

Review

Geographic range limits: achieving synthesis

Kevin J. Gaston*

Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

Understanding of the determinants of species' geographic range limits remains poorly integrated. In part, this is because of the diversity of perspectives on the issue, and because empirical studies have lagged substantially behind developments in theory. Here, I provide a broad overview, drawing together many of the disparate threads, considering, in turn, how influences on the terms of a simple single-population equation can determine range limits. There is theoretical and empirical evidence for systematic changes towards range limits under some circumstances in each of the demographic parameters. However, under other circumstances, no such changes may take place in particular parameters, or they may occur in a different direction, with limitation still occurring. This suggests that (i) little about range limitation can categorically be inferred from many empirical studies, which document change in only one demographic parameter, (ii) there is a need for studies that document variation in all of the parameters, and (iii) in agreement with theoretical evidence that range limits can be formed in the presence or absence of hard boundaries, environmental gradients or biotic interactions, there may be few general patterns as to the determinants of these limits, with most claimed generalities at least having many exceptions.

Keywords: births; deaths; emigration; immigration; population size; range limits

1. INTRODUCTION

Relative to the expanses of land and sea, the great majority of species are absent from most places and restricted in occurrence to rather few. The fundamental importance of determining what limits their geographic ranges has long been recognized in many research fields, including ecology, evolution, epidemiology and physiology. However, for no single species do we yet have a comprehensive understanding. The need to resolve this situation has become yet more pressing given that the knowledge bears on some of the most significant environmental challenges presently facing humankind (e.g. biological invasions, habitat loss, climate change, emerging diseases, food security).

One reason for the failure to provide a comprehensive answer to the question of what limits the geographic ranges of species has been the rather poor integration of different strands of research. While answers have been proffered at different levels of biological organization (e.g. genes, populations, communities) and from different perspectives (e.g. genetics, physiology, population dynamics, forestry, fisheries), these have tended to take place in relative isolation, and the associated literatures have tended to remain surprisingly distinct (Gaston 2003). Likewise, something of a disjunction has persisted between the literature addressing the theory of range limits and empirical studies of those limits. The latter have lagged substantially behind developments in the former, and continue essentially to constitute a large set of case

studies conducted in a heterogeneous fashion and with only limited synthesis.

A number of frameworks have been suggested to integrate the wide variety of perspectives on range limits. These variously distinguish between, for example, constraints posed by abiotic and biotic factors; intrinsic and extrinsic factors; ultimate (historical) and proximate (functional) factors; unmodifiable environmental factors, modifiable environmental factors and natural enemies; and physiological/ecological adaptation and extinction/colonization (e.g. Caughley *et al.* 1988; Brown & Lomolino 1998; Hochberg & Ives 1999). These have undoubtedly helped to crystallize thinking on key topics in range limitation. However, there are two recurrent problems with such schemes. First, while often very explicitly recognizing that this is not the case, they tend nonetheless to encourage a view of the different possible factors that may limit ranges as mutually exclusive alternatives. Second, and in a related vein, they can sometimes be seen to confound the differentiation of different kinds of constraints on ranges with the differentiation of different levels of explanation of those constraints. For example, although genetic, physiological and population dynamic constraints are often distinguished, the first may shape the second, and the first two are played out through their effects on the third.

Here, I provide a broad overview of the determinants of range limits, attempting to draw together much of the disparate material. While far from entirely resolving previous problems, in so doing I take a different approach to both integrating the various perspectives on range limits and drawing together theoretical insights and empirical findings. Rather than focus on attempting to distinguish

*k.j.gaston@sheffield.ac.uk

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between different kinds of factors that may limit geographic ranges, I consider, in turn, how influences on the different terms of the simple single-population equation $N_{t+1} = N_t + i + b - d - e$ can determine range limits, where N is population size; t is time; i is the number of immigrants; b is the number of births; d is the number of deaths; and e is the number of emigrants. Throughout, I attempt to extract some broad generalizations, acknowledging that the factors determining the limits to geographic ranges can vary between species, between different parts of the range of any given species and between different times (Porter *et al.* 2002; Gaston 2003; Morin *et al.* 2007).

2. IMMIGRATION (*i*)

The geographic ranges of most, and perhaps all, species are dispersal limited; there are areas which at any one time are unoccupied because individuals have not managed to get there (as evidenced by numerous successful accidental and intentional species introductions). Among the more cosmopolitan species, this may be a temporary state of affairs, but for the vast majority, most substantial land masses or water bodies, however suitable the environmental conditions, will remain unoccupied (an alternative interpretation is that this is an indicator of the role of history in determining where species occur, with ranges shaped by the interaction between dispersal ability and the timing of events that lead to barriers to movement being formed and destroyed). The extent to which the immediate limits of geographic ranges are dispersal limited is, however, a more contentious issue. Nonetheless, species undoubtedly exist for which range limits (i) are not at equilibrium, but rather are expanding or contracting (particularly in the face of natural and anthropogenic climate and habitat change), with immigration clearly playing a key role in enabling the former and potentially slowing the latter, (ii) extend well beyond the point at which local births exceed local deaths, and recurrent immigration thus maintains sink populations (Järvinen & Väisänen 1984; Pulliam 1988), (iii) are not entirely comprising sink populations, but extinctions of local populations may be so frequent that in the absence of a sufficient number of dispersing individuals, and, in some cases, thus some form of metapopulation dynamics, these limits would contract (Wilson *et al.* 2002; Nielsen *et al.* 2008), (iv) are extended because immigration may reduce the risk of extinction of small populations from demographic stochasticity, particularly serving to reduce the time spent at very low numbers (Holt *et al.* 2005), (v) are created by insufficient numbers of immigrants because all local adult populations are entirely dependent on recruitment of dispersers (e.g. planktonic larvae) from elsewhere (e.g. Gilman 2006), or (vi) are created because the pattern of flow of water and air currents, and potentially other dispersal routes, limits the immigration of individuals into otherwise suitable habitat (Gaylord & Gaines 2000).

Transplants of species to areas somewhat, but not markedly, beyond their geographic range limits may often be key to understanding the determinants of those limits. They have been used experimentally to differentiate between dispersal limitation and other factors limiting ranges (Woodward 1990), to enhance responses to environmental gradients making them easier to detect (Prince & Carter 1985) and to facilitate determination of

whether further evolution is necessary for range expansion (Geber & Eckhart 2005; Griffith & Watson 2006). While still small in number and often in levels of replication, some of these experiments have demonstrated persistence of transplanted populations (table 1), suggesting evidence for dispersal limitation. Unfortunately, to date, most such experiments have only been conducted for short periods, limiting the insight that they provide. Indeed, there is a significant need for more long-term transplant experiments. However, other observational and experimental studies have demonstrated dispersal limitation of species distributions more generally at local and regional scales for some taxa (Lawton & Woodroffe 1991; Primack & Miao 1992; Eriksson 1998; Svenning & Skov 2004; Beisner *et al.* 2006; Munguía *et al.* 2008), suggesting that this may play an important role in the range limitation of at least some kinds of species (e.g. those with limited dispersal abilities).

The likelihood that individuals will reach otherwise suitable habitat at range limits has two broad components (Bennett 2003). The first is a behavioural component, the innate dispersal abilities and the response of individuals to the physical structure of habitat patches. The second is a structural component, the spatial arrangement of those habitat patches. Although dispersal limitation tends predominantly to be thought of in terms of the former, both are important. A decrease in the proportion of suitable habitat patches can itself result in range limits, even when the quality of the suitable habitat remains constant, if this results in patch colonization rates being exceeded by patch extinction rates (Holt & Keitt 2000).

(a) *Gene swamping*

The level of dispersal into local populations at range limits may not only determine the persistence of those populations, but may also influence their capacity to adapt to local conditions (thereby increasing birth rates or decreasing mortality rates). Indeed, the ranges of many species could be dispersal limited in the rather different sense that the high ratio of immigrants from more central populations to those populations at range limits restricts possible local adaptation by introducing alleles adapted to those more central populations (Hoffmann & Blows 1994; Kirkpatrick & Barton 1997; Lenormand 2002); the numbers of immigrants may only need to be low in absolute terms, if high in relative ones. Such effects will be exacerbated by the typically much greater overall numbers of individuals in populations away from the range limit, any tendency for populations at range limits to be smaller (see §6), the inevitably rather unidirectional flow of immigrants into populations at range limits and the steepness of any environmental gradients. They would be weakened by tendencies for dispersing individuals to move preferentially to areas for which they were pre-adapted, and if phenotypic plasticity allowed adaptive adjustment to local conditions (Case & Taper 2000).

The extent to which ranges are in practice limited by immigration restricting local adaptation is poorly understood. Appropriate studies are still required for the magnitude and directionality of gene flow for local populations distributed in different parts of the geographic range of a species. There are examples of apparently marked through to weak adaptive differentiation between populations from the limits and other parts of the geographic ranges of species (e.g. Carbonell *et al.* 2003;

Table 1. The outcomes of experiments that have transplanted individuals of species beyond the limits to their geographic ranges (extensively modified and expanded from Gaston 2003). (Source, whether (E) or not (N) transplant was established from individuals from populations at the edge of native range; life stage, the life stage used in establishing transplant; and duration, period over which the experiment was conducted.)

species	source	life stage	duration (years)	outcome	source
transplanted beyond the extent of occurrence					
plants					
brown algae <i>Fucus serratus</i>	N	thalli	2	successfully grew and reproduced	Arrontes (1993)
annual phlox <i>Phlox drummondii</i>	N	seed	1	successfully grew and reproduced, albeit at a reduced level	Levin & Clay (1984)
<i>Clarkia xantiana xantiana</i>	N, E	seed	2	fitness 5–10% of that in native range and not sufficient for persistence	Geber & Eckhart (2005)
<i>Clarkia xantiana parviflora</i>	N, E	seed	2	fitness 5–10% of that in native range and not sufficient for persistence	Geber & Eckhart (2005)
wall pennywort <i>Umbilicus rupestris</i>	N	seed and mature plant	?	successfully grew and reproduced	Woodward (1990)
grass vetchling <i>Lathyrus nissolia</i>	?	?	?	successfully grew, reproduced and persisted	Carter & Prince (1981)
wood spurge <i>Euphorbia amygdaloides</i>	E	seed and mature plant	1	successfully germinated, grew and fruited	Shulz & Bruehlheide (1999)
round-leaved fluellen <i>Kickxia spuria</i>	?	?	?	successfully grew, reproduced and persisted	Carter & Prince (1981)
cocklebur <i>Xanthium strumarium</i>	N, E	seedling	1	individuals survived to the end of the first growing season, but did not successfully reproduce	Griffith & Watson (2006)
prickly lettuce <i>Lactuca serriola</i>	N	seed and seedling	~1	successfully grew and reproduced	Prince & Carter (1985)
bluebell <i>Hyacinthoides non-scripta</i>	N	bulb	45	reproducing populations in 41% of introduced sites after 45 years	van der Veken <i>et al.</i> (2007)
velvetleaf <i>Abutilon theophrasti</i>	E	seed	2	successfully grew and reproduced beyond the southern range limit; grew slowly and died before reproducing beyond the northern limit	Andersen <i>et al.</i> (1985)
jack pine <i>Pinus banksiana</i>	N	seedling	9	successfully grew, but cones produced contained no viable seed	Asselin <i>et al.</i> (2003)
sugar maple <i>Acer saccharum</i>	E	seed	10	lower germination than at the range edge, but higher seedling survival	Kellman (2004)
gambel oak <i>Quercus gambelii</i>	?	seedling	?	most survived the first year; only a few survived beyond two summers	Neilson & Wullstein (1983)
<i>Eucalyptus paliformis</i>	?	seedling	2	grew, but poorly	Prober (1992)
grass sp. <i>Hordeum murinum</i>	N	seed	4	grew and reproduced successfully in the first year, poor establishment in the second year and reproduction declined until none germinated by the fourth year	Davison (1977)
animals					
Baltic clam <i>Macoma balthica</i>	N	adult	1	some survived at least 10 months after translocation (not known if reproduced), but subsequent absence may be due to emigration or mortality	Hummel <i>et al.</i> (2000)
mud fiddler crab <i>Uca pugnax</i>	N	benthic	1	grew and survived well	Sanford <i>et al.</i> (2006)
thimbleberry aphid <i>Masonaphis maxima</i>	E	adult	1	successfully reproduced but new generation failed to produce sexual progeny and population failed to persist	Gilbert (1980)
[butterfly] sachem skipper <i>Atalopodes campestris</i>	N	larva	1	no significant differences in survivorship, fecundity or predation rate compared with other populations; slower development time	Crozier (2004b)

(Continued.)

Table 1. (Continued.)

species	source	life stage	duration (years)	outcome	source
transplanted beyond the elevation limit					
plants					
stonecrop sp. <i>Sedum rosea</i>	?	seed	1	successfully grew and reproduced	Woodward & Pigott (1975)
orpine <i>Sedum telephium</i>	?	seed	1	successfully grew and reproduced	Woodward & Pigott (1975)
vervain <i>Verbena officinalis</i>	N	seed and mature plant	8	poor flowering and germination	Woodward (1990)
<i>Carex curvula</i>	N	mature plant	2	successfully grew, flowered and fruited	Wagner & Reichegger (1997)
<i>Carex firma</i>	N	mature plant	2	successfully grew, flowered and fruited	Wagner & Reichegger (1997)
[monkey flower] <i>Mimulus cardinalis</i>	N, E	seedling	3	high survival in the first year, reduced growth, few able to reach reproductive maturity and did not bear mature seeds	Angert & Schemske (2005)
[monkey flower] <i>Mimulus lewisii</i>	N, E	seedling	3	most individuals died within 1 month, all within 1 year	Angert & Schemske (2005)
animals					
[psyllid] <i>Craspedolepta nebulosa</i>	N	adult	~1	no evidence of successful reproduction and population extinct within a year	Bird & Hodkinson (2005)
[psyllid] <i>Craspedolepta subpunctata</i>	E	adult	~1	no evidence of successful reproduction and population extinct within a year	Bird & Hodkinson (2005)

Santamaría *et al.* 2003; Angert & Schemske 2005, Geber & Eckhart 2005; Sanford *et al.* 2006). However, at least in some cases, even marked differentiation of individuals at range edges could occur in the face of high gene flow, if immigrants were subject to strong recurrent selection during dispersal (Sanford *et al.* 2006).

The flow of locally deleterious alleles into populations at range limits certainly will often not be sufficiently high as to limit local adaptation, and this may typically be the case. What then prevents adaptation that would enable expansion of range edges? The most common explanation is that this is a consequence of strong stabilizing selection and/or limited genetic variation arising from some combination of Allee effects, genetic drift and the lack of sufficient gene flow into populations at range limits to fuel adaptive potential (Hoffmann & Blows 1994; Bridle & Vines 2007). Indeed, Allee effects alone may be sufficient to prevent the continued spread of a species into otherwise entirely suitable habitat (i.e. in the absence of any environmental gradients; Keitt *et al.* 2001). In other words, it may in part be the very lack of immigrants in these cases which prevents range expansion.

The levels of genetic variation within a population can have a variety of influences, including on productivity/biomass, fitness components, behaviour and responses to disturbance (Hughes *et al.* 2008). If populations at range limits are smaller, experience higher rates of colonization and extinction and receive relatively low levels of immigrants, they would be predicted to have lower levels of genetic diversity, and to be more highly genetically differentiated, than populations more central to the range. Indeed, populations at range margins commonly do have lower genetic diversity or variation than more central populations (e.g. Yeh & Layton 1979; Yamashita & Polis 1995; Lammi *et al.* 1999; Hutchison 2003; Krauss *et al.* 2004; Arnaud-Haond *et al.* 2006; Beatty *et al.* 2008). However, high levels of immigration, in particular, would serve to increase levels of genetic diversity at range limits and reduce the level of genetic differentiation between populations, and there are ample examples in which no decline in diversity is observed (e.g. Garner *et al.* 2004; Gapare *et al.* 2005). Eckert *et al.* (2008) document that 64 per cent of 134 published studies detected a decline in within-population genetic diversity, and 70 per cent an increase in among-population genetic differentiation, towards range margins using nuclear molecular genetic markers. In most cases, the differences in genetic diversity were small, and it is unclear whether such trends are reflected in quantitative genetic trait variation, or whether they are ecologically significant (see also Hoffmann *et al.* 2003). Moreover, few studies have attempted to determine the relative roles of historical and contemporary factors in shaping variation in genetic diversity and differentiation across ranges, although their relative importance could be expected to differ markedly among species (Gaston 2003; Eckert *et al.* 2008). A high proportion of field studies of spatial patterns of genetic diversity and differentiation have concerned species whose geographic ranges have in the past been strongly influenced by glacial events, and have subsequently expanded their distributions; range expansion may deplete genetic variation in populations at range limits as a consequence of colonization bottlenecks (Pujol & Pannell 2008).

3. BIRTHS (b)

Inadequate levels of successful reproduction are probably one of the most common demographic explanations for range limits. Indeed, there is much evidence for reduced or outright failure of reproduction at range limits, particularly among plants (where, if taking place, it is more readily observed), and a sense that this may often be more important in range limitation than subsequent survival of offspring. Depending on taxon, changes in reproduction at range limits can variously include reductions in length of the breeding season (Sexton *et al.* 1992), levels of sexual reproduction (Dorken & Eckert 2001; Tremblay *et al.* 2002; Beatty *et al.* 2008), levels of cross-fertilization (Herlihy & Eckert 2005; Darling *et al.* 2008), levels of pollination (Murphy & Vasseur 1995), levels and timing of flowering or fruit ripening (Levin & Clay 1984; Griffith & Watson 2006; Morin *et al.* 2007), seed production and fertility (Pigott & Huntley 1978; Pigott 1981; García *et al.* 2000; Jump & Woodward 2003; Sugiyama 2003; Angert 2006), clutch sizes (Sanz 1997), germination rates (Levin & Clay 1984; Sugiyama 2003) and numbers of offspring (Sanz 1997, Ontiveros & Pleguezuelos 2003; Hassall *et al.* 2006). While readily interpreted as evidence of negative influences on reproduction at range limits, many of these changes may nonetheless constitute adaptive responses, particularly to low population sizes.

Of course, caution needs to be exercised in interpreting changes in particular reproductive traits towards range limits in isolation, as the picture can often be complicated by trade-offs between different such traits (e.g. numbers and sizes of offspring, short-term and long-term reproductive output). For example, while Peakall (1970) found that the eastern bluebird *Sialia sialis* in North America had larger clutches at the height of the breeding season in the centre of its range, and that the breeding season is longest at mid-latitudes where breeding density is highest, there was no geographic pattern in breeding success. Moreover, there are examples in which measures of reproductive output do not change or even sometimes increase towards range limits (Lammi *et al.* 1999; Angert 2006; Lester *et al.* 2007). Indeed, some reproductive traits exhibit systematic patterns of latitudinal variation across the geographic ranges of species, such that they may be more exaggerated or better developed at one range limit (usually at the higher latitude) than towards the range centre, and less pronounced at the other range limit (e.g. Fleming & Gross 1990; Jenkins & Hockey 2001; Sugiyama 2003). These latitudinal effects can only be detected by large-scale studies, and their existence often cannot be ruled out from those that have been more constrained, emphasizing the need for investigations of range limits to maintain a broad perspective (and the potential for local studies to prove misleading).

This said, the importance of reproductive failure or reduction at range limits is reinforced by the results of a number of the experimental transplants of populations beyond those limits (table 1). Again, these experiments have been predominantly of plant species, for which they are obviously much easier to conduct, and use of a wider range of organisms would be desirable. Typically, such changes in reproduction are argued to result from declines in the availability of resources (through declines in their quantities and/or accessibility), and increasing demands

on resources for maintenance at the expense of reproduction (e.g. as a consequence of changing climatic conditions). Several studies have demonstrated such effects at range limits (e.g. Järvinen & Väisänen 1984; Bost & Jouventin 1991; Hummel *et al.* 2000; Joyner-Matos *et al.* 2007). They may also be manifested in declines in growth rates and body sizes at range limits (e.g. Crozier 2004b; Angert & Schemske 2005; Jump *et al.* 2006; Peguero-Pina *et al.* 2007; Gutiérrez *et al.* 2008), and in increases in measures of developmental instability (Kark 2001; but see Pérez-Tris *et al.* 2000). Reductions in resource availability could result from the presence of competitors, with the limits to the ranges of some species apparently being influenced by such biotic interactions (Hersteinsson & Macdonald 1992; Bullock *et al.* 2000; Gross & Price 2000; Edwards & Hernández-Carmona 2005).

The range limits of longer lived species may be determined by sporadic successful reproduction events. This may be particularly true of some tree species, for which populations at range limits may show atypical age structures that are significantly shaped by levels of recruitment, often reflecting long-term temporal variation in climate (e.g. Pigott 1989; Kullman 1992; Tremblay *et al.* 2002). It is also true of some intertidal organisms, experiencing recruitment from planktonic populations, which may be highly susceptible to climatic variability. Whether this also occurs for some terrestrial animals remains unclear. It would tend to be more characteristic of species with no or low adult dispersal abilities, but as these tend to be smaller and shorter lived, the potential for population persistence without successful reproduction may be limited.

Many species at their range limits occupy a particular subset of those habitats that they occupy elsewhere, or even a different set of habitats altogether (Ehleringer & House 1984; Conkey *et al.* 1995; but see Meilleur *et al.* 1997; Herlihy & Eckert 2005). This seems commonly to reflect responses to climate, with the breadth of habitats exploited increasing when climatic conditions ameliorate (Thomas *et al.* 2001), and successful reproduction is enabled.

4. DEATHS (d)

Arguably, relatively too much attention is paid to range limitation as a consequence principally of increasing mortality rather than that of numbers of births. Much of this attention is implicit, with, for example, extensive documentation and discussion of relationships between the physiological tolerances and capacities of organisms (usually measured in the laboratory) and the environmental conditions prevailing at range limits (e.g. Root 1988; Jenkins & Hoffmann 2001; Dunham *et al.* 2003). Direct observation of the consequences of physiological tolerances and capacities failing or being overwhelmed at range limits is typically extremely difficult, particularly for animals where the demise of individuals has often to be surmised, and mortality and emigration are often hard to measure separately. Nonetheless, there are empirical examples of high levels of mortality at range limits (e.g. Iversen 1944; Dekker & Beukema 1993; Ungerer *et al.* 1999; Edwards & Hernández-Carmona 2005; Angert 2006), and in transplants beyond those limits (table 1), and of greater levels of physiological stress

(e.g. Tomanek & Somero 1999; Sorte & Hofmann 2004). In many cases, these high rates of mortality occur during or shortly after extreme environmental events. It is thus noteworthy that, conversely, most (especially 'correlative') modelling of the distributions of individual species, particularly in the context of predicting responses to climate change, employs spatial variation in mean not extreme environmental conditions (Gaston 2003). It may not always, however, be the extreme events *per se* that are significant but the interaction between these events and resource availability, such that insufficient resources are available to enable organisms to cope with the demands of those events. In this sense, physiological and resource limitations on species distributions may be strongly confounded.

While physiological tolerances and capacities tend foremost to be measured for adult organisms, mortality of pre-reproductive individuals may be much more important in setting range limits for many species (e.g. St Clair & Gregory 1990; Bengtsson 2000; Zacherl *et al.* 2003; Crozier 2004a), often apparently occurring as a consequence of development times becoming too extended (e.g. Crozier 2004b; Angert & Schemske 2005; Sanford *et al.* 2006). In other cases, however, it may indeed be the larger individuals that experience differential mortality, particularly where this is a consequence of failure to meet overall energy demands, which scale with body size (e.g. Pörtner & Knust 2007).

Spatial coincidence between environmental conditions and the physiological tolerances and capacities of species are almost invariably interpreted as providing evidence that these tolerances and capacities limit distributions. However, causality may potentially flow in the opposite direction (Gaston 2003). If there are sufficient costs of maintaining broad physiological tolerances and capacities, then selection may favour those individuals that lose them, leading to physiological tolerances and capacities coinciding with environmental conditions for this reason. Differentiating between these two alternatives is extremely difficult. Heritability studies and artificial selection experiments have regularly demonstrated that physiological tolerances and capacities (along with morphological and life-history traits) often have marked genetic variance (Spicer & Gaston 1999; Blows & Hoffmann 2005). Indeed, these tolerances and capacities can be modified substantially. Why then would these traits constrain the distributions of species? First, such variances may not be typical of many wild populations, perhaps particularly in populations at range limits if these are small, and experience limited gene flow and/or inbreeding (Blows & Hoffmann 2005). Second, range expansion may often necessitate changes in more than one trait, particularly because environmental parameters commonly covary (e.g. temperature and precipitation), and this may be much more difficult to achieve. Indeed, there may be trade-offs in selecting for different traits.

(a) *Predation and parasitism*

Natural enemies have widely been held to be relatively unimportant in determining geographic range limits. This is based on the assumption that specialist natural enemies would become locally extinct before driving their prey to this state, and mortality pressure from generalist natural enemies would decline at low abundances as they would

switch to alternative prey. Rather few empirical studies have examined the influence of natural enemies across range limits. Nonetheless, some support for these inferences is based on observed reductions in levels of mortality or infection by natural enemies at range limits (e.g. García *et al.* 2000; Alexander *et al.* 2007). However, there are also a number of empirical examples in which rates of predation (including herbivory; e.g. Pienkowski 1984; Bruelheide & Scheidel 1999; deRivera *et al.* 2005) or parasitism (e.g. Price *et al.* 1988; Briers 2003) may play a role in range limitation. Of course, exploitation (and in some cases persecution) by humans may be particularly significant in constraining the ranges of some species (e.g. Lensink 1997).

Contrary to the above propositions, theory suggests that specialist natural enemies can generate range limits in prey species if these enemies exhibit sufficient dispersal rates that their populations in sites where the prey is nearly eliminated can be sustained by sites in which it is not, and if the prey species exhibits some gradient in productivity (Hochberg & Ives 1999; Case *et al.* 2005). Equally, generalist natural enemies can create range limits in prey species when different prey species are differentially productive or vulnerable to predation across a gradient, and apparent competition is exerted (Case *et al.* 2005). They may also do so if the additional costs of capturing rare prey species are relatively unimportant, as is often the case with human harvesting (e.g. fisheries, bushmeat trade).

When other constraints on geographic ranges are removed, the resulting expansion can allow species to escape from natural enemies (Menéndez *et al.* 2008), with presumably important consequences for mortality profiles (the contribution of different factors to overall levels of mortality) if not necessarily for overall levels of mortality. How these profiles change over the geographic range of a species has seldom been documented, although Brewer & Gaston (2003) reported huge variation for the holly leafminer *Phytomyza ilicis*, with different mortality factors predominating towards different range limits.

5. EMIGRATION (e)

The role of emigration in influencing the position of geographic range limits has received surprisingly little explicit attention. Nonetheless, if populations at range limits are more fragmented, and many are demographic sinks, then dispersal from these populations may be selected against. Alternatively, if habitat quality varies spatially and temporally (including through an improving trend), there is interference or pre-emptive competition, or competition among kin, then dispersal from populations at range margins may be selected for (Holt 2003). The bulk of empirical examples have documented increases in dispersal at range limits (e.g. Cwynar & MacDonald 1987; Hill *et al.* 1999; Thomas *et al.* 2001; Darling *et al.* 2008), although attention has focused on expanding range limits, it may be that such effects have disproportionately been sought, and it is often difficult to differentiate between such an effect being caused by the arrival of more dispersive individuals in edge populations from elsewhere and genuine *in situ* selection (Geber 2008).

In practice, the whole shape of dispersal kernels, the frequency distributions of dispersal distances, may change

systematically with the nature of range limits (Phillips *et al.* 2008). Where ranges are expanding, the individuals at the limits will tend to be those with better dispersal abilities, having dispersed further than others, resulting in a spatial sorting of dispersal ability. If some component of dispersal ability is heritable, then the offspring of individuals at the range limit will also tend to have higher dispersal ability. This process, repeated generation after generation, potentially leads to continual selection for increased dispersal at range limits, akin to a runaway evolutionary process (Phillips *et al.* 2008).

(a) Behaviour

One of the reasons that deaths do not occur at geographic range limits at the high frequency that seems often to be supposed is that more mobile organisms can exhibit behaviours that lead to their departing areas when conditions become less favourable. In general, the interaction between range limits and behaviour has been rather poorly studied, although it has been suggested both that such responses are observed (e.g. Ontiveros & Pleguezuelos 2003) and that some such limits reflect the inadequacy of certain behaviours (e.g. the American bison *Bison bison* no longer being able to paw through snows to obtain winter forage: Daubenmire 1985; the Indian crested porcupine *Hystrix indica* no longer having sufficient nocturnal foraging time: Alkon & Saltz 1988).

6. POPULATION SIZE (N)

The outcome of the levels of immigration, births, deaths and emigration at the range limit of a species is its population size there. The notion was long championed that the local densities and population sizes of species declined from the core of their distributions towards their range limits (Hengeveld & Haeck 1982; Brown 1984). Indeed, such a pattern is assumed in much theory about the structure of ranges and the determinants of range limits. However, it is now apparent that there is limited empirical evidence for such systematic patterns in density (Sagarin & Gaines 2002a,b; Gaston 2003; Herlihy & Eckert 2005; Kluth & Bruelheide 2005; Poulin & Dick 2007; Samis & Eckert 2007). By contrast, it is widely accepted that levels of occupancy often decline towards range limits, with marked fragmentation of population structure being commonplace (Gaston 2003; Gilman 2006; Yakimowski & Eckert 2007; but see Samis & Eckert 2007). This suggests the possibility that observed changes in density towards range limits are dependent on spatial scale, with local densities not demonstrating any systematic pattern, but declines perhaps becoming more apparent when densities are averaged over large areas and thus reflecting the declining level of occupancy. However, there could also be an important effect of the spatial extents of studies, with declines in local abundances perhaps more frequent from closer to range edges rather than across the full span of central to range-edge populations. Clearer differentiation needs to be made between an 'abundant-centre' hypothesis, in which abundances are predicted to decline from the core to the periphery of a geographic range, and a 'rare-periphery' hypothesis, in which abundances are predicted to be low at the range limit with no necessary wider pattern.

The population structure of geographic ranges is a key issue for understanding how range limits are determined. As well as being an outcome of demographic forces, and an influence on these forces (through density dependence), the local population size at range limits itself can be an important influence on the potential for local adaptation and thus demographic change. This occurs through its interaction with genetic variation, Allee effects, genetic drift and the numerical dominance or otherwise of immigrants from other parts of the range. The level of isolation of local populations at range limits is also significant, as it strongly shapes the influence immigrant individuals are likely to have on local adaptation.

If levels of immigration, births, deaths and/or emigration are temporally quite variable at range limits, as seems likely often to be the case, then one would predict that abundances would also often exhibit substantial variation. Indeed, there is evidence both of greater temporal variability in abundances at range edges and of a higher frequency of local population extinctions, the latter being exacerbated by small population sizes (Thomas *et al.* 1994; Mehlman 1997; Williams *et al.* 2003; McClenachan & Cooper 2008). Again, these dynamics can have important consequences for the ability of populations at range limits locally to adapt, particularly through the loss of genetic variation from stochastic drift, and for the evolution of dispersal.

7. PUTTING THE PIECES TOGETHER

It is clear that, under some circumstances, there is theoretical and empirical evidence for systematic changes towards range limits in all four of the demographic parameters considered here (i , b , d and e), and that these can contribute to range limitation. Equally, under other circumstances, no such changes may take place, or they may occur in the opposing direction, with limitation still occurring. This is important in several ways. First, it suggests that rather little about range limitation can be inferred from the vast majority of empirical studies, which document change in only one of these demographic parameters, and often only a component of that parameter. Second, it suggests a pressing need for studies that document variation in all of the parameters, and a search for study organisms that would be best suited to such work (they may be difficult to find). Third, in agreement with theoretical evidence that geographic range limits can be formed in the presence or absence of hard boundaries, environmental gradients or biotic interactions, there may be few truly general patterns as to the determinants of the limits of geographic ranges, with most claimed generalities at least having many exceptions (e.g. that range limits are typified by lower densities, lower genetic variation, lower fitness, higher mortality).

This last point follows from the fact that only small changes in i , b , d or e may be sufficient to bring about a range edge (Lensink 1997; Gaston 2003). This is particularly so if these parameters are strongly nonlinear functions of environmental conditions and/or population density. Laboratory studies suggest that this is often the case, with asymmetric responses of demographic parameters to environmental gradients being common, in which critical thresholds are reached at which these parameters change very rapidly (Gaston 2003). One consequence is that it has

often proven frustratingly difficult to explain what determines the limits of a particular species at a given place and time.

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