On the evolutionary ecology of species' ranges

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ABSTRACT

A species' range limits may shift in space either because of changes in ecological factors (e.g. climate, the abundances of interacting species) or because the traits which influence range limits (e.g. dispersal, niche characteristics) evolve by natural selection. In *Geographical Ecology*, Robert MacArthur (1972) provided a synthesis of the evolutionary factors that may drive range dynamics. In this paper, I revisit this theme in the light of recent theoretical studies of evolution in heterogeneous environments. These studies suggest that a rich range of evolutionary patterns in species' ranges may occur, including expansions or contractions, leading to dynamism in ranges even in epochs without strong directional environmental change.

Keywords: biogeographic theory, niche conservatism, range shifts, species' ranges.

INTRODUCTION

Elucidating the factors that shape species' ranges has long been a central concern of both ecology (e.g. Caughley *et al.*, 1988; Krebs, 1994; Lawton *et al.*, 1994; Brown *et al.*, 1996; Brown and Lomolino, 1998) and evolutionary biology (e.g. Jablonski, 1987). This concern was evident in Robert MacArthur's (1972) magisterial work, *Geographical Ecology*, whose 30th anniversary we celebrated last year. It seems to me to be an opportune moment to reflect on the current state-of-the-art in range theory and the extent to which our understanding has advanced since 1972. I think it is fair to state that when ecologists reflect on MacArthur's contribution to biogeography, they mainly think of island biogeography and the role of interspecific interactions in community assembly. Yet MacArthur had a long-standing interest in single species' ranges in continental settings, as witnessed by the following quote: 'future [biogeographic] theory will concentrate on the boundaries of species ranges as they are encountered on ecologically uniform or continuously varying terrain' (MacArthur and Wilson, 1967: 182). His principal published work focusing on species' ranges is chapter 6 of *Geographical Ecology*, entitled 'Species distributions'. In this chapter, MacArthur synthesized themes and ideas from many thinkers (stemming back to Charles Darwin), leavened them with his own fresh perspectives, and put them into a logical, quantitative and internally consistent framework. For me, a salient feature of MacArthur's thinking on species' distributions as sketched in this chapter is his interweaving of

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ecological and evolutionary perspectives. For instance, MacArthur notes that habitat specialization may be an important determinant of range limits, and then states, 'even where this factor [habitat specialization] does limit a species' distribution, we can legitimately ask why the species has not adapted to a wider range of habitats' (MacArthur, 1972: 142). The answer, he suggests, involves adaptive trade-offs between habitats.

Before proceeding, it is useful to reflect on general concepts that underlie analyses of ranges. Interpreting the causes of species' range limits requires one to pay attention to three things: niches, spatial variation in environments, and dispersal (Brown and Lomolino, 1998). A species' niche is that set of environmental factors (both abiotic and biotic) which permits populations to persist. As used in the quote from MacArthur above (and in the text below), the term 'habitat' denotes spatial variation in one or more of the environmental factors that define a species' niche. To a first approximation, a species' range is governed by how well its niche requirements match a spatially varying template of environmental factors (Brown, 1984). When this match fails, it is usually because of dispersal or the lack thereof. Dispersal can permit a species to occupy habitats in which its niche requirements are not met (sink populations; Holt, 1985; Pulliam, 2000). Conversely, barriers and constraints on dispersal can prevent a species from occupying perfectly suitable habitats.

In most species, there is likely to be genetic variation in niche requirements and in dispersal propensities among individuals. Species' ranges thus can potentially reflect evolution both in niches and in dispersal. These two evolutionary modalities interact. Dispersal defines how organisms experience habitats and thus channels the direction of adaptive evolution to particular habitats. In turn, spatial and temporal variation in local habitat conditions provides the context for understanding many of the selective advantages of dispersal. The evolutionary dynamics of species' ranges involves the co-evolutionary interplay of selection on dispersal on the one hand, and adaptation to habitats on the other.

My goal is to highlight important issues in the evolution of species' ranges and to point out how current thinking echoes the synthesis provided in *Geographical Ecology*. In his book, MacArthur touches on a number of evolutionary topics – the evolution of habitat specialization, the evolution of dispersal, density-dependent habitat selection, the evolutionary impact of temporal variability in the environment, and co-evolution between interacting species – that are still at the heart of contemporary discussions of the evolutionary dynamics of species' ranges.

TOWARDS AN EVOLUTIONARY ECOLOGY OF RANGE LIMITS

MacArthur observes that many species' range boundaries are not fixed but instead fluctuate greatly (p. 144). A dramatic expression of the dynamic character of ranges comes from studies of mammal communities. Species found today in the same communities, often with broadly overlapping ranges, have often arrived there from historically non-overlapping ranges (Graham *et al.*, 1996). Standard explanations for range shifts seek out changes in ecological factors (e.g. changes in climate, the breaking of dispersal barriers, the arrival of competitors, anthropogenic environmental degradation) as drivers for range dynamics (see Brown and Lomolino, 1998, for an excellent summary of such effects). MacArthur, for instance, notes the impact on ranges of climatic fluctuations and anthropogenic influences (e.g. hunting).

Such explanations for observed range shifts usually make the tacit assumption that species' traits are fixed, so that ranges change because environments change. Recent theory

(e.g. Kirkpatrick and Barton, 1997, and see below) suggests that evolutionary dynamics within a species can also lead to range expansions or contractions, even with no contemporaneous directional trends in the environment. Moreover, even if environmental change is the primary determinant of range dynamics, evolutionary responses by a species can modulate the magnitude, direction and pattern of its range shift. Over long temporal scales, changes in species' ranges almost surely reflect the impact of evolution in heterogeneous environments (Hoffmann and Blows, 1994; Kirkpatrick and Barton, 1997; G. Stevens, personal communication). Indeed, empirical evidence is increasingly showing that dynamism in range boundaries involves evolution in species' traits (Enquist *et al.*, 1995; Davis and Shaw, 2001; Thomas *et al.*, 2001).

Although species' ranges are very complex spatial entities, I suggest that useful insights can be gained from considering models for the evolution of dispersal and habitat specialization (or generalization) in simple landscapes. Most ranges span large spatial scales, relative to the spatial domain of individual mobility. It is unlikely that dispersal over short time-scales links all the far-flung populations in an entire geographic range into a seamless evolutionary unit. Instead, ranges comprise many local evolutionary arenas, and the range as a whole evolves because of the accumulated impact of evolution at local scales. Sometimes this may consist of an adaptation that arises in one place and then spreads throughout a species' distribution, leading to a range shift. But, in other cases, evolutionary changes in ranges involve local adaptation.

At the scale of these local arenas – for instance, at the periphery of a species' range – range dynamics arise from the addition or subtraction of particular habitats or ecological variables (e.g. resources) from the local suite of such habitats or variables utilized by a species. Some theoretical models (e.g. Case and Taper, 2000) examine range dynamics along smooth environmental gradients. In others (e.g. those below), a species is assumed to occupy a landscape with two or more discrete habitats. Evolution of habitat generalization or specialization at this local or regional scale can define the potential for the ultimate expansion of the species over a much larger area.

This scenario of a species' range being comprised of a small number of coupled habitat patches can literally apply to some phases in the life history of a species, including the initial stages of a species formed in a small peripheral isolate and the initial beachhead of colonization into a new island or continent. But even if not literal descriptions of a species' range, simple spatial scenarios such as the two-habitat models explored below also provide useful conceptual tools that help to elucidate key processes at work in the evolutionary dynamics of species' ranges, even at much broader scales. MacArthur likewise used models of population growth and habitat selection (for example, his Figures 6-12 and 6-13) in simple landscapes with discrete habitats to reflect creatively on geographical range dynamics.

EVOLUTION OF DISPERSAL

Species' ranges would not exist if individuals did not disperse from their natal sites. Consider a species newly introduced at a single point in space. If the environment is homogeneous and there are no dispersal barriers, the rate of range expansion typically scales with a measure of the average distance moved by individuals from birth to reproduction (Okubo, 1980; Turchin, 1998). The evolution of dispersal rates (the fraction of individuals who move away from where they are born) and parameters that define the dispersal 'kernel' (the probability density of distances moved) can thus influence the temporal unfolding of

a species' range. As an introduced species invades into favourable terrain, it is likely to experience selection favouring dispersal, thus accelerating the rate of invasion. Given genetic variation in dispersal rates, individuals with higher dispersal rates will tend to be found in increasing frequency near the range limits (simply because they move more), hence the rate of range expansion will tend to increase over time. Many introductions have an initial lag, during which invasion occurs sluggishly, followed by a more rapid expansion. This pattern is to be expected if there is selection towards greater dispersal rates. An alternative plausible mechanism for accelerated invasion is a phase of improved adaptation to the novel environment. Thomas *et al.* (2001) have recently demonstrated that the evolution of increased dispersal rates and habitat breadth are both involved in accelerated responses of several butterfly and cricket species to warming trends in Britain.

Once the invasion stalls, three factors that favour continued dispersal are (Clobert *et al.*, 2001): (1) spatiotemporal variability in local fitnesses (dispersal as a bet-hedging strategy; Holt, 1997; McPeek and Holt, 1992); (2) interference or pre-emptive competition (dispersal as the best of a bad lot; Morris, 1991); and (3) competition among kin (dispersal to reduce local sib competition; Hamilton and May, 1977; Comins, 1982). All can influence range dynamics, but here I focus on the first mechanism favouring the maintenance of dispersal.

Consider a simple case where, after colonization, an invasion quickly stalls because of local landscape heterogeneity. The initial range includes a source habitat in which a population can persist without immigration, surrounded by a sink habitat in which emigration from the source maintains the population (Pulliam and Danielson, 1991; Dias, 1996; Pulliam, 1996). The realized initial range of the species thus consists of the source and sink habitats. Other patches of potential source habitats may be available, but can only be reached if individuals traverse sink habitats. Assume for a moment that there is no direct interference among individuals (i.e. all individuals in the source have equal access to resources) and stable population dynamics.

MacArthur (1972: 150–151) provides a succinct verbal argument for why dispersal is disfavoured in stable source–sink systems. He does not use 'source–sink' terminology, but his Figure 6–12 (p. 150) provides a clear, graphical model of the demographic consequences of asymmetrical flow between habitats, leading to sources and sinks. As he notes, because of dispersal into the sink, the source population is kept below its local carrying capacity, K, leading to an absolute fitness there (successful offspring produced per resident) greater than one. The sink will maintain a positive density, despite having on average fitness less than one. Because more individuals leave the source than return from the sink, on average dispersers move down fitness gradients in stable source–sink environments (Holt, 1985, 1993). MacArthur notes that such dispersal should surely be selectively disadvantageous. Formal analyses (reviewed in Johnson and Gaines, 1990; McPeek and Holt, 1992) show that, without constraints on dispersal (e.g. due to interference), the evolutionarily stable state of the population in a stable environment indeed typically leaves it restricted to the source. [The main exception to this conclusion is when there are multiple sources and sinks, and it is much easier to disperse between sources and sinks than among sources (Wilson, 2001).]

Thus, the evolution of dispersal in stable environments can shrink a species' initial range, if the initial range includes sink habitats, and dispersal into sinks is selectively disadvantageous. This conclusion depends upon the assumption that the source has stable dynamics. Recent theory suggests that dispersal into sinks can persist at an evolutionary equilibrium if source populations have unstable dynamics and sinks are not too unfit (Holt, 1997; Jansen and Yoshimura, 1998; Holt and Barfield, 2001). In effect, sink habitats can be utilized as

part of a 'bet-hedging' strategy, permitting individuals to buffer temporal variability in fitness in source populations (Holt, 1997), provided individuals (or their descendants) can at times successfully re-enter sources (Morris, 1991). Moreover, in some systems, no habitat may be a permanent source (e.g. because of successional dynamics or climatic variation). In such landscapes, dispersal is both selectively favoured and required for species' persistence (Ronce *et al.*, 2001).

This conclusion updates the thoughts of MacArthur (1972: 151), who recognized the importance of temporal variability in fostering the evolution of dispersal. If the initial range of a species is a single habitat and this habitat has unstable dynamics, dispersal into a sink habitat may become advantageous. This implies that the array of habitats used by the species should expand. Such expansion can have both a direct effect on the range – namely, the sink habitat as well as the source is now being used by the species – and an indirect effect. The indirect effect arises because once dispersal is selectively advantageous, there are likely to be 'mistakes' in dispersal, permitting dispersal barriers to be surmounted and range expansion to occur. At geographical (rather than landscape) scales, the latter effect is almost surely the more important.

There are three general implications of dispersal evolution for range dynamics:

1. *Range evolution in the absence of directional environmental change*. The simplest expectation is that a species' range may change in size, even without contemporaneous, directional environmental change such as climate warming. For instance, an introduced species with poor dispersal capabilities may remain stalled in its invasion until appropriate genetic variants appear that permit long-distance dispersal, at which time it may expand rapidly. Moreover, depending upon initial conditions and shifts in the magnitude of temporal variation in sources, one might observe either range contractions or expansions arising due to selection on dispersal, as sink habitats are added to or removed from the habitat repertoire of a species.

2. *The importance of a mesoscale perspective*. Habitats can be added to and subtracted from the range, not only because of changes in local conditions occurring at the range limits, but because of environmental change elsewhere in the range. Imagine that in our two-habitat scenario for a species that has newly invaded (or evolved in a peripheral isolate), the initial condition involves use of both source and sink habitats in a temporally constant environment. In a broad range of circumstances (see above), dispersal is disadvantageous. Selection against dispersal implies that the species should evolve towards a shrunken range, as fewer and fewer individuals disperse from source to sink. If the environment remains constant, eventually the species should be restricted to the better source habitat.

Now imagine that the source environment begins to experience greater temporal variation. For instance, a specialist pathogen may invade the source, cause recurrent epidemics and thus create temporal variation in host fitness in the source. This in turn favours increased use of the sink habitat (where fitness may be more stable because pathogens are less likely to cause epidemics in low-density populations). Provided appropriate genetic variation is available, a species' realized range could wax and wane, driven by environmental change in core habitats, even if conditions in peripheral habitats remain constant.

3. *Indirect effects of the evolution of dispersal*. For dispersal to be selectively favoured at a landscape scale (the domain of local population dynamics), there must be back-dispersal to the natal site (Morris, 1991; Wilson, 2001). One cost of dispersal is that individuals leave their natal site and enter habitats from which there is no return dispersal. This loss in space

is equivalent to mortality and so tends to disfavour dispersal. Such losses are particularly likely in species utilizing passive modes of dispersal.

This individual cost of dispersal at the level of local landscapes, however, provides an indirect benefit at the level of the species, since in effect lost dispersers comprise a pool of dispersers available for colonizing far-flung habitats, from which return dispersal to the natal site is exceedingly unlikely. For many taxa, much of the observed range at continental scales may be an epiphenomenon (viewed through the lenses of local ecological and evolutionary dynamics, at the scale most relevant to natural selection), emerging because of rare dispersal events at very large spatial and temporal scales (e.g. jump dispersal; Brown and Lomolino, 1998). The size of the pool of dispersers available for long-distance episodes of colonization should tend to increase, with increasing benefits maintaining dispersal at a local, landscape scale. An increase in local temporal variability should tend to favour an increased number of individuals leaving sources and residing in sinks, which should, in turn, indirectly increase the pool of dispersing individuals potentially involved in long-distance dispersal. This argument suggests there may be an emergent relationship between the stability of local population dynamics and determinants of range dynamics at much broader spatial and temporal scales (see Discussion).

Evolution in heterogeneous landscapes reflects the interplay of local and regional processes. This interaction of processes at different scales is important for understanding the evolution of dispersal. In turn, the pattern and rate of dispersal influences the evolutionary dynamics of habitat specialization and generalization (Kawecki and Holt, 2002). Concentrating on local factors alone to determine why a given habitat is added to or lost from the species' range ignores this fundamental evolutionary fact. An important indirect effect of dispersal on evolutionary range dynamics operates via the influence of dispersal on hampering, or promoting, local adaptation. This theme is the focus of the next section of the paper.

NICHE CONSERVATISM, EVOLUTION AND SPECIES' RANGES

Evolution can influence species' ranges via the sculpting of adaptation by natural selection. The most familiar quip in all evolutionary ecology may well be that popularized by MacArthur: 'a jack of all trades is a master of none'. The issue of trade-offs is fundamental throughout evolutionary ecology, as trade-offs can influence the evolution of life-history parameters, dietary specialization, interspecific interactions and, quite generally, all aspects of ecological specialization versus generalization (Rosenzweig, 1995). In the context of species' ranges, trade-offs must be considered when environments are spatially varying and selection favours different phenotypes in different places.

The selective consequences of trade-offs can be modulated by density dependence. MacArthur was an early champion of Steve Fretwell's theory of habitat selection (Fretwell, 1972), which examined the consequences of density dependence and adaptively sensible individual decision rules for the distribution of species in spatially variable environments. MacArthur prominently featured Fretwell's graphical model of habitat selection in his chapter 'Species distributions' in *Geographical Ecology*, and he clearly considered this model to provide a useful perspective on geographical ranges. The rules an organism uses in habitat selection in effect define a biased template of available environments, against which novel mutations are 'tested'.

Population geneticists have long recognized that natural selection favouring adaptation to local environments can be inhibited by gene flow, particularly in low-density populations (Antonovics, 1976). Ernst Mayr (1963) argued that range limits arise because asymmetrical gene flow from central, abundant populations hampers local adaptation in peripheral, sparse populations (Kirkpatrick and Barton, 1997). Recent theoretical studies (Brown and Pavlovic, 1992; Holt and Gaines, 1992; Kawecki, 1995; Holt, 1996a,b,c, 1997; Holt and Gomulkiewicz, 1997a,b; Kirkpatrick and Barton, 1997; Gomulkiewicz et al., 1999; Tufto, 2001; Kawecki and Holt, 2002) have clarified the importance of considering simultaneously dispersal, demographic asymmetries and adaptive trade-offs among habitats when analysing the direction and rate of evolution in heterogeneous landscapes. Local density dependence is particularly important in achieving evolutionarily stable range boundaries (Kirkpatrick and Barton, 1997; Case and Taper, 2000); in low-K environments, immigration elevates populations above carrying capacity, reducing fitness and hampering the evolution of local adaptation (Gomulkiewicz et al., 1999).

Consider again a source–sink system. The theoretical studies cited above show that in many (but not all) circumstances, the force of selection may be weak for fostering adaptation to sink environments, particularly if dispersal rates are low, absolute fitness in the sink is initially low and density dependence is strong (Kawecki, 1995; Holt, 1996a,b; Gomulkiewicz et al., 1999). Generally, the lower the fitness in the sink, the weaker the selection is to improve adaptation there. Those ecological factors restricting a species to a subset of habitats can automatically weaken the power of natural selection to expand the range of habitats utilized by that species.

The weak force of selection in sinks may even foster niche contraction; a species may become progressively better adapted to habitats in which it is initially well-adapted, at the expense of adaptation to sink habitats. If the species initially occupies both habitats, selection may thus lead to a contraction in habitat range, even in a stable environment. Holt and Gomulkiewicz (1997b) suggest that even if a habitat is not a sink, but merely has a low carrying capacity, selection may at times disfavour adaptation to it, leading ultimately to an evolutionary loss of ability to use this habitat and thus a reduction in the species' range. George Stevens (personal communication) has suggested that species' ranges may often shrink as species evolve, driven by the evolutionary dominance (via gene flow) of abundant, core populations over less abundant, peripheral populations. The conclusion that species can lose their ability to utilize habitats in which their abundance is initially relatively low arises in a wide range of evolutionary models differing in their detailed ecological and genetic assumptions (e.g. van Tienderen, 1991; Kirkpatrick and Barton, 1997). It appears to be a reasonably robust conclusion that in the evolution of species' ranges, as elsewhere, a useful rule-of-thumb is 'success breeds success'.

However, these theoretical models provide for a rich array of evolutionary scenarios. In some settings, the force of selection may be strong for improving adaptation to the sink or low-K habitats (Holt, 1996b), so that a species initially largely confined to one habitat may evolve habitat generalization and expand its range. I here present results from one simple model that illustrates this range of potential effects of adaptive evolution on range size, in a landscape where neither habitat is initially a demographic sink. The basic idea is to splice together the evolution of habitat choice [using the results of McPeek and Holt (1992), but ultimately stemming back to Fretwell (1972)] and the evolution of habitat specialization or generalization [using the formalism of, for example, Holt (1996a), but ultimately rooted in the trade-off concept].

Prior theoretical studies of niche conservatism (cited above) have explored the evolution of specialization or generalization, given fixed patterns of exposure (via dispersal) to different habitats. However, as noted in the Introduction, range dynamics should reflect the intraspecific co-evolution of characters that determine local fitness, and those which define how a lineage experiences different habitats (via habitat choice or dispersal) (Holt, 1987; Rosenzweig, 1987). Here I present the flavour of how such co-evolutionary dynamics influence species' ranges, without dwelling on algebraic or computational details.

I assume a species has intrinsically stable population dynamics, perturbed only by modest environmental variation, and haploid genetics. Rare mutations with small effects arise that affect either habitat choice or habitat-specific fitnesses, but not both traits simultaneously. If mutations arise sufficiently infrequently, one can first examine the direction of evolution in dispersal, given fixed adaptive responses. Then, given that habitat choice is at an evolutionary equilibrium, one may ask how adaptation to particular habitats evolves. If such adaptation occurs, this may alter local carrying capacities, which then feeds back to influence the evolution of dispersal. I imagine that this intraspecific co-evolutionary process recurs iteratively.

First consider the evolution of habitat choice, given fixed adaptive abilities to use different habitats. The model I use is that of McPeek and Holt (1992), who explored a model for the evolution of dispersal between non-sink habitats. A species is assumed to have discrete generations. Each habitat has local density dependence in fitness, described by a monotonically declining function $W_i(N_i)$. The carrying capacity of habitat i, K_i, is that local population size where $W_i(K_i) = 1$. Each newborn individual has a propensity to move between habitats, a propensity which may vary by natal habitat (the 'conditional dispersal strategy' of McPeek and Holt, 1992; Ronce et $al.$, 2001). To maintain dispersal and permit an evolutionary equilibrium to be dominated by a single dispersal syndrome (rather than a neutrally stable line of equilibrium; McPeek and Holt, 1992), we assume that there is a small amount of spatially uncorrelated temporal variation and no direct cost to habitat choice.

I start with a limiting case of this scenario, which permits a simple, analytically tractable solution. Consider a species whose juveniles all enter a well-mixed pool of dispersal propagules, from which they sort out into two breeding habitats. Dispersal occurs whenever an individual is born in habitat i but settles into habitat j. Given small amounts of temporal variation and low dispersal costs, a single conditional dispersal strategy beats all alternatives (McPeek and Holt, 1992). Computer simulations that relax this assumption (and in particular permit philopatry and localized dispersal) suggest that the qualitative conclusions we draw from this limiting case characterize a much broader range of systems (R.D. Holt and M. Barfield, unpublished results).

At the evolutionarily stable state (ESS) of the population, individuals disperse from habitat 1 to habitat 2 at a per capita rate equal to $K_2/(K_1 + K_2)$ and from habitat 2 to habitat 1 at a rate $K_1/(K_1 + K_2)$ (McPeek and Holt, 1992). Local, per capita dispersal rates should thus be inversely related to local carrying capacity. This prediction is closely related to the ideal free distribution. Theoretical models of the evolution of dispersal reveal that populations tend to evolve towards an ideal free distribution (Fretwell, 1972), in which fitnesses are equilibrated across occupied habitats (Fryxell and Lundberg, 1998; Holt and Barfield, 2001). Given density dependence in fitness, for fitness to be equilibrated across space, individual movements must not perturb local densities; hence, as many individuals should immigrate into each patch as emigrate from it. This pattern of 'balanced dispersal' has been observed in a number of detailed field studies of vertebrate movements, including migratory

songbirds (Doncaster *et al.*, 1997) and oldfield rodents (Diffendorfer, 1998; Lin and Batzli, 2001).

We now turn to the evolution of habitat specialization and generalization, given that the population is at its ESS dispersal strategy. The McPeek-Holt model predicts relatively more turnover in low-*K* habitats (Doncaster *et al.*, 1997; Diffendorfer, 1998). Intuitively, it can be seen that this pattern of dispersal will weaken the strength of selection for adaptation to the low-*K* habitat. Consider a mutant allele which increases fitness in the low-*K* habitat by a small amount, with no effect in the high-*K* habitat. If there is ongoing dispersal, this mutant spawns a lineage with descendants found in both habitats. Because of the asymmetry in dispersal produced by the ESS 'balanced dispersal' syndrome, most of these descendants will end up in the high-*K* habitat, where they have no fitness advantage. This asymmetry in dispersal reduces the potential fitness advantage of a novel type that is advantageous in the low-*K* habitat. If an increase in fitness in the low-*K* habitat comes at a cost in the high-*K* habitat, because more individuals experience the latter the cost will outweigh the benefit and the species will not tend to improve adaptation in the habitat in which it is initially rarer.

We now examine the evolution of habitat specialization more closely. Let λ denote the overall growth rate of a novel haploid mutation when it is rare relative to the resident type, and the resident type is at demographic equilibrium. Imagine that the mutant increases fitness in habitat 1 by a small amount, but at some cost to fitness in habitat 2. The mutant type moves among habitats at the same ESS rates as does the resident. The impact of a small increase in fitness in habitat 1 on overall fitness, averaged over both habitats, is:

$$\frac{\partial \lambda}{\partial W_1} = \left(\frac{K_2}{K_1 + K_2}\right)\left(\frac{\partial W_2}{\partial W_1}\right) + \left(\frac{K_1}{K_1 + K_2}\right) \tag{1}$$

The term $\partial W_2/\partial W_1$ describes a fitness trade-off between the two habitats. The other terms in parentheses describe how natural selection 'weights' the two habitats. By inspection of (1), it is clear that if habitat 2 has a relatively low carrying capacity, selection is weak towards improving fitness there, because the main determinant of the spread of the allele is its effect in whichever habitat has the higher *K*. Previous theoretical studies assuming fixed dispersal patterns (i.e. non-ideal habitat selection, leading to sources and sinks) have similarly shown that, in a spatially heterogeneous environment, natural selection is biased towards whichever habitat makes the larger contribution to the total breeding population (e.g. van Tienderen, 1991; Brown and Pavlovic, 1992; Holt and Gaines, 1992; Kawecki, 1995; Holt, 1996a). Natural selection is thus a weak force for improving or maintaining adaptation to any habitat in which a species is initially relatively rare, compared with other habitats where it is more abundant.

If the novel allele spreads to fixation, local carrying capacities may change. If so, the original settlement rules used by individuals will no longer be ideal-free. Selection should then act on these rules, until the population returns to an ideal free distribution.*

If selection has improved fitness in habitat 1, at the expense of fitness in habitat 2, habitat choice should tend to evolve so that fewer individuals utilize habitat 2. This further weakens the evolutionary importance of habitat 2. This positive feedback can potentially lead to the

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* *Technical point*: The maintenance of dispersal by selection requires temporal variation in this model (McPeek and Holt, 1992). Given small amounts of such variation, selection on dispersal leads to populations with an ideal free distribution (with fitness equilibrated on average among habitats), with a single persistent dispersal strategy (McPeek and Holt, 1992; Holt and Barfield, 2001).

evolutionary loss of rare habitats for a species (Holt, 1987; Rosenzweig, 1995). However, this tendency towards loss of particular habitats can be kept in check, depending on the nature of adaptive trade-offs between habitats. Moreover, note we have assumed only a small amount of temporal variation; as discussed below, temporal instability that is large in magnitude can both directly and indirectly foster the evolutionary maintenance of habitat generalization.

To make further headway in an analysis of co-evolution between habitat choice and local fitness requires a quantitative characterization of trade-offs in fitness among habitats. As an illustrative example, assume local fitnesses in the McPeek-Holt discrete generation model are given by the Ricker equation, in which r_i is the intrinsic growth rate of habitat i and d is a measure of density dependence:

$$W_i = e^{(r_i - dN_i)} \tag{2}$$

The carrying capacity of habitat i is $K_i = r_i/d$. We assume that the variation potentially available for selection is described by a fitness set (Levins, 1969), the outer boundary of which is given by a function $r_2 = \varphi(r_1)$ with negative slope (the examples used below are shown in Fig. 1). Richard Levins' concept of a fitness set is a graphical formalization of the trade-off concept. Because fitness is a joint function of phenotype and the environment, the shape of the fitness set will reflect the interplay of internal constraints on phenotypic variation (e.g. developmental constraints), and spatial variation in the environmental factors influencing fitness (e.g. resource availability or predation pressure).

Evolution requires genetic variation. I assume that available mutations have phenotypes in a small neighbourhood of the initial state of the population. The initial state of the population is assumed to be at a particular point on the outer bound of the fitness set; evolution occurs if a mutant arises with values for r_i slightly different from the resident, or slightly different habitat selection rules, and this mutant increases when rare. In the particular model explored here, with iterative selection on dispersal and ability to utilize habitats, stable protected polymorphisms are not observed, so the evolutionary trajectory of the population can be envisaged as movement of a point along the outer boundary of the fitness set.

After substitution of the fitness function (2) into the ESS condition [expression (1) set equal to 0], a necessary condition for the species to be at an evolutionary equilibrium and still be a habitat generalist (with respect both to habitat utilization and movement between habitats) is

$$\partial r_2/\partial r_1 = -(r_1/r_2) \tag{3}$$

Figure 1 depicts several idealized examples of fitness trade-offs between the habitats. Graphically, expression (3) states that, if a population is at evolutionary equilibrium at a point on the outer bound of the fitness set, a line between that point and the origin is perpendicular to the tangent of the fitness set.

In all cases, if the initial distribution of the species is complete habitat specialization on one habitat, there is no selective force for improved adaptation to the other habitat. If all individuals are found in just one habitat, novel mutants that arise that could potentially improve fitness in the other habitat do not have any opportunity to express their potential fitness advantage (Holt and Gaines, 1992). Without exposure to the habitat in which this fitness advantage can be made manifest, selection has no traction.
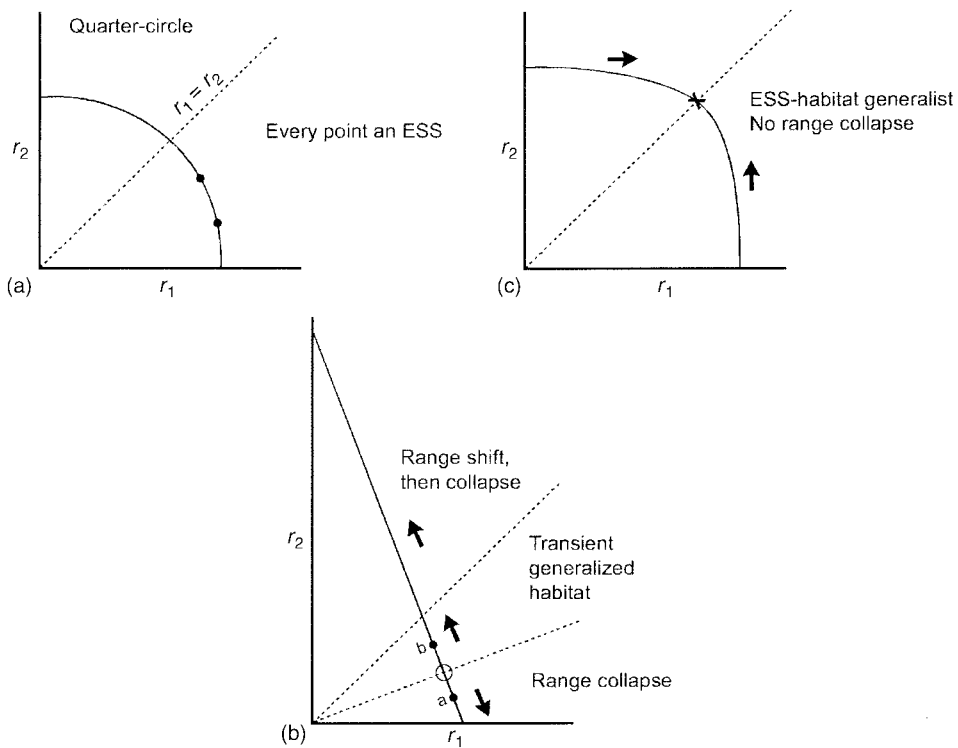
Fig. 1. Examples of trade-offs between habitats and potential evolutionary trajectories. Using the density-dependent Ricker model of the text, the carrying capacity of habitat i is proportional to the intrinsic growth rate in habitat i, r_i. A fitness set (*sensu* Levins, 1968) bounds potential genetic variation in a lineage; for simplicity, we assume clonal or haploid genetic variation. Initially, a species is monomorphic for a single combination of habitat-specific growth rates, along the outer bound of the fitness set, and has a higher growth rate (and thus equilibrial abundance) in habitat 1 than in habitat 2. Evolution is constrained to variation arising along the fitness set. Habitat use is determined at a second genetic locus, which also can evolve. Using the arguments in the text (and detailed simulations; R.D. Holt and M. Barfield, unpublished results), one can gauge the deterministic fate of novel mutations, differing slightly in growth rates. The evolutionary direction is shown by arrows. At the ESS, the line passing through the origin is perpendicular to the tangent of the fitness set. (a) The fitness set is a semi-circle, along which there is evolutionary neutrality. (b) The fitness set is bounded by a line with slope of magnitude greater than one; for instance, habitat 2 may have lower density-independent mortality rates. As discussed in the text, the species may exhibit alternative trajectories (increasing specialization towards habitat 1, or a transient phase of generalization followed by specialization on habitat 2), depending upon initial conditions. (c) Specialization to either habitat imposes large costs in the other habitat. If the species is very nearly specialized to either habitat, it still evolves towards complete specialization, but otherwise the species should evolve towards habitat generalization.

In the special case of Fig. 1a, the trade-off is a quarter-circle centred on the origin. In this special case, each point on the trade-off function defines an evolutionary equilibrium in both movement rates and local adaptation. There is no directional force tending to move the

population along the curve, which describes a line of neutrally stable evolutionary equilibria.

Now consider Fig. 1b, which shows a linear trade-off between the two habitats. The open circle denotes the only point of evolutionary equilibrium containing both habitats. At any other point along φ, iterative selection on dispersal and local adaptation alters the species' distribution. For instance, if the species is initially at point 'a', it will have a much higher carrying capacity in habitat 1 than in habitat 2. Because of this demographic asymmetry, selection is automatically skewed towards habitat 1.

But now assume the initial condition of the species is at point 'b' on the fitness set. Although there is still a demographic asymmetry between the two habitats, it is less pronounced. The magnitude of the slope of φ is greater than one. This implies that a unit increase in fitness in habitat 2 leads to a decrease in fitness in habitat 1 that is smaller in magnitude. This asymmetry in the fitness trade-off between the two habitats outweighs the demographic asymmetry due to the initial difference in carrying capacities. An allele increasing fitness in habitat 2 thus tends to increase (supplanting the original type). This then shifts selection on the movement rules, which equilibrate with relatively more individuals using habitat 2. As this iterative process of evolution occurs, the population in effect moves along the fitness surface; its carrying capacity increases in habitat 2 and decreases in habitat 1. Because the initial condition in this example assumes the species is moderately specialized to habitat 1, there is a phase of increasing generalization, as the two carrying capacities converge. But eventually the population will be increasingly specialized on habitat 2 and lose its ability to utilize habitat 1.

In Fig. 1c, the fitness set bows out strongly from the origin. Given an initial state in which the species is moderately restricted to either habitat, adaptive variants that improve fitness in one habitat have little cost in the other habitat. The evolutionarily stable pattern of its habitat utilization is for it to be a habitat generalist, even if in its initial state it was somewhat specialized to a single habitat. The particular example depicted assumes a symmetrical fitness function (relative to rotation around a line with slope of unity), which leads to equal abundances in the two habitats at the ESS (denoted by the 'X'). More generally, asymmetric fitness functions can lead to moderately unequal abundances across habitats at the ESS.

This model suggests that the evolutionary dynamics of species' ranges can go in a number of different directions, depending jointly on both the nature of adaptive trade-offs among habitats and the initial habitat distribution of the species. Species which initially are sufficiently close to habitat specialists, and in which habitat choice is adaptive (which implies few individuals reside in low-K habitats), are likely to remain specialized. Indeed, such species are likely to become more specialized with time, as selection trims low-K habitats from the habitat repertoire of the species. By contrast, species that are habitat generalists can remain generalists, provided improved fitness in one habitat comes at too great a cost in the other habitat. However, habitat generalists may also evolve towards complete specialization if large fitness benefits in one habitat incur little cost in the other habitat. Moreover, alternative evolutionarily stable habitat distributions are possible, as in Fig. 1b, where small differences in initial conditions could lead to divergent evolutionary trajectories. One can construct fitness sets, such that a species may evolve towards being either a specialist or a generalist, depending on its initial condition. Finally, species can exhibit transient phases of habitat generalization during evolutionary switches from specializing on one habitat to another.

The above results describe a particular model, in which all individuals enter a mating pool each generation. This may accurately describe the dynamics of some species' ranges (e.g. migratory birds which winter in one area, but disperse to breed in several different regions), but more generally we expect dispersal to be limited, with many individuals remaining in the habitat where they were born. Numerical studies of models with limited dispersal and the stepwise evolution of dispersal rates followed by the evolution of habitat-specific traits suggest that the loss of low-K habitats may frequently occur, and that the conclusions sketched above regarding the evolutionary trajectories expected given the trade-off functions shown in Fig. 1 apply even with limited dispersal (R. Holt and M. Barfield, unpublished results).

Although I have focused on the range dynamics of a single species, as stressed by MacArthur (1972) interspecific interactions such as competition and predation can be important determinants of a species' habitat utilization and range limits over both eco-logical and evolutionary time-scales. Some interspecific interactions can be folded into trade-off functions and so are implicit in the model. For instance, imagine that a generalist predator invades habitat 1, which initially has the higher carrying capacity for a prey species. In the absence of predation, the prey species gradually evolves towards increasing specialization on habitat 1. Following predator invasion, the added mortality lowers r_1 and so in our model lowers the realized carrying capacity of habitat 1, thus changing the trade-off function. If the added mortality is sufficiently great, a species evolving greater specialization on habitat 1 may experience a reversal in its evolutionary trajectory. [More complex approaches are needed if the species is locked into co-evolutionary interactions with other species (e.g. Hochberg and van Baalen, 1998).]

Our focus has been on microevolution within a single species, without speciation, and we have assumed that individuals have rigid habitat choices, which evolve but at different times and with a different genetic basis than abilities to utilize habitats. If instead there is flexible habitat choice by individuals, or genetic correlations between habitat preference and performance, and habitat choice can be coupled to individual differences in adaptive capaci-ties in different habitats (as in some models of competitive speciation; Rosenzweig, 1995), then instead of a single species evolving towards habitat specialization or generalization, a lineage may split into two species, each specialized to a different habitat (Rosenzweig, 1995; J.S. Brown, personal communication). After speciation, the arguments presented above still hold within each species and with even greater force: the presence of a superior competitor restricted to a given habitat usually entails that habitat will be a demographic sink for an inferior competitor, and so selection in the latter will automatically discount adaptation there, relative to a habitat where the superior competitor is absent. Negative interspecific interactions can sharpen spatial variation in fitness. This is part of the reason competitive interactions hone increasing specialization over evolutionary time-scales in adaptive radiations (Schluter, 2000) and can produce stable range limits along environmental gradi-ents (Case and Taper, 2000).

DISCUSSION

Evolution by natural selection acting either on dispersal or adaptive characters can lead to 'range collapse', where a species that originally occupied a variety of habitats becomes increasingly specialized over time and thus shrunken in its range, relative to its ancestral state. Habitat loss may also occur due to evolutionary processes not involving adaptive

trade-offs between habitats. For instance, Kawecki *et al.* (1997) argued that a habitat-specific accumulation of deleterious mutations can lead to loss of marginal habitats.

However, we have also seen that habitat loss is not inevitable, provided specialization to either habitat is too costly as measured in terms of fitness reductions in the other. Other factors can also facilitate the evolutionary retention of a broad habitat distribution and a wide geographical range for a species. These include:

1. *Modest limitations on dispersal.* With limited dispersal (e.g. due to dispersal costs, leading to strong philopatry), theoretical studies suggest that gene flow may not always counter strong selection favouring local adaptation (e.g. Antonovics, 1976). A recent study by Kirkpatrick and Barton (1997) of evolution of species' ranges along a smooth environmental gradient suggests that high rates of dispersal may be required for gene flow to constrain a species' geographical range. In their model, there is a rate of movement among habitats, below which gene flow does not constrain a species' distribution along a smooth environmental gradient. Case and Taper (2000) argue that interspecific competition of two partially sympatric species distributed along a gradient can reduce the level of dispersal needed for gene flow to hamper local selection, basically because competition can lower density and so may inflate the impact of a given amount of immigration upon local selection. Indeed, the greatest scope for local adaptation at the edges of species' ranges may be at modest (rather than zero, or large) rates of dispersal, because immigration can provide more genetic variation for selection to act upon than is provided by local mutation alone (Holt and Gomulkiewicz, 1997a; Gomulkiewicz *et al.*, 1999), and modest rates of dispersal are not likely to swamp strong selection.

2. *Non-ideal habitat distributions.* The model leading to the evolutionary trajectories illustrated in Fig. 1 assumed that populations evolve towards an ideal free habitat distribution, such that fitnesses are equalized across all occupied habitats. Either direct interference or constraints on individual abilities to discriminate among habitats can lead to evolutionarily stable, non-ideal distributions, even in stable environments. At times, such constraints on dispersal can lead to substantial numbers of individuals being exposed to low-quality habitats, which then automatically become more important in selection. With a non-ideal distribution of individuals, the strength of selection may be even stronger for adaptation to a sink than to the source habitat sustaining that sink (Holt, 1996b).

However, there is no uniform effect of non-ideal habitat distributions. The models of Kirkpatrick and Barton (1997) and Case and Taper (2000) assume uniform, passive dispersal and spatially uniform density dependence. In a heterogeneous landscape, these assumptions entail a non-ideal-free distribution with sources and sinks (Holt, 1985). Immigration into a sink with strong density dependence depresses fitness, in turn making it harder for selection to improve local adaptation (Gomulkiewicz *et al.*, 1999). If dispersal is not free to evolve, it acts as a constraint within which natural selection must act (Brown and Pavlovic, 1992; Kawecki and Holt, 2002). Strong density dependence coupled with asymmetrical dispersal can lead to selection being more effective in sinks than in sources (Holt, 1996b; Kawecki and Holt, 2002).

3. *Unstable population dynamics.* In the above analysis of the evolution of habitat specialization, I assumed very modest temporal variability to maintain selection for dispersal and permit convergence to a single ESS. Strongly unstable dynamics due either to environmental fluctuations or endogenous instability can dramatically shift how natural selection responds to spatial environmental variation. MacArthur (1972: 167) makes a point

which is the mirror image of this: namely, a species' use of space influences the direction of selection in temporally varying environments (this conjecture arose with reference to how dispersal governs the evolution of germination strategies).

Temporal variation can both directly and indirectly influence the evolution of species' niches and thus their geographical ranges. Stevens (1989) made the perceptive observation that if one considers variation in a particular environmental factor or suite of factors (e.g. temperature), then evolution to cope with temporal variation at a single location may, as a by-product, imply an ability to deal with such variation expressed spatially, and so permit a species to occupy a wide geographical range.

In addition to this direct effect of local temporal variation, there are several indirect effects. Expression (1) describes how selection 'weights' alternative habitats differing in carrying capacity in environments that are relatively stable. If environments are strongly unstable, measures of relative abundance do not fully capture how selection weights alternative environments. Theoretical studies (e.g. Holt *et al.*, 1999) have suggested that in spatially varying environments in which a fixed pattern of dispersal couples different habitats, temporal variation can radically alter the selective consequences of trade-offs between habitats. Consider, for instance, a metapopulation in which there is a mix of persistent populations, occupying one kind of habitat buffered from disturbance, and transient, low-density populations, occupying a suite of different habitats exposed to disturbances sufficiently severe to cause extinction. Relatively few dispersal propagules emanate from the low-density, transient populations. Any local adaptations that build up in the latter habitats are thus likely to be expunged by extinction; in the long run, individuals who leave descendants, including in transient populations, are likely to be those residing in stable sources.

Moreover, as noted earlier, temporal variability is a potent driver of evolution in dispersal. Stable environments should evolve towards lower dispersal rates, which can imply that gene flow is less likely to hamper local adaptation or range expansion (Kirkpatrick and Barton, 1997). However, very stable environments may lead to such a low pool of dispersers that a species will not be likely to leap dispersal barriers and occupy new terrain. As noted above, it may be selectively advantageous for a species to utilize low-quality stable sink habitats, if source habitats are sufficiently unstable (Holt, 1997). This maintains a pool of dispersers and indirectly fosters adaptation to the sink conditions. This argument holds even if the specific factors of the sink environment to which adaptation occurs are not present in the source habitat at all.

The direct and indirect consequences of temporal variation for evolutionary range dynamics may depend upon whether central or peripheral populations exhibit the greater variance in fitness. There are some systems in which peripheral populations have more stable dynamics than central populations (e.g. the snowshoe hare, *Lepus americanus*, in Wisconsin versus further north; Keith, 1990). Ecological theory suggests many mechanisms lead to unstable dynamics in habitats with high average abundances. In exploitative ecosystems, for instance, increases in productivity can destabilize dynamics (e.g. the 'paradox of enrichment'; Rosenzweig and MacArthur, 1967; Rosenzweig, 1995). A potent source of instability in many populations is provided by specialized parasites and pathogens. Such specialist enemies are not likely to persist in low-density host populations, and so unstable dynamics (e.g. due to recurrent epidemics) are more likely in habitats with high host abundance (Hochberg and van Baalen, 1998). If central, abundant populations tend to be more variable, the evolutionary tendency towards increasing specialization to high-quality

habitats may be held in check. Such instability favours continued dispersal into peripheral habitats that are low in quality, but demographically stable (Holt, 1997; Holt and Barfield, 2001). The continued exposure of individuals to low-quality habitats automatically ensures that adaptation to conditions there remains selectively relevant.

By contrast, if habitats in which abundance is low also have more unstable dynamics, selection may be even more heavily weighted towards abundant central populations than suggested by the results of Kawecki (1995) and Holt (1996a,b). Maurer and Taper (2002) argue that low-density peripheral populations may typically be more unstable and extinction-prone than central populations. If so, this makes it less likely that natural selection can sculpt adaptations to the conditions experienced by these peripheral populations. The spatial patterning of population stability may thus be a key indirect determinant of the evolution of species' ranges.

CONCLUSIONS

This paper has focused on conceptual issues regarding the dynamics of species' ranges, rather than empirical patterns. The theoretical models discussed above suggest that a variety of evolutionary trajectories should be observed in species' ranges, including range collapse, expansions and directional shifts. One factor that warrants much more attention is the role of unstable population dynamics in the evolution of species' ranges. Unstable local dynamics may indirectly facilitate the evolution of broader species' ranges, through its effects on the evolution of both dispersal and habitat specialization. Further advances in the evolutionary analysis of species' range dynamics require a more refined understanding of spatial and temporal variation in the factors driving local population dynamics.

Because dispersal links habitats, range shifts can arise not only because of changes in the regions actually experiencing a species' advance or retreat (near the range margin), but also because of environmental change elsewhere in the range, driving evolution towards either dispersal or adaptation to local habitat conditions. Evolutionary dynamics can occur on the same time-scale as environmental change (Thompson, 1998). In a continuously changing environment, the realized range dynamics will reflect the interplay of both rates of environmental change and rates of evolutionary responses (e.g. Pease *et al.*, 1989). Evolutionary lags can lead to shifts in the positions of ranges, long after the environmental change which initiated this dynamic. Even in the absence of secular environmental trends, one of the clear messages of the body of theory reviewed above is that a prime driver of range dynamics at broad spatial scales may be patterns of temporal variation in population dynamics at much more local scales.

MacArthur (1972) expressed dissatisfaction with single-species biogeography in the opening lines of his Chapter 6: 'The ranges of single species would seem to be the basic unit of biogeography. Curiously enough, the history of science often proceeds in a reverse order from expectations and this is very true of biogeography. Patterns on islands, of species diversity, and of tropical communities are already clear and even moderately well understood, while patterns of single species' ranges still seem to be catalogs of special cases. In this chapter an attempt is made at classifying kinds of range boundaries and the kinds of flow of populations that take place within those boundaries, but no very pleasing pattern emerges' (p. 127).

One wonders what MacArthur would think today. In recent years, there has been an upsurge of interest in analyses of species' ranges. Part of this surely reflects technological

developments, including geographic information systems (GIS), remote sensing, systematics databases and computational technologies. Part of this interest surely expresses growing societal concern with climate change, invasive species and other aspects of environmental degradation (Brown and Lomolino, 1998). Part may also be due to a growing appreciation of the profound impact of evolutionary processes acting over short time-scales (Thompson, 1998; Davis and Shaw, 2001; Thomas *et al.*, 2001). The development of macroecological approaches (Brown, 1995; Maurer, 1999; Gaston and Blackburn, 2000) has revealed many intriguing range patterns (Brown *et al.*, 1996), including correlations between range size and local abundance (Gaston and Blackburn, 2000), heavily skewed frequency distributions for local abundances (Brown *et al.*, 1995) and 'collapses' towards range margins for species under the onslaught of environmental change (Lomolino and Channell, 1995).

We may not have all the patterns clearly in hand that characterize single-species ranges, but I suspect we do have an increasingly firm handle on the basic processes at work which shape range limits. A full interpretation of range dynamics will surely in the end incorporate the effects of both environmental instability and the fluidity of dispersal rates and niche requirements as evolved traits of species. I suggest that many of the key processes that govern the evolutionary dynamics of species' ranges were synthesized 30 years ago by Robert MacArthur, whose last major work, *Geographical Ecology*, still warrants careful study. I hope he would be pleased to see that the framework he helped to synthesize at that time still resonates today.

REFERENCES

Antonovics, J. 1976. The nature of limits to natural selection. *Ann. Missouri Bot. Gard.*, **63**: 224–247.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.*, **124**: 255–279.

Brown, J.H. 1995. *Macroecology*. Chicago, IL: University of Chicago Press.

Brown, J.H. and Lomolino, M.V. 1998. *Biogeography*. Sunderland, MA: Sinauer Associates.

Brown, J.H., Mehlman, D.W. and Stevens, G.C. 1995. Spatial variation in abundance. *Ecology*, **76**: 2028–2043.

Brown, J.H., Stevens, G.C. and Kaufman, D.M. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.*, **27**: 597–623.

Brown, J.S. and Pavlovic, N.B. 1992. Evolution in heterogeneous environments – effects of migration on habitat specialization. *Evol. Ecol.*, **6**: 360–382.

Case, T.J. and Taper, M.L. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nat.*, **155**: 583–605.

Caughley, G., Grice, D., Barker, R. and Brown, B. 1988. The edge of the range. *J. Anim. Ecol.*, **57**: 771–785.

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

Comins, H.N. 1982. Evolutionary stable strategies for localized dispersal in 2 dimensions. *J. Theor. Biol.*, **94**: 579–606.

Davis, M.G. and Shaw, R.G. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**: 673–679.

Dias, P.C. 1996. Sources and sinks in population biology. *TREE*, **11**: 326–330.

Diffendorfer, J.E. 1998. Testing models of source–sink dynamics and balanced dispersal. *Oikos*, **81**: 417–433.

Doncaster, C.P., Clobert, J., Doligez, B., Gustafsson, L. and Danchin, E. 1997. Balanced dispersal between spatially varying local populations: an alternative to the source–sink model. *Am. Nat.*, **150**: 425–445.

Enquist, B.J., Jordan, M.A. and Brown, J.H. 1995. Connections between ecology, biogeography, and paleobiology – relationship between local abundance and geographic distribution in fossil and recent mollusks. *Evol. Ecol.*, **9**: 586–604.

Fretwell, S. 1972. *Populations in Seasonal Environments*. Princeton, NJ: Princeton University Press.

Fryxell, J. and Lundberg, P. 1998. *Individual Behavior and Community Dynamics*. London: Chapman & Hall.

Gaston, K.J. and Blackburn, T.M. 2000. *Pattern and Process in Macroecology*. Oxford: Blackwell Science.

Gomulkiewicz, R., Holt, R.D. and Barfield, M. 1999. The effects of density dependence and immigration on local adaptation and niche evolution in a black-hole sink environment. *Theor. Pop. Biol.*, **55**: 283–296.

Graham, R.W., Lundelius, E.L., Graham, M.A. *et al.* 1996. Spatial response of mammals to late quaternary environmental fluctuations. *Science*, **272**: 1601–1606.

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

Hochberg, M.E. and van Baalen, M. 1998. Antagonistic coevolution over productivity gradients. *Am. Nat.*, **152**: 620–634.

Hoffmann, A.A. and Blows, M.W. 1994. Species borders – ecological and evolutionary perspectives. *TREE*, **9**: 223–227.

Holt, R.D. 1985. Population dynamics in two-patch environments – some anomalous consequences of an optimal habitat distribution. *Theor. Pop. Biol.*, **28**: 181–208.

Holt, R.D. 1987. Population dynamics and evolutionary processes: the manifold effects of habitat selection. *Evol. Ecol.*, **1**: 331–347.

Holt, R.D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. In *Species Diversity in Ecological Communities* (R. Ricklefs and D. Schluter, eds), pp. 77–88. Chicago, IL: University of Chicago Press.

Holt, R.D. 1996a. Demographic constraints in evolution: towards unifying the evolutionary theories of senescence and niche conservatism. *Evol. Ecol.*, **10**: 1–11.

Holt, R.D. 1996b. Adaptive evolution in source–sink environments: direct and indirect effects of density-dependence on niche evolution. *Oikos*, **75**: 182–192.

Holt, R.D. 1996c. Rarity and evolution: some theoretical considerations. In *The Biology of Rarity* (W.E. Kunin and K.J. Gaston, eds), pp. 209–234. London: Chapman & Hall.

Holt, R.D. 1997. On the evolutionary stability of sink populations. *Evol. Ecol.*, **11**: 723–731.

Holt, R.D. and Barfield, M. 2001. On the relationship between the ideal-free distribution and the evolution of dispersal. In *Dispersal* (J. Clobert, E. Danchin, A.A. Dhondt and J.D. Nichols, eds), pp. 83–95. Oxford: Oxford University Press.

Holt, R.D. and Gaines, M.S. 1992. Analysis of adaptation in heterogeneous landscapes – implications for the evolution of fundamental niches. *Evol. Ecol.*, **6**: 433–447.

Holt, R.D. and Gomulkiewicz, R. 1997a. How does immigration influence local adaptation? A reexamination of a familiar paradigm. *Am. Nat.*, **149**: 563–572.

Holt, R.D. and Gomulkiewicz, R. 1997b. The evolution of species' niches: a population dynamic perspective. In *Case Studies in Mathematical Modelling: Ecology, Physiology, and Cell Biology* (E.G. Othmer, F.R. Adler, M.A. Lewis and J.C. Dallon, eds), pp. 25–50. Englewood Cliffs, NJ: Prentice-Hall.

Holt, R.D., Hochberg, M.E. and Barfield, M. 1999. Population dynamics and the evolutionary stability of biological control. In *Theoretical Approaches to Biological Control* (B. Hawkins and H. Cornell, eds), pp. 219–230. New York: Academic Press.

Jablonski, D. 1987. Heritability at the species level – analysis of geographic ranges of Cretaceous mollusks. *Science*, **238**: 360–363.

Jansen, V.A.A. and Yoshimura, J. 1998. Populations can persist in an environment consisting of sink habitats only. *Proc. Natl. Acad. Sci. USA*, **95**: 3696–3698.

Johnson, M. and Gaines, M.S. 1990. Evolution of dispersal: theoretical models and experimental tests using birds and mammals. *Annu. Rev. Ecol. Syst.*, **21**: 449–480.

Kawecki, T.J. 1995. Demography of source–sink populations and the evolution of ecological niches. *Evol. Ecol.*, **9**: 38–44.

Kawecki, T.J. and Holt, R.D. 2002. Evolutionary consequences of asymmetric dispersal rates. *Am. Nat.*, **160**: 333–347.

Kawecki, T.J., Barton, N.H. and Fry, J.D. 1997. Mutational collapse of fitness in marginal habitats and the evolution of ecological specialisation. *J. Evol. Biol.*, **10**: 407–429.

Keith, L.B. 1990. Dynamics of snowshoe hare populations. *Curr. Mammal.*, **2**: 119–195.

Kirkpatrick, M. and Barton, N.H. 1997. Evolution of a species' range. *Am. Nat.*, **150**: 1–23.

Krebs, C.J. 1994. *Ecology: The Experimental Analysis of Distribution and Abundance*. New York: HarperCollins.

Lawton, J.H., Nee, S., Letcher, A.J. and Harvey, P.H. 1994. Animal distributions: patterns and processes. In *Large-Scale Ecology and Conservation Biology* (P.J. Edwards, R.M. May and N.R. Webb, eds), pp. 41–58. London: Blackwell.

Levins, R. 1968. *Evolution in Changing Environments*. Princeton, NJ: Princeton University Press.

Lin, Y.-T. and Batzli, G.O. 2001. The influence of habitat quality on dispersal, demography, and population dynamics of voles. *Ecol. Monogr.*, **71**: 245–276.

Lomolino, M.V. and Channell, R. 1995. Splendid isolation: patterns of range collapse in endangered mammals. *J. Mammal.*, **76**: 335–347.

MacArthur, R.H. 1972. *Geographical Ecology*. New York: Harper & Row.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Maurer, B.A. 1999. *Untangling Ecological Complexity*. Chicago, IL: University of Chicago Press.

Maurer, B.A. and Taper, M.L. 2002. Connecting geographic distributions with population processes. *Ecol. Lett.*, **5**: 223–232.

Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, MA: Belknap Press.

McPeek, M.A. and Holt, R.D. 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.*, **140**: 1010–1027.

Morris, D.W. 1991. On the evolutionary stable dispersal to sink habitats. *Am. Nat.*, **137**: 907–911.

Okubo, A. 1980. *Diffusion and Ecological Problems: Mathematical Models*. New York: Springer-Verlag.

Pease, C.M., Lande, R. and Bull, J.J. 1989. A model of population growth, dispersal and evolution in a changing environment. *Ecology*, **70**: 1657–1664.

Pulliam, H.R. 1996. Sources and sinks: empirical evidence and population consequences. In *Population Dynamics in Ecological Space and Time* (E. Rhodes, R.K. Chesser and M.H. Smith, eds), pp. 45–70. Chicago, IL: University of Chicago Press.

Pulliam, H.R. 2000. On the relationship between niche and distribution. *Ecol. Lett.*, **3**: 349–361.

Pulliam, H.R. and Danielson, B.J. 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. *Am. Nat.*, **137**: S50–S66.

Ronce, O., Olivieri, I., Clobert, J. and Danchin, E. 2001. Perspectives on the study of dispersal evolution. In *Dispersal* (J. Clobert, E. Danchin, A.A. Dhondt and J.D. Nichols, eds), pp. 341–357. Oxford: Oxford University Press.

Rosenzweig, M.L. 1987. Habitat selection as a source of biological diversity. *Evol. Ecol.*, **1**: 315–330.

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

Rosenzweig, M.L. and MacArthur, R.H. 1967. Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.*, **97**: 209–223.

Schluter, D. 2000. *The Ecology of Adaptive Radiations*. Cambridge: Cambridge University Press.

Stevens, G.C. 1989. The latitudinal gradient in geographical range – how so many species coexist in the tropics. *Am. Nat.*, **133**: 240–256.

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.

Thompson, J.N. 1998. Rapid evolution as an ecological process. *TREE*, **13**: 329–332.

Tufto, J. 2001. Effects of releasing maladapted individuals: a demographic-evolutionary model. *Am. Nat.*, **158**: 331–340.

Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sunderland, MA: Sinauer Associates.

van Tienderen, P.H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution*, **45**: 1317–1331.

Wilson, H.B. 2001. The evolution of dispersal from source to sink populations. *Evol. Ecol. Res.*, **3**: 27–35.