# The effects of spatial patterns in habitat quality on community dynamics within a site

R. T. CLARKE[1], J. A. THOMAS[1], G. W. ELMES[1] AND M. E. HOCHBERG[2]

[1] *Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset BH20 5AS, UK*
[2] *Laboratoire d'Écologie, Université Pierre-et-Marie-Curie, (CNRS–URA 258), 7 quai St. Bernard, Bat.A, 7ème étage, 75232 Paris Cedex 05, France*

## SUMMARY

Metapopulation studies of single species have shown that the size and spatial arrangement of patches of assumed uniformly 'suitable' habitat can influence their population dynamics and persistence. We investigated whether variation in the spatial arrangement of 'suitable' habitat of varied quality within a single site can affect the abundance and persistence of interacting species. We accomplished this by extending a field-based spatial simulation model of four interacting species at two trophic levels (an endangered butterfly, its larval food-plant, and two ants). The habitat on sites with the same average and range of qualities was rearranged to give varying degrees of local spatial heterogeneity or 'site ruggedness'. We found that the ant species that acts as host to the butterfly caterpillars decreased with site ruggedness. The impact on the butterfly was more substantial: it often failed to persist on very rugged sites. Despite being free-ranging over the whole area, the butterfly's persistence depends on the arrangement of habitat quality at a finer spatial scale, due to its interactions with species possessing narrower habitat niches and more localized dispersal. Ruggedness also influenced the rate of recovery of the host ant, and hence community structure, for more than a century following the butterfly's extinction.

## 1. INTRODUCTION

Two aspects of habitat change are widely accepted as the reasons why local rates of extinction among butterflies (and probably other insects) have exceeded those of plants and vertebrates this century within surviving ecosystems in intensively managed regions of the Palaearctic (Thomas 1991; Thomas & Morris 1994; New *et al.* 1995; Ae *et al.* 1996):

(i) Habitat quality: the niches occupied by the immature stages of many insects have proved to be narrower than was once thought, and apparently trivial changes in vegetation structure, often associated with altered management, may change the quality of a species' habitat within a site, greatly affecting its intrinsic rate of increase and the site's carrying capacity (Thomas 1991).

(ii) Habitat availability: where habitat of suitable quality for a species still exists, the size, shape, isolation and dynamics of habitat patches across the landscape may have profound effects on the persistence of populations, due to the comparatively poor dispersal shown by many insects (Thomas *et al.* 1992; Hanski & Thomas 1994; Hanski *et al.* 1995).

All the studies leading to these explanations involved considerable simplifications. Work on habitat quality was conducted within individual sites and either considered changes in the average quality for a species' habitat over time (reviewed in Thomas (1991); New *et al.* (1995)) or showed that the existence of heterogeneity in habitat quality within a site increases persistence (e.g. Singer 1972; Sutcliffe *et al.* 1997).

In contrast, multi-site and spatial (metapopulation) studies have usually considered binary systems in which the availability of uniformly 'suitable' or 'unsuitable' patches of habitat has varied in a landscape. For the same reasons of practicality, both types of study have involved single or pairs of species, despite recent evidence that very different conclusions about community dynamics, individual species' persistence and abundance may be obtained by studying the dynamics of systems containing more than two interacting species (Begon *et al.* 1996; Holt 1997). However, such community studies have assumed that the quality of a species' habitat, if considered at all, was uniform and constant in space and time.

The influence of differences in habitat niche, competitive or dispersal abilities on the coexistence of spatially interacting species has been variously modelled by the use of partial differential equations (Holmes *et al.* 1994), spatial 'lottery' models where plant species compete for possession of vacant cells made vacant by individual deaths or disturbance (Shmida & Ellner 1984) or more spatially explicit cellular automaton simulation models (Colasanti & Grime 1993; Halley *et al.* 1994).

In this paper we consider a new combination of some of the variables employed by these approaches to population dynamics and community structure. We employ an existing field-based spatial simulation model

(Hochberg *et al.* 1994) of four interacting species (a butterfly, a plant and two ants) to investigate whether variation in the spatial arrangement of habitat of varied quality within a single site (referred to as 'habitat ruggedness'; see Methods) can affect the abundance and persistence of these species, as well as the rate of reassembly of the community after one species becomes extinct. We again considered a simplified system. It involved only one isolated habitat patch or site that remained constant in size, shape and average quality over time: we simply rearranged the spatial distribution of the micro-areas of slightly different, but suitable, habitat within it. The results demonstrate a potential role of spatial habitat heterogeneity *within* sites in population and community ecology.

## 2. METHODS

### (*a*)  *The biological system*

The species studied comprise the endangered 'Large Blue' butterfly, *Maculinea rebeli*, its early larval food plant, *Gentiana cruciata*, and two competing species of *Myrmica* ant that are parasitized by *M. rebeli* in its final instar (Thomas *et al.* 1989, 1993; Elmes *et al.* 1991*a, b*, 1996). *M. rebeli* has one generation per year, *G. cruciata* is perennial, and unparasitized *Myrmica* colonies typically live for ten or more years, producing two cohorts of brood a year and workers that live for less than two years. Sites supporting this community are generally isolated, 0.25–1 ha in size, and have clear-cut boundaries defined by the distribution of *G. cruciata* (Elmes *et al.* 1996). Adult butterflies remain within these boundaries, ovipositing throughout the site on flowering gentians. The young caterpillar develops rapidly on gentian flowers, falls to the ground and awaits discovery by a foraging *Myrmica* worker, which mistakes it for an ant larva and carries it back to the ant nest. Over the next ten months, the caterpillar feeds on the resources inside its ant nest, increasing over 50-fold in weight before pupating. In the wild, *M. rebeli* is adopted with equal alacrity by any of the three to four *Myrmica* species living on the site (Elmes *et al.* 1991*a*). However, it survives well in the nests of only one species, *Myrmica schencki*, termed here the 'host' species in contrast to 'Other *Myrmica*' (Hochberg *et al.* 1992). Thomas *et al.* (1989) found 89% of mature *M. rebeli* larvae on French sites in host ant nests, and since the study has been extended to include other sites in France, this estimate has risen to over 95%. Moreover, at the Spanish site for which the model was parameterized, 100% of recorded emergences were from *M. schencki* nests (unpublished data). Although higher survival rates to maturity have been recorded for Other *Myrmica* in the laboratory, reared under optimal conditions where food is not limiting (which seldom occurs naturally) (Elmes *et al.* 1991*b*), survival was still significantly greater in *M. schencki* nests. Caterpillars cause substantial damage to infested host ant nests and some proportionally less harm to Other *Myrmica* nests. Although we have estimated that, on average, the relative damage ($\mu$) of adopted caterpillars to Other *Myrmica* is 50% (Hochberg *et al.* 1994), in the wild it may be considerably less than this.

It is important to note that the populations of gentians, butterflies and ants operate at different spatial scales within our definition of a site. Both the plant and the adult butterfly exist as single discrete populations that can potentially occupy every part of a site, whereas each ant colony occupies only about 11 m² , and is in many respects comparable to a separate population. Furthermore, each species of *Myrmica*

inhabits a narrower niche than either the gentian or adult butterfly (Thomas 1995), and a typical site contains some subareas that are unsuitable for *M. schencki*, others that are unsuitable for Other *Myrmica* and many subareas where both ants compete with varying degrees of dominance. Thus although the entire site represents one continuous habitat patch for the butterfly and the gentian, for each ant species it is more akin to a landscape containing a metapopulation of colonies exploiting many habitat patches with varying degrees of connectivity.

### (*b*)  *The spatial model*

Hochberg *et al.* (1994) constructed a spatially explicit mechanistic model for the interactions of these species based on measurements of 19 life-table and other parameters measured in the field or laboratory. The 'site' consisted of a grid of $30 \times 30$ cells equal to a total area of 1 ha, with each cell corresponding to the foraging range of a typical *Myrmica* colony. The sloping grassland site for which the original model was calibrated contained a continuous physical gradient of habitat in which gentians grew and over which the butterflies flew, ranging from cool moist to hot dry grassland (Hochberg *et al.* 1994). This is represented by a simple gradient of 30 steps ($=$ cells) across the $x$ axis (figure 1*a*). Each species of *Myrmica* had a narrower niche than either the gentian or the adult butterfly, and had different growth rates and nest capacities according to their positions across this gradient (figure 1*b*). Our study used the same model specification and parameter values as in Hochberg *et al.* (1994), except that (i) the probability, $P_{jx}^{bud}$, of an ant colony of species $x$ in habitat type $j$ budding into a vacant adjacent cell was made a more realistic function, $(2W/\epsilon_j^x - 1)$, of colony size, $W$, relative to cell colony capacity, $\epsilon_j^x$, and (ii) there was an 8% density-independent annual mortality of whole ant colonies (Brian 1972).

In the absence of the butterfly, the ants established a dynamic equilibrium across the gradient, with *M. schencki* predominating towards the hotter end and Other *Myrmica* peaking in cooler moister cells (figure 1*c*); this balance altered in favour of non-host species when the butterfly was introduced due to the greater harm it does to its host ant's colonies (figure 1*d, e*). Thus this site contained a range of subareas within it that varied in quality from strongly productive sources to absolute sinks for each species (Watkinson & Sutherland 1995). We have since shown that this same model is valid on other sites containing similar variation and patterns of habitat quality to the original one (Elmes *et al.* 1996).

### (*c*)  *Adaption of the model to study within-site effects of spatial heterogeneity in habitat quality*

The simple linear gradient in habitat quality in the basic model (figure 1*a*) was rearranged to examine whether different degrees of habitat spatial heterogeneity within a site affect the balance between competing *Myrmica* species and the site's carrying capacity for the butterfly. In each case, the same 1 ha size of site was used as in the basic model, and we kept precisely the same amounts (30 cells) of each of the 30 slightly different types of occupiable habitat within it. However, instead of distributing these cells as a simple slope from cool damp (type 1) to hot dry (type 30) (figure 1*a*), we rearranged them to create sites with $k$ (1, 2, 4, 8, 16, 32 or 64) dry 'hills' set among damper areas (figure 1*f, g*) and, as an extreme case, we also distributed each cell type randomly.

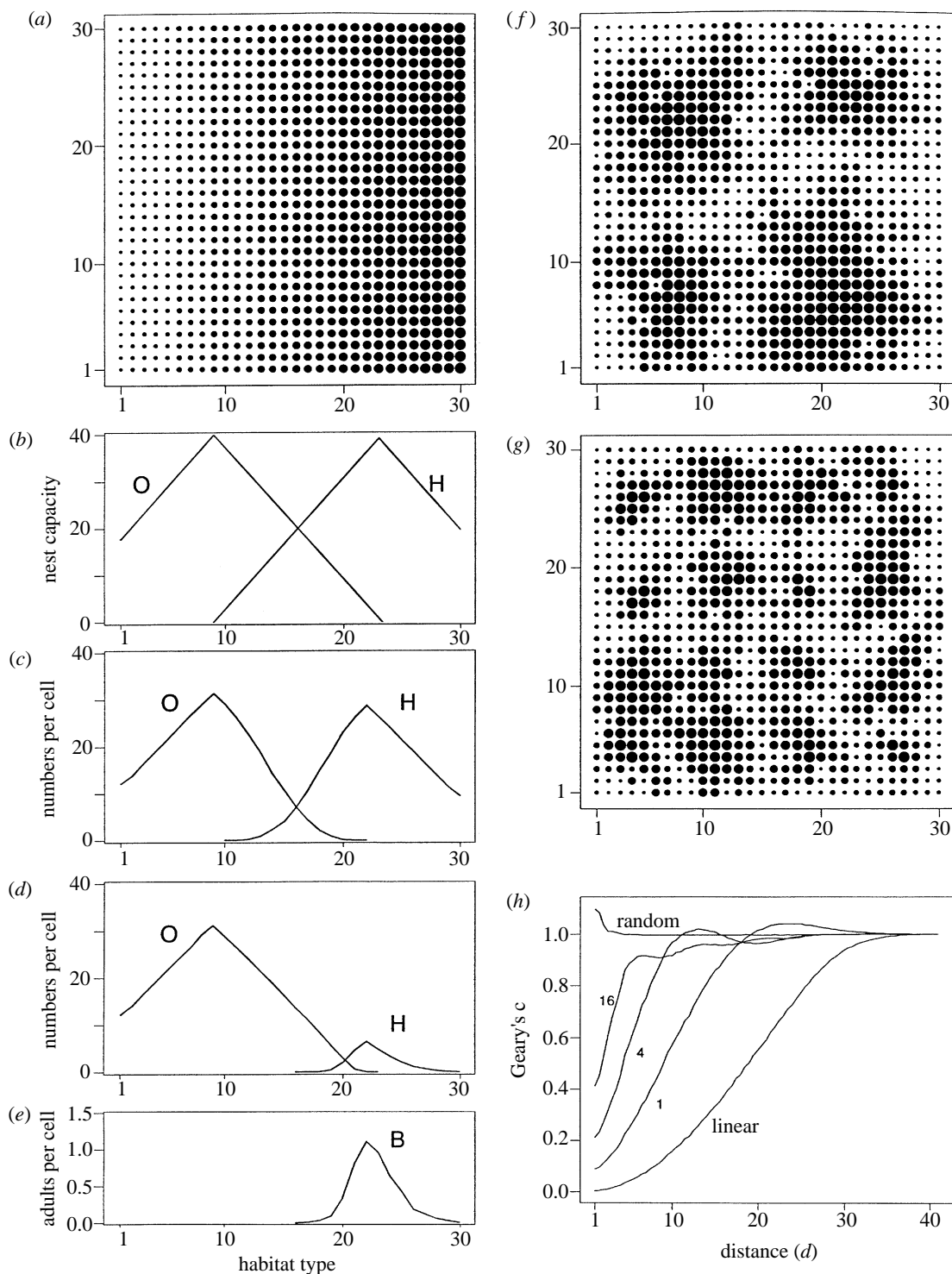These spatial arrangements were generated by the following algorithm:

Figure 1. Spatial patterns of habitat within sites and population effects. (*a, f, g*) Notional 1 ha sites each comprising a grid of 30 × 30 cells with cell habitat-type ranging from cool and wet (smallest circles, type 1) to hot and dry (largest circles, type 30), arranged as (*a*) linear gradient, (*f*) four dry 'hills' and (*g*) 16 dry 'hills'. (*b*) The size of host ant *Myrmica schencki* (H) and other non-host *Myrmica* (O) colony supported per cell (expressed in butterfly equivalents) in the absence of interspecific competition at different positions along the linear habitat gradient (*a*). (*c*) and (*d*) Average size of colonies in each habitat type when the two *Myrmica* species compete and the butterfly is (*c*) absent or (*d*) present. (*e*) Average number of butterflies (B) produced per cell. (*h*) Plot of Geary's standardized spatial semi-variance, $c_d$, of habitat in cells up to a distance *d* cells apart for sites with habitat arranged in a linear gradient, 1, 4 or 16 dry 'hills', or randomly. (*c*)–(*e*) show the means of the last 10 years of 50 simulation runs, each of 120 years duration with one butterfly introduced in year 50 on sites with a linear habitat gradient.
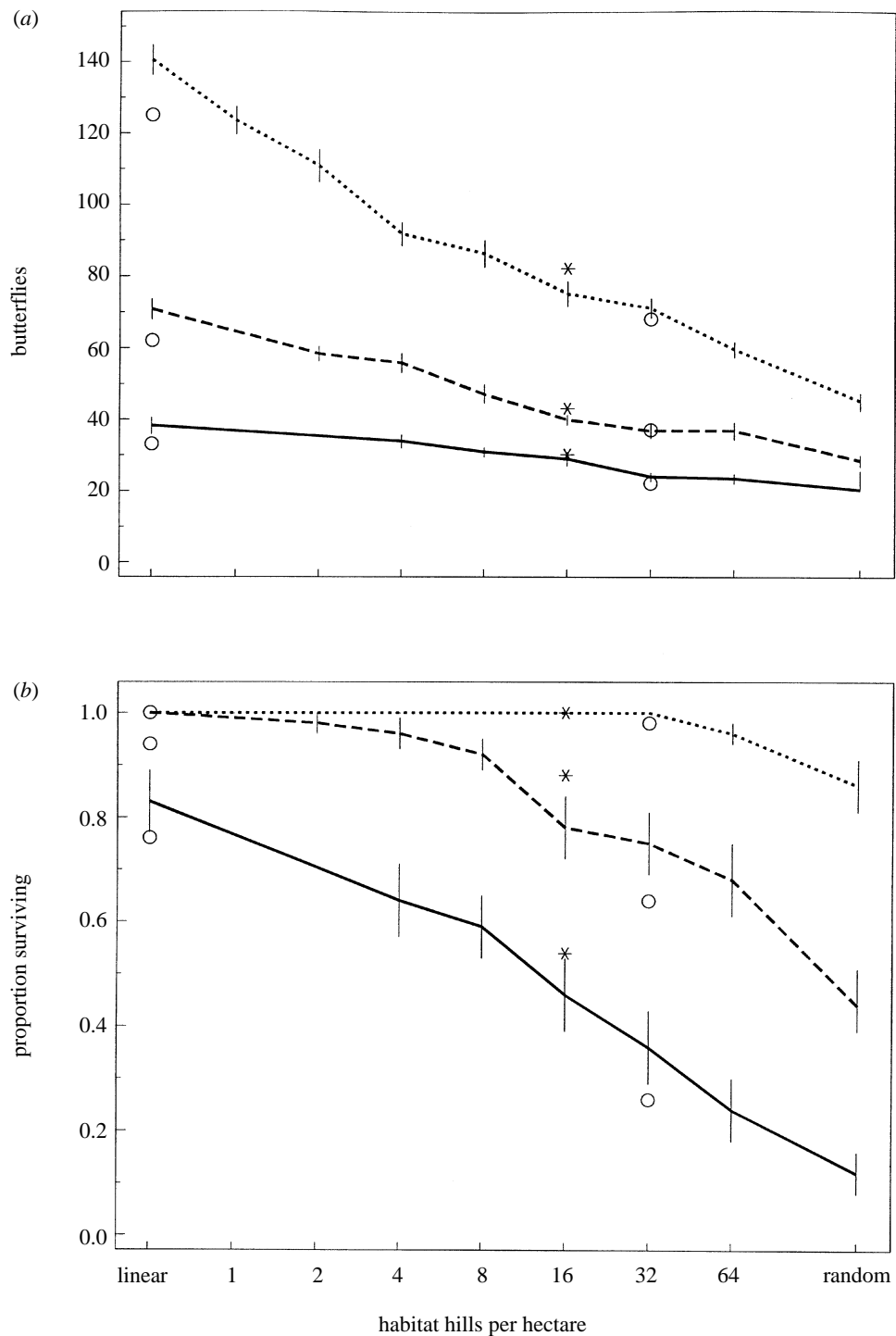
Figure 2. Effects of habitat ruggedness on (*a*) the average adult abundance (when persisting) and (*b*) the persistence of *M. rebeli* butterfly populations on sites of three different sizes: 0.25 (solid line), 0.5 (dashed line) and 1 ha (dotted line). The ruggedness of sites varied from the simple linear gradient base-line (linear), through an increasing number of hot/dry hilltops (1, 2, 4, 8, 16, 32, 64 per ha); greatest ruggedness was obtained by distributing the cells of habitat randomly. Results show the means (±s.e.) of the last 10 years of 50 simulation runs, each of 120 years duration with one butterfly introduced in year 50. Stars denote the equivalent results for each of the three sizes of site when habitat is arranged to give a density of 16 'damp hollows' per hectare. Open circles denote results for sites with annual variation in cell habitat quality (see methods) with linear habitat and 32 'dry hilltops' per hectare.

(i) Arrange the habitat type values $(1-m)$ of all cells on the site in decreasing order in a one-dimensional array, X, i.e. the $n_m$ values of type $m$ first, then the $n_{m-1}$ values of $m-1$, and so on. (In our 1 ha site, $m = 30$ and $n_i = 30$, $i = 1, ..., m$.)

(ii) Evenly space the required $k$ 'hilltops' on the site and assign them the habitat type of the first $k$ values in X.

(iii) Assign the next unallocated value in array X to a randomly chosen cell on the site, subject to the restrictions that the cell must be currently unassigned and that either at least two of the immediately surrounding cells must be already assigned or the cell is next to a hill currently comprising only one cell.

(iv) Repeat step (iii) until all cells on the site have been assigned habitat types.

This produces a sequence of sites for which adjacent cells are progressively more variable in habitat type. This increased localized habitat variability makes a site more fragmented for both of the ant species and hence for the later immature stages of the butterfly, because these ant colonies spread by stepping-stone dispersal (Kimura & Weiss 1964) into adjacent vacant cells (Hochberg *et al.* 1994). Habitat spatial heterogeneity can be quantified by Geary's standardized index of spatial semi-variance, $c_d$, defined as half the average squared difference in habitat types of all pairs of cells whose centres are at most '$d$' cells apart, divided by the variance of all cell habitat types on the site (Legendre & Fortin 1989) (figure 1$h$). A value of $c_d = 1.0$ implies approximate spatial randomness of habitat exists on the site when viewed in spatial units of size $d$. Average habitat heterogeneity of adjacent cells (first-order spatial heterogeneity) is measured by $c_{\sqrt{2}}$. As the term 'spatial heterogeneity' is ambiguous, without a definition of the spatial scale to which it refers (Dutilleul & Legendre 1993), and 'fragmented' habitat inappropriately implies isolated patches or islands of non-differentiated 'suitable' habitat, we will refer to Geary's $c_{\sqrt{2}}$ for the habitat as the 'ruggedness' of the site, high values corresponding to very rugged sites (figure 1$h$). The ruggedness does not affect the distribution of the food plant or adult egg-laying, which both operate on the scale of the whole site.

The algorithm was also used to derive model 1 ha sites with the inverse habitat patterns of 'damp hollows' surrounded by drier cells, achieved by arranging all the habitat values in increasing rather than decreasing order in step (i). The average value of Geary's $c_d$ is the same for sites with $k$ dry hills as with $k$ damp hollows hence, as defined, both types of site have the same degree of habitat ruggedness. Simulations were also repeated using smaller sites of 0.5 ha $(21 \times 21$ cells) and 0.25 ha, which are more typical of the size of real sites elsewhere (Elmes *et al.* 1996).

We also simulated the effects of temporal fluctuations in cell habitat quality (e.g. due to annual variation in weather) on the above results. In the standard model of Hochberg *et al.* (1994) and figure 1$b$, the nest capacity (in butterfly equivalents), $\epsilon_j^x$, of ant species $x$ in a cell of habitat $j$ is given by:

$$\epsilon_j^x = C^x - b|j - j_{xm}| \qquad (1)$$

where $b = 2.8$; $C^x = 39.2$ and $j_{xm} = 22$ for $x = $ host; $C^x = 40$ and $j_{xm} = 9$ for $x = $ Other *Myrmica*.

Temporal variation was incorporated by making the optimum habitat, $j_{xmt}$, for each species in generation $t$ a variable, defined as

$$j_{xmt} = j_{xm} + y_t \qquad (2)$$

where $y_t$ was a random normal deviate with a mean of zero and standard deviation of 2.0. This assumes all cells across the site would be affected in the same way (e.g. as in a dry year).

## 3. RESULTS

Any increase in the ruggedness of habitat quality within a site results in a fall in its carrying capacity for the butterfly, *Maculinea rebeli* (figure 2$a$). There is also a considerable fall in the persistence of the butterfly, especially on small sites (figure 2$b$). The explanation is simple although the results were unexpected (see §4). As each micropatch of habitat of a given quality becomes increasingly isolated from cells of similar quality, continuous blocks of near optimum habitat for the host ant become rarer within the site. In this situation, the nest sites of individual colonies of *Myrmica schencki* that are driven extinct by *M. rebeli* are more likely be colonized by non-host *Myrmica* which, once established, are hard to dislodge. It is remarkable, however, that the simple arrangement of patches, without changing the overall quality of a site, should have such profound effects on butterfly numbers and persistence. This shows that a natural enemy population (here the butterfly) can become increasingly vulnerable to extinction as the spatial scale of habitat heterogeneity in resource (ant) growth rates approaches that over which individuals of the resource population disperse.

For a given level of ruggedness, almost identical results were obtained using damp hollows instead of dry hills (figure 2: star symbols). Similarly, adding realistic annual fluctuations to cell habitat quality hardly altered the effects of habitat ruggedness on the butterfly population (figure 2: open circles)

Whenever the butterfly became extinct there was an immediate return to the original level of competition between the ants. We simulated the recovery of the host ant, *M. schencki*, on small (0.25 ha) sites, using the same spatial variations in habitat quality and keeping size and average habitat quality constant (figure 1$a$, $f$–$g$). Striking differences between these otherwise identical sites were found (figure 3). At the point of extinction, the average number of host ant nests remaining (10–11 colonies) was the same for all site types. The recovery of the host ant following butterfly extinction was most rapid when the habitat was arranged as a simple linear gradient and slowest when the same cells were randomly distributed within the site (figure 3). This 'ghost effect' of the butterfly was detectable in the balance of ant nest densities 100 years after the extinction took place. Even after this period, the density of host ant nests in the most rugged sites had recovered to less than half the density on a site with the same habitat arranged as a simple gradient.

## 4. DISCUSSION

This study, which investigates how the spatial distribution of habitat quality within a site impinges on the persistence and dynamics of interacting species in a community, suggests considerable population changes on more rugged sites.

In the case of the ants one would expect fewer colonies of each species to be predicted on rugged sites by any model that was restricted to direct (pairs of
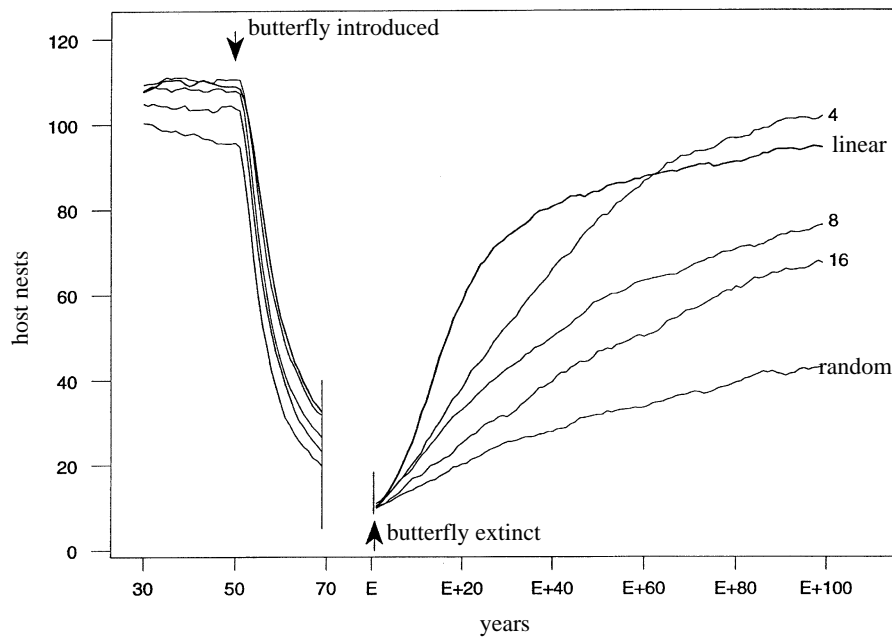
Figure 3. The effect of habitat ruggedness on the pattern of recovery of the host ant species *Myrmica schencki* following the extinction of the myrmecophilous butterfly *M. rebeli* on 0.25 ha sites. Increasing levels of habitat ruggedness were represented by sites ranging from a linear gradient (linear), through 4, 8 or 16 dry 'hills', to a random distribution (random). Results are based only on those simulation runs where the butterfly became extinct within 70 years of its introduction. For each level of ruggedness, we show the mean number of host ant species' colonies for the last 20 years prior to the butterfly's introduction, the first 20 years after introduction (prior to any population extinction); and for the first 100 years following the extinction of the butterfly.

species) interactions or which ignored intraspecific variation in habitat quality. This is because every microhabitat patch (i.e. cell) present can support a single colony of *Myrmica*, each of which behaves as a discrete population with poor dispersal, resembling a unit of a greater population. As the site also contains some terrain that is unsuitable for each ant species the effect of increased ruggedness is to produce smaller areas of above-average quality habitat set among less suitable land, with reduced connectivity between similar habitat types. This results in higher exposure to interspecific competition and smaller 'refuge' areas. In our model neither ant shows any significant decline as its patches of productive habitat become more fragmented until the competitive balance between them is altered by a third species, the butterfly, which differentially impacts on them both (figure 3). Both *Myrmica* species then respond like any conventional metapopulation where local extinction exceeds colonization, although the distribution and abundance of *Myrmica schencki* is greatly reduced relative to Other *Myrmica*. However, if the relative impact of adopted caterpillars on Other *Myrmica* nests is less than assumed (see §2), the model predicts that Other *Myrmica* increase, especially on rugged sites, because the higher extinction rate of its competitor releases additional patches of vacant marginal habitat to colonize in the 'landscape'.

A more interesting prediction is that the butterfly itself is the main loser under increased ruggedness. For at the spatial scale of the adult, little appears to have changed: the whole site remains one discrete habitat patch of unchanged overall quality, supporting a single population of *M. rebeli*. However, the butterfly declines because the main resource of its (inconspicuous) juvenile stage functions at a finer spatial scale, and so it too depends on habitat heterogeneity at this scale. We doubt whether this is a unique property of myrmecophilous insects; similar differences in spatial scale exist between the adult and larval stages of typical phytophagous butterflies.

These predictions have implications for the conservation of *Maculinea rebeli*, now threatened with global extinction (Anon. 1990). We have yet to confirm them in the field, but observations at our main study sites (near Panticosa in the Pyrénées and Gap in the Alps) suggest the simulated microhabitat patterns are representative of real sites, at least to the level of 64 'hills' per hectare. Unfortunately, these are unsuitable places to test spatial predictions, as they are the European strongholds of *M. rebeli*: several sites exist in close proximity in both regions, and all experience frequent immigrations of adult *M. rebeli*, negating the periodic local extinctions we predict for isolated sites with rugged habitat. But as more sites are destroyed, we expect that populations will increasingly become restricted to solitary habitat patches, even in current strongholds. At this stage—and probably already in large parts of *M. rebeli*'s range—low levels of ruggedness may be an important criterion when designating the best areas to conserve. This runs counter to the intuitions of most conservation managers. However, we stress that we are not arguing that species persist better on sites with habitat that is homogeneous in quality (e.g. Thomas *et al.* 1997), rather that for a given range of habitat qualities within sites, some

species' chances of persisting may be greater on sites where the spatial distribution of that habitat is least rugged, especially if sites are small.

These results have wider implications than their application to the conservation of an IUCN Red Data Book species. We predict, for example, that among communities that are dominated by species with partially overlapping niches and which spread mainly by stepping-stone colonization—including those dominated by keystone ant genera such as *Myrmica* and some *Formica*—maximum realized biodiversity will occur on sites with the least first-order spatial heterogeneity in habitat quality. Pacala & Tilman (1994) showed how environmental and spatial heterogeneity can influence the prediction of coexistence of competing plant species in relation to their variability in life history traits. Our study suggests that habitat ruggedness may also influence plant community structure and diversity, especially where there is strong pre-emptive competition for space, where dispersal is very localized (e.g. vegetative) and where species are differentially prone to external stresses, for example from pest infections or herbivores. The analogy may also extend to effects on the structure of communities after a component species has left a site. In our example, the host ant took much longer to recover on rugged sites after the butterfly became extinct (figure 3). Indeed, anyone investigating these sites, say, 20 years after *M. rebeli* had disappeared would find a community structure of ants present, plus a spatial pattern of 'apparent competition' between *M. schencki* and gentians (Hochberg *et al.* 1994; Holt & Lawton 1994), that were inexplicable in terms of the population dynamic interactions of the species found there. We do not know how generally these effects may apply, but suggest that our algorithm and index of local spatial heterogeneity might usefully be employed for assessing the impact of habitat spatial pattern in other model communities.

Finally, our predictions have implications for butterfly metapopulation studies, despite being simulated from one continuous habitat patch of constant size. In work at the landscape scale, it has been a major accomplishment for field biologists to define and map the overall boundaries of 'suitable' habitat for any species with sufficient precision for effects of patch size and isolation on population persistence to be studied. Our results suggest that in ignoring (or over-simplifying) intraspecific variation in habitat quality, an additional parameter is overlooked that may be driving the population dynamics of certain species. We reiterate that the changes in abundance and persistence presented here result simply from the rearrangement of the same amounts of heterogenous habitat quality within a site: these effects would undoubtedly be amplified if, as often occurs in nature, the overall quality of each species' habitat within a site also changed in time.

## REFERENCES

Ae, S. A., Hirowatari, T., Ishii, M. & Brower, L. P. (eds) 1996 *Decline and conservation of butterflies in Japan III*. Osaka: Lepidopterological Society of Japan.

Anon. 1990 *IUCN Red list of threatened animals*. Gland: IUCN.

Begon, M., Sait, S. M. & Thompson, D. J. 1996 Predator–prey cycles with period shifts between two- and three-species systems. *Nature, Lond.* **381**, 311–315.

Brian, M. V. 1972 Population turnover in wild colonies of the ant *Myrmica*. *Ekol. Polska* **20**, 43–53.

Colasanti, R. L. & Grime, J. P. 1993 Resource dynamics and vegetation processes: a deterministic model using two-dimensional cellular automata. *Funct. Ecol.* **7**, 169–176.

Dutilleul, P. & Legendre, P. 1993 Spatial heterogeneity against heteroscedasticity: and ecological paradigm versus a statistical concept. *Oikos* **66**, 152–171.

Elmes, G. W., Clarke, R. T., Thomas, J. A. & Hochberg, M. E. 1996 Empirical tests of specific predictions made from a spatial model of the population dynamics of *Maculinea rebeli*, a parasitic butterfly of red ant colonies. *Acta ecologica* **17**, 61–80.

Elmes, G. W., Thomas, J. A. & Wardlaw, J. C. 1991*a* Larvae of *Maculinea rebeli*, a large blue butterfly, and their *Myrmica* host ants: wild adoption and behaviour in ant nests. *J. Zool.* **223**, 447–460.

Elmes, G. W., Wardlaw, J. C. & Thomas, J. A. 1991*b* Larvae of *Maculinea rebeli*, a large blue butterfly, and their *Myrmica* host ants: patterns of caterpillar growth and survival. *J. Zool.* **224**, 79–92.

Halley, J. M., Comins, H. N., Lawton, J. H. & Hassell, M. P. 1994 Competition, succession and pattern in fungal communities: towards a cellular automaton model. *Oikos* **70**, 435–442.

Hanski, I., Pakkala, T., Kuussaari, M. & Lei, G. 1995 Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* **72**, 21–28.

Hanski, I. & Thomas, C. D. 1994 Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biol. Conserv.* **68**, 167–180.

Hochberg, M. E., Thomas, J. A., & Elmes, G. W. 1992 The population dynamics of a large blue butterfly, *Maculinea rebeli*, a parasite of red ant nests. *J. Anim. Ecol.* **63**, 375–391.

Hochberg, M. E., Clarke, R. T., Elmes, G. W. & Thomas, J. A. 1994 Population dynamic consequences of direct and indirect interactions involving a large blue butterfly and its plant and red ant host. *J. Anim. Ecol.* **63**, 375–391.

Holmes, E. E., Lewis, M. A., Banks, J. E. & Veit, R. R. 1994 Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology* **75**, 17–29.

Holt, R. D. 1997 Community modules. In *Multi-trophic interactions in terrestrial systems* (ed. A. Gange). Oxford: Blackwell. (In the press.)

Holt, R. D. & Lawton, J. H. 1994 The ecological consequences of shared natural enemies. *A. Rev. Ecol. Syst.* **25**, 495–520.

Kimura, M. & Weiss, G. H. 1964 The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics* **49**, 561–576.

Legendre, P. & Fortin, M. 1989 Spatial pattern and ecological analysis. *Vegetatio* **80**, 107–138.

New, T. R., Pyle, R. M., Thomas, J. A., Thomas, C. D. & Hammond, P. C. 1995 Butterfly conservation management. *A. Rev. Ent.* **40**, 57–83.

Pacala, S. W. & Tilman, D. 1994 Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am. Nat.* **143**, 222–257.

Singer, M. C. 1972 Complex components of habitat suitability within a butterfly colony. *Science* **176**, 75–77.

Shmida, A. & Ellner, S. D. 1984 Coexistence of plant species with similar niches. *Vegetatio* **58**, 29–55.

Sutcliffe, O. L., Thomas, C. D., Yates, T. J. & Greatorex-Davies, J. N. 1997 Correlated extinctions, colonizations and population fluctuations in a highly correlated ringlet butterfly metapopulation. *Oecologia*. (In the press.)

Thomas, C. D., Jordano, D., Lewis, O. T., Hill, J. K., Sutcliffe, O. L. & Thomas, J. A. 1997 Butterfly distributional patterns, processes and conservation. In *Conservation in a changing world* (ed. G. M. Mace, A. Balmford & J. R. Ginsberg). (In the press.)

Thomas, C. D., Thomas, J. A. & Warren, M. S. 1992 Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* **92**, 563–567.

Thomas, J. A. 1991 Rare species conservation: case studies of European butterflies. In *The scientific management of temperate communities for conservation* (ed. I. Spellerberg, B.

Goldsmith & M. G. Morris), pp. 149–197. Oxford: Blackwell.

Thomas, J. A. 1995 The ecology and conservation of *Maculinea arion* and other European species of large blue butterfly. In *Ecology and conservation of butterflies* (ed. A. S. Pullin), pp. 180–197, London: Chapman & Hall.

Thomas, J. A., Elmes, G. W. & Wardlaw, J. C. 1993 Contest competition among *Maculinea rebeli* butterfly larvae in ant nests. *Ecol. Ent.* **18**, 73–76.

Thomas, J. A., Elmes, G. W., Wardlaw, J. C. & Woyciechowski, M. 1989 Host specificity of *Maculinea* butterflies in *Myrmica* ant nests. *Oecologia* **79**, 452–457.

Thomas, J. A. & Morris, M. G. 1994 Patterns, mechanisms and rates of decline among UK invertebrates. *Phil. Trans. Roy. Soc.* B **344**, 47–54.

Watkinson, A. R. & Sutherland, W. J. 1995 Sources, sinks and pseudo-sinks. *J. Anim. Ecol.* **641**, 26–130.