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Review

Geographic range limits: achieving synthesis

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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

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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 *Fucus serratus*	N	thalli	2	successfully grew and reproduced	Arrontes (1993)
annual phlox *Phlox drummondii*	N	seed	1	successfully grew and reproduced, albeit at a reduced level	Levin & Clay (1984)
Clarkia xantiana xantiana	N, E	seed	2	fitness 5–10% of that in native range and not sufficient for persistence	Geber & Eckhart (2005)
Clarkia xantiana parviflora	N, E	seed	2	fitness 5–10% of that in native range and not sufficient for persistence	Geber & Eckhart (2005)
wall pennywort *Umbilicus rupestris*	N	seed and mature plant	?	successfully grew and reproduced	Woodward (1990)
grass vetchling *Lathyrus nissolia*	?	?	?	successfully grew, reproduced and persisted	Carter & Prince (1981)
wood spurge *Euphorbia amygdaloides*	E	seed and mature plant	1	successfully germinated, grew and fruited	Shulz & Bruelheide (1999)
round-leaved fluellen *Kickxia spuria*	?	?	?	successfully grew, reproduced and persisted	Carter & Prince (1981)
cocklebur *Xanthium strumarium*	N, E	seedling	1	individuals survived to the end of the first growing season, but did not successfully reproduce	Griffith & Watson (2006)
prickly lettuce *Lactuca serriola*	N	seed and seedling	~1	successfully grew and reproduced	Prince & Carter (1985)
bluebell *Hyacinthoides non-scripta*	N	bulb	45	reproducing populations in 41% of introduced sites after 45 years	van der Veken *et al.* (2007)
velvetleaf *Abutilon theophrasti*	E	seed	2	successfully grew and reproduced beyond the southern range limit; grew slowly and died before reproducing beyond the northern limit	Andersen *et al.* (1985)
jack pine *Pinus banksiana*	N	seedling	9	successfully grew, but cones produced contained no viable seed	Asselin *et al.* (2003)
sugar maple *Acer saccharum*	E	seed	10	lower germination than at the range edge, but higher seedling survival	Kellman (2004)
gambel oak *Quercus gambelii*	?	seedling	?	most survived the first year; only a few survived beyond two summers	Neilson & Wullstein (1983)
Eucalyptus paliformis	?	seedling	2	grew, but poorly	Prober (1992)
grass sp. *Hordeum murinum*	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 *Macoma balthica*	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 *et al.* (2000)
mud fiddler crab *Uca pugnax*	N	benthic	1	grew and survived well	Sanford *et al.* (2006)
thimbleberry aphid *Masonaphis maxima*	E	adult	1	successfully reproduced but new generation failed to produce sexual progeny and population failed to persist	Gilbert (1980)
[butterfly] sachem skipper *Atalopedes campestris*	N	larva	1	no significant differences in survivorship, fecundity or predation rate compared with other populations; slower development time	Crozier (2004*b*)

(*Continued.*)

Table 1. (*Continued.*)

species	source	life stage	duration (years)	outcome	source
transplanted beyond the elevation limit					
plants					
stonecrop sp. *Sedum rosea*	?	seed	1	successfully grew and reproduced	Woodward & Pigott (1975)
orpine *Sedum telephium*	?	seed	1	successfully grew and reproduced	Woodward & Pigott (1975)
vervain *Verbena officinalis*	N	seed and mature plant	8	poor flowering and germination	Woodward (1990)
Carex curvula	N	mature plant	2	successfully grew, flowered and fruited	Wagner & Reichegger (1997)
Carex firma	N	mature plant	2	successfully grew, flowered and fruited	Wagner & Reichegger (1997)
[monkey flower] *Mimulus cardinalis*	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] *Mimulus lewisii*	N, E	seedling	3	most individuals died within 1 month, all within 1 year	Angert & Schemske (2005)
animals					
[psyllid] *Craspedolepta nebulosa*	N	adult	∼1	no evidence of successful reproduction and population extinct within a year	Bird & Hodkinson (2005)
[psyllid] *Craspedolepta subpunctata*	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 2004*b*; 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 2004*a*), often apparently occurring as a consequence of development times becoming too extended (e.g. Crozier 2004*b*; 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 2002*a*,*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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REFERENCES

Alexander, H. M., Price, S., Houser, R., Finch, D. & Tourtello, M. 2007 Is there reduction in disease and pre-dispersal seed predation at the border of a host plant's range? Field and herbarium studies of *Carex blanda*. *J. Ecol.* **95**, 446–457. (doi:10.1111/j.1365-2745.2007.01228.x)

Alkon, P. U. & Saltz, D. 1988 Foraging time and the northern range limits of Indian crested porcupines (*Hystrix indica* Kerr). *J. Biogeogr.* **15**, 403–408. (doi:10.2307/2845271)

Andersen, R. N., Menges, R. M. & Conn, J. S. 1985 Variability in velvetleaf (*Abutilon theophrasti*) and reproduction beyond its current range in North America. *Weed Sci.* **33**, 507–512.

Angert, A. A. 2006 Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. lewisii*). *Ecology* **87**, 2014–2025. (doi:10.1890/0012-9658(2006)87[2014:DOCAMP]2.0.CO;2)

Angert, A. L. & Schemske, D. W. 2005 The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. *Evolution* **59**, 1671–1684. (doi:10.1554/05-107.1)

Arnaud-Haond, S., Teixeira, S., Massa, S. I., Billot, C., Saenger, P., Coupland, G., Duarte, C. M. & Serrão, E. A. 2006 Genetic structure at range edge: low diversity and high inbreeding in southeast Asian mangrove (*Avicennia marina*) populations. *Mol. Ecol.* **15**, 3515–3525. (doi:10.1111/j.1365-294X.2006.02997.x)

Arrontes, J. 1993 Nature of the distributional boundary of *Fucus serratus* on the north shore of Spain. *Mar. Ecol. Prog. Ser.* **93**, 183–193. (doi:10.3354/meps093183)

Asselin, H., Payette, S., Fortin, M-J. & Vallée, S. 2003 The northern limit of *Pinus banksiana* Lamb. in Canada: explaining the difference between the eastern and western distributions. *J. Biogeogr.* **30**, 1709–1718. (doi:10.1046/j.1365-2699.2003.00935.x)

Beatty, G. E., McEvoy, P. M., Sweeney, O. & Provan, J. 2008 Range-edge effects promote clonal growth in peripheral populations of the one-sided wintergreen *Orthilla secunda*. *Divers. Distrib.* **14**, 546–555. (doi:10.1111/j.1472-4642.2008.00469.x)

Beisner, B. E., Peres-Neto, P. R., Lindström, E. S., Barnett, A. & Longhi, M. L. 2006 The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology* **87**, 2985–2991. (doi:10.1890/0012-9658(2006)87[2985:TROEAS]2.0.CO;2)

Bengtsson, K. 2000 Long-term demographic variation in range-margin populations of *Gypsophila fastigiata*. *Folia Geobot.* **35**, 143–160. (doi:10.1007/BF02803093)

Bennett, A. F. 2003 *Linkages in the landscape: the role of corridors and connectivity in wildlife conservation*. Gland, Switzerland & Cambridge, UK: IUCN.

Bird, J. M. & Hodkinson, I. D. 2005 What limits the altitudinal distribution of *Craspedolepta* species (Sternorrhyncha: Psylloidea) on fireweed? *Ecol. Entomol.* **30**, 510–520. (doi:10.1111/j.0307-6946.2005.00719.x)

Blows, M. W. & Hoffmann, A. A. 2005 A reassessment of genetic limits to evolutionary change. *Ecology* **86**, 1371–1384. (doi:10.1890/04-1209)

Bost, C. A. & Jouventin, P. 1991 The breeding performance of the Gentoo Penguin *Pygoscelis papua* at the northern edge of its range. *Ibis* **133**, 14–25. (doi:10.1111/j.1474-919X.1991.tb04804.x)

Brewer, A. M. & Gaston, K. J. 2003 The geographical range structure of the holly leaf-miner. II. Demographic rates. *J. Anim. Ecol.* **72**, 82–93. (doi:10.1046/j.1365-2656.2003.00682.x)

Bridle, J. R. & Vines, T. H. 2007 Limits to evolution at range margins: when and why does adaptation fail? *Trends Ecol. Evol.* **22**, 140–147. (doi:10.1016/j.tree.2006.11.002)

Briers, R. A. 2003 Range limits and parasite prevalence in a freshwater snail. *Proc. R. Soc. B* **270**(Suppl.), S178–S180. (doi:10.1098/rsbl.2003.0046)

Brown, J. H. 1984 On the relationship between abundance and distribution of species. *Am. Nat.* **124**, 255–279. (doi:10.1086/284267)

Brown, J. H. & Lomolino, M. V. 1998 *Biogeography*, 2nd edn. Sunderland, MA: Sinauer Associates.

Bruelheide, H. & Scheidel, U. 1999 Slug herbivory as a limiting factor for the geographical range of *Arnica montana*. *J. Ecol.* **87**, 839–848. (doi:10.1046/j.1365-2745.1999.00403.x)

Bullock, J. M., Edwards, R. J., Carey, P. D. & Rose, R. J. 2000 Geographical separation of two *Ulex* species at three spatial scales: does competition limit species' ranges? *Ecography* **23**, 257–271. (doi:10.1111/j.1600-0587.2000.tb00281.x)

Carbonell, R., Pérez-Tris, J. & Tellería, J. L. 2003 Effects of habitat heterogeneity and local adaptation on the body condition of a forest passerine at the edge of its distributional range. *Biol. J. Linn. Soc.* **78**, 479–488. (doi:10.1046/j.0024-4066.2002.00156.x)

Carter, R. N. & Prince, S. D. 1981 Epidemic models used to explain biogeographical distribution limits. *Nature* **293**, 644–645. (doi:10.1038/293644a0)

Case, T. J. & Taper, M. L. 2000 Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nat.* **155**, 583–605. (doi:10.1086/303351)

Case, T. J., Holt, R. D., McPeek, M. A. & Keitt, T. H. 2005 The community context of species' borders: ecological and evolutionary perspectives. *Oikos* **108**, 28–40. (doi:10.1111/j.0030-1299.2005.13148.x)

Caughley, G., Grice, D., Barker, R. & Brown, B. 1988 The edge of the range. *J. Anim. Ecol.* **57**, 771–785. (doi:10.2307/5092)

Conkey, L. E., Keifer, M. & Lloyd, A. H. 1995 Disjunct jack pine (*Pinus banksiana* Lamb.) structure and dynamics, Acadia National Park, Maine. *Ecoscience* **2**, 168–176.

Crozier, L. 2004*a* Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* **85**, 231–241. (doi:10.1890/02-0607)

Crozier, L. G. 2004*b* Field transplants reveal summer constraints on a butterfly range expansion. *Oecologia* **141**, 148–157. (doi:10.1007/s00442-004-1634-z)

Cwynar, L. C. & MacDonald, G. M. 1987 Geographical variation of lodgepole pine in relation to population history. *Am. Nat.* **129**, 463–469. (doi:10.1086/284651)

Darling, E., Samis, K. E. & Eckert, C. G. 2008 Increased seed dispersal potential towards geographic range limits in a Pacific coast dune plant. *New Phytol.* **178**, 424–435. (doi:10.1111/j.1469-8137.2007.02349.x)

Daubenmire, R. 1985 The western limits of the range of the American bison. *Ecology* **66**, 622–624. (doi:10.2307/1940411)

Davison, A. W. 1977 The ecology of *Hordeum murinum* L. III. Some effects of adverse climate. *J. Ecol.* **65**, 523–530. (doi:10.2307/2259498)

Dekker, R. & Beukema, J. J. 1993 Dynamics and growth of a bivalve, *Abra tenuis*, at the northern edge of its distribution. *J. Mar. Biol. Assoc. UK* **73**, 497–511.

deRivera, C. E., Ruiz, G. M., Hines, A. H. & Jivoff, P. 2005 Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. *Ecology* **86**, 3364–3376. (doi:10.1890/05-0479)

Dorken, M. E. & Eckert, C. G. 2001 Severely reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). *J. Ecol.* **89**, 339–350. (doi:10.1046/j.1365-2745.2001.00558.x)

Dunham, J., Rieman, B. & Chandler, G. 2003 Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. *N. Am. J. Fish. Manage.* **23**, 894–904. (doi:10.1577/M02-028)

Eckert, C. G., Samis, K. E. & Lougheed, S. C. 2008 Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. *Mol. Ecol.* **17**, 1170–1188. (doi:10.1111/j.1365-294X.2007.03659.x)

Edwards, M. S. & Hernández-Carmona, G. 2005 Delayed recovery of giant kelp near its southern range limit in the North Pacific following El Niño. *Mar. Biol.* **147**, 273–279. (doi:10.1007/s00227-004-1548-7)

Ehleringer, J. & House, D. 1984 Orientation and slope preference in barrel cactus (*Ferocactus acanthodes*) at its northern distribution limit. *Great Basin Nat.* **44**, 133–139.

Eriksson, Å. 1998 Regional distribution of *Thymus serpyllum*: management history and dispersal limitation. *Ecography* **21**, 35–43. (doi:10.1111/j.1600-0587.1998.tb00392.x)

Fleming, I. A. & Gross, M. R. 1990 Latitudinal clines: a trade-off between egg number and size in Pacific Salmon. *Ecology* **71**, 1–11. (doi:10.2307/1940241)

Gapare, W. J., Aitken, S. N. & Ritland, C. E. 2005 Genetic diversity of core and peripheral Sitka spruce (*Picea sitchensis* (Bong.) Carr) populations: implications for conservation of widespread species. *Biol. Conserv.* **123**, 113–123. (doi:10.1016/j.biocon.2004.11.002)

García, D., Zamora, R., Gómez, J. M., Jordano, P. & Hódar, J. A. 2000 Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. *J. Ecol.* **88**, 436–446. (doi:10.1046/j.1365-2745.2000.00459.x)

Garner, T. W. J., Pearman, P. B. & Angelone, S. 2004 Genetic diversity across a vertebrate species' range: a test of the central–peripheral hypothesis. *Mol. Ecol.* **13**, 1047–1053. (doi:10.1111/j.1365-294X.2004.02119.x)

Gaston, K. J. 2003 *The structure and dynamics of geographic ranges*. Oxford, UK: Oxford University Press.

Gaylord, B. & Gaines, S. D. 2000 Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* **155**, 769–789. (doi:10.1086/303357)

Geber, M. A. 2008 To the edge: studies of species' range limits. *New Phytol.* **178**, 228–230. (doi:10.1111/j.1469-8137.2008.02414.x)

Geber, M. A. & Eckhart, V. M. 2005 Experimental studies of adaptation in *Clarkia xantiana*. II. Fitness variation across a subspecies border. *Evolution* **59**, 521–531. (doi:10.1554/04-265)

Gilbert, N. 1980 Comparative dynamics of a single-host aphid. I. The evidence. *J. Anim. Ecol.* **49**, 351–369. (doi:10.2307/4251)

Gilman, S. E. 2006 The northern geographic range limit of the intertidal limpet *Collisella scabra*: a test of performance, recruitment, and temperature hypotheses. *Ecography* **29**, 709–720. (doi:10.1111/j.0906-7590.2006.04572.x)

Griffith, T. M. & Watson, M. A. 2006 Is evolution necessary for range expansion? Manipulating reproductive timing of a weedy annual transplanted beyond its range. *Am. Nat.* **167**, 153–164. (doi:10.1086/498945)

Gross, S. J. & Price, T. D. 2000 Determinants of the northern and southern range limits of a warbler. *J. Biogeogr.* **27**, 869–878. (doi:10.1046/j.1365-2699.2000.00440.x)

Gutiérrez, N. L., Martínez, A. & Defeo, O. 2008 Identifying environmental constraints at the edge of a species' range: scallop *Psychrochlamys patagonica* in the SW Atlantic Ocean. *Mar. Ecol. Prog. Ser.* **353**, 147–156. (doi:10.3354/meps07184)

Hassall, M., Walters, R. J., Telfer, M. & Hassall, M. R. J. 2006 Why does a grasshopper have fewer, larger offspring at its range limits? *J. Evol. Biol.* **19**, 267–276. (doi:10.1111/j.1420-9101.2005.00967.x)

Hengeveld, R. & Haeck, J. 1982 The distribution of abundance. I. Measurements. *J. Biogeogr.* **9**, 303–316. (doi:10.2307/2844717)

Herlihy, C. R. & Eckert, C. G. 2005 Evolution of self-fertilization at geographical range margins? A comparison of demographic, floral, and mating system variables in central vs. peripheral populations of *Aquilegia canadensis* (Ranunculaceae). *Am. J. Bot.* **92**, 744–751. (doi:10.3732/ajb.92.4.744)

Hersteinsson, P. & Macdonald, D. W. 1992 Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64**, 505–515. (doi:10.2307/3545168)

Hill, J. K., Thomas, C. D. & Blakeley, D. S. 1999 Evolution of flight morphology in a butterfly that has recently expanded its geographic range. *Oecologia* **121**, 165–170. (doi:10.1007/s004420050918)

Hochberg, M. E. & Ives, A. R. 1999 Can natural enemies enforce geographical range limits? *Ecography* **22**, 268–276. (doi:10.1111/j.1600-0587.1999.tb00502.x)

Hoffmann, A. A. & Blows, M. W. 1994 Species borders: ecological and evolutionary perspectives. *Trends Ecol. Evol.* **9**, 223–227. (doi:10.1016/0169-5347(94)90248-8)

Hoffmann, A. A., Hallas, R. J., Dean, J. A. & Schiffer, M. 2003 Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science* **301**, 100–102. (doi:10.1126/science.1084296)

Holt, R. D. 2003 On the evolutionary ecology of species' ranges. *Evol. Ecol. Res.* **5**, 159–178.

Holt, R. D. & Keitt, T. H. 2000 Alternative causes for range limits: a metapopulation perspective. *Ecol. Lett.* **3**, 41–47. (doi:10.1046/j.1461-0248.2000.00116.x)

Holt, R. D., Keitt, T. H., Lewis, M. A., Maurer, B. A. & Taper, M. L. 2005 Theoretical models of species' borders: single species approaches. *Oikos* **108**, 18–27. (doi:10.1111/j.0030-1299.2005.13147.x)

Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N. & Vellend, M. 2008 Ecological consequences of genetic diversity. *Ecol. Lett.* **11**, 609–623. (doi:10.1111/j.1461-0248.2008.01179.x)

Hummel, H., Bogaards, R. H., Bachelet, G., Caron, F., Sola, J. C. & Amiard-Triquet, C. 2000 The respiratory performance and survival of the bivalve *Macoma balthica* (L.) at the southern limit of its distribution area: a translocation experiment. *J. Exp. Mar. Biol. Ecol.* **251**, 85–102. (doi:10.1016/S0022-0981(00)00208-2)

Hutchison, D. W. 2003 Testing the central/peripheral model: analyses of microsatellite variability in the eastern collared lizard (*Crotaphytus collaris collaris*). *Am. Midl. Nat.* **149**, 148–162. (doi:10.1674/0003-0031(2003)149[0148:TTCPMA]2.0.CO;2)

Iversen, J. 1944 *Viscum*, *Hedera* and *Ilex* as climate indicators. *Geol. Foren. Forhandl. Stockh.* **66**, 463–483.

Jenkins, A. R. & Hockey, P. A. R. 2001 Prey availability influences habitat tolerance: an explanation for the rarity of peregrine falcons in the tropics. *Ecography* **24**, 359–367. (doi:10.1034/j.1600-0587.2001.d01-634.x)

Jenkins, N. L. & Hoffmann, A. A. 2001 Distribution of *Drosophila serrata* Malloch (Diptera: Drosophilidae) in Australia with particular reference to the southern border. *Aust. J. Entomol.* **40**, 41–48. (doi:10.1046/j.1440-6055.2001.00197.x)

Joyner-Matos, J., Chapman, L. J., Downs, C. A., Hofer, T., Leeuwenburgh, C. & Julian, D. 2007 Stress response of a freshwater clam along an abiotic gradient: too much oxygen may limit distribution. *Funct. Ecol.* **21**, 344–355. (doi:10.1111/j.1365-2435.2007.01230.x)

Jump, A. S. & Woodward, F. I. 2003 Seed production and population density decline approaching the range edge of *Cirsium* species. *New Phytol.* **160**, 349–358. (doi:10.1046/j.1469-8137.2003.00873.x)

Jump, A. S., Hunt, J. M. & Peñuelas, J. 2006 Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob. Chang. Biol.* **12**, 2163–2174. (doi:10.1111/j.1365-2486.2006.01250.x)

Järvinen, A. & Väisänen, R. A. 1984 Reproduction of pied flycatchers (*Ficedula hypoleuca*) in good and bad breeding seasons in a northern marginal area. *Auk* **101**, 439–450.

Kark, S. 2001 Shifts in bilateral asymmetry within a distribution range: the case of the chukar partridge. *Evolution* **55**, 2088–2096. (doi:10.1554/0014-3820(2001)055[2088:SIBAWA]2.0.CO;2)

Keitt, T. H., Lewis, M. A. & Holt, R. D. 2001 Allee effects, invasion pinning, and species' borders. *Am. Nat.* **157**, 203–216. (doi:10.1086/318633)

Kellman, M. 2004 Sugar maple (*Acer saccharum* Marsh.) establishment in boreal forest: results of a transplantation experiment. *J. Biogeogr.* **31**, 1515–1522. (doi:10.1111/j.1365-2699.2004.01128.x)

Kirkpatrick, M. & Barton, N. H. 1997 Evolution of a species' range. *Am. Nat.* **150**, 1–23. (doi:10.1086/286054)

Kluth, C. & Bruelheide, H. 2005 Central and peripheral *Hornungia petraea* populations: patterns and dynamics. *J. Ecol.* **93**, 584–595. (doi:10.1111/j.1365-2745.2005.00997.x)

Krauss, J., Schmitt, T., Seitz, A., Steffan-Dewenter, I. & Tscharntke, T. 2004 Effects of habitat fragmentation on the genetic structure of the monophagous butterfly *Polyommatus coridon* along its northern range margin. *Mol. Ecol.* **13**, 311–320. (doi:10.1046/j.1365-294X.2003.02072.x)

Kullman, L. 1992 Climatically induced regeneration patterns of marginal populations of *Pinus sylvestris* in northern Sweden. *Oecol. Mont.* **1**, 5–10.

Lammi, A., Siikamäki, P. & Mustajärvi, K. 1999 Genetic diversity, population size, and fitness in central and peripheral populations of a rare plant *Lychnis viscaria*. *Conserv. Biol.* **13**, 1069–1078. (doi:10.1046/j.1523-1739.1999.98278.x)

Lawton, J. H. & Woodroffe, G. L. 1991 Habitat and the distribution of water voles: why are there gaps in a species' range? *J. Anim. Ecol.* **60**, 79–91. (doi:10.2307/5446)

Lenormand, T. 2002 Gene flow and the limits to natural selection. *Trends Ecol. Evol.* **17**, 183–189. (doi:10.1016/S0169-5347(02)02497-7)

Lensink, R. 1997 Range expansion of raptors in Britain and the Netherlands since the 1960s: testing an individual-based diffusion model. *J. Anim. Ecol.* **66**, 811–826. (doi:10.2307/5997)

Lester, S. E., Gaines, S. D. & Kinlan, B. P. 2007 Reproduction on the edge: large-scale patterns of individual performance in a marine invertebrate. *Ecology* **88**, 2229–2239. (doi:10.1890/06-1784.1)

Levin, D. A. & Clay, K. 1984 Dynamics of synthetic *Phlox drummondii* populations at the species margin. *Am. J. Bot.* **71**, 1040–1050. (doi:10.2307/2443379)

McClenachan, L. & Cooper, A. B. 2008 Extinction rate, historical population structure and ecological role of the Caribbean monk seal. *Proc. R. Soc. B* **275**, 1351–1358. (doi:10.1098/rspb.2007.1757)

Mehlman, D. W. 1997 Change in avian abundance across the geographic range in response to environmental change. *Ecol. Appl.* **7**, 614–624. (doi:10.1890/1051-0761(1997)007[0614:CIAAAT]2.0.CO;2)

Meilleur, A., Brisson, J. & Bouchard, A. 1997 Ecological analyses of the northernmost population of pitch pine (*Pinus rigida*). *Can. J. For. Res.* **27**, 1342–1350. (doi:10.1139/cjfr-27-9-1342)

Menéndez, R., González-Megías, A., Lewis, O. T., Shaw, M. R. & Thomas, C. D. 2008 Escape from natural enemies during climate-driven range expansion: a case study. *Ecol. Entomol.* **33**, 413–424. (doi:10.1111/j.1365-2311.2008.00985.x)

Morin, X., Augspurger, C. & Chuine, I. 2007 Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology* **88**, 2280–2291. (doi:10.1890/06-1591.1)

Munguía, M., Peterson, A. T. & Sánchez-Cordero, V. 2008 Disperal limitation and geographical distributions of mammal species. *J. Biogeogr.* **35**, 1879–1887. (doi:10.1111/j.1365-2699.2008.01921.x)

Murphy, S. D. & Vasseur, L. 1995 Pollen limitation in a northern population of *Hepatica acutiloba*. *Can. J. Bot.* **73**, 1234–1241. (doi:10.1139/b95-134)

Neilson, R. P. & Wullstein, L. H. 1983 Biogeography of two southwest American oaks in relation to atmospheric dynamics. *J. Biogeogr.* **10**, 275–297. (doi:10.2307/2844738)

Nielsen, C. L. R., Wakamiya, S. M. & Nielsen, C. K. 2008 Viability and patch occupancy of a swamp rabbit metapopulation at the northern edge of its distribution. *Biol. Conserv.* **141**, 1043–1054. (doi:10.1016/j.biocon.2008.01.016)

Ontiveros, D. & Pleguezuelos, J. M. 2003 Influence of climate on Bonelli's eagle's (*Hieraaetus fasciatus* V. 1822) breeding success through the Western Mediterranean. *J. Biogeogr.* **30**, 755–760. (doi:10.1046/j.1365-2699.2003.00860.x)

Peakall, D. B. 1970 The eastern bluebird: its breeding season, clutch size, and nesting success. *Living Bird* **9**, 239–256.

Peguero-Pina, J. J., Camarero, J. J., Abadía, A., Martín, E., González-Cascón, R., Morales, F. & Gil-Pelegrín, E. 2007 Physiological performance of silver-fir (*Abies alba* Mill.) populations under contrasting climates near the south-western distribution limit of the species. *Flora* **202**, 226–236.

Phillips, B. L., Brown, G. P., Travis, J. M. J. & Shine, R. 2008 Reid's paradox revisited: the evolution of dispersal kernels during range expansion. *Am. Nat.* **172**, S34–S48. (doi:10.1086/588255)

Pienkowski, M. W. 1984 Breeding biology and population dynamics of Ringed plovers *Charadrius hiaticula* in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding. *J. Zool. Lond.* **202**, 83–114.

Pigott, C. D. 1981 Nature of seed sterility and natural regeneration of *Tilia cordata* near its northern limit in Finland. *Ann. Bot. Fenn.* **18**, 255–263.

Pigott, C. D. 1989 Factors controlling the distribution of *Tilia cordata* Mill at the northern limits of its geographical range IV. Estimated ages of the trees. *New Phytol.* **112**, 117–121. (doi:10.1111/j.1469-8137.1989.tb00316.x)

Pigott, C. D. & Huntley, J. P. 1978 Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range I. Distribution in north-west England. *New Phytol.* **81**, 429–441. (doi:10.1111/j.1469-8137.1978.tb02648.x)

Porter, W. P., Sabo, J. L., Tracy, C. R., Reichman, O. J. & Ramankutty, N. 2002 Physiology on a landscape scale. *Integr. Comp. Biol.* **42**, 431–453. (doi:10.1093/icb/42.3.431)

Poulin, R. & Dick, T. A. 2007 Spatial variation in population density across the geographical range in helminth parasites of yellow perch *Perca flavescens*. *Ecography* **30**, 629–636. (doi:10.1111/j.2007.0906-7590.05139.x)

Price, P. W., Westoby, M. & Rice, B. 1988 Parasite-mediated competition: some predictions and tests. *Am. Nat.* **131**, 544–555. (doi:10.1086/284805)

Primack, R. B. & Miao, S. L. 1992 Dispersal can limit local plant distribution. *Conserv. Biol.* **6**, 513–519. (doi:10.1046/j.1523-1739.1992.06040513.x)

Prince, S. D. & Carter, R. N. 1985 The geographical distribution of prickly lettuce (*Lactuca serriola*): III. Its performance in transplant sites beyond its distribution limit in Britain. *J. Ecol.* **73**, 49–64. (doi:10.2307/2259767)

Prober, S. M. 1992 Environmental influences on the distribution of the rare *Eucalyptus paliformis* and the common *E. fraxinoides*. *Aust. J. Ecol.* **17**, 51–65. (doi:10.1111/j.1442-9993.1992.tb00780.x)

Pujol, B. & Pannell, J. R. 2008 Reduced responses to selection after species range expansion. *Science* **321**, 96. (doi:10.1126/science.1157570)

Pulliam, H. R. 1988 Sources, sinks, and population regulation. *Am. Nat.* **132**, 652–661. (doi:10.1086/284880)

Pérez-Tris, J., Carbonell, R. & Tellería, J. L. 2000 Abundance distribution, morphological variation and juvenile condition of robins, *Erithacus rubecula* (L.), in their Mediterranean range boundary. *J. Biogeogr.* **27**, 879–888. (doi:10.1046/j.1365-2699.2000.00457.x)

Pörtner, H. O. & Knust, R. 2007 Climate change affects marine fishes through the oxygen limitaion of thermal tolerance. *Science* **315**, 95–97. (doi:10.1126/science.1135471)

Root, T. 1988 Energy constraints on avian distributions and abundances. *Ecology* **69**, 330–339. (doi:10.2307/1940431)

Sagarin, R. D. & Gaines, S. D. 2002*a* Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *J. Biogeogr.* **29**, 985–997. (doi:10.1046/j.1365-2699.2002.00705.x)

Sagarin, R. D. & Gaines, S. D. 2002*b* The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecol. Lett.* **5**, 137–147. (doi:10.1046/j.1461-0248.2002.00297.x)

Samis, K. E. & Eckert, C. G. 2007 Testing the abundant center model using range-wide demographic surveys of two coastal dune plants. *Ecology* **88**, 1747–1758. (doi:10.1890/06-1153.1)

Sanford, E., Holzman, S. B., Haney, R. A., Rand, D. M. & Bertness, M. D. 2006 Larval tolerance, gene flow, and the northern geographic range limit of fiddler crabs. *Ecology* **87**, 2882–2894. (doi:10.1890/0012-9658(2006)87[2882:LTGFAT]2.0.CO;2)

Santamaría, L., Figuerola, J., Pilon, J. J., Mjelde, M., Green, A. J., de Boer, T., King, R. A. & Gornall, R. J. 2003 Plant performance across latitude: the role of plasticity and local adaptation in an aquatic plant. *Ecology* **84**, 2454–2461. (doi:10.1890/02-0431)

Sanz, J. J. 1997 Geographic variation in breeding parameters of the Pied Flycatcher *Ficedula hypoleuca*. *Ibis* **139**, 107–114. (doi:10.1111/j.1474-919X.1997.tb04509.x)

Sexton, O. J., Andrews, R. M. & Bramble, J. E. 1992 Size and growth rate characteristics of a peripheral population of *Crotaphytus collaris* (Suaria: Crotaphytidae). *Copeia* **1992**, 968–980. (doi:10.2307/1446626)

Shulz, C. & Bruelheide, H. 1999 An experimental study on the impact of winter temperature on the distribution of *Euphorbia amygdaloides* L. in Central Germany. In *Recent shifts in vegetation boundaries of deciduous forests, especially due to general global warming* (eds F. Klötzli & G.-R. Walther), pp. 121–150. Basel, Switzerland: Birkhäuser Verlag.

Sorte, C. J. B. & Hofmann, G. E. 2004 Changes in latitudes, changes in aptitudes: *Nucella canaliculata* (Mollusca: Gastropoda) is more stressed at its range edge. *Mar. Ecol. Prog. Ser.* **274**, 263–268. (doi:10.3354/meps274263)

Spicer, J. I. & Gaston, K. J. 1999 *Physiological diversity and its ecological implications*. Oxford, UK: Blackwell Science.

St Clair, R. C. & Gregory, P. T. 1990 Factors affecting the northern range limit of painted turtles (*Chrysemys picta*): winter acidosis or freezing? *Copeia* **1990**, 1083–1089. (doi:10.2307/1446492)

Sugiyama, S. 2003 Geographical distribution and phenotypic differentiation in populations of *Dactylis glomerata* L. in Japan. *Plant Ecol.* **169**, 295–305. (doi:10.1023/A:1026081122985)

Svenning, J.-C. & Skov, F. 2004 Limited filling of the potential range in European tree species. *Ecol. Lett.* **7**, 565–573. (doi:10.1111/j.1461-0248.2004.00614.x)

Thomas, J. A., Moss, D. & Pollard, E. 1994 Increased fluctuations of butterfly populations towards the northern edges of species' ranges. *Ecography* **17**, 215–220. (doi:10.1111/j.1600-0587.1994.tb00096.x)

Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M. & Conradt, L. 2001 Ecological and evolutionary processes at expanding range margins. *Nature* **411**, 577–581. (doi:10.1038/35079066)

Tomanek, L. & Somero, G. N. 1999 Evolutionary and acclimation-induced variation in the heat-shock responses of congeneric marine snails (genus *Tegula*) from different thermal habitats: implications for limits of thermotolerance and biogeography. *J. Exp. Biol.* **202**, 2925–2936.

Tremblay, M. F., Bergeron, Y., Lalonde, D. & Mauffette, Y. 2002 The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range. *J. Biogeogr.* **29**, 365–373. (doi:10.1046/j.1365-2699.2002.00665.x)

Ungerer, M. J., Ayres, M. P. & Lombardero, M. J. 1999 Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *J. Biogeogr.* **26**, 1133–1145. (doi:10.1046/j.1365-2699.1999.00363.x)

van der Veken, S., Rogister, J., Verheyen, K., Hermy, M. & Nathan, R. 2007 Over the (range) edge: a 45-year transplant experiment with the perennial forest herb *Hyacinthoides non-scripta*. *J. Ecol.* **95**, 343–351. (doi:10.1111/j.1365-2745.2006.01208.x)

Wagner, J. & Reichegger, B. 1997 Phenology and seed development of the alpine sedges *Carex curvula* and *Carex firma* in response to contrasting topoclimates. *Arct. Alp. Res.* **29**, 291–299. (doi:10.2307/1552143)

Williams, C. K., Ives, A. R. & Applegate, R. D. 2003 Population dynamics across geographical ranges: time-series analyses of three small game species. *Ecology* **84**, 2654–2667. (doi:10.1890/03-0038)

Wilson, R. J., Ellis, S., Baker, J. S., Lineham, M. E., Whitehead, R. W. & Thomas, C. D. 2002 Large-scale patterns of distribution and persistence at the range margins of a butterfly. *Ecology* **83**, 3357–3368. (doi:10.1890/0012-9658(2002)083[3357:LSPODA]2.0.CO;2)

Woodward, F. I. 1990 The impact of low temperatures in controlling the geographical distribution of plants. *Phil. Trans. R. Soc. B* **326**, 585–593. (doi:10.1098/rstb.1990.0033)

Woodward, F. I. & Pigott, C. D. 1975 The climatic control of the altitudinal distribution of *Sedum rosea* (L.) Scop. and *S. telephium* L.I. Field observations. *New Phytol.* **74**, 323–334. (doi:10.1111/j.1469-8137.1975.tb02620.x)

Yakimowski, S. B. & Eckert, C. G. 2007 Threatened peripheral populations in context: geographical variation in population frequency and size and sexual reproduction in a clonal woody shrub. *Conserv. Biol.* **21**, 811–822. (doi:10.1111/j.1523-1739.2007.00684.x)

Yamashita, T. & Polis, G. A. 1995 A test of the central–marginal model using sand scorpion populations (*Paruroctonus mesaensis*, Vaejovidae). *J. Arachnol.* **23**, 60–64.

Yeh, F. C. & Layton, C. 1979 The organization of genetic variability in central and marginal populations of lodgepole pine *Pinus contorta* spp. *latifolia*. *Can. J. Genet. Cytol.* **21**, 487–503.

Zacherl, D., Gaines, S. D. & Lonhart, S. I. 2003 The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852). *J. Biogeogr.* **30**, 913–924. (doi:10.1046/j.1365-2699.2003.00899.x)