs' parameters differ by a factor of more than ten, but this is unlikely to be the case for real species.

2.3.2 Numerical simulations

Numerical simulations were carried out to check that the speeds predicted analytically using the linear conjecture gave the same results as those observed experimentally for the nonlinear system of equations (2.1) and (2.2). The simulations were carried out by approximating the spatial derivatives by finite differences and then carrying out simulations in R (R Development Core Team, 2011). This model was initially motivated by a metapopulation model in which the morphs' establishment abilities described the colonisation of empty patches and subsequent population growth of each morph, and patches became extinct at a constant rate. In metapopulation models interactions between species are effectively neutral because the nonlinear terms in these models come from the availability of patches. This initial motivation, and the fact that analysis revealed that the invasion speed does not depend upon the competition coefficients, meant that I first investigated the simple case where both morphs have the same carrying capacity and there are neutral interactions ($m_{ee} = m_{ed} = m_{de} = m_{dd} = 1/K$).

Initially simulations were carried out with no mutation between morphs. In this case both coexist neutrally at equilibrium, however, during an invasion whichever morph has the faster invasion speed in isolation will invade the empty landscape and reach its carrying

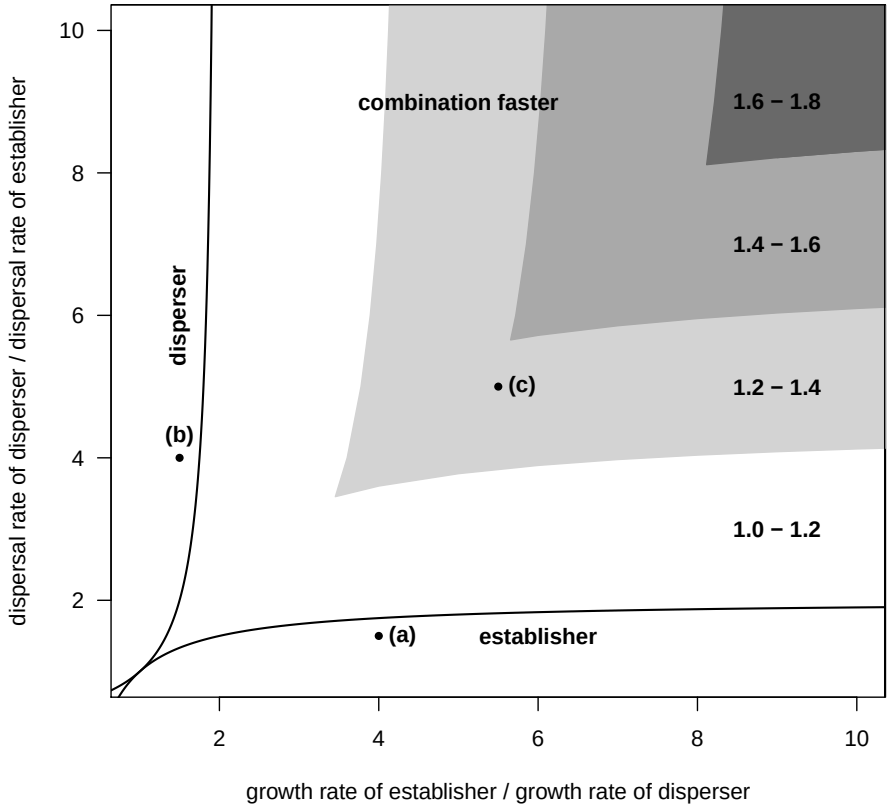

Figure 2.1: Parameter regions where each invasion speed occurs. The area between each of the curves (given by Eqns. (2.14) and (2.15)) and the axes is where the polymorphic invasion occurs at approximately the same monomorphic speed as one of the phenotypes. The area above the curves is where the polymorphic invasion occurs faster than either monomorphic invasion, with the shading from white to grey representing the extent to which the polymorphic invasion is faster. (a), (b) and (c) show the parameters used in Fig. 2.3. The area where the ratio of the net growth rates and dispersal rates is less than one is not shown in this figure because that region of parameter space violates my assumption of net growth rate of establisher $>$ net growth rate of disperser and dispersal rate of disperser $>$ dispersal rate of establisher. If there were a trade-off in only one of the traits, for example, if both morphs have the same net growth rate but different dispersal rates then the ratio of growth rates would be 1, and so the invasion would follow the speed of the disperser. Similarly if the morphs only differed in their net growth rate then the invasion would follow the speed of the establisher.

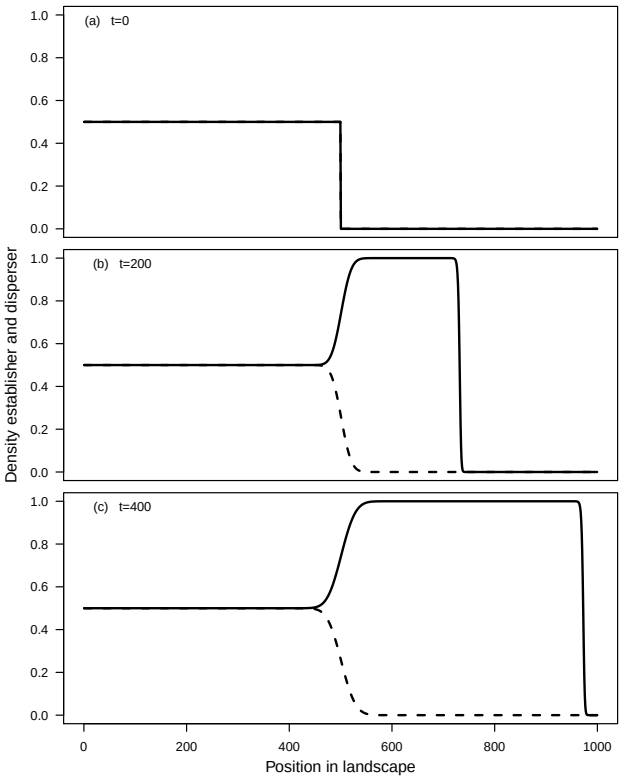

Figure 2.2: Invasion profile when there is no mutation between phenotypes. At the start of the simulation half of the landscape was filled with both morphs, each at half of the carrying capacity, and the other half of the landscape was unoccupied. This is an example of the case where the establisher morph (solid line) has the fastest single invasion speed, and so this phenotype invades through the landscape and the disperser morph (dotted line) remains in its initial location. (a) represents t=0, (b) t=200, and (c) t=400. The parameter values used for this simulation were $K = 1$, $r_e = 0.8$, $r_d = 0.2$, $D_d = 0.6$, $D_e = 0.4$.

capacity (Fig. 2.2). The interface between coexistence of phenotypes and dominance of the faster morph moves very slowly (Fig. 2.2).

I found that the addition of a small amount of mutation between phenotypes allows both morphs to coexist during an invasion. Again, I initially looked at the simple case of symmetrical mutation between morphs. Here the three different invasion speeds that were found analytically are observed (Fig. 2.3). These three invasion speeds occur as a result of differences in the dispersal and establishment abilities of the two phenotypes. When the dispersal abilities of the disperser and establisher are similar but the population growth rate of the establisher is much higher than that of the disperser, the invasion occurs at the speed of the establisher (Fig. 2.3a). When the population growth rates of each morph are

similar but the dispersal rate of the disperser is much higher than the dispersal rate of the establisher, the invasion occurs at the speed of the disperser (Fig. 2.3b). However, when there is a big difference between the two phenotypes in terms of both their dispersal and establishment abilities, the invasion occurs faster than either single morph (Fig. 2.3c).

The analysis predicts that the carrying capacity and mutation rate do not affect the invasion speed. To check this, simulations were also carried out with different mutation rates between morphs (Fig. 2.4i), non-neutral interactions (Fig. 2.4ii), and non-neutral interactions with different mutation rates and different carrying capacities (Fig. 2.4iii). It was found, as was predicted, that none of these parameters has an effect on the invasion speed, although they could change the shape of the invasion profile. It is only the morphs' population growth rates and dispersal abilities that were found to affect the species' invasion speed.

2.3.3 Investigating the effect of the mutation rate on the invasion speed

The invasion speeds found from numerical simulations where $\mu = 0.001$ are compared to the analytical predictions in the limit $\mu \to 0$ in Fig. 2.5. These two different measurements of the invasion speed can be seen to agree, suggesting that the mutation rate does not have a big effect on the speed observed. To quantify this effect I have analytically investigated whether the speed changes with different μ, by expanding Eqn. (2.9) to the lowest non-trivial order in μ. This is done to obtain a more accurate estimate of q^2. To do this I have let $q^2 = \alpha$, and have assumed, as I have previously, that the mutation rates are small but not necessarily the same, and so have substituted $\mu_e = e\mu$ and $\mu_d = d\mu$ into Eqn. (2.9). I then carry out a perturbation expansion, by substituting an expansion of the form

$$\alpha = \alpha_0 + \mu\alpha_1 + \mu^2\alpha_2 + \ldots,$$

into Eqn. (2.9) up to order μ.

Equations are then generated by equating coefficients of powers of μ on the left and right

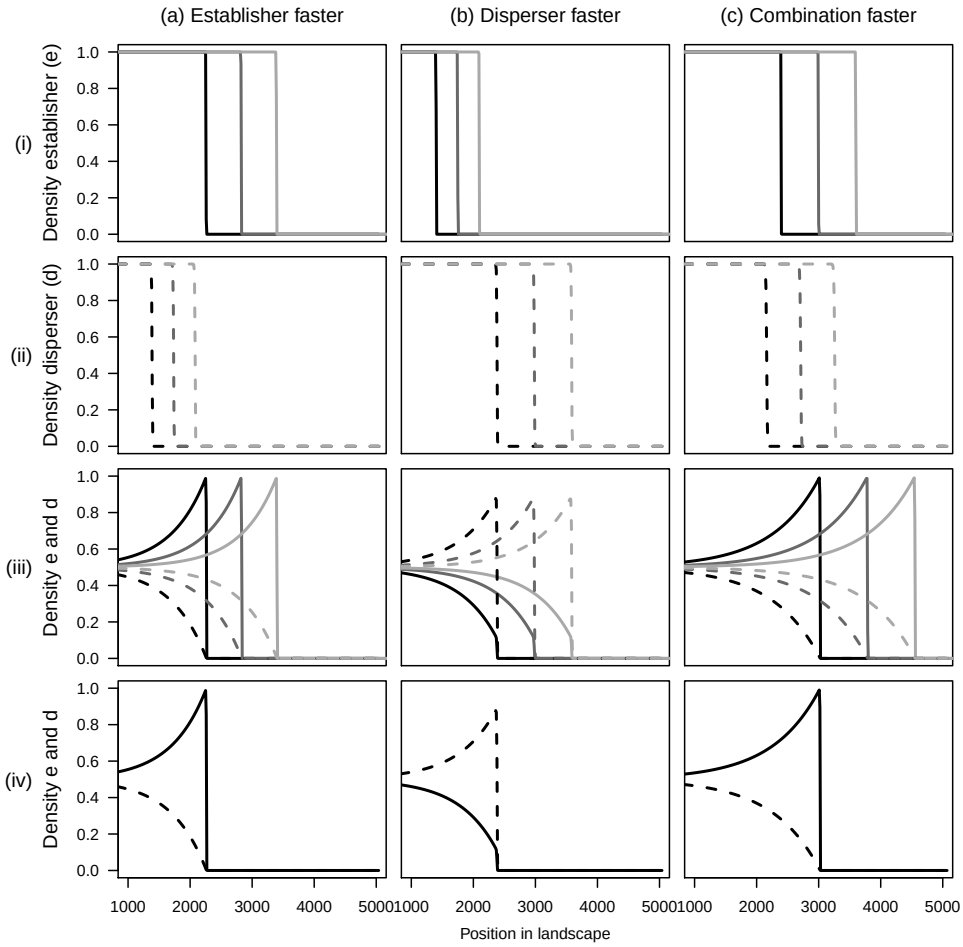

Figure 2.3: Invasion profiles of the establisher morph (solid line) and disperser morph (dashed line) when present in the landscape on their own (rows (i) and (ii)), and when mutation allows both to be present (row (iii)). Row (iv) shows the same data as row (iii), but the invasion waves are shifted by (speed) times (time) to illustrate that the wave maintains its shape as it travels. The simulations were initiated with the first 100 cells occupied by each phenotype at its equilibrium population density and the remaining cells unoccupied. The simulations were run on a lattice consisting of 8000 cells, using a space increment of 0.1. For all graphs each line represents the density profiles at a different time point, shown by the different shades of grey, with each time point 500 units apart. In column (a) the polymorphic invasion speed is the same as the monomorphic establisher speed; in column (b) the polymorphic invasion speed is the same as the monomorphic disperser speed, and in (c) the polymorphic invasion speed is faster than either monomorphic invasion. For all simulations K=1, μ=0.001, and in (a) r_e=0.8, r_d=0.2, D_d=0.6, D_e=0.4; (b) r_e=0.6, r_d=0.4, D_d=0.9, D_e=0.2; (c) r_e=1.1, r_d=0.2, D_d=1.5, D_e=0.3.

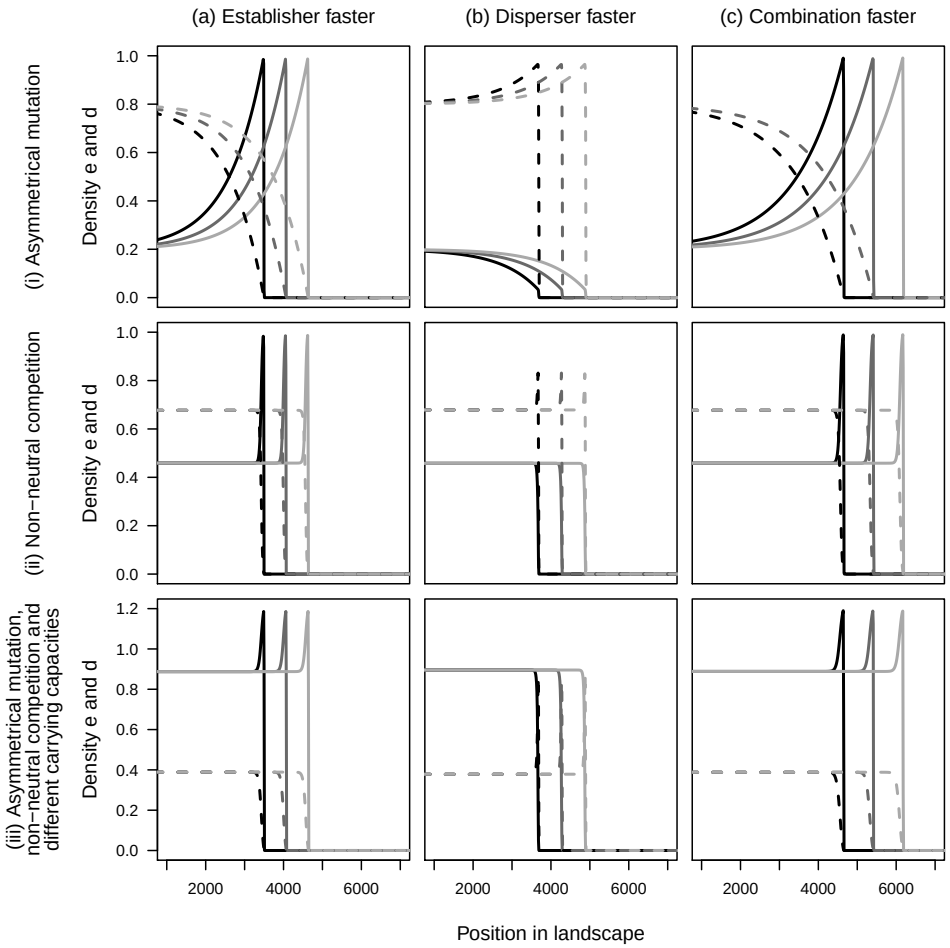

Figure 2.4: Invasion profiles showing that invasion speeds are the same when (i) morphs have asymmetrical mutation rates, (ii) there is non-neutral competition and (iii) morphs have asymmetrical mutation, non-neutral competition and different carrying capacities. The simulations were initiated with the first 100 cells occupied by each phenotype at its equilibrium population density and the remaining cells unoccupied. The simulations were run on a lattice consisting of 8000 cells, using a space increment of 0.1. For all graphs each line represents the density profiles at a different time point, shown by the different shades of grey, with each time point 500 units apart. In column (a) the polymorphic invasion speed is the same as the monomorphic establisher speed; in column (b) the polymorphic invasion speed is the same as the monomorphic disperser speed, and in (c) the polymorphic invasion speed is faster than either monomorphic invasion. For all the simulations the parameters used are the same as in Fig. 2.3 apart from in (i) have that μ_e=0.001 and μ_d=0.00025, in (ii) α_{de}=0.8, α_{ed}=0.7, where α is the competition coefficient, and in (iii) have both the parameters used in (i) and (ii) and additionally K_e=1.2 and K_d=1.

hand sides of the equation. First coefficients of μ^0 are found to be given by:

$$\begin{aligned}\mu^0: \quad & (D_d-D_e)^2(D_d+D_e)^2\alpha_0^4 - 2(D_d-D_e)(D_d+D_e)^2(r_e-r_d)\alpha_0^3 \\ & - 2(D_d-D_e)^2(D_d+D_e)(r_e+r_d)\alpha_0^3 + (D_d-D_e)^2(r_e+r_d)^2\alpha_0^2 \\ & + 4(D_d-D_e)(D_d+D_e)(r_e-r_d)(r_e+r_d)\alpha_0^2 + (D_d+D_e)^2(r_e-r_d)^2\alpha_0^2 \\ & - 2(D_d-D_e)(r_e-r_d)(r_e+r_d)^2\alpha_0 - 2(D_d+D_e)(r_e-r_d)^2(r_e+r_d)\alpha_0 \\ & + (r_e-r_d)^2(r_e+r_d)^2 \\ & = (D_d-D_e)^4\alpha_0^4 - 2(D_d-D_e)^2(r_e-r_d)^2\alpha_0^2 + (r_e-r_d)^4.\end{aligned}$$

This can be factorised to give:

$$\begin{aligned}& \Big(r_e-r_d-\alpha_0(D_d-D_e)\Big)^2\Big(r_e+r_d-\alpha_0(D_d+D_e)\Big)^2 \\ & = \Big(\big(r_e-r_d-\alpha_0(D_d-D_e)\big)\big(r_e-r_d+\alpha_0(D_d-D_e)\big)\Big)^2.\end{aligned}$$

Taking the square root of both sides of this equation gives Eqn. (2.10) with $\alpha_0 = q^2$. This therefore gives the same three values of q^2 as when I took the limits $\mu_e \to 0$ and $\mu_d \to 0$.

Now equating terms of order μ on the left and right hand sides of the equation gives:

$$\begin{aligned}\mu: \quad & \alpha_1\Big(2(D_d-D_e)^2(D_d+D_e)^2\alpha_0^3 - 3(D_d-D_e)(D_d+D_e)^2(r_e-r_d)\alpha_0^2 \\ & + 3(D_d-D_e)^2(D_d+D_e)(r_e+r_d)\alpha_0^2 + (D_d-D_e)^2(r_e+r_d)^2\alpha_0 \\ & + 4(D_d-D_e)(D_d+D_e)(r_e+r_d)(r_e-r_d)\alpha_0 + (D_d+D_e)^2(r_e-r_d)^2\alpha_0 \\ & - (D_d-D_e)(r_e-r_d)(r_e+r_d)^2 - (D_d+D_e)(r_e-r_d)^2(r_e+r_d)\Big) \\ & + (D_d-D_e)^2(D_d+D_e)(d+e)\alpha_0^3 - (D_d-D_e)(D_d+D_e)^2(d-e)\alpha_0^3 \\ & + 2(D_d-D_e)(D_d+D_e)(r_e-r_d)(d+e)\alpha_0^2 - (D_d-D_e)^2(r_e+r_d)(d+e)\alpha_0^2 \\ & + 2(D_d-D_e)(D_d+D_e)(r_e+r_d)(d-e)\alpha_0^2 + (D_d+D_e)^2(r_e-r_d)(d-e)\alpha_0^2 \\ & + 2(D_d-D_e)(r_e-r_d)(r_e+r_d)(d+e)\alpha_0 - (D_d-D_e)(r_e+r_d)^2(d-e)\alpha_0 \\ & - 2(D_d+D_e)(r_e-r_d)(r_e+r_d)(d-e)\alpha_0 + (D_d+D_e)(r_e-r_d)^2(d+e)\alpha_0 \\ & - (r_e-r_d)^2(r_e+r_d)(d+e) + (r_e-r_d)(r_e+r_d)^2(d-e) \\ & = 2(D_d-D_e)^4\alpha_0^3\alpha_1 - (D_d-D_e)^2(r_e-r_d)(d-e)\alpha_0^2 \\ & - 2(D_d-D_e)^2(r_e-r_d)^2\alpha_0\alpha_1 + (r_e-r_d)^3(d-e).\end{aligned}$$

To calculate α_1, each α_0 needs to be substituted into this equation. Substituting

$\alpha_0 = \frac{r_e - r_d}{D_d - D_e}$ into this equation, gives:

$$3(D_d + D_e)(r_e + r_d)\alpha_1 + (r_e - r_d)\frac{2(D_d + D_e)(d + e) + (D_d - D_e)(d - e)}{D_d - D_e} = 0,$$

giving:

$$\alpha_1 = -\frac{(r_e - r_d)(3dD_d + dD_e + eD_d + 3eD_e)}{3(D_d - D_e)(D_d + D_e)(r_e + r_d)}.$$

Since I am assuming that $D_d > D_e$ and $r_e > r_d$, this means that α_1 will always be negative. Therefore, assuming that $q^2 = \alpha = \alpha_0 + \mu\alpha_1$, means that the addition of μ will always make q^2 smaller, and hence the invasion speed v slower.

Substituting $\alpha_0 = \frac{r_e}{D_e}$ and $\alpha_0 = \frac{r_d}{D_d}$ into this equation give long equations for α_1, and so to reduce the number of parameters I make the additional substitutions $e = xd$, $r_e = rr_d$ and $D_d = DD_e$, where $x > 0$, $r > 1$ and $D > 1$. Then for $\alpha_0 = \frac{r_e}{D_e}$, I get:

$$\alpha_1 = \frac{-d}{2D_e}\left(\frac{r^3(3D^2 + 2D - 2) - r^2(3D^2 + 2D + 4) + 9r - 3}{r^3(4D^3 - 7D^2 + D + 3) + r^2(3D^3 - 2D^2 - 3D - 1) + r(4 - D) - 1}\right.$$
$$\left. + \frac{x\big(r^3(2D^3 - 3D^2 + 6D - 6) + r^2(-3D^2 + 2D + 4) - r(2D + 1) + 1\big)}{r^3(4D^3 - 7D^2 + D + 3) + r^2(3D^3 - 2D^2 - 3D - 1) + r(4 - D) - 1}\right), \quad (2.16)$$

and for $\alpha_0 = \frac{r_d}{D_d}$, I get:

$$\alpha_1 = \frac{-d}{2DD_e}\left(\frac{-D^3r^3 + r^2(D^3 + 2D^2) + r(-4D^3 - 2D^2 + 3D) + 6D^3 - 6D^2 + 3D - 2}{D^3r^3 + r^2(-4D^3 + D^2) + r(D^3 + 3D^2 + 2D - 3) - 3D^3 - D^2 + 7D - 4}\right.$$
$$\left. + \frac{x\big(3D^3r^3 - 9D^3r^2 + r(4D^3 + 2D^2 + 3D) + 2D^3 - 2D^2 - 3D\big)}{D^3r^3 + r^2(-4D^3 + D^2) + r(D^3 + 3D^2 + 2D - 3) - 3D^3 - D^2 + 7D - 4}\right). \quad (2.17)$$

It is not obvious just from looking at these two equations whether α_1 will be negative or positive, and so I numerically investigated the signs of these two equations by drawing contour plots of the terms inside the brackets of each equation. This revealed that in the region of parameter space that I am interested in, so below curve (2.15) for Eqn (2.16), and below curve (2.14) for Eqn. (2.17), these equations for α_1 will always be negative. This shows that the addition of mutation between morphs will always result in slower speeds than predicted using Eqns. (2.11-2.13).

I have also numerically solved Eqn. 2.9 for $\mu = 0.001$ for the case where $q^2 = \frac{r_e - r_d}{D_d - D_e}$, which is shown in Fig. 2.5. It can be seen from this figure that even when the mutation rate is $\frac{1}{100}$, which is larger than would be realistically expected in most organisms (Falconer,

1989), the change in speeds when mutation between morphs is included is minuscule. This suggests that using Eqns. (2.11-2.13) to calculate the invasion speeds give a very good approximation.

2.4 Discussion

This study investigated the effect that the presence of two dispersal phenotypes has on the invasion speed of a species. I found that if there were differences in both the morphs' establishment and dispersal abilities then the invasion speed can be faster than the speed of either morph on its own. This effect becomes significant when both traits differ by a factor of two or more, and for reasonable parameter values the combined invasion speed can be up to twice as fast as either monomorphic speed. It was found that this effect persists when the mutation rate between the morphs tends to zero, which is surprising because in this case each morph has a minuscule effect on the other morph in the leading edge of the invasion front. This effect has been shown to be robust to the other parameters in the system, such as non-neutral interactions and differences in mutation rates.

Mathematically, there is no reason to expect that the invasion speed of a community of phenotypes should follow the speed of any particular phenotype. It has been shown that in both cooperative and competitive two-species models there are conditions which allow both species to invade at the same speed (Lewis et al., 2002; Weinberger et al., 2002). Weinberger et al. (2007) have also observed that in strongly cooperative systems anomalous spreading speeds can evolve. They found that in a model of a two-allele, one-gene-locus diploid species, the presence of both homozygotes and heterozygotes results in the homozygotes spreading at a faster speed than they do in the absence of the heterozygotes, but which is also faster than the speed that the heterozygotes spread at (Weinberger et al., 2007). However, this anomalous spreading speed was observed in a system where there is strong cooperation between phenotypes. In this model I found that anomalous speeds persist when mutation between morphs is vanishingly small, and so have shown that faster speeds can be observed in competing systems where there is effectively no cooperation.

In this study, the analytical method of van Saarloos (2003) gave values for the invasion speed that agreed with the numerical predictions. This model is quite generic and so it is expected that the phenomenon of anomalous invasion speeds will occur in a wide variety of systems. This is because the method used to predict the invasion speed is

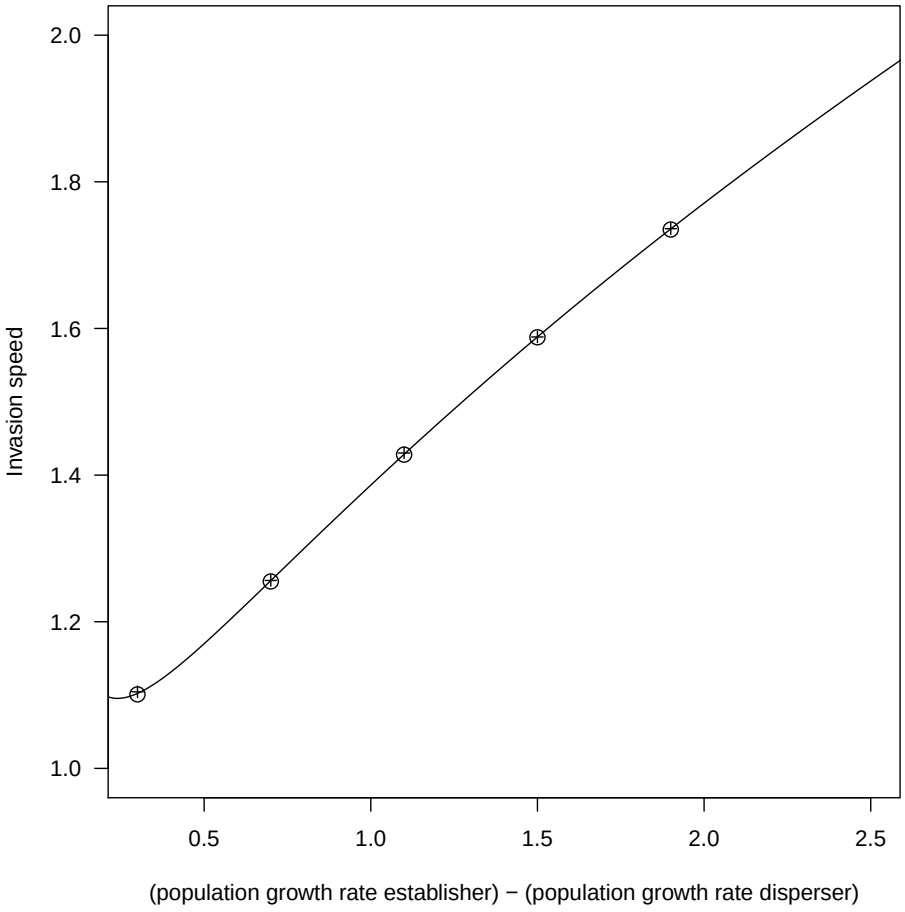

Figure 2.5: Comparison of analytical and numerical predictions of the invasion speed when polymorphism results in faster invasions than either single morph. The curve represents the analytical predictions of the invasion speed in the limit $\mu \to 0$ given by Eqn. (2.13). The crosses represent numerical predictions calculated numerically using Eqn. (2.9), and the circles the numerically integrated predictions, when $\mu = 0.001$ using a space increment of 0.1. Parameter values used were $r_d = 0.3$, $D_d = 1$, $D_e = 0.2$ and $K = 1$. For the analytical prediction r_e was varied and for the numerical simulations the values of r_e used were 0.6, 1, 1.4, 1.8 and 2.2.

appropriate for any model with 'pulled' wavefronts (van Saarloos, 2003), and its results depend solely on the linearised behaviour of the partial differential equation close to the unstable equilibrium. Clearly, there will be many different systems of reaction-diffusion equations which have the same linearised form at low density, so it would be expected that polymorphism should affect invasion speeds in a very wide class of problems. For instance, in metapopulations the colonisation process is local but depends on the availability of habitat (Jansen and Vitalis, 2007), which in a spatial model would lead to a nonlinear diffusion term (Ovaskainen and Cornell, 2006). I have studied numerically and analytically invasive waves for two competing morphs in a spatial metapopulation system, and since the nonlinearity in the diffusion term is unimportant at low densities, the same invasion speeds as in the population model described in this chapter were found.

Having observed the faster invasion speed I was interested in whether the invasion is occurring at the speed of a morph that is both a better disperser and better establisher. Comparing the polymorphic speed v_p with v_b, a 'best of both worlds' morph, where $v_b = 2\sqrt{r_e D_d}$, it was found that $\frac{1}{2}v_b < v_p < v_b$. The polymorphic wave speed is therefore always slower than the 'best of both worlds' case. When anomalous invasion speeds occur the species does benefit from having both good dispersers and good establishers present at the front of the wave. However, the faster speeds are observed in the limit where mutation tends to zero, and so the faster speeds are not occurring as a result of mutation of morphs into each other at the invasion front. Mutation is required for the travelling wave of invasion to occur, however, another mechanism other than mutation that allowed both morphs to travel at the same speed would give the same results. More complex dynamics are therefore resulting in anomalous invasion speeds.

These results suggest that polymorphism is an important factor that needs to be considered when investigating species' invasions, and so speeds should not be predicted by only looking at the fastest single morph. In terms of the invasion of exotic species this may be of concern if introduced species spread faster than expected threatening native species. However, for species shifting their range as a result of climate change this may be encouraging as it may mean that more species than previously thought will be able to keep up with the rate of change.

Species may experience these faster range expansions as a result of both morphological and behavioural differences in phenotype. For example, many flowering plants exhibit seed polymorphism where large seeds remain near the site of the parent plant and small seeds are wind dispersed to sites further away (Sorensen, 1978). These morphological

differences may allow faster range expansions to occur. Species may also have different dispersal strategies, such as the western bluebird, *Sialia mexicana*, where aggressive males are more dispersive than non-aggressive males. It has been found that these two phenotypes are maintained in populations as each are advantageous in different stages of range expansions (Duckworth, 2008).

In insects that have wing polymorphism, where one morph is capable of flight and the other is not, trade-offs between dispersal ability and reproductive ability are observed (reviewed in Zera and Denno, 1997). The anomalous invasion speeds reported in this chapter require both traits to differ by a factor of two, and so anomalous invasion speeds would be expected if the growth rate of the flightless morph is more than twice that of the winged morph, but otherwise the invasion would follow the speed of the disperser morph.

I have modelled the invasion here of a species where dispersal ability trades-off with population growth rate. Although in some species, such as the speckled wood butterfly, individuals with increased dispersal ability are less fecund and hence will have slower population growth rates (Hughes et al., 2003), this trade-off is not always observed. It has been suggested that because dispersal and reproductive rate are complex traits it is unlikely that they will directly trade-off against one another, and that either may actually trade-off against other traits (Phillips et al., 2010b). For example, Burton et al. (2010) showed that dispersal and reproduction can trade-off with competitive ability when invading into a landscape occupied by another species. If a competitor is present in the expanding range it may therefore be that the trade-off required for faster invasions may not occur, as investing more in competitive ability is more important for a species to be able to expand its range. The relationship between dispersal and reproduction has been found in some species to be positive, with for example, more dispersive cane toads, *Bufo marinus*, having faster growth rates (Phillips, 2009), and more dispersive Glanville fritillary butterflies, *Melitaea cinxia*, investing more in reproduction (Hanski et al., 2006; Saastamoinen, 2007). The result of faster range expansions found using this model may not be transferable to species such as these where there is no trade-off between dispersal and establishment.

A general theory emerging from the literature is that during range expansions there is evolution towards increased dispersal (Burton et al., 2010; Hughes et al., 2007; Kubisch et al., 2010; Travis et al., 2009, 2010). There is also a view that spatial sorting can lead to increased dispersal at the range edge, through fast-dispersing individuals dispersing further and then random mating at the range edge of these individuals (Shine et al., 2011).

While these results agree that having good dispersers at the invasion front allows the population to invade faster, if there is a trade-off in dispersal and establishment ability it is also important to have good establishers present. Indeed under some parameter conditions, for example see Fig. 2.3c(iii), these results suggest that for faster speeds to occur the density of good establishers at the invasion front is higher than the density of good dispersers. During range expansions, these results suggest that establishment ability (i.e. local population growth rate) is just as important as dispersal ability, and that there will be selection for both to evolve.

These conclusions were made based on the results of a simple deterministic model in which the landscape was modelled as one-dimensional and continuous. These simplifying assumptions were made to make the model analytically tractable but in doing so have made the model less realistic. Modelling using a simple deterministic approach can sometimes give results that are an artefact of the model. Carrying out simulations of a stochastic version of the model will help to determine if these results are robust, and will give predictions for when these results are expected to occur. Stochastic simulations may also help to further explain why faster invasions occur when there are differences between the two phenotypes, and so this will be my next step in this research.

Species expanding their range as a result of climate change are likely to invade into landscapes where the habitat is not continuous, and where there may be patches that are unevenly spaced and of different quality (Travis and Dytham, 2002). Future work investigating what impact this may have on species' invasions may help more accurate predictions for the rate of range expansions as a result of climate change to be made. Also explicitly modelling a shifting climate would improve understanding of the effect that the loss of suitable habitat at the rear of a species' range has on invasions.

The structure of the landscape in terms of availability of habitat and its spatial distribution is also an important factor that needs to be considered for species expanding their ranges. The evolution of dispersal distances and dispersal polymorphism have been found to be affected by landscape structure (Bonte et al., 2010). It has been predicted that as a result of species having dispersal polymorphism there may be geographic variation in range expansion speeds (Bonte et al., 2010). The results found in this chapter implying that dispersal polymorphism can lead to faster range expansions may lead to even further geographic differences.

In this model I have assumed perfect heritability of the dispersal trait, however, there is increasing evidence that species responses to climate change can be plastic (reviewed

by Gienapp et al., 2008). Indeed it has been shown that spatial and temporal variation in the environment can result in selection of different dispersal strategies as a result of phenotypic plasticity (McPeek and Holt, 1992). If plasticity could result in differences in morphs' establishment and dispersal abilities then this could aid the range expansion of species that are not genetically polymorphic. This could result in increased invasion speeds for more species than would be predicted by the present model.

I have shown that the presence of two phenotypes can lead to unexpected results for the speed of biological invasions. Not only can invasion speeds adapt due to evolutionary selection of more invasive phenotypes, but polymorphism itself plays a role in determining invasion speeds. It is hoped that these results motivate further research into understanding the importance of dispersal polymorphism in determining shifting species' ranges.

3. Are anomalous invasion speeds robust to demographic stochasticity?

3.1 Introduction

The range expansion of species either as a result of climate change or from the introduction of exotic species has important consequences for conservation management. There is increasing evidence that species are shifting their distributions as a result of climate change (Chen et al., 2011; Hickling et al., 2006; Parmesan and Yohe, 2003; Root et al., 2003), but predicting whether these species can keep up with the rate of change, or whether, and by how much, they lag behind is a challenge. The introduction of exotic species that then spread (Sakai et al., 2001), and especially those that become pests (Ziska et al., 2011), can have important consequences for biodiversity (Gurevitch and Padilla, 2004). Being able to predict the rate at which they spread is key for minimising the impact these species have on ecosystems.

The rate of spread of species' invasions has long been investigated using simple deterministic models (Fisher, 1937; Skellam, 1951). Since these early models more complex techniques have been developed and used to model the spread of species. These include new analytical methods such as integrodifference equations, and more computational methods such as individual-based models (IBMs) which often incorporate a greater number of parameters and include stochasticity (see Hastings et al., 2005; Jongejans et al., 2008, for reviews of these developments). Deterministic models are often used because they are elegant and give simple predictions. However, they do not explicitly model individuals or consider random demographic events, and so stochastic models are expected to give more realistic results which can be more useful when making decisions for conservation management.

Predicting the speed of invasions of polymorphic species using simple deterministic models has revealed that anomalous speeds, where the population invades faster than either single phenotype, may be observed (Elliott and Cornell, 2012; Weinberger et al., 2007). In Chapter 2 it was found that if there are differences in the dispersal and establishment abilities of two morphs in a population, and there is mutation between morphs, then faster rates of spread can occur than if there is only one morph present.

Surprisingly it was found that this effect persists when the mutation rate between morphs tends to zero (Elliott and Cornell, 2012). The reason behind this is unclear because the invasion speed is determined by what happens at low density, and in this limit the number of individuals of the minority morph tends to zero. The question therefore arises as to whether anomalous speeds occur as an artefact of the model, or if they are still present in more complex models where there is the possibility that at low density only one morph can be present at the invasion front. In this chapter a stochastic version of the model will be developed in the hope that it will shed some light on the answer to this question.

The use of deterministic and stochastic models for predicting the rate of spread of species has highlighted some important differences. In density independent models demographic stochasticity does not generally slow invasions (Kot et al., 2004). This was also found by Mollison (1991), who showed that linear stochastic models often give the same result as deterministic models, and that speeds predicted using these provide an upper bound for the more realistic nonlinear stochastic case. Incorporating demographic stochasticity into density dependent models has provided further insight into whether stochasticity affects invasion speeds (Clark et al., 2001; Lewis, 2000; Lewis and Pacala, 2000; Snyder, 2003). These models reach varying conclusions with Snyder (2003) finding that the addition of demographic stochasticity results in marginally slower invasions, and Clark et al. (2001) finding that adding stochasticity can turn accelerating invasions into constant speed invasions. Kot et al. (2004) also demonstrated that in contrast to the density independent case, the combined effect of stochasticity and density dependence can slow invasions.

Travis et al. (2011) have also highlighted the importance of using both deterministic and stochastic modelling approaches when predicting invasion speeds. They found that although both models produced similar trends, their analytical model predicted significantly higher speeds than their stochastic IBM (Travis et al., 2011). They found that the greater the amount of stochasticity incorporated into the model, through increasing the number of age classes, the greater the difference in the speed predicted by the two models. Their results revealed that looking at both stochastic and deterministic models can help to more accurately predict the speed at which a species expands its range.

A general result appearing in the literature is that incorporating demographic stochasticity into density dependent models leads to slower invasion speeds. Based on these results (Kot et al., 2004; Snyder, 2003; Travis et al., 2011) it may be expected that a stochastic version of the dispersal polymorphism model developed in Chapter 2 has slower invasion speeds than the deterministic version. If this is the case then it may be that anomalous

speeds do not arise in stochastic models. In this chapter I investigate whether anomalous speeds are preserved in a model incorporating demographic stochasticity using a discrete time and space stochastic model. The model follows Chapter 2 so that there is a polymorphic population with morphs that differ in their dispersal abilities. Numerical simulations of this model are carried out in order to determine the invasion speed of the population and to find the conditions (if any) under which anomalous speeds are produced.

3.2 Model

3.2.1 Derivation of the model

The model used is based on the work in Chapter 2 which looks at the invasion of a species that has two dispersal phenotypes. This model uses partial differential equations (PDEs) which were used because they are elegant and give simple results. In this chapter the spatially-explicit general Lotka-Volterra model is adapted so that it is now discrete in time and space. This is done because the stochastic equivalent of PDEs are complex and it is more straightforward to make a link between deterministic and stochastic models that are discrete rather than continuous. I will therefore first develop a discrete time and space deterministic model, and then compare the results of this model to a stochastic discrete time and space version.

The model has the same two phenotypes with mutation between morphs as in the model in Chapter 2. The phenotypes differ in their dispersal and establishment abilities in the following way. There is:

- an establisher morph, e, that after establishment has a higher growth rate but is a poorer disperser; and
- a disperser morph, d, that has a lower growth rate after establishment but is a better disperser.

The model simulates the invasion of these two morphs with discrete generations. Population density of the species is denoted by N_i with $i \in \{e, d\}$ representing density of each morph. Population dynamics and dispersal then occur in discrete steps, so that in each time step the order of events occurs as follows. First a fraction b of each morph reproduces and produces offspring, with a fraction μ of these offspring being of the other

phenotype. This gives the number of individuals of morph $i \neq j$ at time t and position x after recruitment to be

$$B_i(t,x) = (1+b)N_i(t,x) + \mu b(N_j(t,x) - N_i(t,x)). \tag{3.1}$$

A fraction of each morph then dies. A Ricker-like density dependence is assumed, which gives the survival probability of morph i to be

$$P_i = \exp\left[-m_i^0 - m_i^1(B_i(t,x) + B_j(t,x))\right]. \tag{3.2}$$

The number of individuals of morph i after the mortality step is then given by

$$M_i(t,x) = P_i B_i(t,x). \tag{3.3}$$

Density dependence was chosen to act on mortality rather than birth rate because it makes the calculations simpler, and it is expected that qualitatively similar results would be obtained if density dependence acted on birth. Finally a fraction D_i of each morph disperses, so that the number of individuals of morph i that disperse is given by

$$\tilde{N}_i(t,x) = D_i M_i(t,x). \tag{3.4}$$

In the 1D case each morph disperses with equal probability to the left and right, and in the 2D case with equal probability to the 8 neighbouring cells. This gives two discrete time and space equations that represent the population dynamics and dispersal of a polymorphic population. In 1D the iteration equation for morph i is therefore

$$N_i(t+1,x) = M_i(t,x) - \tilde{N}_i(t,x) + \frac{1}{2}\tilde{N}_i(t,x+1) + \frac{1}{2}\tilde{N}_i(t,x-1). \tag{3.5}$$

3.2.2 Reparameterisation of the model

I reparameterise this model so that the parameters can be related to the continuous time model in Chapter 2. This is so that the results of the two models can be more easily compared, and to reduce the number of parameters that need to be varied in the discrete model. To do this I first look at the non-spatial single morph model which is given by:

$$N_i(t+1) = (1+b)N_i(t)\exp(-m_i^0 - m_i^1(1+b)N_i(t)).$$

For the purpose of this model I want the carrying capacity K to be fixed by the equilibrium population density, and so calculate the equilibrium density N_i^* by setting $N_i(t+1) = N(t)$. This gives the equilibrium to be $N_i^* = \frac{\log(1+b)-m_i^0}{m_i^1(1+b)}$ and so I then set $K = N_i^*$.

The nonspatial version of the continuous model in Chapter 2 is given by $\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K}\right)$. To relate the population growth rate term to the parameters in the discrete model it is assumed that when N_i is small there is exponential growth in one time step. It can therefore be assumed that $N_i << K$, which gives $N_t = N_0 e^{r_i t}$, where N_0 is the initial population size and t is time. In the discrete model assuming $N_i << K$ gives $N_t = RtN_0$ where $R = (1+b)e^{-m_i^0}$. The continuous and discrete models can therefore be related by $R = e^{r_i}$, which gives $r_i = \log(1+b) - m_i^0$.

This reparameterisation gives $r_i = log(1+b) - m_i^0$ and $K = \frac{\log(1+b)-m_i^0}{m_i^1(1+b)}$ where r_i is the population growth rate and K the carrying capacity. In the full spatial model the parameter D_i is defined in the same way as in Chapter 2, and so parameter values used for the dispersal rate in the two models are directly comparable. Simulations are then carried out with different values of r_i and D_i to determine the effect each morphs' dispersal and establishment abilities have on the invasion speed.

3.2.3 Assumptions of the stochastic model

The stochastic version of the model is an individual-based model that uses the same mean birth, death and dispersal rates as in the deterministic model. However, there are now random demographic processes, and the number of individuals $N_i(t,x)$ of morph i at site x and time t is an integer. In the recruitment step, I assume that each individual independently produces a Poisson-distributed number of offspring with mean b. Offspring are assumed to have the same phenotype as their parent with probability $1-\mu$, and the other phenotype with probability μ. It is then assumed that each individual survives (statistically independently) with probability given by P_i in Eqn. (3.2). Each individual then independently chooses to disperse with probability D_i. If an individual disperses it moves with equal probability to a randomly chosen neighbouring site, and if not remains at the same site. Since the sum of Poisson-distributed random variables also has a Poisson distribution, and the sum of Bernoulli random numbers has a binomial distribution (Derman et al., 1973), these individual-based processes can be implemented in the model by generating Poisson-distributed pseudorandom numbers with mean given by $B_i(t,x) - N_i(t,x)$ in Eqn. (3.1) for the total number of births of each morph at each site, and using binomial distributed pseudorandom variables to generate the total number of

individuals of each morph surviving (using probability P_i from Eqn. (3.2)) and dispersing (using probability D_i) at each site. This is formally equivalent to an individual-based model, but much more computationally efficient than generating separate pseudorandom numbers for each individual.

In the stochastic model I am interested in the effect that the carrying capacity of the population, K, has on the invasion speed. It is expected that the stochastic model will be most similar to the deterministic model at high carrying capacities, and that when the carrying capacity is small stochasticity will have a bigger effect on the invasion speed. This is because the population density at the invasion front, which is where the invasion speed is determined (Snyder, 2003), will be lowest in this case so demographic fluctuations will have a bigger effect. Simulations were therefore run with the carrying capacity K ranging from $K = 100$ to $K = 10^{14}$ whilst keeping the other parameters constant, as a way of looking at how stochasticity affects the invasion speed.

In the stochastic case I am also interested in the effect that the mutation rate, μ, has on the invasion speed. This is because mutation between morphs allows both morphs to be present at the invasion front, and so the size of the mutation rate will influence the numbers of the minority morph present at the front. In Chapter 2 I found the surprising result that when the mutation rate is small, changing it has no effect on the invasion speed. I therefore vary the mutation rate in both models in the present chapter to see if the same results are observed. I predict that in contrast to the previous model changing the mutation rate will affect the speed, in particular that the smaller the mutation rate the bigger the effect that stochasticity will have on determining the invasion speed. This is because when the mutation rate is smaller there will be fewer individuals of the minority morph present at the front, and so fluctuations in population density are likely to have a bigger effect on whether both morphs will be present in the leading edge of the invasion wave.

3.2.4 Analysis

This model was analysed using both semi-analytical and numerical techniques. The method of front propagation (van Saarloos, 2003) was used to calculate the invasion speed for the deterministic model, this led to equations that were solved numerically. Simulations of the deterministic and stochastic models were then carried out in R (R Development Core Team, 2011), by simulating the invasion of an introduced species into a previously unoccupied landscape on a lattice that in the 1D case has dimensions

15000×1 and in the 2D case 15000×10.

The simulations were initialised with half the landscape occupied by the population at its stable equilibrium density and half the landscape unoccupied. Reflecting boundary conditions were used at the end of the lattices. These were implemented by assuming that if an individual disperses out of the landscape it is reflected back in, and remains in the cell where it began before the dispersal step. These simulations produced travelling waves which rapidly approached a constant speed as the invasion progressed. The simulations were run for 10 000 time steps which was sufficient to show that constant speed travelling waves were produced. The invasion speed was estimated by plotting the density profiles at different times and adjusting by eye the distance that the profiles needed to be displaced in order to lie on top of each other. To check that the simulations had reached a constant invasion speed these calculations were carried out at several time points.

Invasions were modelled on both a one and two-dimensional landscape because in contrast to the deterministic case where there is no difference between the results, the number of dimensions does matter in the stochastic case. In particular there are more fluctuations in 1D, and so if anomalous speeds are observed in this case the results can be considered to be robust. In addition carrying out simulations in 1D is computationally cheaper than in 2D, and so most of the results presented will be in 1D, with 2D simulations carried out to check that the same results are observed. Examples of the R code used in the simulations are given in Appendix B, an example of both morphs dispersing in a 1D landscape is given in Appendix B.1 and an example of a single morph dispersing in a 2D landscape is given in Appendix B.2.

3.3 Results: Deterministic model

Deterministic simulations were first carried out to investigate how the invasion speed varied with different parameter values. These results were then compared to those found for the PDE model in Chapter 2. These simulations were carried out by iterating equations (3.1-3.4) in R (R Development Core Team, 2011). Simulations were first carried out with each morph present in the landscape on its own and then with both morphs present. The simulations were carried out on both a 1 and 2D landscape, and as the same speeds were observed in both, only the results from the 1D simulations are presented here.

I observe the same phenomenon as was found in the PDE model in Chapter 2; i.e. that there are three possible wavespeeds (Fig. 3.1). These three invasion speeds occur as a

result of differences in the dispersal and establishment abilities of the two phenotypes. When the dispersal abilities of the disperser and establisher are similar but the population growth rate of the establisher is much higher than that of the disperser, the invasion occurs at the speed of the establisher (Fig. 3.1a). When the population growth rates of each morph are similar but the dispersal rate of the disperser is much higher than the dispersal rate of the establisher, the invasion occurs at the speed of the disperser (Fig. 3.1b). However, when there is a big difference between the two phenotypes in terms of both their dispersal and establishment abilities, the invasion occurs faster than either single morph (Fig. 3.1c).

The main difference observed between the continuous and discrete time models is that with comparable parameter values all of the invasion speeds are slightly slower in the discrete version. In particular the difference between the anomalous speed and the fastest single morph speed is not as big. For example, for the parameter values used in Fig. 3.1c, when both morphs are present the invasion speed is 1.24 times faster than the fastest single morph, however, in the PDE model for the same ratio of dispersal and establishment rates between morphs, the invasion speed is 1.38 times faster. This means that a population consisting of two morphs with big differences in their establishment and dispersal abilities does not have as significant an effect on the invasion speed. Nevertheless the invasion does still occur faster than would be predicted from a single morph's invasion speed.

3.3.1 Calculation of invasion speed

The front propagation method of van Saarloos (2003) was used to calculate the invasion speed of this polymorphic population. Here the results of this method are presented for the case where both morphs are present; the invasion speed was also calculated using this method for the single morph cases but these results are not presented as they are similar to the more complex two morph case. The general system of spatially uniform equations has two equilibria: an unstable extinction state where $(N_e, N_d) = (0, 0)$, and a stable coexistence state which I will denote by (N_e^*, N_d^*). The front propagation method involves linearising the equations about the unstable steady state, which gives:

$$\begin{aligned} N_e(t,x) =& e^{-m_e^0}[(1+b-\mu b)[(1-D_e)N_e(t,x) + \frac{1}{2}D_e(N_e(t,x+1)+N_e(t,x-1))] \\ &+ \mu b[(1-D_e)N_d(t,x) + \frac{1}{2}D_e(N_d(t,x+1)+N_d(t,x-1))]], \end{aligned} \tag{3.6}$$

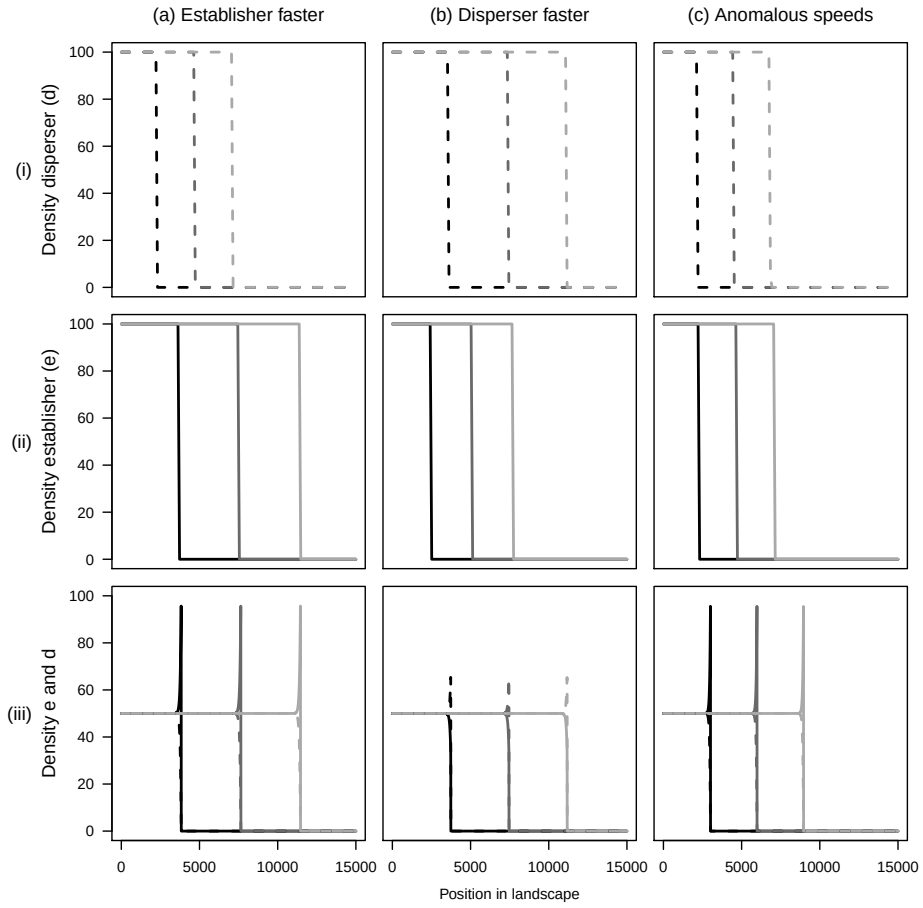

Figure 3.1: Invasion profiles of the disperser morph (dashed line) and establisher morph (solid line) when present in the landscape on their own (rows (i) and (ii)) and when mutation allows both to be present (row (iii)). The simulations were initiated with the first 100 cells occupied by each phenotype at its equilibrium population density and the remaining cells unoccupied. The simulations were run on a lattice consisting of 15000 cells. For all graphs each line represents the density profiles at a different time point, with each time point 500 units apart. In column (a) the polymorphic invasion speed is the same as the monomorphic establisher speed, in column (b) the polymorphic invasion speed is the same as the monomorphic disperser speed, and in (c) the polymorphic invasion speed is faster than either monomorphic invasion. For all simulations $K = 100$, $\mu = 0.01$, and in (a) $r_e = 0.8$, $r_d = 0.2$, $D_d = 0.6$, $D_e = 0.4$; (b) $r_e = 0.6$, $r_d = 0.4$, $D_d = 0.8$, $D_e = 0.2$; (c) $r_e = 0.8$, $r_d = 0.14$, $D_d = 0.8$, $D_e = 0.1$.

$$N_d(t,x) = e^{-m_d^0}[(1+b-\mu b)[(1-D_d)N_d(t,x) + \frac{1}{2}D_d(N_d(t,x+1)+N_d(t,x-1))] + \mu b[(1-D_d)N_e(t,x) + \frac{1}{2}D_d(N_e(t,x+1)+N_e(t,x-1))]]. \quad (3.7)$$

Here it is assumed that the speed calculated using the linear system (3.6) and (3.7) also applies to the nonlinear system (3.1-3.4). This linear speed is known to be a lower bound of the invasion speed but it is not always exact (Weinberger et al., 2002). These results are therefore compared to those found from the numerical simulations to check that this linear conjecture is valid.

Using these linearised equations, and following van Saarloos (2003), I substitute $\begin{pmatrix} N_e \\ N_d \end{pmatrix} \propto \begin{pmatrix} n_e \\ n_d \end{pmatrix} \exp(-i\omega(k)t + ikx)$, where $\omega(k)$ is the dispersion relation of Fourier modes of the linearised equations (3.6), (3.7), and k is the spatial wavenumber. This gives the equations:

$$[e^{-m_e^0}[(1+b-\mu b)(1-D_e+D_e\cos k)] - e^{-i\omega(k)}]n_e + e^{-m_e^0}\mu b(1-D_e+D_e\cos k)n_d = 0, \quad (3.8)$$

$$e^{-m_d^0}\mu b(1-D_d+D_d\cos k)n_e + [e^{-m_d^0}[(1+b-\mu b)(1-D_d+D_d\cos k)] - e^{-i\omega(k)}]n_d = 0. \quad (3.9)$$

This leads to an eigenvalue problem, with solutions

$$\omega(k) = i[log[(1+b-\mu b)[e^{-m_e^0}(1-D_e+D_e\cos k)+e^{-m_d^0}(1-D_d+D_d\cos k)]\pm R] - \log 2], \quad (3.10)$$

where $R^2 = [(1+b)^2-2\mu b(1+b)][e^{-m_e^0}(1-D_e+D_e\cos k)-e^{-m_d^0}(1-D_d+D_d\cos k)]^2 + \mu^2 b^2[e^{-m_e^0}(1-D_e+D_e\cos k)+e^{-m_d^0}(1-D_d+D_d\cos k)]^2$. This implies

$$\frac{d\omega(k)}{dk} = i\left(\frac{-(1+b-\mu b)(e^{-m_e^0}D_e\sin k + e^{-m_d^0}D_d\sin k) \pm \frac{dR}{dk}}{(1+b-\mu b)[e^{-m_e^0}(1-D_e+D_e\cos k)+e^{-m_d^0}(1-D_d+D_d\cos k)] \pm R}\right). \quad (3.11)$$

The wave speed is then calculated by finding k^*, where k^* is the linear spreading point (van Saarloos, 2003), such that

$$\frac{d\omega(k^*)}{dk^*} = \frac{\Im\omega(k^*)}{\Im k^*}, \quad (3.12)$$

where $\Im$ denotes the imaginary part. These equations represent a biological invasion so n_e and n_d cannot be negative, so I can deduce that k^* is purely imaginary. I can then assume $k^* = iq$ with q real, which I substitute into (3.12). The realised wavespeed is

obtained by finding the real solution q that corresponds to the largest speed $v = \frac{\Im\omega(iq)}{q}$ (van Saarloos, 2003). Substituting into Eqn. (3.12) gives an equation which cannot be solved analytically. I therefore solve this numerically and then calculate the invasion speed v using this value of q.

I find that this analytical method does give the same invasion speed that I found using the numerical simulations, as can be seen in Fig. 3.2. This suggests that the linear conjecture does give the correct wave speed for the full non-linear model and that the numerical simulations give accurate predictions.

3.4 Results: Stochastic model

I next investigated what effect demographic stochasticity has on the invasion speed. A version of the model that includes demographic stochasticity was set up in the way described in the Model section. The model was then simulated in the same way as the deterministic model, with simulations run on both a one and two dimensional landscape. I ran 10 replicates of each simulation, which proved to be a sufficient number as there was little variation between repeats, as can be seen by the small error bars in Fig. 3.3. For the stochastic simulations the effect that the carrying capacity of the population has on the invasion speed was investigated, as it is known that stochasticity has a bigger effect at low population densities. I was therefore also interested in whether there was a threshold population size for stochasticity to no longer have an effect on the invasion speed, and so larger populations than would be realistically expected were investigated to show that the stochastic model converged to the deterministic model.

It was found that for all parameter values having a small carrying capacity results in the invasion occurring slower than the deterministic prediction. Demographic stochasticity does therefore result in slower invasions as has previously been found (Snyder, 2003; Travis et al., 2011). However, I found that as the carrying capacity of the population increases, the invasion speed also increases approaching the deterministic speed (Fig. 3.3). The stochastic model does therefore behave like the deterministic model when the population is big enough.

The same pattern as in the deterministic model was found in that when the dispersal abilities of the disperser and establisher are similar, but the population growth rate of the establisher is much higher than that of the disperser, the invasion follows the speed of the establisher (Fig. 3.3a). Also when the population growth rates of each morph are

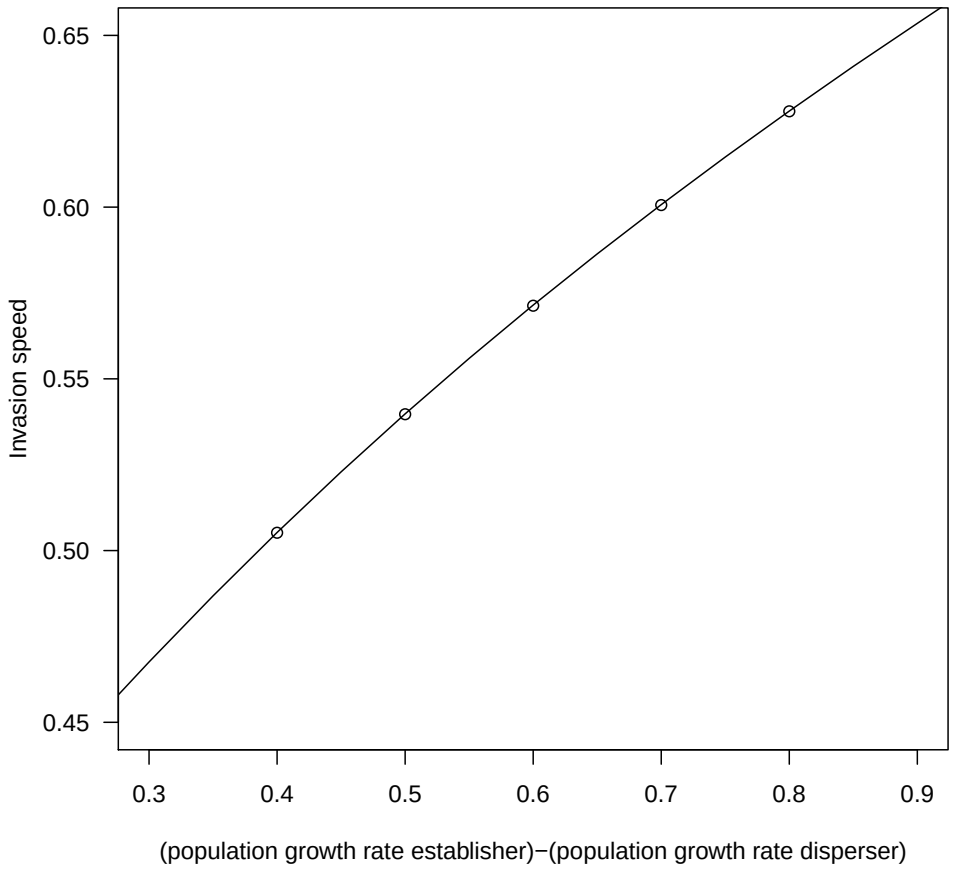

Figure 3.2: Comparison of analytical and numerical predictions of the invasion speed when polymorphism results in faster invasions than either single morph. The circles represent numerical predictions calculated from simulations, and the curve numerical predictions found using the van Saarloos (2003) method. Parameter values used were $r_d = 0.1$, $D_d = 0.8$, $D_e = 0.15$, $K = 100$, $\mu = 0.01$ and the values of r_e used for the numerical simulations were 0.5, 0.6, 0.7, 0.8 and 0.9.

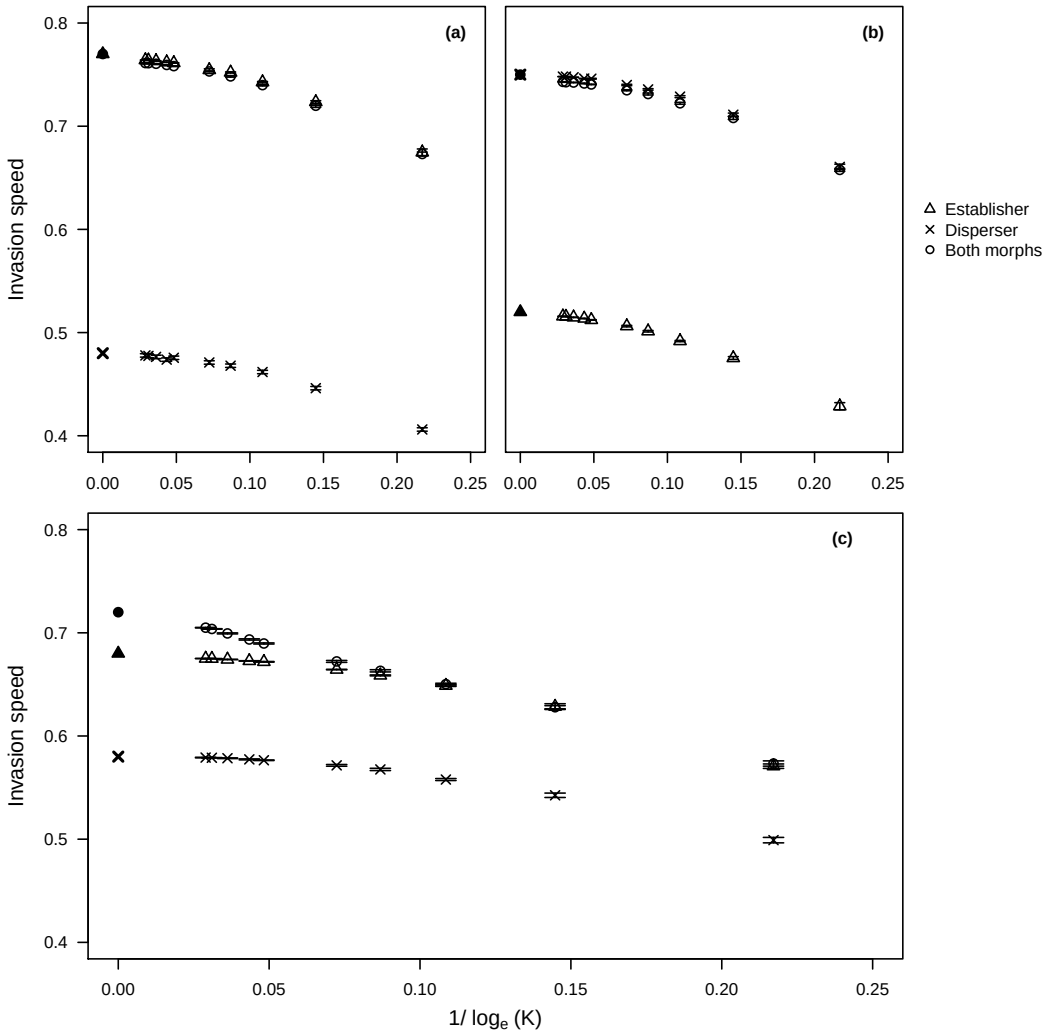

Figure 3.3: Comparison of stochastic and deterministic invasion speeds at different carrying capacities. The filled symbols represent the deterministic prediction and the empty symbols the stochastic predictions. The triangle represents the establisher morph's speed, the crosses the disperser morph's speed and the circles the invasion speed when both morphs are present. The error bars show 1 standard error of the mean. In (a) the polymorphic invasion speed is the same as the monomorphic establisher speed, in (b) the polymorphic invasion speed is the same as the monomorphic disperser speed, and in (c) the polymorphic invasion speed is faster than either monomorphic invasion at high K. Parameter values used in (a) and (b) are the same as in Fig. 3.1 (a) and (b), and in (c) the parameter values used were $r_e = 1$, $r_d = 0.2$, $D_d = 0.9$, $D_e = 0.2$ and $\mu = 0.01$ with K ranging from $K = 100$ to $K = 10^{14}$.

similar, but the dispersal rate of the disperser is much higher than the dispersal rate of the establisher, the invasion follows the speed of the disperser (Fig. 3.3b). In the case where there is a big difference between the two phenotypes in terms of both their dispersal and establishment abilities, I find that at the lower carrying capacities the invasion follows the speed of the faster morph. However, there is a threshold carrying capacity where the invasion starts to be faster than the monomorphic speed, and as the carrying capacity increases further this increases to approach the anomalous deterministic speed (Fig. 3.3c).

For simulations carried out in 2D it was found that the invasion speed evolved to follow the same three possible scenarios (Fig. 3.4). In this case the stochastic speed approaches the deterministic speed at lower carrying capacities than was found in 1D, and so behaves like the deterministic model at lower population densities. As these results were found to follow the same pattern as in 1D, the simulations for the remainder of this chapter were performed in 1D.

I investigated how the mutation rate affects the threshold value for anomalous invasion speeds to occur for the case observed in Fig. 3.3c. It was found that the higher the mutation rate, the lower the threshold carrying capacity is for anomalous invasion speeds to occur (Fig. 3.5). High mutation rates ($\mu = 0.05$ and $\mu = 0.1$) result in anomalous invasion speeds even when the carrying capacity is very low ($K = 100$). Smaller mutation rates ($\mu = 0.001$ – $\mu = 0.01$) do not result in anomalous invasion speeds until the carrying capacity is much higher. This is in contrast to both the continuous and discrete deterministic models where it was found that mutation rate had no effect on the invasion speed. This suggests that a higher mutation rate allows the morphs to keep up with each other better at the front of the invasion wave. A higher mutation rate therefore means that there are more of the morph that is at lower density present at the invasion front, which in this case is the disperser morph, and so there are more good dispersers along with the good establishers present at the front which results in faster invasions particularly when the carrying capacity is lower.

I then investigated whether the invasion speed changed if there was no longer a symmetrical mutation rate between morphs. I was interested in whether having more mutation into one morph than the other has an effect the invasion speed. For example, it may be predicted that if the mutation rate from the establisher morph into the disperser morph is higher, then there would be faster invasions as this would result in a higher number of dispersers present at the invasion front. However, this was not found to be the case, as Fig. 3.6 shows, the higher symmetrical mutation rate ($\mu = 0.01$) gives the fastest

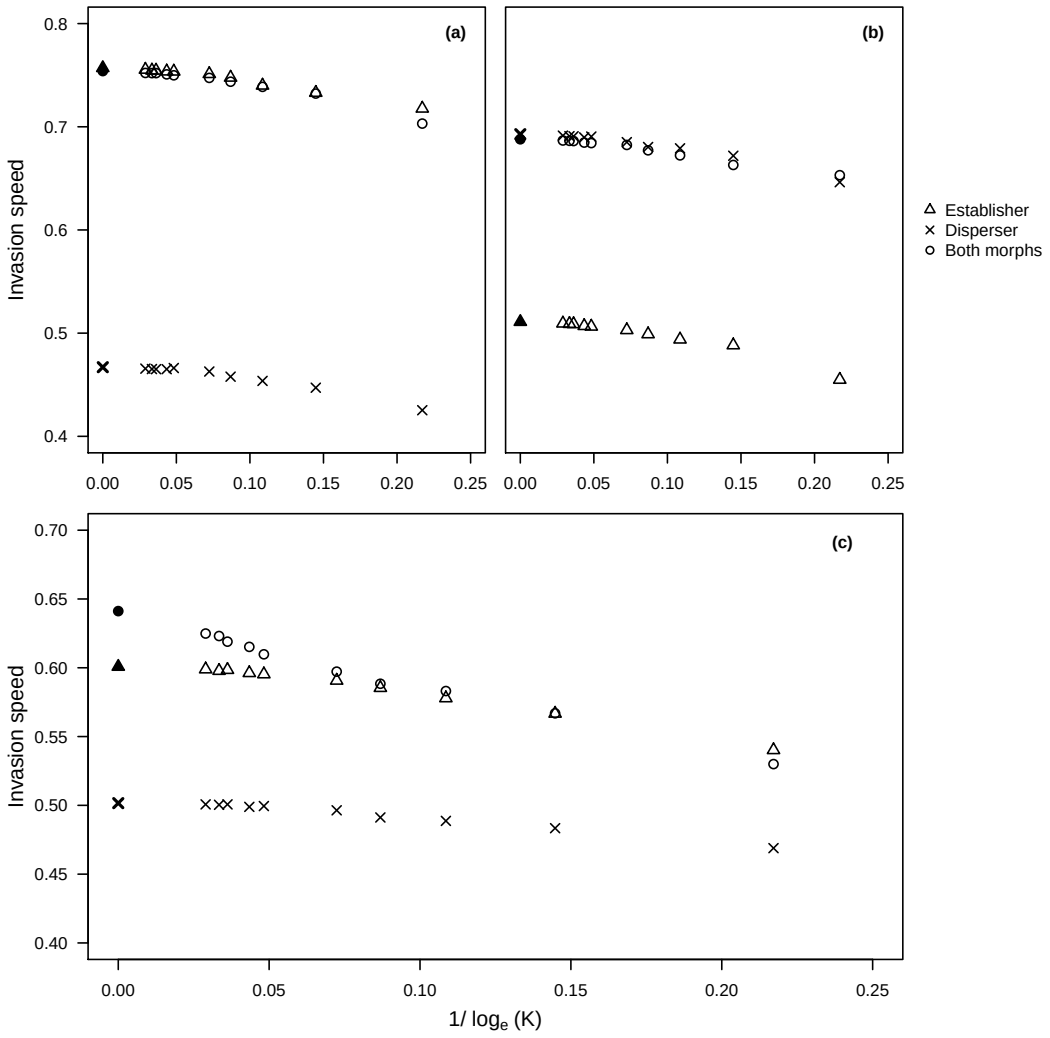

Figure 3.4: Comparison of stochastic and deterministic invasion speeds for simulations carried out in 2D. The filled symbols represent the deterministic prediction and the empty symbols the stochastic predictions, where these were calculated by averaging the population density across the rows of the lattice and then using the same method as in 1D. The triangle represents the establisher morph's speed, the crosses the disperser morph's speed and the circles the invasion speed when both morphs are present. In (a) the polymorphic invasion speed is the same as the monomorphic establisher speed, in (b) the polymorphic invasion speed is the same as the monomorphic disperser speed, and in (c) the polymorphic invasion speed is faster than either monomorphic invasion. Parameter values used for r_e, r_d, μ and K are the same as in Fig. 3.3(a-c), with in (a) $d_e = 0.53$, $d_d = 0.8$, in (b) $d_e = 0.26$, $d_d = 0.93$ and in (c) $d_e = 0.186$, $d_d = 0.93$.

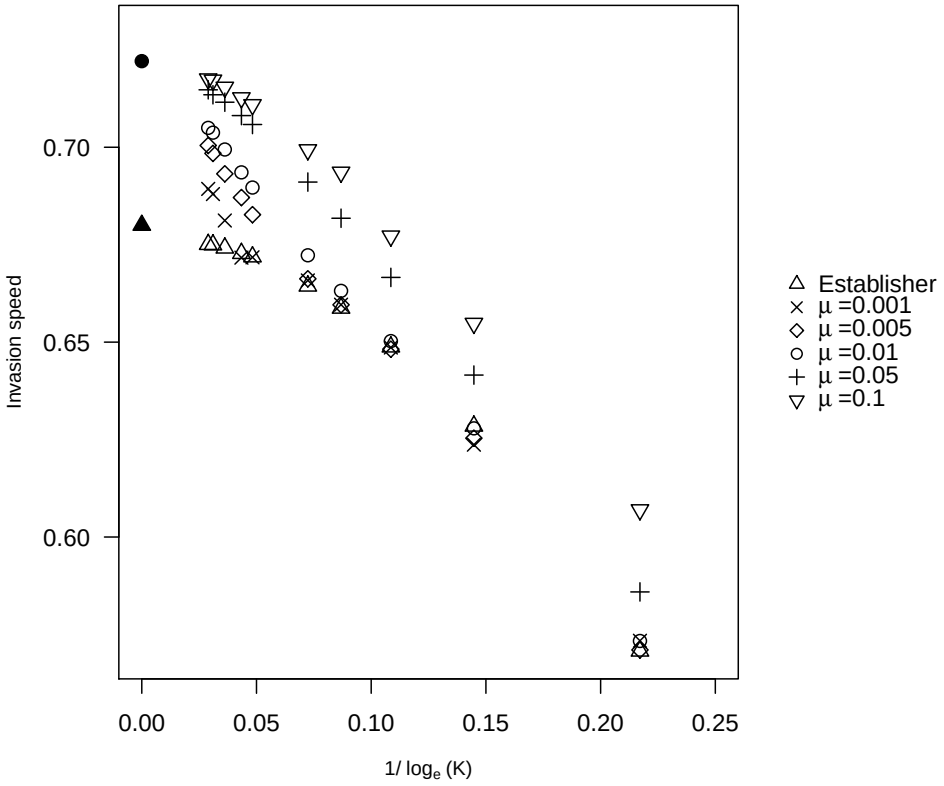

Figure 3.5: Comparison of invasion speeds with different values of μ. The parameter values are the same as in Fig. 3.3(c) with the value of μ varied from $\mu = 0.001$ (crosses), $\mu = 0.005$ (diamonds), $\mu = 0.01$ (circles), $\mu = 0.05$ (plus) and $\mu = 0.1$ (triangles point down). The filled circle represents the polymorphic deterministic speed which is the same for all mutation rates. The triangles point up represent the fastest single morph's speed, which here is the establisher, with the filled triangle the deterministic speed.

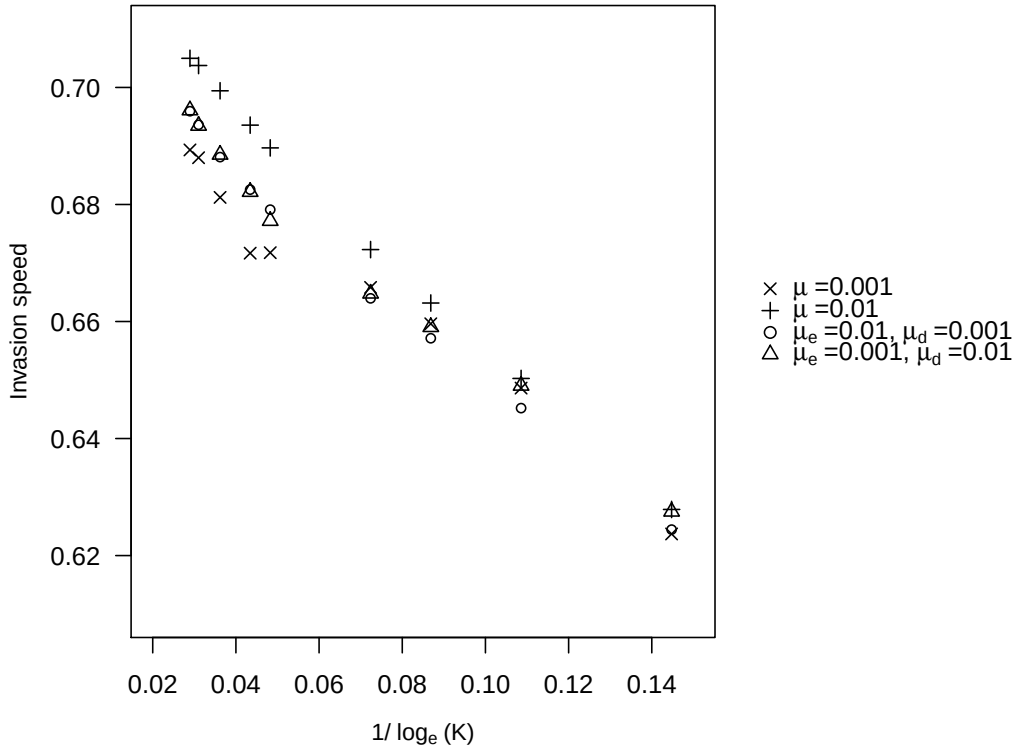

Figure 3.6: Comparison of invasion speeds with asymmetrical mutation rates between morphs. The parameter values are the same as in Fig. 3.5 with the crosses representing the symmetrical mutation rate $\mu = 0.001$ and the plus the symmetrical rate $\mu = 0.01$. Asymmetrical mutation rates are given by the circles and triangles. The circles represent $\mu_e = 0.01$ and $\mu_d = 0.001$ so more mutation from the establisher morph into the disperser morph, and the triangles represent $\mu_e = 0.001$ and $\mu_d = 0.01$ so more mutation from the disperser morph into the establisher morph.

invasion speed, with the lower symmetrical mutation rate ($\mu = 0.001$) giving the slowest speed. The asymmetrical mutation rates were found to result in invasion speeds that lay between the symmetrical lower and upper mutation rates used. The fastest invasion speeds are therefore found with high symmetrical mutation rates, again suggesting that it is important for there to be both good establishers and good dispersers present at the invasion front for anomalous speeds to be observed.

I also investigated what happens if different parameter values are used so that the trade-off between the morphs' establishment and dispersal abilities means that the two morphs' monomorphic speeds are similar. Here I find that when both morphs are present anomalous invasion speeds are observed from lower carrying capacities. For $\mu = 0.001$ the lowest mutation rate investigated, I find that anomalous speeds can be observed from a

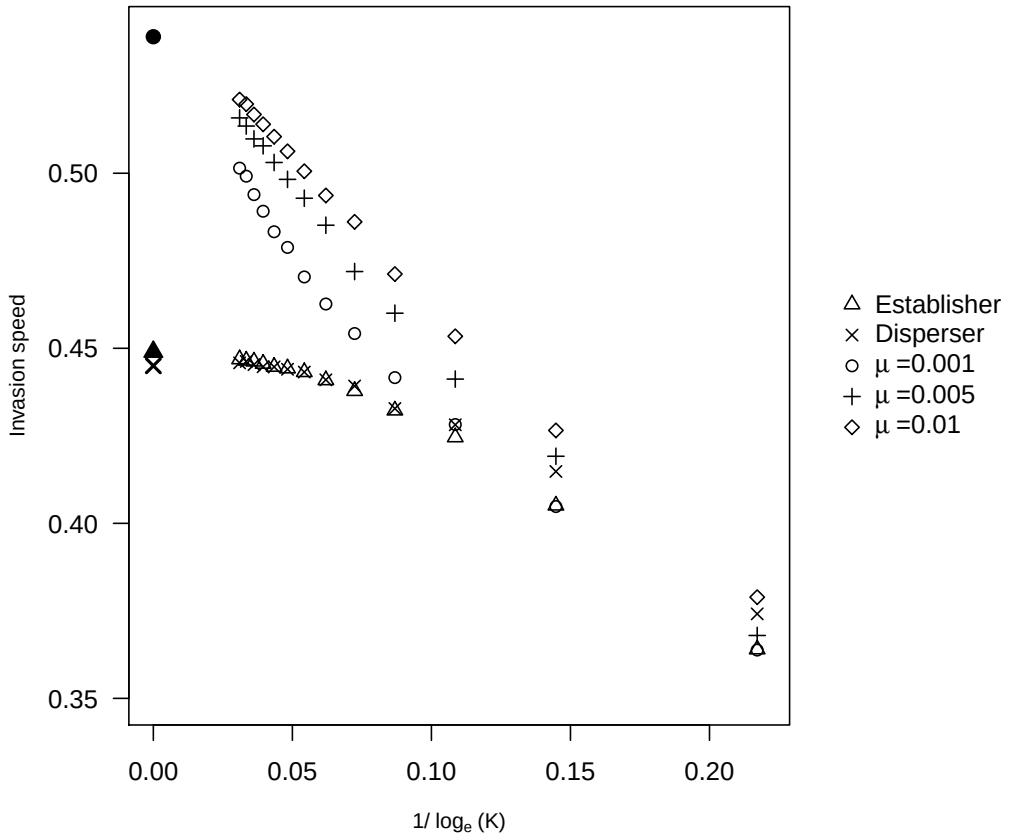

Figure 3.7: Anomalous invasion speeds when individual morph speeds are similar. The triangles represent the establisher morph's speed, the crosses the disperser morph's speed and the circles the invasion speed when both morphs are present with $\mu = 0.001$, the plus when $\mu = 0.005$ and the diamonds when $\mu = 0.01$. The filled symbols represent the deterministic speeds. Parameter values used were $r_e = 0.56$, $r_d = 0.13$, $D_d = 0.8$, $D_e = 0.15$ and K ranges from $K = 100$ to $K = 10^{13}$.

carrying capacity of $K = 10^4$ (Fig. 3.7), whereas for the parameter values used in Fig. 3.3 anomalous speeds were not observed at this mutation rate until $K = 10^{11}$. For higher mutation rates $\mu = 0.005$ and $\mu = 0.01$, anomalous speeds are observed from even lower carrying capacities ($K = 1000$ and $K = 100$ respectively).

3.4.1 Density profiles at the invasion front

The conditions under which anomalous invasion speeds are observed were then investigated by numerically exploring the density profiles. Typically it was found that when anomalous speeds occur the establisher morph is at higher densities just behind the invasion front, but in the leading edge the disperser morph is at higher density (Fig. 3.8).

This is in contrast to the case where the invasion follows the speed of either the establisher or disperser, as here whichever is the faster morph in isolation is at higher density in the leading edge (Fig. 3.9). As can be seen in Fig 3.8, the qualitative pattern is that as the carrying capacity gets higher, and so there are higher densities of both morphs at the invasion front, anomalous speeds are observed. For anomalous speeds to occur it is therefore important for both establishers and dispersers to be present at high enough densities at the invasion front.

However this is not always the case, as Fig. 3.8a shows, there are some cases where as the carrying capacity is increased, and so there is a higher density at the invasion front, anomalous speeds are not observed until the carrying capacity becomes even bigger. For example, for the parameter values used in Fig. 3.8a, anomalous speeds are not observed until carrying capacities in the order of $K = 10^{11}$, however, both morphs are at high densities with the disperser at the highest density in the leading edge from a carrying capacity of $K = 10^{8}$. It is therefore difficult to determine what exact conditions are required for these speeds, and as yet I have been unable to do so. As can be seen though the phenomenon described above, where there is a switch in the morph that is at higher density at the invasion front, does seem to be a necessary condition for anomalous speeds to occur although it does not always result in them.

3.5 Discussion

In this chapter I have investigated what effect the presence of two dispersal phenotypes has on a species' invasion speed, using both a deterministic and stochastic discrete time and space model. It was found that if the morphs differ in both their dispersal ability and growth rate, then the invasion speed can be faster than the speed of either morph on its own. It has been shown that anomalous invasion speeds persist in a model incorporating demographic stochasticity. Primarily anomalous invasion speeds were found to depend upon a high mutation rate and high carrying capacity (see Fig. 3.5). However, if the establisher and dispersers monomorphic speeds were similar, anomalous invasion speeds were observed at lower mutation rates and carrying capacities (see Fig. 3.7).

This model agrees with previous models that adding demographic stochasticity results in slower invasion speeds, with the deterministic speed predicting an upper bound for the stochastic speed (Lewis, 2000; Mollison, 1991; Snyder, 2003). Travis et al. (2011) showed that the greater the amount of stochasticity, the bigger the difference in the speeds

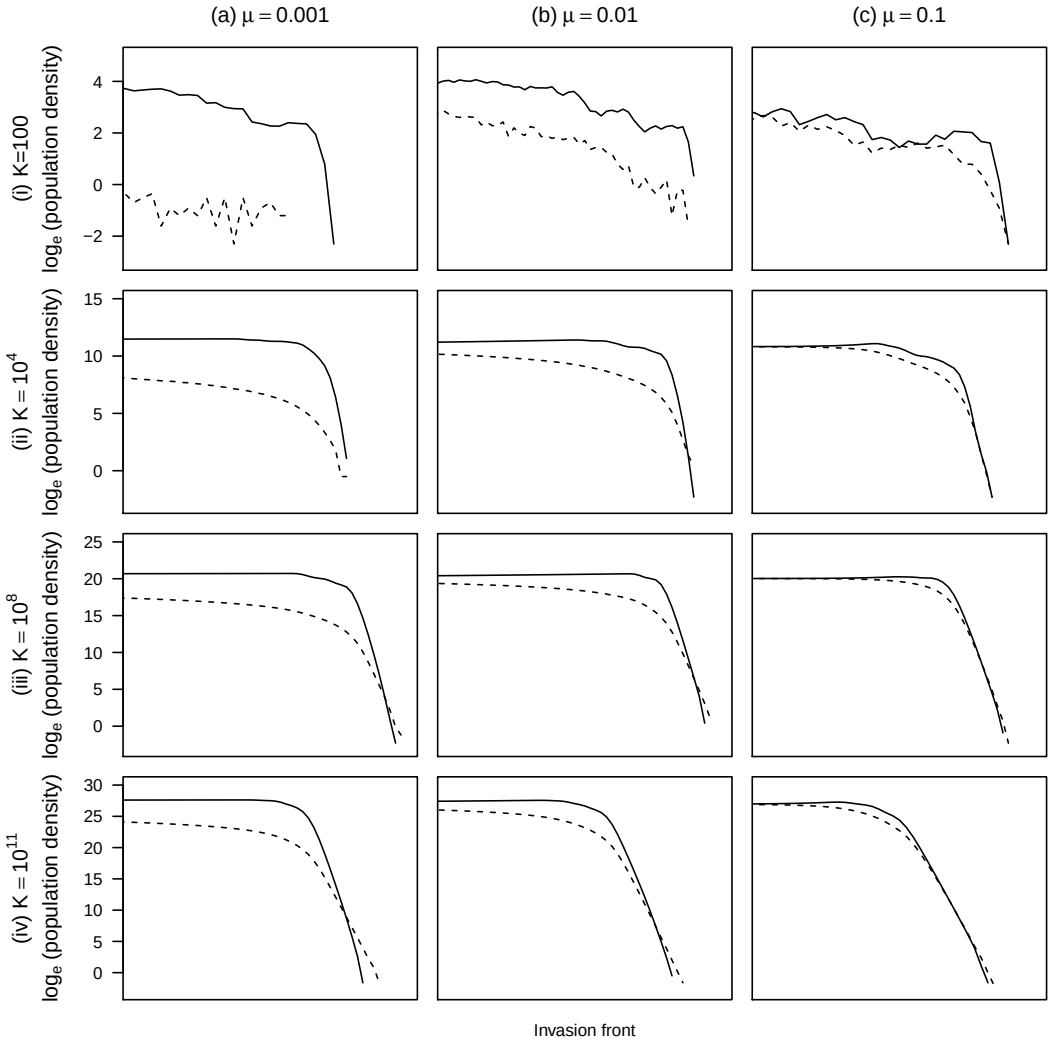

Figure 3.8: Comparison of population densities at the invasion front for the case where anomalous speeds occur. Log_e(population density) for the front 50 cells occupied by the population at time $t = 8000$ is plotted, where the solid line is the establisher morph and the dashed line the disperser morph. In (a) μ=0.001 and here anomalous speeds were only found for carrying capacity (iv), however the disperser is at a higher density from (iii) (see Fig. 3.5 for details of when anomalous invasion speeds are observed). In (b) μ=0.01 and anomalous speeds occur from carrying capacity (iii), which is the first time the disperser is at higher density at the invasion front. In (c) anomalous speeds occur from (i) and the disperser morph is at higher density for all carrying capacities. Parameter values used are the same as in Fig. 3.5.

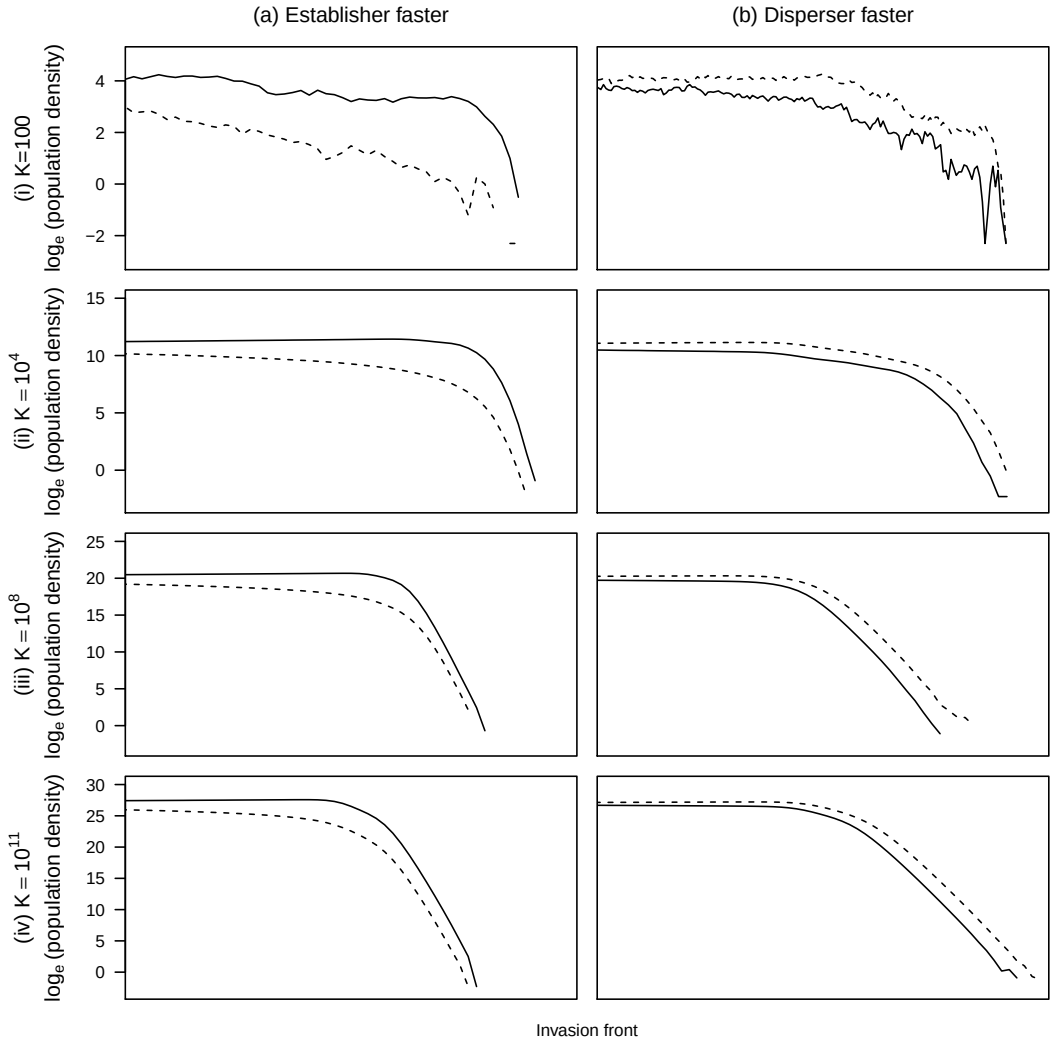

Figure 3.9: Comparison of population densities at the invasion front, where in (a) when both morphs are present the invasion follows the speed of the establisher morph, and in (b) the invasion follows the speed of the disperser morph. Log_e(population density) for the front 50 cells occupied by the population at time $t = 8000$ is plotted, where the solid line is the establisher morph and the dashed line the disperser morph. In (a) the establisher morph is at higher density at the invasion front for all carrying capacities and in (b) the disperser morph is at higher density for all carrying capacities. Parameter values used are the same as in Fig. 3.3.

predicted by their deterministic and stochastic models. These results also demonstrate this as I have shown that as the carrying capacity of the population increases, and hence the degree of stochasticity in the model decreases, the difference between the two speeds is smaller, with the stochastic speed tending towards the deterministic one.

These results suggest that for anomalous invasion speeds to occur both morphs need to be present in the leading edge at high enough densities. Higher mutation rates and higher carrying capacities both mean that the rarer morph will be present at the invasion front in higher densities. Numerically exploring the density profiles at the invasion front suggests that this is the case (see Fig. 3.8). Anomalous invasion speeds were only observed when there was a trade-off between the two morphs' dispersal and establishment abilities, and when both were present at high densities in the leading edge. However, in some cases anomalous speeds were not found to occur when these conditions were all satisfied (e.g. Fig. 3.8a). The emergent phenomena of anomalous invasion speeds observed here must occur as a result of the establisher and disperser morphs being at high density in the leading edge. However, so far a quantitative criterion to predict exactly when anomalous invasion speeds are expected to be observed in the stochastic model has not been found.

At low mutation rates the carrying capacity required for the population to invade faster than either single morph is typically high – higher than the carrying capacity of many species. For example, despite some species exhibiting differences in their establishment and dispersal abilities, such as the western bluebird, *Sialia mexicana*, which has morphs with different dispersal behaviours (Duckworth, 2008), and flowering plants which exhibit seed polymorphism (Sorensen, 1978), these examples will not have populations with large enough carrying capacities to observe anomalous speeds. For low mutation rates the carrying capacity needs to be in the order of $10^4 - 10^{11}$ for faster speeds to be observed. Adding demographic stochasticity to the model does therefore rule out a large number of species that may exhibit these anomalous invasion speeds.

There are, however, species that have very large populations, in particular populations with carrying capacities in the order of 10^4 may realistically expect to be found, and so it may be that anomalous invasion speeds are observed for species such as these. For example, many insect species exhibit trade-offs in their establishment and dispersal abilities through wing polymorphism (reviewed in Guerra, 2011; Zera and Denno, 1997), and also have very large population densities. In particular anomalous invasion speeds may be expected to be observed in insects such as crickets (Roff et al., 1999), planthoppers (Langellotto et al., 2000) and aphids (Braendle et al., 2006) to name a few. Anomalous

invasion speeds may also be observed in other taxa, for example, microorganisms can have very large population sizes, and some species of protists have been found to have trade-offs in their dispersal and establishment abilities (Fjerdingstad et al., 2007).

As was discussed in Chapter 2, an assumption of this model is that dispersal ability trades-off with population growth rate. It is known that this assumption applies to some species, such as the insects discussed previously and others such as the speckled wood butterfly, *Pararge aegeria*, (Hughes et al., 2003). However other species such as Glanville fritillary butterflies, *Melitaea cinxia*, (Hanski et al., 2006; Saastamoinen, 2007) and cane toads, *Bufo marinus*, (Phillips, 2009) show positive relationships between dispersal and growth rate. Anomalous invasion speeds are therefore unlikely to be observed in these species where there is no trade-off between dispersal and establishment.

The stochastic model developed in this chapter highlights that bigger trade-offs are more likely to result in anomalous invasion speeds, as these speeds are observed at lower carrying capacities and at lower mutation rates when the individual morph's invasion speeds are similar (see Fig. 3.7). The individual morphs have similar speeds as a result of there being a bigger difference between each morphs' dispersal and establishment rates. Species that have more extreme trade-offs, such as wing-polymorphic insects, where one morph is capable of flight and the other is not (see Guerra, 2011; Zera and Denno, 1997), may therefore be more likely to experience anomalous invasion speeds than other species that have smaller trade-offs.

I have modelled the invasion of a polymorphic species on a homogenous landscape which is not very realistic. Introducing spatial heterogeneity into the model would more realistically reflect the natural environment, and so would be a natural extension to this model. I am also interested in whether dispersal polymorphism resulting in anomalous invasion speeds can help a species to keep up with the rate of climate change. The next step in this research will therefore be to explicitly model a range expansion as a result of a shifting climate.

I have shown that the presence of two phenotypes can lead to unexpected results for the speed of biological invasions. These results reveal that demographic stochasticity can slow invasions, however, this is dependent on the carrying capacity of the population and the mutation rate between morphs. Anomalous invasion speeds were found to persist in models including demographic stochasticity when carrying capacities or mutation rates between morphs are high. It is hoped that these results motivate further research into understanding the difference between deterministic and stochastic models, and the

implications that anomalous speeds have for predicting the rate of range expansions.

4. Dispersal polymorphism: helps or hinders a species' ability to keep up with the rate of climate change?

4.1 Introduction

Over the past century mean global temperatures have increased by 0.6°C (IPCC, 2007) with future rapid increases in temperature predicted. To survive periods of climate change species can respond in one of two different ways. Species can respond to the new climatic conditions in their current location, either by adjusting to the new conditions by means of phenotypic plasticity, or by adapting to the new conditions genetically; or they may shift their ranges with the climate conditions they are already adapted to. If a species fails to respond in either of these ways then it may become extinct. There is evidence that different species are responding in all three of these ways as a result of the current threat from climate change.

There are signs that some species have already become extinct as a result of recent climate change. For example, increased night time temperatures in the tropics has led to the spread of fungal pathogens in the harlequin frog, which has resulted in approximately 67% of these frogs having gone missing presumed extinct in recent years (Pounds et al., 2006). Predictions about future extinctions as a result of climate change also paint a depressing picture, with one study estimating that between 18 and 35% of terrestrial species could become extinct by 2050 depending on the level of warming (Thomas et al., 2004).

There is more encouraging evidence that species are responding positively to climate change. It has been observed that some species are responding to new climates in their current locations. For example, there is evidence that the timing of phenological events, such as bird nesting, first flowering and frog breeding has become earlier in response to increased temperatures (reviewed in Parmesan and Yohe, 2003). These changes in timing are thought mostly to be plastic responses to climate change, however, genetic responses to increased temperatures have also been observed. For example, in Canadian red squirrels, *Tamiasciurus hudsonicus*, advanced parturition dates as a result of warmer springs, have been shown to be a genetic response resulting in earlier breeding in this

squirrel (Réale et al., 2003).

The most commonly observed response to climate change is species shifting their ranges with the conditions they are currently adapted to. There is lots of evidence that species are shifting their ranges polewards in response to recent warming (Chen et al., 2011; Hickling et al., 2006; Parmesan and Yohe, 2003; Root et al., 2003). Using a meta-analysis, Chen et al. (2011) have estimated that the distributions of species have shifted to higher latitudes at a median rate of 16.9 km per decade, and to higher elevations at a median rate of 11.0 m per decade. However, they also concluded that responses to climate change varies greatly within taxonomic groups and between individuals (Chen et al., 2011). With rates of climate change also expected to vary between spatial locations (Loarie et al., 2009), the number of species that will be able to keep up with the rate of change in the long term is still unknown.

Evolution during range expansions may increase species' chances of keeping up with climate change. Dispersal ability is a key trait in determining whether a species can keep up with the rate of change and indeed, evolution of increased dispersal has been observed to help species survive periods of change (Hill et al., 2011). For example, in recently colonised sites it has been observed that there are changes in flight morphology in butterflies (Hill et al., 1999a), and bush crickets (Simmons and Thomas, 2004). Historical data from the pollen record shows that survival of trees during the Quaternary period was a result not only of range shifts, but also of adaptive evolutionary change, with species adapting locally to new climates throughout their ranges (Davis and Shaw, 2001).

The question with modern climate change, which is predicted to be more rapid than historical climate change is, will species be able to keep up with the rate of change? Although during Quaternary climate change there is evidence that trees were able to evolve and shift to survive, future climate change is predicted to be faster than species may be able to evolve, in which case they may go extinct (Davis and Shaw, 2001). In marine ecosystems species will also be affected as seas warm, for example, it is predicted that 20% of Lessepsian migrants will not be able to spread fast enough to keep up with climate change, which may lead to biodiversity loss (Hiddink et al., 2012).

I am interested in whether there are any other aspects of a species' ecology that may help it to keep up with rates of climate change. I have previously shown using both a deterministic model in Chapter 2 (Elliott and Cornell, 2012) and a discrete time and space stochastic model in Chapter 3 (Elliott and Cornell, 2013), that if a population is polymorphic then a species' invasion can be faster than if the population only consists of

a single morph. This was found to be the case if a population consists of two morphs that differ in their dispersal abilities, one having a higher dispersal rate and the other having a higher establishment rate. These faster invasion speeds in polymorphic populations have been defined as anomalous invasion speeds (Weinberger et al., 2007), and in Chapter 2 I find that they occur when there is a big difference between the morphs in both of these traits. In the stochastic version of the model these anomalous speeds occur only if the carrying capacity is high, the mutation rate between morphs is high, or the individual morph's invasion speeds are similar (Chapter 3).

I am interested in whether these anomalous invasion speeds help a population to keep up with a shifting climate when otherwise a single morph population may become extinct. The stochastic dispersal polymorphism model that was developed in Chapter 3 is adapted so that there is a finite domain in which the species can exist. This domain is then shifted through the landscape simulating a shifting climate. The rate at which the climate is shifted is varied to determine under what conditions a species can keep up.

4.2 Methods

The model that was developed in Chapter 3 is used and instead of allowing the population to invade an infinite landscape I introduce a finite domain in which the species can exist. The basis of the model is briefly described here, with parameters used given in Table 4.1, but for full details see Chapter 3. I model the invasion of a species that consists of two phenotypes: there is an establisher morph e that after establishment has a higher population growth rate but a lower dispersal rate; and a disperser morph d that has a lower growth rate after establishment but a higher dispersal rate. The model is discrete in time and space, and so population dynamics and dispersal occur in discrete steps. First reproduction occurs, where there can be mutation between morphs so that offspring of one morph can be of the other type. Next there is a mortality step where each morph has a survival probability, so that a certain number of each morph die. Finally there is a dispersal step with each morph having a dispersal probability, so that a number of each morph disperses. The range shifting dynamics were simulated in one dimension because it is computationally cheaper than in two dimensions, and it was found in Chapter 3 that the results were qualitatively the same in two dimensions. It is therefore assumed that each morph has equal probability of dispersing to the left and the right.

Demographic stochasticity was introduced by modelling the birth rate, mutation rate,

Table 4.1: Notation of parameters used in the model

notation	parameter
N_i	population density of morph i
r_i	population growth rate of morph i
D_i	dispersal rate of morph i
K	carrying capacity of the population
μ	mutation rate between morphs

survival probability and dispersal rate as stochastic processes. For details of how this was carried out and for the full model equations see Chapter 3. In contrast to the previous model where the population invaded an infinite landscape there is now a finite domain within which the species can exist. For example, there is a domain that is 300 cells long which is shifted through a bigger landscape to simulate a shifting climate. Every two time steps I shift the landscape by one cell, so that a cell that the population can survive in is added to the leading edge of the domain and a cell is removed from the trailing edge. Every two time steps any individuals present in the trailing edge therefore die. I have chosen parameter values so that to keep up with the shifting landscape the population invades at or above the speed of 0.5.

First simulations with a single morph that has an invasion speed of 0.5 were carried out to check that for this simple version of the model the population can keep up with the shifting landscape. I then investigated what happens when both morphs are present. For this, parameter values were chosen to match each of the three possible scenarios that the invasion speed was found to evolve to in Chapters 2 and 3:

1. Establisher morph is faster – if both morphs had similar dispersal rates but the establisher had a higher establishment rate than the disperser, then when both morphs were present it was found that the invasion evolved to follow the speed of the establisher. So for this case parameter values were used so that the establisher morph has the speed of 0.5 lattice spacings per time step but the disperser is slower, and investigated whether the polymorphic population could keep up with the shifting landscape.

2. Disperser morph is faster – if both morphs had similar establishment rates but the disperser morph had a higher dispersal rate than the establisher, when both morphs were present the invasion was found to evolve to follow the speed of the disperser.

So for this case parameter values were used so that the disperser morph has the speed of 0.5 lattice spacings per time step but the establisher is slower, and investigated whether the polymorphic population could keep up with the shifting landscape.

3. Anomalous invasion speeds – I found that if the morphs had both a big difference in their establishment and dispersal rates then when both morphs were present the invasion evolved to be faster than either morph's individual invasion speed. So in this case parameter values were chosen so that when present on their own both morphs' invasion speeds were slower than 0.5 lattice spacings per time step, and investigated whether the polymorphic population could keep up with the shifting landscape.

For the third case I investigated how much slower than the shifting landscape the single morphs could be for the polymorphic population to still keep up with the shifting climate.

In previous work I found that the carrying capacity K of the population, and the mutation rate between morphs μ, had an effect on the invasion speed (Chapter 3). It was found that the higher the carrying capacity the faster the invasion speed, and that in the case where anomalous speeds were observed, the higher the mutation rate for a given carrying capacity the faster the invasion speed. I therefore investigated the effect that both the carrying capacity and mutation rate have on whether a polymorphic population is able to keep up with a shifting climate for the three scenarios described above. I also investigated how the size of the finite domain in which the species exists affects whether the species can keep up, as it has previously been observed that larger habitat availability means a species is more likely to survive a period of climate change (Travis, 2003).

The simulations were carried out in R (R Development Core Team, 2011), and were run on a lattice size of 50 000 cells and for up to 100 000 time steps. Simulations were run starting with a carrying capacity of $K = 10^{14}$, and then decreasing K by a factor of 10 each time until the smallest carrying capacity of $K = 100$. The parameters were scaled so that the invasion speed of the population was 0.5 lattice spacings per time step for the highest carrying capacity, and then looked at how decreasing the carrying capacity affected whether the population kept up with the shifting landscape. Larger carrying capacities than would be realistically expected were investigated to show that the stochastic model converged to the deterministic model. Two different finite domain sizes were investigated: $n = 300$ representing a small habitat availability, and $n = 3000$ representing a large habitat availability for the species. Simulations were carried out for

each K and at each domain size for four different mutation rates $\mu = 0.01$, $\mu = 0.001$, $\mu = 0.005$ and $\mu = 0.0001$. For the cases where it was found that the population could not keep up with the shifting landscape the time to extinction of the population was recorded.

4.3 Results

Simulations were first carried out at the largest carrying capacity investigated, which was $K = 10^{14}$. For these simulations parameter values that represent each of the three scenarios described in the Methods section were chosen. In the first case, where the establisher's invasion speed is the same as the rate at which the landscape is shifted and the disperser is slower, as expected the establisher shifting on its own can keep up but the disperser cannot. Then when both morphs are present in the landscape both morphs are able to keep up with the shifting landscape (Fig. 4.1). Similarly in the second case when the disperser's invasion speed is the same as the rate at which the landscape is shifted and the establisher is slower, again as expected the disperser shifting in the landscape on its own can keep up but the establisher cannot. Then when both morphs are present mutation between morphs allows both the establisher and disperser to keep up with the shifting landscape (Fig. 4.2).

In the third case where in Chapter 3 anomalous invasion speeds were observed, the simulations were carried out with the establisher and dispersers speeds both slower than the rate at which the landscape was shifted. In this case, as predicted, the establisher and disperser morphs when shifting in the landscape on their own are not able to keep up and quickly become extinct. However, when both morphs are present mutation between morphs once again produces faster invasion speeds, and so both morphs are able to keep up with the shifting climate (Fig. 4.3). In this case having both morphs present in the population greatly increases the chances of the population surviving a period of climate change.

As it was found in the model in Chapter 3 that larger carrying capacities had faster invasion speeds, I then looked at how the size of the carrying capacity affects whether a species is able to keep up with the shifting landscape. It was found that as the size of the carrying capacity decreased for all three scenarios the invasion speed became slower, and the likelihood that the population kept up with the rate of climate change decreased. For the cases where the population was unable to keep up with the rate of change, the time it took for the population to become extinct was recorded. For all simulations it was found

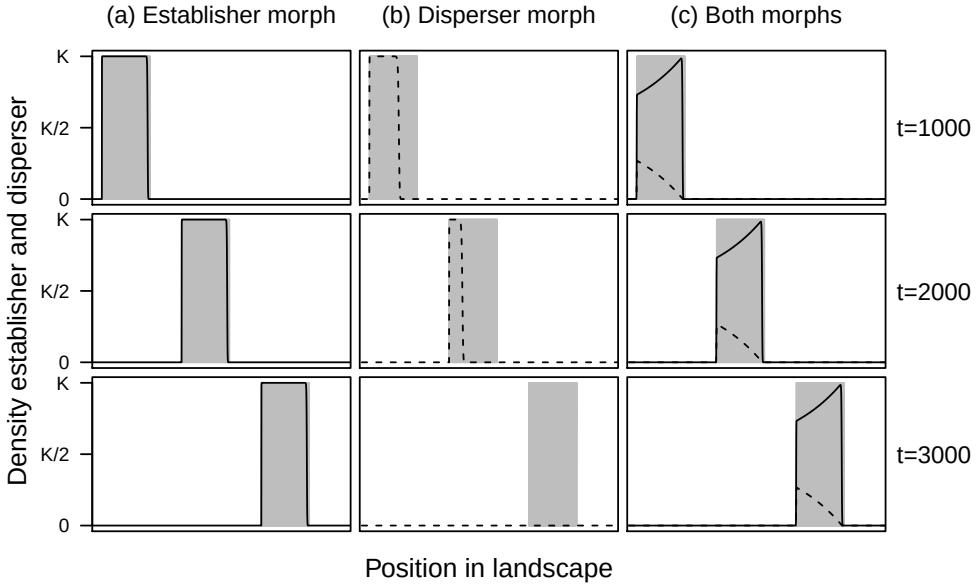

Figure 4.1: Range shifting of the population when the establisher is the faster morph. This is an example of the case where the establisher morph is expected to keep up, the disperser's invasion speed is slower than the shifting landscape speed, and it was found that when both morphs were present they were both able to keep up. In (a) the establisher morph is present on its own, in (b) the disperser morph is on its own and in (c) both morphs are present. Each row represents a different time point with each time point 1000 units apart. The shaded area represents the area in which the population can survive, and the solid line shows the density in space of the establisher morph and the dashed line the disperser morph. The parameter values used for these simulations were $r_e = 0.4$, $r_d = 0.15$, $D_e = 0.32$, $D_d = 0.55$, $K = 10^{14}$ and $\mu = 0.001$.

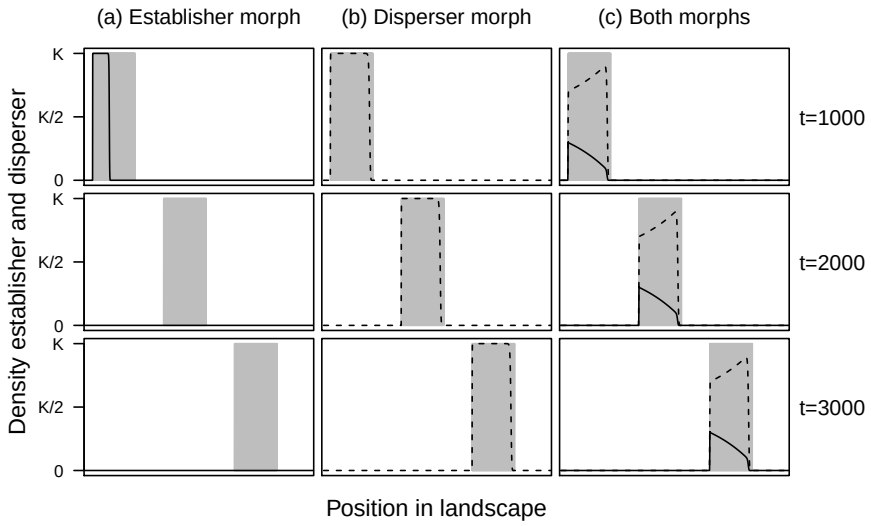

Figure 4.2: Range shifting of the population when the disperser is the faster morph. This is an example of the case where the disperser morph is expected to keep up, the establisher's invasion speed is slower than the shifting landscape speed, and it was found that when both morphs were present they were both able to keep up. In (a) the establisher morph is present on its own, in (b) the disperser morph is on its own and in (c) both morphs are present. Each row represents a different time point with each time point 1000 units apart. The shaded area represents the area in which the population can survive, and the solid line shows the density in space of the establisher morph and the dashed line the disperser morph. The parameter values used for these simulations were $r_e = 0.25$, $r_d = 0.17$, $D_e = 0.2$, $D_d = 0.8$, $K = 10^{14}$ and $\mu = 0.001$.

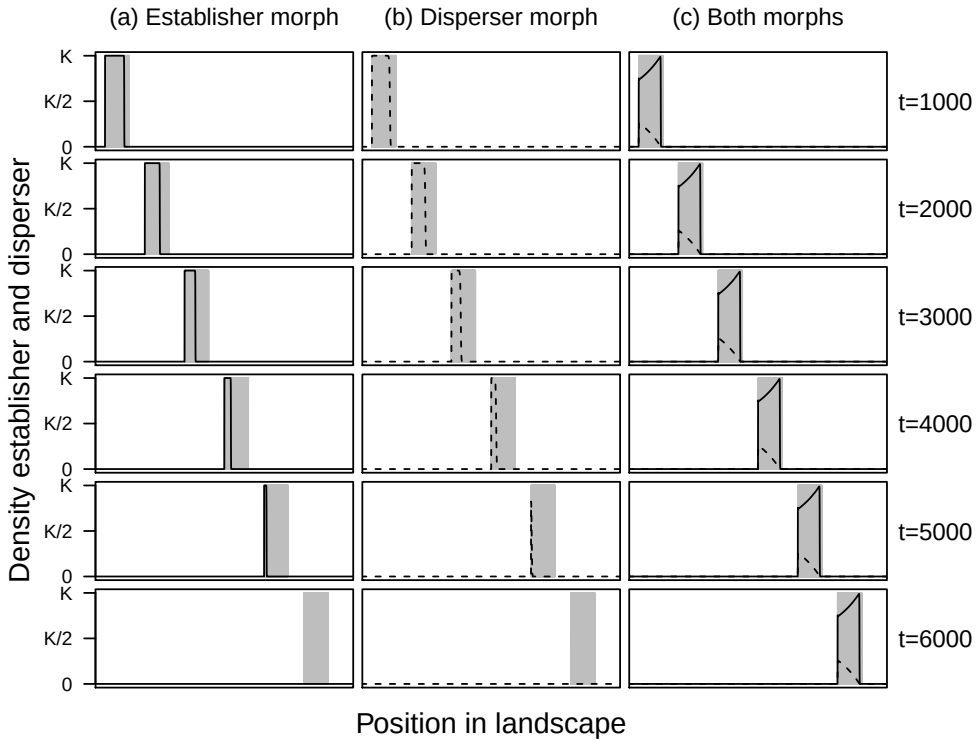

Figure 4.3: Range shifting of the population when the individual morphs are slower than the rate of shifting, but when both morphs are present they keep up. In (a) the establisher morph is present on its own, in (b) the disperser morph is on its own and in (c) both morphs are present. Each row represents a different time point with each time point 1000 units apart. The shaded area represents the area in which the population can survive, and the solid line shows the density in space of the establisher morph and the dashed line the disperser morph. The parameter values used for these simulations were $r_e = 0.56$, $r_d = 0.13$, $D_e = 0.15$, $D_d = 0.8$, $K = 10^{14}$ and $\mu = 0.001$.

that the fastest time to extinction of the population was at the lowest carrying capacity (Fig. 4.4). Then as the carrying capacity increased the population was able to keep up with the shifting landscape for longer, and so went extinct at a later time, until at the largest carrying capacities the population was able to keep up with the shifting landscape and could persist.

I then investigated what effect changing the mutation rate had on the time to extinction, and found that high and low mutation rates have different effects depending on which scenario is being investigated. For the first two scenarios (Fig. 4.4a and b), where one morph is faster than the other, low mutation rates between morphs, $\mu = 0.0001$ and $\mu = 0.001$, resulted in time to extinction of the polymorphic populations being very similar to the individual morphs. However, as the mutation rate increased to $\mu = 0.005$ and $\mu = 0.01$, at the bigger carrying capacities there were quicker times to extinction for the polymorphic population than the individual morphs. Higher mutation with a morph that is slower than the shifting landscape therefore means that the polymorphic population becomes extinct faster than a population that consists of only a single morph.

In the third case where anomalous speeds are observed it was found that higher mutation rates had the opposite effect (Fig. 4.4c). Here, when mutation rates were low, $\mu = 0.0001$, the time to extinction of the polymorphic population was only marginally slower than the individual morphs, and this was only when the carrying capacity of the population was very high. However, as the mutation rate becomes bigger, the time it takes for the polymorphic population to become extinct is much longer than for the individual morphs. For example, at a carrying capacity of $K = 10^7$ and a mutation rate of $\mu = 0.01$ it takes approximately 10.5 times longer for the polymorphic population to become extinct than a population that just consists of either the establisher or disperser morph. In this case, where there is a trade-off between dispersal and establishment, having both morphs present results in the population surviving longer, with the slowest extinction times for the higher mutation rates. More mutation between morphs is therefore a benefit when there is a trade-off between establishment and dispersal, but is costly when morphs are similar in one trait but have large differences in their other trait.

For the case where anomalous speeds were observed I investigated how much slower than the landscape individual morphs could be for the polymorphic population to still keep up with the shifting climate. I was interested in how rapid a period of climate change a polymorphic population could survive when a monomorphic population would become extinct. It was found that the mutation rate and carrying capacity of the population

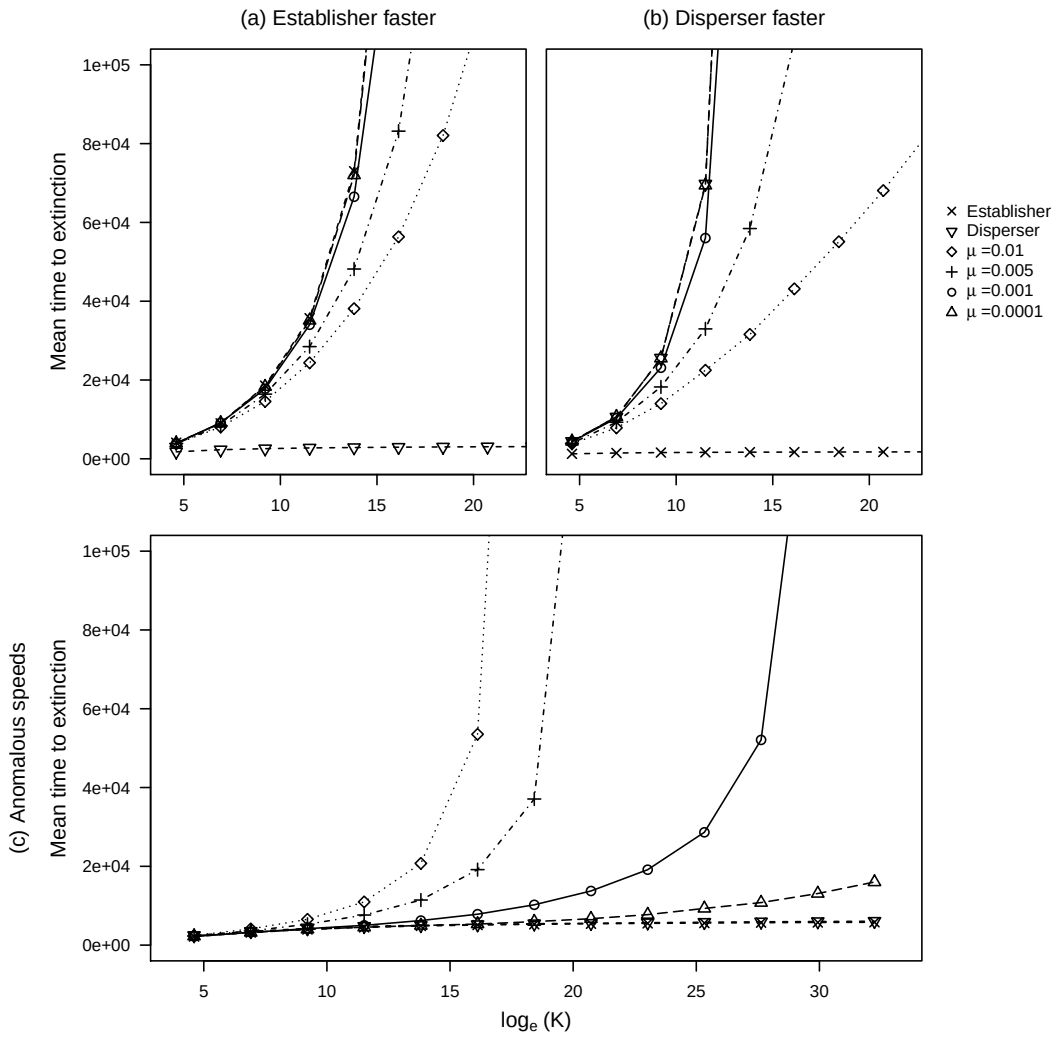

Figure 4.4: Mean time to extinction of the population against log(carrying capacity). In each graph the crosses represent the establisher morph shifting through the landscape on its own, the triangles point down the disperser morph on its own, and the other symbols when both morphs are present with different mutation rates between morphs. The diamonds represent $\mu = 0.01$, the plus $\mu = 0.005$, the circles $\mu = 0.001$ and the triangles point up $\mu = 0.0001$. Each point represents the mean of twenty replicates. Error bars are not included on these graphs because they obscure the points. In (a) the establisher morph is the faster morph, in (b) the disperser is faster and in (c) both morphs have similar speeds but are both slower than the speed of the shifting landscape. In (a) the parameter values used are the same as in Fig. 4.1, in (b) as Fig. 4.2 and in (c) the same as in Fig. 4.3 with K ranging from $K = 100$ to $K = 10^{14}$.

determine how much slower than the shifting landscape individual morphs can be, but both morphs still keep up. For example, for the parameters used in Fig. 4.3, at the biggest carrying capacity $K = 10^{14}$ the establisher and disperser morph are approximately 0.89 $\times$ the speed of the landscape, and at the highest mutation rate $\mu = 0.01$ both morphs keep up with the shifting landscape, but at the lowest mutation rate $\mu = 0.0001$ both morphs become extinct. Different combinations of parameter values will therefore determine how much slower than the shifting landscape individual morphs can be for both morphs to keep up.

The final variable that I was interested in was the size of the shifting landscape. The results presented so far are for a landscape consisting of 300 cells in which the species could survive, which was the smaller of the two landscape sizes investigated. For the bigger landscape size of 3000 cells, it was found as it has been previously (Travis, 2003), that a population is more likely to keep up with the shifting climate, and that if it is unable to it takes longer to become extinct (Fig. 4.5). For the two cases where one morph is faster than the other, it was found that time to extinction decreases for all mutation rates when comparing the same carrying capacities for the two different landscape sizes (compare Fig. 4.4a and b with Fig. 4.5a and b). Having a larger area in which the population can live therefore results in a species that consists of a superior morph being able to survive a period of climate change for longer. For the third case where anomalous speeds mean that both morphs can shift their range faster than a single morph, it was also found that a larger landscape decreases the time to extinction (Fig. 4.5c). For even the lowest mutation rate there is a greater improved chance of survival with this bigger shifting landscape. These results suggest that the size of habitat that a species can survive in will have a big effect on whether a species will survive periods of climate change, with a bigger habitat availability improving the chances of survival for all three scenarios investigated here.

4.4 Discussion

Climate change is affecting the habitats in which species live, and to survive many species will shift their ranges with their current habitats. These results suggest that having a polymorphic population may either help or hinder a population's ability to keep up with a shifting climate. I found that if there is a trade-off between dispersal and establishment between two morphs then having a polymorphic population is beneficial, as this population is able to keep up with the shifting climate when a monomorphic

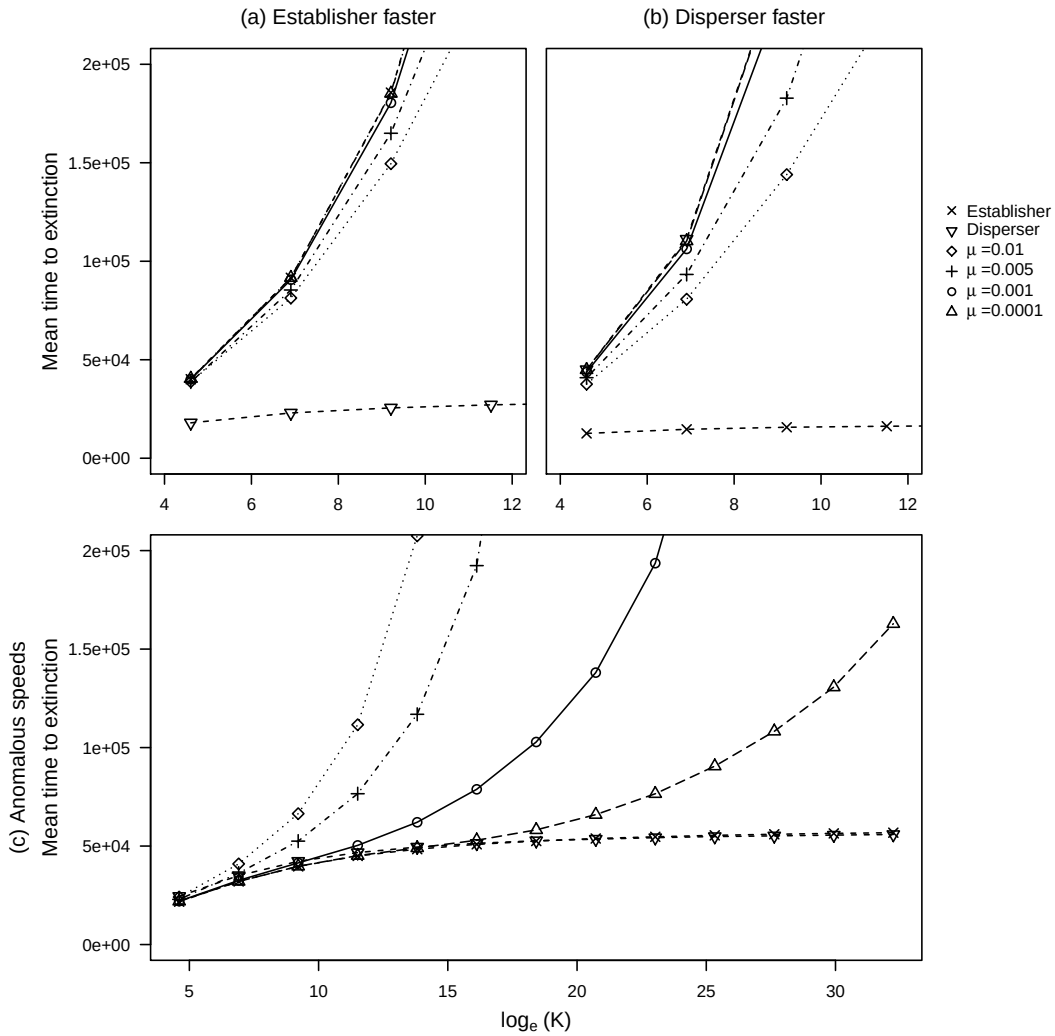

Figure 4.5: Mean time to extinction of the population against log_e(carrying capacity) for a larger shifting landscape. The symbols and parameter values are the same as in Fig. 4.4 with the exception that the size of the landscape that the population could exist in was bigger at 3000 cells.

population is unable to. However, if one morph is superior, so if one morph is either a much better disperser or much better establisher, then mutation between morphs slows the population down, and so having a polymorphic population can result in the population not being able to keep up with a shifting climate when the faster superior morph would be able to.

These results agree with my previous work in Chapters 2 and 3, that large differences in the morphs' establishment and dispersal abilities results in anomalous invasion speeds, which when there is a shifting climate means that the polymorphic population is able to keep up with the rate of change, whereas the monomorphic populations are not able to. In this case having a polymorphic population improves the chances of survival of the species. Here it was found that the higher the mutation rate between morphs, the greater the chance that the population will keep up with the shifting climate, and the longer it will take for the population to become extinct if it does not. Higher mutation means that there is more mutation into the disperser morph which is at lower density at the invasion front. This results in more dispersers being present at the invasion front which is beneficial because the establisher morph is a poorer disperser. There are therefore both good establishers and good dispersers present at the invasion front, and so the population has a faster invasion speed. This results in the population keeping up with the shifting climate better, or persisting for longer, than a monomorphic population which just consists of either good establishers or good dispersers is able to.

It was found that as long as the invasion speed of the population was the same or greater than the speed of the shifting landscape, then the species will always keep up with the rate of change. During a period of simulated climate change it was therefore found that a population travels at the same speed as it would when invading an infinite landscape. This suggests that if a species' invasion speed and the rate at which the climate is shifting are known, then it is possible to predict whether a species will be able to shift with the climate.

These results are encouraging for species that exhibit dispersal polymorphism, as they suggest that polymorphism may save them from becoming extinct as a result of climate change. For example, many insect species exhibit wing polymorphism (Guerra, 2011; Zera and Denno, 1997), and so it may be that these species are able to keep up with climate change when other monomorphic insects may not be able to.

For the two cases where one morph is superior, either in terms of being a better establisher or better disperser, it was found in Chapters 2 and 3 that during an invasion the population

evolves to follow the speed of the faster morph. Here it was found that at low mutation rates, as long as the faster morph is able to invade at the speed of the shifting landscape, the polymorphic population will keep up with the shifting climate. However, at higher mutation rates the polymorphic population can become slower than the shifting climate and lag behind. In this case higher mutation means that more of the poorer morph is present at the invasion front which slows the invasion down, and so the population is less able to keep up with the shifting climate and becomes extinct faster. These results are particularly worrying for species that have a superior disperser morph because these results suggest they may not be able to keep pace with a shifting climate. For example, there is evidence from several insect species, such as bush crickets (Simmons and Thomas, 2004) and butterflies (Hill et al., 1999a), that there is evolution of traits associated with increased dispersal during range expansions. The results from this model suggest that if there is still mutation with slower morphs then in the long run this could result in these species not being able to keep up with the rate of climate change.

For all but the smallest carrying capacities, the size of the mutation rate between morphs that is beneficial depends on the scenario that is being looking at. A high mutation rate is advantageous in the case where there is a trade-off between the morphs' establishment and dispersal abilities, but is disadvantageous when one morph is superior. In nature mutation rates are typically low, and so it is likely that the highest mutation rates investigated here may not occur. This is good news for the two cases where one morph is superior, as low mutation rates increase chances of survival. However, for the trade-off case low mutation rates only increase chances of survival at high carrying capacities, so it may be that at lower carrying capacities having a polymorphic population will not give as big an advantage as the results from this model predict, if these mutation rates do not occur.

These results also illustrated that the size of habitat in which the species lives has an effect on whether a species survives a period of climate change. It was found, as has been shown previously by Travis (2003), that wide habitat ranges mean a species is more likely to survive. This suggests that generalist species that can exploit a wider range of habitats will be more likely to keep up with the rate of change than specialist species. That generalist species are more likely to keep up with climate change has been found to be the case in many British butterflies (Warren et al., 2001) and birds (Julliard et al., 2004) to name a few.

The model that has been used in this chapter is a simple representation of a range expansion of a species as a result of climate change. In particular I have made the

simplification that the landscape is homogenous which is not realistic. Previous models have shown that the combined effects of climate change and habitat fragmentation can slow down range expansions (Anderson et al., 2009), and result in even faster rates of extinction of species (Travis, 2003). It may therefore be that if habitat loss is included in this model times to extinction could be faster. Future work could investigate what the combined effects of climate change, habitat loss and dispersal polymorphism are on whether a species is able to keep up with a shifting climate. In particular it would be interesting to investigate whether anomalous invasion speeds would still help a species to survive climate change if habitat loss is included.

The majority of research looking at the range expansion of species as a result of climate change has focused on the expanding cooler range edge that is at higher latitudes and altitudes, and there is less known about what is happening at the lower latitude range edge (Chen et al., 2011; Parmesan and Yohe, 2003; Root et al., 2003). At lower latitude range edges there are two extremes of what can occur; either the species' range could completely shift resulting in latitudinal displacement, or a fraction could persist with range expansions at the higher latitude margin without complete contraction at the lower latitude (Hampe and Petit, 2005). Here a range expansion that follows the first scenario has been modelled whereby the new climate window is completely non-overlapping of the window prior to climate change. History shows that these kinds of displacement have occurred with, for example, the entire range of boreal species such as spruce in North America having shifted as a result of a warming climate during the Quaternary period leading to glacial retreat (Williams et al., 2004).

There is evidence that, as a result of modern day climate change, some European butterfly species are shifting their ranges at both their high and low latitude range edges (Hill et al., 1999b). Other montane butterfly species in both the UK (Franco et al., 2006) and Spain (Wilson et al., 2005) have been found to have range contractions at their lower latitude range margins, however, at least for the Spanish montane butterflies there is no evidence that they are expanding their northern range margins (Wilson et al., 2005). During Quaternary climate change the melting of vast ice sheets enabled large species' range shifts. It may be that with modern climate change whether species have future non-overlapping regions will be influenced by other factors, such as obstacles to dispersal like oceans, or reaching the tops of mountains, that prevent them from expanding their ranges further. The model developed here will not therefore be applicable to species such as these, and for these species to survive climate change adaptation to the new climatic

conditions or human intervention will be required.

If species' low latitude ranges are not contracting as a result of climate change, or are contracting at a rate slower than climate change, then it may be that species have a better chance of surviving than this model would suggest. The speeds predicted from this model would still influence the expanding range edge, but instead of going extinct the population may just lag behind the shifting climate at a rate determined by the mutation rate and carrying capacity of the population. For example, many butterfly species in Europe have expanded their northern range margin but their southern range margin has not contracted (Parmesan et al., 1999). Also where these range expansions are occurring they tend to be lagging behind the shifting climate (Hill et al., 1999b; Menendez et al., 2006; Parmesan et al., 1999). However, range contractions may be occurring in more species than has so far been recognised as it has been suggested that it is harder to observe extinctions at the rear of a species' range than it is to observe range expansions (Franco et al., 2006). These model predictions for time to extinction of populations give a worst case scenario if range shifts cause latitudinal displacement. If range contractions happen at slower rates than range expansions then it is likely that more species would be able to survive periods of climate change than this model predicts.

These results highlight the importance of looking at the entire population of phenotypes when predicting whether a species will be able to survive a period of climate change. Having a polymorphic population can either help or hinder a species' ability to keep up with the rate of change. These results are particularly encouraging for species that have trade-offs in their establishment and dispersal abilities as I predict that polymorphism can significantly improve their chances of surviving. It is hoped that these results encourage more research into how polymorphism affects range expansions and in particular inspire empiricists to investigate whether these results can be observed in a real system either in the laboratory or in the field.

5. Species' range margins: adaptation versus dispersal evolution along an environmental gradient

5.1 Introduction

The question as to why species have a limited range is one that has long been investigated both theoretically and empirically (see reviews in Bridle and Vines, 2007; Gaston, 2003). However, a clear understanding as to what causes range margins to be formed has been difficult to come by (Gaston, 2009). In some cases range margins may be formed as a result of obstacles preventing further dispersal, abrupt changes in the environment or by interactions with other species (Gaston, 2003). However, often there are no such obvious boundaries to prevent species further expanding their ranges and in these cases margins may be formed as a result of failing to adapt to the environment. There are two classic arguments as to why adaptation at range margins fails (reviewed in Bridle and Vines, 2007). The first argument is that gene swamping may occur as a result of gene flow from central well-adapted populations to the range edge where these genes prevent adaptation to the edge conditions. The second is that there is insufficient genetic variation at the range edge to allow adaptation, which may either be as a result of Allee effects, genetic drift or low rates of mutation.

Whether gene flow from central populations to edge populations results in populations failing to adapt has been investigated using quantitative trait models (reviewed in Lenormand, 2002). These models look at how the mean value of a quantitative trait, for example body size, varies along an environmental gradient, such as temperature. In these models population dynamics are related to how closely the trait mean matches the optimum at each point on the gradient. When the population density reaches zero, the trait mean is far from the optimum, and so a range margin is formed.

Kirkpatrick and Barton (1997) found that if the mean value of the trait is able to match the optimum along the gradient, then the species' range expands without limit, and the population is at its carrying capacity across all space. However, if the environmental conditions change too rapidly, i.e. the gradient is too steep, then the species can only

exist in a limited region, and if the gradient is even more extreme then the population becomes extinct. In this case gene swamping occurs as migration of genes from central well-adapted populations prevent marginal populations from adapting. In this model genetic variance was assumed to be constant, whereas in reality it can evolve as a result of migration, mutation and selection (Bridle and Vines, 2007). Barton (2001) extended the model so that genetic variance could evolve, and found that if this is the case then populations can always adapt to the environmental gradient, and so the species expands its range without limit. If the environmental optimum changes in both time and space the same range margin scenarios were found. If genetic variance does not evolve then for steep gradients the species has a limited range, whereas if genetic variance evolves or there are shallower gradients then uniform adaptation occurs (Polechova et al., 2009).

These models would therefore suggest that if the environmental gradient is shallow, or genetic variance evolves, then there are no limits to adaptation and a species should have an unlimited range. However, species do have range margins and fail to adapt beyond these, and so these models must be missing something that explains a species' failure to adapt. One limitation of these models is that they do not include stochastic effects, and so for example, do not take into account increased extinction risk at low population densities which in reality would be found.

Bridle et al. (2010) developed a stochastic model to see how the predictions for adaptation at range margins compared to those of deterministic models. They found that at high carrying capacities the same results are observed as in the deterministic models (Barton, 2001; Kirkpatrick and Barton, 1997). However, when population densities are smaller, adaptation to the environment is predicted to occur for a smaller range of parameters than predicted in the deterministic models. Whether the population could adapt to the gradient depended on not only dispersal and steepness of the gradient, but also the local carrying capacity (Bridle et al., 2010). Including demographic stochasticity meant that population extinction occurred at shallower gradients than found using the deterministic models.

Another limitation of these models is that there is no cost to adapting to the environment, however, it would be expected that if increased energy is used for adapting to different conditions then there is less energy available for other life-history processes. There is lots of evidence that life-history traits trade-off with one another (for reviews see, Roff and Fairbairn, 2007; Zera and Harshman, 2001), as organisms only have a limited amount of energy to invest and have to choose how to allocate this. One common trade-off observed is between allocation of energy invested in traits related to increased fecundity, and traits

related to increased dispersal ability. For example, in wing polymorphic insects, the flight-capable morph has large functional flight muscles and high lipid stores, whereas the flightless morph has reduced lipid stores and small non-functional flight muscles (Zera and Harshman, 2001). However, the ability to fly comes at a cost as ovaries are much bigger in the flightless morph (Zera and Harshman, 2001), and so this morph has higher fecundity.

As discussed above trade-offs between traits are commonly observed. It is possible therefore that adaptation to new environments comes at a cost to some other trait, and so range margins may be formed as a result of the costs associated with adaptation. In this chapter I will therefore investigate whether range margins along environmental gradients are formed as a result of trade-offs between adaptation and another trait. In particular I am interested in the trade-off between adaptation and dispersal, as dispersal directly affects a species' ability to expand its range.

There is evidence that adaptation to new environments does trade-off with dispersal. A well studied species that exists along a latitudinal gradient is the Atlantic silverside, *Menidia menidia*. Across the range of *M. menidia* the growing season declines by a factor of 2.5 with increasing latitude (Conover and Present, 1990). To compensate for the shorter growing season it has been found that fish from northern latitudes have faster growth rates than fish from southern latitudes (Conover and Present, 1990). This increased growth occurs as a result of approximately two times higher rates of food consumption by northern fish (Present and Conover, 1992). These fish have therefore adapted to the shorter growing season by increasing their rate of food consumption, and hence their growth rate. Increased growth rate in northern fish does come at a cost though, as these fish have diminished locomotory capacity (Billerbeck et al., 2001). Trade-offs between adaptation to shorter growing seasons and dispersal ability have also been found to occur in other organisms, for example in other fish species (Cano and Nicieza, 2006) and in amphibians (Arendt, 2003; Ficetola and De Bernardi, 2006). This would suggest that these species have an optimal body plan that maximises both survival and dispersal, and so adaptation to different environmental conditions results in a compromise of this optimal body plan. For these examples, this compromise comes in the form of faster growth occurring at a cost to dispersal.

In this chapter, I will develop a quantitative trait model that investigates whether range margins are formed as a result of trade-offs between dispersal and adaptation. The model is based on the model by Kirkpatrick and Barton (1997) but is discrete in time and

space. There is a quantitative trait where the optimum value for survival varies along an environmental gradient, but the trait also affects dispersal ability. The trade-off is modelled so that in the centre of the species' range where the optimum value of the trait is zero, dispersal is highest. Along the environmental gradient as the optimal value of the trait for survival increases, dispersal is lower. Away from the centre of the range there is therefore a cost to adapting to the environment in terms of reduced dispersal. I am therefore assuming a trade-off such as the one described for the above examples, so that the body plan of this species is optimised to one particular strategy. The trait then describes how far the species has had to deviate from this plan to be able to adapt to the environment. I will investigate how changing different parameter values affects the formation of range margins. I will then allow the trait to vary in both time and space in a similar way to Polechova et al. (2009), to investigate whether under climate change this trade-off influences a species' ability to expand its range.

5.2 Model

The model that I use in this chapter is based on the model of Kirkpatrick and Barton (1997). They use partial-differential equations to jointly model the evolution of population density and the mean value of a quantitative trait along an environment that changes in space. I adapt this model so that it is discrete in time and space. This was done because PDEs are an approximation to reality as they assume events happen continuously in time and space. By using a discrete model it is assumed that there are discrete generations, and that there are discrete patches in which a species lives, making the results easier to interpret in terms of individuals. In this model the density of individuals with trait z at time t and position x is given by $n(z, x, t)$. Population dynamics occur in discrete steps in the order of mortality, dispersal and then reproduction.

Following Kirkpatrick and Barton (1997) the following assumptions are made:

1. The phenotypic trait z is normally distributed with variance, v, which is assumed to be constant (Falconer, 1989), so that

$$n(z, x, t) = N(x, t)\frac{1}{\sqrt{2\pi v}} \exp\left(\frac{-(z - \bar{z}(x, t))^2}{2v}\right),$$

   where $\bar{z}(x, t)$ is the trait mean at point x and time t.

2. At each point x there is a value of the trait, $\theta(x)$, that maximises survival and

reproduction. This optimum changes as a linear function of space $\theta(x) = bx$, where b is the steepness of the environmental gradient.

3. Individuals whose phenotype z differs from their local optimum have reduced viability, and the probability of survival for a phenotype z at location x within a generation is
$$\exp\left(\frac{-(z-\theta(x))^2}{2\omega}\right),$$
where ω is the variance of the Gaussian fitness function.

In addition to these assumptions, I am making the further assumption that adaptation to the environment trades-off with dispersal ability, and so dispersal also depends upon the trait z. The dispersal function was chosen to be modelled as

$$\delta(z) = \frac{1}{d}\exp\left(\frac{-z^2}{2\beta}\right), \tag{5.1}$$

where d is the fraction of individuals that disperse, and β is the variance of the dispersal function. This shape of the dispersal function was chosen because this means that as the value of θ increases, and so to be perfectly adapted to the environment z will also need to increase; $\delta(z)$ will tend to zero, as can be seen in Fig. 5.1. This allows an explicit trade-off between adaptation to the environment and dispersal to be modelled.

This leads to the population dynamics being modelled as follows. First mortality is given by

$$n_m(z,x,t) = n(z,x,t)\exp\left(-m_0 - m_1 N(x,t) - \frac{(z-\theta(x))^2}{2\omega}\right), \tag{5.2}$$

where a Ricker-like density dependence is assumed. A fraction of the population then disperses so that

$$n_d(z,x,t) = (1-2\delta(z))\, n_m(z,x,t) + \delta(z) n_m(z,x+1,t) + \delta(z) n_m(z,x-1,t), \tag{5.3}$$

where $\delta(z)$ is defined in Eqn. (5.1). Finally a fraction, r, of the population reproduces and produces offspring, where there is mutation at rate μ of offspring away from their parents' phenotype. This leads to the population density after one time step being given by

$$n(z,x,t+1) = r(1-\mu) n_d(z,x,t) + r\mu \int M(z,z') n(z',x,t) dz', \tag{5.4}$$

where it is assumed that mutation behaves as a Gaussian function with variance u, which acts on the phenotype, $M(z,z') = \frac{1}{2\pi u}\exp\left(\frac{-(z-z')^2}{2u}\right)$.

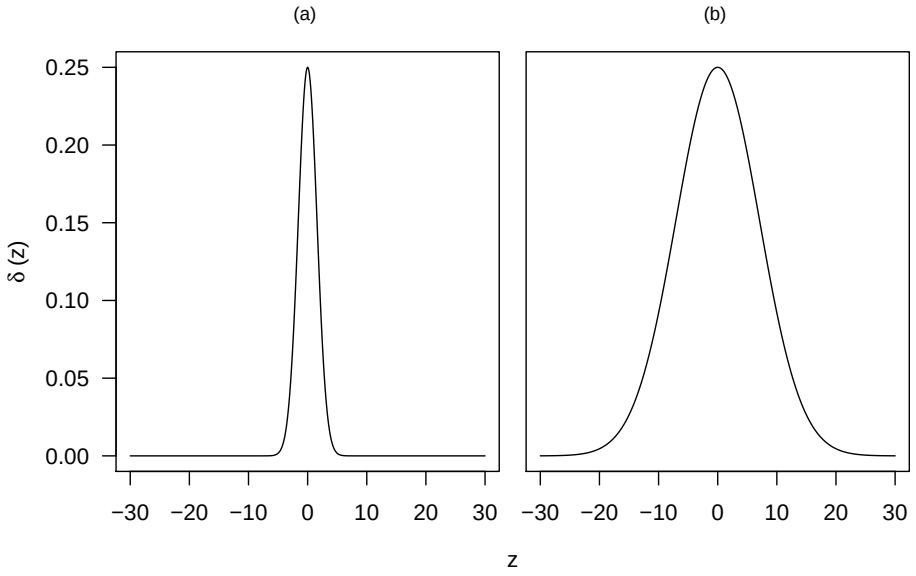

Figure 5.1: Form of dispersal function given by Eqn. 5.1, with two different values of the variance β. In both $d = 4$, and in (a) $\beta = 2.5$, representing a strong trade-off because as z increases $\delta(z)$ tends to zero quickly; and in (b) $\beta = 50$, representing a weaker trade-off because $\delta(z)$ tends to zero slower as z increases.

Then, following other authors, (García-Ramos and Kirkpatrick, 1997; Kirkpatrick and Barton, 1997) approximate iteration equations can be derived for $N(x,t) = \int n(z,x,t)dz$ and $Y(x,t) = \int zn(z,x,t)dz$. In doing this a first order Gaussian moment closure with constant variance is performed. Carrying out these approximations means that the dependence on μ drops out. This leads to two equations, the first describes the change in population density, and the second describes the change of the trait mean in time and space:

$$
\begin{aligned}
N(x,t+1) &= \alpha A N(x,t) \exp\left(-m_1 N(x,t) - \frac{(\bar{z}(x,t)-\theta(x))^2}{2(\omega+v)}\right) \\
&+ \frac{\alpha}{d} B \left[N(x+1,t) \exp\left(-m_1 N(x+1,t) - C\left[\bar{z}(x+1,t) - \frac{\beta\theta(x+1)}{\omega+\beta}\right]^2 - \frac{\theta(x+1)^2}{2(\omega+\beta)}\right)\right. \\
&+ N(x-1,t) \exp\left(-m_1 N(x-1,t) - C\left[\bar{z}(x-1,t) - \frac{\beta\theta(x-1)}{\omega+\beta}\right]^2 - \frac{\theta(x-1)^2}{2(\omega+\beta)}\right) \\
&\left. -2N(x,t) \exp\left(-m_1 N(x,t) - C\left[\bar{z}(x,t) - \frac{\beta\theta(x)}{\omega+\beta}\right]^2 - \frac{\theta(x)^2}{2(\omega+\beta)}\right)\right], \qquad (5.5)
\end{aligned}
$$

$$
\begin{aligned}
Y(x,t+1) = {} & \alpha D[\omega Y(x,t) + v\theta(x)N(x,t)] \exp\left(-m_1 N(x,t) - \frac{(\bar{z}(x,t)-\theta(x))^2}{2(\omega+v)}\right) \\
& + \frac{\alpha}{d} E\Bigg[[\omega Y(x+1,t) + v\theta(x+1)N(x+1,t)] \exp\Bigg(- m_1 N(x+1,t) \\
& -C\left[\bar{z}(x+1,t) - \frac{\beta\theta(x+1)}{\omega+\beta}\right]^2 - \frac{\theta(x+1)^2}{2(\omega+\beta)}\Bigg) \\
& + [\omega Y(x-1,t) + v\theta(x-1)N(x-1,t)] \exp\Bigg(- m_1 N(x-1,t) \\
& -C\left[\bar{z}(x-1,t) - \frac{\beta\theta(x-1)}{\omega+\beta}\right]^2 - \frac{\theta(x-1)^2}{2(\omega+\beta)}\Bigg) \\
& - 2[\omega Y(x,t) + v\theta(x)N(x,t)] \exp\Bigg(- m_1 N(x,t) \\
& -C\left[\bar{z}(x,t) - \frac{\beta\theta(x)}{\omega+\beta}\right]^2 - \frac{\theta(x)^2}{2(\omega+\beta)}\Bigg)\Bigg], \qquad (5.6)
\end{aligned}
$$

where $\alpha = r\exp(-m_0)$ is density independent population growth, $Y = \bar{z}N$ and where the following parameters have been redefined to simplify the equations: $A = \sqrt{\frac{\omega}{\omega+v}}$, $B = \sqrt{\frac{\omega\beta}{\beta v+\omega v+\omega\beta}}$, $C = \frac{\omega+\beta}{2(\beta v+\omega v+\omega\beta)}$, $D = \sqrt{\frac{\omega}{(\omega+v)^3}}$ and $E = \sqrt{\frac{\omega\beta^3}{(\beta v+\omega v+\omega\beta)^3}}$.

Solving these equations at stationarity shows that two equilibria always exist. The first equilibrium is when the population density is at carrying capacity,

$$N = \frac{1}{m_1}\left(-m_0 - \log\left(\frac{1}{r}\sqrt{\frac{w+v}{w}}\right)\right),$$

and the trait is perfectly adapted, $\bar{z} = bx$. The second equilibrium occurs when the population is extinct everywhere, $N = 0$. To investigate whether there were any other equilibria whereby the species had a limited range, numerical simulations were carried out. Simulations were run in R (R Development Core Team, 2011), on a one-dimensional lattice of varying sizes. The simulations were initiated with the first 100 cells of the lattice occupied by the population at its stable equilibrium density, and the trait perfectly adapted to the environment. Reflecting boundary conditions were used at the end of the lattices. The simulations were run until the population formed a range boundary. The parameters b, β, ω and v were varied to see what effect the steepness of the environmental gradient and the three different variance parameters had on the formation of range margins.

Having carried out these simulations and found where the populations had formed range margins, I then allowed the optimal value, θ, of the trait z to change as a linear function

of both space x and time t so that

$$\theta(x,t) = b[x - ct], \tag{5.7}$$

where as before b is the steepness of the environmental gradient, and c is the rate of change of the optimum in time. This leads to the same two equations (Eqn. (5.5) and (5.6)) with $\theta(x)$ replaced by $\theta(x,t)$. As before numerical simulations of this model were carried out, with the speed, c, at which the environmental gradient shifts varied. This simulated a shifting climate, and I used this to investigate whether dispersal evolution helps a population to keep up with the rate of climate change.

5.3 Results

5.3.1 No environmental gradient

First the case $b = 0$ was investigated, so that the environmental gradient is constant across all space. In this case equations (5.5) and (5.6) reduce to

$$\begin{aligned} N(x,t+1) = \alpha A N(x,t) \exp\left(-m_1 N(x,t) - \frac{\bar{z}(x,t)^2}{2(\omega+v)}\right) \\ + \frac{\alpha}{d} B \Big[N(x+1,t) \exp\left[-m_1 N(x+1,t) - C\bar{z}(x+1,t)^2\right] \\ + N(x-1,t) \exp\left[-m_1 N(x-1,t) - C\bar{z}(x-1,t)^2\right] \\ - 2N(x,t) \exp\left[-m_1 N(x,t) - C\bar{z}(x,t)\right] \Big], \end{aligned} \tag{5.8}$$

$$\begin{aligned} Y(x,t+1) = \alpha D \omega Y(x,t) \exp\left(-m_1 N(x,t) - \frac{\bar{z}(x,t)^2}{2(\omega+v)}\right) \\ + \frac{\alpha}{d} E \Big[\omega Y(x+1,t) \exp\left[-m_1 N(x+1,t) - C\bar{z}(x+1,t)^2\right] \\ + \omega Y(x-1,t) \exp\left[-m_1 N(x-1,t) - C\bar{z}(x-1,t)^2\right] \\ - \omega Y(x,t) \exp\left[-m_1 N(x,t) - C\bar{z}(x,t)\right] \Big]. \end{aligned} \tag{5.9}$$

In this case where there is no environmental gradient, the value of the phenotypic trait that maximises survival is zero, which is also the value of the phenotypic trait that maximises dispersal, and so these conditions select for a species' optimal body plan. There is therefore no trade-off in this version of the model, and so it was expected that

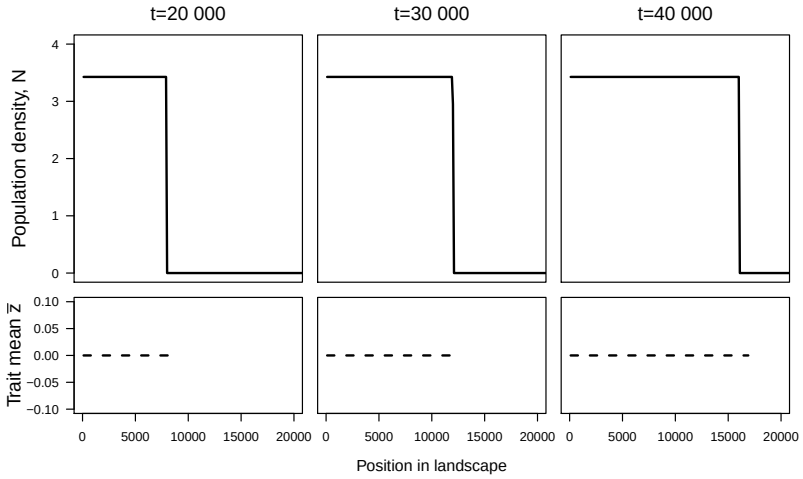

Figure 5.2: Travelling wave of invasion with no environmental gradient. For all simulations the population density evolved to be at carrying capacity (top row), and the trait mean to zero (bottom row), at all locations. Each column represents the invasion at a different time point. The parameter values used for these simulations were $r = 1.2$, $m_0 = 0.01$, $m_1 = 0.05$, $d = 4$, $\omega = 500$, $\beta = 50$, $v = 1$. For these parameter conditions the invasion speed was found to be 0.3908.

this population would invade throughout space and be at carrying capacity at all locations. This was verified by numerically simulating the invasion of this species, by iterating equations (5.8) and (5.9) in R (R Development Core Team, 2011). It was found that these simulations approached a travelling wave at the invasion front, which rapidly approached a constant speed as the invasion progressed. The population density was found to be at carrying capacity, and the mean value of the phenotypic trait zero, at all locations for all parameters investigated (Fig. 5.2).

It was found that the speed of the invasion was affected by the three types of variance included in the model. Faster speeds were observed when the variance v, of the phenotypic trait is smaller, when the variance β, of the dispersal function is bigger and when the variance ω, of the Gaussian fitness function is bigger. Smaller v means that there are fewer phenotypes present in the population, and so more individuals will have a phenotype that is at or close to zero, which both maximises survival and dispersal. Bigger β means that the dispersal function tends to zero slower for bigger values of the phenotypic trait z, and so there will be more dispersive phenotypes present in the population. Finally bigger ω means that the cost of the phenotypic trait not being the optimum value for survival is smaller, and so the population has higher mean fitness.

Calculation of invasion speed

To check that the speeds observed numerically were correct, the front propagation method of van Saarloos (2003) was used. In equations (5.8) and (5.9) the mean value of the trait depends upon space and time which makes linearising these equations difficult. In the simulations I investigated what happens when the mean value of the trait evolves, which revealed that when the landscape is homogenous the mean value of the trait always evolves to zero at all times across all space. It would be interesting to check whether the speed observed corresponds to the maximum wavespeed across all values of $\bar{z}$. This can be checked by calculating what the invasion speed would be if $\bar{z}$ is constant, and so if I set the phenotypic trait to be a constant value, equations (5.8) and (5.9) become even simpler. If the phenotypic trait is constant then the change in time and space of the trait mean is zero, so Eqn. (5.9) $= 0$, and then Eqn. (5.8) reduces to

$$N(x,t{+}1) = (\rho{-}2\gamma)N(x,t)e^{-m_1 N(x,t)}{+}\gamma[N(x{+}1,t)e^{-m_1 N(x+1,t)}{+}N(x{-}1,t)e^{-m_1 N(x-1,t)}], \tag{5.10}$$

where $\rho = \alpha A \exp\left(\frac{-\bar{z}^2}{2(w+v)}\right)$ and $\gamma = \frac{\alpha}{d} B \exp\left(-C\bar{z}^2\right)$. Eqn. (5.10) can then be easily linearised around the unstable steady state $N = 0$, giving

$$N(t, x+1) = (\rho - 2\gamma)N(x,t) + \gamma[N(x+1,t) + N(x-1,t)].$$

Using these linearised equations and following van Saarloos (2003), as I have in earlier chapters, I substitute $N \propto n\exp(-i\omega(k)t + ikx)$, where $\omega(k)$ is the dispersion relation of Fourier modes of the linearised equation (5.10), and k is the spatial wavenumbers. This gives the equation:

$$e^{-i\omega} = (\rho - 2\gamma) + \gamma(e^{ik} + e^{-ik}).$$

This leads to an eigenvalue problem, with solutions

$$\omega(k) = i\log\left(\rho - 2\gamma + 2\gamma\cos k\right). \tag{5.11}$$

This implies

$$\frac{d\omega(k)}{dk} = \frac{-i2\gamma\sin k}{\rho - 2\gamma + 2\gamma\cos k}. \tag{5.12}$$

The wave speed is then calculated by finding k^*, where k^* is the linear spreading point

(van Saarloos, 2003), such that

$$\frac{d\omega(k^*)}{dk^*} = \frac{\Im\omega(k^*)}{\Im k^*}, \tag{5.13}$$

where $\Im$ denotes the imaginary part. This equation represents a biological invasion so n cannot be negative, so I can deduce that k^* is purely imaginary. I can then assume $k^* = iq$ with q real, which I substitute into (5.13). The realised wavespeed is obtained by finding the real solution q that corresponds to the largest speed $v = \frac{\Im\omega(iq)}{q}$ (van Saarloos, 2003). Substituting into Eqn. (5.13) gives an equation which cannot be solved analytically. I therefore solve this numerically and then calculate the invasion speed, v, using this value of q.

I found that this method gives the same invasion speed as was found from the numerical simulations. As $\bar{z}$ was found to evolve to zero during the simulations, invasion speeds for other constant values of $\bar{z}$ were calculated using Eqn. (5.13) to check that the population was evolving to invade at the maximum speed across values of $\bar{z}$. Indeed, Fig. 5.3 confirms that the maximum invasion speeds occur for $\bar{z} = 0$, and that the speeds predicted using the front propagation method agree with those from numerical simulations when $\bar{z}$ evolves to zero. Interestingly, it can be seen from this figure that when there is a bigger trade-off between adaptation and dispersal (grey lines), a higher amount of phenotypic variance (dashed line), results in faster speeds than a small amount of phenotypic variance for bigger values of the mean phenotypic trait. This is because when the mean value of the trait is far from the optimum, more variance means that there will be a greater number of 'good' phenotypes in the population, i.e. phenotypes that will have higher dispersal and survival, than if there was less variance, and so the population has a faster invasion speed.

5.3.2 Environmental gradient varies across space

I then investigated the case where the optimum value of the trait for survival varies linearly in space. In this case it was expected that range margins would be formed because as the optimum value of the trait for survival increases, dispersal tends to zero, and so there will become a point when the population cannot invade any further. To investigate if this was the case numerical simulations were carried out by iterating equations (5.5) and (5.6) in R (R Development Core Team, 2011). These simulations revealed that as predicted range margins were formed, with the size of the range that arose determined by the different parameters used.

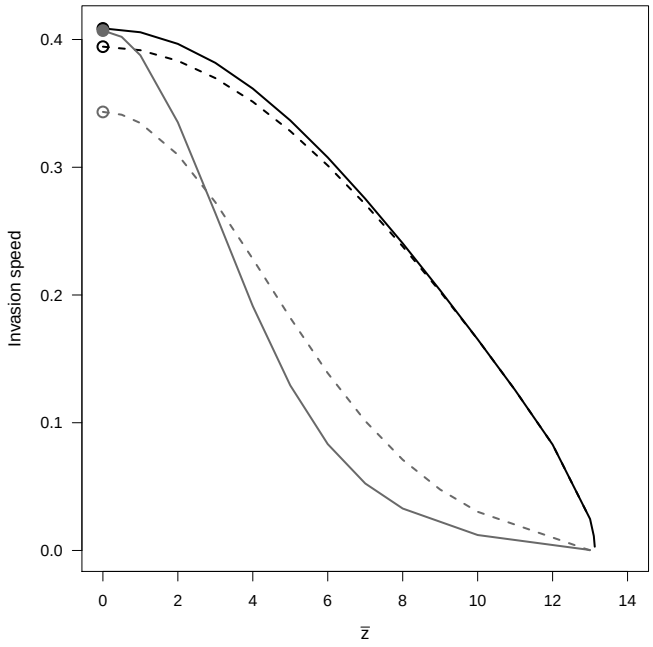

Figure 5.3: Invasion speed for different values of $\bar{z}$. The points represent predictions of the invasion speed from numerical simulations of Eqns. (5.8) and (5.9), when $\bar{z}$ is allowed to evolve. As was shown in Fig. 5.2 $\bar{z}$ always evolved to zero, and so these points are plotted at $\bar{z} = 0$. The curves represent numerical predictions of the invasion speed using the van Saarloos (2003) method, when $\bar{z}$ is set to be a fixed value in Eqn. (5.8). For all simulations the parameter values used were $r = 1.2$, $m_0 = 0.01$, $m_1 = 0.05$ and $\omega = 500$. The solid lines represent $v = 0.1$ and the dashed $v = 5$, with $\beta = 5$ used for the grey lines and $\beta = 50$ for the black lines. The speeds for negative z are the same as for positive so are not shown on this graph. It can be seen that the numerical predictions of the invasion speed when $\bar{z}$ evolves are the maximum speeds across all fixed values of $\bar{z}$ for each set of parameter values.

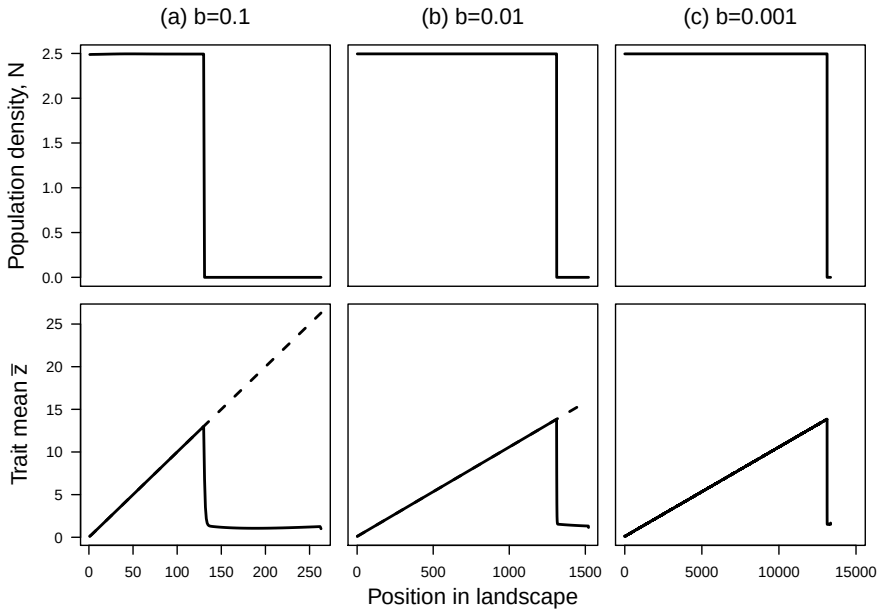

Figure 5.4: Formation of range margins for three different values of the environmental gradient, b. The dashed line shows the optimum value of the trait for survival. The parameters used in these simulations were $r = 1.2$, $m_0 = 0.01$, $m_1 = 0.05$, $\omega = 50$, $\beta = 2.5$, $v = 5$ and $d = 4$. In (a) the environmental gradient has slope $b = 0.1$, in (b) $b = 0.01$, and in (c) $b = 0.001$.

As expected, the steepness of the environmental gradient greatly influenced the size of range that evolved. Across all parameter space bigger ranges were observed for shallower environmental gradients, as can be seen in Fig. 5.4. This is because a shallower gradient means that the dispersal function evolves to zero further along the gradient, and so the population can disperse further. A steeper gradient results in the optimum value of the trait for survival reaching the value at which dispersal evolves to zero faster. Therefore if the trait mean matches the optimum, then a steep gradient means the population will not be able to invade very far before adaptation to the environment results in dispersal evolving to zero.

In these simulations I defined a range margin as having been formed when over consecutive time steps the position of the range front had not changed. This was determined by plotting invasion profiles, such as those given in Fig. 5.4, at different time points until the population density had not changed in space for a minimum of 10^4 time steps. The range size was then defined as the number of cells in the landscape that had a population density greater than half of what would be the equilibrium population density in a homogenous environment. To check that the range size that formed was independent of the initial conditions, simulations were carried out with different proportions of the

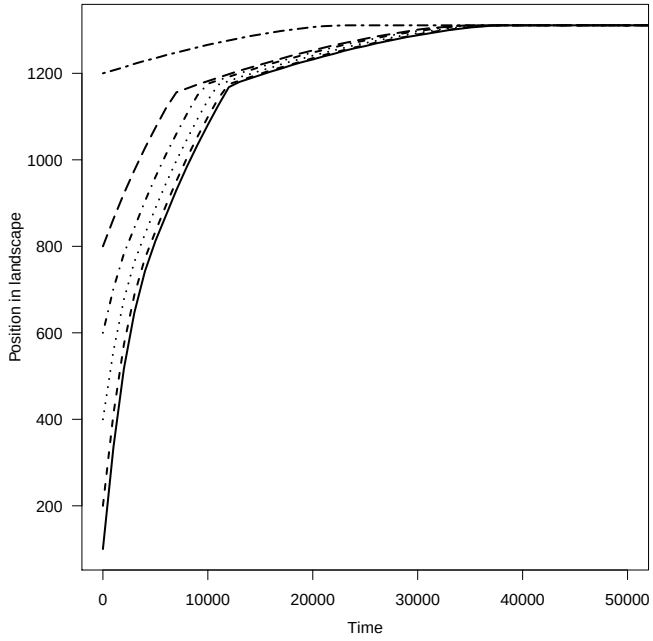

Figure 5.5: Formation of range margins with different initial conditions. The lines represent different initial conditions, from the first 100 cells of the lattice occupied by the population, to the first 1200 cells, all of which were found to form range margins at the same position in the landscape (cell 1311). The parameters used in these simulations were the same as in Fig. 5.4b.

landscape initially occupied. It was found that the same range size was formed with different starting conditions, giving numerical evidence for the evolution of a range margin (Fig. 5.5).

I next investigated how the size of the range that arose depended on the other parameters that were varied in the model. To do this I calculated the range size for different parameter values, and then multiplied these by the steepness of the environmental gradient that the simulations were run on. The range size multiplied by the gradient gives the optimum value of the trait for survival, θ, at which range margins are formed. I then plotted these values against the log of the phenotypic variance (Fig. 5.6).

This figure reveals three patterns for the formation of range margins. The first is that bigger ranges were formed when there was a smaller trade-off between dispersal and adaptation (bigger values of β). The second is that bigger ranges were formed when the amount of phenotypic variance, v, is small, and the third is that when there is weaker stabilising selection towards the optimum phenotype (bigger ω), large amounts of phenotypic variation result in the range being bigger in proportion to the gradient when the gradient is steeper (see Fig 5.6ii).

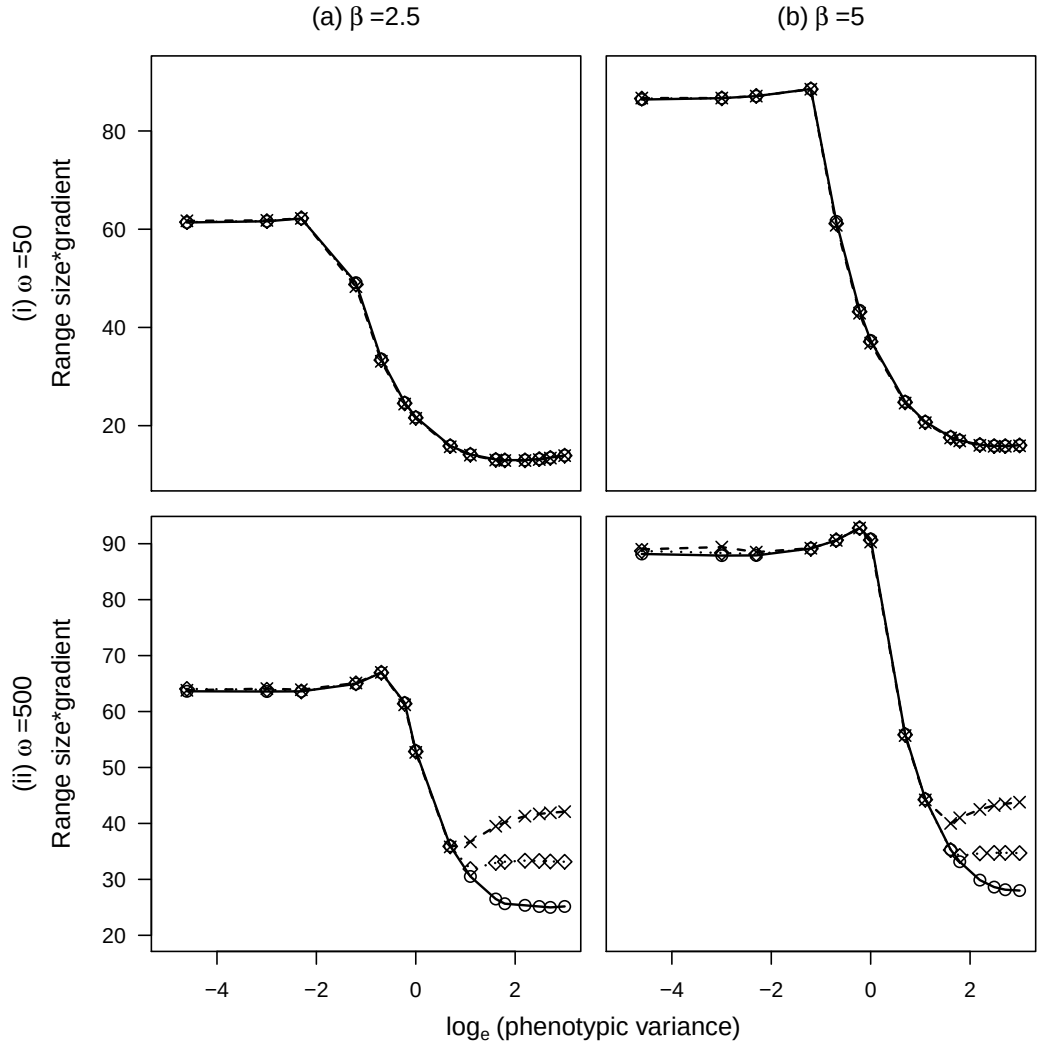

Figure 5.6: Range size scaled by the steepness of the environmental gradient as a function of the phenotypic variance. In (i) there there is strong stabilising selection towards the optimum phenotype ($\omega = 50$), and in (ii) there is weak stabilising selection ($\omega = 500$), with (a) and (b) representing two different variances of the dispersal function. The crosses represent an environmental gradient of $b = 0.1$, the diamonds $b = 0.05$, and the circles $b = 0.01$. The parameters used in these simulations were $r = 1.2$, $m_0 = 0.01$, $m_1 = 0.05$ and $d = 4$, with in (a) $\beta = 2.5$, and in (b) $\beta = 5$.

The first pattern, that bigger ranges are observed when the variance, β, of the dispersal function is larger, occurs because this means the dispersal rate tends to zero slower. There is therefore a smaller trade-off between dispersal and adaptation, and so the population can expand its range further before dispersal evolves to zero, resulting in bigger ranges being formed.

The second pattern observed was that bigger ranges are formed when the amount of phenotypic variance is small. When there is a smaller amount of phenotypic variance, evolution of the phenotypic trait is slower, and so there are fewer phenotypes present in the population. Offspring are therefore more likely to have phenotypes closer to their parents, and so they will be better adapted locally. It also takes longer for the mean phenotype to evolve to match the optimum value for survival, which means there will be more dispersal and so the population can invade further. However, as can be seen in Fig. 5.6, very small amounts of phenotypic variance do not result in the biggest ranges. This is because if the amount of phenotypic variance is too small, evolution occurs very slowly, and so the population takes longer to adapt to the environment, and so has lower fitness. The population cannot therefore invade as far as a population that has a slightly higher amount of variance, which means it can adapt a bit faster to the environment and consequently has higher population fitness. The size of the variance that results in the biggest range sizes is smaller, when there is stronger stabilising selection. This means there is stronger selection towards the optimum phenotype, so despite evolution being slow more phenotypes will be closer to the optimum value for survival, and so the population has higher fitness.

When there was strong stabilising selection towards the optimum phenotype, it was found that the size of a species' range is proportional to the steepness of the environmental gradient (Fig 5.6i). The population therefore stops invading at the same value of θ, and so the upper limit of θ where the population can still disperse and be adapted to the environment is proportional to the steepness of the gradient. This was also found to be the case when there was weak stabilising selection and small amounts of phenotypic variance. However, the third pattern observed was that when there were larger amounts of phenotypic variance, the population could extend further in proportion to the gradient when the gradient was steeper (Fig 5.6ii). This suggests that when there is weak stabilising selection phenotypes can be quite maladapted without causing a cost to the fitness of the population. More phenotypic variance means that there will be a greater number of phenotypes present in the population, some of which will be less well-adapted but they will have higher dispersal ability. This results in the population expanding its

range further. This effect is stronger when the environmental gradient is steeper because the spatial scale is smaller, and so dispersal is occurring over smaller distances.

5.3.3 Environmental gradient varies across time and space

Having found where a population with this trade-off between dispersal and adaptation forms range margins, I then investigated what happens if the environmental gradient also varies in time. Simulations were performed where the optimum value of the trait θ now depends not just on the spatial location x, but also the time t, as described in the Model section. θ was defined so that if $x - ct < 0$, then I set $\theta = 0$. This simulates the gradient shifting forwards in space, with the environment becoming homogenous behind the shifting gradient.

It was found that if the gradient shifts at a slow enough speed then the population can invade at the speed at which the gradient is shifted. If this is the case then, the slower the gradient is shifted, the further into the area where the optimum value of the trait is not zero that the population remains. Very slow speeds result in the population maintaining the same size range where $\theta \neq 0$ as it did when the environmental gradient is static in time. Faster shifting speeds result in a reduction of this range size.

Even faster speeds result in the population lagging behind the speed at which the environment is shifted. It was found that the threshold speed for which the population could invade at the speed of the shifting gradient, is the invasion speed of the population in the absence of a gradient. For speeds faster than this, the population is then only invading through the landscape where $\theta = 0$, and so if the trait mean matches the optimum, then the population has both optimal survival and the highest dispersal. It was found that the trait mean did evolve to be zero to match the optimum, and travelling waves of invasion such as those found in simulations with no environmental gradient (Fig. 5.2) were observed.

When the gradient was shifted at speeds slower than that at which the population could invade in the absence of a gradient, it was found that a fluctuation in population density was sometimes observed at the invasion front. A noticeable fluctuation was observed when the environmental gradient was steep and there was a small amount of phenotypic variance (Fig. 5.7a). When the gradient was shallower and variance higher, although from Fig. 5.7b there does not appear to be a fluctuation, closer examination revealed that there was a very small deviation from the equilibrium population density at the invasion front (Fig. 5.8).

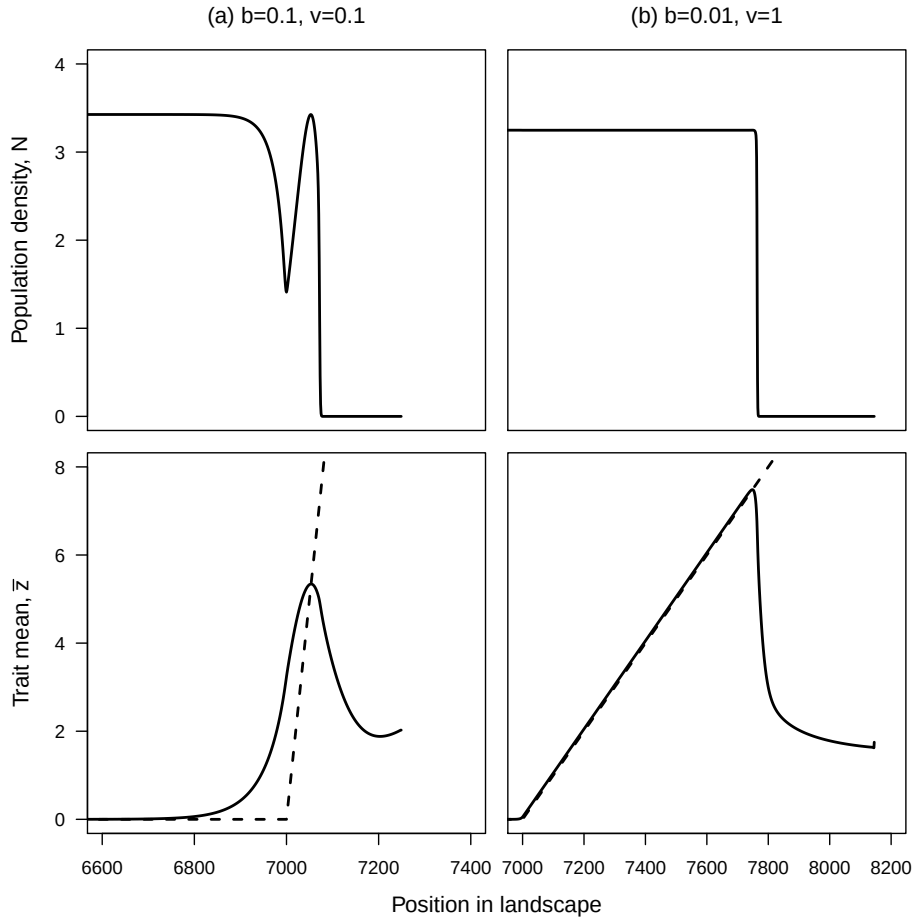

Figure 5.7: Shape of the travelling wavefront when the gradient is shifting in time. In (a) the environmental gradient is steep and there is a small amount of phenotypic variance, and here there is a noticeable fluctuation in population density at the leading edge. In (b) the environmental gradient is shallower and there is larger phenotypic variance, and no noticeable fluctuation in population density. For both simulations the gradient was shifted at speed $c = 0.1$. The lines show the shape of the travelling wavefront at one time point. The dashed line on the bottom two panels represents the value of the trait that maximises population growth. The parameters used in these simulations were $r = 1.2$, $m_0 = 0.01$, $m_1 = 0.05$, $d = 4$, $\omega = 50$ and $\beta = 5$ with in (a) $b = 0.1$ and $v = 0.1$, and in (b) $b = 0.01$ and $v = 1$.

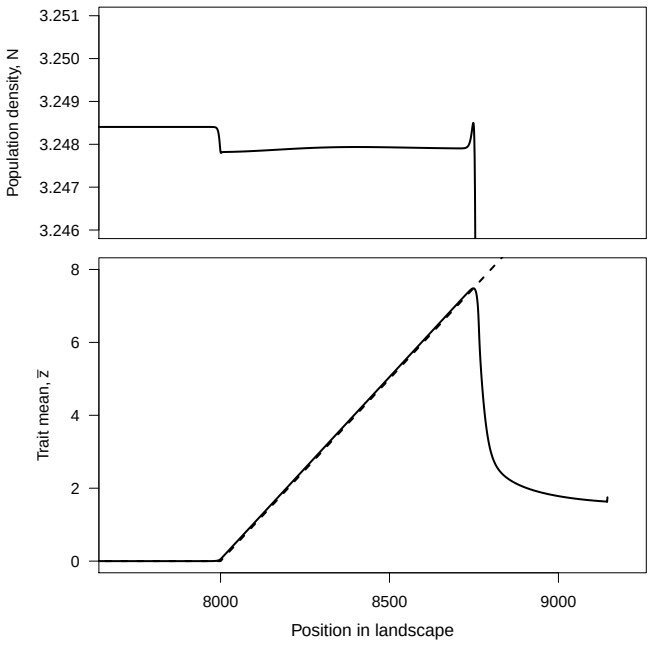

Figure 5.8: Closer examination of the fluctuation in population density for shallower environmental gradients. This figure shows a close-up of the front for the invasion wave in Fig. 5.7b. It is now evident that there is a small fluctuation in population density along the environmental gradient.

This fluctuation in population density at the invasion front was found to begin at the transition between where there is no gradient, and where there is a gradient (see Fig. 5.8 for a clear example of this). Where the mean phenotype matches the optimum value of the trait for survival, population density is at equilibrium. However, because the trait mean, $\bar{z}$, is continuous, in the area where the optimum changes from being zero to being greater than zero, the trait mean is unable to match the optimum. Higher dispersal of phenotypes from the area where the optimum value of the trait is zero results in dispersal of maladapted phenotypes along the gradient, preventing the trait mean from matching the optimum. This maladaptation results in lower survival, and so there is a decrease in population density. The trait mean then evolves to match the optimum at some point along the gradient, and so again here the population density is higher. Further along the gradient the trait mean is lower than the optimum to allow dispersal at the expanding range edge. This is at the expense of higher fitness, and so the population density again decreases.

This maladaptation of the trait either side of where the trait mean matches the optimum value for survival along the gradient results in the fluctuation in population density observed. Bigger fluctuations are observed when the gradient is steeper because there will be higher maladaptation around the optimum. When the phenotypic variance is small, bigger fluctuations also occur because there are fewer phenotypes present, and so it will take longer for the trait mean to evolve to match the optimum.

There are two possible strategies that a species with the body plan described in this model can adopt. The species can either adapt to the environment at all points along the environmental gradient with the consequence that it is unable to disperse at the range front, or the species can disperse at the range front and so expand its range but at the cost of being maladapted and hence have lower survival. In the case where the environmental gradient was fixed in time, it was found that far along the environmental gradient the cost of dispersing on survival became too high, and so range margins were always formed (see Fig. 5.4). However, when the gradient shifts in time the species was found to expand its range. In this case it can be seen from the lower two panels of Fig. 5.7 that at the invasion front the trait mean rapidly decreases, so that the mean is much smaller than the value of the trait that maximises population growth. It can also be seen from Fig. 5.1 that more dispersal occurs when the value of the trait z is smaller, and so in order for dispersal to occur, and the population to invade at the range front, the trait mean needs to be much lower than the optimum value for survival. This large degree of maladaptation at the range front is greater than the degree of maladaptation observed in models that do

not include a trade-off between dispersal and adaptation. For example, in the models of both Kirkpatrick and Barton (1997) and Alleaume-Benharira et al. (2006), there is not a steep decrease in the trait mean at the range edge. In these models, more dispersal means more gene swamping of maladapted phenotypes from the centre of the range, preventing the population from adapting at the range edge. However, in the model in this chapter, because of the trade-off between dispersal and adaptation, range expansions along an environmental gradient can only occur if there is some maladaptation at the range edge.

5.4 Discussion

The formation of range margins as a result of a failure to adapt to unfavourable conditions beyond a species' current range has long been investigated both theoretically and empirically, and yet there is still not a clear understanding as to why evolution does not allow adaptation to occur. The model developed in this chapter suggests that range margins may be formed as a result of a trade-off between dispersal and adaptation. I have found that along an environmental gradient if adaptation comes at the cost of reduced dispersal, then at some point the species will always be unable to expand any further. The largest ranges were found when the environmental gradient was shallower, the trade-off between adaptation and dispersal was smaller, and the amount of phenotypic variance was smaller.

The introduction of a trade-off between dispersal and adaptation has, therefore, resulted in an interesting proposition: could it be that range margins are formed as a result of adaptation to the environment at the range edge at the cost of dispersal, rather than maladaptation at the range edge? Theoretical models to date have assumed that it is a failure to adapt to the environment that results in the formation of range margins (e.g. see Sexton et al., 2009, for a review). However, in this model, because adaptation to the environment comes at the cost of reduced dispersal, it is adaptation to the environment itself, that prevents a species from expanding its range.

In contrast to models where adaptation to the environment does not come at a cost (Bridle et al., 2010; Kirkpatrick and Barton, 1997), I found that range margins are always formed. In previous models unlimited adaptation was found to occur for shallower gradients, but here it was found that because of the trade-off between dispersal and adaptation, range margins were formed even when the gradient was shallow. The largest ranges were found when the gradient was shallower because dispersal evolved to zero further along

the gradient.

It was also found that the stronger the trade-off between dispersal and adaptation, the smaller range a species had. This is because a bigger trade-off means that to adapt to the environment there are bigger deviations from a species' optimal body plan, and so dispersal evolves to zero quicker. If species are found to have trade-offs between adaptation and dispersal, then it may be that the size of their range is related to the strength of this trade-off.

In this model small amounts of phenotypic variance resulted in the biggest ranges. This result is different to that found when there is no trade-off, as then adaptation to any steepness of gradient was found to occur because of the increased evolutionary potential resulting from higher genetic variance (Barton, 2001). However, in this model, higher amounts of variance means that the trait evolves to match the optimum value for survival everywhere which is detrimental for dispersal. Dispersal therefore evolves to zero faster, and so a smaller range is formed.

When there was weak stabilising selection towards the optimum phenotype, larger amounts of phenotypic variance resulted in bigger ranges in proportion to the environmental gradient, when the gradient was steeper. In this case the phenotypic trait, z, varies more without causing a cost to fitness. Here, because there is weaker selection towards the optimum phenotype, more variance means that there are more dispersive phenotypes present in the population. The population is therefore able to invade further in proportion to the gradient. For steep gradients the spatial scale is smaller and so the observed effect is bigger. Small amounts of phenotypic variance still result in the biggest ranges, but these results suggests that a larger amount of variance is better than an intermediate amount, as even though there may be more maladapted phenotypes there will also be more dispersive phenotypes present in the population.

There is empirical evidence of trade-offs between dispersal and adaptation in several fish and amphibian species (e.g. Atlantic silversides (Billerbeck et al., 2001) and anuran toads (Arendt, 2003) to name a few). In these species the evolution of faster growth rates at higher latitudes, where the growing season is shorter, has been found to come at the cost of dispersal. It may therefore be that these species have been prevented from further expanding their ranges as a result of this trade-off. It would be interesting to investigate whether the evolution of even faster growth rates in these species is prevented because further deviations from their optimal body plan comes at too great a cost.

In this model when the environmental gradient was shifted in time, it was found that a species with this trade-off was then able to expand its range. If the environment shifted slower than the speed at which the species could invade when there is no gradient, then the species was found to keep up. However, if the speed was faster then the species lagged behind. If this was the case then the species expanded its range at its invasion speed in the absence of a gradient.

When the gradient was shifted in time, and so the species was able to expand its range, it was observed that there was a large degree of maladaptation at the invasion front. This was observed because for the species to be able to invade along an environmental gradient, there must be dispersive phenotypes present at the range front. In this model, the body plan of the species means that if it is dispersive it will not be adapted to the conditions at the front, and so the mean value of the trait will be below the optimum value for survival. In contrast to models without a trade-off (e.g. see Kirkpatrick and Barton, 1997), dispersal of phenotypes from the centre of the species' range to the range edge is beneficial, as this increases the number of dispersive phenotypes present here, and so the population can expand its range.

In models with no trade-off between adaptation and dispersal, species are predicted to survive greater rates of change if they have larger amounts of genetic variance (Duputié et al., 2012; Pease et al., 1989; Polechova et al., 2009). However, with a trade-off it was found that faster speeds are observed with smaller amounts of phenotypic variance, and so here more phenotypic variance does not help a species to invade. This is because more phenotypic variance means that more phenotypes evolve to match the optimum value for survival, which results in less dispersive phenotypes at the range front. This model therefore predicts that species that have smaller amounts of phenotypic variance will be able to keep up with the fastest rates of change.

These results suggest that species that have restricted ranges as a result of a trade-off between adaptation and dispersal may be able to undergo range expansions with climate change. This is because if climate change means that environmental gradients shift in space, then there will always be a region where the species is able to disperse, and so the species will be able to shift its range. For example, if climate change results in longer growing seasons at higher latitudes, then for the species previously mentioned that exhibit a trade-off between fast growth and dispersal, a longer growing season will mean that growth does not need to be as fast. Individuals at higher latitudes may then be able to grow slower, and so their body plan will not deviate so far from the optimal plan. This

will mean that these individuals will be more dispersive and so can expand their range. Indeed, there is some evidence to suggest that with climate change the Atlantic silverside has expanded its range further north (Sargent et al., 2008).

In this model I have assumed that when the environment has shifted the landscape behind it has become homogenous. When the environment shifts faster than a species can invade at, the species was then still able to persist. If instead the trait became negative when the gradient shifted, the species would then need to adapt to these new conditions. If the gradient shifted too fast in this case, a species may no longer be able to persist, and the speed at which it goes extinct may be not be the same as the speed at which it is able to invade.

A major simplifying assumption made in this model is that the same trait that determines adaptation to the environment also determines dispersal, where it is assumed that adaptation to new environments evolves much more rapidly than dispersal does. This is unlikely to be the case for real species. Instead it would be better to use a multi-trait model where there is an interaction between the trait that determines adaptation and dispersal. However, this would make the model a lot more complicated, and so this approach was not used here. Multi-trait quantitative genetics models have been developed (e.g. see Duputié et al., 2012), and so developments of this model could use a similar approach to see if range margins are formed in the same way. Alternatively a model similar to the approach used in this chapter, but where dispersal evolves more rapidly, could also more realistically model this trade-off.

Another simplifying assumption made in this model is that genetic variance is constant. When genetic variance evolves it is found that parameters that give limited adaptation with constant variance (Kirkpatrick and Barton, 1997) result in unlimited adaptation (Barton, 2001). It may be that if genetic variance evolves in this model then instead of unlimited adaptation, maximum range sizes for each steepness of environmental gradient and degree of trade-off are always able to evolve, and so investigating this would be a natural extension to this model.

This model has revealed that range margins may be formed as a result of trade-offs between adaptation to environmental gradients and dispersal. Larger ranges were found when conditions meant that this trade-off was not as strong. If the gradient shifted in time then this meant there was always a region into which the species could disperse, and so the species expanded its range. Further research is needed into understanding whether trade-offs between adaptation to different environments and other traits, in particular dispersal,

can explain the formation of range margins.

6. General discussion

One of the major threats to global biodiversity is modern day climate change, which together with land cover changes such as habitat fragmentation and habitat destruction, poses a challenge to the survival of many species. Being able to predict the rate at which species spread is important for preserving biodiversity, as these rates will have an impact on whether species will be able to shift with climate change. There is evidence that some species are shifting their ranges in the direction predicted by climate change (e.g. Chen et al., 2011), but also that other species are lagging behind (Menendez et al., 2006; Warren et al., 2001) or are experiencing range contractions (Franco et al., 2006; Wilson et al., 2005). There is also evidence that species have survived past periods of climate change, but modern change is occurring faster than previously observed (Davis and Shaw, 2001), and so the number of species able to keep up with rates of change in the long term is unknown.

Invasions by exotic species are also increasingly occurring, as a result either directly or indirectly of human activities (Sakai et al., 2001). These species can have big impacts on ecological systems threatening local wildlife (Gurevitch and Padilla, 2004). Being able to predict the rates at which species spread, and understanding population dynamics during invasions will be important for trying to control these species.

Mathematical models have long been used to investigate what affects the rate of spread of species, with a strong focus in recent years in predicting species' responses to climate change. Increasing evidence from these models is that dispersal can evolve during range expansions (for reviews see, Le Galliard et al., 2012; Travis and Dytham, 2012). However, few models look at whether, and how, dispersal trades-off with other traits during invasions (but see Burton et al., 2010; Travis et al., 2012, 2010).

The purpose of this thesis was to investigate how trade-offs between dispersal and other traits affect the rate of range expansions. In this discussion I will summarise the key findings of this thesis, and then discuss them in the context of the wider literature indicating implications for future research.

6.1 Overview of the thesis

6.1.1 Trade-offs between dispersal and reproductive rate

The first three data chapters in this thesis model a trade-off between dispersal and population growth rate. Chapters 2 and 3 look at the invasion of a species that exhibits dispersal polymorphism, and Chapter 4 introduces a shifting climate into the model. These models look at the invasion of a species where there is a trade-off between dispersal and establishment ability, so may for example, represent a wing polymorphic insect, where investment in flight come at the cost of reduced fecundity (Zera and Denno, 1997).

The key finding of Chapter 2 is that anomalous invasion speeds were observed when there is a large trade-off between dispersal and establishment. These speeds had previously been observed in strongly cooperative systems (Weinberger et al., 2007), but the model used in this chapter revealed that these speeds also evolve when mutation between morphs is vanishingly small, and so there is effectively no cooperation. The anomalous invasion speeds were found to be up to twice as fast as a single morph's invasion speed for realistic parameter conditions, suggesting that if a species is polymorphic, trade-offs between traits can result in faster invasion speeds than may be predicted from looking at a single morph.

It was surprising that anomalous invasion speeds were found to persist when the mutation rate between morphs tends to zero because the invasion speed is determined by what happens at low density, and in this limit the number of individuals of the minority morph present at the invasion front tends to zero. It may be then that anomalous invasion speeds occurred as an artefact of the fact that densities can be arbitrarily small in this model. To investigate whether these speeds were still observed in more complex models, where at low densities only one morph can be present at the invasion front, a stochastic version of this model was developed in Chapter 3. This model showed that anomalous speeds persist when there is demographic stochasticity, but for a smaller range of conditions than found by the deterministic model. Anomalous speeds were found to occur when the population had a high carrying capacity, when mutation between morphs was high, or when the individual morph's invasion speeds when invading on their own in the landscape were similar.

Investigation of why these speeds arose showed that they only occur when there is a trade-off between the morphs, and when both the establisher and disperser are at high enough densities at the invasion front. High densities can occur as a result of any of

the three factors that were found to result in anomalous invasion speeds. When densities are lower, so the model is more stochastic, these speeds are less likely to be observed. Demographic stochasticity does therefore mean that large trade-offs between dispersal and establishment may not have as big an effect on invasion speeds as was predicted by the deterministic model.

Together the results of these two chapters suggest that when predicting invasion speeds it is important to take into account the whole community of phenotypes, and not just look at a single morph's invasion speed. For example, predicting the speed of invasion of a wing polymorphic species just from the speed that the flight-capable morph can invade at may give incorrect predictions. All phenotypes present in the population need to be taken into account, as the presence of more than one morph may mean that anomalous invasion speeds occur. This could have implications for controlling the spread of invasive species because if the species is invading in high densities, and is polymorphic, it may spread faster than expected.

Having established that anomalous speeds do still persist in stochastic models, I then added a shifting climate to the model in Chapter 4 to investigate whether dispersal polymorphism helps a species to keep up with the rate of change. It was found that anomalous invasion speeds may help species to survive climate change. For the case where there is a large trade-off in the morphs' establishment and dispersal abilities it was found that for some rates of change the presence of both morphs meant the population could keep up, when the two morphs by themselves would become extinct. However, it was found that if one morph is superior, either in terms of being a better establisher or better disperser, and there is not a big difference in the other trait, then mutation between morphs can slow invasion speeds, and may result in a species being unable to keep up with the rate of change. It was found that if the climate was shifted slower than the speed at which a species was predicted to invade at in Chapter 3, then it would be able to keep up with the rate of change, but if the climate shifted faster than this, the species would always become extinct. These results suggest that if a species' invasion speed is known, then this may help predict whether species will be able to survive periods of climate change by shifting their range.

These models show that a trade-off between dispersal and reproductive rate can alter range shifting dynamics, and can affect whether a species will be able to keep up with rates of climate change. These results highlight the importance of taking into account all phenotypes present in a population when predicting species' responses to climate change.

6.1.2 Trade-offs between dispersal and adaptation to an environmental gradient

Chapter 5 investigates how a different trade-off with dispersal may affect species' responses to climate change. Here, I investigated a trade-off between dispersal and adaptation to an environmental gradient. In this model it was assumed that a species has an optimal body plan that maximises both dispersal and survival, and that if adaptation to another environment is required this comes at the cost of reduced dispersal. To model this trade-off, a quantitative genetics model was used, this was because I was interested in what happened if there were lots of different phenotypes present in the population so that the species could adapt to different conditions. I therefore needed to model a continuous spectrum of phenotypes, rather than use a model with two distinct phenotypes as I did in Chapters 2-4.

Here it was found that if there was no environmental gradient then a species evolves to follow the speed of the phenotype that maximises dispersal and survival, with faster speeds observed when there was a smaller cost to dispersing. The invasion speed was also found to be faster when there was a smaller amount of phenotypic variance. The invasion speed here is not the same as if there is only a single phenotype present because a mixture of phenotypes means there will be maladapted phenotypes in the population which slows the invasion speed.

The introduction of an environmental gradient meant that range margins were formed. This is because at some point along the gradient the trade-off between dispersal and adaptation will be so great that dispersal is effectively zero, and so the species cannot invade any further. If there are trade-offs between adaptation and dispersal then this may explain why range margins are formed when other models that do not include trade-offs suggest that a species will always be able to adapt to the environment (Bridle et al., 2010; Kirkpatrick and Barton, 1997).

If the gradient then shifts in time, so that behind the shifting gradient the conditions are optimal for the body plan of the species, then the species is able to expand its range. This simulates an expansion of optimal conditions. The speed at which the environment shifts determines whether the species is able to keep up with the rate of shifting. The threshold speed for a species keeping up with the shifting environment was found to be the speed at which the species is able to invade at in the absence of a gradient. If the environment shifts slower than this, the species is always able to keep up.

In the absence of a gradient, faster invasion speeds were observed when there was a smaller amount of phenotypic variance. When the environmental gradient was shifted in space, species with less phenotypic variance could therefore keep up with faster rates of change, however, they were also more maladapted along the gradient, and so had lowered survival resulting in bigger fluctuations in population density at the invasion front. Models that do not incorporate trade-offs between adaptation and dispersal predict that species will survive greater rates of change if they have larger amounts of genetic variance (Duputié et al., 2012; Pease et al., 1989; Polechova et al., 2009). The results from this model reveal that if there are trade-offs, although if there is more variance a species may be better adapted to the environment, this does not help a species invade, and so species are predicted to survive greater rates of change if they have smaller amounts of phenotypic variance.

These results suggest that deviations from a species' optimal body plan result in the formation of range margins. Under a simulated shifting gradient, a species is better able to keep up with the rate of change when there is a smaller trade-off between adaptation and dispersal. A trade-off between adaptation and dispersal may therefore affect a species' ability to respond to climate change. If adaptation to novel conditions comes at the cost of dispersal, and if a shifting environment results in the reduction of the optimal conditions for a species, then species may not be able to keep up with rates of change.

The results of this thesis suggest that trade-offs between dispersal and other traits can affect the rates of range expansion of species, and so it is important to consider these when predicting whether species will be able to keep up with rates of spread. The models used in this thesis are simple and do not incorporate many factors that other models have found to influence range shifting, and so these results will now be discussed in the context of the wider literature.

6.2 Future directions and wider perspectives

6.2.1 Trade-offs between dispersal and other traits

Two different trade-offs between dispersal and other traits were investigated in this thesis: the first was a direct trade-off between dispersal and reproductive ability, and in the second adaptation to different environments was found to come at the cost of reduced dispersal,

both of which suggest that trade-offs can affect the rate of species' range expansions. A trade-off between dispersal and reproduction is the most commonly modelled assumption (Phillips et al., 2010b). There is evidence that dispersal does trade-off with fecundity in expanding populations. For example, populations of the speckled wood butterfly in more recently colonised sites were found to have increased dispersal ability but were less fecund (Hughes et al., 2003), and so it is important to understand how this trade-off affects range shifting dynamics.

However, other species that are undergoing range expansions do not seem to be experiencing such trade-offs. For example, at the range front where cane toads have evolved increased dispersal, they also have faster population growth rates (Phillips, 2009). Instead it has been suggested that there may be trade-offs with other traits that are not related to fitness at the invasion front, for example, if range expansions mean that species escape their natural enemies, increased dispersal may evolve at the cost of defence against natural enemies (Phillips et al., 2010b). In the case of the cane toads it appears that an enhanced dispersal rate is associated with spinal injuries (Brown et al., 2007; Shilton et al., 2008), and it has been found that toads at the front have reduced investment in immune defence (Llewellyn et al., 2012). For this species it has been suggested that this may provide a mechanism for controlling their spread (Brown et al., 2007). For species that are expanding their range as a result of climate change, trade-offs between increased dispersal and immune defence could be a concern in the long term. Modelling these different observed trade-offs will be important in understanding what impact they will have on species persistence.

Few theoretical studies to date have investigated the consequences of increased evolution of dispersal during range expansions. One theoretical study that has investigated trade-offs has shown that dispersal and reproductive ability can evolve at the expense of competitive ability (Burton et al., 2010). When invading into an area with a competitor this can reduce the rate of dispersal evolution. In this model simulations were either performed with a species invading into an area in the absence of a competitor, or into an area fully occupied by a competitor. The case where a species undergoes a period of range expansion before encountering a competitor was not investigated. It may be in this case, if a competitor is encountered at a time later in the expansion when dispersal has already evolved at the cost of competitive ability, the species is now a poorer competitor and so fails to establish and expand its range any further. Other models have found that evolution of increased dispersal can act as a barrier to further dispersal, by preventing adaptation to

new environments (Phillips, 2012). It would be interesting to investigate whether similarly evolution of increased dispersal could act as a barrier to further dispersal as a result of reduced competitive ability. More work investigating how trade-offs between dispersal and competitive ability affects a species' ability to expand its range is therefore required.

There are many other costs associated with dispersal (review, see Bonte et al., 2012) and more work needs to be carried out to investigate how these may affect range shifting dynamics. One recent advance has been in modelling a trade-off with increased dispersal in plants. In this model the evolution of taller plants, so that seeds can be dispersed over longer distances, comes at the cost of fewer seeds produced (Travis et al., 2010). This can result in different range shifting dynamics depending on the strategy that evolves across fragmented landscapes.

The results from the models in Chapters 2-4 of this thesis suggest that the presence of both good dispersers and good establishers at the invasion front can result in faster range expansions. In relation to the model of Travis et al. (2010), this would suggest that faster range expansions would be observed if there were both plants that are taller, so disperse over longer distances but produce fewer seeds, and shorter plants that produce more seeds but don't disperse as far. However, Travis et al. (2010) observe that typically there is evolution of taller plants, so selecting for longer dispersal distances during range expansions. It would be interesting to model the evolution of dispersal rate during the range expansion of a polymorphic population such as that modelled in Chapters 2-4 to see if similarly, evolution results in increased dispersal of all phenotypes, when results of the models in this thesis where dispersal doesn't evolve, suggest that populations could experience faster range expansions if a community of phenotypes with large trade-offs between morphs are present. There is therefore a need to understand how different kinds of trade-offs with dispersal, and how these evolve, will impact on speeds of range expansions.

6.2.2 More realistic modelling of dispersal

The models used in this thesis modelled dispersal using a simple emigration rate. However, this only encompasses one aspect of the dispersal process, as was discussed in the Introduction. Costs incurred during dispersal can be during any of these stages, and there may be feedback between the different phases of dispersal (Bonte et al., 2012). More complex modelling of dispersal that takes into account other aspects rather than just an emigration rate, has been found to affect the rate of range expansions. For example,

inclusion of density-dependent dispersal (Travis et al., 2009), evolution of a dispersal kernel rather than just an emigration rate (Boeye et al., 2013; Travis et al., 2010), or modelling temporally variable dispersal (Ellner and Schreiber, 2012) all result in faster range expansions.

However, most of these models (except Travis et al., 2010) do not incorporate trade-offs with other traits, which the results from the models in this thesis and others (e.g. Burton et al., 2010) suggest will be important. The model developed by Travis et al. (2010) provides a good starting point for the incorporation of more mechanistic modelling of dispersal. Other mechanistic models which incorporate more realistic dispersal have begun to be developed (e.g. Bartoń et al., 2012), and so incorporation of trade-offs with other traits needs to be integrated into these.

Travis et al. (2012) have made a further development in the advancement of modelling trade-offs with dispersal and other traits. They have developed a stochastic IBM, which investigates the costs associated with different stages of the modelling process. They model a trade-off between investment in safer movement ability and fecundity, and found that the shape of this trade-off influences the joint evolution of the three dispersal parameters modelled.

In the models used in this thesis, it is implicitly assumed that during a species' development period, increased investment in movement ability, e.g. in Chapters 2-4 in terms of investing in flight apparatus if the species is a wing polymorphic insect, means that a species can move more efficiently during the movement phase. In the model of Travis et al. (2012) explicitly modelling these stages results in different dispersal strategies evolving depending on the shape of the trade-off. If investment in movement ability to reduce the costs of transferring through inhospitable matrix has a low cost to fecundity, then safe movement and high emigration rates evolve. If investment in movement ability comes at a bigger cost to fecundity, low investment in movement ability and low emigration rates evolve. In a patchy landscape it may therefore be that the high emigration rates and low reproductive rates that I have assumed a morph can have, do not evolve when different stages of dispersal are modelled and there are costs to dispersing into unsuitable areas. In this case slower invasion speeds than predicted from the models in this thesis may be observed. To predict if this is the case, and to understand species' responses to climate change, increasingly models such as the stochastic approach developed by Travis et al. (2012) will be needed.

6.2.3 Increasing spatial complexity

The models used in Chapters 2-4 investigate range shifting dynamics of a polymorphic population in a homogenous environment. The evolution of polymorphism in dispersal distance strategies has been found to be affected by landscape structure, with long and short dispersal distances evolving with different properties of the landscape (Bonte et al., 2010). It would be interesting to add a heterogenous landscape into the models that I developed to investigate whether anomalous invasion speeds still arise, and whether they are more beneficial in certain landscape structures.

The model developed in Chapter 5 suggests that taking into account trade-offs with dispersal along environmental gradients is important. If adaptation to novel conditions comes at the cost of dispersal then this may slow range expansions. However, if climate change results in the environment shifting then this may mean that these species are able to expand their range. In this model I again assumed a pre-emigration cost to dispersal, where for example, faster growth occurs at the cost of development of structures that aid dispersal. If trade-offs between adaptation and different stages of dispersal were explicitly modelled, it would be expected that a trade-off with this stage would greatly influence range shifting dynamics. Along an environmental gradient this will feedback on the movement and settlement stages of dispersal, as reduced investment in structures that aid dispersal will result in less efficient movement, and dispersal itself moves individuals to sites where they may be maladapted. Modelling each of these stages may help to explain how the costs of dispersal at each stage trade-off with adaptation, and how these different costs affect a species' ability to expand its range.

Other models investigating the range expansion of species along environmental gradients have shown that the structure of the landscape can affect a species' ability to expand its range. For example, Phillips (2012) found that if a species underwent a period of range expansion before an environmental gradient was encountered, then the evolution of increased dispersal could prevent adaptation to the new environment, and so act as a barrier to further dispersal. However, in a fragmented landscape the evolution of increased dispersal can help a species to disperse beyond unsuitable patches and continue expanding its range (Travis et al., 2010). In the model by Travis et al. (2012) the shape of the trade-off between dispersal and fecundity in a patchy landscape was found to have an outcome on the evolutionary potential of a species, highlighting the importance of incorporating trade-offs in other models with heterogenous landscapes. Increasingly species will encounter

different human influenced landscapes, and so understanding species' responses through these landscapes is important.

6.3 Concluding thoughts

As rates of climate change are set to increase and may be variable (Loarie et al., 2009), understanding the rates at which species spread is important. The models developed in this thesis and others (Burton et al., 2010; Travis et al., 2012, 2010) suggest that trade-offs between dispersal and other life-history traits need to be considered when making predictions. The models developed in this thesis are simple in their assumptions but are useful in giving predictions about how trade-offs might influence range shifting dynamics.

There is a growing literature on how dispersal evolves during range expansions, and so it is time to incorporate trade-offs into more complex models in order to predict species' responses to climate change. Adding more detail into these models will increase their complexity, however, now that we have a better understanding of the predictions gained from simpler models, more complex models are needed if predictions are going to be useful for conservation management. An understanding of the long-term consequences of increased dispersal will be important in determining species persistence in a changing world.

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Appendices

A Calculation of invasion speeds by looking for travelling wave solutions

A common method used to calculate range expansion speeds is to look for travelling wave solutions, as was described for the example of the Fisher equation in section 1.2.4 of the Introduction. Here I will explain what can be obtained from using this method to solve the PDEs of the dispersal polymorphism model described in Chapter 2. In the spatially homogenous situation of Eqns. (2.1) and (2.2), it was shown in Chapter 2 that there are two steady states, an unstable extinction state $(n_e, n_d) = (0, 0)$ and a stable coexistence state given by $(n_e, n_d) = (n_e^*, n_d^*) = \left(\frac{m_{dd}-m_{ed}}{m_{ee}m_{dd}-m_{ed}m_{de}}, \frac{m_{ee}-m_{de}}{m_{ee}m_{dd}-m_{ed}m_{de}}\right)$. I am therefore looking for travelling wavefront solutions to Eqns. 2.1 and 2.2 for which $0 \leq n_e \leq n_e^*$ and $0 \leq n_d \leq n_d^*$.

If a travelling wave solution exists it can be written in the form $n_e = F(z)$, $n_d = G(z)$, where $z = x - ct$ and c is the wave speed. This travelling wave form can then be substituted into Eqns. (2.1) and (2.2) in Chapter 2 to give:

$$-cF' = D_eF'' + r_eF(1 - m_{ee}F - m_{ed}G) + \mu_dG - \mu_eF,$$

$$-cG' = D_dG'' + r_dG(1 - m_{de}F - m_{dd}G) + \mu_eF - \mu_dG,$$

where prime means differentiation with respect to z. These can then be written as a set of first order differential equations:

$$F' = H,$$

$$G' = J,$$

$$H' = \frac{1}{D_e}\Big(\mu_eF - \mu_dG - r_eF(1 - m_{ee}F - m_{ed}G) - cH\Big),$$

$$J' = \frac{1}{D_d}\Big(\mu_dG - \mu_eF - r_dG(1 - m_{de}F - m_{dd}G) - cJ\Big).$$

In (F, G, H, J) phase space the two steady states are $(0, 0, 0, 0)$ and $(F^*, G^*, 0, 0)$, and so there is the possiblity of a travelling wave from $(0, 0, 0, 0)$ to $(F^*, G^*, 0, 0)$, where I have defined $F^* = \frac{m_{dd}-m_{ed}}{m_{ee}m_{dd}-m_{ed}m_{de}}$ and $G^* = \frac{m_{ee}-m_{de}}{m_{ee}m_{dd}-m_{ed}m_{de}}$. For a rightward moving

travelling wave I therefore look for solutions to the set of 1st order differential equations given above with the boundary conditions:

$$\lim_{z\to-\infty}(F,G,H,J)\to(F^*,G^*,0,0),$$

$$\lim_{z\to+\infty}(F,G,H,J)\to(0,0,0,0).$$

The Jacobian, or stability matrix A, is then found to be:

$$A=\begin{pmatrix} 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ \frac{\mu_e-r_e(1-2m_{ee}F-m_{ed}G)}{D_e} & \frac{r_em_{ed}F-\mu_d}{D_e} & \frac{-c}{D_e} & 0 \\ \frac{r_dm_{de}G-\mu_e}{D_d} & \frac{\mu_d-r_d(1-m_{de}F-2m_{dd}G)}{D_d} & 0 & \frac{-c}{D_d} \end{pmatrix}.$$

A can then be evaluated at the two steady states and the characteristic equations found. The characteristic equation of the steady state $(F^*,G^*,0,0)$ is found to be

$$\begin{vmatrix} -\lambda & 0 & 1 & 0 \\ 0 & -\lambda & 0 & 1 \\ \frac{1}{D_e}\left(\mu_e+\frac{r_em_{ee}(m_{dd}-m_{ed})}{m_{ee}m_{dd}-m_{ed}m_{de}}\right) & \frac{1}{D_e}\left(\frac{r_em_{ed}(m_{dd}-m_{ed})}{m_{ee}m_{dd}-m_{ed}m_{de}}-\mu_d\right) & \frac{-c}{D_e}-\lambda & 0 \\ \frac{1}{D_d}\left(\frac{r_dm_{de}(m_{ee}-m_{de})}{m_{ee}m_{dd}-m_{ed}m_{de}}-\mu_e\right) & \frac{1}{D_d}\left(\mu_d+\frac{r_dm_{dd}(m_{ee}-m_{de})}{m_{ee}m_{dd}-m_{ed}m_{de}}\right) & 0 & \frac{-c}{D_d}-\lambda \end{vmatrix}=0.$$

The eigenvalues are then given by

$$\lambda_{1,2}=\frac{1}{2D_e}\left(-c\pm\sqrt{c^2+4D_e\left(\frac{r_em_{ee}(m_{dd}-m_{ed})}{m_{ee}m_{dd}-m_{ed}m_{de}}+\mu_e\right)}\right),$$

$$\lambda_{3,4}=\frac{1}{2D_d}\left(-c\pm\sqrt{c^2+4D_d\left(\frac{r_dm_{dd}(m_{ee}-m_{de})}{m_{ee}m_{dd}-m_{ed}m_{de}}+\mu_d\right)}\right).$$

There is coexistence of the two morphs, which means that there are stronger interactions within than between morphs, and so $m_{ee}m_{dd}>m_{ed}m_{de}$ and $m_{dd}>m_{ed}$, $m_{ee}>m_{de}$. This means that two eigenvalues are positive and two are negative, so $(F^*,G^*,0,0)$ is an unstable saddle point.

The characteristic equation of the steady state $(0,0,0,0)$ is then found to be

$$\begin{vmatrix} -\lambda & 0 & 1 & 0 \\ 0 & -\lambda & 0 & 1 \\ \frac{\mu_e - r_e}{D_e} & \frac{-\mu_e}{D_e} & \frac{-c}{D_e} - \lambda & 0 \\ \frac{-\mu_d}{D_d} & \frac{\mu_d - r_d}{D_d} & 0 & \frac{-c}{D_d} - \lambda \end{vmatrix} = 0.$$

The eigenvalues are then given by

$$\lambda_{1,2} = \frac{-c \pm \sqrt{c^2 - 4D_e(r_e - \mu_e)}}{2D_e},$$

$$\lambda_{3,4} = \frac{-c \pm \sqrt{c^2 - 4D_d(r_d - \mu_d)}}{2D_d}.$$

I am assuming that μ_e and μ_d are small, which means that the terms in the brackets of the eigenvalues are positive. Therefore if $c^2 < 4D_e(r_e - \mu_e)$ and $c^2 < 4D_d(r_d - \mu_d)$ then $(0,0,0,0)$ is a stable spiral, and so around the origin F and G oscillate. However, if $c^2 > 4D_e(r_e - \mu_e)$ and $c^2 > 4D_d(r_d - \mu_d)$ then the origin is a stable node. For travelling wave solutions to occur between the two steady states it is therefore required that

$$c \geq 2\sqrt{D_e(r_e - \mu_e)},$$

$$c \geq 2\sqrt{D_d(r_d - \mu_d)}.$$

These two conditions correspond to two of the invasion speeds found in Chapter 2 (see Eqns. (2.11) and (2.12)). However, this method does not give the conditions for the third invasion speed found in Chapter 2, which corresponds to the anomalous invasion speeds observed using both the front propagation method method (van Saarloos, 2003) and numerical simulations.

This has shown that although in many cases, e.g. the Fisher equation, the method of looking for travelling wave solutions does give the correct conditions for the wavespeed, it does not always reveal all observed wavespeeds. In the case of the model developed in Chapter 2 I have shown that this method does not give the conditions for the third set of possible wavespeeds that were found using the alternative front propagation method and, which I have shown from running numerical simulations can be observed. It is for this reason that I have included the calculations of the invasion speed using the front propagation method (van Saarloos, 2003) in Chapter 2, and used this method to calculate range expansion speeds for the remainder of this thesis.

Once the conditions for which which a travelling wave to exist have been found it then needs to be proven that these are sufficient conditions for them to exist. This can be done by looking for a heteroclinic connection between the two steady states. This is fairly straightforward to do for equations in 2D phase space, e.g. see an example of this analysis for the Fisher equation in Kot (2001). However, in higher-dimensional systems these are generally more difficult to find (Guckenheimer and Holmes, 2002). For the equations I am looking at in Chapter 2, this would mean looking for a heteroclinic condition in 4D phase space. This has proven too difficult to do, and since I have shown by numerically integrating the equations that travelling wave solutions do exist with the speeds predicted analytically, this analysis will not be included in this thesis.

B Stochastic dispersal polymorphism code

B.1 Example of code used for simulations in 1D

Below is an example of the code that was used to perform the stochastic simulations of the discrete time and space dispersal polymorphism model in Chapter 3. This is an example of an invasion of both morphs in one dimension, for a population with a carrying capacity of a 100. In the code e represents the establisher morph and d the disperser morph. I have annotated the code for the establisher morph to explain what each line means, the code for the disperser morph is defined in the same way and so is not annotated.

```
#libraries required to shift a matrix
library(abind)
library(magic)

#parameters used in the simulations
b<-2 #birth rate
K<-100 #carrying capacity
mu<-0.001 #mutation rate between morphs

#population growth rates of each morph
re<-1
rd<-0.2

#survival parameters
m0e<-log(b+1)-re
m0d<-log(b+1)-rd
m1e<-(log(b+1)-m0e)/(K*(1+b))
m1d<-(log(b+1)-m0d)/(K*(1+b))

#dispersal rates of each morph
de<-0.2
dd<-0.9

n<-10000 #size of landscape on which simulations are run
e<-matrix(rep(0,n),nrow=1)
d<-matrix(rep(0,n),nrow=1)

#initial conditions - each morph is present at half the carrying capacity
e[1:100]<-K/2
d[1:100]<-K/2
```

```
t<-0 #start time
tmax<-10000 #max time simulations run for
tnext<-100 #interval between times at which the data is saved

allz<-cbind(e,d) #matrix containing initial conditions

while(t<tmax){
    while(t<tnext){

    birthse<-rpois(e,b*e) #number of offspring that each establisher produces
    birthsemutation<-rbinom(birthse,birthse,mu) #number of establisher's
        offspring that are dispersers
    birthsd<-rpois(d,b*d)
    birthsdmutation<-rbinom(birthsd,birthsd,mu)

    e<-e+birthse-birthsemutation+birthsdmutation #total number of establishers
        after recruitment
    d<-d+birthsd-birthsdmutation+birthsemutation
    N<-e+d #total population size

    sprobe<-exp(-m0e-m1e*N)  #survival probability of establishers
    e<-matrix(rbinom(e,e,sprobe),nrow=1) #number of establishers that survive
    sprobd<-exp(-m0d-m1d*N)
    d<-matrix(rbinom(d,d,sprobd),nrow=1)

    movee<-matrix(rbinom(e,e,de),nrow=1) #number of establishers that disperse
    prighte<-rbinom(movee,movee,0.5) #number that disperse to the right
    plefte<-movee-prighte #number that disperse to the left

    #enforce reflective boundary conditions: establishers at edges reflect back
         into cell 1 or n
    plefte[1]<-0 #probability that disperse out of landscape is zero at edges
    prighte[n]<-0
    movee[1]<-prighte[1] #update number that disperse at edges to only be those
         that disperse inside the landscape
    movee[n]<-plefte[n]

    #shift number that move to the left and right in each of these directions
    lefte<-matrix(shift(plefte,-1),nrow=1)
    righte<-matrix(shift(prighte,1),nrow=1)
    e<-e-movee+lefte+righte #position of establishers in landscape after the
        dispersal step
```

```
    moved<-matrix(rbinom(d,d,dd),nrow=1)
    prightd<-rbinom(moved,moved,0.5)
    pleftd<-moved-prightd
    pleftd[1]<-0
    prightd[n]<-0
    moved[1]<-prightd[1]
    moved[n]<-pleftd[n]
    leftd<-matrix(shift(pleftd,-1),nrow=1)
    rightd<-matrix(shift(prightd,1),nrow=1)
    d<-d-moved+leftd+rightd

    t<-t+1 #update time
    }
e<-e
d<-d
newz<-cbind(e,d) #matrix containing e and d after tnext

allz<-rbind(allz,newz) #join matrices after each tnext
tnext<-t+100 #update tnext
}
```

B.2 Example of code used for simulations in 2D

Here is an example of the code for a simulation in two dimensions. As the code is longer, I have just included the code for a simulation of a single morph, here the establisher morph. Parameter values used are the same as in the code above, with the exception of the dispersal rates so will not be repeated. I have only annotated the code where it differs from the code for simulations in 1D.

```
de<-(4/3)*0.2 #dispersal rate multiplied by 4/3 so that there is the same
    amount of dispersal to the left and right as in the 1D model

Nrow<-10 #width of landscape
Ncol<-10000 #length of landscape
n<-Nrow*Ncol #total area of landscape
e<-matrix(rep(0,n),nrow=Nrow)

e[1:Nrow,1:100]<-K #initial condition
t<-0
tmax<-10000
```

```
tnext<-1000

allz<-e

while(t<tmax){
    while(t<tnext){

    birthse<-rpois(e,b*e)
    e<-e+birthse

    sprobe<-exp(-m0e-m1e*e)
    e<-matrix(rbinom(e,e,sprobe),nrow=Nrow)

    movee<-matrix(rbinom(e,e,de),nrow=Nrow) #number of establishers that
        disperse
    prighte<-matrix(rbinom(movee,movee,0.125),nrow=Nrow) #number that disperse
        to the cell on the right
    movee2<-movee-prighte #number of establishers that remain to disperse (this
         is updated after the number that disperse in each direction is
        calculated)
    plefte<-matrix(rbinom(movee2,movee2,1/7),nrow=Nrow) #number that disperse
        to the cell on the left
    movee3<-movee2-plefte
    pupe<-matrix(rbinom(movee3,movee3,1/6),nrow=Nrow) #number that disperse to
        the cell above
    movee4<-movee3-pupe
    pdowne<-matrix(rbinom(movee4,movee4,1/5),nrow=Nrow) #number that disperse
        to the cell below
    movee5<-movee4-pdowne
    puplefte<-matrix(rbinom(movee5,movee5,0.25),nrow=Nrow) #number that
        disperse to the cell diagonally up to the left
    movee6<-movee5-puplefte
    puprighte<-matrix(rbinom(movee6,movee6,1/3),nrow=Nrow) #number that
        disperse to the cell diagonally up to the right
    movee7<-movee6-puprighte
    pdownlefte<-matrix(rbinom(movee7,movee7,0.5),nrow=Nrow) #number that
        disperse to the cell diagonally down to the left
    pdownrighte<-matrix(movee7-pdownlefte,nrow=Nrow) #number that disperse to
        the cell diagonally down to the right

    #reflective boundary conditions - establishers at edge of the landscape do
        not disperse out
    plefte[1:Nrow,1]<-0
    prighte[1:Nrow,Ncol]<-0
```

```
    pupe[1,1:Ncol]<-0
    pdowne[Nrow,1:Ncol]<-0
    puplefte[1,1:Ncol]<-0
    puplefte[1:Nrow,1]<-0
    puprighte[1,1:Ncol]<-0
    puprighte[1:Nrow,Ncol]<-0
    pdownlefte[Nrow,1:Ncol]<-0
    pdownlefte[1:Nrow,1]<-0
    pdownrighte[Nrow,1:Ncol]<-0
    pdownrighte[1:Nrow,Ncol]<-0

    #update number that disperse at the edges to only be those that disperse
        inside the landscape
    movee[2:(Nrow-1),1]<-prighte[2:(Nrow-1),1]+pupe[2:(Nrow-1),1]+pdowne[2:(
        Nrow-1),1]+puprighte[2:(Nrow-1),1]+pdownrighte[2:(Nrow-1),1]
    movee[2:(Nrow-1),Ncol]<-plefte[2:(Nrow-1),Ncol]+pupe[2:(Nrow-1),Ncol]+
        pdowne[2:(Nrow-1),Ncol]+puplefte[2:(Nrow-1),Ncol]+pdownlefte[2:(Nrow-1)
        ,Ncol]
    movee[1,2:(Ncol-1)]<-prighte[1,2:(Ncol-1)]+plefte[1,2:(Ncol-1)]+pdowne
        [1,2:(Ncol-1)]+pdownrighte[1,2:(Ncol-1)]+pdownlefte[1,2:(Ncol-1)]
    movee[Nrow,2:(Ncol-1)]<-prighte[Nrow,2:(Ncol-1)]+plefte[Nrow,2:(Ncol-1)]+
        pupe[Nrow,2:(Ncol-1)]+puprighte[Nrow,2:(Ncol-1)]+puplefte[Nrow,2:(Ncol
        -1)]
    movee[1,1]<-prighte[1,1]+pdowne[1,1]+pdownrighte[1,1]
    movee[1,Ncol]<-plefte[1,Ncol]+pdowne[1,Ncol]+pdownlefte[1,Ncol]
    movee[Nrow,1]<-prighte[Nrow,1]+pupe[Nrow,1]+puprighte[Nrow,1]
    movee[Nrow,Ncol]<-plefte[Nrow,Ncol]+pupe[Nrow,Ncol]+puplefte[Nrow,Ncol]

    #shift number that disperse in the correct directions
    lefte<-matrix(ashift(plefte,c(0,-1)),nrow=Nrow)
    righte<-matrix(ashift(prighte,c(0,1)),nrow=Nrow)
    upe<-matrix(ashift(pupe,c(-1,0)),nrow=Nrow)
    downe<-matrix(ashift(pdowne,c(1,0)),nrow=Nrow)
    uprighte<-matrix(ashift(puprighte,c(-1,1)),nrow=Nrow)
    uplefte<-matrix(ashift(puplefte,c(-1,-1)),nrow=Nrow)
    downrighte<-matrix(ashift(pdownrighte,c(1,1)),nrow=Nrow)
    downlefte<-matrix(ashift(pdownlefte,c(1,-1)),nrow=Nrow)

    #position of establishers in the landscape after dispersal
    e<-e-movee+lefte+righte+upe+downe+uplefte+uprighte+downrighte+downlefte

    t<-t+1
    }
e<-e
```

```
newz<-e

allz<-cbind(allz,newz)
tnext<-t+1000
}
```