# The role of landscape structure in determining eco-evolutionary dynamics during environmental change

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The candidate confirms that the work submitted is his 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 overleaf. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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## Abstract

Climate change may produce a variety of responses in populations' ecological and evolutionary dynamics. At opposing limits of populations' ranges, the responses are expected to differ. Some lag in response may be expected due to the rapidity of climate change, with the strength and type of lags varying across space. Importantly responses may contain both ecological and evolutionary components. This thesis provides significant contribution to understanding how structure in populations and the landscape may determine the nature of populations' responses to climate and environmental changes.

A number of models and a microcosm experiment are presented. The results show how alternate temporal and spatial population structures are developed when individuals move in space. From defining percolation routes, patterns of gene flow or spatial selection, landscapes provide a large role in determining populations' responses. Even without landscape structure, populations exhibit large levels of regional structure, and indeed substructure, due to localised interactions. This spatial structure may deform during climate change, producing new characteristics of equilibrium spatial distributions. During range deformation the feedback between spatial structure and dynamics can alter populations' evolvability by changing the patterns and strength of intraspecific competition, or the maintenance of genetic variation. These changes produce dynamics that will be sensitive to individual differences in a population. Changes in populations' age and sex structure may modulate ecological and evolutionary interactions.

The research presented here highlights an increased importance of understanding populations' *spatio-temporal* structure and dynamics within heterogeneous landscapes. This is especially so as ecological and evolutionary processes can converge to different degrees during climate change, depending on the landscape a population inhabits. Prediction of populations' responses may require a greater understanding of spatial processes and how range deformation affects the evolution of different kinds of traits. All the above areas feed into a greater understanding of the genesis and maintenance of diversity in any situation.

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**3. Range shifting on a fragmented landscape**

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# 1. Populations' responses to climate change.

## 1.1 Introduction: The fundamental reasons for climate change biology

Fundamentally populations are expected to respond to climate change because of the links between climatic environment and organism functioning (e.g. Humphries et al. 2002; Helmuth et al. 2005, 2006). For instance, temperature may affect the activation of genes controlling specific reactions (Helmuth et al. 2006) and determine the energetic gains from living in different environments (Humphries et al. 2002). These processes of metabolism and physiological function can then affect the available resources that are partitioned amongst individuals' reproduction, movement, and survival (Stearns 1989). Climate also plays a 'harder' role in individual functioning by affecting organisms' structural integrity, and so extreme climate conditions can be a direct cause of death (Allen & Breshars 1998; Laurance & Williamson 2001; McDowell et al. 2008). Arguably all organisms exhibit some adaptation to climate (Andrewartha & Birch 1958), especially temperature (West et al. 1997), and these relationships have effects spanning huge biological scales, from gene to ecosystem.

The relationship between climate, other biotic and abiotic environmental factors, and population regulation has long been conceptualised as the ecological niche (Hutchinson 1957). The niche is a discrete set describing the set of conditions in which populations may persist (Chase & Leibold 2003). At least conceptually, a map exists that links climatic conditions (and other environmental factors), individual functioning and population dynamics (Lawton 1992; Sibly & Hone 2002; Gaston 2003; Coulson et al. 2006). Thus the predicted changes in climate are expected to alter individuals' ability to grow, reproduce and survive on account of trade offs made at the physiological level (Helmuth et al. 2005).

In the following sections, I first introduce some aspects of populations' biology in temporally and spatially varying climates. This illustrates some of the complexity underlying climate change responses. Following this I present the hypotheses with which many climate change studies approach their research. Finally I introduce some of the landscape effects that may be considered in future research and underpin the research presented in this thesis.

## 1.2 Populations' relationships with climate

### *1.2.1 Temporal relationships with climate*

Populations encounter climate variation over a variety of time scales. Some variation is predictable in terms of natural selection, such as annual and daily changes in temperature and light. Other climate variation may not be directly linked to the timing of individual activities (e.g. Milankovitch cycles (see Dynesius & Jansson 2000) or ENSO (see Lima et al. 1999)) but produce predictable population reponses (Coulson et al. 2001). Selection may act on traits where there is a long-term change in the average climate (Dynesius & Jansson 2000). Climatic variation over short time scales may also be unpredictable and would be termed stochastic, and known as 'weather' (Stenseth et al. 2002). Thus within the long-term (~30yr) mean of conditions that defines climate, there is cyclic variation at small scales (Seasons, Days) and longer temporal scales (Milankovitch cycles, ENSO), surrounded by less predictable weather (Stenseth et al. 2002). The iteration of populations means that generations may encompass weather variation around a climate average in different ways dependent on life history (e.g. Morris et al. 2008).

Climate fluctuations can have considerable consequences for the dynamics of the population due to its affects on individual function (Coulson et al. 2001). One excellent example demonstrates this point particularly well. Helmuth et al. (2006) illustrate the complicated relationship of climate, other environmental factors and the life history of the Limpet, *Patella depressa*. Sea temperature, air temperature, desiccation, wave action, wind speed, turbulence, currents, irradiance, habitat suitability and food availability all play different roles throughout a limpet's life history (figure 1 in Hemluth et al. 2006). Individual responses to climate variation may also be manifested in different ways depending on the sex, age, phenotype or genotype of an individual (Coulson et al. 2001).

Furthermore individuals' responses may depend on the population context, as represented by sex and age structure, the distribution of phenotypes and genotypes, and population size (Benton et al. 2006). The population response may be dependent on prevailing environmental conditions and also those in the recent history of the population via maternal effects (Roach & Wulff 1987; Rossiter 1996).

### *1.2.2 Spatial relationships with climate*

At any single instance, populations also encounter variation in climate across space (Andrewartha & Birch 1958). The temporal relationships with climate were introduced first because they are a subset of the spatial variation in climate; temporal variation also occurs across space. Across global and regional scales broad patterns emerge such as decreasing temperature from equator to pole, or from low to high latitudes. Broad scale gradients may also be found with increasing depth in aquatic environments. Other gradients exist in relation to landmasses, proximity to water bodies and vegetation patterns that may not themselves be spatially correlated or follow a broad scale pattern. The smaller scale variation in climate across space is often referred to as microclimate. Microclimates are the "weather" of spatial variation in climate: variation which determines local conditions, but within a larger scale trend.

The relationship with climate across space has long been recognised (Merriam 1894; Grinnell 1917, 1924). Gaston (2003) cites an example where plants' spatial distributions were advocated as a means to correct climate maps (Boyko 1947). Gaston (2003) also presents direct evidence for why correlative relationships between range limits and climatic conditions should exist. These are exactly the same reasons for why populations would respond to temporal changes in the climate outlined above: climate affects individual functioning that in turn affect mortality, reproduction and development (Gaston 2003). However there is a profound difference in the effects of spatial variation. A population solely encountering temporal variation has the effects manifested through individuals' lifetimes and the generations of populations. Through space, however, individuals may move, migrate, emigrate and immigrate, creating a wide range of ecological and evolutionary effects (Macarthur 1977; Tilman & Kareiva 1997; Clobert et al. 2001; Hanski & Gaggiotti 2004; Dieckmann & Ferriére 2004).

Spatial variation in climate can generate large differences in population dynamics across space (Kendall et al. 1998), providing texture and pattern to populations' ranges (Lawton 1993). The manner with which abundance varies across space is complicated and few general rules appear (Sagarin et al. 2006). However most populations are rare in many places and only a few localities exhibit great abundance (Brown et al. 1996; Gaston 2003). Underlying large-scale gradients is a distribution of microclimates that may be unpredictably arranged, producing patterns of abundance that do not adhere to the predictions of simple theory (e.g. Gilman 2005). Populations may exhibit 'permanent' clines in abundance, decreasing or increasing towards range limits (Vucetich & Waite 2003), or more complicated patterns (Sagarin & Gaines 2002). Coulson et al. (2001) demonstrated that the form and strength of density dependence differs according to the pattern of temporal variation in the climate, and it can similarly vary across space (also see Firbank et al. 1995). For instance, contrary to the simplest of predictions (e.g. Brown 1984) density dependence may be stronger at a range limit than the range centre (Kluth & Bruelheide 2005). However this pattern is not expected to operate in all circumstances (Samis & Eckert 2007). The evidence suggests we may expect different environmental conditions to affect populations in different ways at different localities (Kendal et al. 1998; also see Coulson et al. 2001). This is far from trivial as dispersal can mediate interactions between populations that experience different environmental conditions (Pulliam 1988; Tilman & Kareiva 1997).

Populations constrained to an island may exhibit no spatial movement in response to climate changes (e.g. Oguto & Owen-Smith 2003) and so responses are manifested in temporal changes in abundance rather than spatial chanages. However, populations less restricted by landscape have altered their range in response to temporal cycles such as the ENSO (Brown & Suharson 1990; Murawski 1993; Hawkins et al. 2000) and Milankovitch cycles that can operate over tens of thousands of years (Dynesius & Jansson 2000). Vast changes in biodiversity have appeared across space during earth's history (Hewitt 2000; Davis & Shaw 2001; Mayhew et al. 2008). Ice ages have included large-scale movement of climates and populations (Bennett et al. 1991), with remnant populations left over from populations' past distributions illustrating the distance with which populations have moved (e.g. West 1989; Colinvaux et al. 1996). The existence of hybrid zones is evidence of such climate changes; where populations are split during a climatic change and divergence during periods of allopatry prevent hybrid viability (Hewitt 2000; Hewitt & Lister 2004).

### *1.2.3 The climate is set to change*

The present climate is set to change. Last century a temperature change of 0.6 ± 0.2 ° C was exhibited with temperature change over the next century forecasted to be in the region of 2.1-4.6 °C (Houghton et al. 2001). Given the examples presented in the previous sections we would expect considerable ecological effects to occur in both space and time. Contemporary climate change differs from past episodes of change in three main ways. Firstly the rate of change is expected to be 2-5 times faster than previous 'natural' episodes of climate warming (Davis & Shaw 2001). However estimates vary (e.g. Kerr & Kharouba 2007) being dependent on the scenario (Malcom et al. 2002) and also because of differences in the magnitude of effects between locations (Thuiller 2007, e.g. America vs. Europe). Secondly the peak average temperature of climate warming is expected to be higher than at any time in the last 2 million years (see Kerr & Kharouba 2007). The maximum global mean surface temperature estimated to have occurred in the last 125,000 years is 15.5°C (Houghton et al. 2001). By 2100 the global mean surface temperature is predicted to reach between 15.5 and 19 °C (Houghton et al. 2001). Finally many of the 'confounding factors' have been caused by anthropogenic actions mainly occurring over the last century. Populations have many other 'confounding' factors acting upon their dynamics, such as landscape alterations, pollution, exploitation, and persecution. The role of landscape in populations' responses to climate change is a central theme of the whole thesis and is revisited in much more detail later in this chapter.

## 1.3 The simple hypotheses... Move adapt or die

Gaston (2003, pp 21) suggests we can understand limitation of population success at three levels. At the first level are factors that prevent a population's spread across space, such as "*physical barriers (e.g. mountain chains, rivers), climatic factors, the absence of essential resources, or the impact of competitors, predators or parasites*" (Gaston 2003). Every population has range limits; there are no Darwinian demons that can exploit all available conditions (Law 1979). The second concerns a dynamical view of populations, where populations persist where they do because the "*net addition of individuals exceeds the net loss*" (Gaston 2003). Thus a single Darwinian demon may be able to live in all conditions but a population of demons may not be successful due to dynamic factors such as Allee effects (Stephens et al. 1999). We could view these two explanations as 'proximate' explanations of why populations occur where they do. They are proximate because an answer to these questions explains: 'given a population, where will it exist?'

Gaston's third level of explanation concerns the ultimate explanations for populations' ranges. The previous proximate explanations are only limitations given the characteristics of the population, so we can ask 'what determines a population's characteristics, and so where it will exist'. For example why doesn't a population evolve characteristics that would permit further spread in 'static' climates (Antonovics 1976; Macarthur 1972)? Or indeed, evolve characteristics that result in less extensive spread? These proximate and ultimate explanations equally apply to limitations of populations in time as well as space. For instance within an annual cycle why do populations reproduce, mature and die *when* they do (rather than *where* they do)? Temporal restrictions occur for most of the same reasons such as climatic variation such as absence of other resources, or because of intra-specific interactions. There are also ultimate explanations for why a population does not exploit more temporal variation, such as frequency dependent selection (Janzen 1976).

Given that populations may be limited in these different ways what are the expectations, what are our hypotheses regarding climate change responses? Climate change responses may be manifested in a number of different ways broadly delimited as "*move, adapt or* *die*", a division made by numerous authors (e.g. Fields et al. 1993; Helmuth et al. 2005; Davis et al. 2000). The "movement" of populations is a shift in the distribution of abundance through space. However, changes in density, phenology, morphology and genetic frequencies may contribute to populations' responses (Root et al. 2003). Climate change effects could result in no change in spatial distribution if moderated by changes in other traits. For instance densities could change without a change in spatial distribution, or a population may respond via direct or plastic changes in traits. If climate change effects are small, then a populations' spatial distribution needn't be altered. However intense changes may necessarily cause alterations to the distribution of abundance through space.

### *1.3.1 Move*

Thuiller (2007) suggests that for every 1°C of warming ecological zones may be expected to shift 160 km. This is similar to "Hopkins' Bioclimatic law" where 1°C equates to 100km latitudinal or a 130m-altitudinal change (Hopkins 1920, in Kerr & Kharouba 2007). We might then expect considerable spatial shifts in patterns of diversity as populations *move* with climate conditions in which they can survive and reproduce, driven by two perceivable mechanisms.

Firstly, at one extreme, populations may actively *track* existing condition, in a manner conceptually similar to migrations. Where some degree of habitat selection is involved, populations may migrate from areas becoming unsuitable to areas becoming suitable (for instance change in settlement during migration). If populations exhibit choice in the locations of sites that they occupy, then some degree of an "ideal free distribution" (Fretwell & Lucas 1969) may be approached. This assumes an immediate response of individuals to climate, and intelligent dispersal.

If there is little or no direct habitat selection the response may be viewed as a *range shift*, where previously suitable areas become unsuitable and previously unsuitable areas become suitable (Parmesan 1996). Here individual 'choices' are not immediate. At lower latitudes, local extinctions may occur leading to extirpation from these areas as warming leads to negative population growth rates. At higher latitudes, areas that were previously unsuitable and unoccupied become suitable and occupied by colonisation of dispersing individuals. This change in net colonisations and extinctions across the range can produce a range shift (extinctions>colonisations at low latitudes and extinctions<colonisations at high latitudes) (Parmesan 1996). This type of response may typically occur over more than 1 generation and inherently involves a lagged response (Hill et al. al. 1999b; Walther et al. 2002; Parmesan & Yohe 2003).

Some authors have taken a community-focused view, suggesting that "warm" adapted species will increase in frequency within a community as the climate warms (e.g. Sagarin et al. 1999; Peñuelas & Boada 2007) (or conversely a decrease in cold adapted species would occur). As previously discussed, considerable climatic variation is found through the year. Within annual cycles temperature may vary by as much as 25°C (Bradshaw & Hozapfel 2006) depending on latitude (Gaston & Chown 1999). Thus populations may maintain their spatial location by moving their responses in time (Visser 2008). "Move" responses relate to proximate, ecological limitations to a population's spatial and temporal range; they are "given the population" responses explanations that assume population characteristics do not change.

### *1.3.2 Adapt or Die*

Populations' characteristics may change, such that "*average fitness for the shifted phenotypic distribution is higher than that of the original distribution when compared within the current environment*" (Visser 2008). The shift in the distribution of phenotypes may be due to phenotypic plasticity (Roy & Sparks 2000; Bradley et al. 2000) or selection (Balanya et al. 2006). In the case of phenology, a change in the timing of environmental conditions may track changes in climate related cues through a season (Visser 2008), for instance the coincidence with temperature and day length. Morphology may change as life history factors are determined by environments experienced by an organism (Millien et al. 2006) or previous generations (Thompson &

Ollason 2001). Phenotypic plasticity allows for a change in the distribution of phenotypes but without any necessary change in the distribution of genotypes within a population. Individuals may alter the allocation of resources amongst traits or alter different developmental processes to produce different phenotypes better suited to the prevailing environment (Helmuth et al. 2005). The distribution of phenotypes may have non-random changes even if responses are plastic, if parts of the distribution exhibit higher fitness than others and produce an evolutionary change. A change in phenotypes due to change in the genotype distribution may be expected if there is some correlation and so directional selection on trait variation exhibited across space or time. Across yearly cycles not all individuals respond at exactly the same time and some of this variation can have a genetic component (Filchak et al. 2000). Similarly, across space local adaptations to different climates may exist (Norton et al. 1995, 1999; Davis & Shaw 2001; see references and discussion in Jump & Penuealas 2005). Adaptive explanations, whether plastic or evolutionary, tend towards the ultimate level of Gaston's scheme, as there is a change in the characteristics of the population, and so the response.

Some studies investigating the *paleo* record suggest previous climate change responses have been mostly been range shifting events rather evolutionary responses (see Davis & Shaw 2001; though see Mayhew et al. 2008). However contemporary studies reveal that both range shifts and evolutionary changes have occurred in response to climate fluctuations. Some suggest that *paleo* studies inevitably focus on populations that exhibit range shifts (Lyons 2003). Many evolutionary changes have been recorded during contemporary climate changes (Davis & Shaw 2001; Parmesan 2006), which I present in a later section.

If populations can neither adapt nor move, and the magnitude of climate change is sufficient, then populations will go extinct (Lynch & Lande 1993). Local extinction is a central mechanism for range shifting, though it may be harder to demonstrate than colonisation events (Thomas et al. 2006). The mechanistic route to extinction is poorly understood (Mclaughlin et al. 2002) though studies have shown that the related physiological stress may reduce population growth rates (Waite & Strickland 2006).

McLuaghin et al. (2002) show how climate change increases environmental variability and could alter population persistence through causing wider population fluctuations. Indirect links between extinction and climate change have been shown in harlequin frogs. Pounds et al. (2006) suggest that climate has allowed proliferation of pathogenic fungal epidemics outbreaks out in the frog species. Interest in the conditions and processes leading to mortality are of increasing interest to better describe populations' responses to climate change (McDowell et al. 2008).

Watkinson & Gill (2002) suggest that populations could actually exhibit five responses: "*no response, persistence, adaptation, extinction and dispersal*". This is an addition of *no response* and *persistence* upon the *move, adapt or die* schematic. It is worth highlighting the fact that populations may not exhibit a response to climate change, especially during the early stages of climate change. Climate may not be the primary determinant of a populations range (Gaston 2003), and factors such as landscape availability or biotic interactions could have a larger effect on distribution. We can conceptualise this as the realised niche being much smaller than the fundamental niche. Thus a large change in the environmental conditions may be necessary to take a population beyond the limits that define population viability. The result of climate change would depend on where in niche space that population lies. It is likely that there will be some consequences of altering the relationship between climate and niche due to the disequilibrium introduced. Similarly a population could have a realised niche that is larger than the fundamental niche (Pulliam 1988). Understanding the effects of climate change on this last scenario is more complicated, as realised niches larger than the fundamental may only manifested by spatial interactions or biotic interactions. An understanding of population dynamics resulting from a niche may then be necessary to predict the consequences of climate change.

## 1.4 The coherent finger prints of climate change

A variety of studies and meta-analyses have shown that many populations already exhibit responses that carry the "*fingerprint*" of contemporary climate change (Root et al.

2003). Indeed a *"globally coherent fingerprint"* exists (Parmesan & Yohe 2003). The evidence shows that considerable changes have occurred in populations' spatial distribution (e.g. Birds, Thomas & Lennon 1999; Butterflies, Parmesan 1996. Parmesan et al. 1999; fish, Perry et al. 2005; dragonflies, Hickling et al. 2005). Altitudinal changes have also been observed (Grabherr et al. 1994; Pauli et al. 2007), with warming increasing extinctions at low elevations and colonisations increasing at the colder conditions of high elevations. Data fitting these broad hypotheses is also found across a broader suite of taxa (Parmesan & Yohe 2003; Hickling et al. 2006). The breeding (Thomas & Lennon 1999) and over wintering (Austin & Rehfisch 2005) ranges of bird species have followed this trend (also see Visser 2008), though habitat selection may be involved in these responses.

The meta-analysis of Root et al. (2003) demonstrates a trend for earlier timing of life history events in relation to climate change across taxa. The same trend is found in a broader study conducted by Parmesan & Yohe (2003). Potentially a phenological shift could occur in two directions with earlier initiation of spring events and later onset of events tied to the autumn (Walther et al. 2002). Phenological and spatial shifts could both comprise a population's responses, though no studies have investigated the dual effects on a single population.

In *situ* changes in responses during climatic changes have been demonstrated in a wide variety of taxa (Bradshaw & Hozapfel 2006; Parmesan 2006). Changes in phenology are, in some cases, due to plastic responses (e.g. changes in body size, Millien et al. 2006; Yom-Tov et al. 2006) or result from selection. (Berteaux et al. 2004; Jump & Penuelas 2005). The examples of evolutionary responses are generally limited to phenological change (Visser 2008; Bradshaw & Hozapfel 2006) but have shown the rapidity of evolutionary change in response to climate (Balayna et al. 2006). Changes in the timing of key life history events have been documented (Reale et al. 2003), especially where resource availability is determined by the change in another species (Visser 2008).

The majority of documented evolutionary responses to climate change consist of changes in phenology (Bradshaw & Holzapfel 2006). These studies show populations are responding to changing climates via alterations to reproductive timing or by changing how information on day length is related to temperature. In this second case evolutionary change in day length cues allow exploitation of warmer conditions where days of that length were previously colder and would induce dormancy (Bradshaw 2001, 2004). These studies show evolution towards different timing to coincide with when conditions are exhibited within a year, rather than to changes in actual differences between conditions at the same time of year. Bradshaw & Holzapfel (2006) suggest this is due to the relative differences in temperature occurring throughout the year. For instance the latitudinal variation in climate conditions may be more related to winter temperatures than summer (also see Lima et al. 2007). This could lead to an expansion in the growing year that is larger in magnitude than the absolute change in maximum temperature within a year.

In many of these cases the evolutionary change does not constitute a change in the niche, but changes in the mechanisms that optimize its exploitation (e.g. recognition of day length, Visser 2008). The same niches are available during the year but change in their temporal position, moderating any spatial change in a populations range. Similarly, Thomas et al. (2001) document a case where a population shifts resources to maintain the same climate niche. Evolution tied to temperature maximums has however been shown (Balanya et al. 2006). In *Drosophila*, European (Rodrıguez-Trelles et al. 1998), Australian (Umina et al. 2005) and North American populations (Levitan 2003) have exhibited an increase in genotypes with greater heat tolerance (also see figure 1 of Balanya et al. 2006). Similar evolutionary responses in *Drosophila* have also been observed over annual climate cycles (Dobzhansky 1943, 1947a, b) supporting a view that evolution may occur rapidly in response to new conditions (Hairston et al. 2005).

## 1.5 The incoherent responses to climate change

The meta-analyses introduced in the previous section measured the correlative relationship between the results found in a variety of studies with some simple predictions regarding populations' climate change responses. Not all the populations respond in the expected manner. Under the simple hypothesis that climate change would shift a populations' range, an extension of its previous occupancy would be expected at the northern limit whilst a retraction would be expected at its southern limit (Parmesan 1996). For 14 of the 35 butterfly species studied by Parmesan et al. (1999) an extension in the northern limit was associated with stability at the southern limit. Ten species exhibited stability at both limits and 7 the expected change of extension and retraction at northern and southern limits respectively. The remaining species exhibited differing responses, from extension of both limits to southern shifts in populations range (table 3, Parmesan et al. 1999). Similar results were found for the British Birds studied by Thomas & Lennon (1999), with "*individualistic*" population responses present within the general trend for a shift of ranges northwards.

A variety of factors could generate the individualistic responses. For instance the apparent regional stability of range limits could occur when organisms shift locally to higher elevations (Parmesan et al. 1999). A similar effect could occur due to the differences between latitudinal and annual variation (Bradshaw & Holzapfel 2006; Lima et al. 2007), or because other factors determine the range limit (Davis et al. 1998a, b; Fielding et al. 1999; Gaston 2003). Few authors relate evolutionary changes to spatial responses (but see Thomas et al. 2001). For instance evolution, or plastic changes, in phenology may allow a population to stay in the same location (e.g. Root et al. 2003). Extinctions may also be less observable than colonisations at the coarse scales of the available data (Thomas et al. 2006; Franco et al. 2006). Perry et al. (2005) show distinct differences in life history traits exist between fish species that have shifted their range and those that remain stationary.

Without any criticism of the studies mentioned, it is clear that the simplicity of the hypotheses presented in such analyses do not represent the complexity of the systems and the environments that they inhabit. Some 'complexities', relating to landscape effects, are explored later in this chapter (also see Opdam & Wascher 2004). The conclusions previously made focus on rates of change at northern range limits, with figures on the rates of range shift presented only for northern range (Parmesan et al. 2001: Thomas & Lennon 1999; but see Franco et al. 2006). The figures of southern limit shifts are not provided and, given the data presented, are expected to be much smaller. Some of the difference may be accounted for by the variation in the rates of climate change across latitude, with northern climates warming at faster rates than southern latitudes (e.g. Thuiller 2007). What is clear though is that there are differences in the response throughout a populations range and in many cases this has led to extension of the population's range.

## 1.6 Landscape as a confounding factor

In the rest of this chapter I shall investigate how understanding variation in the landscape may be important to climate change biology. Landscape effects can be formalised as sensitivity of processes to spatial patterning (e.g. Pickett & Cadenasso 1995; With 2004) and may provide valuable insights into the potential future distributions of species both from ecological and evolutionary perspectives (Collingham & Huntley 2000; Hampe 2004; Opdam & Wascher 2004).

For many populations, currently occupied habitats are unlikely to remain available throughout the present period of climate change (Thomas, Rose et al. 1999), which may influence spatial patterning (Ohlemüller et al. 2006). The most obvious effect of landscape is on levels of connectivity that determine which areas can be accessed (Collingham & Huntley 2000; Wiens 2001; Gaston 2003). Some areas may be reached from a large number of other areas, whilst other areas may be isolated and reached by only a few. Levels of connectivity may not be determined by distance alone as movements may also depend on the habitat type between habitat areas. This is the matrix.

whose characteristics can determine the relative costs of movement (Clobert et al. 2001) and determine whether an individual will even attempt movement (Wiens 2001). These effects of individuals' perception of the landscape can affect population dynamics by determining population size and viability in a patch (Kawecki 1995), interactions between patches (Kawecki & Stearns 1993) and the extent to which a population may spread through a given landscape (With et al. 2007).

Given the considerable effects landscape characteristics can have on spatial processes (Tilman & Kareiva 1997), and potential for highly non-linear responses (Harrison & Bruna 1999), it is striking how consistently their effects are excluded when projecting spatial responses to climate change (Opdam & Wascher 2004 and references therein). Landscape effects are, due to the context and data, removed from analyses investigating the simple hypotheses regarding climate change (Parmesan et al. 1999; Thomas & Lennon 1999; Parmesan & Yohe 2003). It may be argued that removal of populations that are isolated or have poor dispersal abilities distracts from those populations that may be of greatest conservation importance.

Warren et al. (2001) investigated the effects of habitat on climate change responses in 46 non-migratory butterfly species that have their northern range limit in Britain. Over the period of recording it might be expected that there would be some expansion of the range to the north as habitats become increasingly suitable. However, landscape alterations have led to widespread loss of habitat, with around 70% loss of semi natural habitat due to agricultural intensification since 1940 (Warren et al. 2001). Thus, there are opposing effects of climate change (+ve) and habitat loss (-ve) on the butterfly species studied, 75% of which exhibited a negative change in distributional area between recordings made in 1970-82 and 1995-99. Sedentary and specialist species tended to exhibit the most negative changes; presumably because habitat is not available to facilitate a range shift (expansion) and those species are less able to do so (Warren et al. 2001). Hill et al. (2001) show that there is a clear effect of landscape on the modelled expansion of the *Pararge aegeria* butterfly. In areas with lower amounts of woodland expansion of the range was slower. The authors suggest that lack of habitat may be preventing many populations from responding to climate changes, like those excluded from the meta-analyses of Parmesan & Yohe (2003) and Parmesan et al. (1999). For such populations there may be a double cost of habitat loss. Franco et al. (2006) showed that the low latitude range margins of 4 butterfly species exhibited shifts due to both habitat loss and climate change, with the relative importance of different factors dependent on species.

## 1.7 A deadly anthropogenic cocktail

Historical climate change events occurred in a world where human populations had not converted almost a quarter of the landscape into an agricultural, industrial and urbanised landscape; a landscape without road and rail linking production and people; a landscape with fewer barriers to dispersal. Landscape alteration is also an incredibly extensive problem; humans have altered almost 25% of the Earth's surface through cultivation (www.millenniumassessment.org). It is expected that modern landscapes are less permeable to population's movement when range shifting (Schwartz 1992; Pitelka et al. 1997; Collingham & Huntley 2000; Opdam & Wascher 2004). This is the "*deadly anthropogenic cocktail*" (Travis 2003).

Range shifts rely on colonisation of habitat that becomes newly available. Habitat fragmentation can simply and directly impact population's ability to reach suitable areas if dispersal distances are too great (Collingham & Huntley 2000; Fahrig 2003; McInerny et al. 2007). Habitat may be lost or fragmented, two processes that can have differing but synergistic effects on populations (Harrison & Bruna 1999). For instance there are sharp threshold of population persistence associated with patch connectivity and this threshold may be less intense if patches are correlated in space (Dytham 1995; With & King 1999a,b; Hill & Caswell 2001; Fahrig 2001). Dispersal ability and reproductive output play a large role in determining how fragmented a landscape is (With & King 1999a).

The vast majority of populations' distributions were determined before man altered the landscape, or introduced populations to new areas; so present distributions may not represent actual dispersal ability. Populations also have no guarantees that suitable habitat will exist in the future (Ohlemüller et al. 2006) and if it will, habitat may not necessarily be with individuals' dispersal range (Shwartz 1992; Pitelka et al. 1997, Opdam & Wascher 2004). This is the simplest level of the climate change problem when considering the landscape. The prime aim of 'landscape ecology' is to determine which landscapes provide stable populations and communities, to produce a "*protected area network*" that can maintain biodiversity within anthropogenic action (With 2004). A central pursuit of contemporary conservation biology is to investigate if such networks would also maintain biodiversity during climate change (Hannah et al. 2002).

The central idea is that populations are forced into an 'island hopping' exercise, a series of colonisation and extinction events as climate change alters where habitat is available. Travis (2003) investigated these ideas in a patch occupancy model. He showed that the rate of climate change has an explicit interaction with landscape, with faster rates of climate change increasing the effects of habitat loss and so reducing the amount of habitat loss that can be tolerated. Collingham & Huntley (2000) show a similar effect where migration rates across a landscape are reduced by habitat loss (also see Schwartz 1992). High dispersal and colonisation abilities could mitigate against the effects of habitat loss and climate change (Travis 2003), as in models investigating landscape effects in static climates (With & King 1999a). Whilst landscape effects are often mentioned in meta-analyses (Parmesan et al. 1999) and bioclimate model investigations (Thomas et al. 2004; Heikkinen et al. 2006) the details of landscape effects are not well-understood in a climate change context. Travis (2003) shows that simple assumptions made in static climates may not hold during climate change. For instance, changes in the threshold of population persistence in response to habitat loss will change during a period of climate change.

## 1.8 Uncertain futures

During climate change habitat availability and/or the levels of fragmentation that previously enforced a range limit may change (Hampe 2004; Ohlemüller et al. 2006; Shoo et al. 2006). There are two main concepts underlying how landscapes will change.

Firstly, Hampe (2004) suggests that the number of "*recruitment sites*" will increase at high altitude limits and decrease at low latitude limits. This patterns result from an expectation that some habitats are near-suitable at high latitudes and more habitats will become within a populations niche than become unsuitable. At low latitudes there is expected to be the opposite situation, with a net decrease in habitat suitability. This predictable concept of landscape change is similar to that held in much of the range shifting literature, where a change in the balance of colonisations and extinctions across a populations range (e.g. Parmesan 1996). An important similarity with this concept is found in the abundance centre hypothesis (ACH) briefly presented later (see Sagarin & Gaines 2002, 2006; Sagarin et al. 2006).

The second concept is of less predictable landscape changes provided in the studies of Shoo et al. (2006) and Ohlemüller et al. (2006). Shoo et al. (2006) showed how the relative amount of habitat would decrease during climate change, in this case for mountain populations being forced to high altitudes. Ohlemüller et al. (2006) demonstrate that variation in the representation of habitat may cause some environmental conditions (or habitats) will become increasingly represented during climate change. These studies present a view of changes in the landscape that will create differences in the spatial relationships within populations. Under the concept encapsulated in the first case (e.g. Hampe 2004) populations will remain a single population. However in the second case, allopatry or indeed sympatry may be driven by changes in the landscape. Importantly populations may experience vicariance as the 'climate window' is shifted across the landscape.

The pattern of habitat may be of further importance as correlated landscapes often provide the greatest viability (With & King 1999a; Hill & Caswell 1999). Dispersers are more likely to encounter habitat and spread their range. Thus movement into more fragmented landscapes may reduce the viability of populations in those areas (Holt & Keitt 2000) and so "*pin*" the range shift (Keitt et al. 2001). This is where habitat area causes a metapopulation to be unviable (Holt & Keitt 2000) or Allee effects arise due to small population sizes. The model by Keitt et al. (2001) demonstrates that under an Allee effect low population sizes may always tend to local extinction. Thus if dispersal rates are low population sizes in the previously uninhabited area may fluctuate within the range where population growth is always negative and so pin an invasion. The strength of the Allee effect may be measured by the ratio between the population size that indicates the threshold of the Allee effect (*C*) (unstable fixed point of population growth) and the carrying capacity (*K*) (stable fixed point) (Keitt et al. 2001). This is similar to a colonisation rate determined by the amount of neighbouring populations, a corollary of propagule pressure, in the metapopulation model of range limits by Holt & Keitt (2000). With a strong Allee effect a population's range shift may be pinned, with a weak Allee effect allowing expansion into the new habitat (Keitt et al. 2001). The width of the region where invasion pinning occurs decreases with increasing dispersal (see fig 5 Keitt et al. 2001). Similarly low colonisation probabilities may reduce metapopulation occupancy in fragmented landscapes and pin the expansion into areas that are fragmented or have low habitat area (Holt & Keitt 2000). This is a more complicated case of dispersal limitation from a direct barrier such as a landmass (see Gaston 2003). Effectively the range edge is a sink as population growth rate is less than zero at the range edge (Pulliam 1988) and so dispersal from a source could unpin the range limit.

Landscape changes may be accompanied by changes in the fecundity of individuals and populations (Hampe 2004). For instance at high latitude range limits we might expect populations to increase in fitness (Chamillé-Jammes et al. 2006) and low latitude populations' fitness to decrease (Waite & Strickland 2006). Such changes in individual fitness may alter the relationship between population and landscape by changing colonisation and extinction rates (McInerny et al. 2007). Changes in population size may alter the strength of Allee effects (Stephens et al. 1999) and dispersal rates (Carmel & Flather 2006), two processes central to the determination of colonisation and extinction rates. Under the previously discussed view of Hampe (2004) suitable habitats increasing in number at high latitudes would be inhabited by populations increasing in fecundity. The resulting increase in habitat availability (and/or de-fragmentation of habitat) and increasing colonisation ability could reduce dispersal limitation within the population (Hampe 2004). Conversely populations would become increasingly dispersal limited at low latitudes, as decreasing fitness and habitat availability increasingly fragment a population.

There is certainly a large gap between theoretical expectations of how climate change–landscape interactions can be manifested and empirical investigation of the interactive effect. As with climate change research, and ecological research in general, data availability precludes more extensive corroboration of our more extensive theoretical understanding. Studies such as Warren et al. (2001) and Hill et al. (2001) use simple hypotheses of landscape effects, primarily equating landscape alteration with the simultaneous effect on habitat loss and fragmentation, and envisaging dispersal as a largely context independent process. Dispersal is a simplistic description of a highly context dependent set of processes (Clobert et al. 2001; Bowler & Benton 2005). The dispersal of an individual may be divided into multiple stages, for example (1) the decision to leave the current location, (2) movement to a new location and (3) decision to settle in a new location (Clobert et al. 2001). All of these stages may be affected by differences between individuals, within populations and environmental variation, contexts that may themselves be liable to alter within the changing climate (e.g. Walters et al. 2006).

The examples presented here suggest considerable potential for synergistic effects between landscape and populations on the ability of species to shift their range in response to climate changes (Opdam & Wascher 2004). Within a "*spatially dissected*" world (Opdam & Wascher 2004), populations tread a transient path through the landscape that may alter in area and pattern. There is a very wide range of possible scenarios that can be conceived (e.g. habitat availability and fragmentation may increase or decrease to different extents as a population shifts its range) with different consequences for the populations inhabiting them who possess different traits. Many of the hypotheses put forward relate to qualitative changes in extinction and colonisation rates of populations across a range and do not examine the quantitative changes that may be exhibited in populations

## 1.9 Populations' spatial structure

The previous section focused on the heterogeneity in the landscape and how this might affect populations that were assumed to be themselves homogenous; for instance where all individuals have the same dispersal ability or resistance to extinction. However local selection regimes frequently produce local adaptations in response to environmental heterogeneity (Kawecki & Eberet 2004) generating spatial structure in the distribution of population traits (Slatkin 1985; Bohonak 1999), sometimes referred to as textures (Lawton 1993). Structures exhibited by populations are more formally described as: discontinuities in the distribution displayed in a population's entire variance, where characters are non-randomly distributed (Loveless & Hamrick 1984). The variance and resultant structure may occur in abundance (Holt et al. 1997, Lammi et al. 1999, Mcgeoch & Price 2004; Sagarin & Gaines 2002), genetic variance (Soule 1973, Shwartz et al. 2003), life history traits (Hallas et al. 2002), reproductive mode (Eckert 2001) and dispersal ability (Jenkins & Hoffman 2000; Simmons & Thomas 2004); indeed, any population characteristic.

Populations may display structure over much shorter scales than their dispersal may suggest. For instance Ehrlich et al. (1975) found a single butterfly population to be made up of 3 distinct units over a scale much smaller than the degree of dispersal displayed by individuals. It is important to distinguish potential and actual vagility (Ehrlich 1961; Grenouillet et al. 2007) as gene flow mediated by dispersers can be restricted by ability to access mates after dispersal (Labine 1964). Such mechanisms may create an 'intrinsic' barrier to the movement of genes (Ehrlich et al. 1975; Bohonak 1999). Population structure over distances of <2km has also been found in bird species (Blondel 1999; Garant et al. 2004; Postma & van Noordwijk 2004); though differences may also be attributable to habitat selection by immigrants and competition between individuals. The majority of information on population structure regards genetic differences (Loveless & Hamrick 1984; Heywood et al. 1991; Bohonak 1999). Because of the explicit link with dispersal and gene flow, generation of genetic structure may depend heavily on landscape pattern (Slatkin 1985, 1987; Bohonak 1999; Ezard & Travis 2006; Alleaume- Benharira

2006; Campbell Grant et al. 2007; Fortuna et al. 2008). The spatial structure of populations may play a central role in describing the responses of populations to perturbation (Huffaker 1958; Hastings & Higgins 1994; Ruxton & Doebeli 1996; May 1999; Thomas & Hanski 2004; Fagan 2002; Fortuna et al. 2006, 2008). A 'perturbation' may not be felt equally throughout the whole population (Hanski 1998; Thomas & Hanski 2004; Campbell Grant 2007), so different traits may be affected to different extents and recovery may depend on how the distribution of traits is affected.

## 1.10 Spatial selection and range expansion

Some authors (e.g. Lawton 1993; Hengeveld et al. 2004) suggest that populations or individuals occurring towards the edge of a range will be of great importance in the range shifting responses to climate change. Due to their spatial proximity, individuals or populations at high latitudes may be 'closer' to habitats that will become suitable. Furthermore if populations towards the range limit exhibit local adaptation, individuals' adaptations may better match the environmental conditions of newly suitable habitat. Thus range limit populations may access newly available habitats more easily and subsequently be more successful in colonising those areas.

This reasoning suggests that understanding spatial structure may be especially relevant during range expansion events. By virtue of range limit populations being closer, they may contribute more to the colonisation of areas becoming suitable. The process of "mutation surfing" (Klopfsetin et al. 2005) embodies this principle, where iterated founder effects are caused by repeated sampling from the populations closest to available habitat (Ibrahim et al. 1996; Edmonds et al. 2004). This simple process of selecting individuals that are most proximate has the consequence that any adaptations those individuals possess may increase in frequency within the population. In some cases a trait with lower fitness than the resident population can proliferate in the low competition environments of an expanding range limit (Currat et al. 2006; Travis et al. 2007).

This 'spatial selection' may act on dispersal (Hastings 1983). Simmons & Thomas (2004) found greater numbers of individuals capable of long distance dispersers at range margins (see also Thomas et al. 2001). Simmons & Thomas (2004) inferred evolutionary forces had generated selection for dispersal and expressed the possibility that long distance dispersers "*may dominate recently colonised populations simply because they can get there*". Long distance dispersers are more likely to have offspring that can disperse further (Simmons & Thomas 2004), but the common garden experiments were carried out over a single generation so environmental and maternal effects could not be entirely disregarded. Similarly, in a model of dispersal in the lesser marsh grasshopper, Walters et al. (2006) investigated how within population variation for long distance dispersal may be selected for.

Other cases of dispersal evolution in butterflies during range expansion have been documented (e.g. Butterflies, Hill et al. 1999a; Hanski et al. 2004; Toads, Phillips et al. 2006). Travis & Dytham (2002) showed in an individual based model that selection of individuals with greater dispersal ability may occur at such expansion fronts, supported by further recent empirical evidence in Cane Toads (Phillips et al. 2006). Any selection towards greater dispersal rates could augment the speed of expansion (Travis & Dytham 2002; Phillips et al. 2006) and is often expected to increase the rate of expansion.

Selection of different modes of dispersal may be dependent on the spatial pattern of the landscape (Thomas et al. 1998). For instance Dynesius & Jansson (2000) demonstrated that some areas are more stable during climate changes, and have lower rates of dispersal evolution when compared to areas that are less stable and require range shifts for survival. Future landscapes may have a different level of dispersal 'risk' than experienced previously and differentially select for dispersal rates, producing different effects on range expansion (e.g. via *invasion pinning*, Keitt et al. 2001). As previously discussed the mode of dispersal that would allow a range expansion might depend on habitat availability, spatial pattern and Allee effects. Dispersal evolution is highly dependent on Allee effects (Travis & Dytham 2002) and so landscape features that enhance or ameliorate an Allee effect could provide a dual effect on population viability and the evolutionary patterns produced. There are circumstances where strong Allee effects in fragmented landscapes could drive dispersal towards a level that does not maintain population viability (Gyllenberg & Metz 2001), a case of "*evolutionary suicide*" (Deickmann & Ferriére 2004).

In some range expansions a niche shift has been inferred (Thomas et al. 2001; Broennimann et al. 2007). Spatial selection may be a potent force for evolution of the niche as the contribution to future generations may be determined by factors that affect spatial proximity (e.g. dispersal (Travis & Dytham 2002) or dormancy (Travis & McInerny submitted)) and adaptations that are more successful in those environments (Thomas et al. 2001). In the best-documented case of a niche shift, the butterfly *Aricia agestis* could not shift its range as the *Helianthemum* species used as a host plant did not occur in the areas that became climatically suitable (Thomas et al. 2001). Rapid evolution to a *Geranium* species allowed the butterfly to track the climate and shift its range. Elsewhere in the range *Aricia* is adapted to the *Geranium* species (Thomas et al. 2001). Any variation present for the alternate host plant trait could rapidly become frequent, simply due to its success in areas that become more suitable. In such situations co-evolution of dispersal and traits determining the niche may occur as generality may beget the greater success of dispersers (Dynesius & Jansson 2000).

Whether individuals that are capable of long distance dispersal are actually found at range limits may depend on numerous taxa specific quantities. In insect species, wing polymorphism and potential facultative dispersal modes are often found (see Zera & Denno 1997; Roff 1990 for reviews: also see Hughes et al. 2003). Density dependent production of individuals capable of dispersing long distance is found in many species, being intensified by resource limitation (Zera & Denno 1975, and refs therein), conditions that may be expected to occur at range edges (Hoffman & Blows 1994; Petit et al. 2004; Hampe & Petit 2005). However for a few aphid and cricket species short distance dispersers exist in stressful environments (Zera & Denno 1997), possibly due to the larger amount of resources required in production of a long distance disperser (Dixon 1985). These different environmental responses may have a large role to play in explaining differences in the immediacy of a climate change response, and the idiosyncrasies displayed in observed responses as many species exhibit spatial structure in the frequency of the different strategies (Zera & Denno 1997). Through habitat suitability, climate change may augment the basis for life history trade offs that determine dispersal ability.

Colonisation of an area may be composed of >1 dispersal events. This means the amount of individuals dispersing into an area alter the strength of selection towards adaptation to local conditions (Kawecki & Ebert 2004). The gene flow arising from dispersal may drive gene frequencies in a different direction to selection (Lenormand 2002) reducing or halting the rate of evolution (Holt & Gomulkiewicz 2004). Kirkpatrick & Barton (1997) suggest that the degree to which gene flow can '*pin*' local adaptations and halt range expansion may depend on the strength of an environmental gradient and dispersal rates.

## 1.11 The changing shape of populations' range

From the previous text it is clear that some landscapes may be better than others for preserving populations viability (e.g. see Table 1 in Thomas & Hanski 2004). Some landscape structures provide greater ecological success, through maintaining connectivity and populations' persistence (Fortuna et al. 2006). During climate change, the degree to which any landscape is maintained or indeed augmented relative to the population's history may be of central interest to the response. There are different views of how heterogeneous the landscape is in the literature. For instance, Hampe (2004) suggested that habitat availability would generally increase and decrease in high and low latitudes respectively. However, whilst this is a reasonable first approximation there may be uncertainty as to whether future habitat will exist and if any increase in habitat availability would be greater than that lost. If *loss>gain* a population's range may contract. Conversely a range may expand when *gain>loss*. This suggests changes could occur in the spatial interactions within a population and alter the strength of processes within a population. For instance the amount of gene flow, regionally and locally, may change, altering evolutionary forces (e.g. Kirkpatrick & Barton 1997; Kawecki 2004) and the spatial proximity of different components of a population's structure may alter the environmental conditions different traits are exposed to. Changes in the shape of populations' ranges have been under investigated, with previous studies focusing on splitting of populations (Hewitt 2000). Meta-analyses have focused on the changes occurring at range limits such as changes in position, and the rate of that change (Parmesan et al. 1999; Thomas & Lennon 1999).

Rapoport (1975) was very interested in how populations' ranges may exhibit "*deformation*" during periods of environmental disequilibrium, such as when populations invade new habitats. Range deformation may occur not only because of environmental heterogeneity (e.g. Parmesan et al. 1999) but differences in the rate of response between interacting species and the relative positions of the species before perturbation. The amount of factors that may be involved in range deformation led Rapoport to state: *"There is a moment when the investigator realizes that only with a computer all the variables and all the restrictions and conditions can be put together in order to simulate expansions and contractions of the areas in isotropic and an-isotropic media (with barriers)"*(Rapoport 1975).

We can now add extensively to Rapoport's view as it is clear that range deformation may occur in a variety of ways. 'Barriers' to dispersal may exist not just because of dispersal limitation, but because population viability is reduced by factors such as Allee effects interacting with the landscape pattern (Keitt et al. 2001). Climate change is not exclusive to the range limits (Jump & Penuelas 2005), climate changes will be expected to occur throughout a populations' range. Climate change effects may vary in strength across a populations range (Thuiller 2007), as can the degree of landscape changes (Thomas, Rose et al. 1999). There will also be variation in the rate of range shifting responses associated with interspecific and intraspecific differences in dispersal abilities (e.g. Travis & Dytham 2002; Walters et al. 2006) and landscape patterning (Hill et al. 1999b). If any of these effects is stronger or weaker through space, or if the strength of lags differs through space, then we may expect the range to deform. Changes in the structure of dispersal and gene flow interactions may have wide consequences for the ecology, genetics and adaptive evolution of populations (Slatkin 1987; Hanski 1998; Lieberman et al. 2005) and those changes may fees back to alter dispersal and gene flow. This interplay between adaptation and migration will be central to understanding population responses to climate change (Davis & Shaw 2001).

## 1.12 Outline of thesis

This thesis investigates some important interactions between climate change and populations' spatial structure. Using simulation models and an experimental microcosm system I take a strategic approach to understanding landscape effects and their consequences for climate change responses. The experimental microcosms provide the opportunity to provide replicated experimental observations whilst the simulation models provide an opportunity to theoretically investigate relevant spatial processes.

**Chapter 2** provides a conceptual overview of how climate change predictions are currently made and how they relate to ecological theory. Climate change research is a huge area of research as climate may have links with nearly every ecological process. Hence this chapter stands back and questions some basic concepts underlying the research

**Chapter 3** investigates how landscape pattern may affect a range shifting response in an individual based model. This study shows how predictions of landscape effects are affected by climate change.

The model investigated in **Chapter 4** demonstrates the ecological and evolutionary importance of landscape geometry during environmental change in an individual based model. By tracking population dynamics and adaptive change in a two patch system comparisons between different landscape geometries are determined.

In **Chapter 5** a model investigation of how populations' spatial structure may change during a directional shift in the environment is undertaken. By monitoring ecological dynamics and the success of mutations, a highly novel study into the determinants and effects of range deformation is presented.

**Chapter 6** uses experimental populations to investigate the effect of emigration on population dynamics and the demographic consequences of intra-specific population structure. Population dynamics are observed during the invasion of different 'landscapes' by soil mite populations.

**Chapter 7** is a research summary and discussion of how these factors may change perceptions of populations' responses to climate change. I discuss how my research suggests a necessity for new considerations for new circumstances.

# 2. "Population Thinking" for Climate Change.

## 2.1 Introduction

In this chapter I outline some of the conceptual background to the research presented in the rest of the thesis. The discussion is made in the context of "*population thinking*", which Ernst Mayr (1959) coined and heralded as an important but overlooked facet of the theory of natural selection. In population thinking, 'population' refers to the variation any trait or phenomena may exhibit, rather than the natural populations we study. Thus I refer to conceptual '*populations*' and natural *populations*. Mayr's treatise of the philosophy contained in natural selection has similarly been proclaimed to be amongst his greatest and less well-recognised contributions to biological thinking (Bock 1994). Many of the key points discussed here are not limited to climate change research and are applicable to any area of research. As such the concepts are drawn from a variety of areas and references do not necessarily mean evidential support or example, but rather may indicate a conceptual link.

## 2.2 Population Thinking

*"The ultimate conclusions of the population thinker and of the typologists are precisely the opposite. For the typologist, the type (eidos) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real." (Mayr 1959)*

Mayr (1959) contended that whilst the *Origin of Species* (Darwin 1859) initiated modern biological science, the importance of the mode of thinking it encapsulated had been somewhat overlooked (also see Mayr 2000). In "*population thinking*" the uniqueness and variation of the natural world was emphasised. Mayr exalted this as a fundamental change in the philosophy and concepts of nature within scientific literature. The previously prevailing '*typological*' way of thinking held that "*the variation* [was] *an illusion*" (Mayr 1959). Quite simply, the switch to population thinking made the mechanisms of natural selection a viable proposition because variation was present upon which selection could act. The typological outlook didn't allow for partial, assortative success as all individuals are considered of the same type; the "*all or nothing*" view of evolution does not work (Mayr 1959). Population thinking provided the key that opened up the theory of natural selection; selective superiority and differential contributions to the gene pool could emerge. The "*invariance*" and "*stability*" view of diversity had reigned since Plato in typological thought (Mayr 2000; typological thought ≈ essentialism, Mayr 1969). As typological thought withdrew from biology, the scientific and cultural world changed forever.

## 2.3 Population thinking in model building

In the 'modern' era such differences in the way of thinking are hard to imagine. Given all we know about individual differences and their effects on the processes we study, it takes a substantial leap to understand a society where the variation is an "*illusion*". However, some considerable analogy can be found in all the scientific models we build to understand the world. Whether analytical, computational or verbal in form, the practicalities of tractability and generality necessitate abstracting variation in the vast majority of a system's components (Levins 1966; Odenbaugh 2006; Benton et al. 2006). We generally treat only a few factors as a 'population'. For example, evolutionary studies tend to abstract environmental heterogeneity and in ecological studies individual differences in genetics are generally ignored, despite their potential effects on process. For instance simple acknowledgment of parameters' variability in population models may yield different points of equilibrium and levels of system stability (Bjørnstad & Hansen 1994). In the scheme of Levins (1966) we trade off generality, realism and precision to understand details of different types of questions. Scientists are actively encouraged to reduce our models appropriately (Ockham's Razor). In many situations the small number of components considered in our models may also be due to the exogenous limitation of data collection (Hengeveld & Haek 1982; Gaston 2003). Our data may have been collected for differing purposes than the concepts we test, or by the means in which we interpret its quantities (Austin 2002, 2007). This matter of model complexity is well illustrated in the "neutral theory of biodiversity" (Hubbell 2001). In neutral theory nearly all 'populations' are disregarded in favour of an ecological nihilistic world - a world that can produce patterns so similar to real world phenomena that there is both much excitement and suspicion (Alonso et al. 2006).

## 2.4 The bio-climate typology

Efforts to project the expected changes in the distributional patterns of biodiversity in response to climate change have produced somewhat of a bifurcation in the research concepts. In one branch, research carries a highly typological concept of species, bioclimate modelling. At their most basic, bioclimate models utilise correlative approaches often over numerous layers of environmental factors that co-occur with the presence of the target species or populations (Huntley 1995; Heikkinen et al. 2006). Environmental factors such as rainfall, temperature and sunlight hours are used to produce a representation of the 'niche' or "*climate envelope*". The dimensionality depends on the inputted environmental variables and researchers' discretion. This climate envelope can then be projected forward with the expected spatial and temporal changes in a single or multiple factors of that modelled niche. The vast majority of the data originates form biogeographic atlases, such as the *Atlas Florae Europapeae* (http://www.fmnh.helsinki.fi/english/botany/afe/; e.g. Thuiller et al. 2005). To spare both reader and writer, there will be no further discussion of the bio-climate methodology though some well connected publications provide sufficient pointers to those interested (e.g. Guisan & Zimmermann, 2000; Heikkinen et al. 2006).

Unsurprisingly the high productivity of bioclimate models in the literature has been tempered by questions levied at the concepts of populations contained in the methodologies employed (e.g. Hampe 2004; Araújo & Guissan 2006; Austin 2007). The vast majority of this methodological appraisal has come from within the bioclimate community, relating to both the concepts of populations used and a large list of statistical considerations. Some criticism has been made because essential processes such as biotic interactions, evolution or dispersal are not included in the models (Hampe 2004; Dytham et al. *unpublished*). Both biotic interactions and dispersal have large effects on the ranges species occupy (Gaston 2003; Hampe 2004) and are seen as processes amenable to incorporation into the bioclimate framework. However, evolution may be far more difficult to incorporate, especially as the role of evolution in determining species ranges is far less well understood (Rappoport 1975; Kirkpatrick & Barton 1997).

## 2.5 Population thinking for climate change - a review is everything

"*If we are to make progress by boldly oversimplifying, we should at least alert ourselves to some of the complications we are temporarily setting aside*" (Dennett 1995).

Opposing the typological school of thought, on the other branch of the conceptual bifurcation, is "population thinking" which suggests that typology prevents real prediction (Berteaux et al. 2008). This branch comprises a disparate literature that has yet to significantly amalgamate and appropriately develop theory in the context of climate change. Here, near all ecological and evolutionary concepts, such as biotic interactions and dispersal, may be considered to be central to our predictive understanding. However this argument is often made in very broad terms (Hampe 2004). Climate has demonstrably large effects on individual functioning that may scale up to population and community dynamics (Gaston 2003; Helmuth et al. 2005; Mustin et al. 2008). Under population thinking this variation could be central to determining the mechanisms and processes underlying climate change responses.

A thorough review of what is relevant to climate change may arguably encompass the whole of the ecological and evolutionary literature. Simply looking at the chapter titles of Begon, Harper & Townsend (1996) reveals subject matter with currently evidenced links with climate change. A review of concepts important to climate change by Kerr & Kharouba (2007) in "Theoretical Ecology" (May & Maclean eds), necessarily skates along the simpler hypotheses of climate change, related topics and evidence for them. In essence the other chapters of *Theoretical Ecology* deal with details of processes that may be relevant during climate change. Climate change may be expected to affect population cohesion (ch2), population dynamics (ch3), spatial dynamics (ch4), predator-prey interactions (ch5), interspecific competition and species' coexistence (ch7), diversity and stability (ch8), dynamics of infectious diseases (ch10), the effects on resources and the interactions with harvesting (ch11), and how this knowledge might sum to affect policy (ch13). Underlying the simple hypotheses of 'move, adapt or die' may be considerable complexities that have not been investigated and there is a paucity of theory upon which studies may be based.

## 2.6 The importance of population thinking – what we ultimately want to know

The consequences of taking a typological view have large ramifications for the quality of science. A central facet of the problem is that all the qualities our system can exhibit are contained in the assumptions and the resultant model. In the case of natural selection, assuming all the component parts were the same type meant evolution was not possible (Mayr 1959). This is a direct comparison with bioclimate models where no evolution is possible. If part of the climate envelope 'dies' during climate change then it can reappear at any time in the future if that climate is again represented. All individuals are typified as the statistical abstraction of their populations range, often despite some considerable geographic and possibly genetic separation.

The model abstraction is assumed to be the niche, the set of the conditions where population growth rates will be greater than zero (Hutchinson 1957). However, it may be the realised niche that is 'measured' and not the fundamental niche (Araújo & Pearson 2005). Moreover, because it is called the 'niche' it doesn't mean that it is the niche; nor does it mean that it appropriately represents a niche ("*Ceci n'est pas une pipe*", Foucault 1973). Importantly the modelled niche is an assumed representation of *all* responses individuals and their populations could possibly exhibit. This is because the bioclimate model relies on populations being at equilibrium with the environment and so occupying all areas where population growth rate is greater than zero and absent everywhere else (Araújo & Pearson 2005). Thus the modelled niche is dependent on the context in which it is measured and there is weak evidence that this context will remain during any environmental disequilibrium (Randin et al. 2006). We should underline that the modelled niche is considered an "effect" with underlying "causes". Another of Mayr's contributions to the philosophy of science is useful here; understanding cause and effect (Mayr 1961, Beatty 1994).

Underlying any biological phenomenon is a number of explanations. Some are proximate and rely on functions of the system that is studied. Others are ultimate explanations and seek to explain the existence of the proximate reasons, asking why do those functions exist? This is similar to Gaston's (2003) three levels of description (see Chapter 1) that we can indulge ourselves in when considering geographic ranges. Typological models may treat 'populations' as phenomena, taking no account of the factors that are important in their genesis, the causal descriptions (O'Hara 2005). Typological (bioclimate) models will often only answer a proximate question, assuming that all events leading to the population's distribution are equally likely to occur in the future and that no other events will. This is important for the obvious reason that it is assumed the niche is conserved through time and any situation; there will be no evolution, adaptation or alternative realisation. Some of the most detailed evidence of climate change responses does not support this view of niche conservatism (Thomas et al. 2001; in contrast to Wiens & Graham 2005). For example, in the case of an invasive species, the niche measured in the home range may predict sites where invasion will be initiated, but poorly predicts the extent of the resultant range (Broennimann et al. 2007). But getting back to the point a paragraph ago, there is no description of how niches are actually manifested and so scope for the realised or fundamental niche to be context dependent. There are many facetious analogies that can be used to illustrate how confusion between cause and effect could cause problems when making predictions.

In the bioclimate literature there is confusion as to whether the modelled niche represents the fundamental or realised (Araújo & Guisan 2006). Araújo & Guisan (2006) suggest that "*a possibility is to discard the fundamental and realized niche concepts altogether, accepting that any characterization of the niche is an incomplete description*". Such an action would side step any responsibility to conform to concepts of ecology systems or theory producing a 'black box' and so avoiding further discussion of its validity. There will be significant consequences for interpretation of the results if there is little understanding of the underlying ecological concepts. The acceptance of black box methods is found in bioclimate modeling by the use of consensus modeling (Thuiller 2003) and especially artificial neural networks (Hilbert & Ostendorf 2001). Here the underlying assumptions of different statistical models may be conflicting (Austin 2007) or in the case of artificial neural networks, non-existent. We should also ask how much variation between taxa could be appropriately applied when investigating large numbers of species with a large number of variables. Austin (2007) seeks to unite "*complex interdependency between theory, data and statistics*", in part by understanding the fundamental shape of environmental response curves. Austin (2007) also points out that few studies have considered the link to underlying ecological theory. The legitimacy of having rogue representations of ecological systems performing conservation assessments may draw some flak.

In a static environment understanding the importance of such arguments relating to the importance of proximate and ultimate causes of our responses are expected to be important (Cabeza et al. 2004). Any argument regarding the reliability of the model increases in importance as we take our study systems outside of the conditions where the initial measurements were made (Thuiller et al. 2004). Here extrapolation may be dangerous (e.g. Tatem et al. 2004) and the statistical methods used can impose a model assumption that is different from the mechanism by which that system would respond (Austin 2002, 2007; Rice 2004). For instance when predicting into conditions that are not observable during measurement, the typological representation may assume that the response is linear or has a different shape than the 'reality' due to constraints on model selection or construction (Norris 2004). Our dependency on the model structure becomes increasingly important. Novel parameter combinations may mean we will miss important threshold effects and ultimately question the model's utility.

## 2.7 Are bio-climate models useful?

Bioclimate modelling has afforded conservation biology a means to rapidly and extensively assess the distribution of climate change's threat to populations (Heikkenen et al 2006; Mitikka 2008). In a single study Morse et al. (1993) investigated the effects of climate change on more than 15,000 species. As briefly mentioned previously, bioclimate models can assess what degree of populations' current ranges will remain 'hospitable'. In this way Midgley et al.'s (2002) bioclimate modelling suggests that only two thirds of the species in their study would maintain >2/3 of their original range, with a third of the species possibly suffering "*complete range dislocation by 2050*".

Some authors have suggested that bioclimate models provide the "absolute limits" to future ranges (Thomas *et al.*, 2004). The reasoning being that as most species do not have perfect dispersal abilities the actual response will lie somewhere between this *absolute,* potential future range and its present range. The absolute limit assumes that '*everything is everywhere, but the environment selects*' (Beijernick's Law, see Sauer 1988). Varying assumptions about dispersal ability can produce very different results, varying from the "*drastic reduction to modest increase*" in populations' ranges (Peterson 2001). We could also question the validity of bioclimate predictions on the basis that they may be expected to become less reliable just when they are required to be more reliable.

Within the home range an assumption that populations can reach all parts of the range may be generally expected to be more reliable than assuming populations can reach all areas that become suitable in the future. Given the previous discussion we could suggest that our confidence in the model itself might change as the population is forced to move further in geographic space to maintain the same 'niche'. We could turn the predictions around and say the degree to which the home range is maintained will increase our confidence in the bioclimate model (as it is the degree to which the population will not experience conditions it has not experienced before). Similarly our confidence may decline with the degree of range dislocation as the context of the environment-population relationship changes, altering the realised niche.

A change in the 'niche' may be more likely when the model is required to make bigger predictions. For instance studies that have investigated the spatial and temporal transferability of bioclimate models suggest that this last point may have particularly large relevance (Thuiller et al. 2004; Randin et al. 2006; Broennimann et al. 2007). However, size of geographic range (Luoto et al. 2005) and species-specific traits (Pöyry et al. 2008) may provide a gauge of when and where models are likely to be effective. Other 'confounding' factors can disrupt populations' equilibrium in the environment (Plaisance 1979) and so reduce the predictive power of bioclimate models. This suggests that incorporation of other factors into bioclimate models requires a better understanding of the synergistic effects rather than modeling the summed effect.

Whilst recognising variation in the environment, bioclimate models accept little variation in populations. Ohlemüller et al. (2006) take this to an interesting extreme and do away with living populations in their studies. Instead they produce "*risk surfaces*" that demonstrate the manner in which the spatial relationships between common environmental conditions change across the landscape; showing which environmental conditions are threatened and which environmental conditions are most spatially separated. This is an interesting typology as it could be taken to suggest that our preferred model, given the data, may not contain a biological component but could be interpreted biologically. We may need to be wary of misleading concepts representing ecology and such reduction of the model, but changing the manner of interpretation may allow us to stick to the fundamental concepts of biology. Bioclimate models comprise a large proportion of the climate change literature and contain a variety of implicit and explicit interpretations of ecological theory. "*One clear indicator of the degree to which separate paradigms are operating in this field is the number of common citations in two recent review papers: precisely zero*" (Austin 2007).

The present discussions have not been made as a tirade on bioclimate research, but as an inspection of some concepts behind prominent methods in climate change biology and rediscover a baseline for future study. For example bioclimate models could provide some information on how to manage the landscape in relation to dispersal (Thuiller 2007). Yet the implicit message from the assumptions of bioclimate models is that the rest of our ecological and evolutionary knowledge is not relevant over the time scales over which the models are predicting.

However it is important to stress that bioclimate models are an invention based on the necessity of understanding, and this is given the data available. The scale of abstraction in bio-climate models is necessarily based on biological recording conventions and so the conventions of cartography, for example the 10km grid square (e.g. Parmesan & Yohe, 2003; Hickling et al. 2005). This is a delimitation of scale and pattern with limited direct biological relevance. The true scales at which the variation occurs and at which its consequences act may be hierarchical and have interspecific and interspecific differences depending on what processes are being considered (Levin 1992). However the 10km grid square "convention" (this convention is not a convention throughout Europe), was not made with biological problems in mind; nor were presence/absence observations made with such a high magnitude conservation problem in mind.

## 2.8 Thinking outside the climate envelope

*"In the end, our failure to think critically about the dynamically relevant objects in systems means that the productive interplay between theory and empiricism becomes uncoupled."* Schmitz (2001).

A fundamental question to ask as a scientist is: where '*populations*' should occur in our model? In understanding these factors and differences we can develop hypotheses that measure appropriate traits and processes. From Mayr's (1959) view, without understanding the effects of abstracting at any given level we may introduce typologies that produce fallacious results and hinder appropriate study of the system (also see Hallett et al. 2004; Helmuth et al. 2006). We might only find the key processes that describe the system by identifying the correct 'populations' (Schmitz 2001) and recognising the interactions between 'populations' in the correct way.

Throughout science huge typological assumptions are made in the name of tractability. The various divisions of our biological sciences are made through disregarding the 'populations' that others focus on. There are many points of view regarding what ecology actually is, each dependent on different underlying questions (Taylor 1936) and inevitably emphasising different concepts for different questions. For instance, macro-ecological concepts of populations as optimal responses (Gaston 2003), versus the more dynamic concepts contained in population ecology; both push aside considerable 'populations' of variation with the changing scale of the questions. In the well-known passage from "*Travels of Praiseworthy Men*" (Suarez 1658, see Borges 1998) such tradeoffs between the manageable and precise are presented with some great quality:

"*In that empire the craft of cartography attained such Perfection that the Map of a Single province covered the space of an entire City, and the Map of the empire itself an entire province. In the course of Time, these extensive maps were found somehow wanting, and so the College of Cartographers evolved a map of the empire that was of the same scale as the empire and coincided with it point to point. Less attentive to the study of Cartography, succeeding generations came to judge a map of such Magnitude cumbersome, and, not without irreverence, they abandoned it to the rigours of sun and Rain. In the western deserts, tattered Fragments of the Map are still to be found, Sheltering on occasional Beast or Beggar; in the whole Nation, no other relic is left of the study of Geography.*"

In climate change research we could suggest that it isn't clear what scale of map is required. We might rightly suggest that the map needs to be a larger scale during climate change so we may explore avenues if they appear valuable routes to take. This means that we need to both represent units appropriately and also provide theory that links 'populations' at many different scales (Coulson et al. 2006). Any approximation made afterwards would at least be based on the best of our knowledge rather than a typology. This is a trend that has started to occur within the movement in ecology towards "eco-evolutionary" models of the world (Ellner & Rees 2006; Visser 2008) (or eco-genetic models (Kokko & López-Sepulcre 2007)). There is increasingly broad acceptance that evolution may happen over short, ecological time scales (Berry 1989; Thompson 1998; Hairston et al. 2005) though it had been advocated for some time (Levins 1966). However this acceptance is now becoming wide spread. Movement away from population models of numerical abundance accepts more complex causation and the importance of detail (Benton et al. 2006). This embodies the concepts behind "population thinking". In this ecological movement we go for the jugular and try to explain the inverse problems that abound in ecology.

There has been a large focus on providing predictions and the climate change literature is swamped by bioclimate predictions and methodological considerations, which far outweigh the theoretical foundations. There are some contrasts between the willingness to accept the underlying differences in concept and model (e.g. Hampe (2004) cited 54 times; Pearson & Dawson (2003), 198 citations; see also Pearson & Dawson 2004). Whilst there has not been enough exploration of the relationship of bioclimate models to theory (Austin 2007), this is accompanied by a paucity of studies that investigate how fundamental ecological theory may be affected by climate change (though see Lewis 2006). If we do not want or have good enough reason to accept black boxes such as bioclimate models as the predictive tool, there will need to be developments in the fundamental framework to our science. If necessity is the mother of invention, we need to have the right components available to build our future predictive machinery.

Firstly, we need to develop theory appropriate to the climate change 'threat' as theoretical development lags behind present empirical findings. This may be due to the increased environmental heterogeneity necessary when considering climate change responses. For example, a range shift may cause a population to occupy a landscape that is by no means guaranteed to be composed of the same amount of habitat and or have the same spatial relations. This is amongst a myriad of biotic and abiotic contexts that could change. We may not be as well equipped to approach understanding climate change responses as the task requires and so developing theory could highlight some of the areas of ecology and evolution that may be more important than others. In Suarez's "*empire*" a very large map would be required to find needles in haystacks, but mapping the details of every haystack would be an intractable task. Pinpointing some clues as to where needles are contained would make the problem more tractable, reducing the number of haystacks to be mapped and avoiding the frustrations that could lead to abandonment of the mapping process.

Secondly, theoretical investigations may aid the development of data collection that is appropriate to the task. The present typologies have essentially emerged from the lack of detailed data available and we need to have the background to provide data when 'populations' are deemed to be important. Thus we need to move beyond occupancy maps, to data that can be used in predictive ways in a number of situations. This will aid testing and developing climate change theory. Data may need to be more detailed and less limiting in the scope of theory to which they can be usefully applied. For instance description of populations' structure through distributions of individuals traits may provide ecological and evolutionary insight (Benton et al. 2006; Grafen 2007; Visser 2008). An important interplay may develop between laboratory and model as microcosms play an increasingly large role as a test bed and inspiration for the theory that drives research (Davis et al. 1998; Benton et al. 2007).

There are signs that research areas investigating questions of different scales will become more integrated, removing subject specific typologies, producing wider scale descriptions that are backed up with mechanistic understanding (Watkinson et al. 2003; Parmesan et al. 2005). Such an omnipotent model of biological systems may be impossible to achieve, but the usefulness of our science is dependent on scientists considering what is important and securing the correct foundations upon which our science develops. In pursuing a more detailed understanding it will be likely that subject areas bud off and provide more tractable study of smaller subject areas; creating new but appropriate typologies.

## 2.9 Coda

"*far better an approximate solution to the right question than... an exact answer to the wrong question*" Tukey (1962).

This chapter has aimed to justify a further search for the appropriate 'populations' in our theory and observation. Bioclimate models were held up as a straw man upon which to beat the 'population' stick. However "population thinking" is a useful exercise in the critique of all our study, questioning what data and concepts we need to approach problems with. Indeed the "*inability to solve applied ecological problems is argued to depend on inherent variability*" in ecological systems (Hansson 2003). This is the fundamental underpinning of "population thinking": what relevant variation are we passing by? In future research, inductive methods (Mentis 1988) and exploratory simulations (Molofsky & Bever 2004) may play a larger role in conceptual development and create a more united framework within which data is collected. There may also be a need to change the process of model construction and selection. For instance, what constitutes the minimum adequate model may differ between conditions and rely on a different structure. We may then need to apply Okham's Razor more frugally for models built in 'equilibrium' circumstances to be applicable to climate change.

The fundamental question of ecology, "*why is what where?*" (Andrewartha & Birch 1958) has been altered. Climate change has added temporal and spatial complexity to the fundamental question, producing a contemporary question: "*why **will** what be where and **when?***". We are asked now to understand why things are in the places that they are and in what amounts, and to use that knowledge to make predictions given an uncertain future. The spatial component of population dynamics underlying range shifting responses has wide consequences for evolutionary processes (Kirkpatrick & Barton 1997; Barton 2001; Jump & Penuelas 2005) and ultimately the generation of diversity (Rapoport 1975). Some discussion of the links between spatial interactions and climate change has been made (Jump & Penuelas 2005). However transformation of the spatial relationships within the environment, caused by concomitant climate changes and landscape alterations

(Opdam & Wascher 2004; Ohlemüller et al. 2006), suggest there may be further alterations to population processes that we do not understand. Our understanding of the outcomes of such environmental and spatial disequilibrium is poorly understood (May 1999). I suggest that the resultant transient dynamics, ecological lags and evolution feedbacks may become research priorities. Let's get "population thinking" about that.

# 3. Range shifting on a fragmented landscape.

## 3.1 Introduction

A large body of evidence demonstrates that range shifts may be caused by contemporary climate change (e.g. Dennis & Shreeve 1991; Parmesan 1996; Parmesan et al. 1999; Thomas & Lennon 1999; Hughes 2000; Parmesan & Yohe 2003; Thomas & Cameron et al. 2004; Thomas & Tefler et al. 2004; Simmons & Thomas 2004; Hickling et al. 2005). The vast majority of these species have survived previous range shifting events during the quaternary (e.g. Bennett et al. 1991; Dyenesius & Jansson 2000; Hewitt 2000; Davis & Shaw 2001). However, two factors make contemporary range shifts distinct from those in the past.

Firstly the characteristics of climate change differ from past episodes (chapter 1). Rates of change are expected that lie outside any previous episode (Houghton et al. 2001; Thuiller 2007), 2-5 times greater than that fastest range shifts found in the fossil record (Davis & Shaw 2001; and references therein). Such increased rates of climate change will be infrequently translated into faster range shifts. Lags in populations' responses are found (Davis1989; Masek 2001), increasing the risk of extinction (see Thomas, Cameron et al. 2004). The absolute amount of climate change expected is also greater (Thuiller 2007), with many scenarios producing predicted global temperatures that exceed those exhibited in the last 125,000 years (Houghton et al. 2001).

Secondly, the characteristics of the landscape have significantly changed (Travis 2003, chapter 1). Human activities have altered large expanses of the world. For instance, it is estimated that 25% of the worlds surface now cultivated (http://www.millenniumassessment.org/en/index.aspx). The link between climate change and range shifts has been made with data sets that exclude habitat-limited populations from the analysis (e.g. Parmesan 1996; Parmesan et al. 1999). The dispersal abilities of many species are expected to be below the threshold required to traverse the fragmented habitats of modern landscapes (Pitelka et al. 1997; Collingham & Huntley 2000; Travis 2003). Even if dispersal abilities are capable of reaching all new habitat populations viability may not be such that populations remain viable (Warren et al. 2001; Keitt et al. 2001; Opdam & Wascher 2004).

Landscape alterations can be divided into two main effects: habitat loss and habitat fragmentation (see Fahrig 2003). Reductions in the absolute amount of habitat available are represented by habitat loss, whilst fragmentation characterises changes in the pattern of remaining habitat. Habitat loss nearly always results in changes in the ratio of habitat that is classified as edge (Fahrig 2003), decreasing patch size and connectivity (Bascompte & Solé 1996; With et al. 1997). Habitat loss and fragmentation affect population's ability to range shift, by altering the relationship between population and environment that are critical to populations' survival (Travis 2003). For example a large body of work has investigated critical thresholds of habitat loss in relation to the degree of habitat fragmentation for population survival (e.g. With & King 1999a, b; see With 2004) and in two species systems (Dytham 1995), but in a static climate. These theoretical studies show populations can normally tolerate more habitat loss if the remaining habitat becomes less fragmented in a static climate (Dytham 1995; Pearson et al. 1996; With & King 1999a;b; Hill & Caswell 2001; Fahrig 2001; Flather & Bevers 2002; Fahrig 2002; see also Ovaskainen & Hanski 2003). Low levels of fragmentation enhance population viability and percolation through a given landscape. The level of connectivity is realised through a populations dispersal ability. Poor dispersers are more likely to 'perceive' fragmentation and so rely on habitat correlation for survival (Doak et al. 1992; Adler & Nuernberger 1994; With & King 1999a). Dispersal ability is not solely related to actual dispersal distances, but also reproductive output (Carmel & Flather 2006). High levels of reproductive output can increase the number of long distance dispersal events (Carmel & Flather 2006), but also support viability in fragmented areas (Hanski 1998; With & King 1999a; Keitt et al. 2001).

Travis (2003) demonstrated the synergistic effects of climate change and habitat loss – the "*deadly anthropogenic cocktail*". Such effects on ecological theory suggest climate change may affect the nature of spatial interactions, further supporting proposals that a concerted effort is needed to understanding how spatial population dynamics develop during range shifting events (Davis & Shaw 2001; Hampe 2004). For instance, if spatial dynamics significantly differ from those in static climates our conservation strategies may significantly differ from those currently in place (Opdam & Wascher 2004). Range shifts may be an important aspect of responses to climate change due to the amount to which populations' present range will become unsuitable (Thomas, Cameron et al. 2004). Thus understanding the mechanics of range shifting may be imperative for appropriate management.

In this study I investigate the relationship between landscape characteristics, habitat loss and fragmentation, and population survival during climate change. Using an individual based meta population model (Levins 1969; Travis 2003), I show the changing relationship between landscape and populations is significantly altered during climate change and is highly dependent on populations phenotypes.

## 3.2 The model

Building on methods employed in similar studies (Dytham 1995; Pearson et al. 1996; With & King 1999a;b; Hill & Caswell 2001; Fahrig 2001; Flather & Bevers 2002) the landscape is represented by a lattice of suitable and unsuitable patches. Suitable patches may be occupied or unoccupied, with colonisations of unoccupied patches determined by $c$, a colonisation probability and extinction of occupied patches determined by $e$. As patches can only be colonized when an occupied patch occurs within a specified neighbourhood, colonisations are affected by aggregation. In the experiments shown here we use three neighbourhoods ($N$), nearest 8, 24 and 48 patches, with the probability of colonisation given as:

$$1 - (1-c)^n \qquad (1)$$

where the absolute probability of colonisation increases with $n$, the number of occupied patches within the focal patch's neighbourhood (Holt & Keitt 2001).

Habitat is classed as unsuitable in two ways. Firstly a proportion of the habitat on the lattice is destroyed. This degree of habitat loss can be manifested in different ways to produce fragmented or clumped landscapes. Habitat may also be unavailable if it occurs outside of a climate window, as in Travis (2003). The climate window defines where climate is suitable, so not all of the patches remaining after habitat loss are available at any one instance. As the climate window shifts across the landscape a range shift is induced as occupied patches falling outside the window become extinct. Populations may only survive by successfully range shifting as the whole of the pre climate change range will eventually become unsuitable. Populations are initialised onto the landscape within a climate window that is at first static and allowed to reach equilibrium before climate change is initiated.

Varying levels of fragmentation are achieved by employing a simple algorithm that determines habitat availability (Travis unpublished). Within the lattice each cell is given an individual, sequential identity. However the order of the sequence through space is determined by the variable *h*. The sequence starts at a randomly chosen cell on the lattice. With probability *h* the next cell in the sequence will be a randomly chosen neighbour from the nearest eight cells; else a randomly chosen cell from the entire landscape continues the sequence. This process is repeated until all cells have received an identity. As cells can have multiple identities, a single identity is randomly selected from that set and the sequence is appropriately adjusted so each cell has a single number in a continuous sequence. The number of cells that will be unavailable through habitat loss is calculated and cells (patches) to be destroyed are those with identities that are less than or equal to the number to be destroyed.

At one extreme entirely random habitats are generated which produce landscapes with no spatial autocorrelation in the relative positioning of habitat. By increasing the parameter *h*, correlation is increased between neighbouring patches. For $h=0$, fragmented landscapes are generated, with increasing clumping of habitat found with increasing values of *h*. Some examples of landscape patterns produced by this algorithm are shown in figure 3.1.

Sensitivity of the model to the rate of climate change was investigated by varying numbers of generations (*g*) between climate shifts. Similarly the effect of varying the climate window size was assessed. Subsequently two large experiments were carried out. Firstly the effects of 4 levels of habitat clumping ($h=0.0$, $h=0.9$. $h=0.99$. $h=0.999$. where $h=0.0$ is the highly fragmented habitat and $h=0.999$ is highly correlated. clumped habitat) were tested across the full range of range of habitat loss (0-1.0 habitat loss. at 0.05 increments). Populations with perfect ($c=1.0$. $e=0.1$) and poor (c=0.02, e=0.1) colonisation abilities were investigated in most detail. The three levels of dispersal capacity were applied for each parameter set, within 20 randomly generated landscapes, totalling 9600 simulation runs. Secondly, the difference in the two extremes of habitat clumping (h=0.0, h=0.999), across the full range of habitat loss, was examined for increasing colonisation ability (5 levels) with a constant extinction probability and similarly for extinction probability (5 levels) with a constant colonisation ability. Dispersal was held constant at N=24 in each of 20 randomly generated landscapes, at each parameter value, totalling 8000 simulations runs.

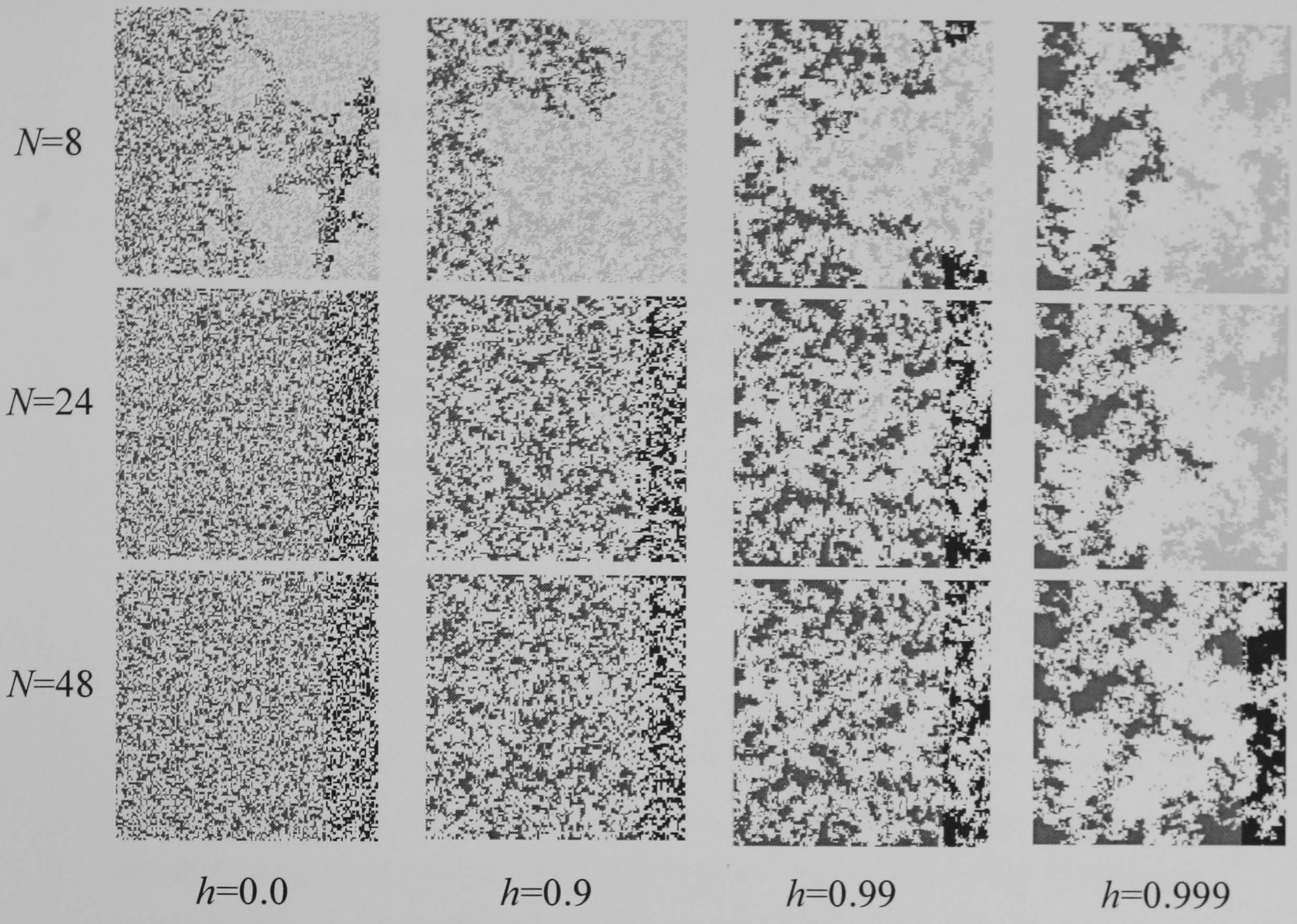

Figure 3.1: Landscapes illustrating the effect of habitat correlation ($h$) on species survival through a period of climate change. Each landscape was used for each level of dispersal ($N$=8, $N$=24, $N$=48), with 0.6 of the habitat lost. White areas represent the unsuitable matrix, light grey areas suitable unoccupied habitat, dark grey areas suitable unoccupied habitat that has been previously occupied and black areas are suitable occupied habitat. Note that the climate window moves left to right, with the window clearly illustrated by the black area of occupied suitable habitat on the right hand side of the $N$=48, $h$=0.999 landscape. ($c$=1.0 & $e$=0.1 in all cases). In 4 of the simulations extinctions are observed, where no black patches appear in the figure ($N$=8, $h$=0.0, 0.9 & 0.999; $N$=24, $h$=0.999).

## 3.3 Results

### *3.3.1 Range shifting and dispersal*

Populations that are most successful during climate change have greater dispersal abilities. Broader dispersal neighbourhoods increase the availability of routes across a landscape for any given level of habitat loss or fragmentation (fig 3.1). This is in agreement with percolation theory developed in static climates (With & King 1999a; b). However, some habitat arrangements can cause extinction just because routes are more tortuous than others. For instance in figure 3.1. the population fails to track climate for n=24, h=0.999. However a number of simulations are found in fig 3.2b. with exactly the same parameters, where populations successfully track a climate change. Some landscapes as a whole do not permit a range shift. Those that do permit a range shift may not do so in entirety and so occupancy often decreases during climate change (e.g. fig 3.1, $n$=8, $h$=0.0). Occupancy is often reduced at lower levels of habitat loss when habitat is clumped. without causing extinction. Populations surviving the period of climate change may also have a reduced range when compared to the initial range size (figure 3.1, $n$=8, compare $h$=0.0 and $h$=0.99). Even if populations cannot survive the whole episode of climate change, dispersal may increase the distance with which species track climate (fig 3.1, h=0.999; fig 3.2).

### *3.3.2 Effect of habitat loss and habitat fragmentation*

As the intensity of habitat loss increases (to the right hand side of fig 3.2), the predictability of populations' responses decreases. As an extinction threshold is reached a populations' survival is determined by the arrangement of habitat. The position of the extinction threshold in relation to habitat loss is highly dependent on dispersal ability. However, colonisation ability and extinction susceptibility determine whether fragmented (h=0.0) or clumped (h=0.999) habitat permitted more successful climate tracking (see figure 3.2 a-e). Unlike theory developed in a static climate, no single pattern of habitat loss best facilitated populations' survival.

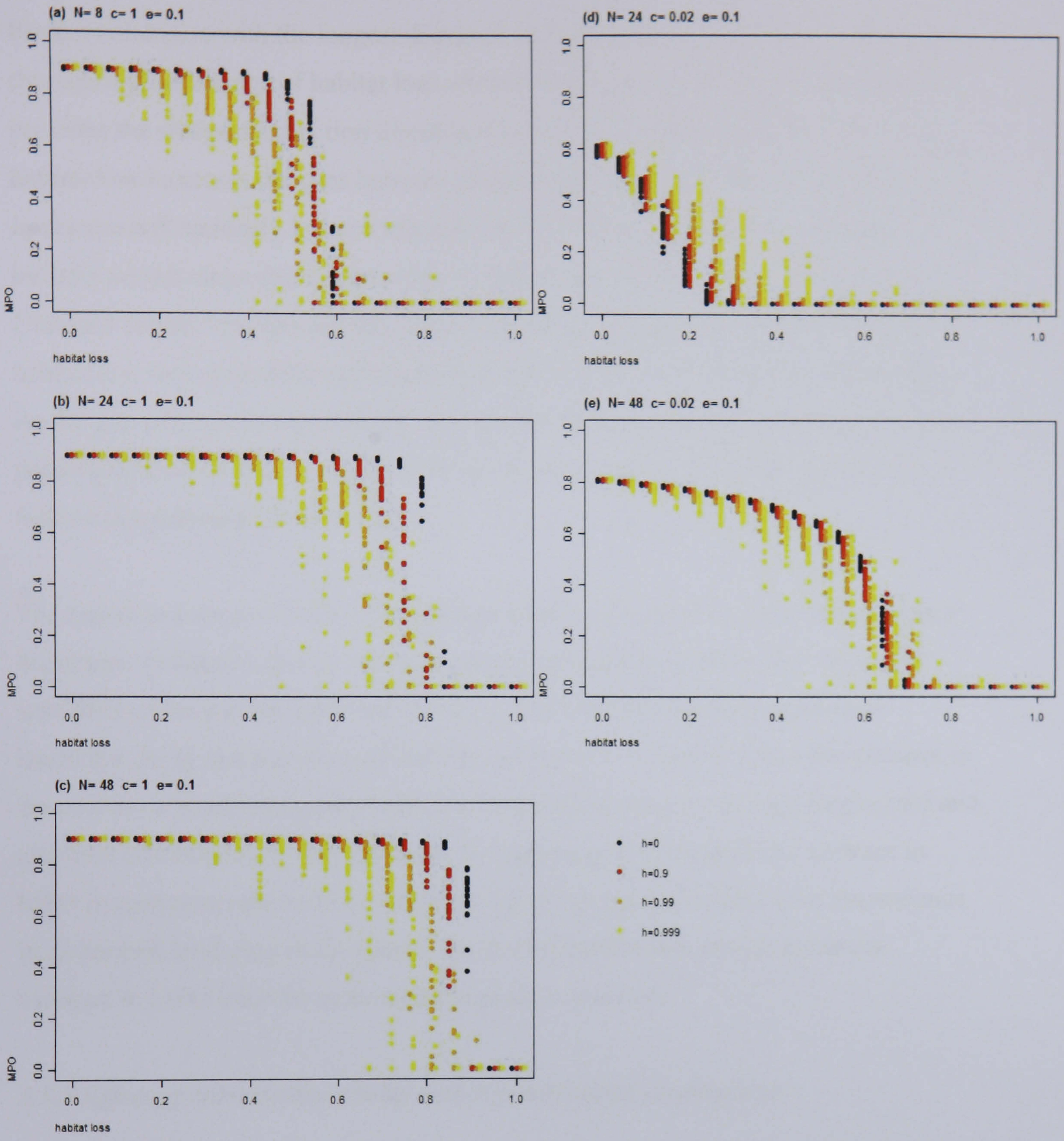

Figure 3.2: Individual data points for the minimum number of patches occupied at any point during a simulation run (Minimum Patch Occupancy- MPO): for a perfect coloniser ($c$=1.0 $e$=0.1) (a) $N$=8, (b) $N$=24, (c) $N$=48, and a poor coloniser ($c$=0.02 $e$=0.1) (d) $N$=24, (e) $N$=48 on landscapes with random, fragmented habitat loss and increasing degrees of clumped habitat loss ($h$=0.9, $h$=0.99, $h$=0.999). Habitat loss is incremented at 0.05 for values; for clarity data points for each landscape at each value of habitat loss are offset. For a poor coloniser with a dispersal capacity of $N$=8 all simulations resulted in extinction.

Perfect colonisers with the longest dispersal abilities ($n$=48) can track climate change through a greater range of habitat loss when h=0.0 (fig 3.2c). Fragmented habitat loss provides the sharpest extinction thresholds as habitat is more evenly distributed. As habitat loss increases the gaps between patches uniformly increases and a fragmented landscape will suddenly become inhospitable. As dispersal decreases, clumped habitats permit range shifts more often at high levels of habitat loss (fig 3.2 a, b). Clumped habitat loss sporadically allows successful climate tracking at levels of habitat loss that exceed the extinction threshold of the more fragmented landscapes. As the gap structure is less uniform for clumped habitat arrangements, there is some probability that those gaps within the populations dispersal range are aligned in a fashion that provides a route to survival.

The switch to increased survival on clumped habitats becomes more obvious in poor dispersers. In figure 3.2a one habitat arrangement permits a successful range shift with 80% of the habitat lost. This is 20% less habitat than the last fragmented landscape (h=0) that permits survival. As can be seen in figures 3.2a-c the variance in the minimum patch occupancy (MPO) of populations moving through fragmented and clumped landscapes are very different. For fragmented landscapes the variance in MPO is comparatively uniform, whilst at any given level of habitat loss, the variance in a clumped landscape is far greater. Increasing habitat loss always enhances variance in MPO until the extinction threshold is reached.

### *3.3.3 Effect of colonisation ability and environmental stochasticity*

Populations with poor colonisation ability (c=0.02 e=0.1) have a less steep extinction threshold and occupy less of the habitat available. For these populations the switch to more successful range shifting on clumped habitats is demonstrated at far lower levels of habitat loss (figures 3.2d & e) than for the perfect disperser. Indeed throughout the range of habitat loss a population with intermediate dispersal abilities may encounter a landscape that permits greater occupancy if it is clumped. In these landscapes a poor disperser (n=8) can never range shift.

The difference between MPO for fragmented and clumped habitats ($\mathrm{MPO}_{h0.0}$ - $\mathrm{MPO}_{h0.999}$) is shown in figure 3.3. At low levels of habitat loss (<0.1) there is little difference in the mean MPO for populations with all colonisation abilities. However, as habitat loss increases, predicting the population response is increasingly dependent on colonisation ability. Generally, as colonisation ability decreases clumped landscapes outperform the fragmented landscape over a greater range of habitat loss. As is the case for clumped habitats occasionally providing better routes for range shifting, clumped habitats also can be arranged such that populations cannot find safe passage. The switching importance of habitat clumping is also found when extinction probabilities increase (figure 3.3b), though the effect is weaker throughout the majority of the parameter values.

### *3.3.4 Sensitivity to the rate of change and size of climate window*

A single rate of climate change and size of climate window were used for all the simulations previously presented. Initial analyses showed the speed of climate change to have little effect on the success of range shifting (figure 3.4), except for extremely small climate window sizes (populations with incredibly narrow ranges). For small climate windows the likelihood that the climate window may surround a tortuous percolation route is low, with only the most direct of routes allowing successful range shifting. For this reason increasing the climate window size increases the amount of habitat loss tolerated during range shifting (see figure 3.5) (see also Travis 2003). Clearly, as the window becomes a greater fraction of the entire landscape percolation routes will have the tendency to increase in number. A perfect coloniser with the greatest degree of dispersal was used for these simulations to mitigate conflicting effects. Undoubtedly reduced colonisation and/or dispersal ability would further reduce successful range shifting.

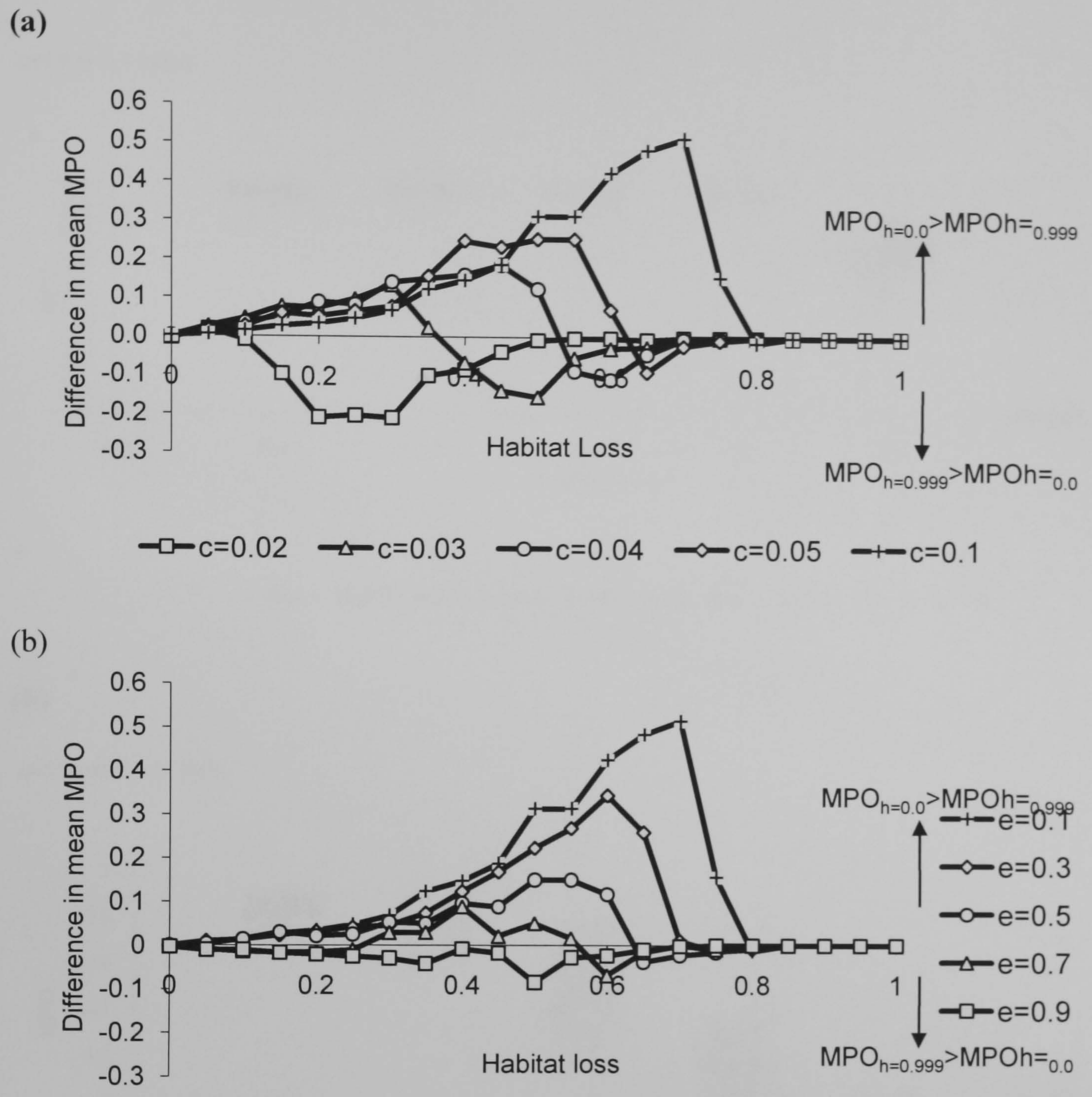

Figure 3.3: The relative performance of range shifting with landscapes suffering from fragmented habitat loss (*h*=0.0) and highly clumped habitat loss (*h*=0.999). Mean minimum patch occupancy (MPO) of twenty simulation runs was recorded for each parameter set and with both forms of habitat loss. The difference between MPO with fragmented habitat and clumped habitat loss ($MPO_{h0.0}$ - $MPO_{h0.999}$) illustrating the relative performance of range shifting on different landscapes. Values >0 show a fragmented landscape better permits a range shift and conversely for values <0. Data are shown for a range of (a) colonisation abilities $0<c<0.1$, $e=0.1$ and (b) extinction rates $0<e<1$, $c=0.1$. Dispersal capacity: $N=24$ in all cases. Note that $e>c$ is possible as the probability of a cell being colonised is also dependent on the number of occupied cells within the neighbourhood (*N*) defined by dispersal capacity.

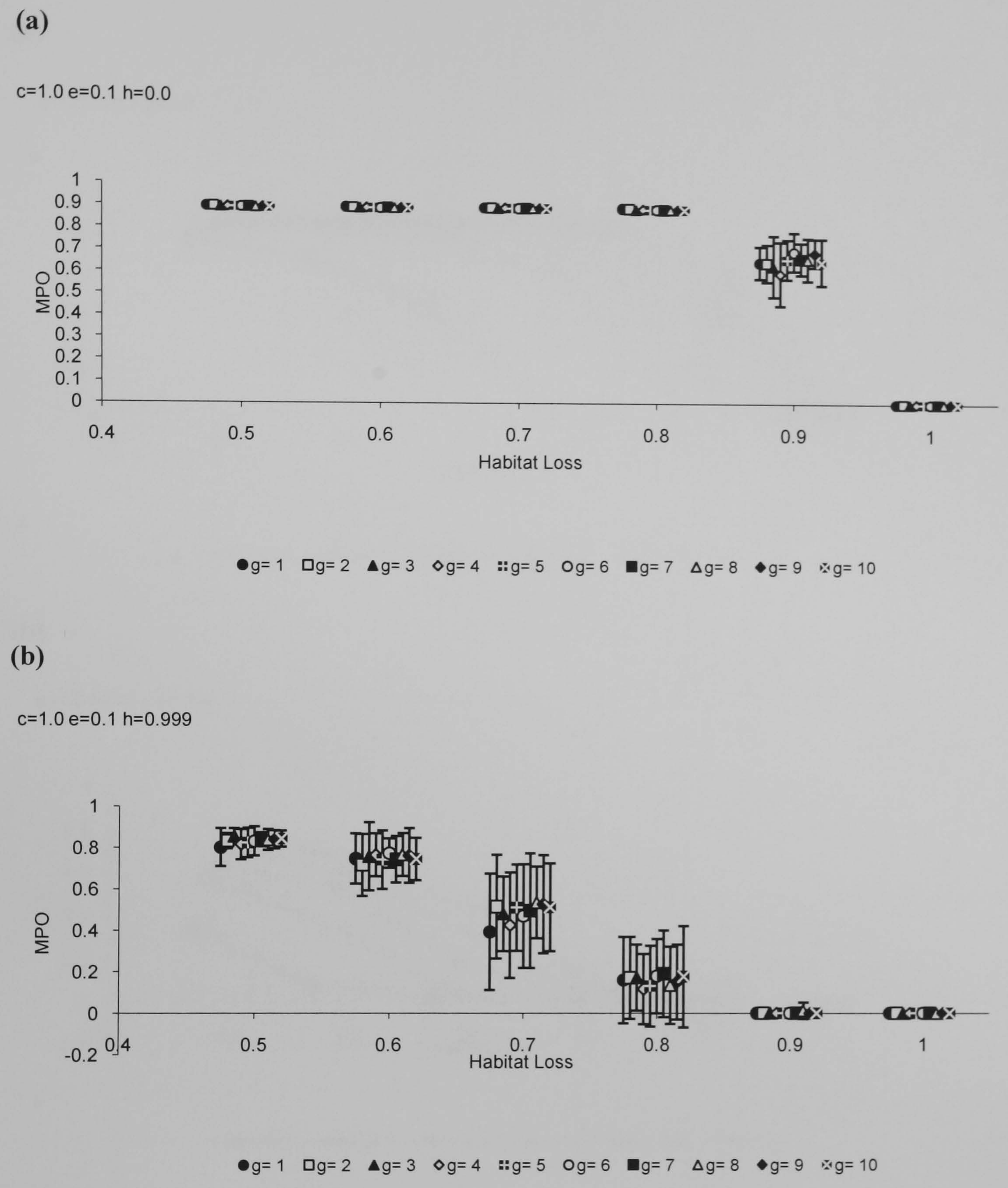

Figure 3.4: The mean minimum patch occupancy (MPO) for 20 simulation runs for a perfect coloniser ($c$=1.0, $e$=0.1, $N$=48) at (a) $h$=0.0 and (b) $h$=0.999, with varying numbers of generations ($g$) between climate shifts (error bars show ± standard deviation). A climate window of 40 units is used in each case. Jitter is added for clarity.

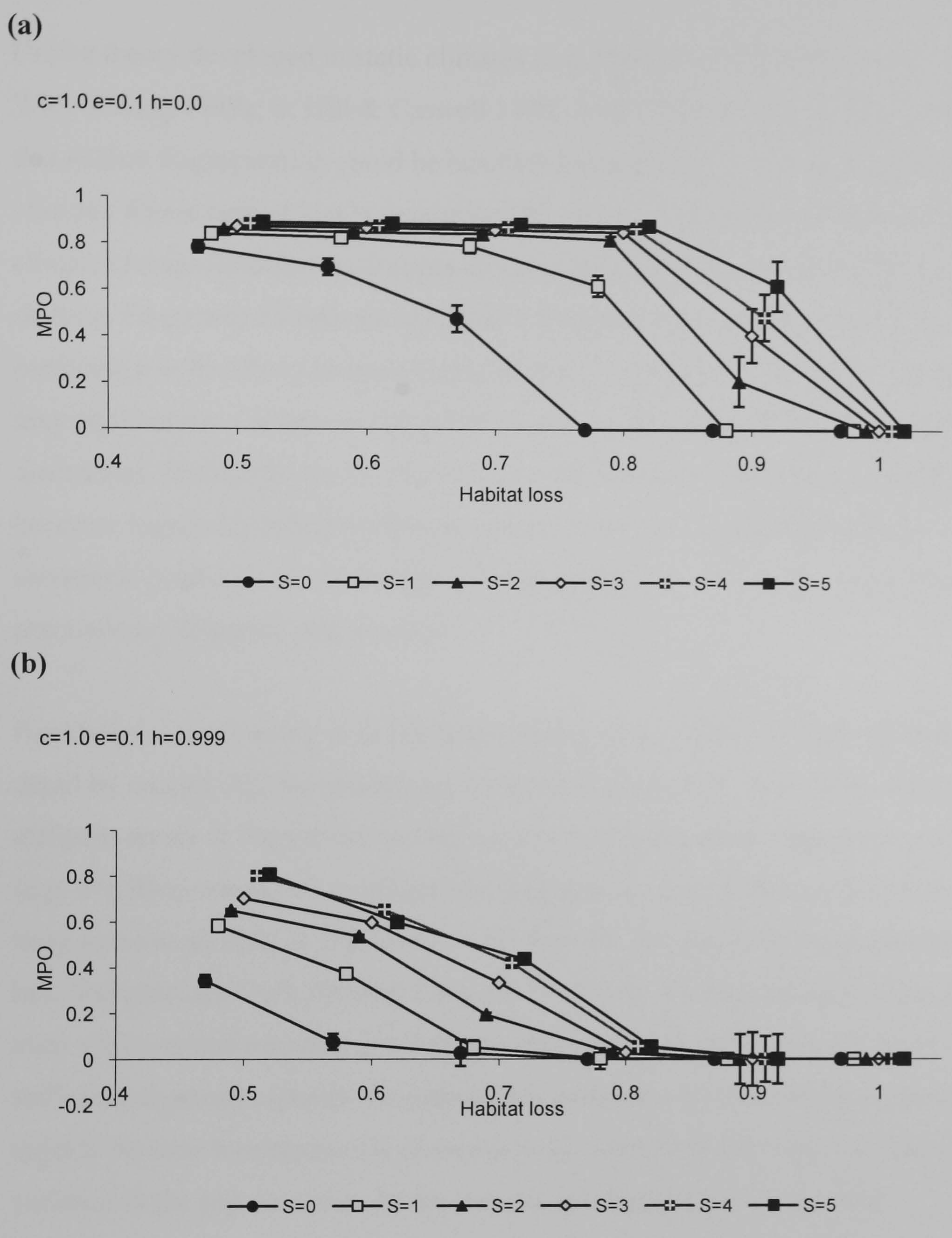

Figure 3.5: The mean minimum patch occupancy (MPO) for 20 simulation runs with varying sizes of climate window (window $=2^S$ units wide), for a perfect coloniser (c=1.0, e=0.1, N=48) at (a) h=0.0 and (b) h=0.999 (error bars show ± standard deviation). 2 generation are allowed between each climate shift. Jitter is added for clarity.

## 3.4 Discussion

Unlike theory developed in static climates (e.g. Dytham 1995; Pearson et al. 1996; With & King 1999a; b; Hill & Caswell 1999; With 2004), the model demonstrates that habitat fragmentation could be beneficial to population survival in a changing climate. Where habitat loss is determined by factors independent of management of climate change, clumped landscapes need not provide a suitable route for range shifting. Fragmented landscapes provide a uniform gap structure that is more predictable in its effects during climate change. In clumped habitats, manageable gaps may not lie in an orientation that permits a range shift, because climate change is directional. The model also shows that near the extinction threshold, prediction becomes highly dependent on knowledge of traits that determine population dynamics. Furthermore, the position of that threshold is dependent on knowledge of populations' dispersal characteristics.

Populations' relationship with landscape during range shifts can be explained in more detail by recognising the restrictions the climate window (or envelope) imposes on different levels of fragmentation. At low levels of habitat loss, fragmented landscapes (e.g. h=0.0) are essentially uniform; the landscape is regionally usable with a single large route to survival at low levels of habitat loss. As shown by the results presented here and previous work (With & Crist 1995; see also Collingham & Huntley 2000) even a fragmented resource is not necessarily perceived as fragmented given sufficient dispersal capacity. As habitat loss increases, fragmented landscapes become quickly become homogenously unusable. Gaps are universally large, as there is little variance in the gap structure. At the extinction threshold, which exhibits comparatively little variation in its position, the prescribed dispersal capacity will be exceeded (Wiens 2001). Thus when a population is tracking climate within its climate window, a fragmented landscape will not greatly differ in its gap structure from one instance to the next. In a fragmented landscape, that supports a range shift, we could reasonably say that the population could keep range shifting indefinitely. That is the climate window does not have a large effect on fragmented landscapes' characteristics.

However, clumped landscapes carry less predictability. Their gap structure exhibits greater variation (Hill & Caswell 1999) and we cannot assume that within the climate window gaps will permit a range shift. This is an important contrast with fragmented landscapes, as clumped landscapes encountered at each of a range shift need not be similar to that encountered before. As landscapes are a finite space, some gaps will inevitably be larger on a correlated landscape causing increased variation in the gap structure. The most parsimonious route for a range shift is when habitat provides an uninterrupted route spanning the entire landscape in the direction of climate change to the future climate space, in the direction of climate change. Deviations from a linear distribution of patches from 'historical' to 'future' range, generates greater variation in the population response. For instance, at the other extreme, habitat could lie in a contiguous distribution that is perpendicular to climate change. Similarly the climate window may reduce the percolation routes available through a landscape, reducing occupancy when the climate window is imposed. This is the prime difference with theory developed in static climates (Pearson et al. 1996; With & King 1999a; b), where populations can take more indirect and tortuous routes through a landscape. Unlike fragmented landscapes, the extinction thresholds for a clumped landscape will depend greatly on the amount of climate change imposed.

Habitat pattern clearly becomes more important during range shifting. Understanding the interaction with population characteristics is similarly simple when we deconstruct the mechanisms of survival. In metapopulation models such as this the colonisation probability of a given patch is a function of the number of neighbouring occupied cells (Holt & Keitt 2000; Fahrig 2002). Fragmentation inhibits these aggregative effects, which permit survival, when habitat loss is at high levels. This is similar to the factors that may lead to pinning of an invasion (Keitt et al. 2001, see chapter 1). For poor colonisers or poor dispersers survival can only be maintained on clumped landscapes where sufficient habitat is found around any given patch. The reduction in aggregative patterns are found with increasing dispersal ability in natural populations, as has been shown for plant species (Quinn et al. 1994). Increasing dispersal neighbourhoods allow populations survival to be reinforced from greater distances, which needn't conform to aggregative spatial patterns (Solé & Bascompte, 2006). Within a clumped landscape only some areas may maintain sufficiently large amounts of habitat for survival (Fahirg 2002; With 2004), so reducing the potential number of routes for a range shift and increasing the variance seen in conditions near the extinction threshold here. Whilst fragmented landscapes can better facilitate range shifting for particularly good colonisers (table 3.1), increasing habitat loss causes such localised aggregative effects nevertheless important, just at a different level of habitat loss. In summary, aggregative effects mean that appropriate management requires sufficient habitat to be found at each stage of a range shift. The exact amount is somewhat unpredictable as high occupancy reduces the amount of habitat required. Occupancies that are greater than specific habitat patterns could normally support may be produced during range shifting as populations take on a transient state.

Like any model, numerous simplifying assumptions are made and the work presented here is a step towards a more detailed understanding of spatial dynamics during range shifting. Future developments could take an immense number of directions, such as investigating the effects of further environmental heterogeneity or inclusion of more detailed population biology and biological traits.

The landscapes presented here are temporally stable and habitat suitability is not affected by any relationship with the climate window. Hampe (2004) suggested expanding range limits may experience decreasing habitat availability and increasing fragmentation (also see Wilson et al. 2004). At trailing range limits suitable habitat may become more common and less fragmented (Hampe 2004; also see Parmesan 1996). Habitat may not remain suitable through all areas of the climate window (Travis & Dytham 2004). Landscapes may change in quality during climate change, for instance microclimates from edge to centre of habitat patches may alter, affecting the realised gaps between patches. Similarly presently occupied habitat may alter, and so increase occupancies to levels that strengthen populations' ability to disperse (Carmel & Flather 2006). Or indeed populations may have reduced occupancy in their present range, reducing the potential to range shift. Thomas, Rose et al. (1999) suggest that whilst habitat could become more widely available, it may not encompass previous habitat (also see Grime 1997; Williams et al. 2005). Even if required range shifts are local, spatial dynamics such as those demonstrated here will be significant in populations' survival.

Table 3.1: The general effect of fragmentation on range shifting at levels of habitat loss before the extinction threshold, for two levels of colonisation.

| | perfect [$e$=0.1 $c$=1.0] | poor [$e$=0.1 $c$=0.02] |
|---|---|---|
| fragmented [e.g. $h$=0.0] | positive effect | negative effect |
| clumped [e.g. $h$=0.999] | negative effect | positive effect |

Whilst many populations have survived previous climate change events, differences in landscape characteristics have elicited different kinds of response (Dynesius & Jansson 2000). Dispersal and generalist/specialist traits may be differentially selected for in different landscapes (Dynesius & Jansson 2000).Dispersal has been presented as an essentially passive process in this model, having most in common with sessile organisms that disperse as propagules before settlement. As has been previously noted, dispersal characteristics determine the scale of heterogeneity that must be considered (Collingham & Huntley 2000; With 2004). Populations capable of 'chance' long distance dispersal events will be more likely to track climate change, being able to exploit routes that would not otherwise have been available. However, Allee effects will likely impact establishment if subsequent propagule pressure is low (Keitt et al. 2001; also see Travis & Dytham 2002). If there is variation in dispersal traits, long distance dispersers may increase in frequency at leading range limits (Thomas et al. 2001; Hughes et al. 2003; Simmons & Thomas 2004; Hill et al. 2004; Phillips et al. 2006). Expansion into areas of pristine habitat are expected to increases in dispersal at the leading range limit (Travis & Dytham 2002).

Dispersal traits can be reduced in to a further set of traits that govern emigration, survival during dispersal and settlement (Clobert et al. 2001). Thus selection may act on other traits such as responses to density within patches, i.e. density dependent dispersal (Travis et al. 1999), and cause divergent responses to habitat loss dependent on landscapes characteristics. Selection for density independent dispersal could conceivably increase at expanding range limits. A similar effect may be found where individuals' dispersal decisions are condition dependent (Ims & Hjermann 2001). Populations may exhibit considerable differences in dispersal depending on the areas they inhabit (Denno et al. 19996), such as dispersal tendency and the period of dispersal (see Table 1 in Ehrlich et al. 1975). Habitat selection (intelligent dispersal) may play a large role in determining how populations respond to habitat fragmentation (Hill et al. 2004) and so may affect the range shifting response. For instance plant species which are animal or wind dispersed may behave very differently when confronted with locating available habitat (Montoya et al. *in press*). Habitat selection and differential settlement between individuals (e.g. Blondel et al. 1999; Postma & van Noordwijk 2005) may drive spatial selection (Garant et al. 2005) and alteration to the dynamics of range shifting. This is especially so where secondary traits co-vary with dispersal ability (e.g. Zera & Denno 1997).

Selection for secondary traits may affect the population parameters we use to describe population dynamics, creating non stationary descriptors of populations that may point to a necessity for increased acknowledgement of individuals traits (Benton et al. 2006; Visser 2008). Recognising the true variation of populations reveals a complex interaction between life history traits, especially as co-variation need not occur in ways that promote a range shift or alleviate Allee effects. For instance tradeoffs occurring with dispersal may reduce fecundity (Hughes et al. 2003), or those individuals able to disperse may be those more able to subsequently have high reproductive output (Simmons & Thomas 2004).The wide range of relationships between dispersal and co-varying traits (Zera & Deno 1997) make understanding such tradeoffs fundamental to understanding populations' range shifting responses. There are a multitude of factors that need to be considered in populations' responses to climate change (Hampe 2004; Pearson & Dawson 2004), the work presented here provides a baseline for understanding the effect of the landscape on species with varied life history and dispersal attributes (With & Crist 1995; With & King 1999a).

In summary, the model presented here has demonstrated that during a period of climate change the effect of fragmentation is highly dependent on species' characteristics and the degree of habitat loss. Incorporating landscape features such as habitat loss and fragmentation at scales relevant to species' characteristics, and to the variation of characteristics within species, will aid identification of conservation priorities and the implications of present reserve networks. We might expect theoretical predictions to fit species which show more immediate response to their changing environment, as has been found with habitat fragmentation studies (Debinski & Holt 2000). Where species are long lived or have overlapping generations, we may expect results that are not immediately concordant with theoretical expectations. The development of lags (Davis 1989), may alter populations' spatial patterning and produce dynamics that differ from those in static climates. It is clear that there is not one landscape 'prescription' that will preserve all species and conservation management needs to acknowledge the variation of responses that are likely. Not all populations perceive landscapes in the same way and understanding how populations utilise landscapes will make general trends more visible.

# 4. Landscape geometry determines spatio-temporal patterns of local adaptation during environmental change.

## 4.1 Introduction

Climate change is an interesting conservation problem as populations can respond by adapting to the new climate conditions *in situ*, or by tracking previous climate conditions through space (Holt 1990; Helmuth et al. 2005; Aitken et al. 2008). There are many factors that may limit either response (e.g. Etterson & Shaw 2001). For instance, genetic variation or habitat availability can constrain adaptive (Bridle & Vines 2007) and range shifting responses respectively (Holt 1990). Theory has investigated adaptive and landscape heterogeneity effects on climate change responses separately (e.g. adaptive, Pease et al. 1989; Buerger & Lynch 1995; landscape heterogeneity, Travis 2003; McInerny et al 2007). However, very little is known about interactions between adaptive and landscape effects in determining populations' responses, despite the expected importance of the interaction (Rapoport 1975; Holt 1990; Edmonds et al. 2004; Burton & Travis *in press*).

If populations neither respond by adaptation or geographic movement they may face fitness costs or extinction (Helmuth et al. 2005; Lynch & Lande 1993). Holt & Gomulkiewicz (2004, pp245) suggest this is fundamentally why "*many conservation problems arise because environmental change forces species' population outside that species' ecological niche*". Outside of the niche, population growth rates, $r$, are $<0$, whilst inside the niche $r>0$ and there is population persistence (Holt & Gomulkiewicz 2004). Here I use the definition of the niche as the 'mapping' of population growth rates onto environmental conditions as in Holt & Gomulkiewicz (2004). However, within the niche population growth rates are not simply a binary condition, i.e. $>0$ or $<0$ (Birch 1953; Austin 1987; Sibly & Hone 2002)(fig 4.1a & b). Environmental change may move a population to an alternative position within the niche altering the population growth rate (fig 4.1 c&d). For example, a change in climate may increase physiological stress leading to a reduction in population growth rates (Waite & Strickland 2006). Alternatively a change in climate could reduce physiological stress (Chamillé-Jammes et al. 2006) and increase the population growth rate. In this way climate change may force a population through its niche, not simply displacing the population outside of it (fig 4.1).

When populations inhabit heterogeneous environments, dispersal can play a large role in determining niche evolution (Kawecki 1995; Kirkpatrick & Barton 1997; Lenormand 2002), or conversely niche conservatism (Holt & Gomulkiewicz 2004). For instance, if a population inhabits two 'patches' with two distinct environmental conditions there are

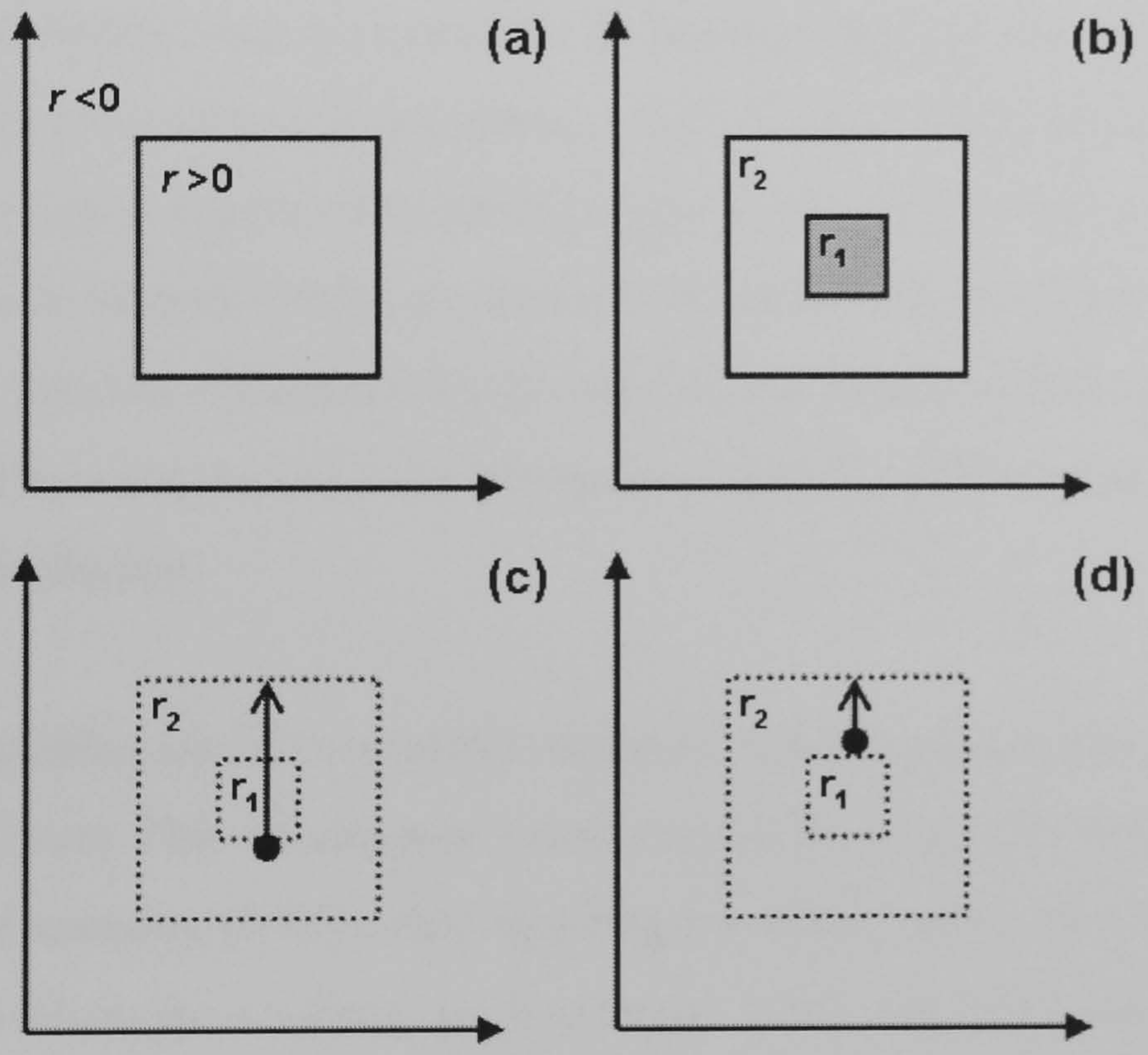

Figure 4.1: (a) The niche may be simply conceived as the set of environmental conditions where population growth rates, *r*, are >0 producing viable populations and <0 producing unviable populations (e.g. Sibly & Hone 2002). (b) However *r* may vary within the set where *r*>0. This may be of great importance when directional environmental change pushes a population through the niche given many different possible start points. Populations may have long (c) or short (d) routes through a niche and encounter different levels of *r* during the journey.

two distinct evolutionary optima. In isolation each population might locally adapt to each optimum. However immigration between patches can divert gene frequencies from the direction of local adaptation, by introducing genes selected for in a different environment (Lenormand 2002). This process is known as gene swamping (Lenormand 2002) or migrational meltdown (Ronce & Kirkpatrick 2001) and it is highly sensitive to the rate and geometry of dispersal (Kawecki & Holt 2002; Kawecki 2004). If dispersal between patches is asymmetric one population may receive fewer immigrants and selection may drive evolution towards that local optimum. For the patch receiving more immigrants gene frequencies may be driven away from the local optimum, and towards that of the source of immigrants producing maladaptation (Lenormand 2002). However if dispersal rates are low, then local adaptation in a patch receiving relatively more immigrants may increase (Kawecki 2004). Such asymmetries in dispersal may be driven by physical properties of the environment (e.g. prevailing winds, Keddy 1981), behavioural responses (Pulliam 1998) or due to simple differences in habitat area or carrying capacity between patches (Kawecki & Stearns 1993) (see Kawecki & Holt 2002 and Kawecki 2004 for further and more detailed examples). I focus on this last example where different patch sizes, represented by carrying capacity, produce asymmetric dispersal and so generate geometry in the landscape.

I consider the tractable case of two patches existing along a climate gradient (North to South, Cold to Warm). The '*landscapes*' could vary in the degree to which they exhibit a Northern Biased Geometry (NBG), having a larger northern patch, or a Southern Biased Geometry (SBG) where the southern patch is larger. NBG and SBG geometries will both produce asymmetry in dispersal, but with opposing geometries in relation to climate warming. The patch receiving more immigrants could be in the north and experience decreasing stress; or in the south and experience increasing stress. As climate change responses may be significantly determined by the "*interplay*" between dispersal and local adaptation (Davis & Shaw 2001), such effects of landscape geometry may be an important consideration in climate change research (Hampe 2004).

I investigate how landscape geometry affects ecological and evolutionary processes during climate change. In a two-patch individual based model I assume that climate plays a large role in determining individual success (though this may be varied by the addition of noise) and that population structure is determined by heterogeneity in the carrying capacities of patches. Carrying capacities may be considered to relate to absolute area of each patch (Kawecki & Stearns 1993) so producing landscapes with differing geometry. I demonstrate that this has considerable consequences for the population, dispersal and niche dynamics.

## 4.2 The Model

The individual based model (fig 4.2) employs similar assumptions to previous models investigating the evolution of an adaptive trait, $z$, which defines the niche along a gradient (e.g. Buerger & Lynch 1995, Kirkpatrick & Barton 1997; Garcia-Ramos & Kirkpatrick 1997; Butlin et al. 2003). Here I consider a landscape consisting of a southern (low latitude) and a northern patch (high latitude)($x_{(south)}$, $x_{(north)}$). A climate gradient passing through the landscape produces discrete ecological optima in each patch ($\theta_{(i)}$) differing by a parameter $b$, where:

$$\theta_{south} - \theta_{north} = b \qquad (1)$$

When $b$=0 a homogeneous climate is represented, with heterogeneity increasing with $b$. Each patch has a proportion of the entire carrying capacity taken from the maximum total population size, $K_{max}$ (fig 4.2b).

$$K_{\max} = K_{south} + K_{North} \qquad (2)$$

The carrying capacities represent a feature of the landscape relating to absolute habitat area (or alternatively patch quality). Varying the proportion of carrying capacity found in the northern patch produces landscapes with opposing geometry in relation to the directional change in the climate gradient; Southern Biased Geometry (SBG) has a larger southern patch, and Northern Biased Geometry (NBG) a larger northern patch. Through the interaction of landscape geometry and dispersal rate (see below) the direction and strength of gene flow is varied. Where there is no bias ($K_{south}=K_{north}$), dispersal rates between patches are, on average, equal. For NBG ($K_{south}<K_{north}$) there is a net flow of individuals to the south and for SBG ($K_{south}>K_{north}$) a net flow to the north. This enforces a '*relative source- sink*' structure (Kawecki 2004) as the smaller patch receives fewer immigrants by virtue of its smaller size (though see results).

A constant, static climate is maintained until quasi-equilibrium is reached, where average adaptation values are maintained over a number of generations. Subsequently, climate change (warming) occurs equally and simultaneously throughout the whole simulation environment, producing a linear change of the ecological optima in both patches (see figure 4.2c):

$$\theta(i) = x(i)b + Ct \qquad (3)$$

where $C$ denotes the amount of change in each time unit, $t$.

Each individual follows an annual, monoecious life cycle and ordering of processes (fig 4.2a). Censuses are made before reproduction for the population sizes or after dispersal when recording patterns of immigration. Generations are discrete and each haploid individual takes part in each process in the same instant. At the beginning of a simulation, optimally adapted individuals are initialised into each patch at the respective carrying capacities. Each individual produces a number of offspring, $E$, where each haploid offspring arises from random within-patch mating and no self-fertilisation is possible (an asexual model was also tested to investigate the generality of results). All adults then die. Offspring settle in the natal patch with probability $1\text{-}m$, and disperse with probability $m$ (fig 4.2c). Dispersers settle in the neighbouring patch or out of the patch system with equal probability ($m/2$). Individuals dispersing outside the patch system are immediately lost, producing a 50% dispersal mortality.

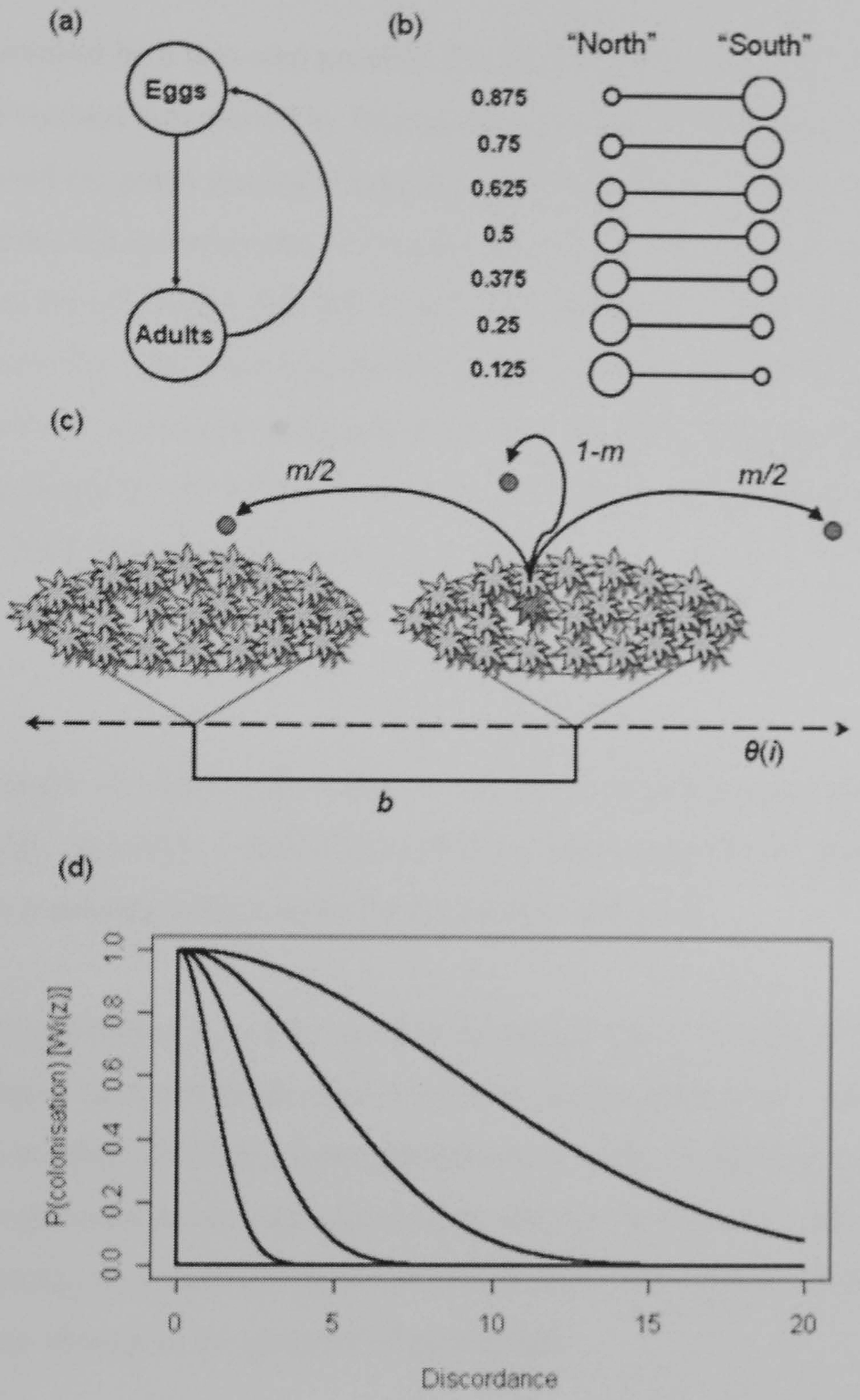

Figure 4.2. Model schematic. The individuals follow a simple annual lifecycle (a). The proportion of the entire carrying capacity ($K_{\max}$) found in the northern patch is varied, producing northern ($K_{north}>K_{south}$), southern ($K_{north}<K_{south}$) or no bias ($K_{north}=K_{south}$)in the landscapes (b). Propagules disperse from this patch with probability $m$ with half the individuals surviving by reaching the second patch (c). The patches are separated on an environmental gradient $\theta(i)$ by $b$ units. The intensity of selection acts on the colonization stage of the life cycle (d) with the strength varied by the parameter $\Omega$ (steepest curve, $\Omega$=1.25; then $\Omega$=5, $\Omega$=20 & $\Omega$=80). See text for details.

Patches are colonised by a two-step process. Firstly, offspring can colonise a patch with a probability of success determined by their adaptation. Both patches potentially confer equal fitness; however patch quality is determined by the degree to which an individual's adaptation matches the environment. For clarity and computational economy a single locus determines the adaptation (but see Holt & Gomulkiewicz 2004). The absolute difference between the adaptation and the climate of the patch experienced gives the concordance between niche and environment ($D = \check{z} - \theta_{(i)}$). This value is then used as the determining parameter for the colonisation rates, $W_{(i)z}$, for each individual (see Holt & Gomulkiewicz 2004; Alleaume-Benharira et al. 2006).

$$W_{i(z)} = e^{-\frac{(D)^2}{2\Omega}} \tag{4}$$

The relative strength of selection in relation to the environment is manipulated by the factor $\Omega$ (fig 4.2d). Secondly, following colonisation determined by the niche, any excess of individuals is randomly culled, reducing population size to $K$.

While, in most simulations, I used the method described above to apply selection at the colonisation stage, I have run further simulations to test the robustness of the results to selection acting at other life stages. I straightforwardly adapt the method to apply selection within the natal patch (reproduction) or selection within the settlement patch (survival to maturity) by relating different processes to $z$. Little effect is found in the dynamics with no change in the patterns of persistence.

The fitness function assumes that perfect adaptation can be achieved. However noise can be added into the model for example representing randomly occurring developmental effects. This has the effect of increasing the population's genotypic variation. Before reproduction mutations may occur (uniform distribution within a range of $\pm 3b$). A mutation rate of $\mu$=0.001 is always employed in obtaining quasi-equilibrium, after which I vary $\mu$ to facilitate a comparison between the "ecological" ($\mu$=0) and "evolutionary" ($\mu$=0.0001, 0.001) responses during climate change.

## 4.3 Results

### 4.3.1 Simple and expected effects of landscape geometry on niche evolution

As theory predicts (Kawecki & Stearns 1993), in a static climate increasing asymmetry in the landscape shifts the niche towards the climate experienced by the largest patch (see fig 4.3 a-d). For Northern Biased Geometry (NBG), individuals exhibit highest fitness ($W$) in the larger northern patch and the opposite holds for Southern Biased Geometry (SBG) (fig 4.3). The distribution of individual niches within the population is unimodal under the levels of noise tested. For the same degree of bias in carrying capacity, NBG and SBG exhibit the same magnitude of local adaptation to the larger patch irrespective of landscape geometry (fig 4.3, compare bias =0.875 vs. 0.125). The level to which the niche is optimised towards one or the other patch is strengthened with increasing dispersal ($m$), selection strength ($\Omega$) and bias between patch carrying capacities (fig 4.3). Where there is no bias in patch size, equivalent $W$ is exhibited and found in each patch; the mean niche being equidistant from the local optimum of each patch.

### 4.3.2 Differences in persistence to climate change with opposing landscape geometry

Differences in persistence are exhibited between different landscape geometries during climate change (figure 4.4). Selection strength ($\Omega$) principally determines persistence, as increasing $\Omega$ decreases the amount of climate change that can be endured. For ecological responses ($u$=0) there is no introduction of new mutations demonstrating resilience of the quasi-equilibrium population. Increasing dispersal rate ($m$) decreases persistence, but the magnitude of this change is determined by landscape geometry (fig 4.4). Landscapes with Southern Biased Geometry (SBG) always have the longest persistence times. Persistence decreases as landscapes become more biased towards the northern patch (NBG). These patterns qualitatively persist when $u$>0 (fig 4.4, a-d vs. e-l), however there are quantitative differences (described later).

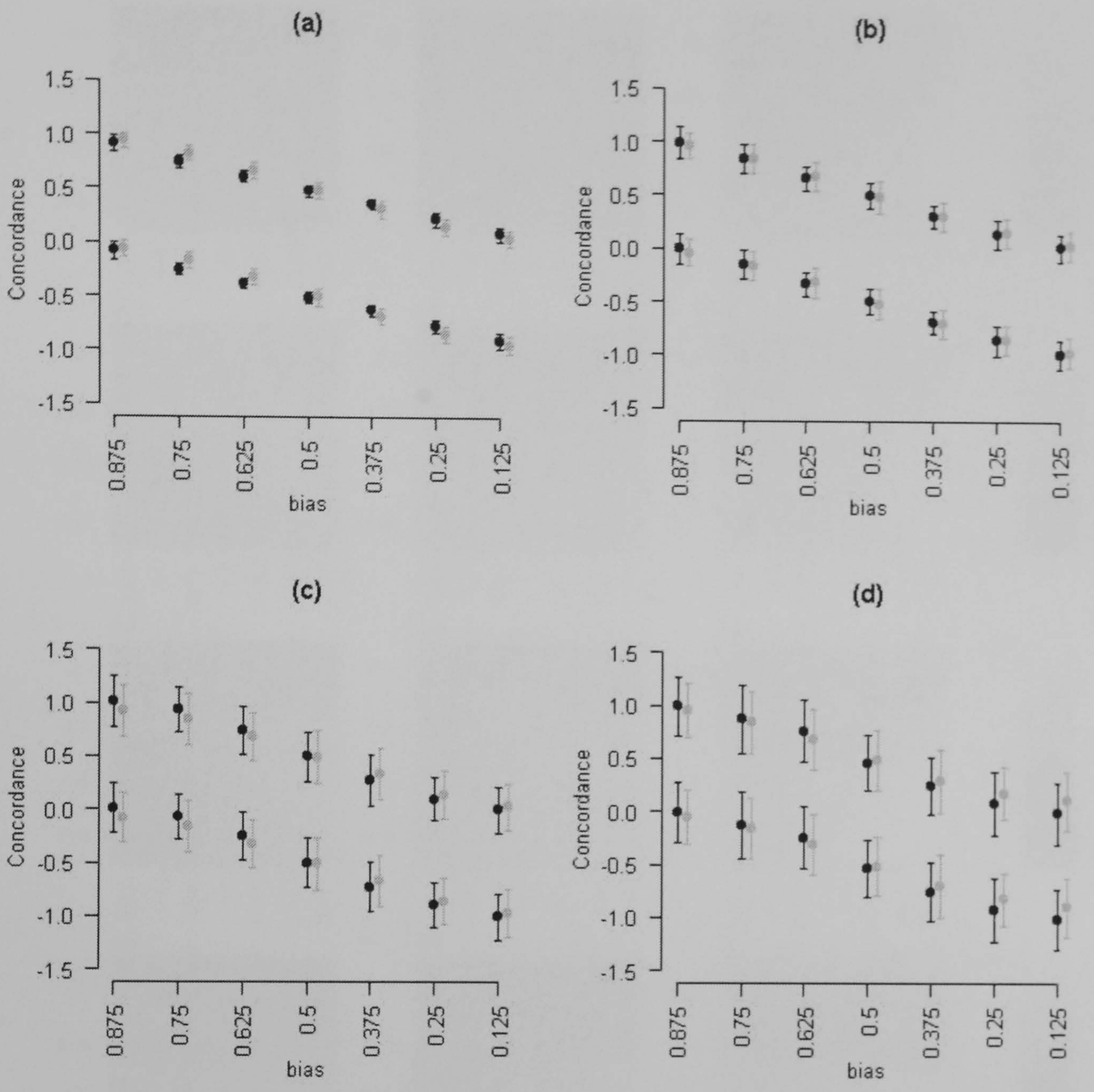

Figure 4.3. The effects of the landscape geometry on adaptation in a static climate. Bias shows the proportion of $K_{max}$ found in the northern patch (also see equation 2), low values producing Southern Biased Geometry (SBG) and high Northern Biased Geometry (NBG). In a-d values deviating from zero show increasing maladaptation to the patch optimum, with equivalent absolute values showing equal levels of maladaptations. The four levels of $\Omega$ (1.25, 5, 20, 80) are shown in chronological order (a-d) with two levels of dispersal rate (low, $m$=0.01, Black; high, $m$=0.5, Grey). $K_{\max}$=400; top line=southern patch, bottom line=northern patch.

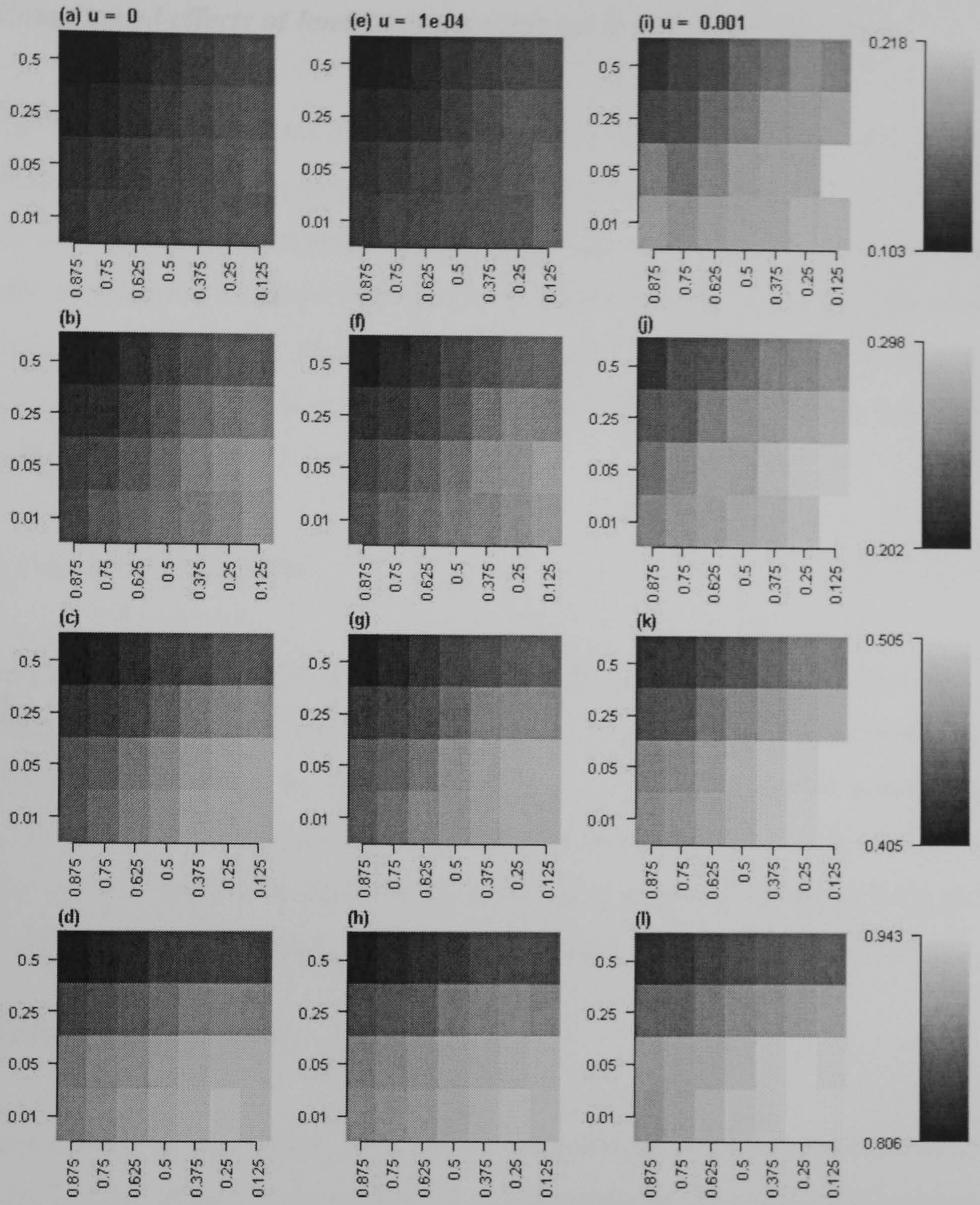

Figure 4.4. Landscape geometry affects persistence during climate change. X axes shows the proportion of the entire carrying capacity contained in the northern patch ($K_{max}$=400), low values producing Southern Biased Geometry (SBG) and high Northern Biased Geometry (NBG). Y axis shows dispersal rate ($m$). Different levels of selection strength ($\Omega$; 1.25, 5, 20, 80) are given by row and mutation rate ($u$) by column. Horizontal shading gradients indicate landscape geometry affects population persistence, with black indicating the lowest levels of persistence. Shading scaled by row. Vertical gradients indicate the effects of dispersal. Mean persistence values are taken from ~80 replicates. Other parameters $b$=1, $c$=0.02, $E$=8.

### 4.3.3 *Complicated effects of landscape geometry on the ecological dynamic*

To understand the mechanisms underlying differences in persistence between landscape geometries I investigated the dynamics in population size dispersal and niche evolution. A consistent effect of landscape geometry is found through parameter space, but to make a detailed presentation of the processes I focus on the dynamics at a few points within parameter space (see fig 4.5; $\Omega$=1.25, $m$=0.5 for $K_{north}$=100, 200 & 300). The patterns in the extinction dynamic are more prominent with lower values of $\Omega$, but are similar across dispersal, selection and mutation parameters.

#### 4.3.3.1 Population dynamics

There are differences in the timing of extinction between the different landscape geometries (fig 4.5, a-c) and the extended persistence of Southern Biased Geometry (SBG) is seen in the dynamics of population size, $N$ (fig 4.5c, population numbers after random cull to $K$). Across all landscape geometries, populations in northern patches generally survive longer than southern patches. This is expected, as the northern patch will always be the last to contain conditions within any of the populations' niches.

#### 4.3.3.2 Dispersal dynamics

In a static climate, a larger patch generally receives fewer immigrants than a smaller patch (fig 4.5, d-f; where the proportion of all offspring that are successful immigrants after selection, $I$, are shown over time $\{I=N_{imigrants}/N_{offspring}\}$, where $N_{offspring}$ is the pre-cull population size and $N_{imigrants}$ is the number which were immigrants). When $I$=0 all offspring originate within the patch and when $I$=1 all offspring are immigrants. Thus $I$ indicates the strength of spatial interactions.

In static climates, $I$ is higher in the larger patch. Patch sizes determine the number of offspring produced, but the probability that these offspring successful colonise is dependent on individuals' niches ($z$). Thus large patches have low $I$, but the immigrants into the source have high fitness ($W$). The smaller patches have higher $I$ but their immigrants have lower $W$ (see fig 4.5, g-i). In the landscape with no bias ($K_{south}= K_{north}$) both patches are the same size and the population is equally adapted (or conversely maladapted) to both climates (fig 4.3), producing equivalent values of $I$ for each patch.

As climate change is initiated ($t \geq 5001$), $I$ always increases in the southern patch regardless of landscape geometry (fig 4.5, d-f). This is due to a decline in $W$ as the southern patch becomes more inhospitable. For the northern patches $I$ initially increases as the north warms and increases $W$ (see next section). However immigration then decreases as, in the southern patch, population sizes become depressed reducing immigrant supply (fig 4.5, d-f).

These general patterns are independent of landscape geometry. However, timing of the immigration increase in southern patches, and the magnitude of changes in immigration for northern patches, is dependent on landscape geometry (fig 4.5, d-f). For Northern Biased Geometry (NBG), $I$ always remains higher in the larger northern patch than in the smaller southern patch (fig 4.5d). However, for Southern Biased Geometry (SBG), whether the small or large patch has higher $I$ depends on the degree of climate change (fig 4.5f). Initially the northern smaller patch receives more immigrants ($I_{south}<I_{north}$) as expected.

However immigration into the northern patch increases as it becomes more suitable ($I_{south}<<I_{north}$). When the southern patch decreases in suitability the smaller northern patch eventually receives fewer immigrants ($I_{south}>I_{north}$) acting qualitatively like a landscape with NBG at equilibrium. Importantly this switching pattern is also found in the homogeneous landscape with no bias ($K_{south}=K_{north}$) where the both patches initially receive the same number of immigrants ($I_{south}=I_{north}$) (fig 4.5e).

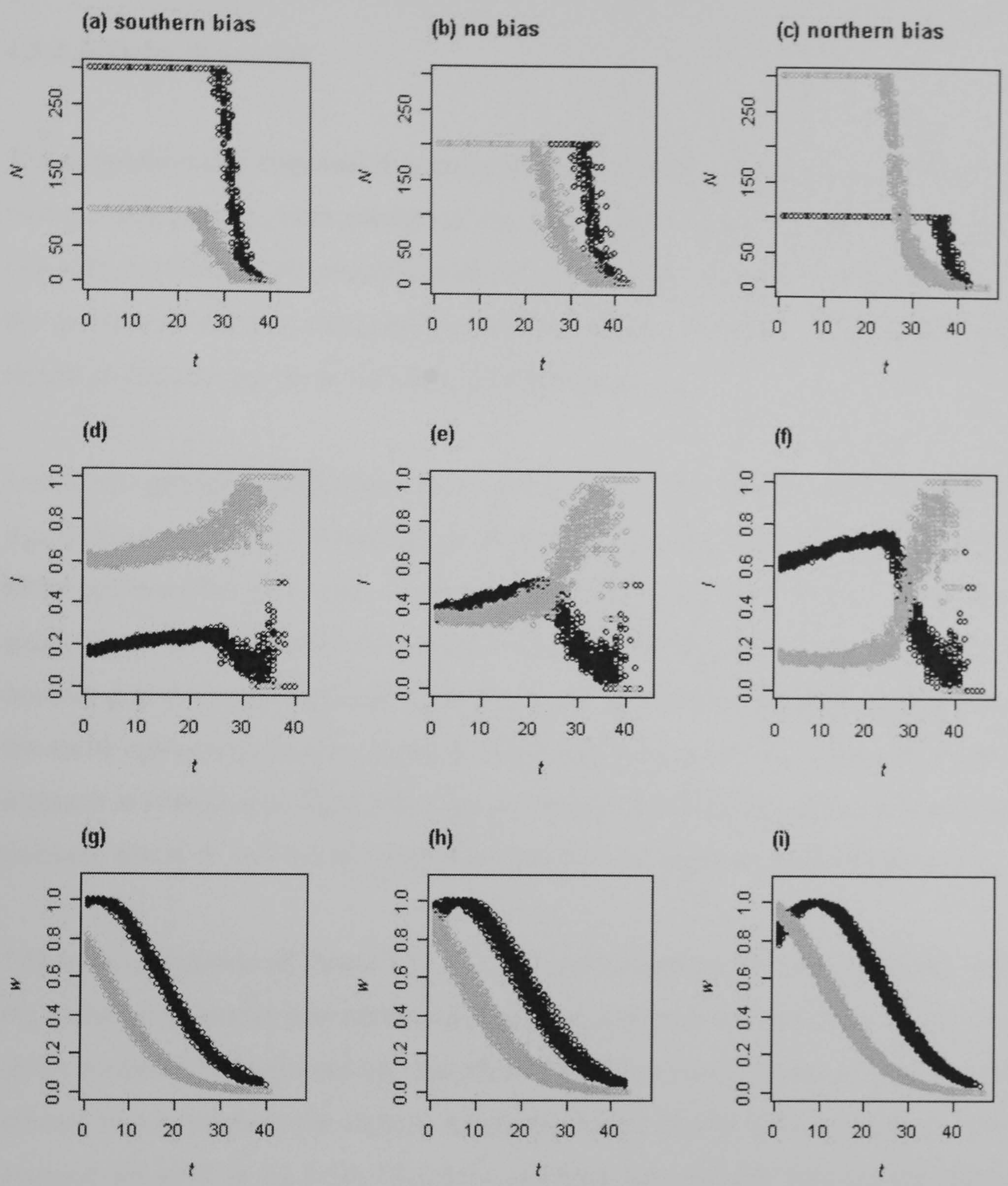

Figure 4.5. The dynamics of population size, immigration and fitness during climate change for a northern bias in the landscape (a, d & g; $K_{north}$=300, $K_{south}$=100), no Bias (b, e & h; $K_{north}$=300, $K_{south}$=300) and a southern bias (c, f & i; $K_{north}$=100, $K_{south}$=300). Top row (a-c) illustrates the extinction dynamic for "northern" (black) and "southern" (grey) patches *after* density dependence. $t$ is the time since climate change was initiated. Middle row (d-f) time series are shown for the numbers of immigrants successfully colonising the "northern" (black) and "southern" patches (grey) *before* density dependence. Bottom row (g-i), average fitness values in "northern" (black) and "southern" patches (grey). Data are derived from ~100 replicates for each parameter set ($b$=1, $c$=0.02, $\Omega$=1.25, $m$=0.5, $\mu$=0, $E$=8).

#### 4.3.3.3 Niche dynamics

The population and dispersal dynamics are explained by changes in the realisation of the niche, $z$. Importantly, both patches of any landscape contain roughly the same genotypes (fig 4.3), but fitness ($W$) depends on their location (fig 4.5, g-i). During the simulations the majority of the original niche is conserved when $\mu$=0. Thus I restrict presentation of results to the average niche for each parameter set.

Landscape geometry determines the position of the niche in relation to the north and the south climates (fig 4.3). When the landscape has Northern Biased Geometry (NBG) the niche optimum lies just south of the northern patch and so $W$ is highest in the northern patch (fig 4.5g). A small level of maladaptation exists due to a degree of selection occurring in the southern patch. Climate change shifts the ecological optimum towards the niche optimum, thus increasing $W$ (fig 4.5g). This accounts for the simultaneous increase in immigrants (fig 4.5d). Climate change subsequently reduces suitability in both patches, where $W$ follows the Gaussian shape of the response curve (equation 4).

The relative increase in fitness ($W$) is higher with Southern Biased Geometry (SBG) as the niche optimum lay just north of the original southern climate (fig 4.3). As climates shifts northwards the previously maladapted northern patch has increasing $W$ as the climate moves towards the niche's optimum (clearly shown by the Gaussian shape mapped out by $W$ in fig 4.5i). The niche optimum was initially further away from the northern patch climate and so a longer period of climate change is taken before the optimum is reached. The southern patch becomes increasingly inhospitable (fig 4.5i, also compare fig 4.1 where 4.1c is akin to the situation found with SBG and 4.1d with NBG). This difference in the position of the niche optimum before climate change accounts for the switch in qualitative immigration dynamics presented above (fig 4.5f). SBG have higher $W$ than NBG when comparing the northern and southern patches at any given level of environmental stress. The differences in persistence between dispersal rates (fig 4.3) are due to the degree to which the population is adapted to a single patch in any landscape.

Importantly the switching effect in immigration (fig 4.5e) and relative fitness is present where the landscape has no bias (fig 4.5h). Before climate change the niche optimum lay equidistant from the equilibrium climate in both patches (fig 4.3, where bias =0.5). As the climate changes, the niche optimum moves towards the conditions experienced in the northern patch creating an asymmetry in *W*, with *W* being lower in the southern patch. This explains why even the unbiased landscape has the switching dispersal dynamic.

### *4.3.4 Landscape geometry generates differential evolutionary rates*

These dynamics have an additional and subtler effect on selection when $\mu$ >0. As shown in fig 4.6 the persistence time increases when mutation rate ($\mu$) is increased to 0.0001 and increases further when $\mu$=0.001. Figure 4.6 shows the proportional change in persistence occurring when the mutation rate is increased from 0 to 0.0001 between each landscape orientation ($TTE_{u=0.0001,\, \Omega,\, m}$ / $TTE_{u=0,\, \Omega,\, m,}$ where *TTE* is the "Time To Extinction" of the entire population shown in fig 4.4). Whilst, under most circumstances, mutation increases persistence, the proportional gain is greatest in landscapes with a Southern Biased Geometry (SBG). The effect of dispersal rate (*m)* and selection strength ($\Omega$) on the proportional gain is highly non-linear. When averaged across all other parameters, SBG always have a greater proportional increase in persistence than NBG. This effect is most dependent on *m*, though is still found when $\Omega$ is varied (fig 4.6a vs. fig 4.6b).

Fig 4.7 shows the dynamics for a population where the phenotype is subject to some noise, promoting generation of variation in the trait $z$. Evolution is slow with NBG, occurring later during the period of climate change (fig 4.7a). Here selection occurs mostly in the northern patch, with the southern patch permanently gene swamped as it always has lower fitness (fig 4.5d). However selection may act in both patches for SBG showing greater evolutionary change over time (fig 4.7c). Firstly, selection of individuals tolerant to the increasingly warm climates is found in the southern patch. Once the effects of gene swamping weaken in the northern patch (fig 4.5f) selection can occur in the northern patch. This extends the range of selection possible and initiates the evolutionary change at an earlier stage, increasing the rate of change in the adaptive trait (fig 4.7c). In a landscape with no bias this effect is present, but to a lesser degree (fig 4.7b). I hypothesise that the reduction is due to the shorter time within which selection may act (e.g. fig 4.4).

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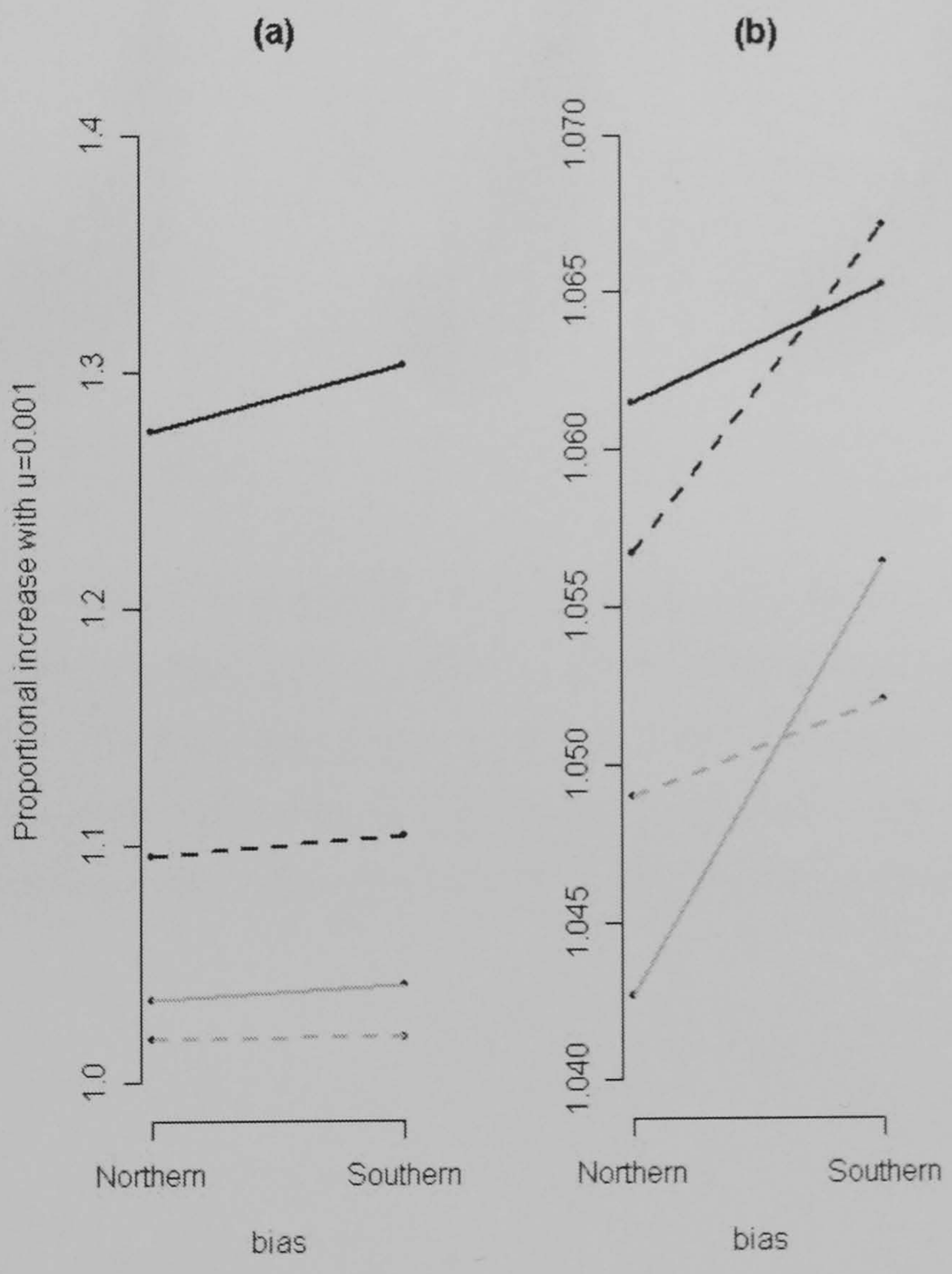

Figure 4.6. The effect of landscape geometry on the rate of evolution. Proportional change in persistence for ($TTE_{u=0.0001,\,\Omega,\,m}$ / $TTE_{u=0,\,\Omega,\,m}$) when *all* results are averaged for each value of $\Omega$ (black, $\Omega$ =1.25; black dashed, $\Omega$ =5; grey, $\Omega$ =20; grey dashed, $\Omega$ =80) and $m$ (black, $m$ =0.01; black dashed, $m$ =0.05; grey, $m$ =0.3; grey dashed, $m$ =0.5). Other parameters $b$=1, $c$=0.02, E=8, for ~80 replications of each parameter set.

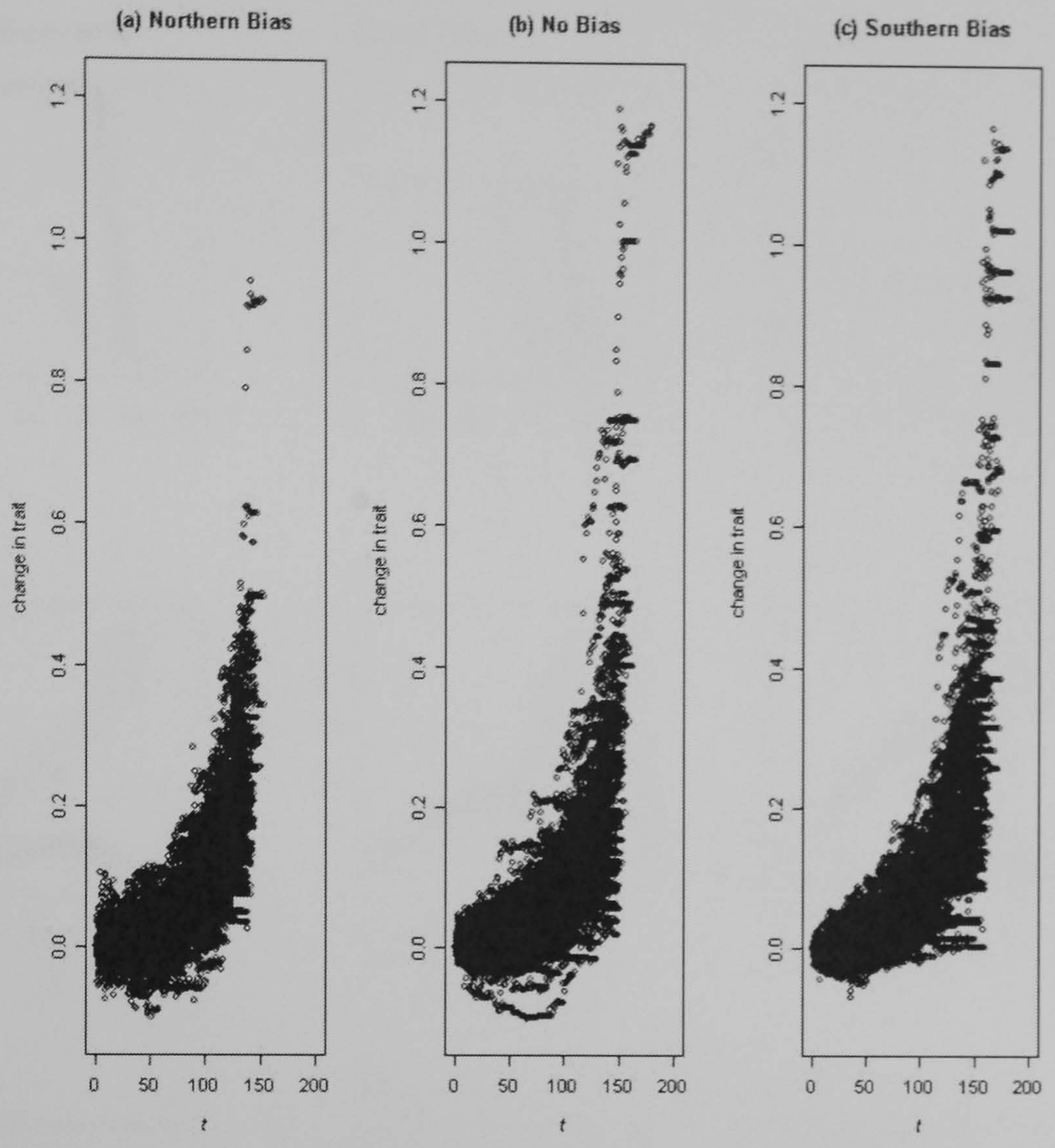

Figure 4.7. The effect of landscape geometry on the dynamics of evolution. The dynamics of adaptation for the previous system with the addition of 50% white noise in the translation of genotype to phenotype to increase the variance upon which selection acts (see methods). Points show the change in the mean trait values form the twenty generation average before the change in the environment is initiated ($\Omega$ =1.25; *m*=0.1; *u*=0.001; for 100 replicate simulations).

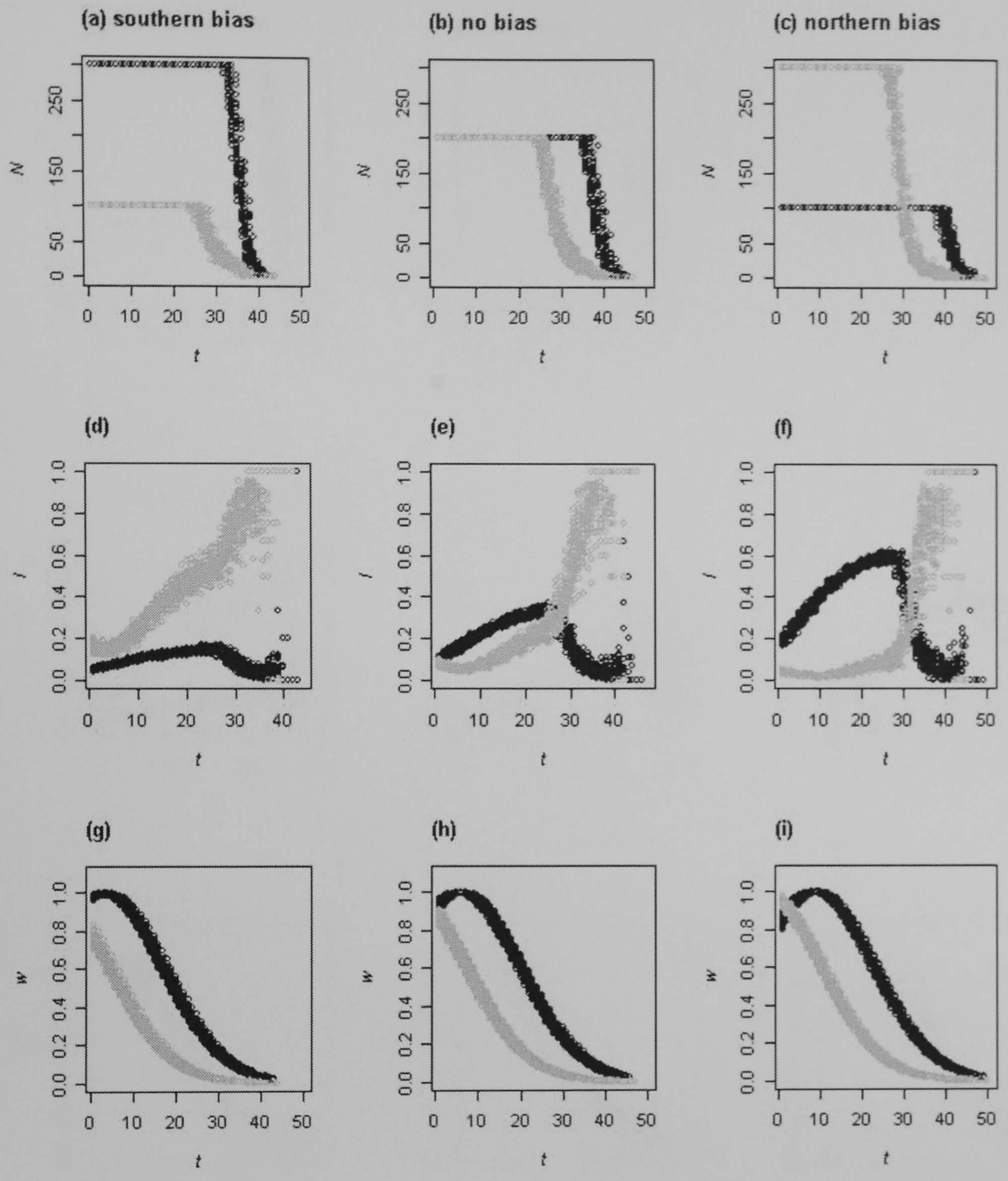

Figure 4.8. The dynamics of (a-c) extinction, (d-f) immigration dynamics and (g-i) fitness. See figure 4.5 for details. ($\Omega$=1.25, $m$=0.9, all other parameters as figure 4.5).

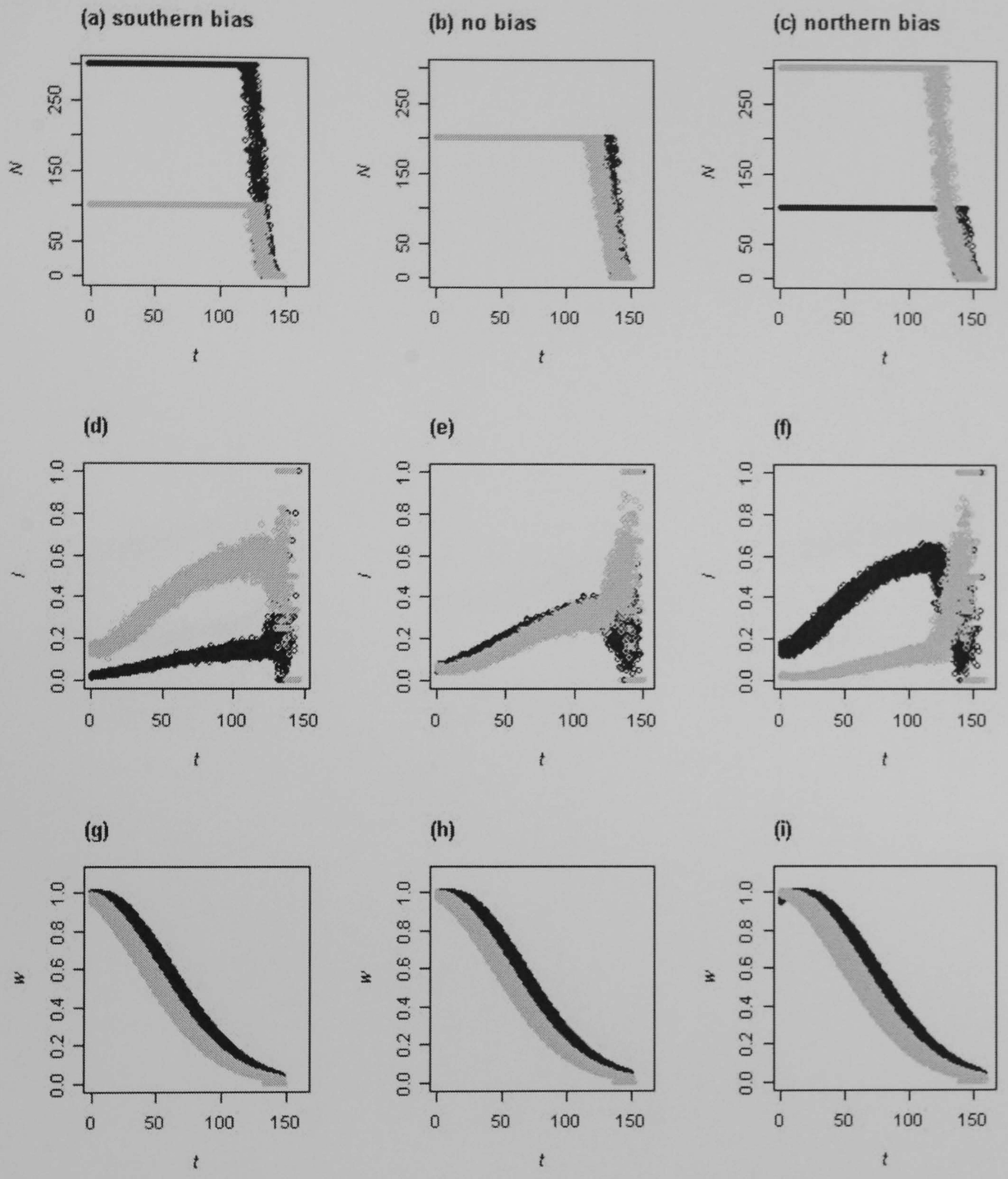

Figure 4.9. The dynamics of (a-c) extinction, (d-f) immigration dynamics and (g-i) fitness. See figure 4.5 for details. ($\Omega$=20, $m$=0.9, all other parameters as figure 4.5).

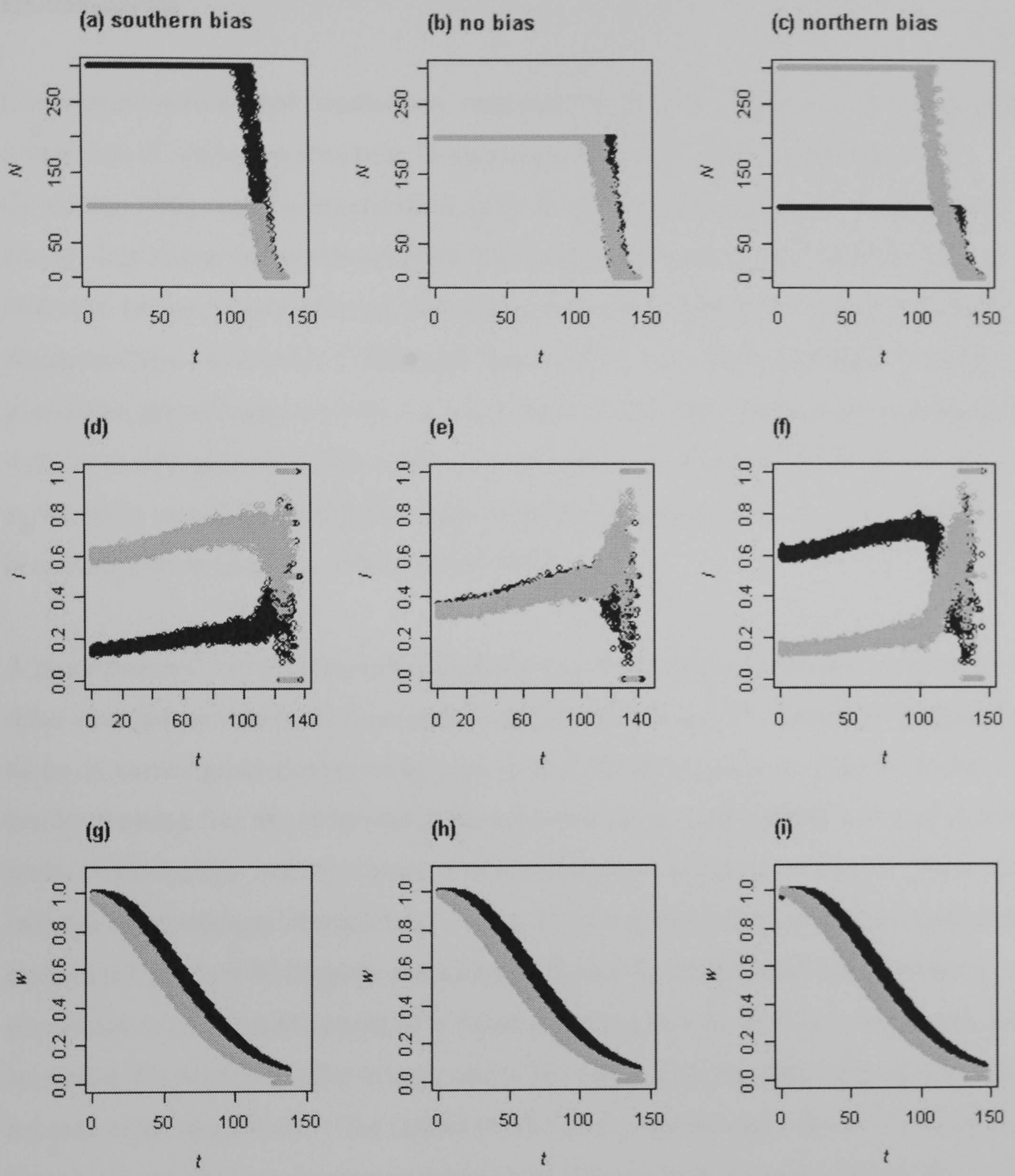

Figure 4.10. The dynamics of (a-c) extinction, (d-f) immigration dynamics and (g-i) fitness. See figure 4.5 for details. ($\Omega$=1.25, $m$=0.5, all other parameters as figure 4.5).

## 4.4 Discussion

I have demonstrated that populations' responses to climate change may vary due to the orientation of landscape structure. Occupying a landscape with Southern Biased Geometry, SBG, may be beneficial as, prior to climate change, the optimum niche already lies nearer the warmer climate. This means that landscapes with SBG take a different, longer journey through the niche space when compared to landscapes with Northern Biased Geometry (NBG) (see figs 4.1 & 4.3). A crude explanation is that population growth rates are >0 for a longer time creating the differences in persistence with landscape geometry. This general result makes sense as equivalent effects are expected at opposing range limits, high latitudes becoming fitter and low latitudes becoming less so (Lawton 1993; Gaston 2003).

A more detailed and complicated explanation of the dynamics is needed to explain how these changes are manifested, encompassing the differences in population, dispersal and niche dynamics generated by landscapes with different geometries. This is given in the results showing that the relationship between climate and adaptations was altered because niche evolution lags behind climate change even when mutations occurred. Thus, the realised niche changes through time even without any change in the fundamental niche. I explain this again following the reasoning of Ronce & Kirkpatrick (2001) where a population is considered generalist if fitness (*W*) is relatively high in both patches and specialist if it is much higher in only one of the patches. In the static climate individuals become more specialised to the largest patch when carrying capacity (*K*) is increasingly biased, irrespective of geometry. Unbiased landscapes have the most generalist populations. During climate change a population occupying a homogenous landscape becomes specialised to the northern patch as effectively climate shifts the niche optimum northwards. This pattern is also found when NBG results in a high degree of specialisation to the northern patch. This is due to the increasing inhospitality of southern climates and increasing suitability of the north. However for SBG, which is at first specialised to the southern conditions, the population becomes at first more generalist, and subsequently specialised to the northern patch before eventual extinction. It is important to emphasise that these changes are despite equivalent dynamics of SBG and NBG in static climates. As the niche is mostly conserved when no mutations enter the populations ($\mu$=0), the populations express different parts of their fundamental niche at different times during climate changes. For instance, if populations' were introduced to a complete gradient (not just patches) the niche breadth (specialisation/generalism) of both SBG and NBG would be exactly the same.

Doebeli (1995) and Kawecki & Holt (2002) show highly asymmetric dispersal may reverse *source-sink* status despite differences in habitat quality. This is essentially the same process demonstrated here (fig 4.5d-f, see figs 4.8, 4. 9 & 4.10 for examples with different selection strength ($\Omega$) and dispersal rates ($m$)). However, in our model absolute dispersal rate *and* selection acting on the parent (reproduction) or offspring (survival to maturity) determines dispersal success (see results). The closest theory to be developed is a model by Holt & Gomulkiewicz (2004) who investigated the effect of abrupt environmental change occurring in a sink. Immigration had a two-fold effect, swamping mutations of small effect but also providing the "*evolutionary opportunity*" of exposure to the new climates (Holt & Gomulkiewicz 2004). Our model differs from that of Holt & Gomulkiewicz (2004) as climate changes strengthen or weaken the effects of gene flow, depending on the landscape geometry (but selection also occurs during reproduction rather than just survival to maturity in Holt & Gomulkiewicz (2004)). Their model also differs from my work as I use a directional environmental change rather than an environmental displacement.

Landscape pattern may influence ecological responses to climate change (Travis 2003; Opdam & Wascher 2004; Jump & Penuelas 2005) by altering the structure of interactions within populations. Simple differences in habitat area and so contribution to the gene pool may also drive different patterns of local adaptation (Kawecki & Stearns 1993). For example "density sinks" (Barton & Hewitt 1989) can generate selection towards a point in environmental space purely due to the high density it can support, even in the face of decreasing fitness (Dias 1996). This is the case in our model. Barton & Hewitt (1989) refer to density sinks as having larger carrying capacities or area; the opposite description used here and in related literature (e.g. Kawecki & Stearns 1993, Kawecki 1995). This is the only aspect of environmental heterogeneity our model captures. Spatial interactions may be determined by differences in a huge number of characteristics exhibited by the environment or an organism's response to that environment (Kawecki 2004). In our model, differences in carrying capacities produces "relative" source-sinks (Kawecki 2004); populations that could persist independently but whose evolution is affected by dispersal interaction (in contrast to "true" source-sinks where the sink has $r>0$ due to immigration, Pulliam 1988; Watkinson & Sutherland 1995)). In this language the SBG may be considered a "*source-sink*" and NBG a "*sink-source*" (where word order equates to increasingly latitude or altitude). Thus another analogy of the changing dynamics shown here is that NBG always remains a *sink-source*, but SBG is initially *source-sink*, then becoming an even stronger *source-sink* and its structure is later switched to *sink-source*.

Our model assumes habitat quality is determined by concordance between individual's adaptations ($z$) and climate. In "*true*" sources and sinks (e.g. Pulliam 1988), sinks cannot persist without immigration as an absolute difference in patch quality is assumed. This assumption would not allow us to test the effect of no landscape bias ($K_{south}=K_{north}$). It is also difficult to conceptualise true sources-sinks in a climate change context as populations would inhabit either an extreme climate gradient ($b$ is large) with highly asymmetric carrying capacities or another factor, such as resource availability, determines habitat suitability. If $b$ is large then shifting in response to climate change (e.g. from low latitudes reducing in quality, to high latitudes increasing in quality) may be precluded as both patches could temporarily become unsuitable and have $r<0$. This also requires an additional assumption regarding changes in absolute habitat quality. For instance does the sink become more like source? Or do the absolute differences remain but local conditions change?

We can consider a hypothetical case where climate plays a small role in determining habitat quality (equivalent to an effect on $r$) but where climate change is sufficient to cause extinction in low latitude populations. If the system is *source-sink* the source may be extirpated leaving an unviable sink and so lead to extinction of the whole population (Pulliam 1988). But if the population is *sink-source* then the source will remain viable and so would not result in wholesale extinction (Pulliam 1998). As we increase the role of climate in determining *r* the situation becomes more complex even for simplified theoretical study. For instance in a *source-sink* the conditions in the sink may become more like the original source (a "cold" sink being warmed). whilst in a *sink-source* the sink becomes more sink like (a "hot" sink being warmed). This assumes that source-sink structure is derived from absolute differences in climate or habitat 'quality'. The complexity of the questions I have outlined here is accompanied by a paucity of relevant theoretical study to begin answering them. A host of real world situations could of course exist as heterogeneity in multiple conditions can be present within and between >2 patches. This is where understanding real world responses could become very difficult indeed (Thomas et al. 2001) and why our model selection rested on a relative source sink structure.

Structural change of the interactions within populations could increase in importance when secondary traits are also concerned, especially for those determining or determined by dispersal. For instance, genetic variation in traits that are not under direct selection by the climate may also be affected by changes in gene flow. Dispersal evolution may also be affected by populations' changing structure (Wilson 2001). One case I consider briefly here is dispersal in a landscape with Southern Biased Geometry (SBG). Here, there is effectively a range shift from south to north accompanying the switch in immigration dynamics. This shift could select for higher dispersal rates producing a 'dispersal amplifier'. Changes in dispersal could cause further changes in selection on traits directly related to climate (e.g. $z$) or on those traits under indirect selection but affected by gene flow. Such feedbacks may produce some complex responses that are very specific to the landscape geometry. For example, dispersal is not independent of $z$ in our model and I showed how dispersal dynamics changed nonlinearly over time despite stationary dispersal rates. Further research into changes in spatial interactions during environmental perturbations is required (May 1999) and may allow us to understand some of the idiosyncrasies in observed climate change responses (Thomas & Lennon 1999; Parmesan et al. 1999; Visser 2008).

Evolutionary theory often uses previous interactions between climate changes and landscape attributes to explain present biodiversity patterns (e.g. Hewitt 2000). In some cases simple environmental features that produce ecological stability, may be associated with increased evolutionary potential (e.g. Dynesius & Jansson 2000). However few investigations have even considered the consequences of adaptation in a dynamic environment (though see Peck & Welch 2004, Desai & Nelson 2005, Burton & Travis *In press*). Our simulations show that landscape pattern could influence the geometry of interactions in such a way as to alter the rates of evolution. For instance selection could occur earlier in the period of change and across a wider set of conditions in landscapes with SBG.

Environments may exhibit considerable changes in spatial structure during climate change (Thomas et al. 1999; Ohlemüller et al. 2006). Populations may become fragmented during stress (Wilson et al. 2004), and the 'evolvability' of fragments with different patterning could determine adaptive responses. Amplification of selection processes due to spatial relationships has been demonstrated in simple and complex static network structures (Lieberman et al. 2006). I demonstrated a related, but more dynamic, concept that I now explain. Source-sink theory suggests that only mutations with large effects may overcome gene swamping (Holt & Gomulkiewicz 2004). Climate change can alter these constraints by altering the structure of interactions. For example, in NBG only mutations of increasingly large effects may affect evolution in the smaller patch as (1) the large patch becomes more productive increasing gene swamping effects in the small patch and (2) the climate in the small patch becomes increasingly different from the optimum niche. This could constrain evolution to the warming climate. However in SBG mutations of lesser effect may succeed in the smaller patch as it becomes nearer the niche optimum and eventually gene swamping may be so reduced that it becomes the source patch. Factors such as these will play a large role in determining evolvability. Considering the effects of climate disequilibrium through space on evolutionary processes (see Desai & Nelson 2005) should become an important area for study. This model suggests that different landscape geometries may affect the convergence of ecological and evolutionary dynamics. For instance NBG suppressed and provided less opportunity for selection during climate change, producing a more ecological response even when $\mu>0$. However SBG may create an environment where selection acts on a wider range of mutation effect sizes.

It is intriguing to think how populations that form more or less evolvable structures may represent the biota before and after climate change. The effects of landscape geometry presented here, or combinations of latitudinal and altitudinal variation may exert forces that disrupt the cohesive nature of populations; or indeed stabilise them. In combination with the theory outlined in the introduction we may start to see how such factors could affect the routes taken when traversing adaptive landscapes (e.g. Peck & Welch 2004, Burton & Travis *In press*): when dynamical geographic landscapes exert amplifying or suppressing forces on the journey towards adaptive peaks.

# 5. Surfing and wiping out: the fate of neutral variation during range shifts.

## 5.1 Introduction

During climate change lags are expected to develop as populations respond at rates slower than the spatial shift in environmental conditions (Jump & Pénuelas 2005). Lags are a feature of a wide range of ecological dynamics in 'static' climates (e.g. Schneider 2001; Benton et al. 2006). However the spatial context of climate change means lags may alter population's spatial structure (biogeographical range) ( Rapoport 1975): a structure with consequences spanning populations' ecology, genetics and adaptive evolution (Hanski 1998).

At opposing range limits lags may be generated in different processes. At range limits leading a range shift, habitat is expected to become increasingly suitable (Parmesan et al. 1999) generating lags when colonisation responses are not immediate (Davis 1989; Grabherr et al. 1994). However at trailing range limits, declining habitat suitability is expected (Parmesan et al. 1999) generating lags in local extinction processes if responses are again not immediate. Lags in different processes needn't operate at the same spatial and temporal scales and so may produce 'deformation' of populations' ranges (e.g. Rapoport 1975, pp22-24). Differences in colonisation and extinction lags could result in expansion or contraction of a range (e.g. Parmesan et al. 1999; Thomas & Lennon 1999). Range limits are the most obvious sites of changes in population-climate relationships, but climate change is of course not exclusively found at range limits (Jump & Pénuelas 2005). More subtle, but nonetheless important, effects could act elsewhere in populations' ranges, such as in the rates of population turnover that underlay patterns of occupancy.

There is a conspicuous lack of studies that have investigated how deformation of ranges might be manifested and impact evolutionary processes. This is despite the importance of historical events in structuring contemporary diversity (Parmesan et al. 1999) and the need to understand range shifting genetics for effective biodiversity management (Opdham & Wascher 2004). At the timescales of 'macroevolution' great emphasis is placed on founder effects, bottlenecks and isolation in generating contemporary biodiversity patterns (Barton & Charlesworth 1984). All these factors could occur over relatively short timescales as populations' ranges change in structure, and in many cases are simultaneously forced through fragmented landscapes (Travis 2003; McInerny et al. 2007).

A number of recent studies suggest that founder effects could be more pronounced at the expanding range limits of invading populations for both neutral (Edmonds et al. 2004, Klopfstein et al. 2005) and non neutral mutations (Travis et al. 2007). These studies show that iteration of founder effects over successive steps of invasion can result in mutations obtaining far higher frequencies and larger spatial distributions than expected in a stationary population (Edmonds et al. 2004; Klopfstein et al. 2005; also see fig 5.1). Klopfstein et al (2005) have dubbed these pronounced founder effects as "*mutations surfing* [] *the wave of range expansion*". The conditions resulting in *mutation surfing* in invading populations are likely to apply to populations' shifting in response to climate changes as individuals colonising newly available habitat are more likely to come from the gene pool at leading range limits. However important differences may exist. Invasion models assume the environment is spatially and temporally constant, whilst the environments of species shifting their range will be both spatially and temporally more complex. For instance shifting populations also have a range limit trailing the range shift which may not be exempt from concomitant genetic change.

Here I report the results from a theoretical study investigating how climate change alters the structure of populations' ranges and the effects this may have on evolutionary processes. Using a well established metapopulation model whose population dynamics have been well studied in a static climate (Lennon et al. 1997; Holt & Keitt

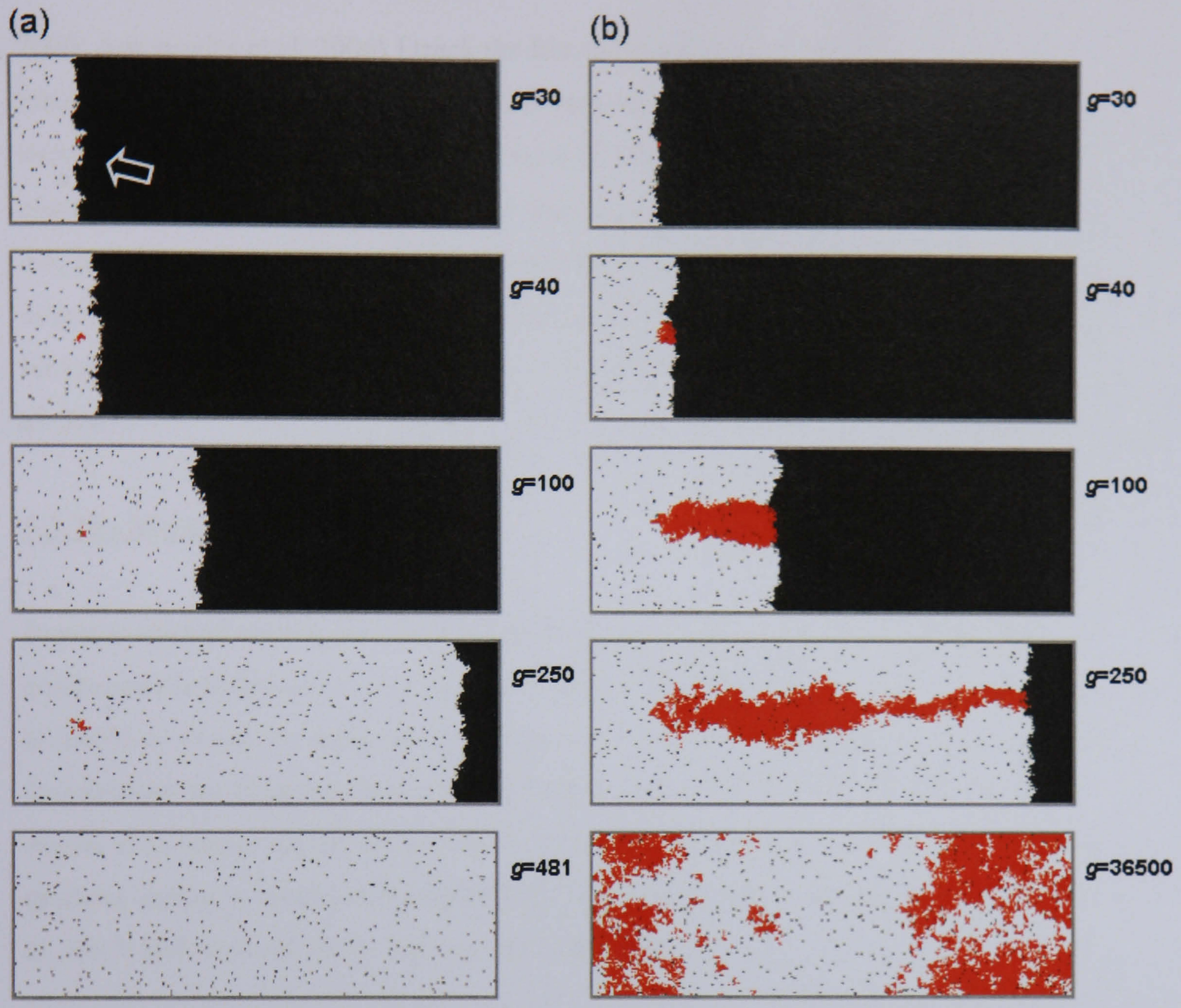

Figure 5.1: The surfing phenomenon (see Edmonds et al. 2004 & Klopfstein et al. 2005) during invasion into pristine landscape (white cells, occupied; black, unoccupied). The population occupies 10 columns of cells at the left hand side until equilibrium is reached. Thereafter, the whole landscape becomes available. A neutral mutation (red cells) occurs when the invasion reaches the 40th column ($g \approx 30$, arrow indicates mutants' location). Mutations do not always surf (a), by g=250 surviving mutants have spatial locations very close to the ancestor's origin. Surfing mutants produce a wider distribution of the mutant (b), with lineages occurring large distances from the ancestor's origin. Lineage shown in (a) is extinct by $g$=481. Surfing mutants may produce lineages persisting for far longer periods (b), with patterns that deform through time (also see Ibrahim et al. (1996)). Other parameters: $e$=0.1, $a$=5, local 'nearest-neighbour' dispersal, 300x100 grid.

2000; Antonovics et al. 2006) I track the fate of neutral variation in a population inhabiting a climate gradient. The gradient may be static or change position through time simulating climate change. The results show that mutation surfing generates considerable changes to gene flow patterns. However those lineages that do not *surf*, those that *wipe out*, are also important in generating genetic structure. The results are of considerable interest to both climate change researchers (e.g. Davis & Shaw 2001) and evolutionary biologists seeking to explain in patterns current diversity (e.g. Currat et al. 2006; Biek et al. 2007).

## 5.2 The Model

Previous studies investigated mutation surfing in populations invading constant environments (Edmonds et al. 2004, Klopfstein et al. 2005, Currat et al. 2006, Travis et al. 2007) or where resources are not replenished (Wei & Krone 2005). Many populations' distributions are in part determined by climate (Gaston 2003), a climate that has or is expected to change rapidly (IPCC 2007). I model a metapopulation inhabiting a climate gradient similar to studies investigating ecological dynamics at range limits (Lennon et al. 1997; Holt & Keitt 2000; Antonovics et al. 2006).

On a cellular lattice each patch is occupied or unoccupied. Occupied patches become extinct with probability $e$, and unoccupied patches become colonised with probability $C$. I model $C$ in a way that facilitates using different dispersal kernels. Each occupied cell produces $\tau$ offspring in each generation ($\tau = 3$ in all simulations), whose dispersal is determined by a dispersal kernel. The results compare the dynamics generated by local dispersal (nearest 4 neighbours) and wide dispersal, a Gaussian function (see Lennon et al. 1997). For wide dispersal the probability of dispersing any distance is EXP(-*ad*), where $a$ modulates the shape of the kernel and $d$ is distance in cells with horizontal or vertical movements. The colonisation probability is then:

$$C = 1 - 1/(1 + e^{aj}) \qquad (1)$$

where $j$ is the sum of offspring entering an unoccupied patch and $a$ modulates the effect of $j$ on $C$. Decreasing $a$ decreases the colonisation probability for any value of $j$.

The value of $a$ is constant, but we apply a linear gradient to the value of $e$ with minimum of $e_{min}$, the population's phenotypic optimum. From $e_{min}$, extinction probabilities increase linearly to 1 ($e_{min}>0$ removes 'immortal' individuals). A linear gradient makes minimal assumptions about the phenotype-climate relationship. Additionally no differences in the rate of climate change across the range are introduced making the mechanisms as transparent as possible. Climate change is modelled as an increase or decrease in extinction values by $v$ in each generation (where <1, values are floored at 1), depending on whether the point is north or south of $e_{min}$, producing a climate shift.

A single offspring that has dispersed to an unoccupied patch is randomly selected as the coloniser. This simplification of the models by Edmonds et al. (2004) and Klopfstein et al. (2005) does not eliminate the spatial processes we wish to investigate (fig 5.1). As mutations come into existence during colonisation we describe the probability that a given lineage will persist ($P_{persistence}$) as the probability that a mutation will take place during a colonisation ($P_{mutation}$), a colonisation will take place ($P_{colonisation}$) and that the lineage survives ($P_{survival}$). This produces the *evolution kernel*, the spatial distribution of probabilities that a mutation will be present in the population, given that the mutation arose at location $[x,y]$ and the amount of time elapsed since it arose at that position. The probability that a mutation is present at time $t$, given that its origin, is produced as the product of the probabilities of mutation, colonisation and subsequent survival:

$$P_{present[x,y,t+n]} = P_{mutation} * P_{colonisaton[x,y,t]} * P_{survival[x,y,t+n]} \qquad (2)$$

Colonisation and survival rates across space can be scaled by a mutation rate to produce the kernel at any point in time, $t$. Results averaged over $[\ ,y]$ revealing the evolution kernel along the climate gradient (i.e. with changing extinction rate).

Within this model we can mark and track any individual cell to understand the effect of range shifting on mutation surfing, or to create the evolution kernel. By marking a group of individuals we can visually observe gene flow patterns, much like a barium meal. Individuals can be marked to track the fate of their lineages. Mutations can also occur at a rate $\mu$ to investigate how diversity is generated and maintained within the population. When tracking any lineage we record where in space it originated from and how long it survives. In all these different ways of observing the effects of the surfing phenomena the population is allowed generous time to reach a quasi- equilibrium before any marking or measurements are taken. The time to quasi equilibrium is dependent on the parameters used with longer distance dispersal and slow rates of climate change showing the shortest times to reach the new equilibrium point.

## 5.3 Results

### *5.3.1 Barium meal: patterns of gene flow.*

The Barium meal given to the range centre shows patterns of gene flow that move towards the range limits in a static climate (Alleaume et al. 2006) (fig 5.2a). Offspring and so their genes disperse down the occupancy gradient. The symmetrical gene flow patterns of a static climate are lost during changing climate (fig 5.2b) as genes flow contrary to the direction of climatic change.

In a static climate, the lineages of cells marked at the range limits eventually die out (fig 5.2c). Barium meals infrequently move into the range centre due to the dispersal differential from high to low occupancy. A changing climate brings a dramatic change in gene flow (fig 5.2d) (Bahn et al. 2006) with the barium meal now flowing through the range centre and marked individuals often taking over the whole population. Marked lineages *surf*, contributing almost entirely to the new range limit as areas at leading limits become increasingly suitable. A concomitant purging of unmarked lineages (*wipe outs*) occurs at trailing limits where extinction rates increase.

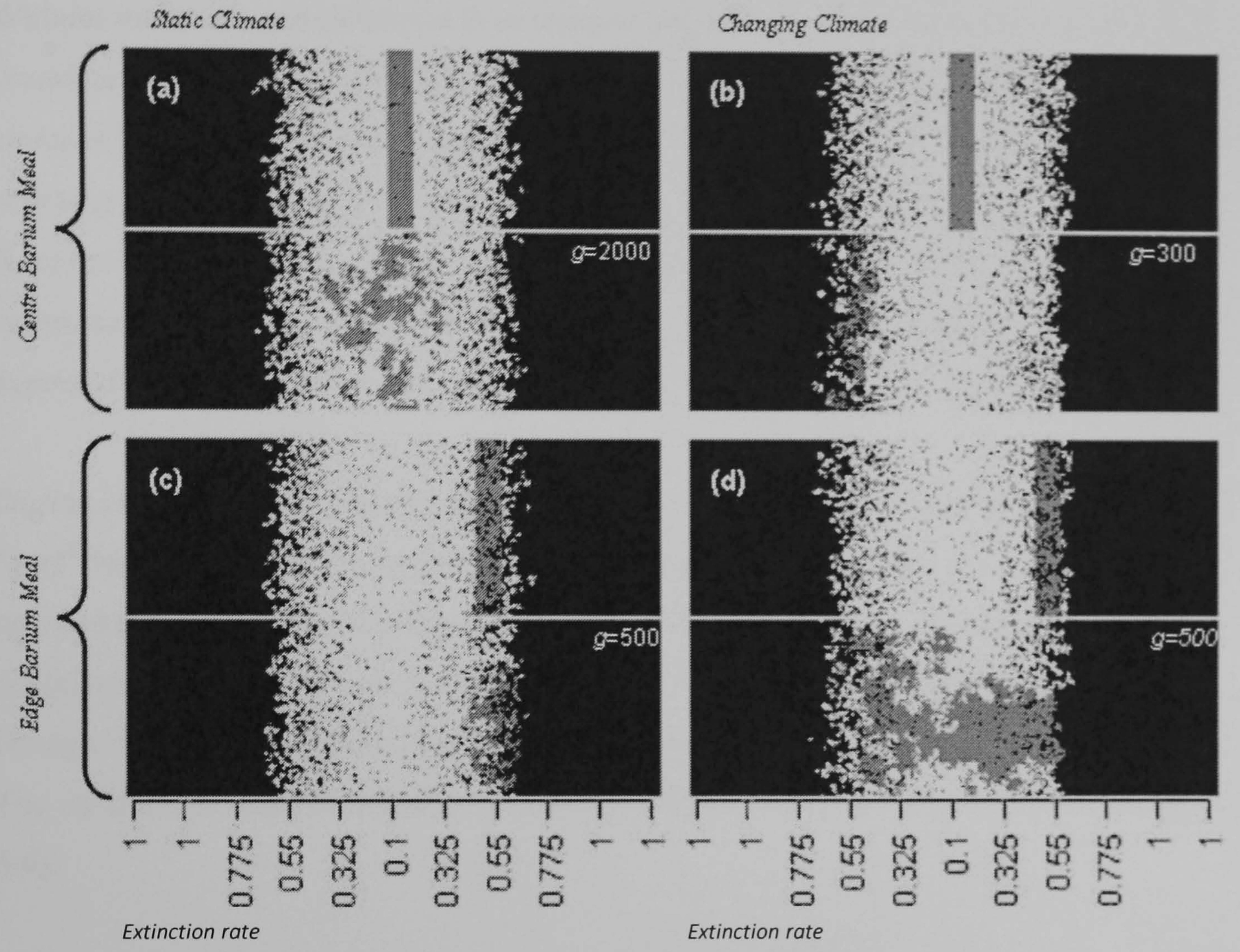

Figure 5.2: “Barium meals” demonstrating the patterns of gene flow in static (a & c) and changing climates (b & d). The barium meals are applied around the point of optimal adaptation at the range centre (a & b) or at low levels of trait-climate concordance towards the range limit (c & d). The upper part of each panel shows the initially marked cells (t=0) and the lower part after the number of generations specified. Black cells are unoccupied, White cells occupied and Grey cells are occupied by individuals form the marked lineage (see text). The climate optimum of the trait effectively moves from the left to the right in the changing climate but the panels are aligned at the climate optimum, $e_{min}$=0.1 (i.e. the “centre” of the population would be 2 cells away every 10 generations under the climate change rate shown). Other parameters, $a$=5, dispersal is local on a 300 by 100 grid with the gradients occurring over 130 cells in each direction away from the optimal climate. $v$=0.0025. Occupancy is shown after the extinction events. See figure 5.3 for wider ranging dispersal.

### *5.3.2 Effects of structure*

Without mutation, populations will eventually originate from a single ancestor (fig 5.3) (multiple ancestors exist if multiple lineages persist to the end of a simulation). In static climates lineages are derived from the range centre (figs 5.3a & b). Dispersal events resulting in colonisation are more likely to occur down the occupancy gradient, away from the range centre. A greater number of dispersers are also produced at the range centre due to high occupancy. The range centre has smaller extinction probabilities and is expected to contribute to future generations over a greater number of generations.

During climate change lineages at or near the leading range limit survive longest as they "*surf*" but also experience decreasing extinction probabilities over time. In contrast, survival decreases at trailing limits with decreasing unoccupied patches available for colonisation in the direction of climate change. This produces reduced survival of lineages towards the trailing limit and the direction flows shown in figure 5.2b & 5.2d. The variation in this effect and its intensity is reduced by wider ranging dispersal (fig 5.4).

### *5.3.3 Evolution kernels: effects of structure and substructure*

Mutations may only be generated by a 'birth' and so substructure (patterns of colonisation; Antonovics et al. 2006) defines mutation occurrence. Structure subsequently affects survival. The *evolution kernel* (see methods) takes this into account (fig 5.5). When a mutation occurs ($g$=0), the kernel equals the colonisation rates along the gradient. Colonisation rates are highest towards range limits. Low population turnover at the range centre, due to the low number of extinctions, creates little space and so few colonisation opportunities. At range limits higher extinction probabilities create space, but low occupancy, and so low offspring input, produces few colonisations. In between space is created by frequent extinctions and occupancy levels produce abundant offspring causing colonisation rates to peak (at equilibrium, colonisations ≈ extinctions) (fig 5.5, $g$=0) (also see Antonovics et al. 2006). For local dispersal (fig 5.5a) colonisation

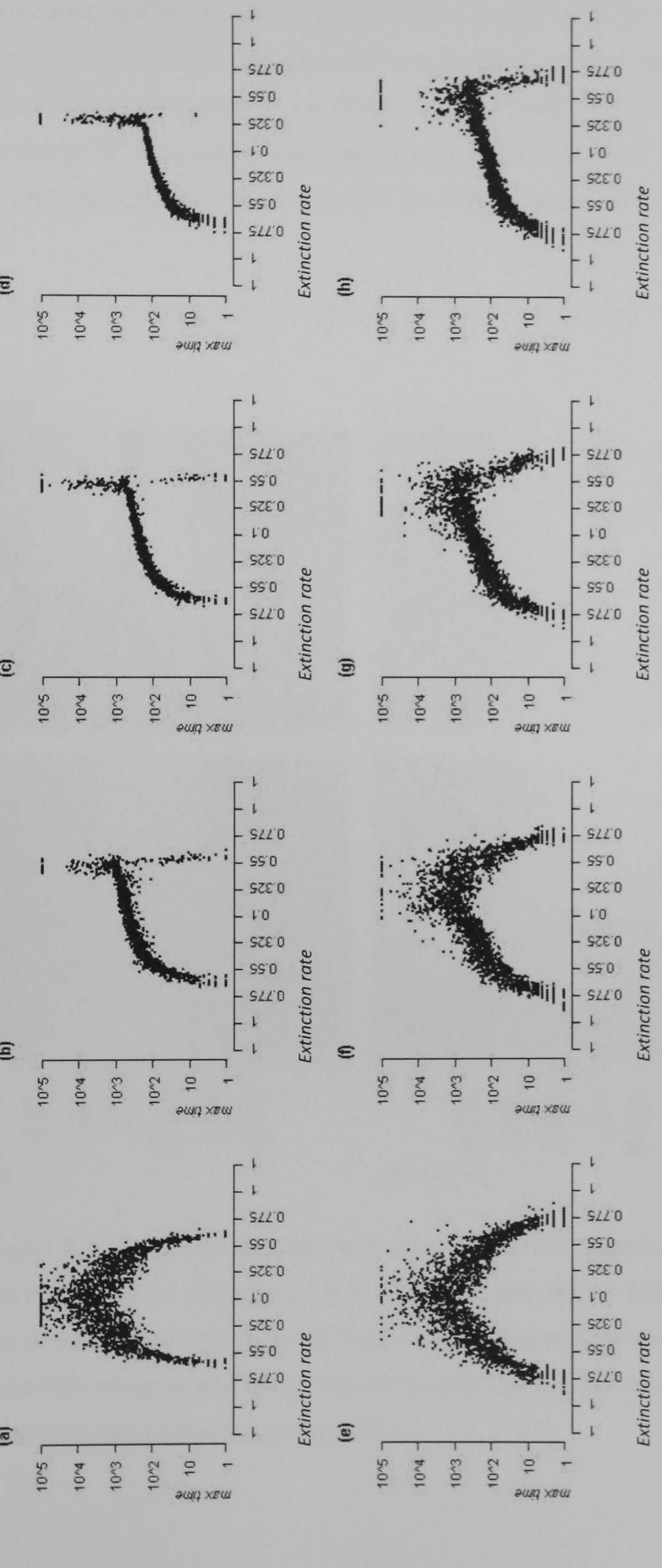
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
max time
10^5
10^4
10^3
10^2
10
1
1
1
0.775
0.55
0.325
0.1
0.325
0.55
0.775
1
1
Extinction rate

Figure 5.3: Contrasting survival of lineages arising from different locations along a gradient for local dispersal (a-d) (nearest neighbour) and wide dispersal (e-h) ($a$=0.3), where a & e are for a static climate. Maximum survival time of lineages arising at points along the climate gradient are shown for three rates of climate changes (b, f, $v$=0.00125; c, g, $v$=0.0025; d, h, $v$=0.00625). The simulations were limited to $10^5$ generations, with data from >1,500,000 lineages. Other parameters, $a$=5, $e_{min}$=0.1, on a 200 by 200 grid with the gradient occurring over 80 cells in each direction.

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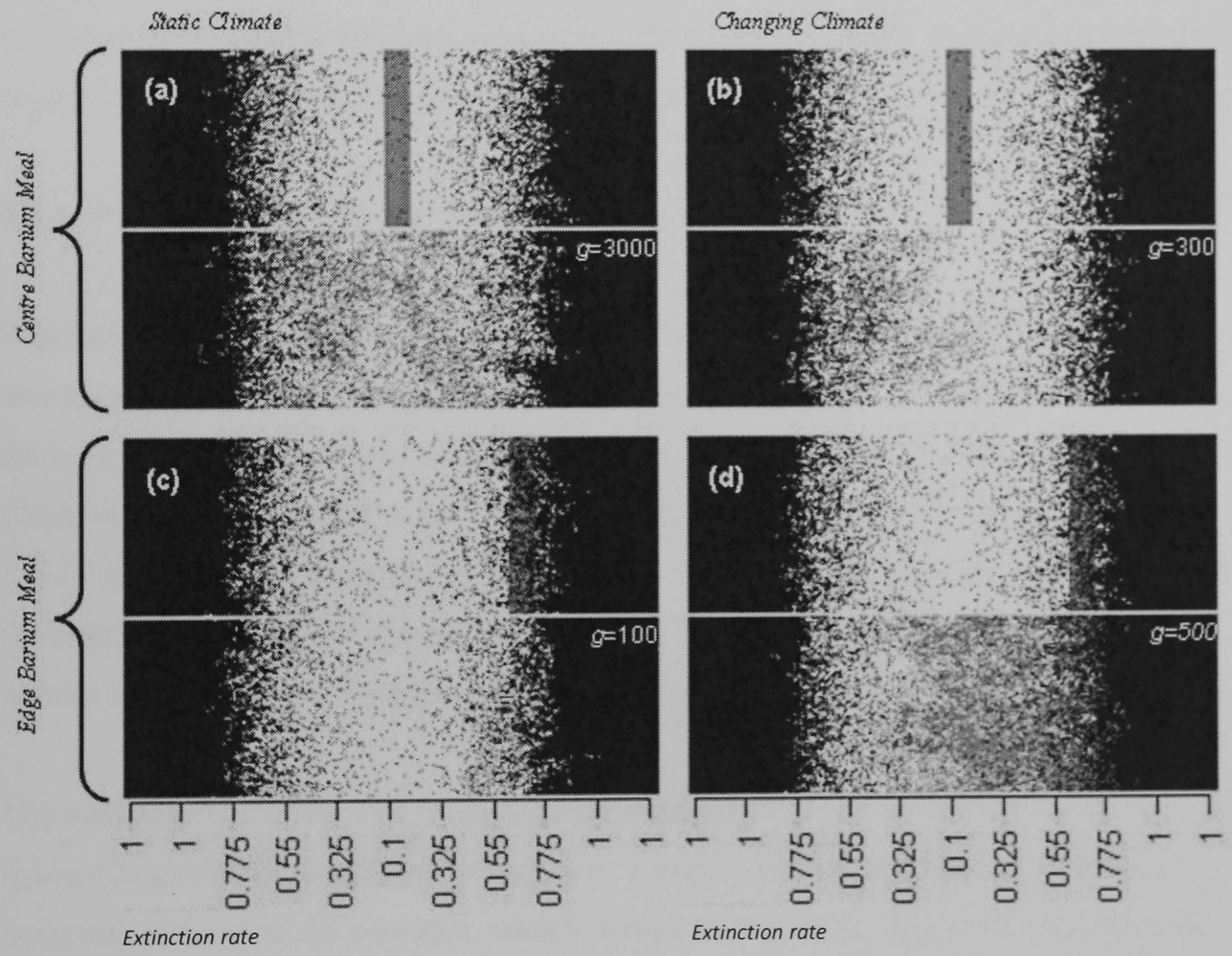

Figure 5.4: As for figure 5.1 "Barium meals" shown in static (a & c) and changing climates (b & d) but with wider ranging, Gaussian dispersal ($a$=0.3). The upper part of each panel shows the initially marked cells (t=0) and the lower part after the number of generations shown. Black cells are unoccupied, White cells occupied and Grey cells are occupied and from the lineage of cells originally marked (see text). All parameters as figure 5.1.

lags at leading limits and extinction lags at trailing limits are visible where there is no overlap with the static climate. Lags are less apparent for wide dispersal (figure 5.5b).

In a static climate the kernel clusters around the highest colonisation rates over short time scales and around the greatest survival probabilities of the range centre at longer time scales. With climate change, increased survival probabilities at the leading limit coincide with high colonisation probabilities (fig 5.5). The association increases the probability that lineages will be derived from the leading limit. Towards trailing limits low survival is associated with low mutation input (compare results for *g*=100). After 100 generations effects of surfing and wiping are obvious at opposing limits. Wide dispersal reduces this coupling (fig 5.5b) producing weakened mutation surfing.

### 5.3.4 *Patterns of diversity loss and gain.*

Populations purge diversity at different rates through time depending on climate change rate and dispersal ability (figure 5.6). In static climates there is a near exponential decrease in diversity (without novel mutations) (black marks figure 5.4). Changing climates maintain diversity at a similar level over short periods, however by *g*=1000 the rate of diversity loss increases sharply (fig 5.6a). This increase in diversity loss indicates the relative success of the surfing individuals at the expense of other lineages. The same pattern occurs, though less intensely for wide ranging dispersal (fig 5.6b).

The evolution kernel shows (1) production of mutations occurs at different rates through space, (2) survival is dependent on mutation's origin and (3) contributions of mutation input and survival to the evolution kernel change through time. These factors affect the regulation of diversity (fig 5.7 a-d). In static climates diversity is greatest towards the range centre (fig 5.7a) and originates from this same locality (fig 5.7e; also see fig 5.3a). With climate change greatest diversity is no longer found at the range centre, with diversity peaking towards the trailing limit (fig 5.7 b-d). Diversity tends to originate at the leading range limit during climate change (fig 5.7 f-h). Mutations are decreasingly likely to have originated anywhere else except where colonisation rates are high (e.g. fig 5.5, $g$=0) and so realised mutation rates are high.

### 5.3.5 *Effects of wide dispersal*

Widening dispersal stabilises population structure during climate change (fig 5.4) by spreading offspring further and so reducing colonisation lags. Faster climate change generates a colonisation lag, increasing mutation surfing depending on the dispersal kernel and the rate of climate change involved (fig 5.8). Faster climate change is necessary to create the areas where founder effects can take place by generating lags.

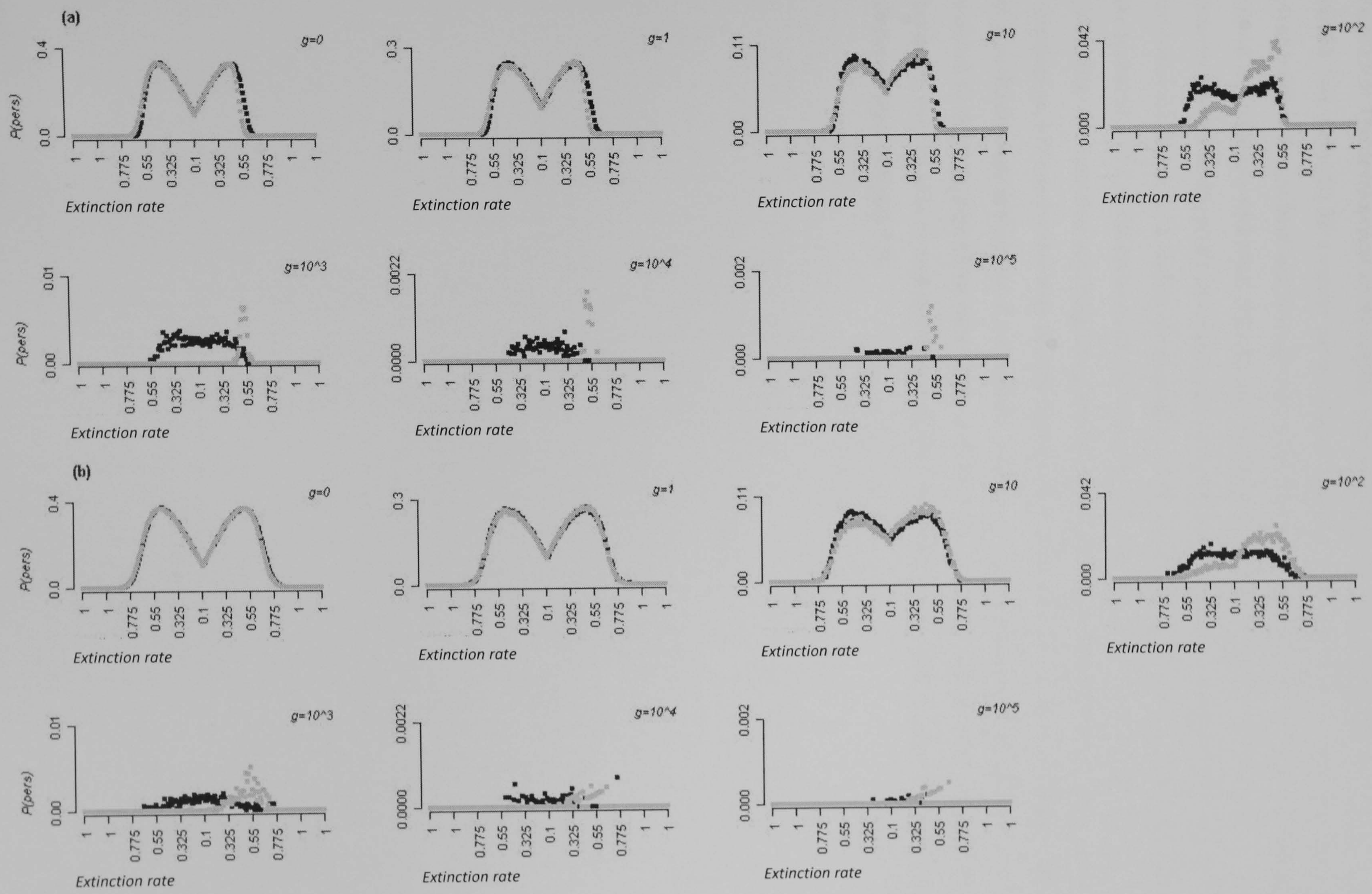
(a)
g=0
g=1
g=10
g=10^2
g=10^3
g=10^4
g=10^5
(b)
g=0
g=1
g=10
g=10^2
g=10^3
g=10^4
g=10^5
P(pers)
0.0
0.4
0.3
0.00
0.11
0.000
0.042
0.01
0.0000
0.0022
0.002
1
0.775
0.55
0.325
0.1
Extinction rate

Figure 5.5: The development of the *surfing* phenomenon over time as shown by the evolution kernels (see methods) for a variety of time steps (the probability that a mutation will arise at a given point of the gradient and then survive to the specified time step). The evolution kernels are shown for mutations with static (Black) and changing (Grey) climate gradients. for local (a) (nearest neighbour dispersal) and wide ranging dispersal (b) ($a$=0.3). Evolution kernels (see methods) are shown for a variety of time steps into the future. Where $g$=0 the kernel is equal to the probability of a colonisation event and so can be scaled by a mutation rate to show the probability of a mutation occurring. As $g$ increases the kernel shows the probability that a new colonisation will survive that time into the future, which again may be scaled by a mutation rate to give the absolute probability of a mutations occurrence at that point of the gradient and survival to that time step. Other parameters, $a$=5, $e_{min}$=0.1, an 200 by 100 grid with the gradient occurring over 80 cells in each direction. $v$=0.0025. Kernels for all climate change scenarios and dispersal types in figure 5.8.

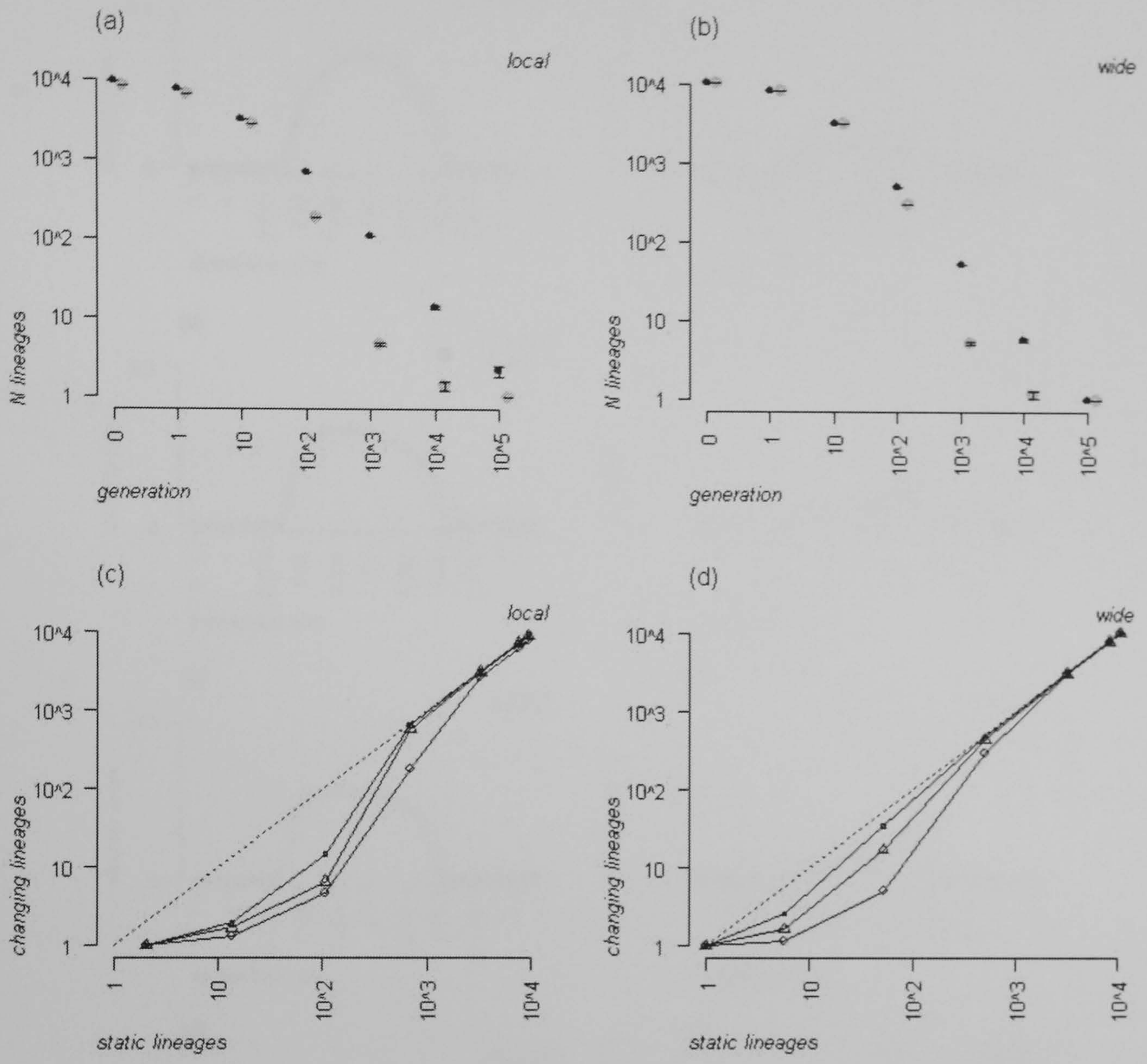

Figure 5.6: Loss of diversity within static (Black) and changing climates (Grey) for ‘local‘ (a) (nearest neighbour dispersal) and (b) ‘wide’ ranging dispersal ($a$=0.3). The climate change rate shown in (a) & (b) is intermediate ($v$=0.0025). The effect of the rate of climate change are shown for local (c) and wide (d) dispersal distances where the number of lineages at each time point in a static climate are plotted against that in a changing climate at the same time step (squares, $v$=0.00125; triangles, $v$=0.0025 and circles, $v$=0.00625). The largest number of lineages are found at $g$=0, with increasing time the number of lineages decreases. All occupied cells at $g$=0 are marked as individual lineages and the average number of survivors (10 replicate simulations) are shown at each time step. All other parameters as previously presented. Jitter added for clarity in a & b.

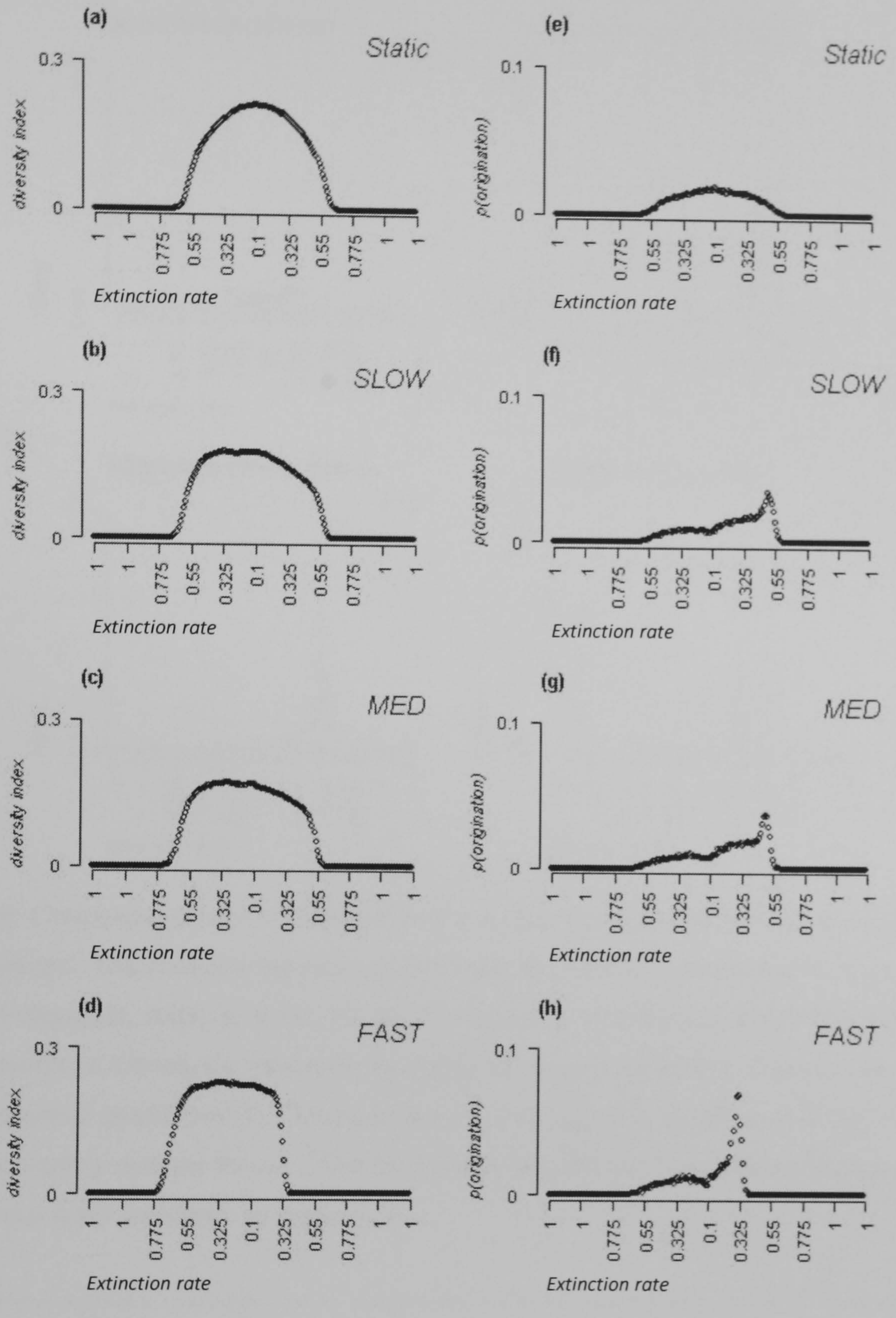

Figure 5.7: Diversity index showing the generation of diversity (a-d) and origins of surviving mutations (e-h) within static (a, e) and changing climates (b-d, f-h; b, f, $v$=0.00125; c, g, $v$=0.0025; & d, h, $v$=0.00625). Mutations occur at rate $\mu$=0.001. Proportions of the entire diversity contained at each point of the gradient (a-d). Probabilities that mutations originated across the gradient (f-h). Data are form a single sample after quasi-equilibrium is reached in each of 561 replicates. Other parameters, $a$=5, $e_{min}$=0.1, local dispersal, a 200 x 200 grid with a gradient over the 80 cells.

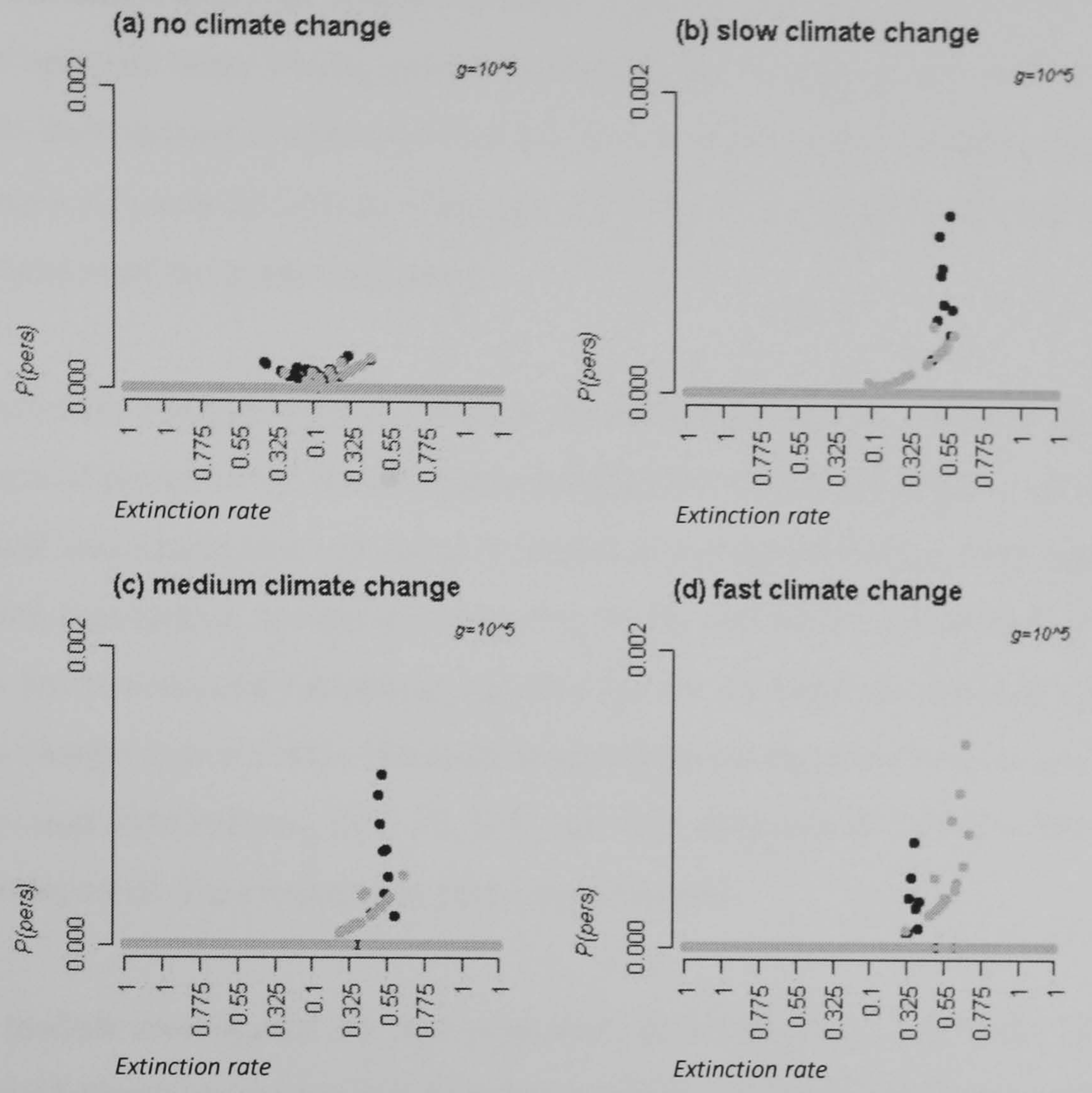

Figure 5.8: Contrasting effects of dispersal on the *surfing* phenomenon with an increasing rate of climate change. The evolution kernels (see methods) at g=100000 are shown for increasing rates of climate change (a, static; b, slow, $v$=0.00125;c medium, $v$=0.0025; & fast, $v$=0.00625). In each case the evolution kernels are shown for local (black) (nearest neighbour dispersal) and wide ranging dispersal (grey) ($a$=0.3). Other parameters, $a$=5, $e_{min}$=0.1, an 200 by 200 grid with the gradient occurring over the 80 cells. The full kernels for all time steps, climate change scenarios and dispersal types are shown in figure 5.10.

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## 5.4 Discussion

This work illustrates the potential for climate change to generate lags in spatial dynamics that can alter the regulation of genetic diversity. Lags occur in different processes at leading and trailing range limits, causing deformation of the range (Rapoport 1975).

Range deformation alters the relative strength of processes (e.g. Drift versus Founder effects) at opposite range limits, generating significant changes in evolutionary patterns. The results demonstrate the potential for climate change to alter (1) patterns of gene flow across ranges, (2) sources of future lineages, (3) sites of subsequent survival, and (4) how these patterns regulate neutral diversity.

The evolutionary changes can be explained by understanding the mechanisms that cause deformation of populations' structure and substructure due to generation of lags, and the populations' movement through space in response to climate change. Very simply, colonisation lags reduce occupancy at leading limits and permit *mutation surfing*, whilst at trailing limits occupancy increases, eliminating the potential for founder effects (figure 5.9). This change in population structure is accompanied by alterations to colonisation rates (the range substructure, fig 5.10, *g*=0; see Antonovics et al. 2006) as shown in a novel development: the *evolution kernel* (see methods).

Previous models investigated the fate of neutral mutations given their point of origin. The proportion of simulations where mutations persisted for 500 generations is often reported (e.g. figure 4a, Klopfstein et al. 2005; fig 6a, Travis et al. 2007). This binary result (survival (by surfing or drifting) vs. extinction (wiping out)) masks further patterns in the temporal distribution of mutation's survival and so the regulation of diversity. As there is finite space in the landscape it is of interest how many individuals receive surfing effects and for how long. The evolution kernel addresses these questions and can be used to understand the generation and regulation of diversity, demonstrating direct links between spatial dynamics and evolutionary patterns. The evolution kernel's concepts can be used to develop models that further investigate the concepts presented here and generate further hypotheses for empirical tests (e.g. Estoup et al. 2004). The results demonstrate a considerable importance of developing theory appropriate to the climate change scenario. Without, we rely on 'equilibrium' patterns that may not apply and make mistakes when challenged to make predictions.

A principle central to the results is that climate change not only affects range limits and this change in pattern affects process. For instance climate change affects leading and trailing limits differentially, causing contractions occurring at leading limits as colonisations lag behind climate change and expansion of trailing limits are generated by extinction lags. The evolution kernel shows longest survival occurs at leading limits (fig 5.3) producing *mutation surfing* as founder effects become iterated and more pronounced (Edmonds et al. 2004; Klopfstein et al. 2005), though for but a few lineages. '*Wiping out*' also occurs where mutations at trailing limits contribute little to future generations. In between limits structural change was visible in alterations to gene flow patterns and sources of diversity. At leading limits colonisation probabilities become aligned with survival, thus most surviving lineages will eventually originate from leading limits.

Surfing does not generate greater diversity at leading limits, as there is finite space at the leading range limit and mutation input is slower than competition between mutants that results in mutation surfing. Small population sizes at range limits can reduce the possible diversity they can contain (Bridle & Vines 2007). The spatial shifts sweep lineages towards trailing limits where diversity peaks. Increased diversity is maintained as more conventional drift acts to reduce diversity at slower rates than the high competition between surfing lineages. Thus mutations do not necessarily survive in the place where they are generated and so have less predictable effects on diversity patterns (fig 5.7 & 5.1). Overall the greatest mutation occurrence is not coupled with greatest survival, except at the leading limits during climate change.

Our metapopulation (or patch-occupancy) approach differs from previous models and has many benefits. The model reduces computing time by tracking patch occupancy. More importantly it doesn't necessitate manipulation of deme sizes or reproductive ability to simulate a climate gradient (the likely candidates from models by Edmonds et al. (2004) and Klopfstein et al. (2005)). A response to a gradient modelled by carrying capacities is not appropriate, as it constitutes a landscape feature shifting with the climate rather than allowing a population to change in structure, a fundamental effect of directional environmental change. Manipulating reproductive ability to a gradient alters the competitive environment at the leading range limits in more complicated ways and should be dealt with at a later stage (see later discussion). An additional benefit is that the ecological dynamics in static climates are well studied (Lennon et al. 1997; Holt & Keitt 2000; Antonovics et al. 2006). The metapopulation parameters (extinction, colonisation and dispersal) can easily be manipulate to maintain the concept of a phenotype-climate interaction avoiding the aforementioned issues. The addition of a climatic gradient incorporates large differences between the invasion models used previously (e.g. Edmonds et al. 2004) and the model presented here.

Firstly, equilibrium gene flow patterns are not homogenous. As occupancy (population size) is determined by phenotypes' responses to climate, then the greatest occupancy coincides with the point of optimal adaptation (Lennon et al. 1997). Declining population sizes away from the optimum generates directional gene flow due to a dispersal differential away from the range centre (Grinnell 1917, Macarthur 1972) (where population size and number of dispersers are positively related). A mutation's lifespan is then related to spatial population dynamics and where it originated. Unlike invasion models this is not solely a diffusion process behind the range limits, and gene flow from high to low densities may affect drift at equilibrium (Alleaume-Benharira et al. 2006). In the invasion scenario the point of optimal adaptation occurs everywhere, as all demographic parameters are homogeneous through space and the important lag is the time since a patch was invaded.

Secondly spatial structure in occupancy is accompanied by substructure in demographic rates (Antonovics et al. 2006). The population exhibits highly non-linear colonisation rates through space (Lennon et al. 1997) and this substructure needn't mirror occupancy patterns (Antonovics et al. 2006). The highest colonisation rates are found where expected lifetimes are short but occupancy is relatively high (Antonovics et al. 2006). This point occurs between the range limit and the range centre, with these extremes having the lowest colonisation rates but for different reasons (Lennon et al. 1997; Antonovics et al. 2006). As colonisations are the opportunity for a mutation to occur, their spatial patterns may be tightly linked to genetic patterns (Hastings & Harrison

1994). The deformation of ecological structure affects evolutionary processes by altering colonisation and extinction patterns that determine gene flow.

Finally and as previously discussed (see introduction), during climate change the difference between responses of edges may deform the range: one edge will be leading whilst the other is trailing.

Mutation surfing has further illuminated how historical events may determine contemporary diversity patterns (Klopfstein et al. 2005, Currat et al. 2006, Travis et al. 2007). Ibrahim et al. (1996) had previously demonstrated this point. Whilst not recognising the surfing process explicitly, they showed "*long-distance migration during range expansion leads to the establishment of pocket populations well in advance of the main wave*". With local dispersal "*pocket populations*" are established within the "*main wave*" (e.g. Edmonds et al. 2004, Klopfstein et al. 2005, fig 5.1). This difference is highlighted by the relative increase in mutation surfing with local dispersal found here (Figure 5.8). At slow rates of climate change wide dispersal does not permit a strong surfing effect (fig 5.4 & 5.8) as the colonisation lag is small and leading limits do not contract (fig 5.10). Fast climate change generates larger colonisation lags (fig 5.9), permitting potentially larger founder effects (fig 5.8). Reduced surfing with local dispersal during fast climate change can be attributed to an increased colonisation lag at leading limits. Colonisation probabilities are then reduced at the leading limit as extinction rates lower and so increases competition amongst lineages at the leading limit (fig 5.8 & 5.10(d), g=0). Elsewhere only nearest neighbour dispersal has been investigated (Edmonds et al. 2004; Klopfstein et al. 2005; Currat et al. 2006; Travis et al. 2007).

Klopfstein et al. (2005) demonstrated links between demographic rates and surfing probabilities: population growth exhibiting a positive relationship, whilst negative relationships with carrying capacity and dispersal rate. Dispersal has wide-ranging effects on various spatial processes and resultant pattern formation, such as genetic structure (e.g. Ibrahim et al. 1996; Charlesworth et al. 2003). I demonstrate that wide range dispersal may permit surfing, but with intensities determined by the magnitude of climate-response lags (fig 5.5 & 5.10). This suggests that interactions between the demographic rates that determine lags (e.g. rate of invasion, see Klopfstein et al. 2005) and the dispersal kernel used are likely.

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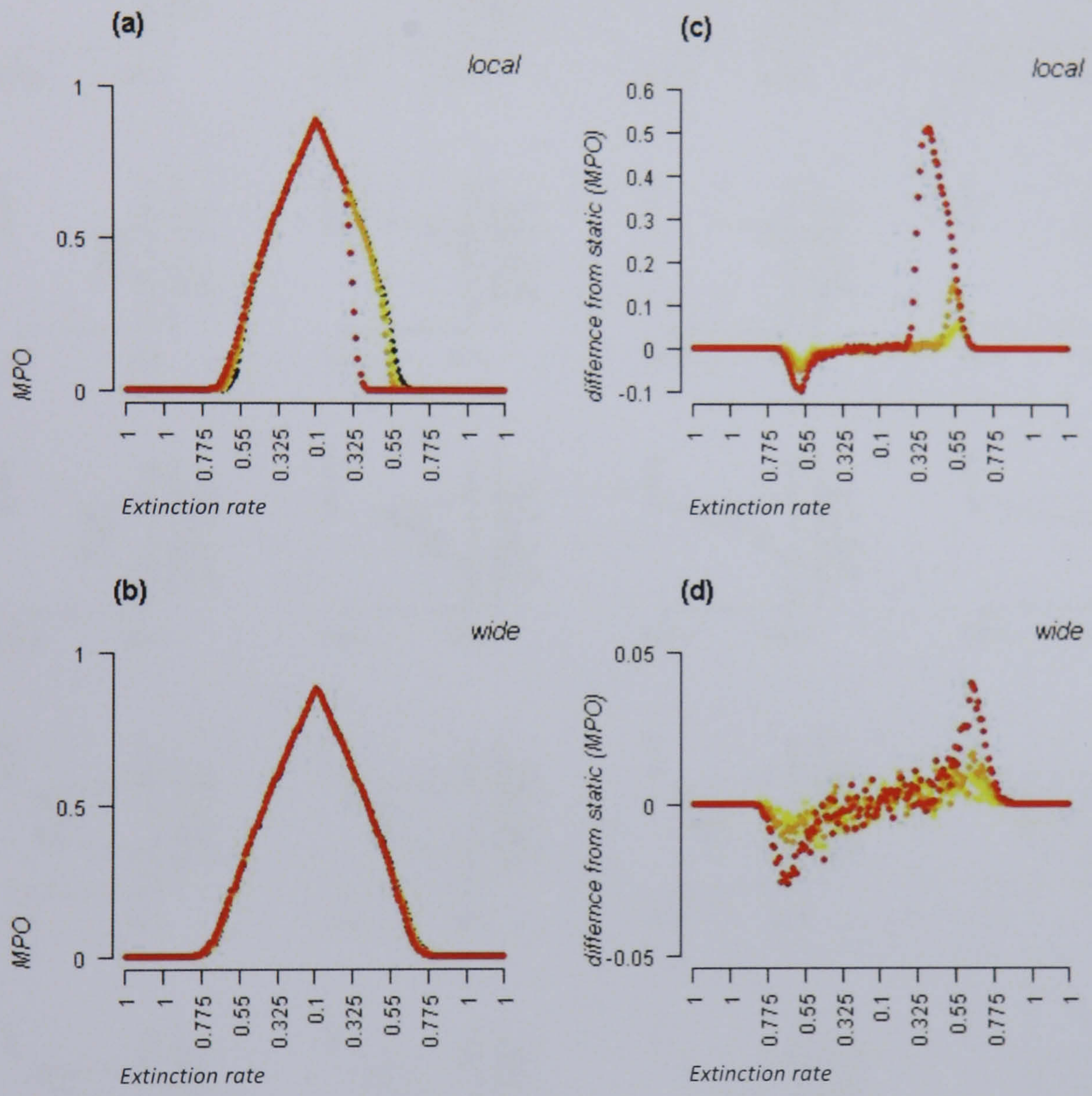

Figure 5.9: Mean patch occupancy (MPO) across the climate gradient (a & b) in a static climate (black) and with three intensities of climate change (yellow, orange, red for $v$=0.00125, $v$=0.0025, $v$=0.00625 respectively). Results shown for local (nearest neighbour dispersal) (a) and wide dispersal (b) ($a$=0.3). The colonisation lag and extinction lags are shown more clearly (c (local dispersal) & d (wide ranging dispersal)) where the difference in MPO in a static climate and a changing climate is shown along the climate gradient. Positive values indicate the MPO in a static climate is greater. The differences are more subtle with wide ranging dispersal.

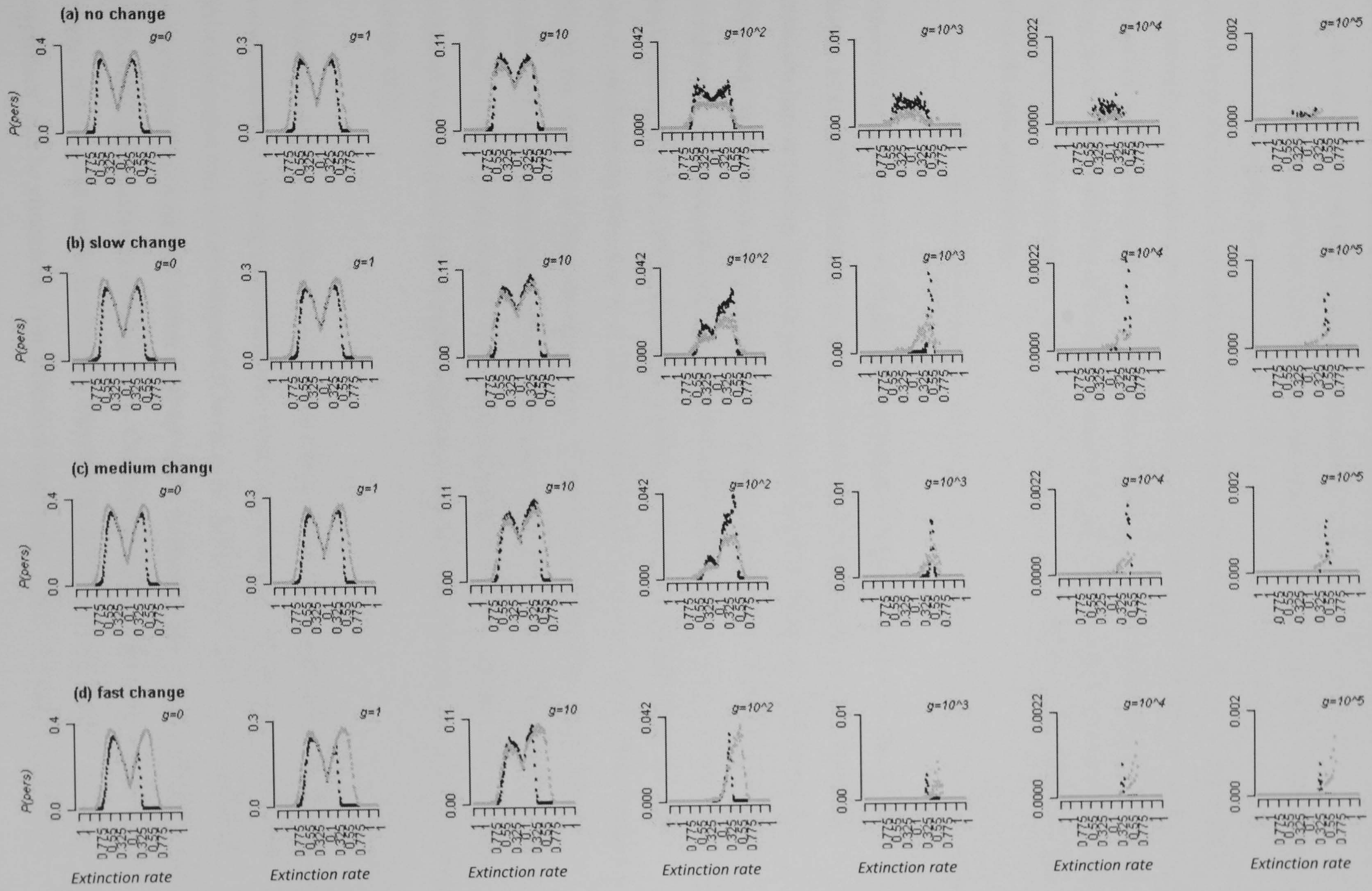
(a) no change
(b) slow change
(c) medium chang
(d) fast change
g=0
g=1
g=10
g=10^2
g=10^3
g=10^4
g=10^5
P(pers)
0.0
0.4
0.3
0.00
0.11
0.000
0.042
0.01
0.0000
0.0022
0.002
1
0.775
0.55
0.325
0.1
Extinction rate

Figure 5.10: Evolution kernels in a static climate (a) and with three intensities of climate change (b, c & d; $v$=0.00125, $v$=0.0025, $v$=0.00625 respectively). The strength of the *surfing* phenomenon is shown over time and contrasted between local (a) (nearest neighbour dispersal) (black) and wide ranging dispersal (b) (grey) ($a$=0.3). As in figure 5.3 where $g$=0 the kernel is equal to the probability of a colonisation event and so can be scaled by a mutation rate to show the probability of a mutation occurring. As $g$ increases the kernel shows the probability that a new colonisation will survive that time into the future, which again may be scaled by a mutation rate, giving the absolute probability of a mutations occurrence at that point of the gradient and survival to that time step. Other parameters, $a$=5, $e_{min}$=0.1, an 200 by 200 grid with the gradient occurring over the 80 cells as previously.

Dispersal rates can evolve to higher rates at invasion fronts (Travis & Dytham 2002; Thomas et al. 2001; Phillips et al. 2006). However, due to increased occupancy the extinction lags at trailing limits could drive lower dispersal rates and lead to further differences in responses across ranges; for instance, when interacting with population growth rates. Inclusion of other traits and evolution in those traits (e.g. life history (Austerlitz et al. 2000, 2003), dormancy (Travis & McInerny *unpublished*) and inter-specific interactions (Brooker et al. 2007)) may alter the manner of range deformation by altering the strength of lags through a range. Furthermore Allee effects may weaken founder effects by permitting colonisations only by large numbers of dispersers, or by "pinning" invasions (Keitt et al. 2001). Even if parameters are stationary, considerable complexities may exist and be highly dependent on the scenario studied, e.g. invasion or climate shift.

Increasing carrying capacity has a negative effect on surfing (Klopfstein et al. 2005). In invasion models carrying capacities have been homogeneous, except where effects of landscape patterning are investigated (Currat et al. 2006, Travis 2007). Such models assume homogenous habitat within a subset of the landscape (see Lawson Handley et al. 2007) creating a qualitative heterogeneity. Carrying capacities may vary considerably between patches and across landscapes. Beyond the results of these studies, surfing 'amplifiers' can be conceived. Amplification may occur where carrying capacities decrease in the direction of range expansion and suppressors where carrying capacities increase. An amplifier may not hinder the ecological expansion of a population, but it may reduce the number of lineages that are carried with the wave front. Conversely a suppressor may allow more lineages to colonise a new area. The potential for such changes in patterns of abundance may be expected during climate change (Shoo et al. 2005; Thomas et al. 2006). For instance for mountain species carrying capacities perceivably decrease and increase during cooling and warming events respectively.

Climate change responses are unlikely to be as simple as portrayed here. Populations perceive few landscapes as homogeneous, and few environmental gradients as perfectly correlated. For instance altitudinal variation may reduce the need for long distance dispersal to track climate changes (Thomas et al. 1999) and so alter the strength of lags that are generated. The buffering effects of altitude could produce range expansion or contraction (e.g. Parmesan et al. 1999; Thomas & Lennon 1999) and these differences in the strength of climate change through space could alter the fundamental stability of ranges (see: Kirkpatrick & Barton 1997; Bridle & Vines 2007). For instance gene flow differentials can drive gene frequencies opposite to the direction of selection, halting populations' spread (Kirkpatrick & Barton 1997). Disruption of these interactions may occur during climate change as relative levels of adaptation and gene flow patterns are altered. Changes in the strength of lags, through ecological and evolutionary mechanisms, makes understanding populations' transformation to a deformed state of increasing importance in the prediction of future diversity. For instance, understanding patterns promoted by climate change 'disequilibrium' may enable us to understand 'equilibrium' patterns as *"it is often hard to be sure that present-day distribution patterns reflect the geographic relations existing at the time of divergence"* (Barton & Charlesworth 1984). Importantly populations themselves may alter in structure in addition to changes in 'geographic relations'. Also the patchiness generated by founder effects during expansion can be misinterpreted as generated by selection at equilibrium (Ibrahim et al. 1996, Currat et al. 2006) and such patterns may persist for many generations (Ibrahim et al. 1996; figure 5.1b, *g*=36500). Additionally moving populations can contain alleles that are otherwise selected against (Travis et al. 2007, Burton & Travis (*in press*)). It is likely that spatial assortment of individuals and range deformation during range shifts may contain further understanding for evolutionary biology.

## 5.5 Summary

The "founder effect" is far from a new concept. Indeed neither is a "*pronounced founder effect*" (Edmonds et al. 2004). Founder effects inevitably vary in strength (Barton & Charlesworth 1984) such as when population foundation is followed by isolation or subsequent influx of individuals (Barton & Charlesworth 1984). However what is new is considering founder effects where populations are dynamically changing, e.g. expanding their range due to translocation (invasive species) or shifting in response to climate change. The form a population takes during such transitions can maintain isolation at leading limits and alter our perceptions of symaptry and allopatry. As such, we need novel theory to understand the differences in evolutionary dynamics climate change can generate (e.g. Desai & Nelson 2005) and the ecological dynamics that describe them. This is illustrated by some different conclusions made in different scenarios (e.g. invasion (Edmonds et al. 2004), climate change (this study) and petri-dish (Wei & Krone 2006)). Understanding the deformation of ranges (Rapoport 1975) and the concomitant evolutionary effects (e.g. Desai & Nelson 2005, Jump & Penualas 2005) under these and other dynamic circumstances may highlight some important details that change our understanding of the processes governing biodiversity.

# 6. The road to nowhere: an experimental study of demographic and evolutionary consequences of emigration.

## 6.1 Introduction

The processes giving rise to population dynamics are birth (*B*) & immigration (*I*) that introduce individuals into a population, and death (*D*) & emigration (*E*) that reduce population numbers (Thomas & Kunin 1999). All of these processes (*BIDE*) may be dependent on the conditions within a given patch, but each of *BDE* may occur even when a patch is isolated and so may be considered the "internal" processes. Even when there is no "external" process in the form of immigration, dispersal may still be of great importance. This will be especially so when emigration affects age and sex classes in different ways to death, resulting in alterations to population structure and the resultant dynamics (Ranta et al. 1999).

Landscape alterations can limit immigration as habitat fragmentation directly reduces populations' dispersal abilities (Fahrig 1997). Dispersal may also interact with environmental conditions such as weather (van Horne et al. 1997) and so populations may also become more fragmented when they are declining for reasons other than habitat loss (Wilson et al. 2004). Though immigration can decline during fragmentation, emigration may still occur. Thus the viability of increasingly isolated populations may not be predicted by solely *BD*, but more accurately by a change in *BDE*. Emigration may then be considered to be at the heart of many contemporary conservation problems as (1) landscape alterations may also affect the propensity of individuals to leave a patch and their subsequent success, (2) creating protected areas may involve decisions to "open" or "close" reserves and (3) range shifts in response to climate change involve emigration from populations and subsequent foundation of populations whose dynamics will also include emigration.

Previously there has been a tendency to focus on immigration due to its effects on (1) colonisation and supplementation to population growth rates (Pulliam 1988). (2) maintenance of regional viability in a metapopulations (Hanski 1998) and (3) synchronisation of population dynamics (Solé & Bacompte 2006). The lack of focus on emigration may be due to an assumption that reduced intra-specific competition compensates for emigration. "Sources" are often viewed as stable, with zero immigration having zero impact on population growth (e.g. Thomas & Kunin 1999). In source-sink dynamics there is the expectation that $E>I$ in sources and that $I>E$ in sinks. Thus any imbalance introduced by dispersal biases between age and/or sex classes may be important in those systems' functioning. As stated previously the effects of emigration and death on population structure could differ, and may operate at different time scales to each other. These time scales needn't be the same as for the processes determining births (fecundity). For instance emigration could potentially occur at any time, but individual growth, maturity and reproduction take time, and ultimately affect when death occurs.

In addition to reducing population size, emigration may alter the effective population size, $N_e$, the breeding population size that describes how genotypes are sampled through the generations (Wright 1931). Different systems of gamete selection, e.g. polygyny vs. polyandry, can affect maintenance of genetic variation (Barrowclough 1980) and fixation of alleles whether the alleles are beneficial or not (Whitlock 2001). $N_e$ may be further sensitive to any other processes that bias gamete selection towards certain classes or some individuals (Crow & Kimura 1970; Husband & Barrett 1992; Nei & Takahata 1993; Whitlock 2001; Hedrick 2005). Sex bias may reduce the effective population size (Wright 1931) as the probability of a given female contributing to the gene pool may be reduced in a female biased population and increased similarly in a male biased population. The effects of sex bias may differ if the alleles in question are linked to specific chromosomes. For example when alleles are "X-linked" in a heterogamous system, females contain two thirds of all the alleles (Hedrick 2005). Individual differences between those that emigrate can then provide a link with effective population size and the resultant evolutionary consequences (see Frankham & Kingsolver 2004; Hedrick 2005). The ecological consequence of low effective population size has been shown in experimental studies (Newman & Pilson 1997: also see Frankham & Kingsolver 2004).

I report an experimental study that investigated the effects of emigration on population dynamics and explore the consequences for $N_e$. Populations of a soil mite, *Sancassania berlesei*, were initiated in experimental landscapes that differ in the amount of emigration permitted away from a focal population. Increasing emigration also incurs an increasing cost and so emigrating individuals returning to the natal patch may be less competitive, if they return at all. I show that emigration can result in changes in demographic dynamics that, through $N_e$, have potential to alter evolutionary process.

## 6.2 Methods

### *6.2.1 Mite populations*

The stock populations of the mite, *Sancassania berlesei*, originate from collections made from agricultural "muck heaps". A number of stock populations are kept in cultures numbering $>10^5$ individuals in unlit incubators at 24 °C. The mites in the current experiment originate from a collection made in 2003 at fields belonging to RJ Young, Waterside Farm, Dunblane. More elaborated introductions to the mite system can be found in Benton et al. (2001), Beckerman et al. (2003), Benton & Beckerman (2005) and Bowler (unpublished). The mites have heterogamous sex determination (XX-XO) (Oliver 1977).

In February of 2007 an excess of mites were removed from the 2003 stock and placed in a plastic funnel that enters an otherwise sealed bottled. Mites are passively cleaned as they move away from the heat and light produced by a desk lamp placed above the funnel. Movement down the funnel removes a large proportion of the detritus from the stock culture by abrasion with a fine plastic mesh contained in the funnel tube (see Bowler unpublished for further details).

Of these cleaned stocks all males and females were removed and kept in separate holding flasks. The mites were then more directly cleaned by pipetting water droplets that catch and drag detritus from mites as water droplets are absorbed into the plaster. 50 males and 50 females were exactingly counted out as the initial population for each focal tube; see below for tube description. All tubes were initiated and recounted on 14/02/07. All construction of equipment occurred before mites enter the focal tube.

### *6.2.2 Experimental design*

Each replicate consisted of a focal tube with four side arms, with treatments differing in the attachments to the side arms (fig 6.1). Tubes are sealed with filter paper and a plastic cap with a hole cut in it allowing gas exchange. The control treatment had a focal tube whose side arms were tightly sealed with cling film and insulating tape. I explored the effects of emigration on population dynamics by adding plastic tubing that either linked a side arm to a neighbouring side arm or a "sink" tube. This produced three treatments:

In the "Low" emigration treatment, pairs of side arms were joined by a piece of 40cm plastic tubing (fig 6.1).

"Medium" emigration treatments had one pair of side arms linked by 40cm of tubing as before, but with the two remaining side arms linked to empty tubes with a single side arm by 20cm of tubing (fig 6.1).

"High" emigration treatments had all side arms separately linked to single armed, empty tubes (fig 6.1).

The total possible distance a disperser could cover, without deviation during its journey, would then be 40cm from leaving any side arm and entering another side arm. This design aimed to control for dispersal costs.

Only focal tubes received food, two balls of dried yeast each day (1.25-1.44mm diameter). The "sink" tubes had no perceivable resources. All tubes were watered to maintain humidity with a 1:100 food colouring to water mix. The amount of watering varies with tube's age and some "stochastic" effects assumed to relate to conditions during filling.

All focal and sink tubes, plastic tubing and plastic caps were fully randomised before assignment to treatments or control when constructing the experiment. The selection of which arms were joined to a neighbour or a sink tube was also randomised, when applicable. This spatial approach to investigating the mite dynamics had previously been investigated more extensively by Beckerman & Benton (unpublished data) and Bowler (unpublished).

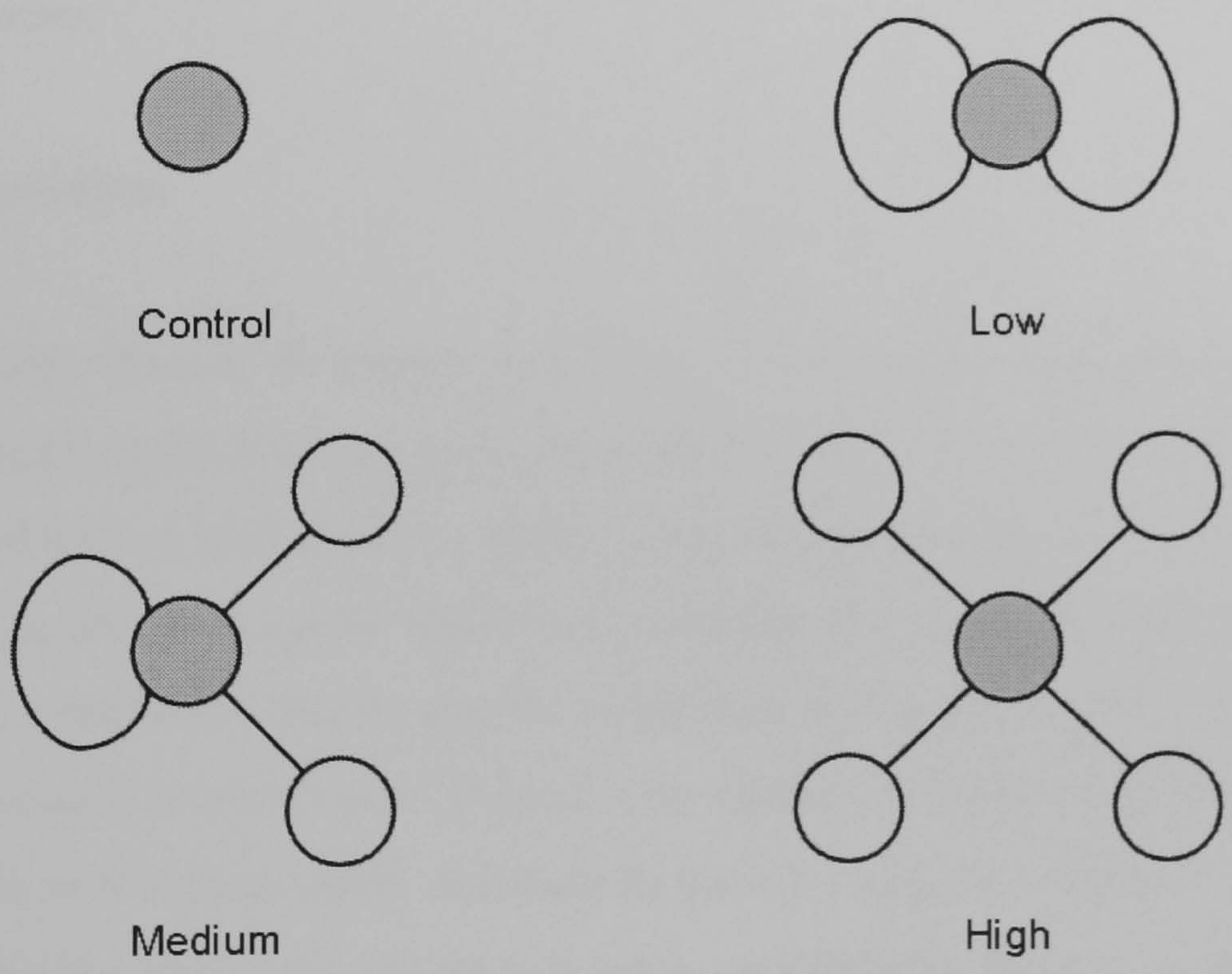

Figure 6.1: Schematic of the experimental design. 4 armed tubes are shown in grey. Pairs of side arms can be connected via plastic tubing, as in the "Low" dispersal treatment, or again via plastic tubing to sink tubes shown in white. Length of tubing differs in each case, see text for details.

### *6.2.3 Tubes*

All tubes were hand made from glass and had the side arm entrance at a height of 35mm, total height of 50mm and diameter of 25mm. Plastic tubing used to link tubes was 9mm in diameter. Tubes were filled with plaster of Paris level with the base of the side arms. A mix of 75ml water to 100g plaster was made by adding plaster to water whilst stirring and the bubbles knocked out of the mix. The mix is poured into the tubes and the surface bubbles removed with a pin. When dry, the plaster surface of focal tubes is divided into quarters by lightly scoring with a craft knife. This aids maintaining orientation when counting under the microscope and also when population estimates are made, see below.

Prior to filling, all tubes were autoclaved to remove any chemicals remaining from manufacture. An excess of tubes were prepared and assessed for surface quality, rate and amount of water uptake, and visual checks that assessed the quality of glass manufacture and potential freedom of mite movement. The highest quality tubes were selected for use in the experiments.

### *6.2.4 Data acquisition*

Successive counts of each life history stage (Egg, Juvenile and Adult) and adult's gender were taken roughly approximately every four days using a Leica MZ8 binocular microscope and a hand held counter. Adult counts encompass all visible individuals. Juvenile and egg densities can be high reach making total counts unfeasible and so counts are taken from a randomly chosen quarter of the tube, including the side arm that quarter contains. However if numbers were judged to be "small" this approximation was discarded in favor of entire counts. Individuals were included in a count if they were anywhere within the focal tube and its side arms, or within a tube quarter and the side arm it contained. The order in which tubes where counted was randomised for every count to remove any biases introduced due to changes in environment between incubator and laboratory (e.g. light, humidity, temperature). Any overtly obvious changes in the tube environment were noted such as excessive dryness or if food was not entirely eaten.

### *6.2.5 **Statistical analysis***

All statistical and graphical analysis was conducted in R (www.Rproject.com). Mean population sizes and sex ratios were estimated using bootstrap re-sampling. Where no overlap existed in the 95% confidence limits of the estimated mean values significant differences were assumed. Benton et al. (2005) employed this method as standard statistical techniques may be confounded by density dependent and highly auto-correlated generation times in the highly plastic mite populations.

The time series can be separated into two distinct periods for analysis. Firstly the initial transient dynamics offer insights into the population growth rate during a transient oscillation, here driven by cohort effects. Following the initial transient the dynamics approach 'equilibrium' allowing insights into stable age and sex structure. A variety of models were fitted to the data (linear model, maximum likelihood mixed-effects model (REML), REML with temporal correlation structure, and generalized linear models). Exploration of the models showed data to be over-dispersed (scale factors <<2) and in all cases a glm with quasi-binomial errors was eventually selected. Differences in tubes were not large enough that REML provided a significantly better fit to the data than a linear model.

Effective population size, $N_e$, was calculated as (Hedrick 2005):

$$N_e = \frac{4N_f N_m}{N_f + N_m} \qquad (1)$$

where $N_m$ and $N_f$ are the number of males and females in the population counts. As the mites have heterogamous males $N_e$ can be estimated for X-linked alleles. $N_e$ is then calculated as (Wright 1931, Hedrick 2005),

$$N_e = \frac{9N_f N_m}{2N_f + 4N_m} \qquad (2)$$

## 6.3 Results

### *6.3.1 General*

The initial population of 100 adults enter a very low competition environment allowing females to have a very high reproductive rate, which leads to over-compensatory dynamics. The resulting transient dynamic can be seen in total population numbers (first column, fig 6.2). Initially high rates of population growth are exhibited, followed by a fall in total population number as the first cohort dies off. As the second cohort matures the population numbers again increase, but with lower amplitude (fig 6.2).

### *6.3.2 Effects of dispersal on population growth rate and transient dynamics*

The initial population increase at low density may be a close approximation for $r_0$, the maximum growth rate. Using $r=\ln(N_{t+1}/N_t)$ (Cameron & Benton 2004; Sibley et al. 2005,2007) , the initial population size ($N_t$=100) and the population size at the first count ($N_{t+1}$), $r_0$ can be estimated (fig 6.3a). Standard statistical tests revealed no significant differences in $r_0$ between treatments (Anova $F_{3,12}$=2.59, $p$=0.10) possibly due to the low power of the small number of replicates and the uncertainty regarding the real distribution in values. A bootstrap of the data demonstrated a significant difference between $r_0$ in the Low dispersal treatment and all other treatments (fig 6.3a, table1). This suggests dispersal may reduce $r_0$ as individuals emigrate reducing the possible contributions to fecundity. One of the $r_0$ estimates is much smaller for the controls, and the bootstrapped estimates (mean & 95% CI) are very sensitive to this point. Removing it from the bootstrap produces a significant difference between the controls and all other treatments (fig 6.3a, table1). Any conclusions drawn from removal of this point are tentative because, although not of similar magnitude, each treatment group has a point with high leverage.

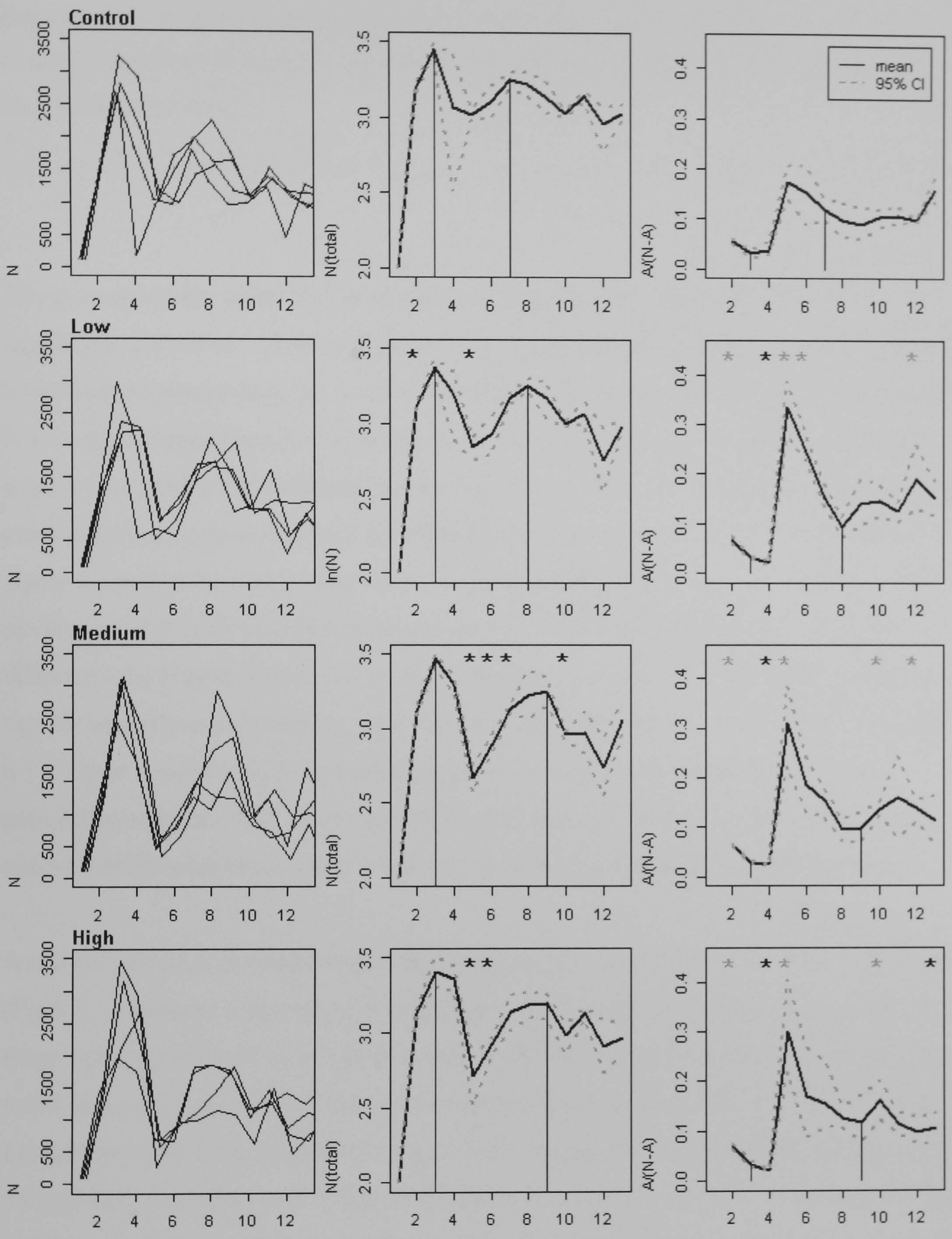

Figure 6.2: In columns from left to right, raw time series for each treatment, bootstrapped time series for total population size (N) and age structure (proportions of Adults:(Juveniles+Eggs)). Bootstraps made from 1000 resampled time series with mean (black lines) and 95% confidence intervals (grey, dashed lines) shown. Stars (*) indicate significant differences between bootstrapped values of dispersal treatments ("Low", "Medium", "High") and the control, with

grey stars indicating the treatment has a significantly larger value and black stars indicating the Control is significantly larger. Vertical lines indicate the timing of the first and second peaks of the transient dynamics.

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The average timing of the first peak was at count 3 in all treatments (fig 6.4). A significant difference in total population size was detectable for the dispersal treatment at count two, accompanying the lower $r_0$ exhibited previously (fig 6.3a, previous section). Following the peak there is a population decline (fig 6.2 second column), where the populations exhibit the minimum values of $r$ ($r_{min}$) during the time series. The Bootstrap estimates of $r_{min}$ reveal there are no differences between values (fig 6.3b, table 6.1). Again a single point had a large effect on the bootstrapped mean of the Control. This point coincided with an observation that drying had occurred in the tube, this was a different tube than that removed when estimating $r_0$. Removal of this point produced significant differences between all dispersal treatments and the Control (fig 6.3b, table 6.1). These significantly larger rates of decline coincide with significantly lower population sizes at count 5 between the Control and all dispersal treatments (fig 6.2), noting that the population sizes where not significantly different at peak numbers.

A second period of population growth occurs as the second cohort becomes established (fig 6.2), leading to a second peak in population numbers. The point of the maximum mean numbers attained in this peak is later with increasing emigration. In controls this point occurs at Count 7. In dispersal treatments peaks occur at Counts 8, 9 & 9 for the Low, Medium & High treatments respectively, suggesting dispersal reduces the speed of the population to recover (e.g. time between peaks: Control, 4; Low, 5; Medium, 6; High, 6). This may be accounted for by the lower total population sizes occurring in the trough at count 5 (and in the count following the trough in the Medium and High dispersal treatments) (fig 6.2). The differences in time between peaks signal asynchrony in the dynamics between treatments. Thus, the significant differences in population size following the trough found between Control and Medium dispersal treatments should be interpreted with some caution as it may be due to a lag between events, but the size of decline appears to be larger after the second peak.

### *6.3.3 Effects on age structure*

Changes in absolute population number are accompanied by changes in age structure as illustrated in fig 6.2. Following the first peak in population numbers. Count 4. all treatments have significantly fewer Juveniles and Eggs per adult than the control (fig 6.2, third column). In the following count, the dispersal treatments have significantly higher proportion of Juveniles and Eggs per adult. In two of the treatments, Low & High dispersal, there is a significantly lower proportion in the following count that is the trough. This can be turned around to the proportion of adults to Juveniles and Eggs to better illustrate differences when immature individuals are at low densities (fig 6.2). For the same population number, dispersal treatments have significantly more adults in the trough. This indicates that there are fewer individuals that will potentially mature and enter the second cohort that will drive the second peak in the dynamics. For example if there are fewer pre-maturity individuals coming through into the second cohort then population growth may lag behind in these dispersal treatments compared to the control.

### *6.3.4 Sex ratio and effective population size*

Throughout the entire time series, treatments have either equivalent or significantly higher proportion of females relative to the control (fig 6.4). Higher female proportions, are found at a total of 1, 3 & 5 of the eight counts during the time series for Low, Medium and High dispersal treatments respectively (fig 6.4). Taking the assumption that the time series is representative of equilibrium population structure I analyse whether these effects represent a general trend.

The degree of bias towards female number is affected by treatment and with an increasing trend towards more females over time, whilst the absolute number of adults remains in the statistical model indicating an expected relationship with density (table

6.2). There are some differences between the number of adults over this period due to Treatment and Count (glm, quasi-binomial, model factors: Treat, $F_{3,124}=22.99$, $p=<0.0001$; Count, $F_{1,123}=461.45$, $p=<0.0001$; Treat:Count, $F_{3,120}=3.0205$, $p=0.03$). Thus I compare effective population sizes as a proportion of the whole Adult population, $N_e/N$ (fig 6.6) (the fraction of the census population that is "effective", see Crow 1954, Hedrick, 2005). The differences in female bias translate to changes in $N_e/N$, though the models differ in structure depending on whether the $N_e/N$ is calculated for a "standard" allele or one which is x-linked (see "*Statistical analysis*")(table 6.3). In both cases all treatments have lower effective population sizes than the control, the two strongest emigration treatments (Medium & High) having lower $N_e/N$ than the other two but not each other (fig 6.6) (table 6.3).

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Table 6.1: Bootstrap estimates of (a) maximum growth rate,$r_0$, and (b) minimum growth rate, $r_{min}$, calculated by $\ln(N_{t+1}/N_t)$ as shown in fig 6.2. Estimated means of the dispersal treatment that significantly differ from that of the control are shown in **bold**. The second estimates are made with the lowest values removed from the treatment data, see text for details.

| | | Control | Dispersal | | |
|---|---|---|---|---|---|
| | | | Low | Medium | High |
| $r_0$ | Mean | 2.70 | **2.55** | 2.56 | 2.60 |
| | 95% CI | 2.60 ↔ 2.79 | 2.52 ↔ 2.59 | 2.50 ↔ 2.62 | 2.51 ↔ 2.66 |
| $r_0$ (point removed) | Mean | 2.75 | **2.55** | **2.56** | **2.59** |
| | 95% CI | 2.69 ↔ 2.79 | 2.52 ↔ 2.58 | 2.49 ↔ 2.63 | 2.51 ↔ 2.66 |
| $r_{min}$ | Mean | -1.35 | -1.63 | -1.86 | 1.82 |
| | 95% CI | -2.29 ↔ -0.75 | -2.00 ↔ -1.22 | -2.24 ↔ -1.47 | -2.37 ↔ -1.26 |
| $r_{min}$ (point removed) | Mean | -0.90 | **-1.62** | **-1.86** | **-1.81** |
| | 95% CI | -1.05 ↔ -0.68 | -2.00 ↔ -1.21 | -2.24 ↔ -1.46 | -2.39 ↔ -1.26 |

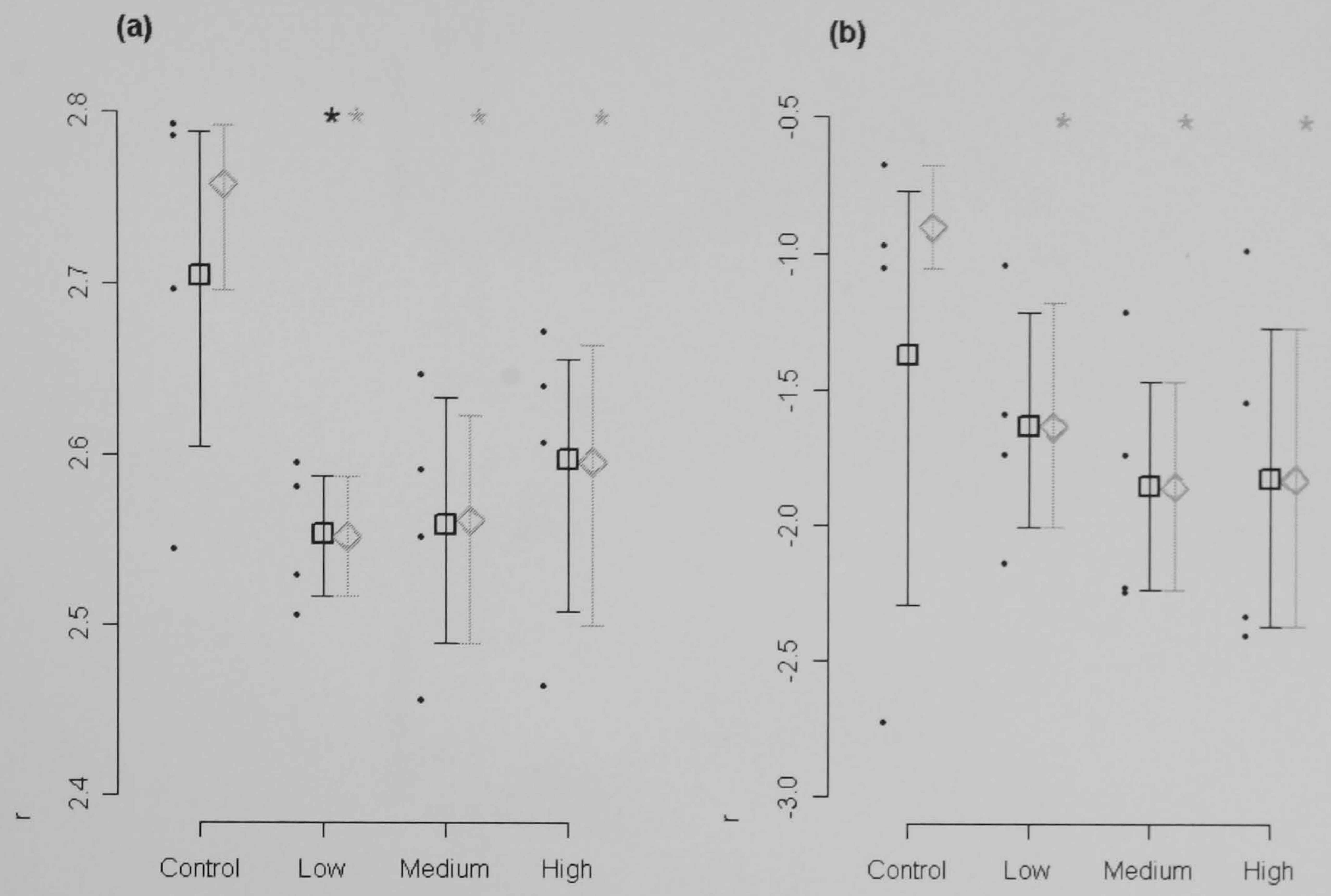

Figure 6.3: Estimates of (a) maximum growth rate,$r_0$, and (b) minimum growth rate calculated by $\ln(N_{t+1}/N_t)$. Raw data (black dots) and the mean (±95% CI) of bootstraps for all data (black) and without the lowest data points in the "none" treatment (grey) are shown. These data points are from different replicates in (a) & (b). Stars demonstrate significant differences between the bootstrapped distributions of the "none" treatment and any other treatment under the two assumptions.

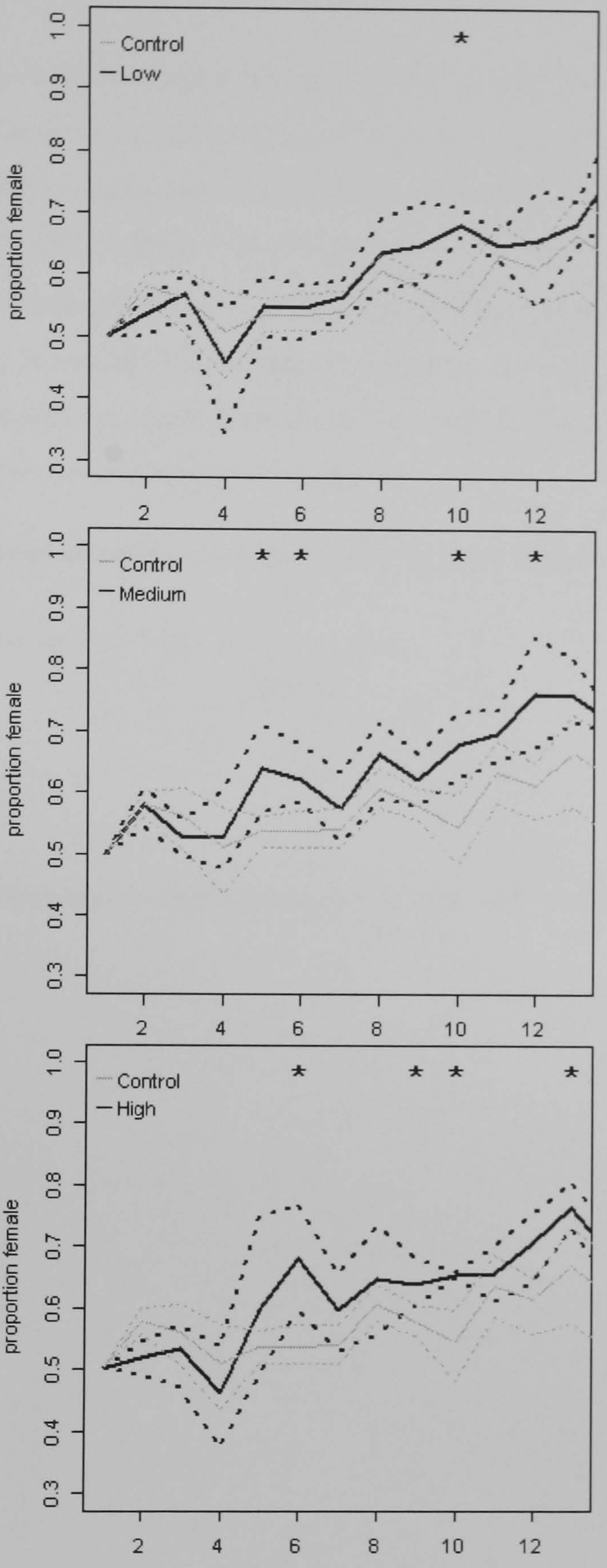

Figure 6.4: Change in sex ratio over time, given by the proportion of Adults that are Female. Bootstrapped time series for "Low", "Medium", "High" treatments (black lines) are compared with the "None" treatment (no dispersal, grey lines). Mean values appear as solid lines and 95% confidence limits as dashed lines (resampled 1000 times). Stars (*) indicate significant differences between bootstrapped values of emigration treatments ("Low", "Medium", "High") and the control.

Table 6.2: Statistical analysis of the female proportion data for the cropped time series in a glm (~Treat + Adult + Count, family = quasibinomial). Exclusion of interaction terms did not significantly affect the model's explanation of the variation (model comparison with all interactions F=1.2515, p=0.2667, with all 2 way interactions F=1.10123, p=0.4263, all other variant models had insignificant effects on explanatory power). Mixed effects models including tube identity, and/or count, as random effects did not perform significantly better than a linear model. The glm shows qualitatively similar effects of the variables but provides a better fit to the data due to the considerable over-dispersion in the data.

| Factor | d.f. | F | P |
|---|---|---|---|
| Treat | 3,124 | 8.6053 | <0.0001 |
| $N_{\text{Adults}}$ | 1,123 | 42.7536 | <0.0001 |
| Count | 1,122 | 24.3104 | <0.0001 |

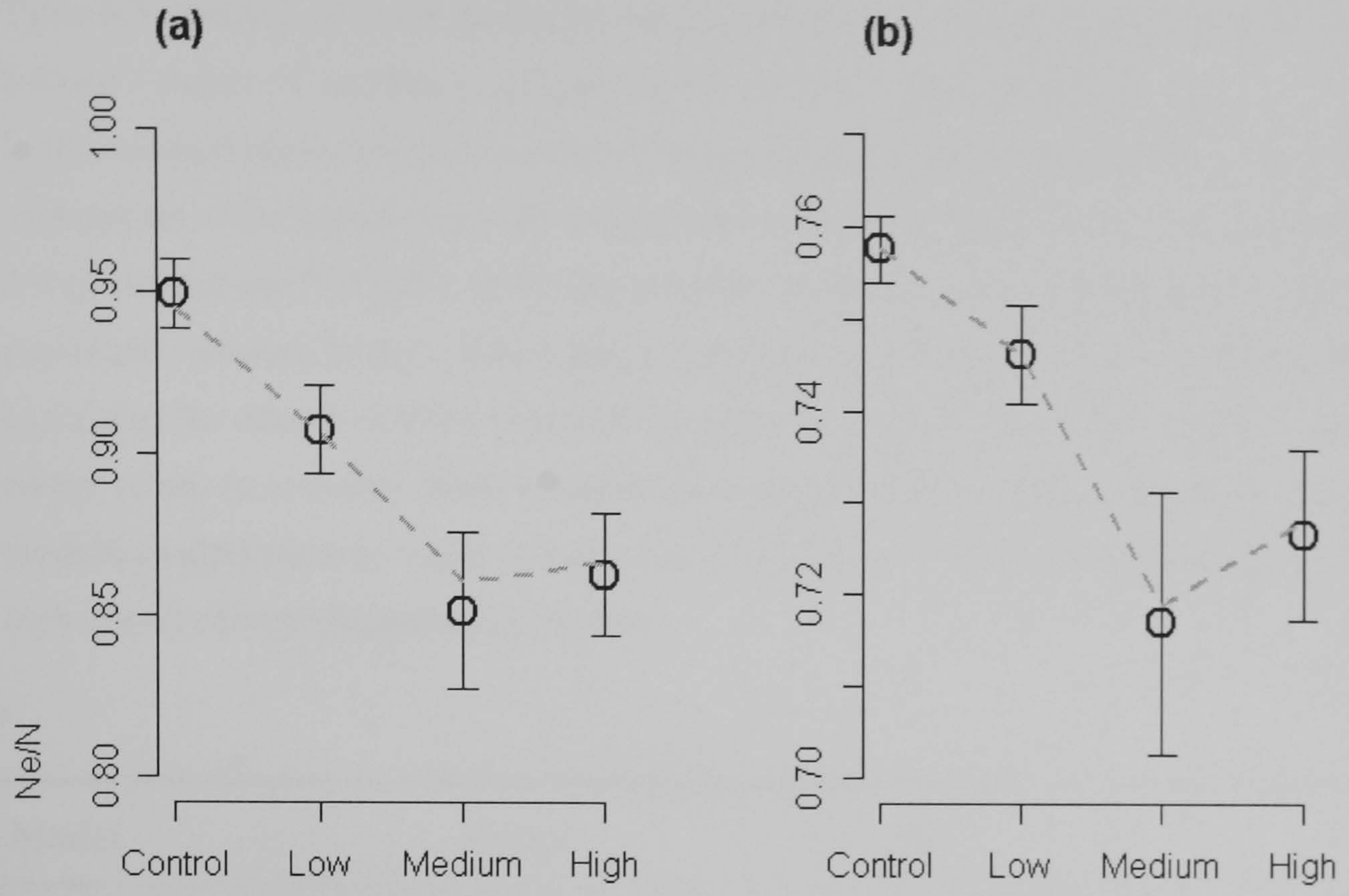

Figure 6.6: Effective population sizes for each experimental treatment accounting for sex bias (*a*) and for an X linked allele (*b*). Means presented with error bars of ± 1se. Lines indicate model predicted values from generalised linear models fitted with quasi-binomial errors to the data and accounting for Treatment, Count and Adult population size. The models in each figure differ in structure, see text and table 6.3 for details. Data are taken from counts 6-13 inclusive (post transient, pre drying).

Table 6.3: Analysis of N*e*/N during the cropped time series using a glm for a standard allele (~Treat + Adult + Count) and an xlinked allele (~Treat * Adult * Count).
In the standard allele model exclusion of interaction terms did not significantly affect the model's explanation of the variation (model comparison with all interactions F=1.4407, p=0.1717, with all 2 way interactions F=1.4362, p=0.1976, all other variant models had insignificant effects on explanatory power). In the x-linked allele model the interaction term has a significant effect on explaining the data (F=3.4555, p=0.01892). Again mixed effects models including tube identity, and/or count, as a random failed to explain the relationships to a greater degree than linear models, so glms (family = quasibinomial) and subsequent F tests where used to cope with the high degree of over-dispersion in the data.

| Model | Factor | d.f. | F | P |
|---|---|---|---|---|
| Standard Allele (negl) | Treat | 3,124 | 7.2574 | 0.0002 |
| | $N_{\text{Adults}}$ | 1,123 | 37.8858 | <0.0001 |
| | Count | 1,122 | 21.1907 | <0.0001 |
| X linked (neglink) | Treat | 3,124 | 3.7977 | 0.0123 |
| | $N_{\text{Adults}}$ | 1,123 | 23.8586 | <0.0001 |
| | Count | 1,122 | 10.8497 | 0.0013 |
| | Treat: $N_{\text{Adults}}$ | 3,119 | 5.6003 | 0.0013 |
| | Treat:Count | 3,116 | 1.7098 | 0.1691 |
| | $N_{\text{Adults}}$ :Count | 1,115 | 13.7271 | 0.0003 |
| | Treat: $N_{\text{Adults}}$ :Count | 3,112 | 3.4555 | 0.0189 |

## 6.4 Discussion

Emigration is not equivalent to death. Even if per capita rates of emigration and death were exactly the same, differences in response between age and sex classes can manipulate population structure and so population dynamics. I have demonstrated that non-random emigration can affect ecological and evolutionary dynamics in ways that a standard density dependent function could not predict. This is due to differences in emigration responses between age and sex classes, producing three main effects: (1) lowering the minimum population growth rate but with no change in the maximum, (2) amplifying lags in the population dynamics through the change in minimum population growth rate and alterations to age structure and (3) reduction in effective population size $N_e$ as emigration was also sex biased.

### *6.4.1 Population growth rate*

There were no differences in maximum population growth rates achieved, but significantly lower minimum population growth rates were found. This suggests that population processes such as density dependence may compensate for emigration during periods of growth where densities are increasing. However, in the following period of decline emigration produces a significantly lower population growth rate. This can be explained as follows. At the peak of population numbers, numbers emigrating would be expected to be highest (Bowler unpublished). In the absence of emigration a trough follows the peak in population numbers because the first cohort produced by the initial population of 100 adults dies off (Benton et al. 2005). Emigration at high densities may combine with the cohort effect to further reduce population numbers during periods of decline. This explanation suggests more individuals emigrate at high density than would have died during the period entering the trough in the absence of emigration. This fact alone could suggest populations with high levels of emigration have higher extinction risk during transient dynamics following colonisation, introduction or invasion. However the combined effect of emigration and the cohort effect produce the low population growth rate, not just emigration. Emigration has been shown to strengthen Allee effects in butterflies (Kuussaari et al. 1998; also see "Population Sieves", e.g. Cronin 2007), which could depreciate growth rates. This effect was not observed as evidence suggests that emigration rates are positively density dependent. However future research could valuably investigate the nature of density dependent emigration between ages and sexes.

### *6.4.2 Changes in age structure*

Lower population growth rates when entering a 'trough' are accompanied by a change in the age structure of the population and a subsequent lag in population growth. Population growth may not be entirely compensating as the contribution of dispersers to the population growth is lost (Lidicker 1962; McMahon & Tash 1988). The effect of emigration on population growth rate will depend on which individuals emigrate and their reproductive value. If juveniles are the only stage to disperse then direct effects of emigration may be reduced, as is the case where juveniles are removed from a population via harvesting (Cameron & Benton 2004) or predation. Population growth rates would, in general, be expected to be highly sensitive to the number of mature individuals. Here, biases in emigration propensity between age classes increased the proportion of mature individuals during the trough. This may have consequences for individuals' life history decisions, which I discuss later.

Previous work has shown the propensity of the mites to emigrate increases with age, with young adults having the high emigration propensity, but emigration declines with age (Bowler unpublished). The effect on sex bias can be dependent on the level of food present during rearing. Low levels of food produce no differences between emigration and rates of each sex, whilst with high food levels male emigration increases and female emigration decreases producing the sex bias (Bowler unpublished). In contrast however, food availability may have the opposite effect in juveniles (Bowler unpublished). During the time series per capita food levels change as an inverse function of population number. This could result in temporal differences in the emigration of any age and sex class and so age structure during any time period. Age structure is numerically dominated by juveniles at many times during the time series presented here. There is always >1 juvenile per adult after initiation of the experimental populations and juveniles can exhibit densities more than 15 times greater than adults. Interpreting the results presented here must be treated with a little caution as numbers of individuals emigrating and their class was not measured. However, the combined consequence of emigration and cohort effects are clearly shown between treatments.

The biology underlying the mite dynamics is complicated. Description of the changing environmental context produced by changes in Adult, Juvenile and Egg density has been well explained elsewhere (see Benton & Beckerman 2005, Benton et al. 2005). Fluctuations are not solely due to changes in age structure and density, but also changes in resource allocation across life history traits. The declining population growth rate was accompanied by reduced relative numbers of immature to mature individuals. This change in age structure may not have an immediate consequence for population dynamics, instead generating a lag in population growth after the trough. If fewer immature individuals mature as the present adult cohort dies off, population growth could be slowed leading to an extension of the lag that is present in the absence of emigration (e.g. bootstrapped times series in fig 6.2). Any individual's response to reduced competition may not be immediate, producing a delay.

This interpretation is supported by previous observations of the mite dynamics (Benton et al. 2005) where the density of pre maturity individuals alters juvenile growth rates and the age at which individuals mature. Age structure may affect juvenile growth rates as inequalities in food consumption and competitive ability between age classes mean per capita food intake is dependent on both population size and age structure (Benton & Beckerman 2005). Food may be monopolised by adults at high densities as they are able to exclude juveniles, and so out-compete juvenile mites at high densities. Lowering per capita food rates of juveniles may cause slow growth and recruitment into the adult stage (Benton & Beckerman 2005). Additional effects may be seen in levels of egg provisioning by mothers (Plaistow et al. 2007). In the experiments presented here, the emigration treatments shifted more towards an adult biased population during the peak of the transient than the control. Such an adult bias could result in low recruitment, as outlined above, and provide a complementary mechanism to understanding the increasingly lagged events generated by emigration.

### *6.4.3 Dispersal and effective population size*

Sex biased dispersal resulted in reduced effective population size. The ultimate causes of male biased dispersal in our populations is unknown but is proximately due to the high mobility of the apparently promiscuous male sex and low mobility of female "egg factories". The reasons suggested for sex biases in dispersal are varied including inbreeding avoidance and asymmetries in resource competition between sexes that determine costs and benefits of dispersal (Lambin et al. 2001).

Wolff (1994) suggested sex biased dispersal may have evolved as a response reducing inbreeding; as *"if one sex disperses, the other does not need to"* (Perrin & Goudet 2001). Inbreeding may be reduced by emigration of a single sex and selection towards which sex disperses more may be sensitive to differences in how successful each sex would be as an immigrant (Perrin & Goudet 2001). Thus differences in resource acquisition within a site may determine the dispersing sex (Perrin & Goudet 2001). Such a difference could also explain why juveniles emigrate. Differences in the costs of dispersal may, however, not be equivalent. Mites exhibit considerable differences in body size between sexes (Benton & Beckerman 2005), suggesting different costs of immigration and emigration could exist. In the mites, like many mammals, there is also a large difference between female and male mites' investment in young, with promiscuous males directly investing only in sperm and being more mobile, possibly to secure matings.

I give a very simple example of the consequences of reducing effective population size. Heterozygosity declines at a rate inversely proportional to the effective population size (Crow & Kimura 1970) with the time until loss of half the original heterozygosity given as roughly $1.39N$ (Hedrick 2005). We can compare the effect of emigration between the "Control" and "Medium" emigration treatments on the half-life of heterozygosity using the mean proportional effective population size ($Ne/N$: Control= 0.950, Medium=0.851).

Then for a population size of $\check{N}$, the increase in half-life of heterozygosity will be 0.136 $\check{N}$, equating to a decrease in half life of 10% when individuals can emigrate. I have used the simplest estimates for effective population size that do not take into account complexity in the demography such as age structure and stage specific survival. As the details of demography have an effect on the estimates made (for instance, differences in survival between the sexes and generation time caused by emigration (Nunney 1993)) I restrict analysis to simple estimates rather than increase complexity without appropriate data.

### *6.4.4 Emigration and contemporary conservation*

Progressing theory and its integration into biodiversity management relies on knowing when and where processes have relevant effects (see Benton et al. 2006). A tool that may be fundamental to predicting populations' futures before they happen is exploration of the effects of environmental change in microcosms and models (Lawton 1994; Benton et al. 2007). Testing some general caricatured features and management scenarios allows more detailed understanding of relevant biological mechanisms to be developed before field study. In a changing world it is important to understand how intraspecific differences drive future dynamics. A fundamental role of research is assessing the potential for evolutionary effects to arise from demographic change and vice versa (Lande 1988; Hairston et al. 2005).

Emigration has received less attention than other processes due to the factors presented in the introduction and additionally because of the great focus on small populations where $I>E$. However, in an increasingly fragmented landscape any population may tend to receive decreasing immigrants shifting the balance towards $E>I$. In many cases populations may become completely isolated (Opdam & Wascher 2004). Dispersal can be viewed as a 3-step process (Clobert et al. 2001) composed of emigration, inter-patch movement and immigration. Each stage is dependent on the first but not successive stages, i.e. inter patch movement is dependent on emigration but not immigration. Understanding the effects of changing environments on emigration and population dynamics of source patches may be fundamental to each other process (Carmel & Flather 2006), especially where immigrants are deemed to be necessary for species survival (e.g. climate change, Parmesan et al. 1999). The results demonstrate the importance of understanding the effects of emigration in demography and evolution. Simple changes in landscape structure may alter the amount of emigration and the type of individuals emigrating, altering population structure in different ways to processes determining birth and death. Individuals emigrating are not randomly selected from a population's structure and biases in the population structure that would not have been predicted without understanding and acknowledging individual differences. Considerable interactions between all these processes undoubtedly exist, as all processes (BIDE) may be dependent on density and structure of populations.

Landscape characteristics can play a large role in determining emigration rates (see Bowler & Benton 2005 for a review). Patch shape (e.g. edge to area ratio) can affect the rates at which individuals experience emigration decisions (Bowler & Benton 2005) or the absolute number of emigration events (Kawecki & Stearns 1993). Where individuals can determine costs of dispersal the characteristics of areas surrounding a patch may affect the decision to emigrate. Inhospitable and hospitable matrix surrounding a patch may deter or encourage the emigration respectively (Wiens 2001). Understanding the landscape context of dispersal on population dynamics may be highly relevant when interpreting model predictions and furthering theoretical research. Global environmental change is likely to alter environments in complicated ways, changing not only patch characteristics (e.g. shape, Fahrig 1997), but also the relative differences in quality between patches and the matrix of the landscape (Opdam & wascher 2004). Again, there may be differences in the perception of emigration costs between sexes, ages, genotypes and phenotypes, and how resistant any given individual is to those costs. The most obvious differences occur when facultative or genetic hetero-morphs exist and these dispersal types are more resistant to the rigours of dispersal, e.g. through specialised body structures (e.g. macropterers) or increased provisioning (Zera & Denno 1997).

I have shown here that landscape differences can provide the stimulus for an inbreeding effect. Landscapes allowing more emigration produce populations with increased inbreeding, due to sex biases in dispersal reducing effective population size. Immigration from other patches is necessary to confer any out-breeding benefit of dispersal, so the consequence of emigration may be negative for isolated populations. Extinction risk may be related to genetic diversity due to inbreeding (Newman & Pilson 1997; Saccheri et al. 1998) and through provision of potential for adaptation to changing environments (Kingsolver & Frankham 2004) (also see Hughes et al. 2008). Understanding and managing landscape effects on emigration should be considered in tandem with the effects of immigration. Inter-deme exchange of individuals may become restricted by fragmentation (Fahrig 1997), reducing the prospects of genetic rescue. However, emigration rates need not be affected. High emigration rates reduce effective population size and given mutation rates are not affected, there is likely to be less new alleles entering high emigration populations. Positive correlations between populations' future evolutionary potential (e.g. potential for adaptation to conditions that drive fragmentation) and effective population size have been found in *Drospohila* (see Kingsolver & Frankham 2004).

Theory investigating evolution in heterogeneous and changing environments does not often acknowledge the effects of individual differences or population structure that is any more complicated than hermaphroditic-annual species (Kawecki 2004; Holt & Gomulkiewicz 2004). Dispersal plays a huge role in determining the strength of selection (Lenormand 2002) and sex biased dispersal may provide further links with evolutionary dynamics. In source-sink systems the flow of dispersers down abundance gradients could alter the sex bias in each patch in opposite directions (e.g. Fraser et al. 2004). A flow of males from source to sink, where dispersal is male biased, may reduce effective population size in the source and sink for different reasons. The source population may then become female biased and a male bias may be generated in the sink. X linked or Y linked alleles may then experience opposite effects in each population, altering the context within which X-linked or Y linked traits evolve. Such differential effects on evolution of female or male linked alleles may be further expounded as the selective background and the costs or benefits of traits may be interpreted differently in either sex (Hedrick 2007). Hedrick (2007) provides numerous examples of differences between sexes in evolutionary relevant traits; such as mutation rate (mutation rates are often higher in males due to the number of cell divisions) and differences in the magnitude of pleiotropic interactions due to selection specific to each sex. Such "sexual antagonism" can act to maintain genetic variance by generating asymmetries in fitness between homozygous and heterozygous individuals (Livingstone 1992; Mackay & Fry 1996). In summary, there is a schematic for complicated compound affects of emigration that feedback into demographic dynamics.

# 7. New Concepts for new circumstances

## 7.1 A change in research

"*Climate change is not a new topic in biology*" (Parmesan 2006). But its contemporary context is new. The world has changed since previous climate change events, predominantly due to human action on the ecosystems and the environments they inhabit (Opdam & Washcer 2004). Studies of contemporary climate change responses will have to at least acknowledge the possibility of modern confounding factors (e.g. habitat loss, habitat fragmentation, habitat deterioration and exploitation (Sutherland 1998)), and future change in the extensity and intensity of those factors.

Considerable differences also exist in the research approaches taken in contemporary study. As changes occur in real time, we are not limited to the fragments of information left in remnant biological matter such as fossils or pollen, and clues of past environments, such as atmospheric and geological deposits. A key facet is our ability to gather data and develop theory as changes occur in real time. It is essential to have an understanding of which processes and mechanisms are important during climate change. Andrewartha & Birch (1984) well summarise the importance of this last point: "*To search for the best concept is no idle conceit, because the experiments that a scientist may devise and therefore the facts he may discover, as well as the explanations that he offers for them, depend on how he conceives nature.*"

However, observation in real time also poses a problem. If climate change is the World's largest ever experiment we need hypotheses that are appropriate to the treatment and cannot rely on gathering information purely by observation. Our experimental material is expected to be reduced during the climate change experiment (Thomas et al. 2004). To address this problem, insights from model and microcosm are needed to accelerate the relative rate at which we can assess the importance of different factors to climate change (e.g. Hutchinson 1957; Schmitz 2001; Benton et al. 2007). The rapidity and magnitude of climate change threatens to overtake our knowledge base before appropriate management measures are taken. Our science may be presently perceived as being poorly equipped. Even if data and theory was available to develop a perfect understanding of dynamics in a 'static' climate, there are nuances specific to climate change scenarios that require investigation. In a more positive light, real time observation of a climate change event could direct research into the fundamental mechanisms underlying the genesis and maintenance of biodiversity.

## 7.2 Summary of research

The work presented here shows how the relative importance of differences between types (age, sex, phenotype or genotype) may alter during climate change and elevate the importance of spatial interactions. Climate change is an even more explicitly spatial scenario than dynamics in a 'static' climate. As such, 'types' may be defined by simple differences in spatial positioning or environmental context, even in the absence of absolute differences between individuals' phenotypes or genotypes. Research contained in this thesis demonstrates not only the importance of this spatial structure, but the interactive effects between landscapes and that structure. The research illustrates how climate change could accentuate the importance of populations' spatial structure in determining ecological and evolutionary dynamics, due to the feedback between the spatial structure and the processes underlying its generation.

**Chapter 3** demonstrated the effects of landscape pattern might differ considerably between static and changing climates. The strength of these differences is dependent on species-specific traits such as dispersal ability, but also traits underlying population dynamic parameters. Here, landscape pattern defines the structure of populations and their viability. During climate change, either a larger amount of absolute habitat is needed to maintain a similar extinction threshold, or the habitat should be more widely distributed throughout the landscape to maintain viable routes for range shifts. This suggests that given less potential area of the habitat we may only reliably conserve those species with higher dispersal abilities. This immediately imposes some considerable selection on what future communities will exist. An important component of the dynamics was a reduction in populations' occupancy during a range shift, under much of parameter space. Reducing populations' distribution may generate further disequilibrium with environmental conditions other than climate where populations are forced through a proportion of any potential range. For example, if heterogeneity in environmental conditions exists longitudinally, then the realised niche may become focused around conditions co-occurring with routes that facilitate latitudinal range shifts. Such an effect may likely affect evolutionary dynamics within a population's spatial structure.

The model presented in **chapter 4** illustrated the effect of different landscape geometries on the positioning of a population's niche. Niches may be sub optimal for at least some portion of a populations sub units, and so create structure in traits that are fundamental to describing populations' dynamics. Crucially, gene flow and environmental heterogeneity can cause selection away from absolute optimality. During directional change in the environment, different positioning of the realised niche within the fundamental niche may produce different dynamics: as would be the assumed, general case at northern and southern range limits. Thus the trajectories through niche space during environmental change may depend on the characteristics of the landscape. Overlaying the ecological differences in dynamics are differences in evolutionary opportunity that also depend on the landscape. As the rate of evolution lags behind the rate of climate change, as shown by alterations to the realised niche, the changing climate produces changes in spatial population dynamics. Patterns of gene flow are altered as the success of reproduction or survival is dependent on relationship of the prevailing climate, producing quantitative differences in the strength of selection between different landscapes. This model showed the manner in which populations experience novel conditions are not exclusively determined by the changing conditions, but also by populations' spatial structure and the processes that produce that structure. Spatial interactions can determine where responses are ecological or evolutionary, by altering the direction gene swamping and adaptive dynamics of the niche.

These themes were further developed in **chapter 5**. As previously shown, climate change responses depend on the positioning of the population within its niche. A simple classification is that opposing range limits will take different routes through the niche, cold limits becoming warmer (a long route) whilst warm limits become even warmer (a short route). The model showed how these forces may deform a population's spatial structure, altering the range of conditions inhabited and the population dynamics through the range. For instance, warm limits may experience conditions outside of the previous niche, where lags in the extinction response exist and populations occupy regions beyond the previous realised niche. The model also showed how *spatial selection* generated during range shifting can alter the degree to which we would consider different areas of a range sympatric. The combination of surfing effects and populations' spatial movement generates altered patterns of competition and gene flow: an effective separation of the edge leading the range shift from the rest of the population. This alteration in the spatial cohesion of a population (i.e. the degree of sympatry) may be expounded by selection for traits affecting the rate of expansion and access to newly suitable areas. Such spatial selection may cause further range deformation, which is by definition a change in the characteristics of environmental disequilibrium exhibited.

**Chapter 6** experimentally investigated the effect of changing populations' landscape context. Fragmentation of populations may not only alter the spatial structure underlying populations' viability, but also the internal structure of populations. Age and sex specific differences in dispersal alter the context of competition within populations, modulating the nature of population dynamic lags. Qualitative and quantitative differences are generated in population's dynamics as individuals lost through emigration differ in 'type' from those lost through death. The competitive context of the population is then altered, a change that would be expected to alter the reproductive decisions made by individuals. As emigration is sex biased in this system, the loss of males compounds the ecological effects by altering the effective population size. The reduced generation of variation may reduce fitness as well as reduce the potential genetic resources upon which selection may act. As fragmentation occurs, populations' structure becomes increasingly spatially separated and reductions in immigration may reduce ecological and genetic rescue effects. These reductions may occur despite the continuation of emigration, further reducing populations capacity to persist.

## 7.3 Understanding complex climate change responses: the Spatial Red Queen

The "*fingerprints*" of climate change have been found on the dynamics of contemporary populations (Chapter 1). Simplicity in the hypotheses necessary to empirically demonstrate that the fingerprints exist (e.g. Parmesan et al. 1999) belies the complexity that is expected in populations' responses. Some important aspects of this complexity have been shown earlier in this thesis. The majority of contemporary and retrospective analyses have investigated "move", "adapt" or "die" responses in isolation (see Chapter 1) (range shifts, Parmesan 1996; evolutionary changes, Bradshaw & Holzapfel 2001). Extinction may be the unavoidable result if neither movement nor adaptation occurs and population growth rates are sufficiently reduced (Lynch & Lande 1993). These are not alternative responses but simple classifications based on the research areas that primarily study the broad categories "*Move, Adapt or Die*." As I have shown in the previous chapters populations' responses may be composed of all three.

Few studies consider interactions between these factors shown (though see Thomas et al. 2001; Hughes et al. 2003). For example, some adaptation reduces the geographic movement a population would potentially need to undertake to avoid extinction. Similarly some geographic movement may reduce the amount of adaptive change necessary. This principle is clearly demonstrated in the absence of climate change, when ranges shifts are caused by evolution of novel traits (Lewontin & Birch 1966; Thomas et al. 2001; Holt 2003). Likewise, loss in fitness may be accompanied by a reduction in a population's range (Wilson et al. 2004). I suggest a framework on which to conceptualise this interplay, the "Spatial Red Queen".

In Lewis Carol's "*through the looking glass*", the Red Queen has to run as fast as she can to maintain her spatial position. If she stood still, she would surely be whisked away. The red queen has been widely used as an analogy for co-evolution between interacting species, from Van Valen's initial presentation of what is known as the Red Queen Hypothesis (Van Valen 1973). The hypothesis describes how populations evolve in response to interacting biotic partners to maintain a foothold in an interspecific interaction. For example better predation would select for better defence, and vice versa. The Red Queen suggests a co-evolutionary arms race may be internally highly dynamic, yet exhibit very little change on the outside; hence '*running to stand still*'. Van Valen (1973) used this analogy to explain the apparent constancy in extinction rates in the fossil record, where failure to keep pace would result in extinction and why extinction rates may be roughly constant within taxonomic groups. However the Red Queen analogy has spread far and wide. In essence the Red Queen describes how environmental changes may necessitate adaptation (Niche Evolution) (see Stenseth & Maynard Smith 1984). This is when "*it takes all the running you can do, to keep in the same place*" (Carroll 1871).

The Spatial Red Queen differs from the red queen as the 'running' may not only occur by direct adaptation to those conditions which change (e.g. Dynesius & Jansson 2000). Populations' can also keep up by 'running' through geographic space. We can visualise the Spatial Red Queen as three axes (fig 7.1a). The first axis represents geographic changes in a populations range, the second the degree of change in populations' traits and the third, the fitness penalties of not moving or adapting (running to extinction). An analogy of "*running to stand still*" in relation to climate change was made by Jump & Penualas (2001). They highlighted the fact that many plant species will not disperse at rates equivalent to climate change, making evolutionary change unavoidable if climates shifted by sufficient magnitude (7.1b).

The Spatial Red Queen schematic is simple. It betrays the realties of multidimensional complexity of real world responses onto a humane three axes. For instance collapsing 'trait' change onto a single axis underemphasizes differences between plastic and evolutionary responses. Furthermore temporal variability could be incorporated into the spatial variability represented by geographic space. For instance, phenological changes may mitigate against a range shifting response (Bradshaw et al. 2004) and we could replace the Geographic for an Environmental axis. However, the Spatial Red Queen summarises the interplay between responses that can occur, providing a useful conceptual tool for understanding climate change responses.

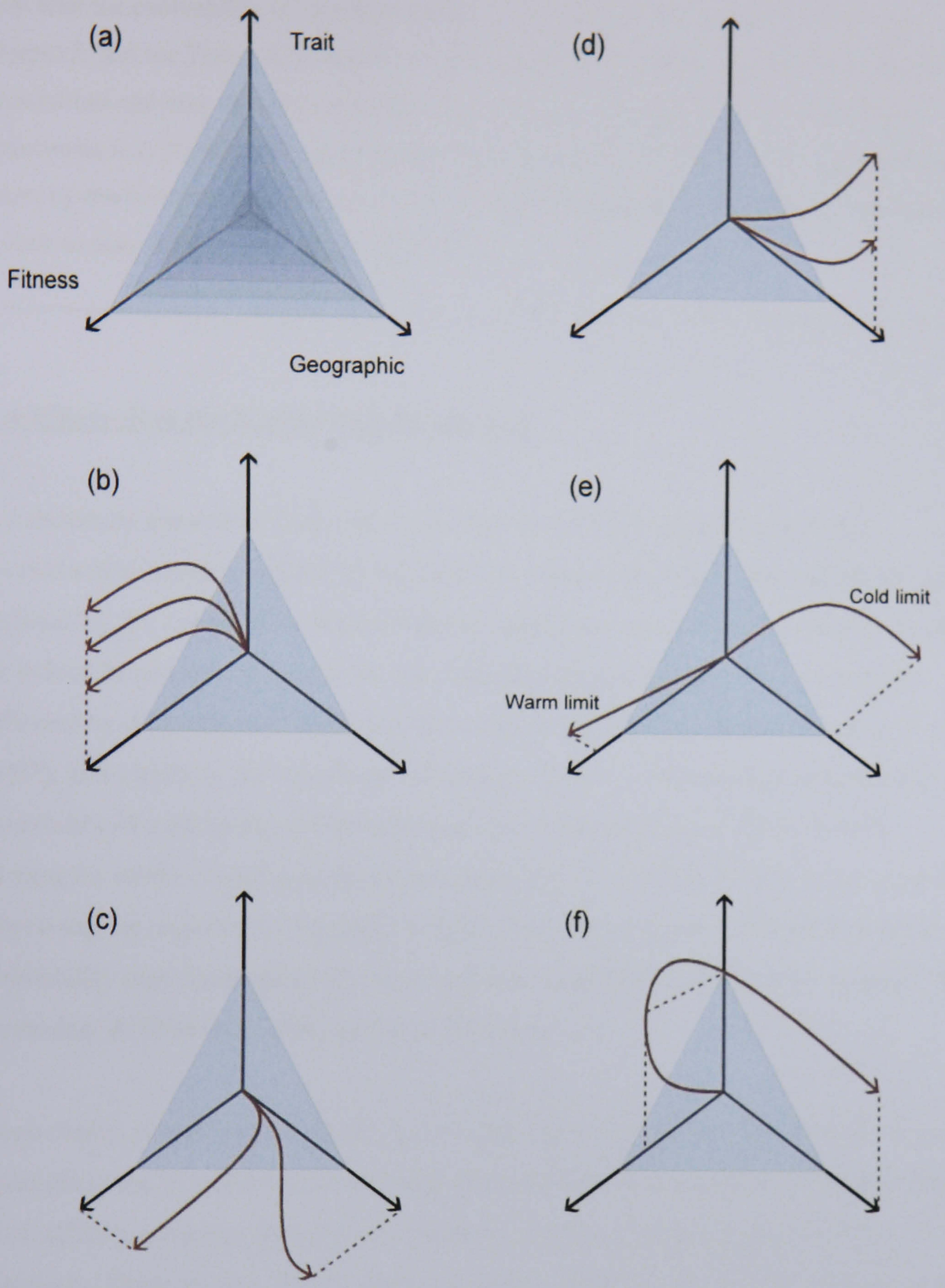

Figure 7.1: The “Spatial **Red** Queen”, a visualisation of the relationships between *Move, adapt, die* schematic. Populations’ responses to climate change can be defined within three axes, ‘Geographic Space’, ‘Trait Space’ and ‘Fitness Space’ (a), demonstrating the compensation possible by ‘running’ through different spaces (see text for details). Limitations to absolute evolvability will create an asymptote in the relationship between Fitness and Trait axes (e.g. Chapter 4, genetic variation, or pleiotropy) (b). Likewise limitations to dispersal (e.g. Chapter 3) may create an asymptote in the relationship between Geographic and Fitness axes (c). Here, reduced occupancy (~fitness) may be produced. The process of range shifting

may alter the evolvability of the population (d), for example by mutation surfing (e.g. Chapter5, and see Travis & Burton *in press*). These trajectories are not equivalent for entire populations and may vary through space (e), such as at opposing range limits different trajectories may be followed (see text). In (f), a hypothetical visualisation of the trajectory taken by the butterfly *Aricia agestis* is shown with the geographic shift only occurring after a switch in plant host (see Thomas et al. 2004).

## 7.4 Where does the Spatial Red Queen run?

As shown by the role of landscape geometry in determining ecological and evolutionary responses (Chapter 4), different trajectories may exist through the space defined by the Spatial Red Queen. Some populations may simply be more evolvable or indeed have more plastic traits. Movement along the geographic axis may be affected by differences in landscape (Collingham & Huntley 2000; McInerny et al. 2007), and similarly the 'topology' of annual climatic variation may determine the possibility of a phenological shift through environmental space (Bradshaw & Holzapfel 2006). Understanding these constraints of running via any axis is central to observing the trajectories populations take. For instance genetic variation and habitat availability may limit adaptive and geographic responses (Wright 1931; Gaston 2003; Svenning & Skov 2004; Hughes et al. 2008)(fig 7.1c).

Importantly, a response in one axis may affect the relationship with another. A good example is the increased fecundity and dispersal rates at range limits found by Hughes et al. (2003), a change that could increase the ability to move geographically. Similarly, Thomas et al. (2001) showed that geographical shift might only occur after evolution in some trait(s) (also see Hill et al. 2004) (fig 7.1d). This evidence underlines the concept set out by Holt & Gomulkiewicz (2004) where conservation problems are due to the inability of populations to adapt (or indeed move) to new conditions. Jump & Penualas (2001) highlight a suite of factors that may affect populations' ability to evolve to new climatic conditions, broadly summarised under the banners of genetic variation, gene flow and pleiotropy (also see Etterson & Shaw 2001), each of which may have different interactions with movement along the other axes. Genetic diversity may be closely tied to ecological processes at a variety of scales (Hughes et al. 2008). Lags and feedbacks can create further non-linearity in populations' responses as a geographic shift may depend on change in a trait. Evolution may operate at varying time scales relative to the rate of climate change, given populations' biology and dynamics. This creates trajectories of differing gradients between the axes of the Spatial Red Queen, with limitations in absolute evolvability producing an asymptote in this relationship.

At opposing range limits there are opposing forces acting on a population that will produce different trajectories through the Spatial Red Queen. At "warm" boundaries populations decline in fitness and have reducing opportunity to move, whilst at "cold" boundaries, increasing fitness and increasing suitability of unoccupied habitat occur (fig 7.1e). These divergent forces could be broadly separated as producing hard and soft selection at opposing range limits respectively, possibly altering which traits selection may act upon. Adaptation at cold range limits may be associated with traits involved in range shifting, such as dispersal and fecundity (Hughes et al. 2003; Simmons & Thomas 2004). At warm limits, adaptation may be associated with traits related to survival and reduced dispersal (Dynesius & Jansson 2000).

These simple examples suggest populations may become increasingly deformed, a sign that different environmental disequilibria are manifested and populations experience different selection pressures (fig 7.1f). Populations' range limits may be coarsely defined as warm or cold (Hampe 2004). However, underlying these proximate descriptions (Chapter 1), there are a number of competing ultimate reasons as to why those range limits are enforced (Antonovics 1976; Hoffman & Blows 1994; Gaston 2003; Bridle & Vines 2007). In the case of range limits enforced by gene flow (Kirkpatrick & Barton 1997; Bridle & Vines 2007), alterations to the relative fitness of interacting populations sub units may affect the evolvability of populations. Different areas of the range may have different ultimate causations, causations that may change with the changing climate.

## 7.5 Away from the 'mean field' is a new topic in biology

Whilst climate change is not a new topic, there are new topics that have been highlighted here and require further exploration. Populations take on a more dynamic context in a more dynamic environment. Alterations to the relationship between environment and population are generated. To maintain the previous 'equilibrium' with the climate populations would need traits that mimic 'mean field' predictions (perfect dispersal) (e.g. Beijernick's Law, see Sauer 1988) – everything would need to be everywhere and the environment would then select. However, populations occur within discrete ranges and have limited dispersal capacities making spatial structure and distance fundamental to the realisation of populations' dynamics and evolution (Hanski 1998). Away from mean field assumptions is a world of differences (Benton et al. 2006). Different species, ages, sexes, phenotypes or genotypes may all potentially have individualistic responses to the environment and space (Clobert et al. 2001). Those components of genetic and phenotypic distributions that respond most positively to climate change will increase in frequency in the next generation (Levitan 2003; Visser 2008), changing populations' traits and so the realisation of the niche.

Changes in the realisation of the niche may co-occur. Populations may inhabit different areas of the fundamental niche, causing changes in dynamics and the relationships with the rest of a community. These changes in environmental relationships can feedback into the deformation of populations' ranges, in turn leading to changes in evolutionary dynamics. As populations' ranges deform away from equilibrium patterns (Rapoport 1975) through evolution or generation of environmental disequilibrium, the competitive environments within which traits originated may also be altered (Edmonds et al. 2004). Simultaneously traits may experience novel environmental conditions, altering the adaptive landscapes across that populations occupy. The combination of these two changes may cause large changes in the adaptive landscape with resultant changes in evolutionary outcomes (Peck & Welch 2004; Brooker et al. 2007; Burton & Travis *in press*).

An interesting new biology is generated during climate change. Populations have uncertain futures that may be translated into changes in fundamental ecological relationships. For instance, range size often has a relationship with a variety of other traits such as abundance, body-size, genetic variation and dispersal ability (see Gaston 2003). These relationships could be disrupted as populations experience conditions outside of the 'equilibrium', producing deviations from the patterns we would expect at present. This is because populations are not guaranteed that the environment will provide equivalent future ranges (Ohlemüller et al. 2006). In a community context such changes are more readily conceived and the ecological effects may be better understood, for instance in the case of species area curves (Thomas et al. 2004; Lewis 2006). It is not known what the effects of altering relationships between range size and co-varying traits may be, however it suggests there may be some dynamic 'relaxation' to restore those processes. This suggests new foci in biology and an increased importance of understanding transient dynamics during running through geographic, trait and fitness spaces. Different transient forms may produce very different outcomes and so appropriate understanding is fundamentally important to prediction. In this thesis I have demonstrated how some of these mechanisms arise and illustrated that climate change study should consider further changes to the spatial dynamics of populations. Range limits have been the 'canaries' of climate change. Now we need to choose the new routes in which we will mine our knowledge.

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# Appendix

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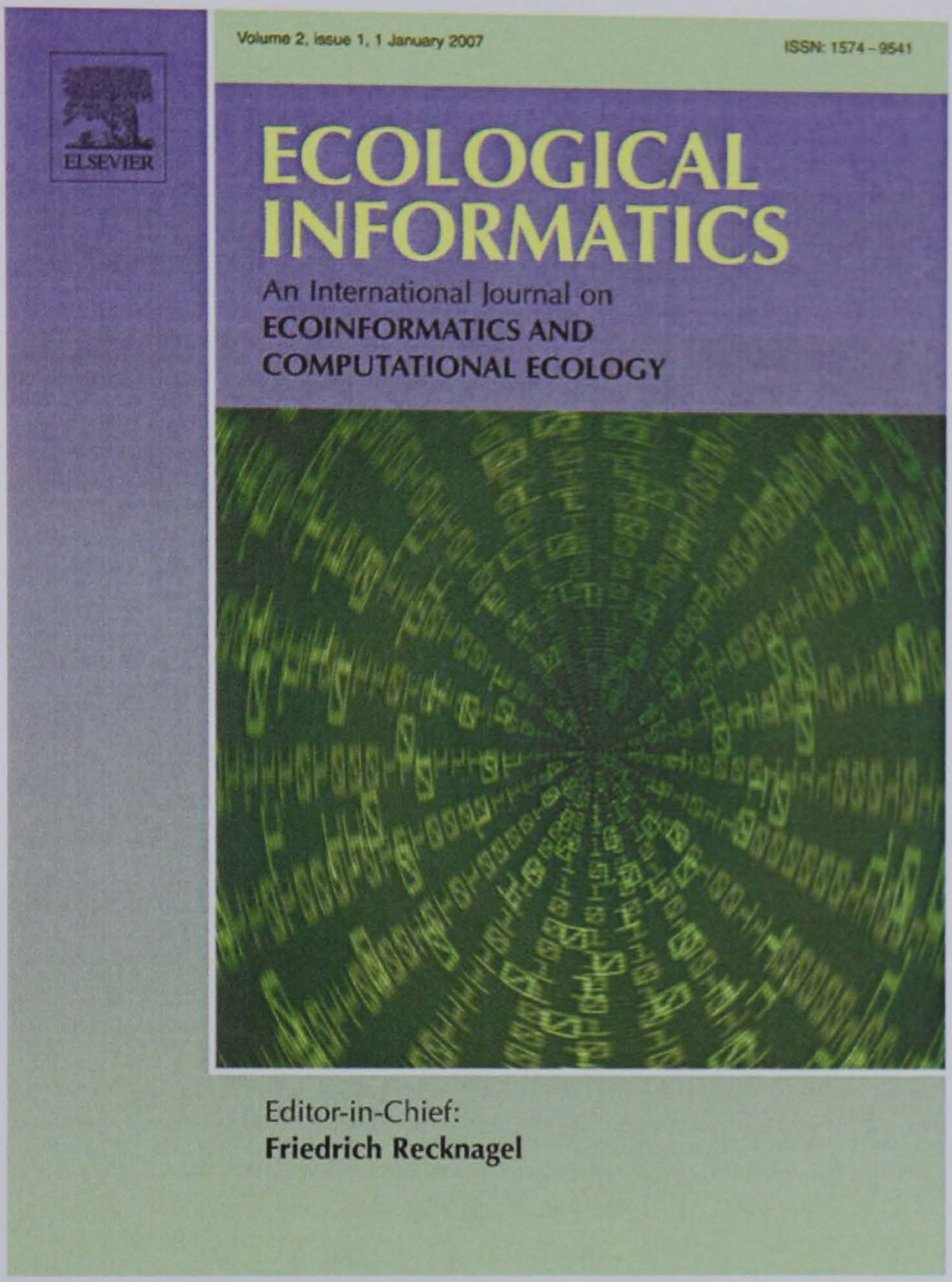

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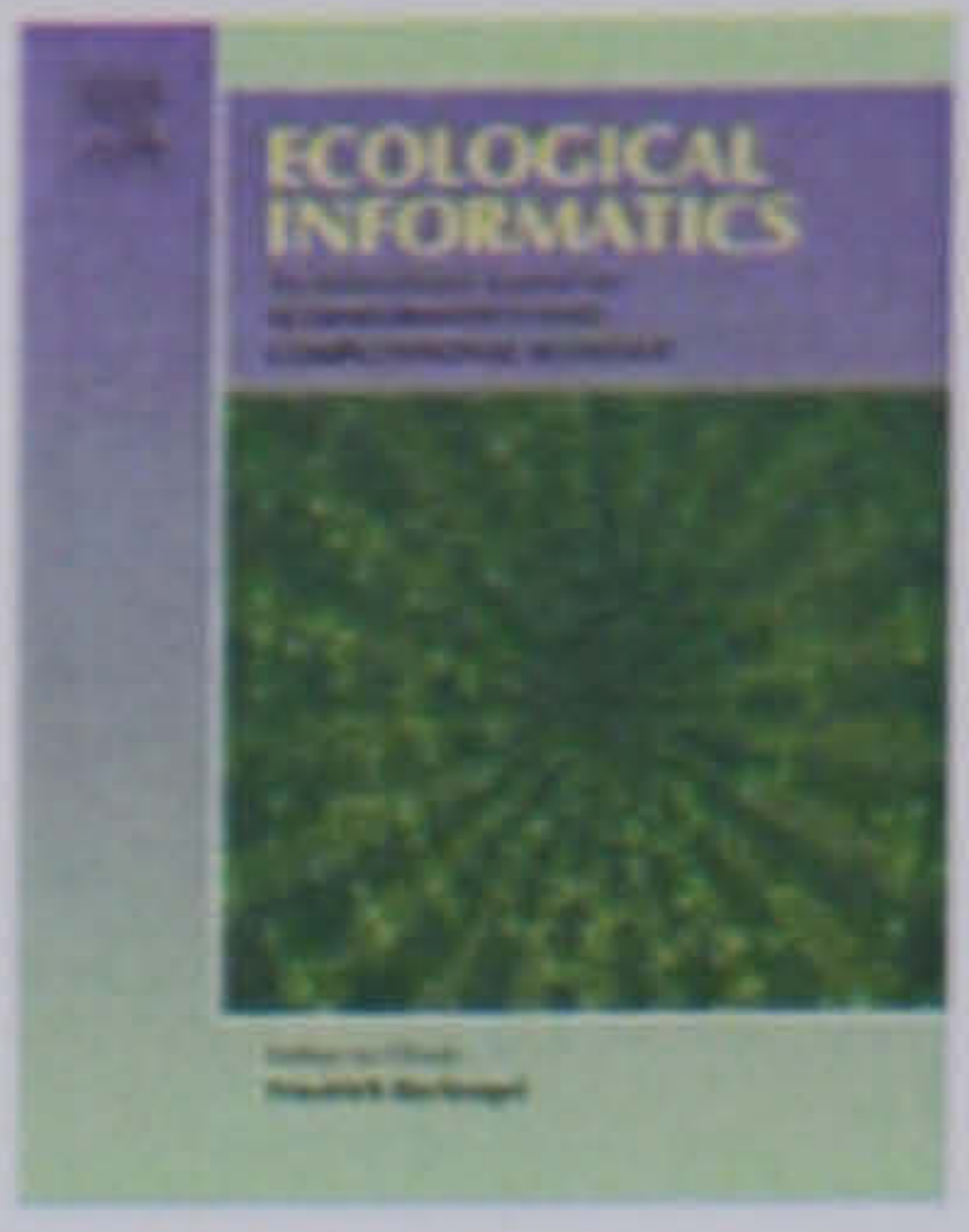

# Range shifting on a fragmented landscape

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## ABSTRACT

Projected responses of species' to climate change have so far included few of the factors that are important determinants of species' distributions within its range. In this paper we utilise a spatially explicit cellular lattice, colonisation–extinction model to investigate the effect of habitat loss, fragmentation and species characteristics on range shifting in response to climate change. Contrary to the predictions of patch occupancy in static climate models we show that fragmentation can have a positive effect on species survival when species have high colonisation rates. For species with low colonisation rates aggregative behaviours prevent success on fragmented landscapes at high levels of habitat loss, and range shifting is more successfully achieved where habitat is correlated. At levels of habitat loss near the extinction threshold, less fragmented landscapes can facilitate range shifting even for the best colonisers. We discuss how imposing a climate window may reduce percolation routes and have implications for the area of usable habitat at any given level of habitat availability. We demonstrate the importance of landscape structure for range shifting dynamics and argue that management of reserve networks needs to consider the requirements of species with different life history characteristics.

## 1. Introduction

In this era of rapid climate change the vast majority species are expected to experience a significant shift in the location of climatically suitable habitat. Evidence of species distributions shifting in response to contemporary climate changes is accumulating rapidly (e.g. Dennis and Shreeve, 1991; Parmesan, 1996; Parmesan et al., 1999; Thomas and Lennon, 1999; Hughes, 2000; Parmesan and Yohe, 2003; Thomas et al., 2004a, b; Simmons and Thomas, 2004; Hickling et al., 2005). Species have previously survived periods of climate change (e.g. Hewitt, 2000; Davis and Shaw, 2001); however, the situation today is very different to past episodes of climate change for two reasons (Collingham and Huntley, 2000; Travis, 2003).

At a global scale climate is changing more rapidly than at any time in the past (IPCC, 2001). It is expected that many species may be unable to alter their distributions at equivalent rates, increasing their risk of extinction (see Thomas et al., 2004a). The estimated speed of contemporary climate change lies 2–5 times outside the fastest rates of range shifting exhibited in the fossil record (Davis and Shaw, 2001; and references therein).

Secondly, humans have significantly altered the landscape, with almost 25% of the worlds surface now cultivated (http://www.millenniumassessment.org/en/index.aspx), causing species' key resources to be liable to fragmentation amongst an inhospitable and sometimes impassable matrix (Pitelka et al., 1997). Landscape alterations have two main effects, habitat loss and habitat fragmentation (see Fahrig, 2003). Habitat loss is the reduction in the amount of habitat available whilst fragmentation is the breaking apart of the habitat; increasing the number of patches and the amount of edge habitat, decreasing patch

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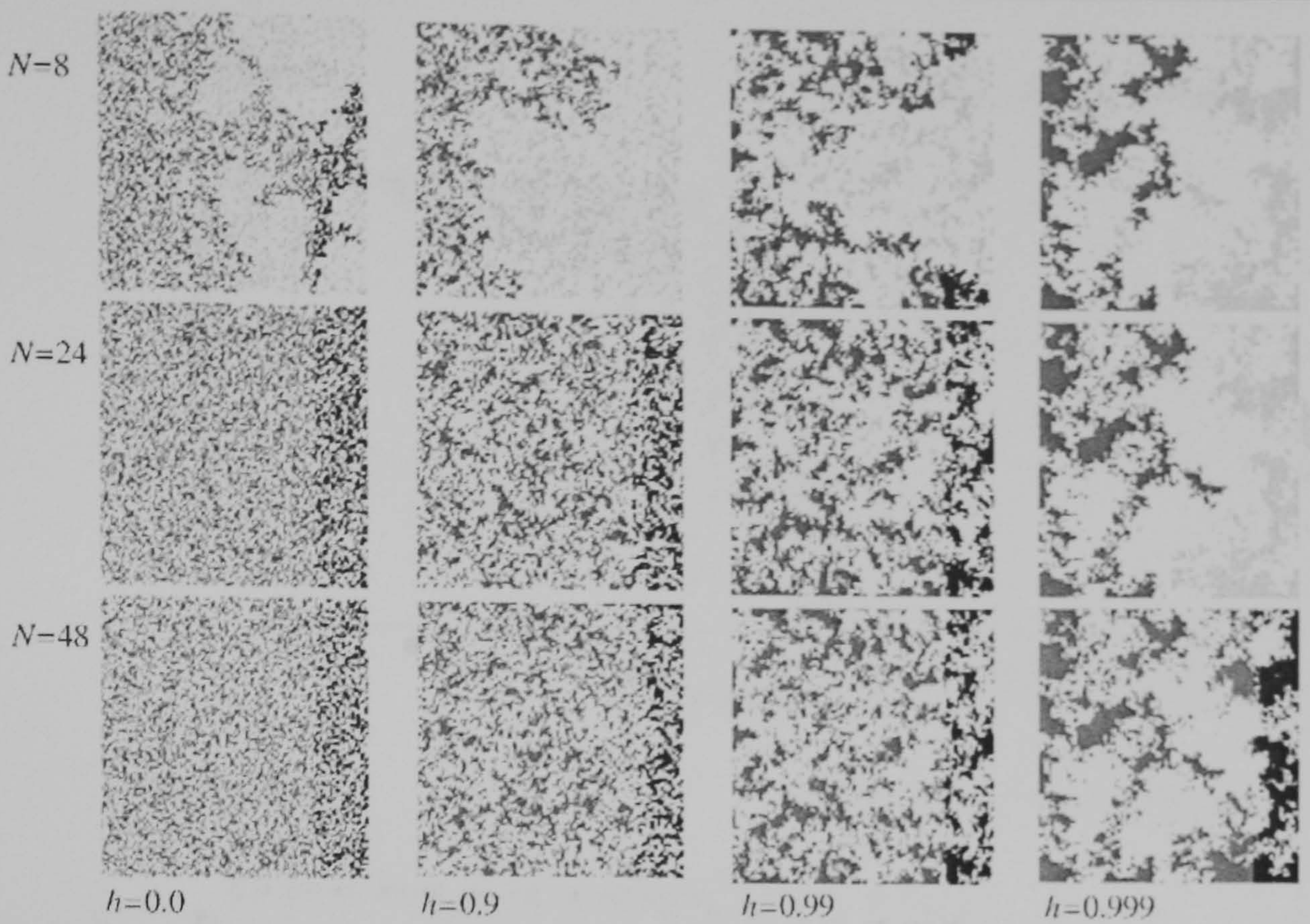

**Fig. 1 – Habitat landscapes illustrating the effect of habitat correlation ($h$) on species survival through a period of climate change. Each landscape was used for each dispersal difference ($N=8$, $N=24$, $N=48$), with 0.6 of the habitat lost. White areas represent the unsuitable matrix, light grey areas suitable unoccupied habitat, dark grey areas suitable unoccupied habitat that has been previously occupied and black areas are suitable occupied habitat. Note that the climate window moves left to right, with the window clearly illustrated by the black area of occupied suitable habitat on the right hand side of the $N=48$, $h=0.999$ landscape. ($c=1.0$ and $e=0.1$ in all cases). In 4 of the simulations extinctions are observed, where no black patches appear in the figure ($N=8$, $h=0.0$, 0.9 and 0.999; $N=24$, $h=0.999$).**

size and reducing connectivity (Bascompte and Sole, 1996; With et al., 1997; Fahrig, 2003). In this paper, we are interested in how the pattern of landscape alteration affects the probability that a particular species will be able to shift its geographic range in response to climate change.

Previous theoretical work utilising spatially explicit models has concentrated on critical thresholds of habitat loss in relation to the degree of habitat fragmentation for individual species (With and King, 1999a,b) and two species systems (Dytham, 1995). In the absence of climate change, the theoretical expectations are clear: a population can ordinarily tolerate more habitat loss if the remnant habitat is less fragmented (Dytham, 1995; Pearson et al., 1996; With and King, 1999a,b; Hill and Caswell, 2001; Fahrig, 2001; Flather and Bevers, 2002; Fahrig, 2002; see also Ovaskainen and Hanski, 2003). The population response is highly dependent on the dispersal capacity, with poorer dispersers more reliant on habitat correlation (Doak et al., 1992; Adler and Nuernberger, 1994; With and King, 1999a). However, large dispersal capacities and high levels of reproductive output may enable relatively high patch occupancy even in a more fragmented landscape (With and King, 1999a).

In agreement with a recent review (Pearson and Dawson, 2003; also see Hampe, 2004; Pearson and Dawson, 2004) we believe that there is a real need for theoretical work investigating how dispersal and population dynamics influence range shifting responses to climate change. Reliable predictions require a better understanding of landscape effects in order to be better placed to optimally direct conservation efforts and maximise species survival. To date few studies have investigated the spatial dynamics of range shifting, with most predictions concerning the response of biodiversity to climate change relying on a climate envelope approach that implicitly assumes perfect colonisation of available habitat (Pearson and Dawson, 2003; Williams et al., 2005). In this paper we extend the methods used by Travis (2003) and explore the consequences of different patterns of habitat loss for range shifting dynamics.

## 2. The model

As in similar studies (Dytham, 1995; Pearson et al., 1996; With and King, 1999a,b; Hill and Caswell, 2001; Fahrig, 2001; Flather and Bevers, 2002) the landscape is represented as a lattice of patches. All landscapes presented here are a 200×200 grid (40,000 patches). Patches can be in one of three states: unsuitable habitat, suitable unoccupied habitat and suitable occupied habitat. Habitat is unsuitable if it is outside of the climate window or if it has been destroyed (i.e. habitat loss). Like Travis (2003), we place a climate window over the lattice that defines the region within which the species can survive. Extinction occurs in all occupied patches outside the climate window and colonisation cannot occur in patches outside of the window. To simulate climate change, the climate window is moved across the landscape. For brevity, we show results for a single rate of climate change (1 lattice column per 2

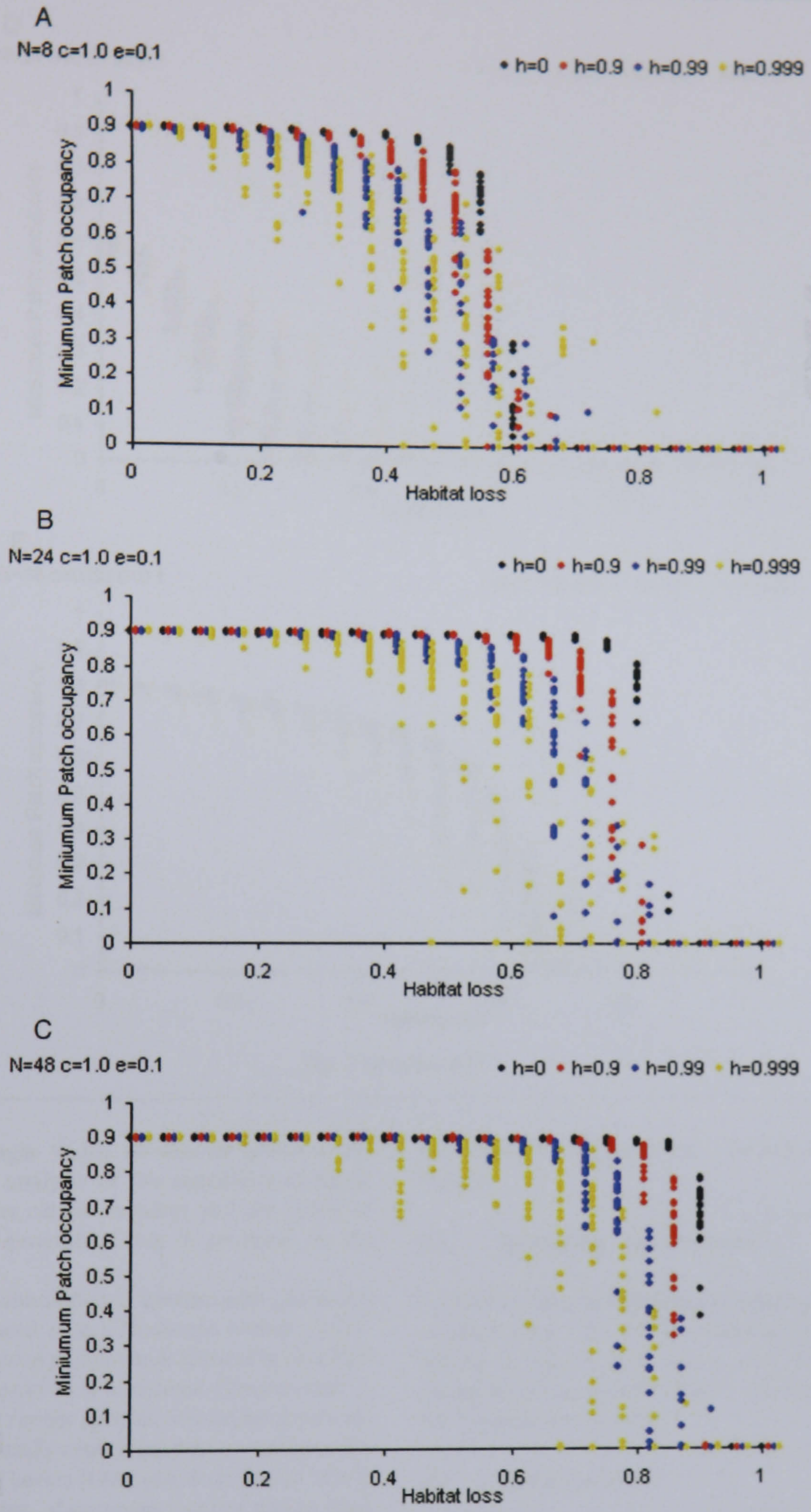

**Fig. 2 – A–E: Individual data points for the minimum patch occupancy (MPO) of each simulation run: for a perfect coloniser ($c=1.0$ $e=0.1$) (A) $N=8$, (B) $N=24$, (C) $N=48$, and a poor coloniser ($c=0.02$ $e=0.1$) (D) $N=24$, (E) $N=48$ on landscapes with random, fragmented habitat loss and increasing degrees of clumped habitat loss ($h=0.9$, $h=0.99$, $h=0.999$). Habitat loss is incremented at 0.05 for values; for clarity data points for each landscape at each value of habitat loss are offset. For a poor coloniser with a dispersal capacity of $N=8$ all simulations resulted in extinction.**

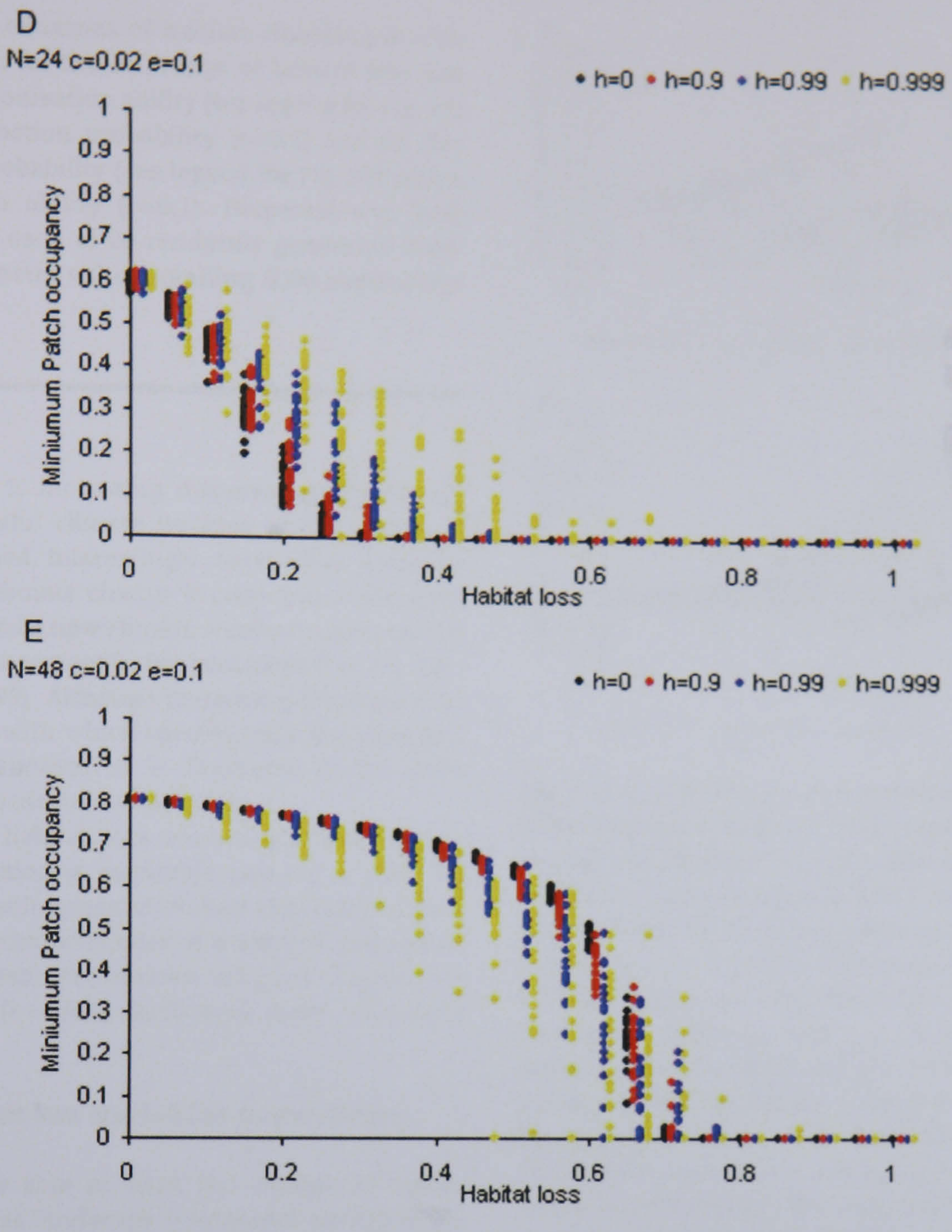

**Fig. 2** (*continued*).

generations) and a single width of climate window (40 columns wide). A brief analysis of the sensitivity of range shifting to the size of the climate window and the speed of change relative to the generation rate is provided in the Supplementary data.

At the start of each simulation a species with particular characteristics is introduced onto a landscape within a presently static climate window. A population is allowed to establish before the species' response to a simulated climate shift is monitored. Within the lattice the species' population dynamics are simulated using a spatially explicit model derived from the metapopulation model of Levins (1969) and described in Travis (2003). Stochastic extinction of occupied patches occurs with probability *e*. Suitable, unoccupied habitat can be colonized if there is an occupied patch within a specified neighbourhood. Here we use three neighbourhood sizes (N): 8 patches, 24 patches and 48 patches. The probability of an empty suitable patch being colonized is

$$1-(1-c)^n$$

where *c* is the probability of colonisation from any one occupied neighbour and *n* is the number of occupied patches within the focal patch's neighbourhood, as specified by the dispersal capacity.

### 2.1. *Generating the landscapes*

A relatively simple algorithm is employed producing patterns of availability that, at one extreme, are highly fragmented having no spatial correlation, and, at the other, are very clumped (or correlated habitat). The algorithm is provided in the Supplementary data.

### 2.2. *The simulations*

The simulations focused on investigating two main areas. Firstly the 4 levels of habitat clumping ($h=0.0$, $h=0.9$, $h=0.99$, $h=0.999$, where $h=0.0$ is the highly fragmented habitat and $h=0.999$ is highly correlated, clumped habitat) were employed over the full range of range of habitat loss (0–1.0 habitat loss, at 0.05 increments) for a perfect coloniser ($c=1.0$, $e=0.1$) and a poor coloniser ($c=0.02$, $e=0.1$). The three levels of dispersal capacity were applied for each parameter set, with 20 randomly generated landscapes, this totalled 9600 simulation runs.

Secondly, the two extremes of habitat clumping ($h=0.0$, $h=0.999$) were utilised for the full range of habitat loss and for (a) five levels of colonisation ability (see legend for Fig. 3A) with a constant extinction probability ($e=0.1$) and (b) five levels of extinction probability (see legend for Fig. 3B) with a constant colonisation ability ($c=0.1$). Dispersal was held constant at $N=24$ for each of 20 randomly generated landscapes, at each parameter value, totalling 8000 simulations runs.

## 3. Results

As is shown in Fig. 1, increasing dispersal ability always allowed more successful climate tracking as the choice of routes always increased. Interestingly, even when a species survives a period of climate change it often has a restricted range, where habitat in its new climate window is inaccessible due to the spatial arrangement in the landscape (see Fig. 1 for $N=8$, $h=0.0$ and $h=0.99$). Although increasing dispersal may increase the distance with which species track the climate it does not guarantee survival as is illustrated in the three dispersal neighbourhoods for $h=0.99$ in Fig. 1.

As the extent of habitat loss increases a threshold is reached where extinction is inevitable (see Fig. 2 A–E). No single degree of habitat fragmentation best facilitated climate tracking. Instead the characteristics of a species' population dynamics and dispersal determined whether fragmented ($h=0.0$) or clumped ($h=0.999$) facilitated more successful climate tracking.

### 3.1. *Effect of habitat loss and habitat fragmentation*

Perfect colonisers are able to track the climate at higher levels of habitat loss as landscape fragmentation increases, except at low levels of dispersal (Fig. 2 A–C). However for a poor disperser (Fig. 2A), clumped landscapes sporadically allow successful climate tracking at levels of habitat loss that exceed the extinction threshold of the more fragmented landscapes. This effect is further illustrated in Fig. 2A–C by comparing the variance in the minimum patch occupancy of populations moving through fragmented and clumped landscapes. For fragmented landscapes the variance in MPO is comparatively uniform, whilst at any given level of habitat loss, the variance in a clumped landscape is far greater. Increasing habitat loss always enhances variance in MPO.

### 3.2. *Effect of colonisation ability and environmental stochasticity*

For a species with poor colonisation ability ($c=0.02$ $e=0.1$) the switch to more successful tracking of climate on clumped habitats is demonstrated at far lower levels of habitat loss (Fig. 2C and D), though the poorest disperser ($N=8$) can never track the climate. As dispersal ability decreases clumped landscapes are more successful through a greater proportion of the range of habitat loss.

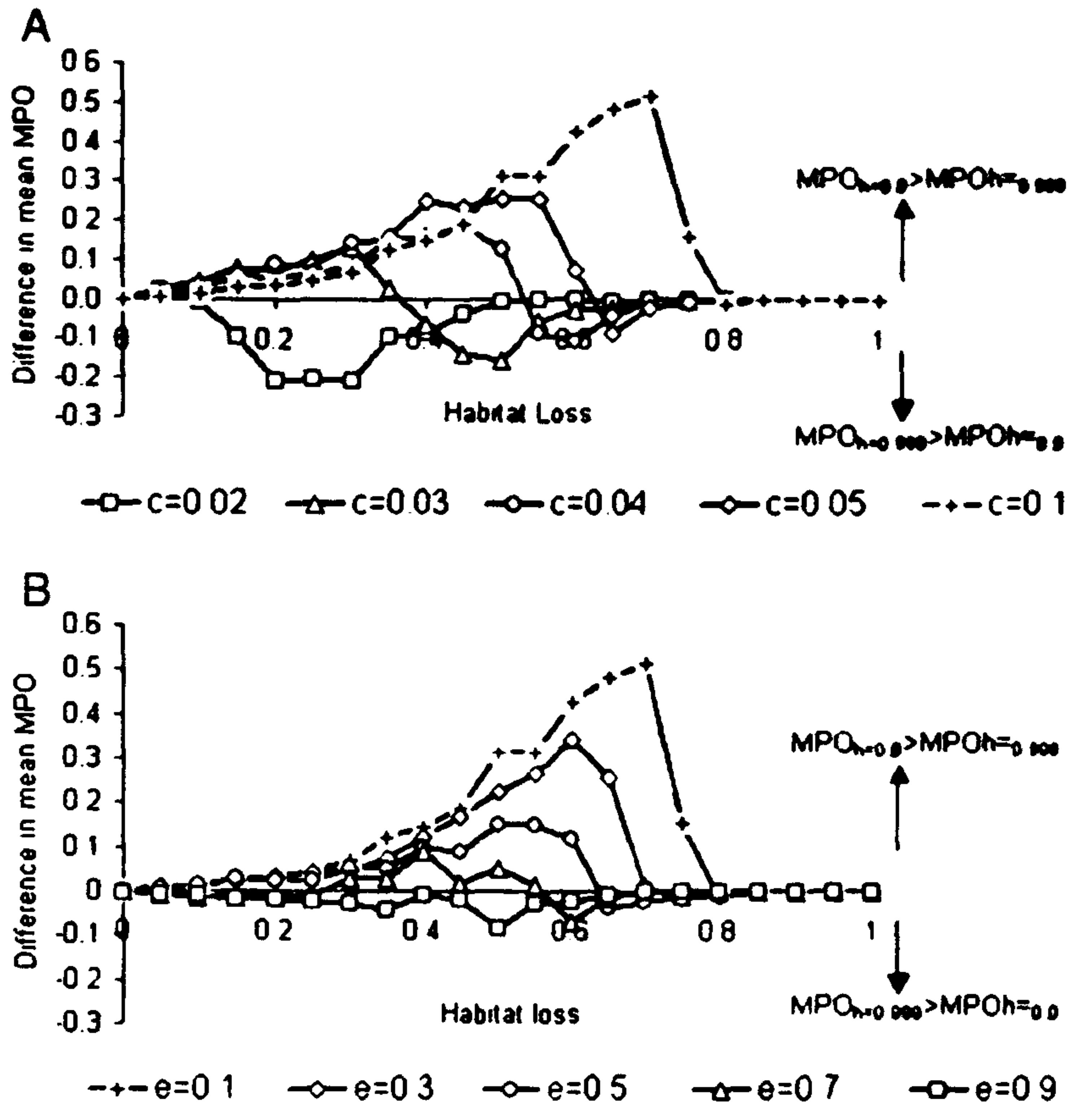

**Fig. 3 – A and B: The relative performance of range shifting with landscapes suffering from fragmented habitat loss ($h=0.0$) and highly clumped habitat loss ($h=0.999$). Mean minimum patch occupancy (MPO) of twenty simulation runs was recorded for each parameter set and with both forms of habitat loss. The difference between the mean MPO with random habitat loss was then taken from that with clumped habitat loss ($MPO_{h0.0}-MPO_{h0.999}$) to illustrate the relative performance of range shifting on different landscapes and for a range of (A) colonisation abilities $0<c<0.1$, $e=0.1$ and (B) extinction rates $0<e<1$, $c=0.1$. Dispersal capacity: $N=24$ in all cases. Note that $e>c$ is possible as the probability of a cell being colonised is also dependent on the number of occupied cells within the neighbourhood ($n$) defined by dispersal capacity. The probability that a suitable, empty patch becomes colonised is then $1-(1-c)^n$.**

Fig. 3A show the difference between the mean MPO for random and highly correlated habitats ($MPO_{h0.0}-MPO_{h0.999}$) for increasing colonisation ability. At low levels of habitat loss (<0.1) there is little difference in the mean MPO for all colonisation abilities. Clumped landscapes outperform the fragmented landscape over a greater range of habitat loss as colonisation ability decreases. The switching importance of habitat clumping is also found when extinction probabilities increase (Fig. 3B), though the effect is weaker throughout the majority of the parameter values.

## 4. Discussion

There are important contrasts between our findings and the predictions of the effect of habitat fragmentation on population persistence in static climates (e.g. Dytham, 1995; Pearson et al., 1996; With and King, 1999a,b; Hill and Caswell, 1999). Specifically we demonstrate that during a period of climate change the effect of habitat fragmentation, at any level of habitat loss, on range shifting is dependent on the species' dispersal characteristics and population dynamics. Here, we have shown that during a period of climate change, a clumped habitat distribution may hinder the range shifting of some species. Turning this around, in effect we demonstrate that fragmentation can increase the success of range shifting. This is most likely to be the case for species with good dispersal, and particularly colonisation abilities. For species exhibiting metapopulation dynamics, and especially for those with poor dispersal ability, range shifting is in general more difficult and for these species a clumped habitat distribution can increase their probability of persistence.

We can understand the shifting response by recognising the restrictions a climate window imposes on different levels of fragmentation. As the gap structure of fragmented landscapes (e.g. $h=0.0$) is essentially uniform, the landscape is regionally usable with a single large route to survival at low levels of habitat loss. However, as habitat loss increases, fragmented landscapes become homogenously unusable. Gaps are universally large, as there is little variance in the gap structure, and at some point the prescribed dispersal capacity will be exceeded. When a climate window is overlaid a fragmented landscape, it can be assumed that the landscape to be encountered at each stage of a shift in climate will not differ greatly in its gap structure. Even a scarce, fragmented resource is not necessarily fragmented given sufficient dispersal capacity (With and Crist, 1995; see also Collingham and Huntley, 2000).

However, for a clumped landscape we cannot assume that the landscape encountered at each stage will be similar to that encountered before. In a clumped landscape, as there is correlation of habitat within a finite space, some gaps will inevitably be larger causing increased variation in the gap structure. Habitat loss may not be exhibited regionally as local areas of habitat are maintained. Habitat correlation effectively homogenises the landscape locally, whilst decreasing habitat loss homogenises the landscape regionally. The spatial arrangement of habitat may inhibit movement where the landscape deviates from the most parsimonious distribution of habitat for range shifting, a contiguous habitat patch spanning the entire landscape in the direction of climate change. Deviations from this distribution generate greater variation in the population response as habitat may be clumped in areas that are perpendicular to climate change, impassable discontinuities exist or the climate window may act as a barrier to percolation where only tortuous routes are available.

At high levels of habitat loss the aggregative effects that permit survival for poor colonisers are only facilitated on less fragmented, clumped landscapes. For models such as that presented here, colonisation of a habitat cell is a function of the number of occupied cells within some neighbourhood (Fahrig, 2002) determined by the dispersal capacity and degree of habitat loss. An empty cell's neighbours reinforce the probability of colonisation producing an aggregative effect, where cells maintain high colonisation rates if the neighbourhood maintains sufficiently large amounts of habitat (Fahrig, 2002). As colonisation ability decreases, the required neighbourhood of habitat will increase. Aggregative properties are reduced with dispersal ability, as has been shown for British plant species (Quinn et al., 1994). Yet, fragmented landscapes can better facilitate range shifting for particularly good colonisers (see Table 1) with the probability of successful range shifting improving on less fragmented landscapes at very high levels of habitat loss.

**Table 1 – The general effect of fragmentation on range shifting at levels of habitat loss before the extinction threshold, for two species types**

| | Perfect coloniser [$e=0.1$ $c=1.0$] | Poor coloniser [$e=0.1$ $c=0.02$] |
|---|---|---|
| Fragmented landscape [e.g. $h=0.0$] | Positive effect | Negative effect |
| Clumped landscape [e.g. $h=0.999$] | Negative effect | Positive effect |

The model presented here makes many simplifying assumptions and we regard it as a first step towards understanding the spatial dynamics of range shifting on fragmented landscapes. There are many directions in which future work could extend these initial results. By way of example we indicate here how more realistic dispersal biology could be incorporated. Dispersal has been presented as an essentially passive process in this model, having most in common with sessile organisms that disperse as propagules before settlement. As has been previously noted, dispersal characteristics determine the scale of heterogeneity that must be considered (Collingham and Huntley, 2000). We have not considered species capable of dispersal, even if sporadically, over very long distances. Such species will most probably find it easier to track climate change and they will be gaining a similar advantage to long distance dispersers at an expanding range front during an invasion (Hill et al., 2004). Other critical traits of dispersal will cause differential responses to habitat fragmentation, such as habitat selection and differential settlement (e.g. Blondel et al., 1999; Garant et al., 2005; Postma and van Noordwijk, 2005), as well as factors that determine condition dependent dispersal responses (see Travis et al., 1999; Ims and Hjermann, 2001). Significant differences in dispersal of populations may be dependent on the characteristics of the regions they inhabit (e.g. Denno et al., 1996), such as dispersal tendency and the period of dispersal (see Table 1 in Ehrlich et al., 1975). Many traits are known to covary with dispersal ability (e.g. Zera and Denno, 1997) and their influence on the spatial dynamics should not be overlooked. It is not possible to generate spatially explicit models for every species and every landscape (With and King, 1999a), though we can provide generality and a baseline for understanding the effect of the landscape on species with varied life history and dispersal attributes using models like that presented here (With and Crist, 1995; With and King, 1999a).

The response of a species to range expansion will inevitably be a complex interaction of life history and behavioural characters. Spread into pristine, suitable habitat will lead to a large increase in dispersal at the range margin (Travis and Dytham, 2002) as appears to be the case in the Speckled wood butterfly (Hughes et al., 2003). Although the story is more complex as an Allee effect will pin an invasion severely (e.g. Travis and Dytham, 2002) and the increase in dispersal ability must be matched by a trade-off, usually, against fecundity (Hughes et al., 2003). Potential interactions are further increased when landscapes and the ability of an individual to find habitat are also considered (e.g. Hill et al., 2004).

Of course, there are further possible complications when dealing with range shifts. Species interactions and evolutionary responses are also going to define species responses to climate change (see Pearson and Dawson, 2003; Hampe, 2004; Pearson and Dawson, 2004). Furthermore, a single rate of climate change and size of climate window were used for the simulations presented (though see Supplementary data). The rate of climate change is likely to impact different taxa in different ways. We might expect theoretical predictions to fit species which show more immediate response to their changing environment, as has been found with habitat fragmentation studies (Debinski and Holt, 2000). Where species are long lived or have overlapping generations, we may expect results that are not immediately concordant with theoretical expectations. For small climate windows the percolation problem is exacerbated, as there is an ever-increasing requirement for the landscape to lie linearly in the direction of change (see Supplementary data).

Our model has treated the landscapes presented in this model as temporally stable and their suitability is not affected by any relationship with the climate window. However, habitat is not expected to remain suitable through all areas of the climate window (see Travis and Dytham, 2004). The expectations of changes in future habitat structure have not been rigorously determined and it is not known how the quantity and quality of habitat will vary spatially and temporally. Thomas et al. (1999) suggest that habitat may become more available, though not necessarily encompassing the entire previous habitat (also see Grime, 1997; Williams et al., 2005). Hampe (2004) noted that differential forces would be acting on populations through a species' range. At the extremes, individuals at retreating margins may experience decreasing availability of habitat, which, is increasingly fragmented. Whilst at expanding margins suitable habitat may become more common and less fragmented (Hampe, 2004).

In summary, the model presented here has demonstrated that during a period of climate change the effect of fragmentation is highly dependent on species' characteristics and the degree of habitat loss. Incorporating landscape features such as habitat loss and fragmentation at scales relevant to species' characteristics, and to the variation of characteristics within species, will aid identification of conservation priorities and the implications of present reserve networks. It is clear that there is not one landscape prescription that will preserve all species, but general trends are more predictable with lower levels of habitat loss.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecoinf.2006.12.001.

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