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Linking habitat use to range expansion rates in fragmented landscapes: a metapopulation approach

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Temperature increases because of climate change are expected to cause expansions at the high latitude margins of species distributions, but, in practice, fragmented landscapes act as barriers to colonization for most species. Understanding how species distributions will shift in response to climate change therefore requires techniques that incorporate the combined effects of climate and landscape-scale habitat availability on colonization rates. We use a metapopulation model (Incidence Function Model, IFM) to test effects of fine-scale habitat use on patterns and rates of range expansion by the butterfly *Hesperia comma*. At its northern range margin in Britain, this species has increased its breadth of microhabitat use because of climate warming, leading to increased colonization rates. We validated the IFM by reconstructing expansions in five habitat networks between 1982 and 2000, before using it to predict metapopulation dynamics over 100 yr, for three scenarios based on observed changes to habitat use. We define the scenarios as “cold-world” (only hot, south-facing 150–250° hillsides are deemed warm enough), “warm-world” in which 100–300° hillsides can be populated, and “hot-world”, where the background climate is warm enough to enable use of all aspects (as increasingly observed). In the simulations, increased habitat availability in the hot-world scenario led to faster range expansion rates, and to long-term differences in distribution size and pattern. Thus, fine-scale changes in the distribution of suitable microclimates led to landscape-scale changes in population size and colonization rate, resulting in coarse-scale changes to the species distribution. Despite use of a wider range of habitats associated with climate change, *H. comma* is still expected to occupy a small fraction of available habitat in 100 yr. The research shows that metapopulation models represent a potential framework to identify barriers to range expansion, and to predict the effects of environmental change or conservation interventions on species distributions and persistence.

The capacity of species to survive climate change will depend on their ability either to adapt in situ to changing conditions, or to colonize regions that become suitable outside their current geographic range. Some bioclimate models predict that future climatically-suitable locations may show little or no overlap with the current ranges of many species (Thomas et al. 2004, Fitzpatrick et al. 2008). Despite reservations regarding the accuracy of such models (Beale et al. 2008, Trivedi et al. 2008, Kriticos and Leriche pers. comm.), a wide range of models (Araújo et al. 2005, Elith et al. 2006) and empirically observed species range shifts (Parmesan 2006) suggest that the conservation of many species will depend on their ability to cross landscapes that have been heavily modified by human activities. Current evidence suggests that a number of habitat generalist or dispersive species have been able to expand their distributions polewards associated with climate change (Warren et al. 2001), but that most species (particularly habitat specialists) are failing to colonize climatically suitable regions as they become available (Menéndez et al. 2006). Indeed, the distributions of many taxa appear not

to have fully occupied available climate space during the present interglacial (Araújo and Pearson 2005, Svenning and Skov 2007, Araújo et al. 2008, Svenning et al. 2008). To aid the conservation of such species in a changing climate, methods are required not only to predict the distribution of future suitable locations (Araújo and New 2007, Beaumont et al. 2007), but also the species traits (Ward and Masters 2007, Massot et al. 2008) and landscape or habitat features that will facilitate species range expansions (Hill et al. 2001, Allouche et al. 2008, Vos et al. 2008).

One important consequence of climate change is that species' regional habitat use may change (Davies et al. 2006). Many species are restricted to hot microhabitats at their high latitude range margins, but occupy a broader spectrum of microhabitats nearer the centres of their ranges (Thomas 1993, Thomas et al. 1999). For such species, climate change might be expected to increase the breadth of habitat requirements towards high latitudes, hence increasing habitat availability, population sizes and colonization rates (Thomas et al. 2001). The important question for

conservationists is whether the increases in habitat availability owing to broader habitat use will be sufficient to allow species to expand their distributions through fragmented landscapes.

In this paper we use a metapopulation model to test how changes to habitat use because of climate change affect a species' distribution at its upper latitude margin. In Britain, the silver-spotted skipper butterfly *Hesperia comma* is restricted to hot microhabitats in calcareous grassland (Thomas et al. 1986), but its breadth of habitat use has recently expanded due to changed environmental conditions (warmer summers; Davies et al. 2006). We show how these changes to habitat use increase habitat availability, before using the Incidence Function Model (Hanski 1994, 1999) to simulate how increased habitat area and connectivity lead to faster rates of range expansion, and to long-term differences in distribution size and pattern. In this system, colonization and extinction dynamics provide a mechanism linking fine-scale changes in habitat use to regional-scale changes in species distributions.

Materials and methods

Study system

In Britain, the silver-spotted skipper butterfly *Hesperia comma* is restricted to short-turfed chalk grassland, where it lays eggs exclusively on short tufts (<10 cm) of sheep's fescue grass *Festuca ovina* (Thomas et al. 1986). During the twentieth century, agricultural intensification, the abandonment of low intensity livestock grazing, and the virtual elimination of rabbits because of myxomatosis led to a dramatic reduction in habitat availability for the species. When a full survey of the British distribution of *H. comma* was undertaken in 1982, it had declined to fewer than 70 populations (Thomas et al. 1986). The vast majority of these refuge populations were in five habitat networks in south-east England (Surrey, Sussex, Chilterns, Kent, Hampshire; Fig. 1), and on south-facing slopes (90% on aspects of 100–300°; 75% on aspects of 150–250°). At the time, the species appeared to select the hottest microhabitats for oviposition, with an estimated optimum sward composition including 41% bare ground (Thomas et al. 1986). In 1991, repeat distribution surveys in Surrey and Sussex showed that a range expansion had begun in Sussex, and that the maximum colonization event was 8.65 km from the nearest 1982 population (Thomas and Jones 1993).

We carried out a repeat survey of the distribution of *H. comma* in 2000, searching for adults and eggs of the species in all areas of chalk grassland containing suitable *F. ovina* plants within 30 km of the 1982 *H. comma* distribution, and within 10–15 km of newly-colonized sites found in 2000. Such a comprehensive search was feasible because suitable habitat occurs only on unimproved calcareous grassland, which is restricted to localized chalk escarpments in south-east England (Fig. 1). We defined habitat patches as areas of suitable grassland bounded by continuous woodland or scrub barriers, or by at least 25 m of unsuitable grassland (Thomas and Jones 1993, Hill et al. 1996), and recorded the area, aspect (°) and vegetation composition of each habitat patch, and of subdivisions of

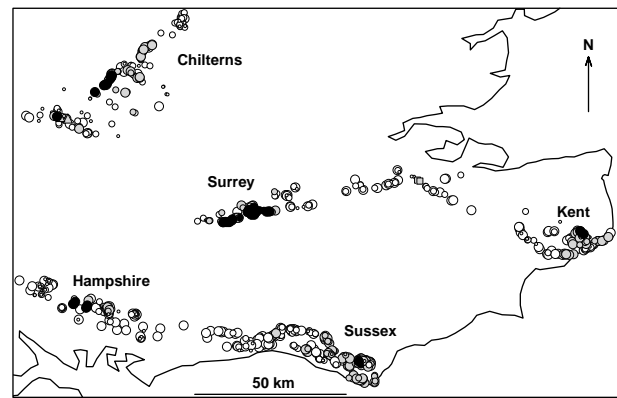


Figure 1. The distribution of *Hesperia comma* in 1982 and 2000 in south-east England. Symbols show occupancy status of habitat patches in five networks: survived (black, occupied 1982 and 2000); colonized (grey, absent 1982, occupied 2000); extinct (grey triangles, occupied 1982, absent 2000); vacant (white, absent 1982 and 2000). Grey squares show populations introduced between 1982 and 2000. Symbol size exaggerates patch area: small <0.1 ha, medium 0.1–1 ha, large >1 ha. Line indicates the coast.

habitat patches where contiguous habitats or aspects varied markedly (Davies et al. 2005). Since 1982, livestock grazing has been reintroduced to many areas of chalk grassland as part of conservation programmes, and rabbit numbers have increased (Davies et al. 2005). In addition, the temperature during *H. comma*'s flight period increased by 2.8°C over 20 yr as a result of direct temperature changes and phenological advancement of the butterfly's flight period (Wilson et al. 2007). At higher ambient temperatures, *H. comma* oviposition rate increases, and oviposition sites are less restricted to hot microclimates (Davies et al. 2006). As a result, optimum sward composition for *H. comma* egg-laying in 2001 and 2002 included a reduced cover of bare ground (21%), and by 2000 the species had colonized north-, east- and west-facing aspects, where bare ground cover and ambient temperature are typically lower than on south-facing slopes (Thomas et al. 2001, Davies et al. 2006). In conjunction with these changes, the species expanded its distribution in Britain, colonizing 179 habitat patches between 1982 and 2000 (Davies et al. 2005). Nevertheless, large areas of suitable habitat remained unoccupied (Fig. 1). In 2002, intensive distribution surveys were again repeated in the Surrey and Sussex networks, showing a limited number of colonization events since 2000.

The metapopulation model

The Incidence Function Model (IFM) (Hanski 1994) is a stochastic patch occupancy model based on the assumptions that 1) extinction risk is inversely related to patch area or population size, and 2) colonization probability is positively related to patch connectivity, where connectivity is a function of the distance to other occupied patches and their size. For each patch *i*, annual extinction risk (E_i) is related to patch area (A_i) by the term $E_i = (e/A_i^x) (1 - C_i)$, where *e* and *x* are species-specific parameters relating extinction risk to area, and $(1 - C_i)$ takes account of the rescue effect by reducing extinction risk for highly

connected patches. Annual colonization probability (C_i) is related to connectivity (S_i) by the term $C_i = S_i^2 / (S_i^2 + y^2)$, where y is a species-specific parameter relating colonization rate to connectivity. Connectivity is estimated as $S_i = \sum \exp(-\alpha d_{ij}) A_j^b$ (Moilanen and Nieminen 2002). Parameter α is a negative exponential dispersal kernel, with the proportion of per generation dispersal over distance d km or greater corresponding to $\exp^{-\alpha d}$; d_{ij} is the distance to patch i from each other patch j ; A_j is the area of each patch j ; and b scales emigration rate to the area of patch j . In this study b was set to 0.5 to account for the tendency of per capita emigration to be greater from smaller habitat patches in this and other species (Hill et al. 1996, Moilanen and Nieminen 2002). The IFM carries out maximum likelihood estimation of parameters e , x , y and α for a species based on snapshots of occupied and vacant habitat patches (Moilanen 1999, 2000). The model was developed to estimate parameters from steady state metapopulations, where observed occupancy is considered to result from approximately equal colonization and extinction rates, although parameters may also be estimated from population turnover without assuming equilibrium dynamics (Moilanen 2000). The estimated parameters can then be used to simulate dynamics for the species in the same or other, potentially non-equilibrium metapopulations, which may be valuable for predicting changes to species distributions following environmental change (Thomas and Hanski 2004).

A metapopulation model is an appropriate framework for modelling *H. comma*'s dynamics in Britain because 1) it has clearly defined, localized habitat patches; 2) most populations are small and at some risk of extinction, with occasional extinctions in 1982–2000 despite generally increasing population sizes (Thomas and Jones 1993, Davies et al. 2005); 3) there is limited dispersal between *H. comma* populations (Hill et al. 1996), and colonization rates decrease with distance from populations (Thomas and Jones 1993, Davies et al. 2005); 4) the probability of habitat patch occupancy increases with patch area and connectivity to other populations of the species (Thomas et al. 1992); 5) the distribution of the species in one population network in the UK (Surrey) remained rather stable between 1982 and 2002 (Davies et al. 2005), allowing us to estimate metapopulation parameters for this network assuming a steady state.

For IFM parameter estimation we used the Monte Carlo Markov Chain method (1000 function evaluations in initiation, 4000 function evaluations in estimation). We assumed, based on field observations, that the minimum area which would support a population from one year to the next without immigration (A_0) was 0.02 ha. For this analysis, we use the parameter estimates of $x = 0.28$, $y = 7.26$, $e = 0.34$, $\alpha = 0.45$ (Thomas et al. 2001) assuming that the distribution of the species in Surrey in 2000 (86 occupied and 30 vacant habitat patches) was representative of a stochastic steady state. We also estimated parameters using information on turnover in Surrey in 1982, 1991, 2000 and 2002, not assuming a stochastic steady state (Moilanen 2000). Simulations using these parameters ($x = 0.39$, $y = 9.44$, $e = 0.22$, $\alpha = 0.45$) are not described in detail since they gave generally similar results to the parameters assuming a steady state in Surrey.

Metapopulation simulations

We tested the effects of habitat use on *H. comma* range expansion rates by simulating metapopulation dynamics through habitat networks based on three different scenarios of habitat availability. In a thermally-restricted or “cold-world” scenario: 1) only areas of habitat with aspects between 150° and 250° were included, corresponding to 75% of occupied habitat patches in 1982. In a “warm-world” habitat definition, broadly corresponding to that used in 1982, 2) aspects between 100° and 300° were included, corresponding to 90% of populations in 1982. In the broadest or “hot-world” habitat definition, corresponding more closely to habitat use in 2000, 3) areas of chalk grassland on all aspects were included in the simulations.

We first validated the model by running 100 IFM simulations of 18 yr using the parameters estimated from the Surrey network, starting with the distribution of the species in each of the five habitat networks in 1982. To test whether the model successfully predicted the relative likelihood that different patches would be occupied in 2000, we used the area under the curve (AUC) of the receiver operating characteristic, a method which allows testing of the significance with which modelled probabilities correctly classify cases (Fielding and Bell 1997). In this case, we calculated whether the proportion of simulations where each patch was occupied was significantly related to observed presence or absence of *H. comma* in 2000 for each network using SPSS v. 15.0 for Windows. To test whether the model accurately predicted distance expanded, we calculated for each network the mean distance to colonized patches in 2000 from the nearest 1982 population. We then calculated the same measure for each 18 yr simulation (from 1982 to 2000), and tested whether observed range expansions lay outside the 95% confidence intervals (2.5th to 97.5th percentiles) of the modelled expansions. In order to test the longer term consequences of habitat use for the range dynamics of *H. comma*, we then simulated metapopulation dynamics for 100 yr for the three habitat use scenarios and five habitat networks. To test whether the distribution pattern used to initiate metapopulation simulations would influence long-term modelled dynamics, we started simulations both from a) the species distribution in 1982, and b) the distribution in 2000.

Results

Network habitat availability

Including habitat from all aspects, we identified 1916.6 ha of suitable habitat for *H. comma* in the five networks (Table 1a). Overall, the area of habitat including all aspects (the “hot-world” scenario) was 1.4 times greater than habitat availability for the “warm-world” scenario of 100–300°, and 2.1 times greater than habitat availability for the “cold-world” scenario of 150–250°. Changes in patch numbers were similar to changes in habitat area: the total number of suitable patches for all aspects was 1.3 times that for the 100–300° scenario, and double that for the 150–250° scenario. However, the difference between the three habitat scenarios differed markedly among networks: there

Table 1. Habitat availability and modelled patch occupancy in the five networks under the three habitat use scenarios: “hot-world” (0–360° aspect), “warm-world” (100–300°) and “cold-world” (150–250°). a) Total habitat area (ha), number of patches in superscript; b) mean proportion of patches occupied after 100 metapopulation simulations of 100 yr starting from the 1982 distribution of *H. comma* (superscript shows patch occupancy starting from the 2000 distribution; values in bold show significant differences from simulations initiated in 1982).

Network	Habitat scenario		
	0–360°	100–300°	150–250°
a) Total habitat area (ha) ^(n patches)			
Surrey	178.7 ⁽¹¹⁶⁾	176.9 ⁽¹¹³⁾	151.9 ⁽⁹⁵⁾
Sussex	713.7 ⁽²¹²⁾	349.3 ⁽¹²³⁾	199.5 ⁽⁶⁷⁾
Chilterns	286.7 ⁽¹⁶¹⁾	251.1 ⁽¹³⁵⁾	166.0 ⁽⁹⁰⁾
Kent	457.7 ⁽¹³⁶⁾	386.8 ⁽¹¹⁰⁾	302.0 ⁽⁷⁰⁾
Hampshire	279.8 ⁽¹¹⁷⁾	168.1 ⁽⁷²⁾	79.6 ⁽³⁵⁾
Total	1916.6 ⁽⁷⁴²⁾	1332.1 ⁽⁵⁵³⁾	898.9 ⁽³⁵⁷⁾
b) Proportion patch occupancy after 100 yr (start 1982) ^(start 2000)			
Surrey	0.74 ^(0.74)	0.73 ^(0.72)	0.64 ^(0.65)
Sussex	0.67 ^(0.70)	0.24 ^(0.28)	0.02 ^(0.03)
Chilterns	0.25 ^(0.31)	0.10 ^(0.13)	0.01 ^(0.01)
Kent	0.53 ^(0.55)	0.43 ^(0.43)	0.29 ^(0.31)
Hampshire	0.22 ^(0.47)	0.01 ^(0.28)	0.00 ^(0.00)

was little difference in habitat availability between scenarios for the predominantly south-facing Surrey network (most sites would already have been sufficiently warm in 1982), whereas in the two networks on the largely north-facing South Downs escarpment (Sussex and Hampshire), habitat availability for the 0–360° scenario was >3.5 times greater than for the 150–250° scenario (Table 1a).

Model validation 1982–2000

Simulations gave good predictions of the relative likelihood that individual patches would be occupied in 2000 in each network, with AUC values of 0.85–0.90 for the 0–360° networks, or of 0.73–0.88 for 100–300° networks (Table 2). AUC values were higher for the 0–360° scenario than for the 100–300° scenario in all networks except Kent, although differences were small.

The observed mean distance to each patch colonized by 2000 from the nearest patch that was occupied in 1982 ranged from 1.3 km in Surrey to 5.8 km in Sussex (Table 2). Observed mean colonization distances lay within the 95% confidence intervals for IFM simulations using the 0–360° habitat scenario for Surrey, Sussex and Hampshire, but were overestimated for Kent and underestimated for the Chilterns (Table 2). Simulations using the 100–300° habitat scenario underestimated range expansions for Sussex, Hampshire, and the Chilterns, and overestimated expansion in Kent. Colonization distance was accurately predicted in Surrey, for both 100–300° and 0–360° scenarios, but this was not surprising because in Surrey the 0–360° scenario was only 1% greater in area than the 100–300° scenario. In contrast, modelled distances expanded over 18 yr were greatly underestimated by the 100–300° scenario in Hampshire and Sussex, where 40 and 51% respectively of potential habitat lay outside the 100–300° range of aspects. Comparison of modelled occupancy in Sussex with that observed after 9, 18 and 20 yr from 1982 suggests that the 100–300° habitat scenario gave rather accurate predictions of occupancy after 9 yr (1991; Fig. 2b), but that by 2000 (18 yr) and 2002 (20 yr) inclusion of 0–360° habitat was necessary to produce accurate predictions

of occupancy (Fig. 2a). The overestimation of colonization distance in Kent appears to be related to a lower percentage cover of larval host plant than in the other networks, and if this is taken into account then observed colonization distances fall within the 95% confidence intervals for 0–360° simulations (Wilson et al. 2009).

100 year metapopulation simulations

Whether simulations were started with the 1982 or 2000 observed distributions of populations, each network showed a lower predicted proportion of patches occupied after 100 yr for the 150–250° habitat scenario than for the 100–300° scenario, and for the 100–300° scenario versus the 0–360° scenario (Table 1b). These differences were significant in all cases (Mann-Whitney U tests for 100 simulations in each scenario, $p < 0.001$), apart from 150–250° versus 100–300° simulations from the 1982 distribution in Hampshire, where most simulations suffered extinction in <100 yr. The difference was particularly marked for Sussex, a landscape that experiences a major increase in habitat availability with climate warming: on average only 2–3% of patches were occupied after 100 yr for the 150–250° simulations, 24–28% were occupied in the 100–300° simulations, and 67–70% were occupied in the 0–360° simulations (Table 1b, Fig. 2). In Sussex, the average number of patches that were occupied after 100 yr in the 0–360° scenario was more than five times that for the 100–300° scenario (Fig. 2).

Four of the habitat networks also showed significant differences in simulated occupancy after 100 yr depending on the starting distribution (1982 versus 2000). This difference appears to result from 1) the higher risk of extinction of 1982 metapopulations, which had fewer populations than in 2000; 2) some observed long-distance colonizations between 1982 and 2000 which led to population networks predicted to be persistent in the long-term. Sussex, Hampshire and the Chilterns all showed significantly higher occupancy when started with the 2000 distribution, both for 0–360° and 100–300° scenarios (Mann-Whitney U tests for 100 simulations in each

Table 2. Validation of metapopulation simulations against observed distribution change in 1982–2000. Average expansion distance is the mean distance to colonized patches from the nearest patch occupied in 1982. Modelled expansions show the median and 95% confidence intervals of 100 Incidence Function Model (IFM) 18 yr simulations; 95% CIs of modelled expansion are shown in bold where they include the observed expansion distance. AUC is calculated for observed patch occupancy in 2000 against proportion occupancy in the 100 simulations.

	Patch occupancy, 2000		Average expansion distance (km)			AUC of modelled patch occupancy		
	n present	n absent	Observed distance	IFM 0–360°	IFM 100–300°	IFM 0–360°	IFM 100–300°	
Surrey	86	30	1.33	0.95 (0.65–1.49)	1.27 (0.71–1.84)	0.88***	0.87***	
Sussex	79	96	5.80	6.21 (4.48–7.21)	2.38 (0–2.93)	0.87***	0.83***	
Chilterns	44	117	3.85	1.93 (0.96–3.41)	1.32 (0.60–2.30)	0.86***	0.86***	
Kent	27	102	3.56	5.42 (4.86–5.98)	5.20 (3.69–5.97)	0.85***	0.88*	
Hampshire	12	105	5.43	6.10 (0.22–8.64)	0 (0–2.18)	0.90***	0.73*	

scenario, $p < 0.01$). Kent showed a significant difference for the 0–360° scenario ($p < 0.001$), whereas Surrey showed no significant differences in occupancy related to the starting distribution, probably because the butterfly was already widespread and had limited capacity to spread in this landscape, and can fully exploit the remaining patches from either starting scenario. For the 150–250° simulations, occupancy did not differ depending on starting conditions, apart from in Sussex where occupancy was marginally higher when starting from 2000 ($p = 0.02$).

Simulated UK distributions for *H. comma* after 100 yr are shown in Fig. 3, based on 2×2 km distribution “tetrads” (commonly used in regional species distribution maps). In total, 287 tetrads with suitable habitat were identified in the five networks, of which 26 were occupied in 1982 and 96 were occupied in 2000. For the 0–360° habitat scenario, *H. comma*’s distribution was predicted to include 136 tetrads after 100 yr (occupied in 50% or more of simulations) when starting with the 1982 distribution, or 164 tetrads when starting with the 2000 distribution. The 100–300° scenario led to a distribution size after 100 yr of 61 tetrads (start 1982) or 81 tetrads (start 2000). The 150–250° scenario led to a predicted distribution size of 31 tetrads when starting with either distribution: for this scenario, the networks in Sussex, Hampshire and the Chilterns were expected to suffer extinction in >50% of simulations (e.g. Fig. 2c, f for Sussex).

Discussion

Here we show how changes in habitat use and availability, as may occur in response to climate change, can influence rates of range expansion through fragmented landscapes. The results shed light on the processes that govern the size and pattern of species distributions, and have implications for the conservation of localized species in a changing climate.

Habitat availability and metapopulation dynamics

We studied the habitat use, distribution and dynamics of the butterfly *Hesperia comma* in its five main UK population networks. The breadth of habitats used by *H. comma* increased between 1982 and 2000 in association with climate warming (Thomas et al. 2001, Davies et al. 2006). Habitat area in the five networks increased by 1.4 times (and the number of patches by 1.3 times) because of an increase in the range of aspects used, from 100–300° in 1982 to 0–360° in 2000. Greater habitat availability should lead to lower rates of local extinction due to larger population sizes; and to higher rates of colonization, because areas of suitable habitat are closer together, and more and larger populations are available to act as sources of colonists. To model these effects, we applied the Incidence Function Model (IFM) (Hanski 1994, 1999) to the dynamics of *H. comma*. The model gave a relatively good fit to patterns and rates of range expansion between 1982 and 2000, capturing the differences in colonization distances among networks varying in habitat area and connectivity (see also Wilson et al. 2009). Furthermore,

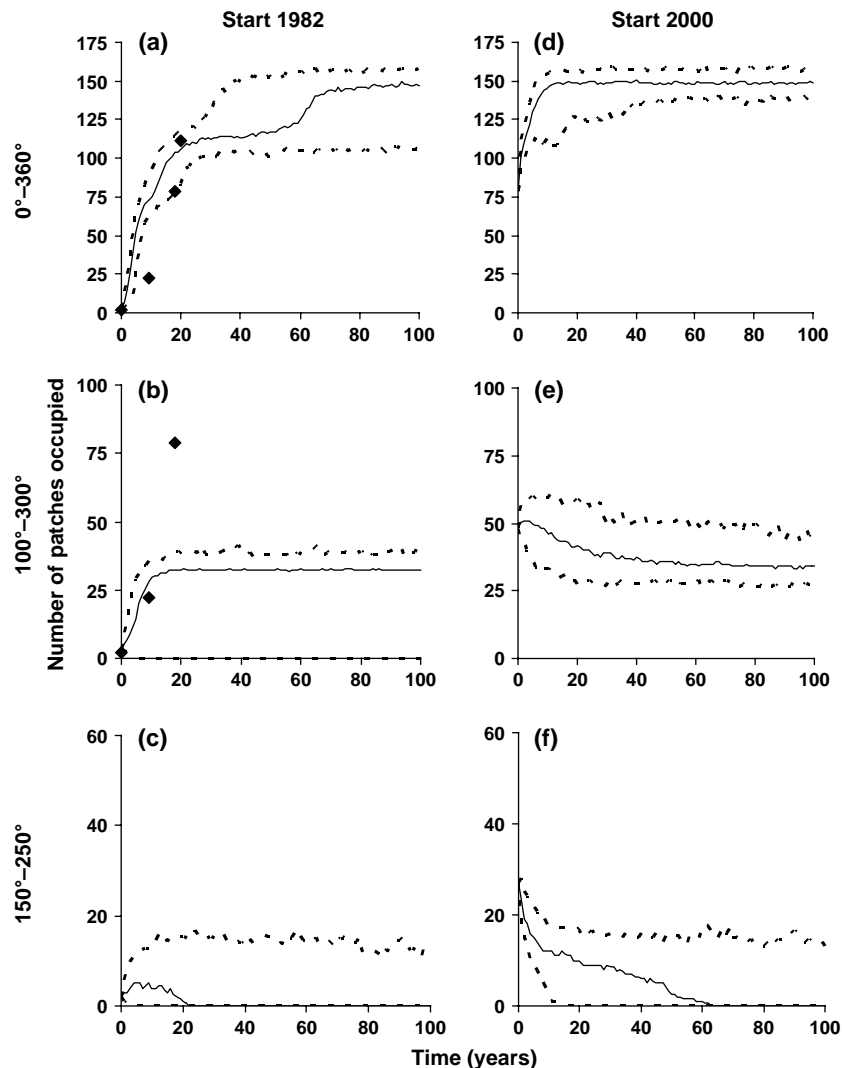


Figure 2. Modelled patch occupancy over 100 yr in Sussex based on different habitat availability and starting distributions. Panels a–c show simulations starting from the 1982 distribution; d–f show simulations from the 2000 distribution. Habitat availability includes all available aspects (a, d), 100–300° aspects (b, e), or 150–250° aspects (c, f). Solid line shows median patch occupancy from 100 IFM simulations, dashed lines show 95% confidence intervals (lower interval reaches zero occupancy in b, c and f). Diamonds in panels a and b show observed occupancy in 1991 (9 yr since 1982), 2000 (18 yr) and 2002 (20 yr).

the model showed how rates of range expansion accelerated through *H. comma*'s population networks associated with wider habitat availability, as demonstrated by the underestimation of empirically observed expansion rates by metapopulation simulations using the 100–300° habitat scenario (Table 2). Our estimated changes to habitat area assume that all aspects were managed appropriately for *H. comma* in 1982 and 2000: in practice, much habitat in 1982 was not managed appropriately for *H. comma*, and subsequent introduction of grazing management as part of conservation programmes and agri-environment schemes has been necessary for the species to exploit potential habitats (Davies et al. 2005). These changes to habitat management may partly explain why observed expansion rate in Sussex in 1991 was overestimated by the simulations (Fig. 2a).

The consequences of greater habitat availability and faster range expansion rates for long-term distribution

patterns were investigated using 100 yr metapopulation simulations, from *H. comma*'s distribution either in 1982 or 2000. Broader habitat use led to a higher proportion of patches occupied after 100 yr (ca 1.5 times more for 0–360° versus the 100–300° scenario; Table 1), which equated to approximately double the number of patches occupied, and double the overall number of 2 × 2 km “tetrads” in *H. comma*'s distribution (Fig. 3). Thus, metapopulation dynamics provided the mechanism linking changes in habitat use to relatively large-scale changes to the species distribution.

Habitat fragmentation and species range shifts

Dispersal failure is potentially hugely important in determining the consequences of climate change for biodiversity. The complete failure of species to expand their distributions

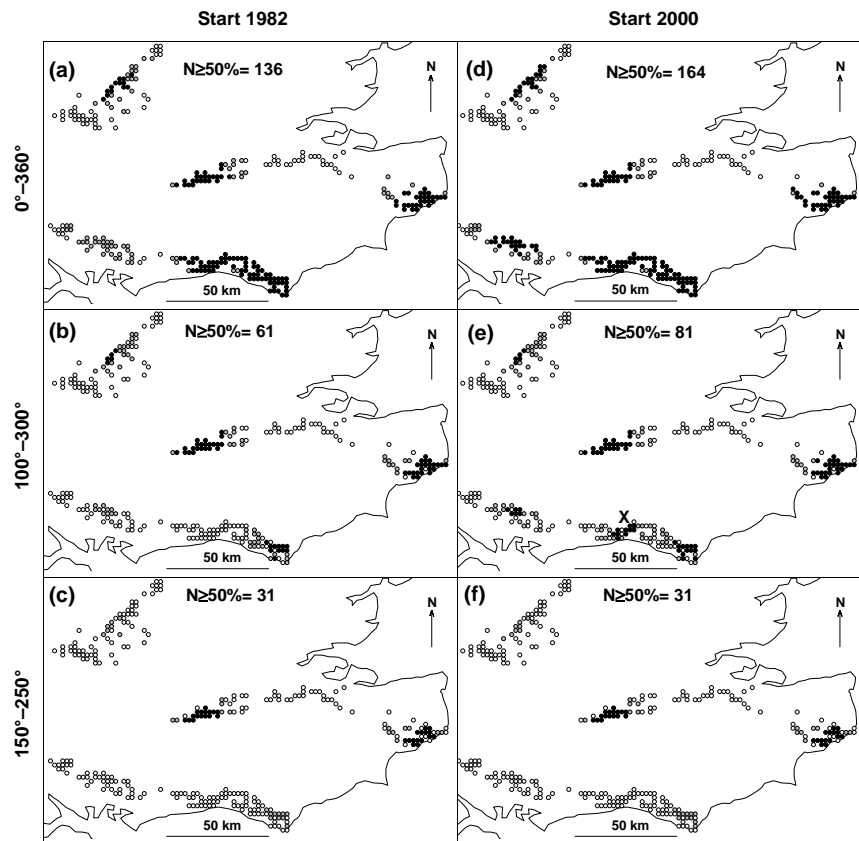


Figure 3. Modelled 100 yr expansions by *Hesperia comma* based on different habitat availability and starting distributions. Maps show the modelled species distribution in 2×2 km squares from 100 IFM simulations. Symbols show: black – occupied in >50 simulations; grey – occupied in 1–50 simulations; white – habitat present but never occupied. Panels a–c show modelled expansions from the 1982 distribution, d–f show modelled expansions from the 2000 distribution. Habitat availability includes all available aspects (a, d), $100\text{--}300^\circ$ aspects (b, e), or $150\text{--}250^\circ$ aspects (c, f). (e) X shows a persistent part of the Sussex network colonized between 1982 and 2000.

into new regions could approximately double extinction rates from climate change, relative to rates that assume full colonization (Thomas et al. 2004). Research on butterflies (Warren et al. 2001, Menéndez et al. 2006) and birds (Julliard et al. 2004) has already shown that more wide-ranging or habitat generalist species have been able to shift their distributions in response to climate change much more readily than sedentary species with localized habitat distributions. Our study species *H. comma* is a habitat-specialist that has been able to expand its distribution (Thomas et al. 2001, Davies et al. 2006). However, despite increasing habitat availability because of climate change, conservation management and agri-environment schemes (Davies et al. 2005), *H. comma*'s range expansion rates have been constrained by habitat fragmentation (Wilson et al. 2009). In this paper, we show that even in the long term the species is only expected to colonize a fraction of its available habitat. The most optimistic “hot-world” metapopulation simulations (with the broadest habitat requirements) suggest that after 100 yr only about a half of existing suitable habitat patches would be occupied by the species (49% if starting with the 1982 distribution; 56% if starting with the 2000 distribution; or 47% of 2×2 km tetrads containing suitable habitat starting from 1982, versus 57% starting from 2000). Should regional habitat requirements become narrower, then the proportion of suitable habitat occupied by the species would likewise be expected to reduce (Fig. 3).

Our results should be considered as indicative of the potential differences in realized range expansions among landscapes differing in topography (slope and aspect) and level of habitat fragmentation, rather than as absolute predictions of range expansion rates. It has been shown that insect dispersal rates may increase related to warmer temperatures (Nieminen 1996, Sparks et al. 2005), potentially leading to faster colonization rates. Furthermore, increased dispersal ability may be selected for in newly established populations (Hanski et al. 2006) and at the expanding front of species distributions (Niemela and Spence 1991, Thomas et al. 2001, Simmons and Thomas 2004). In the case of *H. comma*, individuals in the expanding Sussex network show larger thorax:abdomen size ratios than in the more stable Surrey network (Hill et al. 1999), suggesting that more dispersive forms may indeed have been selected for by the process of range expansion. Nevertheless, parameters estimated from the Surrey network gave relatively good fits to expansion rates and patterns in the other metapopulations (Wilson et al. 2009). Habitat availability at the landscape scale may still be critical in explaining range expansion rates, since a sufficient density of habitat may be necessary to promote colonization in the first place, and therefore to select for dispersive forms.

The differences among the five networks in observed and modelled rates of range expansion, and in future predicted

distributions under the three habitat scenarios, show that there is an important landscape context to species responses to climate change. The metapopulation in one landscape (Surrey) was persistent under all three habitat scenarios, and showed no significant differences in long term distribution patterns related to the distribution used to initiate simulations (1982 versus 2000). In contrast, the Sussex network showed significant differences in long term occupancy among all three habitat scenarios, and between 1982 and 2000 starting conditions; while the Hampshire metapopulation was only predicted to be persistent for 0–360° and 100–300° scenarios started from 2000. There is a relatively small proportion of habitat in Sussex and Hampshire on south-facing slopes, hence the ability to use a wider range of aspects has been critical in allowing *H. comma* to expand its distribution from the regional refuge populations (probably one population in each network in the late 1970s or early 1980s; Thomas et al. 1986). In contrast, the majority of habitat in the Surrey network is south-facing; persistence in this network seems likely, as long as environmental change does not render south-facing slopes unsuitable. Moreover, the proportion of habitat occupied by *H. comma* remains relatively high in Surrey, because although the overall area of habitat is quite small, patches are densely distributed over a relatively restricted area.

Two scenarios could lead to metapopulation declines in Surrey: reduced habitat suitability if south-facing slopes become too hot or dry under climate change, or a reduction in suitable warm microclimates for larval growth because of increasing vegetative growth related to longer growing seasons or nitrogen deposition (WallisDeVries and Van Swaay 2006). In fact, south-facing slopes may be relatively resistant to the latter type of vegetation change because of frequent exposure to drought conditions (Bennie et al. 2006). Simulations suggest that the Surrey metapopulation may be unlikely to expand because of a low density of suitable habitat at its eastern and western extremes (Fig. 1, 3). Nevertheless, a site at the eastern edge of the Surrey network (11.4 km from the nearest 1982 population) was colonized in 2002, suggesting that there is scope for further expansion in this landscape. Metapopulation simulations using parameters derived from the Surrey network should be treated with some caution since they rely on the assumption that the Surrey network in 2000 was at colonization/extinction equilibrium. Furthermore, the uncertain future interactions between climate, habitat condition and habitat use mean that long-term changes to species distributions may be very difficult to predict with any degree of certainty.

Simulations suggest that in many fragmented landscapes, expanding metapopulations do not approach equilibria gradually (e.g. for Sussex see Fig. 2a, d). Instead, high occupancy is achieved quickly among habitat patches close to the starting distribution. Subsequently, relatively rare long-distance colonization events result in colonization of other persistent habitat sub-networks which can achieve high levels of occupancy, leading to what appear as step-changes in metapopulation occupancy (e.g. Fig. 2a, step-changes ca 20 yr and ca 60 yr into the simulation). Such relatively rare colonization events can be important in determining large-scale species distributions, and probably play a key role in explaining why simulations started from

the 2000 distribution achieved greater patch occupancy than those started from the more restricted 1982 distribution. Indeed, there is a risk that models such as that used here might underestimate rates of range expansion because of the role played by rare long-distance colonization events.

Refuge populations for species may reflect historical climate or habitat requirements (Petit and Burel 1998, Helm et al. 2006), and may not necessarily represent the most efficient locations for seeding range expansions into habitats which are suitable now or in the future. The differences in simulation outcomes starting from 1982 versus 2000 distributions show that historical factors can influence long-term distribution size and pattern, and could constrain conservation efforts to facilitate species range shifts in response to climate change. In Sussex, for example, the observed 1982–2000 range expansion resulted in *H. comma* colonizing a part of the habitat-network that is persistent under the 100–300° scenario (Fig. 3e). As a result, 100–300° simulations started with the 2000 distribution achieved significantly higher occupancy than those started with the 1982 distribution (this was not the case in Surrey or Kent, where additional persistent sub-networks had not been colonized between 1982 and 2000). In such circumstances, population translocations could play a part in facilitating species range shifts (Hoegh-Guldberg et al. 2008), and approaches similar to that taken here could assist in identifying habitat networks where species introductions would be more likely to result in range expansions. There is also a message for projects aiming to restore habitat connectivity. The climate-dependent nature of habitat associations may result in climate-driven changes (increases and decreases) to habitat availability which are much larger than those brought about by conservation programmes for particular species and landscapes. Therefore, such schemes need to be carefully targeted if they are to achieve real increases in species' expansion rates.

Conclusions

The majority of species across the world exhibit very small areas of occupancy (Gaston 1994, Kunin and Gaston 1997), as exemplified by the many butterfly species that are restricted to a few tens of km² or less in Britain (Cowley et al. 1999). Many, and probably most, such localized species perceive the environment as heterogeneous, with small areas of suitable habitat surrounded by much larger areas which are unsuitable for reproduction (Soberón pers. comm.). Species of this type shift their distributions by colonizing from one patch of suitable habitat to another, rather than expanding as a continuous front. Even if such species do not exhibit metapopulation dynamics at equilibrium, they are likely to do so during climate change, which is expected to render some existing habitats unsuitable and other previously-unsuitable locations available for colonization. Thus, metapopulation models could provide a suitable framework for the analysis of range shifts by many habitat specialist species. Our research on the butterfly *Hesperia comma* shows how metapopulation models can link fine-scale changes in habitat use to large-scale changes in species distributions. The results of long-term metapopulation simulations show how metapopulations in different

landscapes may respond differently to climate-related changes in habitat use, because of regional differences in habitat area, configuration, and type (in this case, aspect). The implication is that it will be more straightforward to adapt conservation to climate change in some landscapes than in others, and that species-specific responses to adaptation programmes may differ markedly (see also Vos et al. 2008).

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