

Climate change and habitat destruction: a deadly anthropogenic cocktail

J. M. J. Travis

Centre for Conservation Science, The Observatory, Buchanan Gardens, University of St Andrews, St Andrews, Fife KY16 9LZ, UK (justin@mcs.st-and.ac.uk)

Climate change and habitat destruction are two of the greatest threats to global biodiversity. Lattice models have been used to investigate how hypothetical species with different characteristics respond to habitat loss. The main result shows that a sharp threshold in habitat availability exists below which a species rapidly becomes extinct. Here, a similar modelling approach is taken to establish what determines how species respond to climate change. A similar threshold exists for the rate of climate change as has been observed for habitat loss—patch occupancy remains high up to a critical rate of climate change, beyond which species extinction becomes likely. Habitat specialists, especially those of relatively poor colonizing ability are least able to keep pace with climate change. The interaction between climate change and habitat loss might be disastrous. During climate change, the habitat threshold occurs sooner. Similarly, species suffer more from climate change in a fragmented habitat.

Keywords: extinction thresholds; patch occupancy; metapopulation; spatially explicit; dispersal; migration

1. INTRODUCTION

Predicting species' responses to climate change and habitat loss are two of the greatest challenges facing biologists today. On their own, habitat loss and climate change present threats for many species. As biologists we want to know whether a species is likely to be able to persist in a landscape that has suffered from a certain degree of habitat loss. Similarly, we would like to be able to predict whether a species will be able to adapt within its current range to changing climatic conditions, or whether it will be able to migrate to new regions as they become climatically suitable. In this paper, I am interested in the ability of species to change their biogeographical range in response to climate change. I ask which species are more likely to be able to keep pace with climate change? Also, I am interested in the potential interaction between climate change and habitat loss. This leads to the modified question: which species are likely to be able to keep pace with climate change on a fragmented landscape?

A considerable effort has already been expended on theoretical work investigating the potential impacts of habitat loss (Lande 1987; Bascompte & Sole 1996; Ives *et al.* 1998; Neuhauser 1998; Travis & Dytham 1999; With & King 1999; Hiebeler 2000; Ovaskainen *et al.* 2002). Lande (1987), in an analysis of the northern spotted owl, *Strix occidentalis* was the first to demonstrate that a critical threshold level of habitat availability exists, below which the population will go extinct, even though its vital rates are capable of supporting positive population growth in remaining suitable habitat patches. The model of Lande (1987) was an extension of the metapopulation model of Levins (1969) and was spatially implicit: no account was taken of the arrangement of habitat patches in space. Several authors have extended the work of Lande (1987) by using cellular lattice models to look at how the spatial pattern of habitat loss affects the predictions (With & King 1999; Hill & Caswell 1999). The key result of these stud-

ies is that the threshold of habitat loss below which species extinction occurs is determined by the pattern of habitat loss. If habitat loss is spatially correlated, populations can tolerate more habitat destruction than predicted by the spatially implicit model.

Models that predict the future geographical distribution of a species have been developed for a range of different organisms including butterflies (see Fleishman *et al.* 2001), birds (see Peterson *et al.* 2001) and plants (see Sykes *et al.* 1996). These studies most often model the current distribution of a species as a function of easily quantified environmental variables (Fleishman *et al.* 2001). The future occurrence of a species is predicted by projecting its modelled environmental niche onto the future climatic conditions generated by a general circulation model. These models frequently make the assumption that if the environmental conditions become suitable for a species at a particular site, the species will immediately occur at that site. No account is taken of potential dispersal limitation. One noteworthy exception is provided by Collingham & Huntley (2000) who use a spatially explicit model to establish how habitat loss alters the ability of the small-leaved lime (*Tilia cordata*) to migrate in response to climate change. Their results indicate that when habitat availability falls below 25% of the landscape area the migration rate drops dramatically.

In this paper I describe a simple model developed to investigate the combined impacts of climate change and habitat loss on hypothetical species with different characteristics. The model is similar in structure to those used to look at the consequences of habitat loss (With & King 1999; Hill & Caswell 1999). The important extension made here is the incorporation of a climatically suitable range that can shift through time. This allows for different rates of climate change to be simulated and the effects on species occupying landscapes characterized by differing degrees of habitat loss are explored.

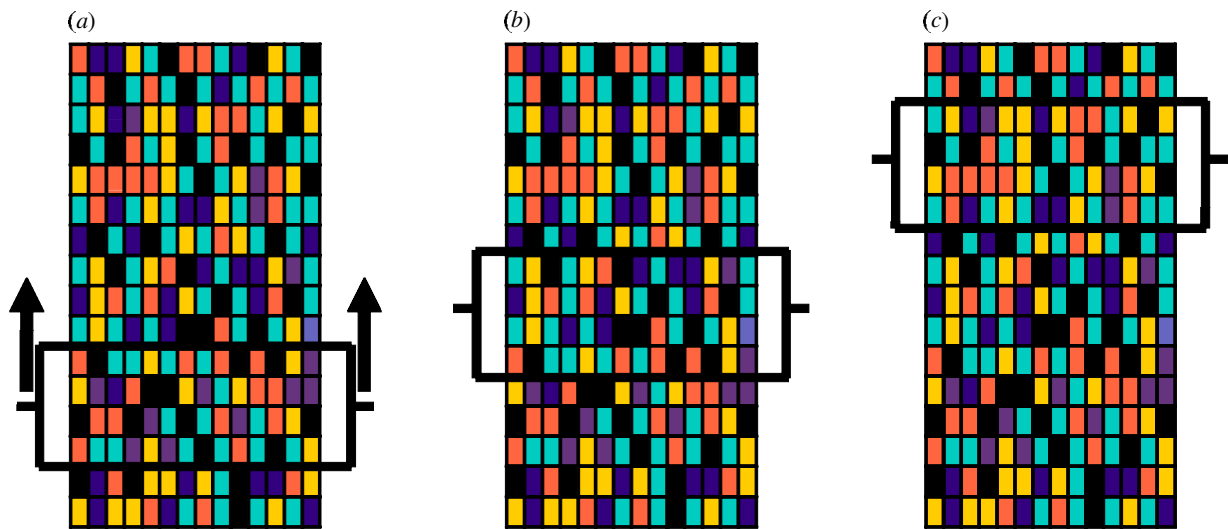


Figure 1. A schematic of the model. Each colour on the lattice represents a different habitat. A climate window is shown within which a species can survive (dark shading). Outside climatic limits the habitat is not available (light shading). (a) The region that is climatically suitable before climate change; (b) and (c) show how this region moves. In (b) there is an overlap between the suitable ranges pre- and post-climate change, whereas (c) represents a greater shift in climate and there is no overlap.

2. THE MODEL

The landscape consists of a series of patches arranged on a lattice. Each patch is assigned at random to one of five habitat types. A climate window is placed over the landscape (see figure 1). This window defines the region in which the species can persist. Within this window the spatial population dynamics are essentially identical to previous cellular patch occupancy models (Hill & Caswell 1999). Each patch can be in one of three states: unsuitable habitat, suitable unoccupied habitat and suitable occupied habitat. For a given species, habitat can be unsuitable for three reasons: if it is outside the climate window of that species, if it has been destroyed (i.e. habitat loss) or if it is the wrong type of habitat. Each simulation starts by introducing a species with particular characteristics onto a landscape that has no habitat loss and stable climatic conditions (i.e. a static climate window). The species is allowed to establish and then a particular habitat loss and climate change scenario is applied, and the species' response is monitored. In § 2a, I consider in more detail how the spatial population dynamics, habitat loss and climate change are implemented.

(a) *Spatial population dynamics*

The population dynamics are simulated using a spatially explicit model derived from the metapopulation model of Levins (1969). The deterministic model of Levins (1969) tracks the total density of occupied and unoccupied patches. Occupied patches go extinct at rate e , and unoccupied patches are colonized at a rate determined by the species' colonization ability and the densities of occupied and unoccupied patches. This model implicitly assumes that colonization is equally likely from every occupied patch.

Numerous authors have used spatially explicit analogues of this type of patch occupancy model (Dytham 1994, 1995; Hill & Caswell 1999) and I employ their methods here. In a spatially explicit, patch occupancy

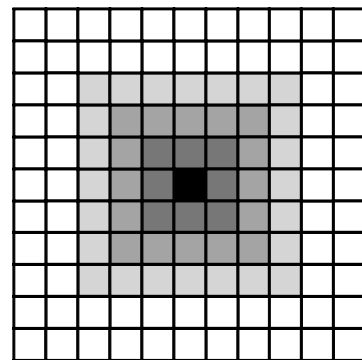


Figure 2. The different neighbourhoods used within the model. In the simulations, the focal patch (black shading) may be colonized from either the nearest eight patches (darkest grey cells), the nearest 24 patches (darkest and mid-grey cells) or the nearest 48 patches (all the grey cells).

model, the landscape is represented by a lattice of habitat patches. Stochastic extinction of occupied patches occurs with probability e . Suitable, unoccupied habitat can be colonized only if there are occupied patches situated within a specified neighbourhood. In most results presented in this paper the nearest 24 patches are considered neighbours and colonization occurs from any occupied neighbouring patch with equal likelihood (see figure 2). The probability that an unoccupied patch is colonized by individuals from a local occupied patch is c . Thus, the probability that an unoccupied patch is colonized can be obtained as follows.

Colonization occurs from each neighbouring patch with probability c , and does not occur with probability $1 - c$. The probability of colonization not occurring from any of n neighbouring occupied patches is $(1 - c)^n$. Hence, the probability that an unoccupied site is colonized is given by $1 - (1 - c)^n$,

where c is the probability of colonization from any one

occupied neighbour and n is the number of occupied patches within the focal patch's neighbourhood.

(b) Habitat loss

In all the results presented in this paper, habitat loss is random and no spatial correlation is imposed on the pattern of loss. The algorithm employed for generating habitat loss is very simple. X and Y coordinates representing a cell on the lattice are repeatedly drawn at random. If the cell is currently suitable habitat then it is degraded. This continues until the required proportion of habitat loss is obtained. In § 4 we suggest how future studies might look at different patterns of habitat availability.

(c) Climate change

I take a very simple approach to model the effect of climate change. I assume that a species is only able to survive on a section of the landscape where suitable climatic conditions occur. To simulate climate change a climate window is moved over the landscape (see figure 1). Extinction occurs at all occupied patches that are outside the climate window. Similarly, colonization cannot occur to patches outside the window. By varying the rate at which the climate window is moved over the landscape it is possible to simulate different rates of climate change. Similarly, by varying the total distance the window is moved it is possible to simulate the effect of different absolute amounts of climate change.

(d) The simulations

All the simulations are run on a lattice that is 100 cells across. Unless stated otherwise the climate window is 20 rows wide. Thus, in the absence of habitat loss, a generalist species has 2000 patches available to it. A population is introduced onto the lattice. Population dynamics are simulated for 500 generations, and then habitat loss or a period of climate change are implemented. After habitat loss the simulation is run for a further 1000 generations and the rate of patch occupancy is recorded each generation. Similarly, patch occupancy is recorded every generation during a period of climate change, and for a further 1000 generations after the climate has stabilized. Here, patch occupancy refers to the proportion of suitable sites that are occupied by the species. A suitable site is one that has the correct habitat characteristics, is within the climate window and has not been destroyed. Minimum patch occupancy (as shown in figures 3–8) indicates the lowest rate of patch occupancy that was recorded during each simulation after the initializing 500 generations. The simulation was implemented once for each of a wide range of different species characteristics, and also for a variety of habitat loss and climate change scenarios.

3. RESULTS

Figure 3 shows the familiar result for habitat loss without climate change. A sharp habitat threshold exists below which the species rapidly becomes extinct (figure 3a). How much habitat has to be destroyed before this threshold is reached depends upon the colonization ability of a species (figure 3b) and on how much of a habitat generalist the species is (figure 3c). Not surprisingly generalist

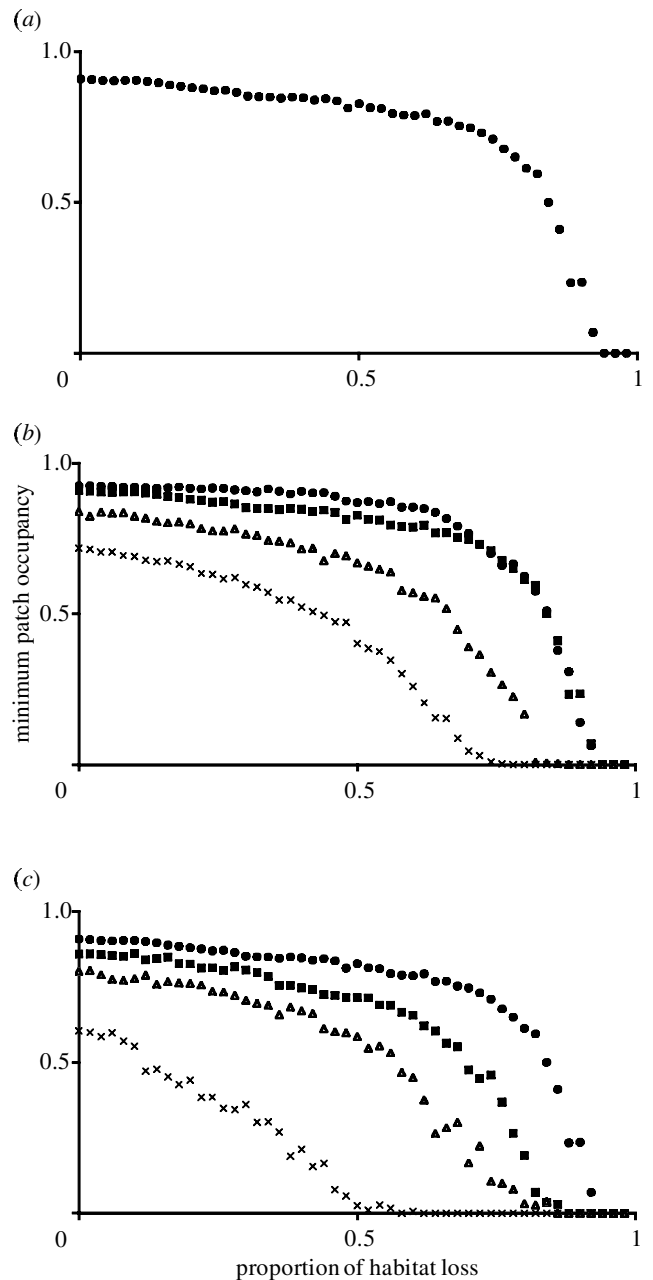


Figure 3. The response of species with different characteristics to habitat loss. Unless otherwise specified $c = e = 0.05$, the species can use all habitat types and the dispersal neighbourhood is 24. (a) A sharp threshold of habitat availability can exist below which a species rapidly approaches extinction. (b) A demonstration of how the response to habitat loss depends upon colonization ability: circles, $c = 0.08$; squares, $c = 0.05$; triangles, $c = 0.02$; crosses, $c = 0.01$. (c) A demonstration of how the response to habitat loss depends upon how much of a generalist a species is. The circles indicate the response of a generalist species that can utilize all five habitat types, the squares a species that utilizes three, the triangles a species that uses two, and the crosses one that uses just one.

species with higher rates of colonization can tolerate the greatest degree of habitat loss. The results obtained for a generalist species on a landscape with 40% habitat loss are equivalent to those obtained for a more specialist species that only utilizes three of the five habitat types. However, separating the two effects within the simulations helps to

better illustrate the probable impacts of habitat loss on species with different habitat requirements.

Figure 4 shows how the rate of climate change affects species persistence within an intact landscape (i.e. with no habitat destruction). In figure 4 the minimum patch occupancy at any time point during climate change is shown. When the climate is changing relatively slowly species are able to maintain a high rate of patch occupancy throughout the period of change. However, an abrupt threshold exists. When the rate of climate change exceeds this threshold the species' minimum patch occupancy rapidly declines until extinction becomes inevitable. Figure 4a shows a typical response to different rates of climate change. The shape of the response is remarkably similar to that for habitat loss (figure 3a). For the parameterization used in figure 3a, the species is able to maintain a high rate of patch occupancy throughout the period of climate change as long as the climate does not change at a rate greater than 16 (meaning the climate window moves 16 rows in 20 generations). When the rate is between 17 and 19, the species survives the period of climate change, but its lowest patch occupancy is considerably lower than it is during a period of climatic stability. For a rate of 20 the species does not shift its range rapidly enough and goes extinct. The exact nature of a species' response to different rates of climate change depends upon colonization ability (figure 4b) and how much of a generalist the species is (figure 4c). For species with lower colonization ability and for specialist species, the threshold occurs at a slower rate of climate change. The characteristics that reduce a species' ability to persist in a fragmented landscape are exactly the same as those that mean a species is less able to keep pace with climate change.

In a fragmented landscape patch occupancy is determined by the ratio c/e (Lande 1987). Thus, doubling the rate of colonization has the same effect as halving the rate of extinction. This is not the case for climate change (see figure 5). When there is a moving climate window, minimum patch occupancy increases as c increases (with the ratio c/e kept constant). This emphasizes that colonization ability is more important than extinction rate in determining a species' ability to keep pace with climate change.

Both the width of a species' climate window and the total amount of climate change influence the response of a species (figure 6). The wider the window, and the less the climate changes, the better a species is able to maintain patch occupancy during climate change. However, even when the total amount of climate change is considerably less than the width of a species' climate window, minimum patch occupancy can be substantially lower than that achieved during periods of climatic stability.

In the type of lattice model formulation adopted in this paper, usually one arbitrary neighbourhood size is chosen. Here, the default neighbourhood has been set at 24—implying that colonization of an empty patch can occur from any one of the 24 nearest-neighbour sites that is occupied. Species that are able to disperse further are likely to have greater neighbourhood sizes. So, by varying the neighbourhood size it is possible to simulate different dispersal abilities. Figure 7 shows how sensitive the model results can be to this parameter. The threshold rate of climate change is much lower for a species that has a neighbourhood size of 8 than for one with 24, and in this

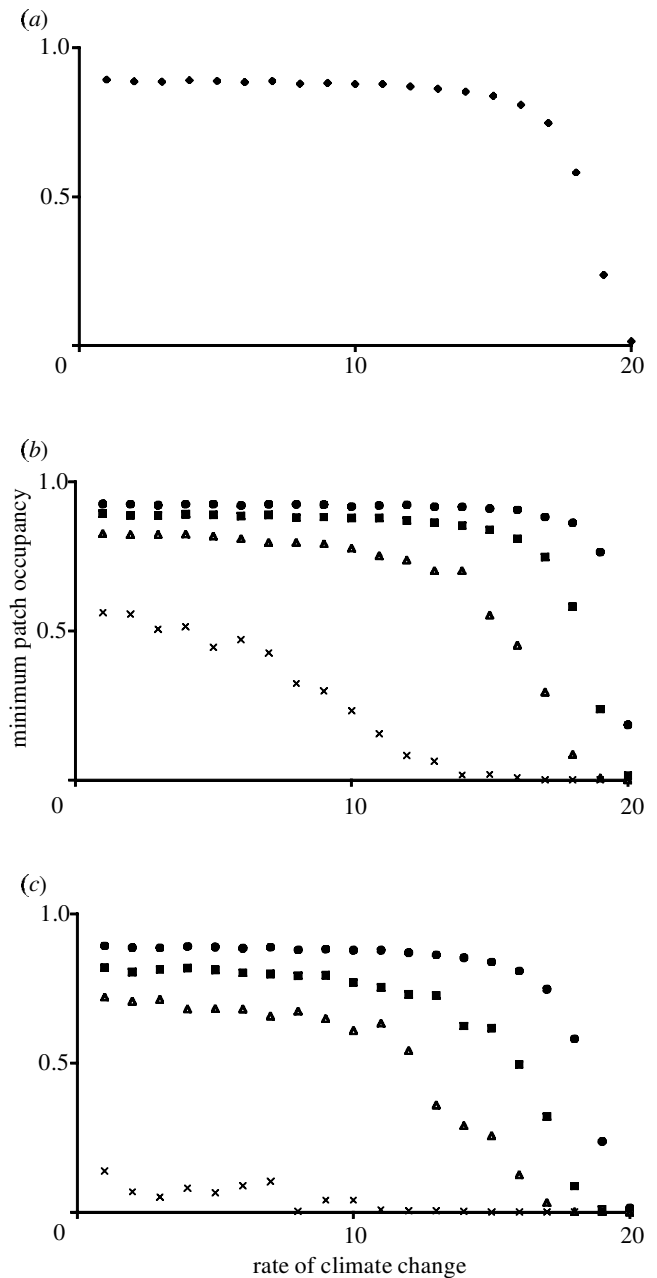


Figure 4. The response of species to climate change in the absence of habitat loss. Unless otherwise specified $c = 0.01$ and $e = 0.01$, the species can use all habitat types and the dispersal neighbourhood is 24. Here, the width of a species range is 20 rows and the climate window moves 30 rows during climate change. The rate of change indicates the number of rows that the climate window moves in 20 generations. (a) A sharp threshold can exist: beyond a critical rate of climate change a species rapidly approaches extinction. (b) A demonstration of how this response depends upon the colonization ability of a species. Here, circles depict $c = 0.02$; squares, $c = 0.01$; triangles, $c = 0.005$; and crosses, $c = 0.002$. (c) An illustration of how the response of generalist species differs from that of specialists. The circles indicate the response of a generalist that can utilize all five habitat types, the squares a species that utilizes three, the triangles a species that uses two and the crosses a species that uses just one habitat type.

example a species with a neighbourhood size of 48 is able to persist even for the most rapid climate change simulated.

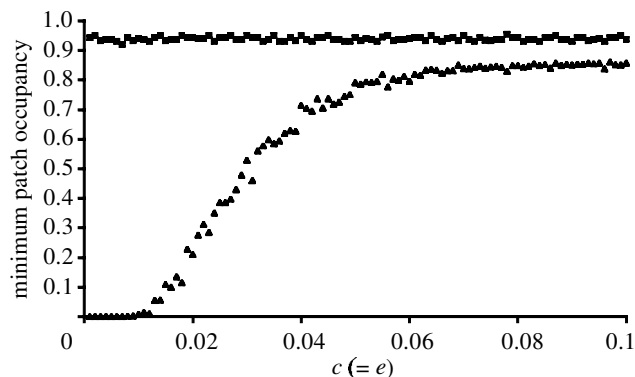


Figure 5. Colonization rate is more important in determining a species' response to climate change than the rate of patch extinction. The figure shows the minimum patch occupancy obtained during a period of climate change (triangles) and when habitat is lost (squares). In the case of habitat loss patch occupancy is determined by the ratio c/e , and thus increasing both by the same amount results in an identical occupancy. The same is not true for a climate change scenario. Now increasing both c and e by the same amount leads to a higher minimum patch occupancy.

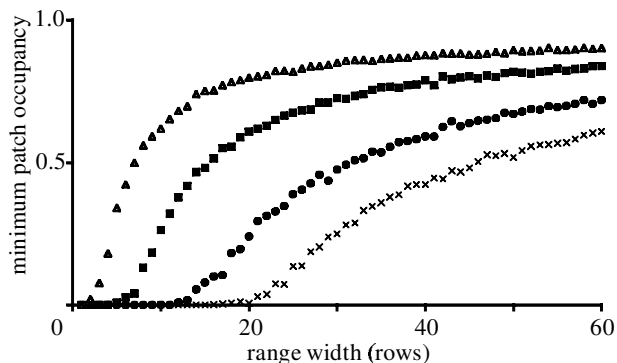


Figure 6. The width of a species range and the amount that the climate changes both influence a species' ability to withstand climate change. For this figure a complete generalist with a dispersal neighbourhood of 24 was assumed. $c = e = 0.01$. Triangles depict the results when the climate window moves five rows, squares 10 rows, circles 20 rows and crosses 30 rows. The rate of climate change is always one row per generation.

Habitat loss can substantially reduce a species ability to keep pace with a changing climate (figure 8). The position of the extinction threshold is modified according to the severity of habitat loss: as more habitat is destroyed a species is liable to go extinct even when the rate of climate change is relatively slow. These results demonstrate that although a species may be able to survive either a particular amount of habitat loss or a rate of climate change when they occur on their own, it may be forced to extinction when the two operate together.

4. DISCUSSION

Predicting extinction risks for populations in a world suffering simultaneously from several sources of anthropogenic change is one of the major challenges facing ecologists and conservation biologists today. Threshold responses, such as a precipitous decline in the regional

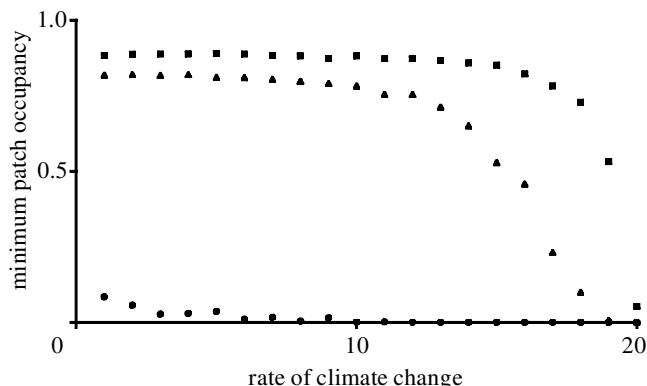


Figure 7. Species with greater dispersal ability can tolerate more rapid climate change. Here, the species can use all five habitat types, $c = 0.005$ and $e = 0.01$. The climate window is 20 rows wide and the window moves a total of 30 rows during climate change. The response of three species with different dispersal abilities is shown. The triangles represent a species that can colonize the nearest 24 habitat patches, the circles represent one that can colonize the nearest eight neighbours, and the squares represent one that can colonize the nearest 48.

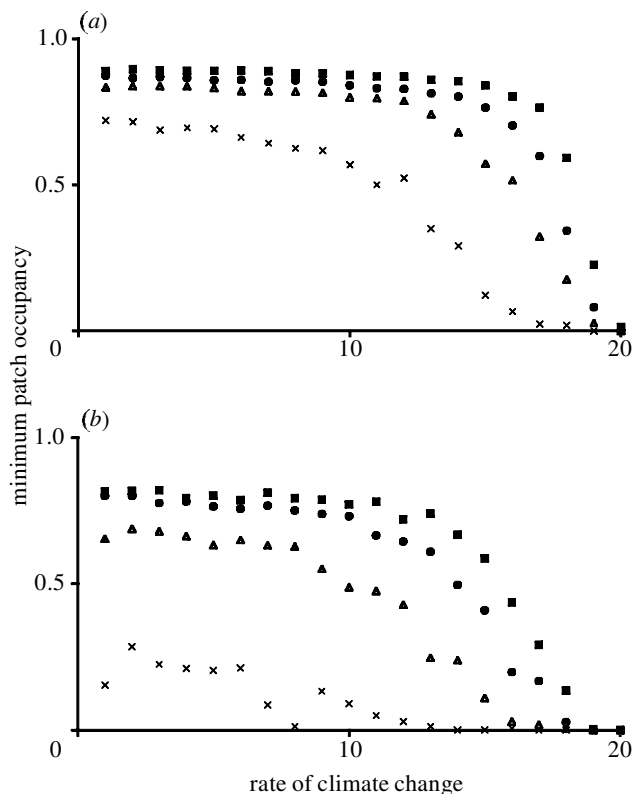


Figure 8. Habitat loss reduces the ability of a species to survive climate change. In (a) the results for a generalist with $c = e = 0.01$ and a dispersal neighbourhood of 24 are shown. The squares show the results for no habitat loss, circles with 20% loss, triangles 40% and crosses 60%. In (b) the results for a species that can only utilize 60% of the habitat are shown. The symbols denote the same amount of habitat loss as in (a).

abundance of a species because of a small loss of habitat near the threshold (figure 3, see With & King (1999) for more examples), serve to make this task both more complex and more urgent.

In the past 10 or so years, numerous authors (Bascompte & Sole 1996; Hill & Caswell 1999; With & King 1999) have used patch occupancy models to investigate the impacts of different amounts and different patterns of habitat loss on species persistence. One of the key results of these previous studies is that a threshold of habitat availability exists above which a species is able to maintain a high degree of patch occupancy and below which the species rapidly approaches extinction. One of the most significant findings of this paper is the one that demonstrates a similar threshold for climate change. Below a critical rate of climate change a species maintains high patch occupancy throughout the period of climate change. Above the critical rate the species is unable to keep pace with climate change and patch occupancy rapidly declines. Our model results demonstrate that species can be expected to show a wide variety of different responses to climate change depending upon their life-history characteristics.

Specialist species that have low colonization ability and poor dispersal are the most prone to extinction during climate change. These characteristics are the same as those that cause a species to be prone to extinction in response to habitat loss. The main difference between habitat loss and climate change relates to the relative importance of colonization and extinction rates. For a habitat loss it is the ratio c/e that determines the patch occupancy, so the two rates can be viewed as equally important. However, colonization rate is more important in determining the response to climate change than extinction rate.

Species with relatively wide ranges are perhaps unsurprisingly the most resilient to the effects of climate change (see figure 6). In general, species that live in the tropics tend to have narrower ranges than those living in temperate regions (Stevens 1989). Given similar rates of climate change in both tropical and temperate areas, we should expect those in the tropics to be most at risk of extinction. One factor that I do not account for in this model is differential adaptation to climate within a species across its range. Any regional adaptation would be likely to reduce a species' resilience to climate change.

Several recent studies have looked at the combined effects of climate change and habitat loss on species (Hill *et al.* 1999; Warren *et al.* 2001). Warren *et al.* (2001) describe climate and habitat change as opposing forces. They investigated 46 species of butterflies that approach their northern climatic range margins in Britain and show that while mobile generalists have generally expanded their ranges, sedentary and specialist species now have more restricted distributions than they did 25 years ago. Their paper concentrated on a range margin, and in this instance climate change has a regional benefit for a species that opposes the negative impacts of habitat loss. Our results emphasize that when the whole of a species range is considered, climate change and habitat loss are not opposing forces. Instead they may act in the same direction, such that their combined negative impacts can drive a species to extinction.

This model makes several simplifying assumptions. Future work relaxing some of these might be revealing. In this paper we assume random patterns of habitat loss. Several papers have already investigated the effect of different patterns of habitat availability on a species' ability to persist in a degraded landscape. These papers frequently use fractals to generate different patterns of habitat loss (Fahrig 1997; With & King 1999). The main result of these studies is that when habitat loss is clumped, a species is able to tolerate greater amounts of loss (see With & King 1999). Future studies are needed to establish whether clumped distributions of habitat make it more likely that a species is able to successfully shift its range. A further assumption made in this model is that the pattern of habitat availability is the same throughout a species range. This is unlikely to be true for many species. The colonization of newly available habitat at range margins is a critical process in the shifting of a species range, and future work developing methods (perhaps using fractals) to simulate realistic patterns of habitat availability at range margins is much needed.

5. CONCLUSION

Extinction thresholds in response to habitat loss are relatively well studied (Lande 1987; Bascompte & Sole 1996; Hill & Caswell 1999). Here, a similar threshold has been demonstrated for climate change. The position of this threshold is sensitive to the amount of habitat loss. This implies that whereas species may have been able to keep pace with past episodes of rapid climate change, today they may be unable to keep pace due to habitat loss.

The author thanks the organizers and participants of the 2002 Extinction Thresholds conference in Helsinki. He also thanks the two anonymous referees whose comments helped to improve this paper.

REFERENCES

- Bascompte, J. & Sole, R. V. 1996 Habitat fragmentation and extinction thresholds in spatially explicit models. *J. Anim. Ecol.* **65**, 465–473.
- Collingham, Y. C. & Huntley, B. 2000 Impacts of habitat fragmentation and patch size upon migration rates. *Ecol. Appl.* **10**, 131–144.
- Dytham, C. 1994 Habitat destruction and competitive coexistence—a cellular model. *J. Anim. Ecol.* **63**, 490–491.
- Dytham, C. 1995 Competitive coexistence and empty patches in spatially explicit metapopulation models. *J. Anim. Ecol.* **64**, 145–146.
- Fahrig, L. 1997 Relative effects of habitat loss and fragmentation on population extinction. *J. Wildlife Mgmt* **61**, 603–610.
- Fleishman, E., MacNally, R., Fay, J. P. & Murphy, D. D. 2001 Modeling and predicting species occurrence using broad-scale environmental variables: an example with butterflies of the Great Basin. *Conserv. Biol.* **15**, 1674–1685.
- Hiebeler, D. 2000 Populations on fragmented landscapes with spatially structured heterogeneities: landscape generation and local dispersal. *Ecology* **81**, 1629–1641.
- Hill, M. F. & Caswell, H. 1999 Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecol. Lett.* **2**, 121–127.

- Hill, J. K., Thomas, C. D. & Huntley, B. 1999 Climate and habitat availability determine 20th century changes in a butterfly's range margins. *Proc. R. Soc. Lond. B* **266**, 1197–1206. (DOI 10.1098/rspb.1999.0763.)
- Ives, A. R., Turner, M. G. & Pearson, S. M. 1998 Local explanations of landscape patterns: can analytical approaches approximate simulation models of spatial processes? *Ecosystems* **1**, 35–51.
- Lande, R. 1987 Extinction thresholds in demographic models of territorial populations. *Am. Nat.* **130**, 624–635.
- Levins, R. 1969 Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* **15**, 237–240.
- Neuhauser, C. 1998 Habitat destruction and competitive coexistence in spatially explicit models with local interactions. *J. Theor. Biol.* **193**, 445–463.
- Ovaskainen, O., Sato, K., Bascompte, J. & Hanski, I. 2002 Metapopulation models for extinction threshold in spatially correlated landscapes. *J. Theor. Biol.* **215**, 95–108.
- Peterson, A. T., Sanchez-Cordero, V., Soberon, J., Bartley, J., Buddemeier, R. W. & Navarro-Siguenza, A. G. 2001 Effects of global climate change on geographic distributions of Mexican Cracidae. *Ecol. Mod.* **144**, 21–30.
- Stevens, G. C. 1989 The latitudinal gradient in geographic range—how so many species coexist in the tropics. *Am. Nat.* **133**, 240–256.
- Sykes, M. T., Prentice, I. C. & Cramer, W. 1996 A bioclimatic model for the potential distributions of north European tree species under present and future climates. *J. Biogeogr.* **23**, 203–233.
- Travis, J. M. J. & Dytham, C. 1999 Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. Lond. B* **266**, 723–728. (DOI 10.1098/rspb.1999.0696.)
- Warren, M. S. (and 14 others) 2001 Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69.
- With, K. A. & King, A. W. 1999 Extinction thresholds for species in fractal landscapes. *Conserv. Biol.* **13**, 314–326.

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.