

Can natural enemies enforce geographical range limits?

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We develop a simple mathematical model to investigate the question as to whether a specialised consumer can be responsible for creating a range limit in the population of its dynamic resource. The model is most attuned for parasitoid-host relationships, but the central results should apply to a broad range of systems. Specifically, at the beginning of each simulation host and parasitoid populations are distributed at random along a string of patches. In each discrete generation and for each patch, host and parasitoid populations grow and interact, and then a constant fraction of those remaining disperses one or more patch distances in either direction according to a geometric distribution. We iterate the model 200 generations, and in any generation for any patch, either host and/or parasitoid can go locally extinct if its population falls below a threshold density. We find that a specialised parasitoid can enforce a limit, and it is even more likely to fragment its host population. The two most important conditions for parasitoid-enforced range limits are: 1) the theoretical host equilibrium density in the presence of the parasitoid be very small at sites eliminated from the host's range, and 2) the parasitoid disperses at high rates. We close by discussing our findings for specialist and generalist natural enemies, and the relevance of our study to the wealth of investigations on the causes of geographical range limits.

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What determines the limits to a species geographical distribution? This is a major and complex question in macroecology (Brown 1984, 1995, Lawton 1993, Gaston 1994), because its solution is likely to be system specific, and integrate notions of historical factors, local adaptation, demography, and environmental variability only to name a few.

Although exceptions abound (Gaston 1994), as a rule-of-thumb species are most abundant toward the centres of their ranges (Hengeveld and Haeck 1982, Brown 1984, Brown et al. 1995, Lawton 1996). This, in many respects, is the basis for the two sets of ecological hypotheses often cited as explaining range limits. The first is that range limits are determined by limits to the physiological or ecological adaptation of the species (e.g., Brown 1984, Holt et al. 1997). Causal factors include low

quality and abundance of resources, competitors, and harsh abiotic environments. Quinn et al. (1997, 1998) have recently shown that for lepidoptera in Britain, herbivore distributions are subsets of their host plants. Second, range limits may be determined by extinction/colonisation phenomena (e.g., Nee et al. 1991, Gyllenberg and Hanski 1992, Hanski et al. 1993, Lennon et al. 1997). Here, species may go locally extinct due to small population size (Halley and Iwasa 1998), or from environmental catastrophes (e.g., drought or flooding). Suitable sites may remain uncolonized due to insufficient dispersal, isolation by space, or abrupt geological or topographic barriers (e.g., mountains or oceans). Lennon et al. (1997) consider the relative scales of dispersal and environmental gradients to be pivotal in determining range limits under the rubric of extinction/colonization.

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In this article, we evaluate an additional proposition which conceptually straddles the two better known ones: natural enemies determine the range limits of their victims. Virtually all organisms in the plant and animal kingdoms have natural enemies, be they predators, parasites, herbivores, pathogens or parasitoids. In the Insecta, it is estimated that the average species is host to about 6 species of insect parasitoid alone (Hawkins 1994). A recent comparative analysis indicated that natural enemies, including parasitoids, are the dominant mortality agents in insects (Cornell et al. 1998). Thus, natural enemy mortality could be sufficient to cause local extinctions of victim populations at sites where the victim species is most vulnerable to extinction anyway; these would include sites where the resources of the victim were sparse and/or of low quality, or there were abundant competitors.

It stands to reason that in order to enforce a range limit, the natural enemy must be capable of causing a series of local extinctions without going extinct at all excised sites until all hosts are gone. If the natural enemy has a large range of victim species at its disposal, this may be little problem (see Holt and Lawton 1993). However, if the natural enemy is specialised on a single species, then local extinction of its victim is likely also to cause the local extinction of the enemy. This will impede the spread of the exterminating power of the enemy, and hence reduce its impact on the victim's potential geographical range. The only way the enemy can keep the victim from reinvading recently cleared areas is that there be sufficient numbers of enemies immigrating into these vacated sites before the victim reinvades. In this paper we describe how such enemy sources may occur.

We develop a simple model for a host-parasitoid interaction over a continuous spatial gradient in productivity over the geographic range of the host. We choose host-parasitoid associations because theory on their population dynamics is particularly well developed (for reviews see Briggs et al. 1999, Hochberg and Holt 1999), parasitoids probably account for the bulk of natural enemy mortalities in the Insecta (Hawkins 1994, Cornell et al. 1998), and a substantial fraction of the earth's biodiversity is insects (Gaston 1991). Although the model specifically considers a single species of monophagous parasitoid (*sensu* Holt and Lawton 1993), we discuss how assemblages of natural enemies and polyphagous natural enemies may modify patterns revealed in our numerical studies.

Model

Consider a coupled host-parasitoid interaction over a string of n patches. Assume the generations of the two species are synchronous with discrete reproductive peri-

ods and non-overlapping age-structure (as would be the case for many temperate arthropods), and denote the densities of adult hosts and parasitoids in patch i as $N_{i,t}$ and $P_{i,t}$, respectively, at the start of generation t . Assume that events within a generation occur in the following order (May et al. 1981): 1) host density dependence, $g\{N_{i,t}\}$, 2) host net reproduction, λ_i , 3) parasitism, $f\{P_{i,t}\}$, 4) parasitoid survival within hosts, c , and 5) dispersal of adult hosts and parasitoids, ε_N and ε_P . After this sequence of events, to approximate demographic stochasticity, sites with population levels < 1 are assumed to go locally extinct. We will consider these five events in turn.

First, host density dependence includes the effects of generalist natural enemies and/or intraspecific competition among hosts. We assume that it is compensating in nature (Bellows 1981), such that adult host survival is

$$g\{N_{i,t}\} = 1/(1 + \theta N_{i,t}) \quad (1)$$

where the parameter θ measures the strength of density dependence. This function yields a locally stable equilibrium when the parasitoid is absent from the system and there is no patch-to-patch movement (e.g., Hassell 1978).

Second, host net reproduction, λ_i , is assumed to vary over its geographic range ($i = 1, 2, \dots, n$), which would be reasonable if there were a gradient in temperature, food abundance, or food quality (see also Caughley et al. 1988). The gradient in host net reproduction is modelled as a modified Gaussian distribution (Brown 1984, Holt et al. 1997),

$$\lambda_i = \lambda_{\max} \exp\{- (0.5(1+n) - i)^2 / 2\sigma^2\} \quad (2)$$

where λ_{\max} is the net rate of increase at the most favourable site for the host (the integer value of i for which $0.5(1+n) - i$ is closest to 0), and σ^2 determines the gradient in net reproduction with larger values corresponding to a shallower gradient.

Third, the function used for parasitism assumes that a constant fraction of the juvenile host population, α , is invulnerable, such that the overall fraction of hosts escaping parasitism, $f\{P_{i,t}\}$, is

$$f\{P_{i,t}\} = \alpha + (1 - \alpha) \exp\{- aP_{i,t}\} \quad (3)$$

where a is the area of search of the host (Hassell 1978). This model has a long pedigree (e.g., Hassell 1978, Holt and Hassell 1993, Hochberg and Hawkins 1994) and reduces to the classical Nicholson-Bailey model as $\alpha \rightarrow 0$. For a single patch in the absence of migration, larger values of α tend to stabilize the population dynamics. In particular, when there is host density dependence, sufficiently large values of α (roughly $\geq 1/\lambda_i$) give rise to stable equilibrium population dynamics when function (1) is employed.

Fourth, the parasitoid survival term, c , incorporates sex ratio (Comins and Wellings 1985), and extra vulnerability of parasitized hosts to generalist natural enemies that act independently of host density (see also Morrison and Barbosa 1987).

Finally, dispersal occurs passively over the string of patches, following a geometric distribution such that the fraction of a population moving from patch i to patch j is

$$\epsilon_{ij} = (1 - \epsilon)e^{j-i}/(2 - \epsilon) \quad (4)$$

where ϵ is the total fraction of emigrants from any one patch. Dispersal rates for the host may differ from those of the parasitoid, so each has a species-specific constant ϵ_N and ϵ_P , respectively. As dispersal rates increase and patch numbers decrease, increasing fractions of dispersers are "lost" from the system (i.e., the boundaries absorb increasing numbers of dispersers). Although other spatial configurations (e.g., reflecting boundaries or toruses) will indeed affect the detailed patterns of host and parasitoid distributions, they do not change the basic conclusions of our study (Ives unpubl.).

Numerical solutions and simulations

The complexity of the model precludes analytical solutions for transient and equilibrium population densities. However, we were able to solve numerically for equilibrium levels and their associated dominant eigenvalues (which reflect the local stability of the equilibrium point) for the case of no movement (Wolfram 1988). In cases with population movement, we had to employ numerical simulations to understand model behaviour.

Numerical simulations were conducted by setting the host and parasitoid populations very close to their expected equilibrium levels if no migration were to occur. The algorithm containing equations 1–4 and the condition for demographic extinction was iterated for 200 generations in each numerical simulation. We observed a wide range of sometimes intricate population dynamics (see e.g., Comins et al. 1992), but only a small set are presented here which pertain to the main question posed in this study.

Results

In the absence of the parasitoid and of host movement, the host equilibrium density equals $(\lambda_i - 1)/\theta$ at any patch i , where λ_i follows the normal distribution set out in equation (2). For comparative purposes to the numerical simulations set-out below with parasitoids in the system, the host density without parasitoids (and in the absence of dispersal) is ca 10^5 in the two central

patches ($i = 25$ and $i = 26$), and the host goes extinct (the equilibrium < 0) at $i \leq 10$ and $i \geq 41$.

The equations that we use to model host-parasitoid interactions produce two distinctly different patterns for the relationship between host net reproduction, λ_i , and the local equilibrium population densities of hosts and parasitoids (i.e., the equilibrium densities that would occur in the absence of dispersal). Depending on the relative importance of intraspecific density dependence and parasitism, increases in λ_i can either increase or decrease the equilibrium host density. When host refuges from parasitoid attack are relatively large (large values of α), intraspecific density dependence dominates the relationship between λ_i and the equilibrium host density, and increases in λ_i increase the equilibrium host density. Conversely, when refuges are relatively unimportant (α small), parasitism dominates, and increases in λ_i decrease the equilibrium host density while increasing the equilibrium parasitoid density. Because we model environmental variation over the potential range of the host as spatial variation in λ_i , these contrasting patterns have a large impact on whether the parasitoid can limit the realized range of the host. Examples showing each of these patterns are given below.

Consider first a case in which the equilibrium host density increases with λ_i over part of the host's potential range (Fig. 1). In the absence of site to site movement (Fig. 1a), towards the center of its range increases in λ_i increase the equilibrium host density. Towards the edge of the range, however, changes in the equilibrium host density are dominated by the parasitoid, and increases in λ_i produce a decrease in the equilibrium density with a concomitant increase in the equilibrium parasitoid density. For sites in which $\alpha > 1/\lambda_i$, the equilibrium point is stable (dominant eigenvalues with magnitude less than one), while towards the edge of the potential host range, the equilibrium becomes unstable.

For the example in Fig. 1a in the absence of site to site movement, the parasitoid is capable of limiting the range of its host; since the population dynamics outside the core area are unstable, extinction in these edge sites is possible. Nonetheless, this depends strongly on initial conditions, as the possible outcomes of the local population dynamics are not only extinction of both host and parasitoid, but also extinction of parasitoid with persistence of host, and for lower values of λ_i , persistence of host and parasitoid in a limit cycle. Of course, complete absence of movement is biologically unrealistic, and numerical simulations show that even small migration rates may (but not necessarily do) lead to persistence of hosts throughout their potential range.

The example in Fig. 1b illustrates the possibility for a mobile parasitoid to limit the range of its mobile host. While both host and parasitoid coexist stably in the core area, both are absent from the areas towards the edge. As we demonstrate below, however, range limitation does not always occur.

The case in Fig. 2 differs from that in Fig. 1 only in that the searching efficiency of the parasitoid, a , is smaller. This leads to greater equilibrium host densities in the areas towards the edge of its potential range (Fig. 2a). With the reduction in the parasitoid searching efficiency and the corresponding increase in equilibrium host density, the dispersing parasitoid cannot limit the range of the host (Fig. 2b).

The host range limitation demonstrated by Fig. 1b also requires high parasitoid dispersal rates. The example in Fig. 3 is identical to that in Fig. 1b, except the dispersal rate of the parasitoid is decreased. The resulting system has hosts and parasitoids persisting over the entire potential range of hosts, with cyclic dynamics occurring towards the edges.

Although the example of range limitation in Fig. 1 has hosts and parasitoids existing at a stable equilibrium

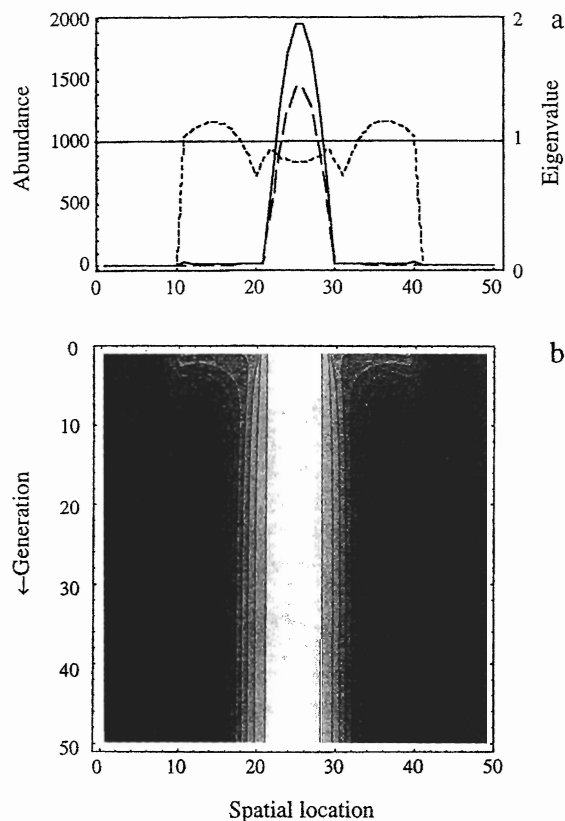


Fig. 1. Population patterns across the geographical gradient of the host. a) Equilibrium population density of host (solid line) and parasitoid (dashed line), and the magnitude of the dominant eigenvalue (dotted line) calculated at equilibrium. Dominant eigenvalues with magnitude less than a value of 1 result in a locally stable equilibrium. b) Host population densities between generations 1 and 50 starting with host and parasitoid abundances at 95% of the equilibrium densities given in the top panel. Lighter shading indicates higher host population density. Parameter values are $n = 50$, $\lambda_{\max} = 10$, $\alpha = 0.12$, $\theta = 0.0001$, $\sigma^2 = 50$, $a = 0.5$ and $c = 0.1$. In (b), host and parasitoid dispersal rates are $\epsilon_N = 0.1$ and $\epsilon_P = 0.75$.

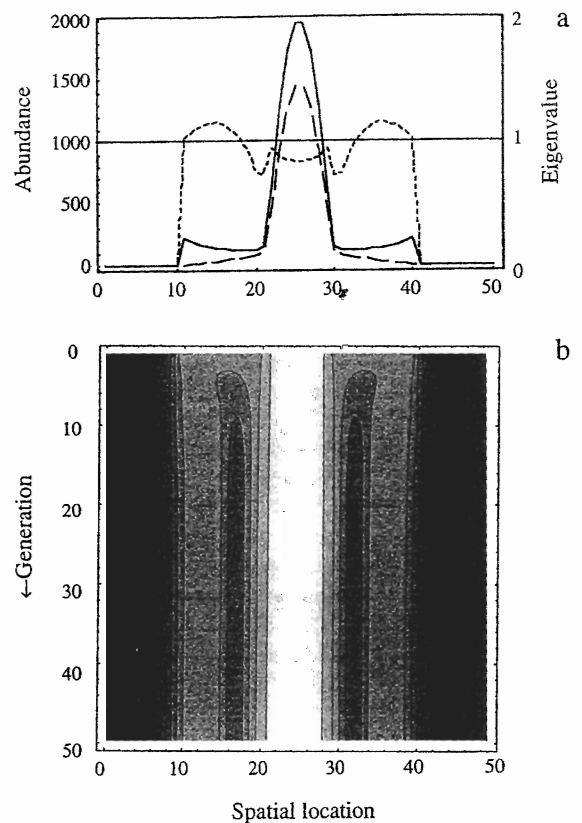


Fig. 2. As in Fig. 1, except the parasitoid searching efficiency is reduced: $a = 0.05$.

at the center of their range, this is not necessary for range limitation. Figure 4 gives an example of a range limitation in which the dynamics are cyclic in the central portion of the range. Nonetheless, extensive simulations suggest that range limitation is more likely when the dynamics at the center of the range are stable. When the dynamics are cyclic, host populations tend to escape from the central region when the parasitoid population is at a trough in its population cycle. This is illustrated in Fig. 5, which is identical to Fig. 4 except the host migration rate is increased from the very low value of 0.0001 (Fig. 4) to 0.01 (Fig. 5).

While Fig. 1 shows that a parasitoid can potentially limit the range of its host, a parasitoid may also have the opposite effect and cause the permanent extinction of the host from the center of its range, as illustrated in Fig. 6. In the simulations leading to this figure, there is no host protection from parasitoid attack (i.e., $\alpha = 0$). This means that, if it were not for non-equilibrium dynamics and parasitoid dispersal, the parasitoid would obtain its maximum density towards the centre of the distribution and the host would attain its maximum density towards the edges (Fig. 6a). Since the equilibrium is unstable, however, a mobile parasitoid can drive the host extinct at the centre of the host's range,

but persist at the fringes (Fig. 6b). Contrast this situation to what happens when the parasitoid and host move at similar, but low rates. In the example of Fig. 7, both species persist everywhere because of the buffering effect of the locally stable fringe sites, which feed small numbers of dispersing hosts and parasitoids into more central sites. Hosts and parasitoids proceed from fringe to center through a combination of site-specific population explosions, and flows of these outbreak populations into more central sites. In effect, Fig. 7 is analogous to Fig. 3, but rather than host and parasitoid populations at the fringe of their ranges being maintained by a central stable core, in Fig. 7 the central unstable area is maintained by the persistent areas at the fringes.

In sum, a parasitoid should be more likely to limit the range of its host in the following situations: 1) the host equilibrium density in the presence of the parasitoid is very small at sites that will be eliminated from the host's range, 2) the parasitoid disperses at relatively high rates, and 3) although not required, range limitation is more likely when host and parasitoid coexist stably at the center of their range.

Discussion

In Chapter 6 of his unpublished doctoral dissertation, Holt (1979) appears to be the first to have recognised the possibility that natural enemies could enforce species range limits. He suggested that this required sufficient dispersal of a predator over a linear gradient in attack rate. In particular, Holt found that this gradient in attack rate should be marked compared to the

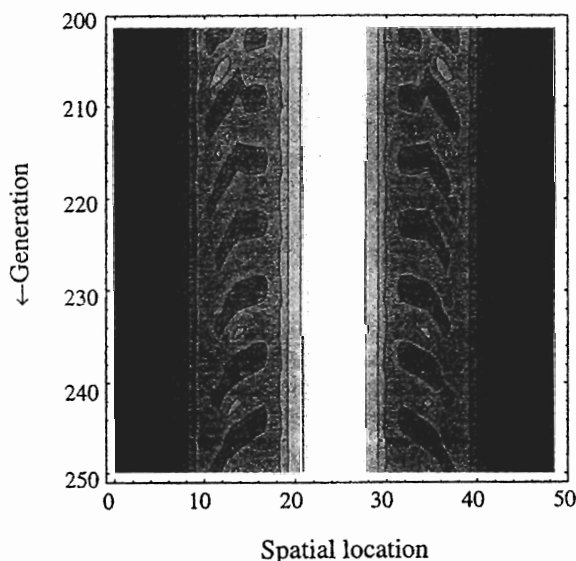


Fig. 3. As in Fig. 1, except the dispersal rate of the parasitoid is reduced: $\epsilon_p = 0.05$.

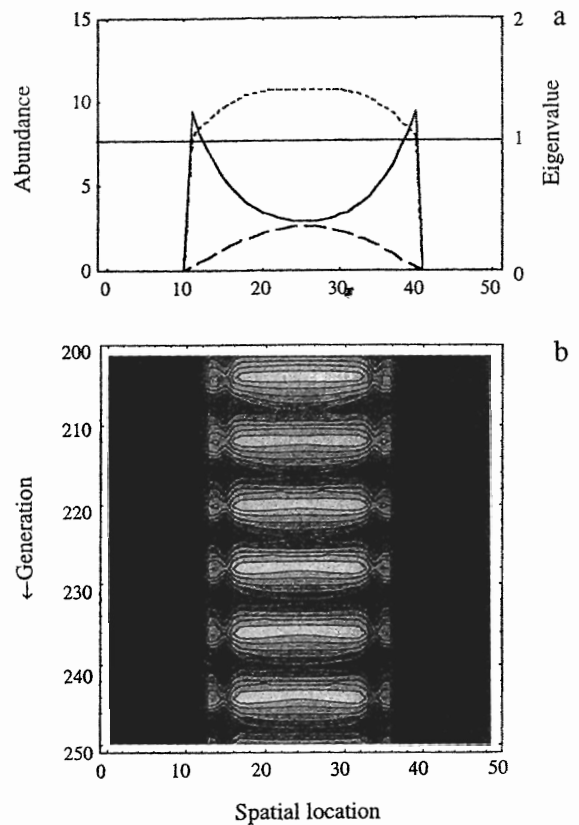


Fig. 4. As in Fig. 1, except the parasitoid searching efficiency is increased to $a = 1.0$, the amount of refuge is reduced to $\alpha = 0.03$, and the host dispersal rate is reduced to $\epsilon_N = 0.0001$.

dispersal distance of the predator, and that of the predator higher than the dispersal of the prey. He also indicated that larger prey carrying capacities should tend to sharpen the predator-enforced prey species border. Our findings, although based on gradients in prey carrying capacity, confirm and extend those of Holt (1979). Caughley et al. (1988) noted that natural enemies could, in principle, create range limits, but they did not propose a detailed mechanism.

Indeed, intuition could lead one to think that a completely specialised natural enemy cannot enforce a range limit on its host, because the geographical distribution of the parasitoid should always be a subset of that of its victim. We have shown, however, that a sufficiently dispersing parasitoid can enforce such a border. Here, parasitoids from persistent sources (e.g. sites with locally stable dynamics) are continuously shunted to more vulnerable host populations. This phenomenon is conceptually very similar to systems of polyphagous parasitoids, where one host population may act as a productive source, the parasitoids produced from which cause the extinction of less productive (or less protected) alternative host species (Holt and Lawton 1993).

There are two additional ways a natural enemy could cause a sharp border that were not considered in our study. One is if there were a sharp cut-off to the host's net reproductive rate, λ_i , and the proportion of protected hosts was somehow positively correlated with λ_i . This would mean that $\alpha_i \lambda_i > 1$ in the most central patches, and $\alpha_i \lambda_i < 1$ towards the edge, and the parasitoid could cause the local extinction of it and the host towards the edge. The conditions for this scenario may be very plausible in cases of ecotones and abrupt topological barriers and host protection from parasitism should increase in more favourable habitats for the host (Hochberg and Holt 1995). Nonetheless, it could equally be argued that the gradient in net growth rate itself is a consequence of a negative trade-off with the ability to be protected (Holt and Hassell 1993).

The second way is if the parasitoid is polyphagous (Holt 1979). Holt (1979) considered this latter scenario in some detail, employing a Lotka-Volterra predator-prey model. He identified cases where a predator could limit the density (or even eliminate) of one of two alternative prey species in regions of overlap. In particular, sharp borders between the two species are possible when there is sufficient overlap in any refuges they may employ to escape predation (for possible example, see Settle and Wilson 1990).

Empirical evidence

We believe that there is a very good reason for why there are apparently no empirical studies indicating that natural enemies can limit the ranges of their victims: first-line evidence requires the observation of the pro-

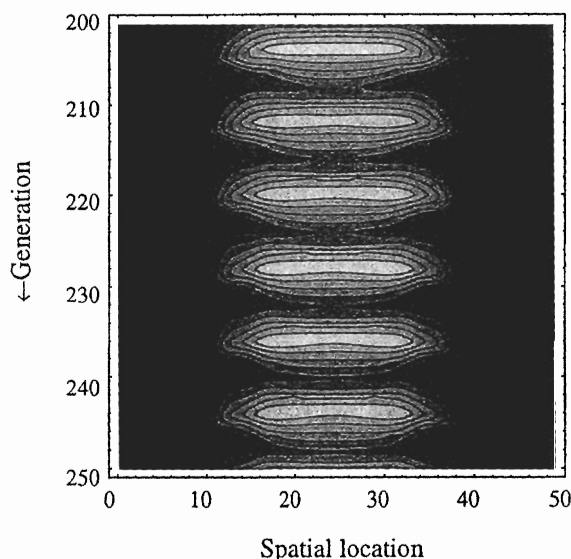


Fig. 5. As in Fig. 4, except the host dispersal rate is increased to $\varepsilon_N = 0.01$.

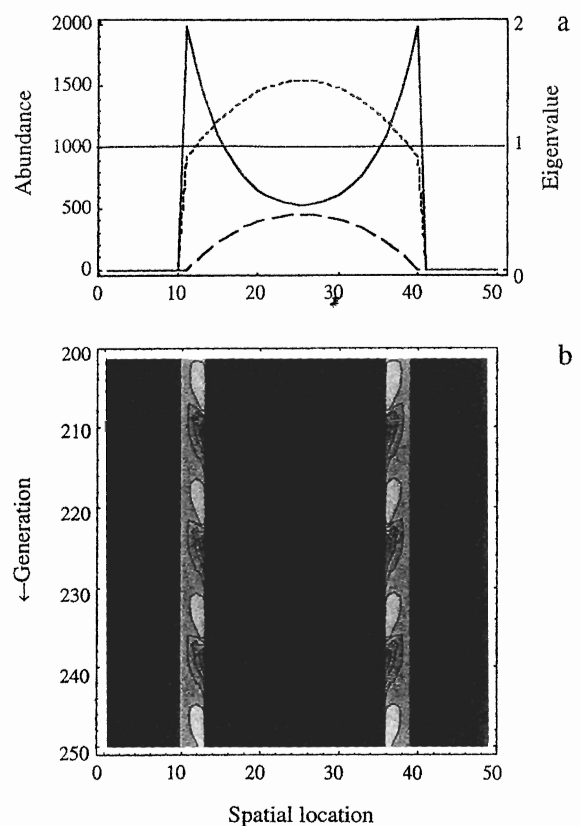


Fig. 6. As in Fig. 1, except the parasitoid searching efficiency is decreased to $a = 0.005$, there are no host refuges, $\alpha = 0$, and host and parasitoid dispersal rates are decreased to $\varepsilon_N = 0.0001$ and $\varepsilon_P = 0.1$.

cess of induced local extinctions at range fringes, and not the final product. Nevertheless, suggestive evidence would be that observed species borders are neither determined by physiological limits nor abrupt and extensive barriers (e.g., ecotones or mountains).

For the parasitoid to enforce a range limit as modelled here, it must disperse over what may often be unrealistically large spatial scales (Roland and Taylor 1997, but see Hastings unpubl.). At smaller spatial scales, Hastings et al. (1997) have shown that pronounced enemy movement can enforce a patch border. Indeed, such small scale movement has been found in two recent empirical studies (Jones et al. 1996, Maron and Harrison 1997), and the movement appears sufficient to explain the containment of outbreaks in the second of these cited host-parasitoid associations. We believe that a most promising way to demonstrate empirically the natural enemy effect would be to monitor species introductions (be they intentional or accidental) and invasions (Nafus 1993). Moreover, as predicted by our model (Fig. 2a, b), it may also be interesting to pay special attention to particularly abundant host species that have unexpectedly restricted geographical ranges (Gaston 1994, Holt et al. 1997).

Some likely scenarios

There are three characteristics of a species which, if occurring separately or together, give the most promise for identifying specialist parasitoids that limit the geographic distributions of their hosts. The first is the extent of the geographic range. Gaston (1994) and Gaston et al. (1997) have presented in some detail how species abundances and geographical extent may or may not be associated (see also Holt et al. 1997). According to our results, parasitoids are increasingly likely to enforce range limits as the scale of dispersal approaches the potential range of the host (see Roland and Taylor 1997). The observations of Maron and Harrison (1997), although not involving the geographic extent of the insect under study, correspond to the extremely small end of this scale.

Small geographical range may or may not also mean small population abundance (Gaston 1994, Holt et al. 1997). In numerical simulations not presented here, we increased or decreased the density dependence parameter θ . (Increasing θ decreases host carrying capacity.) Surprisingly, we observed that the parasitoid was increasingly capable of creating a range limit as density dependence decreased (i.e., carrying capacity increased). This is a reflection of the importance of the density of parasitoids shunted from self-sustaining areas to non-sustaining areas of the host: larger host carrying capacity means more parasitoids shunted, and hence the blanket mortality necessary for the parasitoid to cause a range limit in its host.

Finally, the reduced range effect is often obtained when the host-parasitoid equilibrium is stable at a subset of sites. Arthropod victims with the required

high potential growth rates abound (Hassell et al. 1976), but the extent to which population growth rates vary over species ranges as modelled here is not well understood empirically (Gaston 1994, Lawton 1996). Another possible scenario the range limit effect might be found is where host productivity peaks towards the edges of the distribution and is smallest near the centre (Lawton 1993, Gaston 1994). Here, our results suggest that as long as host protection from the parasitoid is slight, host populations in the most productive (i.e., edge) environments will go extinct, leaving the host and parasitoid to persist in the most inhospitable portions of the host potential distribution (i.e., core) (see Fig. 4b).

A more conservative proposition

Range limits created by the parasitoid are an extreme manifestation of the more common observation we made of the parasitoid fragmenting the host at various sites over the latter's range. Such fragmentation was particularly prevalent when the host was relatively sedentary, and occurs when the host is unlikely to colonise new sites due to the effects of the parasitoid between spatially proximate sites, or along corridors linking occupied and unoccupied sites (Maron and Harrison 1997, Wilson et al. 1999). Numerical results of the same model developed here, but with sites distributed at random around the ring, showed that very small parasitoid dispersal rates could result in local persistent extinctions of the host (see also Hochberg and van Baalen 1998). We may therefore conclude that fragmenting parasitoids may be a common phenomenon when gradients are not smooth (via essentially the same mechanism proposed in Hastings et al. 1997); it can also occur over smooth gradients and the tell-tale sign of this would be relatively ineffective parasitoid populations towards the center of the host's distribution, relatively sparse outbreak populations of the parasitoid and host between center and edge, and less variable populations of the host (usually without the parasitoid) closer to the edge (Hochberg 1996, Turchin and Hanski 1997). For example, Turchin and Hanski (1997) employed sophisticated mathematical techniques to study vole population dynamics along a north-south gradient in vole population growth. Their analysis supports observations that a specialist natural enemy (weasles) was driving cycles in northern latitudes, whilst mobile specialists (kestrels and owls) and generalist natural enemies (foxes, badgers and buzzards) were responsible for more stable dynamics of southerly populations. Our model for host density dependence (eq. 1) could represent such decoupled predation (see also Bellows 1981), and if so, supports the conclusions of Turchin and Hanski (1997) regarding the effects of time scales of density dependence upon popu-

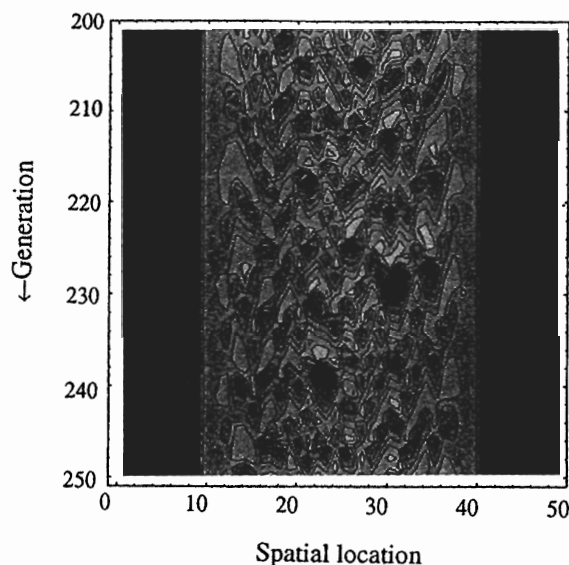


Fig. 7. As in Fig. 6, but with a higher host dispersal rate and a lower parasitoid dispersal rate, $\epsilon_N = 0.01$ and $\epsilon_P = 0.01$.

lation dynamics (i.e., the immobile specialists respond on a slow time scale, whereas the mobile specialists and the generalists respond on faster time scales). Albeit unknown, it would be interesting to see if the immobile specialist predator is capable of fragmenting vole populations, and if the mobile specialists can enforce a range limit.

Community and evolutionary speculations

We close with brief words regarding community ecology and evolution in host-parasitoid systems. There has been some discussion in recent years concerning how the competitive overlap between species may set limits to species distributions. We suggest that under many circumstances, natural enemies and not direct competition will be at the root of spatial patchiness and range limits (e.g., see Settle and Wilson 1990, Martin 1996). This may occur though the direct effects of a specialised parasitoid on its host's distribution, or through the effects of a shared parasitoid in a zone of overlap (see Holt and Lawton 1993). It may well be worth comparing the impacts of natural enemies in zones of species overlap, non-overlap, and potential overlap where one or more species has been eliminated.

By this same token, we wonder to what extent the relative specialisation of insect parasitoids may be linked to their species diversity via the mechanisms discussed in the present study. That is, 1) if parasitoids can fragment their host populations, and/or 2) if the relative specificity of parasitoids is at the root of the elimination of one or more alternative hosts in zones of overlap, then the conditions could arise for reproductive isolation and possibly speciation (Futuyma and Moreno 1988). Mechanism (1) would be supported if relatively fragmented (and sessile) hosts have more diverse parasitoid complexes, whereas mechanism (2) would be supported by data showing phylogenetically closely related parasitoids exploiting different host species with adjacent geographical distributions (Hawkins and Mills 1996).

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