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Dispersal evolution during invasions

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ABSTRACT

Species' range expansions in response to climate change, and the invasion of exotic organisms, are two of the most pressing issues in ecology. Range expansions have already been documented in several taxa, including butterflies, grasshoppers and crickets, and birds, and as climate continues to change we can expect the ranges of many species to alter. Invasion of exotic organisms is of great interest currently because of the damage caused by many invasive species. Within a model, we find that during range expansion, selection generally favours individuals with a higher propensity for dispersal. This character change results in a more rapid spread than expected assuming evolutionary stasis. We show that Allee effects can slow invasion by reducing both selection for increased dispersal and chance of survival for propagules beyond the current range. Understanding how dispersal and other characters might evolve at expanding range margins is important not only for the prediction of range shifts in response to anthropogenic climate change, but also for understanding range shifting during previous natural climate change and for assessing the likely invasion dynamics of an introduced species.

Keywords: Allee effect, climate change, exotic species, migration, range expansion, selection.

INTRODUCTION

Climate change and the deliberate or accidental release of exotic species have led to a world where many thousands of species are expanding their range (Marshall and Haes, 1988; Haes and Harding, 1997; Pitelka *et al.*, 1997; Hill *et al.*, 1999; Parmesan *et al.*, 1999; Thomas and Lennon, 1999; Widgery, 2000; Asher *et al.*, 2001). The progress of these range expansions will be strongly influenced by dispersal strategies, and it is only through a better understanding of dispersal that we can improve predictions relating to invasions. In this paper, we concentrate on the potential for dispersal evolution during range expansion. Recent work has concentrated on establishing how a variety of mechanisms such as kin competition, inbreeding depression and environmental stochasticity influence the rate of dispersal selected for in populations with static ranges (see Clobert *et al.*, 2001). During invasions, dispersing individuals have the opportunity to exploit pristine habitat beyond the

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range edge and hence the selective pressures on dispersal might be quite different to those in populations with static ranges.

At an invasion front, population densities are frequently low, and understanding how populations at these low densities behave is critically important to understanding the dynamics of invasion. Reproduction in small (or sparse) populations is frequently inhibited, with the result that population growth rates exhibit positive density dependence at low densities – the Allee effect (Allee, 1931; Stephens and Sutherland, 1999). Allee effects can be attributed to the increased cost of finding a mate at low densities (Kuussaari *et al.*, 1998), or to social effects such as cooperation or facilitation (Courchamp *et al.*, 2000). Recent work (Cruikshank *et al.*, 1999; Keitt *et al.*, 2001) has shown that the Allee effect can have important consequences for the rate of spread of invasion. At invasion fronts, population densities are characteristically low, and Allee effects become important, lowering the realized population growth rate close to the front, and hence slowing the rate of spread.

Several different approaches have been used to investigate the evolution of dispersal rate and a number of mechanisms have been shown to influence the rate of dispersal that is selected (see Gandon and Rousset, 1999). The rate of dispersal that evolves is likely to be determined by the balance between several different selection pressures. Temporal environmental variability (e.g. van Valen, 1971; Levin *et al.*, 1984; Travis and Dytham, 1999; Travis, 2001), avoidance of inbreeding depression (e.g. Bengtsson, 1978), kin selection (e.g. Hamilton and May, 1977; Comins, 1982; Ronce *et al.*, 2000), chaotic population dynamics (Holt and McPeek, 1996) and demographic and genetic stochasticity (Travis and Dytham, 1998), all promote higher rates of dispersal. The direct costs that dispersal involves (Denno *et al.*, 2001) and spatial variability in the environment (Travis and Dytham, 1999; Travis, 2001) are the main selection pressures acting to lower the rate of dispersal. The desire to understand how dispersal rate may evolve in spatially structured populations such as a metapopulation has motivated most of the recent work on the evolution of dispersal. A common assumption of these models is that the population is at equilibrium. Here, we extend a previous model to examine how dispersal evolves during invasion, a situation in which a population is likely to be far from its equilibrium.

We use an individual-based, spatially explicit simulation model describing invading or spreading populations of up to 500,000 individuals that differ only in their propensity to disperse. We allow dispersal rate to evolve and track the evolution of dispersal strategies during an invasion or range expansion, looking also at how any evolution affects the rate of population expansion. We then extend the model to investigate how Allee effects may impact on the evolution of dispersal during range expansion.

METHODS

The model we use extends those we have used previously to explore the evolution of dispersal (Travis and Dytham, 1998, 1999; Travis, 2001). It is a cellular lattice model and, for all the results presented here, has dimensions of 400 × 400. Each cell represents a habitat patch that can support a population with equilibrium density (N^*) of 10. We employ wrapped (cyclic) boundary conditions except at the ends of rectangular lattices that are absorbing. Genotypes differ only in the dispersal strategy that they exhibit: there is no trade-off between dispersal and competitive ability. We do consider a cost of leaving the natal patch in the form of a probability of dying while dispersing, but reproductive output is otherwise unaffected by propensity to disperse. The model we use simulates a population of an annual species with discrete generations. The order of events for individuals in each generation is as follows: birth, local competition, dispersal (or not), reproduction, death.

We choose to use an individual-based version of Hassell and Comins' (1976) formulation to describe the within-subpopulation dynamics, although this could readily be replaced with an alternative function.

Each individual present in the population at time t gives birth to a number of offspring taken at random from a Poisson distribution with mean μ defined as:

$$\mu = \lambda(1 + aN_t)^{-1}$$

where λ is the rate of increase and a relates to patch quality. The parameter a is calculated from the following expression:

$$a = (\lambda - 1)/N^*$$

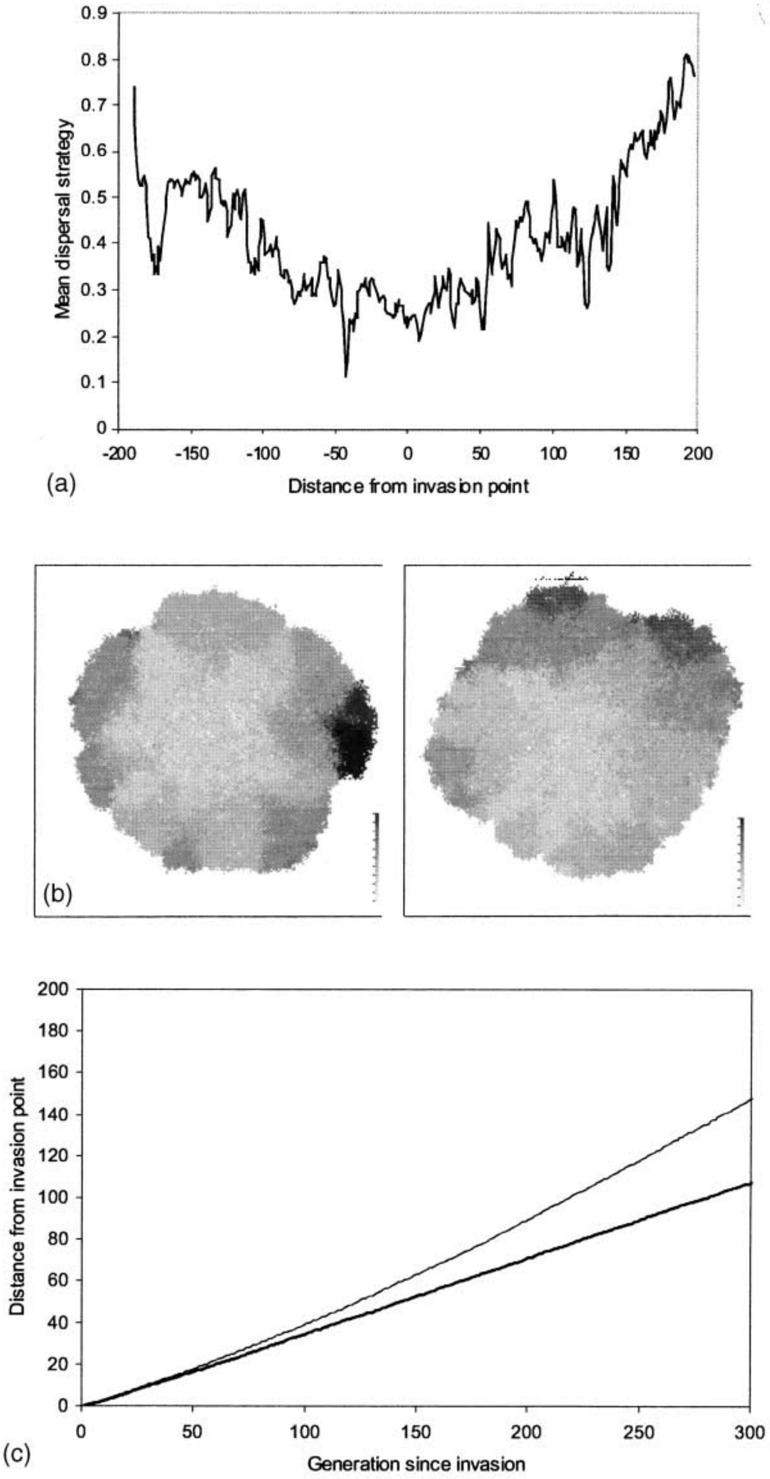
where N^* is the subpopulation equilibrium density. Demographic stochasticity is incorporated through the use of the Poisson function to determine the number of offspring an adult produces, and this stochasticity is likely to play an important role as the population size will frequently be small at the invasion front. When we include an Allee effect, we simply set $\lambda = 0$ for individuals that are alone in a patch.

Offspring inherit their dispersal genotype from their parents, but with a small probability of mutation ($m = 0.005$). The distance of a mutation away from the parental genotype is drawn from a uniform distribution -0.02 to $+0.02$. Dispersal occurs immediately after the within-population dynamics. Individuals disperse with a probability that is dependent upon their genotype. Dispersing individuals move with equal likelihood to one of the eight patches that adjoin their natal patch. In these invasion simulations, individuals never reach the boundary of the arena. The model incorporates an arbitrary explicit cost to dispersal: dispersing individuals die with probability $c = 0.2$ (except where stated otherwise).

The simulations are designed to represent an introduced species expanding into non-native habitat. We assume that the initial colonists come from a population that has been at equilibrium long enough that an equilibrium dispersal rate has evolved. To achieve this, the individuals used to seed the invasion are taken at random from a population that has been living on a lattice of identical shape and size for 10,000 generations – sufficient time for a stable distribution of dispersal genotypes to have evolved. Each realization is initialized by introducing five individuals into one patch at the centre of a square lattice. We track the progression of the invasion and monitor the evolution of dispersal rate.

RESULTS

Figure 1 shows a computer simulation of the invasion by a species into a region previously unoccupied by that species. As the invasion proceeds, the mean dispersal rate at the invasion front increases (Fig. 1a), indicating that individuals with higher propensities to disperse are selected for. These individuals are more likely to be colonizers of new patches, where they are able to exploit the low intraspecific competition and realize higher lifetime reproductive success than conspecifics that remain in more crowded natal patches. The probability of dispersal does not evolve to one in the simulation described here. This is due to the incorporation of a cost to dispersal. The propensity of dispersal that evolves is sensitive


0.9
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Mean dispersal strategy
-200
-150
-100
-50
0
50
100
150
200
(a)
Distance from invasion point
(b)
200
180
160
140
120
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80
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Distance from invasion point
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250
300
(c)
Generation since invasion

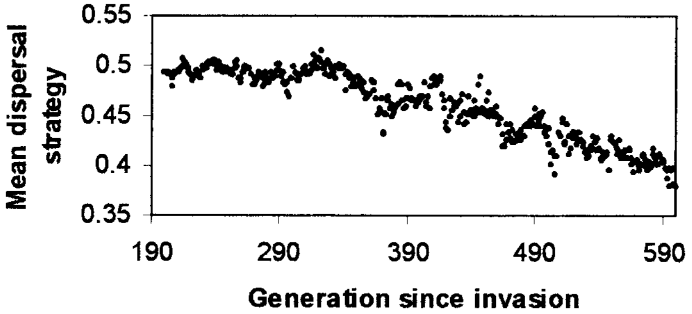

Fig. 2. The reduction in mean dispersal rate after a site is colonized by the invasion. This figure shows the mean dispersal strategy in a patch 80 cells from the centre point of the grid. The individuals that first reach the patch (200 generations after the invasion began) have a high dispersal rate, but the mean dispersal rate of the patch gradually declines as selection acts against higher dispersal rates. Local equilibrium density (N^*) = 10, growth rate (λ) = 2, contest competition.

to the cost incorporated. For example, we found that, with a cost of 10% (i.e. one in 10 dispersing individuals die before reaching their destination), the mean dispersal rate at the invasion front is 0.74, and when the cost is 40%, only 0.52 disperse at the front. However, for all costs, we find that there is an increase in dispersal propensity during invasion. Behind the invasion front there is a decline in the mean propensity to disperse (Fig. 2). As recently colonized areas approach equilibrium density, there is less benefit to be gained from dispersing and, as dispersal carries a cost, there is selection for the optimum dispersal propensity in a saturated environment. If higher costs are incorporated, then selection against dispersal once the invasion front has passed through a region is more intense, and the drop off in dispersal propensity behind the front is more rapid. The evolution of dispersal during range expansion results in an increased rate of spread (Fig. 1c).

Incorporating Allee effects

Allee effects have a huge impact on the results we obtain. When we incorporate an Allee effect into our model, we observe much less intense selection for high dispersal propensity towards the invasion front (Fig. 3a). Individuals that disperse away from their natal patch may move to a site where the population density is low enough that Allee effects become important. This is especially likely for individuals that are born close to the range edge, where they are likely to be colonizers of previously unoccupied habitat patches. Thus, when

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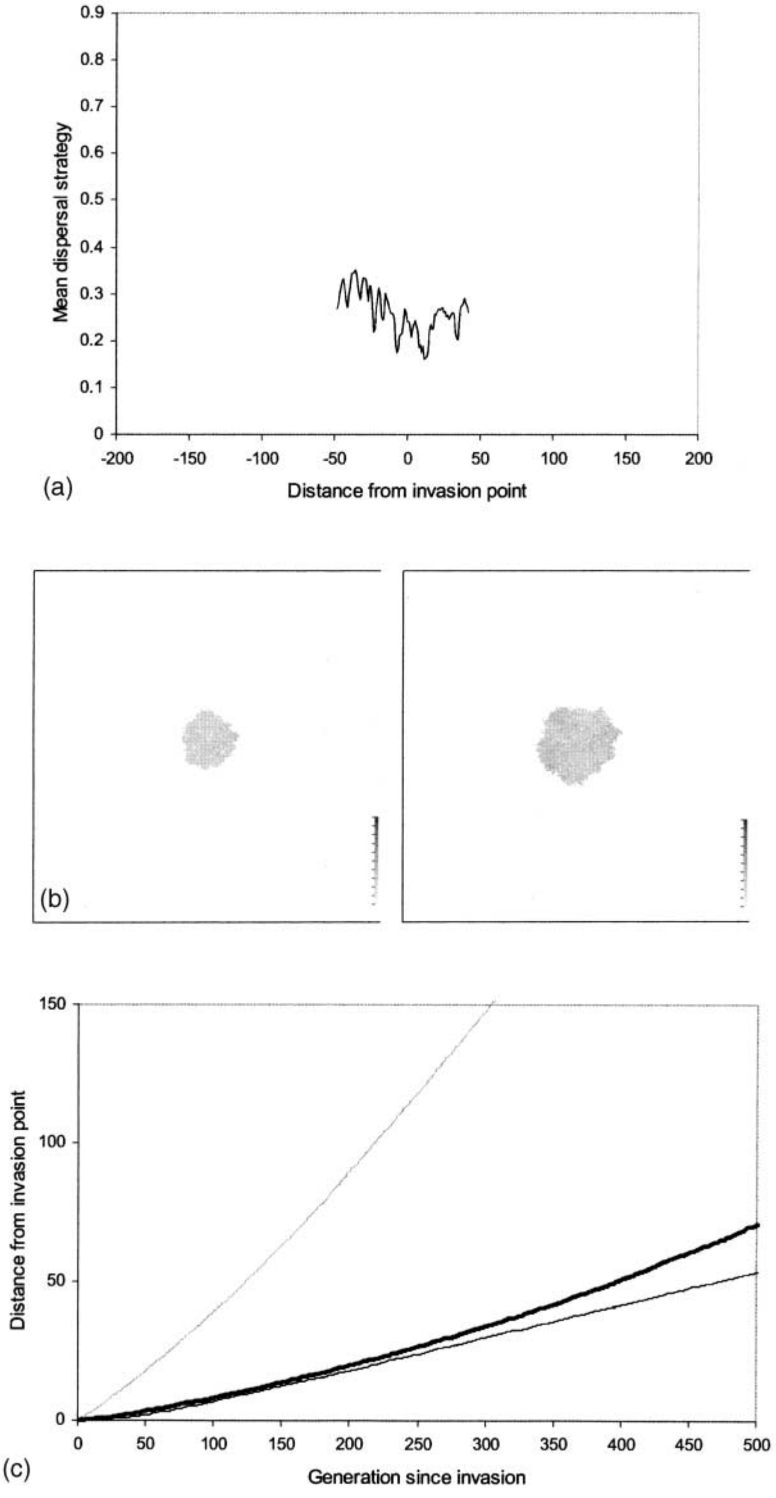
Fig. 1. Evolution of dispersal strategy during an invasion. (a) Profile of mean dispersal strategies 200 generations after five individuals are introduced at the centre point. (b) Two realizations 200 generations after an invasion starting at the centre point. The central 200 * 200 cells of a 400 * 400 lattice are shown. Darker shading indicates higher dispersal strategy (see grey scale). Here black indicates a mean dispersal between 0.9 and 1.0, white between 0.0 and 0.1, and the nine greys the intermediates in increments of 0.1. (c) Distance of invasion front from source with (light line) and without (dark line) evolution of dispersal strategy. Local equilibrium density (N^*) = 10, growth rate (λ) = 2, contest competition.


0.9
0.8
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Mean dispersal strategy
-200
-150
-100
-50
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50
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(a)
Distance from invasion point
(b)
150
100
50
0
Distance from invasion point
0
50
100
150
200
250
300
350
400
450
500
(c)
Generation since invasion

an Allee effect is included, the dispersal propensity that evolves at range margins is considerably lower than when they are ignored. This, in turn, results in slower range expansion (Fig. 3b,c).

DISCUSSION

The results clearly show that the rate of dispersal that evolves during invasions can be very different to that which evolves in a saturated population. Higher rates of dispersal tend to be selected for during invasions and this can result in an increased rate of spread of the population. Thus dispersal evolution could have important implications for the invasion dynamics of exotic organisms. Similarly, it may have an important role to play in range shifting in response to past current climate change. Allee effects are likely to be important during invasions, as population densities towards the invasion front tend to be low. The results demonstrate that species with Allee effects are less likely to evolve increased dispersal rates during invasion and, subsequently, have lower rates of spread.

The model we have described simulates the invasion of an exotic into a new area. Most attempts at predicting whether a species will successfully invade an area, and how the invasion will progress, have been unsuccessful (Williamson, 1999), and it has even been suggested that it may remain effectively impossible (Williamson, 1999). Until now, the evolution of characteristics such as dispersal during invasions has largely been overlooked; evolutionary stasis has been assumed (Coope, 1995; Williamson, 1996). Our results indicate that dispersal evolution can alter the progress of the invasion by increasing the rate of range expansion, and may also increase the probability of an invasion being successful: the more rapidly an invading population increases its range of occupancy, the less likely it is to succumb to stochastic extinction.

In our model, we drop five individuals into a previously uninhabited area. This was designed to simulate the invasion of exotic organisms; extending conclusions based on these results to other situations should be done with care. However, we suggest here that selection pressures acting during the range shifting of species in response to climatic change are likely to be quite similar to those acting during the invasion of an exotic. In both cases, previously unoccupied habitat becomes available, and individuals that arrive first in this new habitat are likely to be at a selective advantage. Thus we would expect that increased rates of dispersal would evolve during range expansion, in much the same way as they do during the invasion simulated in the model described in this paper.

Under current and future climate change, species that possess limited dispersal capabilities will have a higher risk of extinction, as their range shifting is less able to keep pace with

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Fig. 3. An Allee effect reduces the rate of spread during an invasion and lowers the dispersal strategy evolved. Scales identical to Fig. 1 for comparison. (a) Profile of mean dispersal strategies 200 generations after five individuals are introduced at the centre point. (b) Two realizations with an Allee effect 200 generations after an invasion starting at the centre point. The central 200 * 200 cells of a 400 * 400 lattice are shown. (c) Distance of invasion front from source with an Allee effect with (darkest line) and without (lighter line) evolution. For comparison, the distance from the source when there is evolution and no Allee effect is shown (lightest line). Local equilibrium density (N^*) = 10, growth rate (λ) = 2, contest competition. Simple Allee effect applied: individuals alone in a cell produce no offspring.

the changing climate. The unprecedented rapidity of current climate change (Bradley, 2000; Huang *et al.*, 2000), together with habitat fragmentation, serves to make range shifting more difficult, yet more important, for species now than it has ever been in the past. For some species, dispersal evolution may provide an escape from the trap, and it is encouraging that the first evidence is emerging that indeed species are evolving increased dispersal at expanding range margins (Thomas *et al.*, 2001). Dispersal evolution may not 'save' all species, but it may be important for a significant number.

Reid's paradox (Reid, 1899) describes the disparity between the life histories of tree species and their rapid rates of spread at the end of the Pleistocene. Recent work incorporating more complex and realistic dispersal kernels (Kot *et al.*, 1996; Clark, 1998) has begun to resolve the controversy, and dispersal evolution may further explain the disagreement by allowing for the emergence of genotypes with higher dispersal propensity during the period of range shifting, as is the case in the seed morphology of the lodgepole pine during range expansion in western North America (Cwynr and MacDonald, 1987).

One of the main potential differences between the invasion of an exotic and range expansion is the availability of new habitat. An exotic is far more likely to be invading an area of many high-quality patches than a species extending its range. Range edges, almost by definition, are close to the limits of where the species is able to survive, and it is likely that newly available sites are distributed in a fragmented pattern across space. For example, a species shifting its range northwards as the climate warms may, at its northern limit, only be able to survive on slopes with a southern aspect. Thus climate-induced range expansion will frequently be into a more fragmented landscape than the invasion of an exotic organism. A further interesting question exists for range shifting species. That is, what happens to selection pressure at the contracting edge of the population, for example the southern limit of a species whose range is shifting northwards? Clearly, there are some interesting unanswered questions in this area and future studies designed explicitly to investigate the evolution of dispersal during range expansion would be informative. These studies should ideally account for patterns of habitat availability and quality towards range edges, as the nature of these patterns could have a significant impact on the results.

When an Allee effect is incorporated, we observe a significant reduction in the rate of spread. Our results indicate that Allee effects can impact on the rate of spread of invasion in two ways: first, ecologically, through slowing the population growth at the invasion front (Cruickshank *et al.*, 1999; Keitt *et al.*, 2001); and, second, evolutionarily, through selecting for lower dispersal propensity during the invasion process. Interestingly, the evolutionary and ecological effects may interact in a form of positive feedback: the Allee effect makes the evolution of higher propensity for dispersal less likely, and this means that those that do disperse are even more likely to experience severe Allee effects as colonizers. Allee effects are likely to be most serious during expansion through fragmented landscapes, when most new populations are established by few (or single) individuals. Thus, species already suffering from the effects of habitat fragmentation may be the least likely to undertake the evolutionary increase in dispersal propensity required for them to track changes in the distribution of climatically suitable environments.

We implemented only a very mild form of an Allee effect whereby individuals alone in a patch died without reproducing. With two or more individuals present within a patch, there was no Allee effect. Many organisms may suffer more from far stronger Allee effects, and for these species we might expect their rate of spread to be even more limited. The possibility may even exist that a strong Allee effect can cause evolution of reduced rates of dispersal at the edge of ranges, exactly the opposite of the results shown in Fig. 1. We are in no doubt that to understand better the process of invasion, a full understanding on the behaviour of populations at low densities is imperative.

The intrinsic growth rate, the form of competition and the sub-population equilibrium density can all influence the rate of dispersal that evolves (see Travis and Dytham, 1998). In this paper, we have considered one example set of parameters, but it is to be expected that their influence will be in the same direction within an invading population as it is within a population at equilibrium. Thus, scramble competition, higher intrinsic growth rates and lower sub-population equilibrium densities should all select for higher rates of dispersal. The cost of dispersal is an important constraint on the rate of dispersal that evolves. With no cost to dispersal and if the habitat is spatially homogeneous (Travis and Dytham, 1999), dispersal rate evolves close to one. This occurs even when all sub-populations are close to equilibrium density. As the cost is increased, lower rates evolve. Here, we arbitrarily set the cost of dispersal to 0.2. Higher costs would have resulted in the colonists having a lower initial dispersal rate, and also in the dispersal rate obtaining lower rates during invasion. However, qualitatively the results would appear the same.

There has been considerable effort expended in recent years using different types of models to investigate the evolution of dispersal (e.g. Gandon and Rousset, 1999; Ronce *et al.*, 2000; Hovestadt *et al.*, 2001). These models have concentrated almost exclusively on modelling populations at equilibrium. Frequently, the motivation has been to understand the evolution of dispersal within patchy populations or metapopulations. Here, we have extended one model framework to enable the evolution of dispersal during invasion to be investigated. Future studies employing other methods already established within the evolution of dispersal literature could prove insightful. In this paper, we have considered invasion into a patchy environment, where every sub-population has the same equilibrium density, and this remains constant through time. This assumption has been made by most studies investigating dispersal evolution. Rarely, in nature, is the environment so homogeneous. Spatial and temporal environmental variability can have a considerable impact both on the evolution of dispersal rate (see Travis and Dytham, 1999; Heino and Hanski, 2001; Travis, 2001) and dispersal distance (Hovestadt *et al.*, 2001). Generally, temporal variability promotes higher rates of dispersal, while spatial variability selects for lower rates. In general, we would expect the same to be true during an invasion as it is in a population at equilibrium, but further work might be instructive. Until recently, work on the evolution of dispersal had concentrated exclusively on density-independent rates of dispersal. However, a few studies have now begun to tackle the evolution of condition-dependent dispersal (e.g. Ezoe and Iwasa, 1997; Travis *et al.*, 1999; Poethke and Hovestadt, 2002) and also the evolution of dispersal kernels (Hovestadt *et al.*, 2001; Murrell *et al.*, 2002). These advances have been made in work on saturated populations, and it would be interesting to extend them to look at dispersal during invasions.

CONCLUSIONS

Our results imply that predicting how an exotic species will invade and how a species will shift its range in response to climate change requires a thorough understanding of not only its capacity to evolve dispersal strategy, but also its population dynamics at low densities, and interactions between the two. Species that exhibit Allee effects are unlikely to evolve increased dispersal abilities during periods of range expansion. We predict that species with strong Allee effects are much less likely to pose serious threats to alien ecosystems as exotic invaders. We also suggest that such species may be especially at risk of extinction due to the relatively slow rates of range expansion that they are likely to achieve.

REFERENCES

Allee, W.C. 1931. *Animal Aggregations: A Study in General Sociology*. Chicago, IL: University of Chicago Press.

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. and Jeffcoate, S. 2001. *The Millennium Atlas of Butterflies in Britain and Ireland*. Oxford: Oxford University Press.

Bengtsson, B.O. 1978. Avoiding inbreeding: at what cost? *J. Theor. Biol.*, **73**: 439–444.

Bradley, R. 2000. Paleoclimate – 1000 years of climate change. *Science*, **288**: 1353–1355.

Clark, J.S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *Am. Nat.*, **152**: 204–224.

Clobert, J., Danchin, E., Dhondt, A.A. and Nichols, J.D., eds. 2001. *Dispersal*. Oxford: Oxford University Press.

Comins, H.N. 1982. Evolutionary stable dispersal strategies for localized dispersal in two dimensions. *J. Theor. Biol.*, **94**: 579–606.

Coope, G.R. 1995. Insect faunas in ice age environments: why so little extinction? In *Extinction Rates* (J. Lawton and R. May, eds), pp. 55–74. Oxford: Oxford University Press.

Courchamp, F., Clutton-Brock, T. and Grenfell, B. 2000. Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus. Anim. Conserv.*, **3**: 277–285.

Cruickshank, I., Gurney, W.S. and Veitch, A.R. 1999. The characteristics of epidemics and invasions with thresholds. *Theor. Pop. Biol.*, **56**: 279–292.

Cwynr, L.C. and MacDonald, G.M. 1987. Geographical variation of lodgepole pine in relation to population history. *Am. Nat.*, **129**: 463–469.

Denno, R.F., Hawthorne, D.J., Thorne, B.L. and Gratton, C. 2001. Reduced flight capability in British Virgin Island populations of a wing-dimorphic insect: the role of habitat isolation, persistence and structure. *Ecol. Entomol.*, **26**: 25–26.

Ezoe, H. and Iwasa, Y. 1997. Evolution of condition-dependent dispersal: a genetic algorithm search for the ESS reaction norm. *Res. Pop. Ecol.*, **39**: 127–137.

Gandon, S. and Rousset, F. 1999. The evolution of stepping stone dispersal rate. *Proc. R. Soc. Lond. B*, **266**: 2507–2513.

Haes, E.C.M. and Harding, P.T. 1997. *Atlas of the Grasshoppers, Crickets and Allied Insects in Britain and Ireland*. London: The Stationery Office.

Hamilton, W.D. and May, R.M. 1977. Dispersal in stable habitats. *Nature*, **269**: 578–581.

Hassell, M.P. and Comins, H.N. 1976. Discrete time models for two-species competition. *Theor. Pop. Biol.*, **9**: 202–221.

Heino, M. and Hanski, I. 2001. Evolution of migration rate in a spatially realistic metapopulation model. *Am. Nat.*, **157**: 495–511.

Hill, J.K., Thomas, C.D. and Blakeley, D.S. 1999. Evolution of flight morphology in a butterfly that has recently expanded its range. *Oecologia*, **121**: 165–170.

Holt, R.D. and McPeek, M.A. 1996. Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.*, **148**: 709–718.

Hovestadt, T., Messner, S. and Poethke, H.J. 2001. Evolution of reduced mortality and ‘fat-tailed’ dispersal kernels in autocorrelated landscapes. *Proc. R. Soc. Lond. B*, **268**: 385–391.

Huang, S., Pollack, H.N. and Shen, P. 2000. Temperature trends over the past five centuries reconstructed from borehole temperatures. *Nature*, **403**: 756–758.

Keitt, T.H., Lewis M.A. and Holt, R.D. 2001. Allee effects, invasion pinning, and species’ borders. *Am. Nat.*, **157**: 203–216.

Kot, M., Lewis, M.A. and van den Driessche, P. 1996. Dispersal data and the spread of invading organisms. *Ecology*, **77**: 2027–2042.

Kuussaari, M., Saccheri, I., Camara, M. and Hanski, I. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos*, **82**: 384–392.

Levin, S.A., Cohen, D. and Hastings, A. 1984. Dispersal strategies in patchy environments. *Theor. Pop. Biol.*, **26**: 165–191.

Marshall, J.A. and Haes, E.C.M. 1988. *Grasshoppers and Allied Insects of Great Britain and Ireland*. Colchester: Harley Books.

Murrell, D.J., Travis, J.M.J. and Dytham, C. 2002. The evolution of dispersal distance in spatially-structured populations. *Oikos*, **97**: 229–236.

Parmesan, C., Ryrholm, N., Stefanescu, C. *et al.* 1999. Polewards shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**: 579–583.

Pitelka, L.F., Gardner, R.H., Ash, J. *et al.* 1997. Plant migration and climate change. *Am. Sci.*, **85**: 464–473.

Poethke, H.J. and Hovestadt, T. 2002. Evolution of density- and patch-size-dependent dispersal rates. *Proc. R. Soc. Lond. B.*, **269**: 637–645.

Reid, C. 1899. *The Origin of the British Flora*. London: Dulau.

Ronce, O., Gandon, S. and Rousset, F. 2000. Kin selection and natal dispersal in an age-structured population. *Theor. Pop. Biol.*, **58**: 143–159.

Stephens, P.A. and Sutherland, W.J. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *TREE*, **14**: 401–405.

Thomas, C.D. and Lennon, J.J. 1999. Birds extend their ranges northwards. *Nature*, **399**: 213.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. and Conradt, L. 2001. Ecological and evolutionary processes at expanding range margins. *Nature*, **411**: 577–581.

Travis, J.M.J. 2001. The color of noise and the evolution of dispersal. *Ecol. Res.*, **16**: 157–163.

Travis, J.M.J. and Dytham, C. 1998. The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. *Proc. R. Soc. Lond. B*, **265**: 17–23.

Travis, J.M.J. and Dytham, C. 1999. Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. Lond. B*, **266**: 723–728.

Travis, J.M.J., Murrell, D.J. and Dytham, C. 1999. The evolution of density-dependent dispersal. *Proc. R. Soc. Lond. B*, **266**: 723–728.

van Valen, L. 1971. Group selection and the evolution of dispersal. *Evolution*, **25**: 591–598.

Widgery, J. 2000. *Orthoptera Recording Scheme for Britain and Ireland*, Newsletter 26. Huntingdon: BRC.

Williamson, M. 1996. *Biological Invasions*. London: Chapman & Hall.

Williamson, M. 1999. Invasions. *Ecography*, **22**: 5–12.