

Moving beyond assumptions to understand abundance distributions across the ranges of species

Raphael D. Sagarin^{1,2}, Steven D. Gaines³ and Brian Gaylord⁴

¹Institute of the Environment, LaKretz Hall, Suite 300, University of California, Los Angeles, CA 90095-1496, USA

²From September 2006: Nicholas Institute for Environmental Policy Solutions, Duke University, Durham, NC 27708, USA

³Marine Science Institute and Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA

⁴Bodega Marine Lab and Section of Evolution and Ecology, University of California Davis, 2099 Westside Road, Bodega Bay, CA 94923, USA

The assumption that species are most abundant in the center of their range and decline in abundance toward the range edges has a long history in the ecological literature. This assumption has driven basic and applied ecological and evolutionary hypotheses about the causes of species range limits and their responses to climate change. Here, we review recent studies that are taking biogeographical ecology beyond previously held assumptions by observing populations in the field across large parts of the species range. When these studies combine data on abundance, demographics, organismal physiology, genetics and physical factors, they provide a promising approach for teasing out ecological and evolutionary mechanisms of the patterns and processes underlying species ranges.

The importance of abundance

Geographical patterns of the abundance of species underlie some of the most fundamental issues in ecology, including the causes of species range limits, gene flow within populations, population dynamics and explanations for macroecological patterns such as the species-area relationship. Patterns of species abundance have also been used to develop hypotheses about applied issues such as how species will respond to climate change, how to identify probable locations of pest outbreaks and where to situate natural reserves. Given the importance of abundance distributions to ecological theory and applications, it is surprising to find that much of the work on these topics presumes a particular geographical distribution of abundance and makes assumptions about the mechanisms that underlie it.

Here, we discuss how past reliance on simplifying assumptions about range-wide distributions of abundance has hampered pattern recognition in studies of species-abundance distributions and our ability to move beyond simple pattern recognition to mechanistic studies in macroecology. We argue that the emerging picture of geographical complexity in abundance distributions can be seen as an opportunity to reexamine ecological and

evolutionary hypotheses drawn originally on simplistic assumptions about species distributions. In this regard, the breakdown of one generality creates a new window for theory and applied research based on the interaction of biological, ecological, evolutionary and physical factors across entire ranges of species. Recent work reviewed here has capitalized on this opportunity using a range of study systems and emerging techniques.

Assumptions about abundance

A widespread biogeographical assumption is that species are most abundant in the center of their range and decline in abundance toward the range edges. This assumption, which we call the ‘abundant-center hypothesis’, has a long history in theoretical and applied ecology. It has even been called a ‘general rule’ of biogeography [1] and ‘a common feature shared by all species’ [2].

The abundant-center assumption is more than an observational curiosity, because it has also been used extensively in developing ecological and evolutionary hypotheses (Box 1). However, assumptions about species-abundance distributions have rarely been tested empirically, and those tests that have been performed have revealed important limitations. Sagarin and Gaines [3] showed that only 39% of the 145 independent datasets that could be used to test the abundant-center hypothesis could be said to approximate the pattern using even the most lenient criteria possible. These findings are echoed in a simultaneous and independent review by Gaston [4]. Several studies across a range of taxa and locations published since these two studies fail to find general evidence for abundant-center patterns (e.g. South America, bats [5]; Europe, holly leaf-miner [6]; South-west U.S., sawflies [7]; North America, perennial plant [8]; Europe, annual plant [9]; South America, estuarine crab [10]; South America, mole crab [11]; Pacific coast U.S., limpet [12]; North America, trees [13]), or find limited evidence from a subset of the analyzed species [14] or few sites in the range [15,16]. Even in simplified systems, where entire species ranges can be studied, distributions of abundance appear much more complicated and interesting than was assumed previously (Boxes 2 and 3).

Corresponding author: Sagarin, R.D. (sagarin@ucla.edu).
Available online 11 July 2006

Box 1. Hypotheses drawn from the abundant-center assumption

In reviewing primary literature and textbooks, Sagarin and Gaines [3] found that many ecological and evolutionary hypotheses were developed based on the abundant-center assumption. In some cases, different authors drew contradictory hypotheses based on the same abundant-center assumption. The validity of these hypotheses (listed below and adapted from [3]) needs to be re-examined based on the more complex geographic distributions of abundance and other life-history factors that are being revealed in the empirical studies that we review in this paper.

- Speciation is likely to occur at the edges.
- Vicariant events at the edges will have a greater impact than at the center.
- Central populations are more crucial to protect and monitor.
- Edge populations are more crucial to protect and monitor.
- Pest outbreaks are more probable from central populations.
- Reintroduced species will do better in the historical range center.
- Sites near range edges will see gradual population changes as climate change shifts the ranges of species.
- Edge populations are more resistant to climate change.
- The abundant-center pattern leads to the observation of a bimodal distribution of site occupancy and abundance.
- The abundant-center pattern mediates species dynamics within the range.
- The central part of the range is the center of origin.
- Edge population dynamics are more variable.
- Central populations are sources, edge populations are sinks.
- Extinction is more probable at the edges.
- Central populations inhabit a greater variety of habitats.
- Competition is less important at range edges.
- Competition is more important at range edges.
- Competitors and/or parasites might limit species near edges.
- Gene flow from the center will swamp the edges.
- Edge populations are less likely to be swamped by central populations.
- Edge populations are less genetically variable.
- Edge populations are genetically distinct.

Recent studies have acknowledged that this complexity can strongly influence predictions about population variability [16], genetic population structure [17], habitat conservation [18] and species responses to climate change across ranges of species [19] that were based previously on *a priori* assumptions about distributions of individuals. In some cases, acquiring data on the actual distribution of species abundance will go a long way toward testing more appropriate hypotheses or making more accurate

predictions, although abundance distributions alone typically offer only a limited perspective (Box 4).

Moving beyond assumptions

Recognizing both that species distributions do not always exhibit an assumed distribution, and that actual abundance distributions provide limited opportunities for inference, suggests that adding additional layers of data on a geographical scale (including basic population demographics,

Box 2. The complex geometry of ranges

The ubiquity of assumptions about geographical patterns of abundance, despite the lack of convincing support for them, belies several under appreciated difficulties of interpreting and utilizing data gathered at the scale of species ranges.

Even determining the range center can be a challenge that has been left largely to qualitative visual techniques. Without a quantitative determination of the center of a range, there is the danger of self-fulfilling prophecies (i.e. choosing a peak of abundance subjectively somewhere in the interior of the distribution as the center of the range). To obtain an objective, quantitative estimate of the range center, we turn to geometry.

Brown [59] calculated the range center as the intersection of two perpendicular transects that run through the widest points in the range. If ranges were oval in shape, this approach would identify the range center. With more irregularly shaped ranges, however, this method can be skewed easily toward the edge of the range.

A more general solution that does not assume simple range geometries comes from viewing the range center as the 'balance point' of the range. That is, if the shape of the range were cut out of cardboard, the center of the range would be the point where one could balance the cardboard range on a pin (i.e. its centroid). The balance point is readily found analytically. If the range is plotted on a coordinate graph, the range center, (\hat{x}, \hat{y}) , is found using Equation I:

$$\hat{x} = \frac{\int x dA}{\int dA}, \hat{y} = \frac{\int y dA}{\int dA}, \quad [\text{Eqn I}]$$

where the integral of dA is the total area. In practice, this exact solution is typically replaced by a discrete approximation that can be estimated from a range map (Equation II):

$$\hat{x} \approx \frac{\sum x \Delta A}{\sum \Delta A}, \hat{y} \approx \frac{\sum y \Delta A}{\sum \Delta A}, \quad [\text{Eqn II}]$$

where $\sum \Delta A$ approximates the total area.

The range center estimated using this geometrical approach can be different from the center point estimated by the simple intersection of two transects. This, in turn, can lead to different interpretations of the

distribution of species abundance relative to the range center. In the hypothetical species range shown in Figure 1, the center point of the range determined using Brown's method (indicated by the circle) happens to fall in an area of high population density (warmest shading), whereas the center point determined using the method discussed here (indicated by the diamond) falls in an area of relatively lower density.

In cases of discontinuous ranges and ranges with highly irregular shapes, the method that we propose here can place the range center near the range edge or even outside the range entirely. The absurdity of such a situation forces us to look beyond simple pattern analysis and towards a focus on the ecological and evolutionary questions that we seek to address with geographically scaled data.

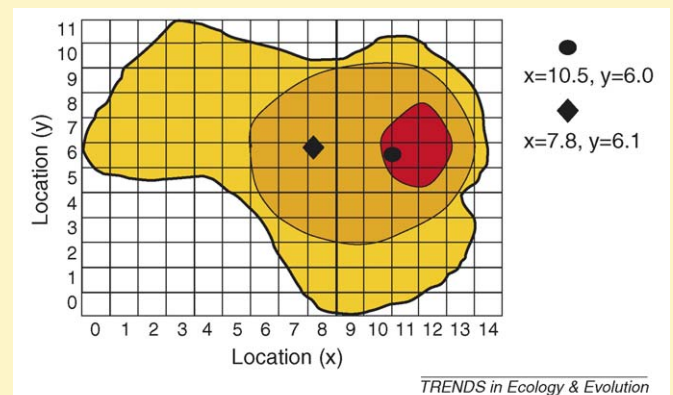
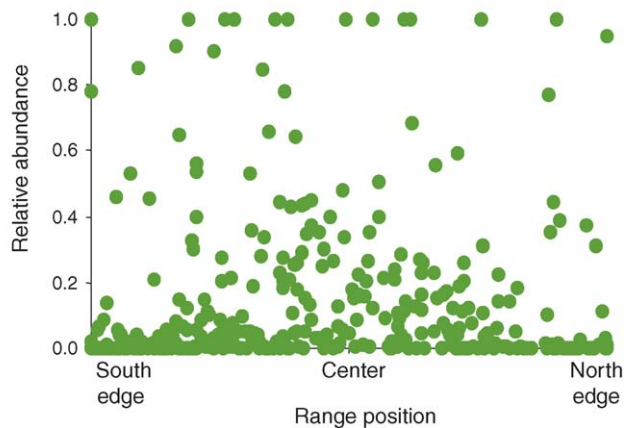


Figure 1. Hypothetical species range where population density is greatest in red and lowest in yellow areas. Determining the range center using the intersection of the longest axes (circle) yields a different location (indicated by numbers on the axes) than determining the range using quantitative analysis (diamond). This leads to different interpretations of where population density is concentrated in the range.

Box 3. Coastal species as an ideal system

Coastal species can be ideal systems to test range-wide hypotheses owing to the unique geometry of their geographical ranges, their physical environment and the distribution of their ranges. These species have ranges that can be thousands of kilometers long, but <0.1 km wide at all points. Defining the range edge and center is relatively simple for these species because their range is essentially one-dimensional. Only two points need to be determined for the edges, and the center can be defined as the midpoint between the edges. The distribution of abundance can be analyzed from population surveys taken at multiple locations within the range. Despite this apparent simplicity, large-scale empirical, synthetic and theoretical studies of coastal systems along the Pacific coasts of North and South America are still revealing the complexity of studying species ranges.

As an example, studies of abundance distributions of 12 intertidal invertebrate species across most or all of their Pacific coast ranges revealed a variety of abundance distributions, including those with highest values at the range edges (Figure 1) [60]. If species conformed generally to abundant-center expectations, the most abundant sites for these species would be clustered toward the center of the range-position axis. In fact, the highest relative abundances (relative abundance = 1) were spread evenly across the axis and high values (i.e. relative abundance >0.75) were found more commonly near the range edges than near the range center. Additionally, the physical environment and physiological responses of species along this gradient are non-linear and non-intuitive, with peaks in heat stress and stress response in the northern part of the gradient [26,28]. These findings contradict both the abundant-center and the similar 'peak and tail' assumptions that have been used previously to infer the processes underlying species distributions.



TRENDS in Ecology & Evolution

Figure 1. Relative abundance (= site-specific abundance/maximum abundance across the range for each species) across the range for 12 intertidal invertebrate species. The data indicate that abundant-center distributions are not more common than other distributions, and that high relative abundances are often found near the range edge. Based on data from [60].

biophysical variables and genetic population structure) will be necessary to narrow the range of viable hypotheses to explain range boundaries and population distributions. Caughley *et al.* [20], for example, layered geographically scaled observations on population density, 'growth rates and' 'well-being' of individuals, or physiological performance to identify the causes of range limits in terrestrial mammals. Their framework, which simplified clines in variables from the range center to the edge as either 'ramps' or 'steps', provided an important benchmark that is ripe for expansion using more natural geographical patterns. For example, further efforts can be devoted to understanding complex causal agents that can produce widely different abundance

Box 4. Using distributions of abundance to test hypotheses

Distributions of abundance are non-existent currently for most taxa, yet they can provide crucial baseline data for monitoring populations and for testing hypotheses related to conservation biology and species responses to climate change. Ceballos and Ehrlich [61] emphasized that conservation efforts should focus on extinctions of populations rather than of species, because the former is a prelude to the latter. The authors used historical range maps to estimate range loss, which they used as a proxy for population loss. However, the authors' attempts to connect patterns of range contraction to human population density remain speculative given that historical data on population sizes in relevant parts of the range were lacking. Likewise, the lack of spatially explicit population data limits the ability to interpret results from Channell and Lomolino's [62] test of the hypothesis that species ranges should collapse toward the range centers. This hypothesis is based on the abundant-center assumption, because it assumes that more-dense central populations will be more resistant to extinction. In fact, the authors found that ranges tended to collapse toward range edges, and argued that the observed pattern points to human-related disturbances that leave only the remote edges intact. The authors did not consider that their study species reached their highest densities originally at their range edges, making these populations more resistant to extinction than the central populations.

Inadequate records of species abundance distributions also limit our ability to determine causes of range shifts [53,63–65]. Sagarin *et al.* [66] were limited in their ability to interpret significant changes in intertidal invertebrate abundance at the Hopkins Marine Station (HMS) in Monterey, CA between the 1930s and the warmer period of the 1990s. They found that species with southern ranges (relative to the HMS) generally increased in abundance and that northern species generally decreased, a result consistent with a simple hypothesis of a climate-related poleward shift in species distributions. Without detailed geographical abundance data, the authors could not make predictions about shifts in the abundance of wide-ranging cosmopolitan species. However, if we assume that the actual distributions of abundance observed in later biogeographical studies of invertebrate abundance [60] had shifted northward past the HMS owing to climate warming, the sign of abundance change for 11 of the 12 species (including five of six cosmopolitan species) would have been predicted correctly.

Nonetheless, hypotheses based on abundance distributions alone rarely provide satisfactory elucidation of underlying causes and can confound multiple causal mechanisms [24]. At the very least, these hypotheses assume that distributions of relative abundance stay constant through time. Indeed, the widely cited 'climate envelope' hypothesis, which holds that species ranges will shift poleward with climatic warming to stay within physiologically optimal conditions, assumes that species are in equilibrium with their environment [8,18]. Recent work suggests that species might be locally abundant at some times but not others [67]. If distributions of species abundance are variable temporally, it is unlikely that higher-order processes such as gene flow between populations, responses of ranges to climate change or source-sink dynamics can be predicted or even approximated based on a single description of a distribution of abundance.

patterns through a single mechanism, as was done by Gaylord and Gaines [21] who showed through models that multiple distributions of abundance could result solely from changes in flow driving larval dispersal. Models [22] and empirical data [23] have also shown that steep gradients in abundance can arise from relatively small changes in environmental conditions rather than abrupt changes as was assumed in Caughley *et al.*'s model.

In the real world, ranges are determined by an 'alignment of different contributory mechanisms' [24], so that range boundaries and population densities can be set by multiple factors that interact in complex ways across ranges and through time. Garrido *et al.* [25] argue that

populations in a species range 'underlie a template of environmental conditions, which is singular at every site.' This point suggests that assumptions about range-wide dynamics made from observations at a few sites are likely to be violated. Recent studies, however, have addressed geographic variability head-on through empirical and experimental analyses on a broad spatial scale. These studies have highlighted the roles that heterogeneous temperature, differential plasticity across the range, population demographics, community interactions (especially those affecting keystone species), biogeographic differences at different range boundaries and variation in the strength of anthropogenic effects play in driving population distributions, range boundaries and species responses to climate change.

Variation in environmental conditions

At the basis of a new view of species distributions is an appreciation of the extreme environmental heterogeneity and lack of spatial autocorrelation of environmental factors that is found even across gradients assumed previously to be relatively monotonic. Helmuth *et al.* [26] showed that across a coastal transect where average water temperatures are strongly negatively correlated with latitude, the intertidal temperatures experienced by organisms are remarkably variable, with some of the highest values being in the northern part of the study range. Moreover, the interaction of multiple physical factors (e.g. temperature, tidal height and wave force for intertidal organisms) has been shown to affect species differently across their ranges [27]. The importance of local environmental heterogeneity is seen clearly in cases where simplistic expectations about species distributions are not met. For example, Sagarin and Somero [28] found that levels of heat-shock proteins (a measure of organismal stress) in an intertidal mussel and snail showed no correlation with position in the species range, but a strong positive correlation with local areas expected to have long daytime exposure during the summer months.

Variable plastic responses

Recent studies give reason to believe that organisms will adapt differently to heterogeneous conditions at different parts of their range, which probably contributes to the deviation of species distributions from the abundant-center pattern. Santamaria *et al.* [29], for example, found high overall performance of an aquatic plant in the center of its European range, but compressed life cycles in the north and perennality in the south, indicating local adaptation. Herlihy and Eckert [8] found no difference between central and northern densities of columbine in North America, but found that northern populations had fewer inflorescences with higher seed density than central populations. Busch [30] found that marginal populations of the flowering plant *Leavenworthia alabamica* were self-compatible whereas conspecifics from the center of the range were self-incompatible, a pattern that the author attributed to genetic bottlenecks at the range edge. Helmuth *et al.* [19] argued that the 'safety factors' attained by intertidal mussels through attachment strength will vary based on geographic variation in storm patterns throughout the year.

Variation in population demographics

Basic population parameters including birth, death, immigration and emigration rates are fundamental in determining species abundance and distribution, but have rarely been studied in the context of entire ranges [31]. Models have been developed recently to address the relationship between population parameters and species distributions [2,31], although some [2] are limited by assumptions of an abundant-center distribution. Williams *et al.* [16], through a study of three North American mammal species, argue that there is no clear *a priori* assumption possible for the relationship between population dynamics and position in the range because of the potentially conflicting roles played by habitat suitability, environmental tolerance and density dependence across the range of the species. This claim is supported by Defeo and Cardoso's [11] work on South American Atlantic mole crabs, which showed marked variability in demographic traits across latitude, including different latitudinal size gradients between males and females, and non-linear trends across latitude in the mortality of both sexes. Kluth and Bruelheide [32] followed up earlier studies of a European annual plant that showed a non-abundant-center distribution of abundance [9] with demographic studies showing weaker density dependence at the range center relative to the range edge.

Variation in species interactions

At the community level, interspecific interactions can alter predicted responses to climate change drastically [33] and affect populations and demographics differentially across the range [34]. Alternatively, community composition is likely to be altered dramatically when a key element of the community is affected by climate or other factors. Abundances of spionid polychaetes in communities across a wide range in the Gulf of California appear to fluctuate with the abundance of the dominant species, *Paraprionospio pinnata*, which itself fluctuates markedly with seasons and sediment types [35]. On the Pacific coast of North America, the keystone predator *Pisaster ochraceus* (the ochre starfish), shows depressed feeding rates under upwelling conditions [36], which are heterogeneous across latitude.

Variation between range edges

In some cases, conditions at one range edge are significantly different than another because of deep geologic history or more recent ecological interactions. Such differences were suggested by the pattern analysis of range boundaries in New World temperate mammals, which showed that northern and southern boundaries were probably caused by abiotic versus biotic factors, respectively [37]. In the field, Garner *et al.* [38] showed no relation between genetic variability and proximity to the range edge (as predicted by the abundant-center hypothesis; see Box 1) across the entire range of Italian agile frogs, but suggested that the observed asymmetric diversity pattern arose from post-glacial range expansion on one edge of the range. In a recent review, Hampe and Petit [18] cited examples of paleontological, phylogeographic and ecological studies showing differences between high- and low-latitude range limits. They noted, for example, that

fundamental differences between northern and southern range boundaries could be at the root of empirical findings that climate-related range shifts in European butterflies and moths were more evident in northern than in southern boundaries [39].

Variation in anthropogenic impacts

Finally, an important factor that is surprisingly neglected in most theoretical treatments of species ranges is the patchy distribution of strong anthropogenic effects on species populations and demographics. Rodriguez and Delibes [40], for example, found that non-natural lynx mortality and associated population demographics were not correlated with the overall distribution of species abundance, but with regional heterogeneity in wildlife-management regimes. Medail *et al.* [41] concluded that, despite physiological and demographic differences between central and northern range edge populations of the palmate windflower *Anemone palmate* in Europe, the marginal populations are threatened primarily by anthropogenic habitat degradation. Garrido *et al.* [25] attributed poor population performance at the northern range edge of the threatened insectivorous plant *Drosophyllum lusitanicum* in the Iberian Peninsula to human land alteration, which occurred to a greater extent in the northern part of the range than the central or southern parts.

Using data to test hypotheses

The growing list of studies like those above provides examples of key factors to address when developing more realistic hypotheses related to species distributions. The multitude of factors points to the need to layer multiple elements of range-scaled data sequentially in an ordered progression to rule out large classes of mechanistic hypotheses. These additional layers of data can be viewed as filters through which a clearer signal can be delivered from noisy abundance data. This new round of hypothesis testing is increasingly possible given development of large-scale ecological monitoring datasets and the emerging strength of cross-disciplinary research, particularly that combining physiology, genetics and ecology.

Some models for this approach have been published recently. In a series of papers outlining extensive geographic research on holly leaf-miners in Europe, Brewer and others [6,42,43] compared population density, physiological tolerances and mortality rates as a result of different sources across the species range. Although several measures were not well correlated with one another, the authors did find strong patterns of spatial correlation within individual factors, thereby providing opportunities for making spatially explicit predictions about population dynamics. Defeo and McLachlan [44] reviewed geographically extensive work on sandy beach mole crab and isopod population densities and demographics, and developed predictive models for the drivers of population control at a range of spatial scales.

Although the authors of these studies argued that their systems are particularly amenable to geographical comparison (see also Box 3), the quest for an ideal study system should not limit advances in biogeographical studies. Even simple demographic parameters such as population size

structure can be used to weigh alternative hypotheses. For example, highly skewed or multi-modal size structures at range edges relative to sites within the range can indicate dispersal, rather than temperature-mediated range boundaries. Zacherl *et al.* [45], for instance, combined size-structure data, abundance data and data on physical factors related to propagule transport to separate the roles of larval transport from climate warming in an analysis of the recent range expansion of the marine snail *Kelletia kelletii*.

Physiological responses to climate are likely to be important drivers of population-abundance patterns, yet Clarke [46] argued that we still lack a clear model linking physiology, climate and macroecology. Empirically, studies of population densities and physiological indicators could be used to test the implicit assumption of the 'climatic-envelope' hypothesis (see Box 4) that populations near the margins of the range will show both relatively low abundance and relatively depressed organismal condition as reflected in reproductive output, growth, stress or other performance measures. Gilman [12], for example, found both higher population densities and no indication of reduced sizes at the northern range boundary of an intertidal limpet relative to populations at the range center, suggesting that neither habitat nor environmental conditions were likely to be limiting the limpet's northern range boundary.

Unraveling the relationship between abundance and genetic diversity will be crucial to understanding the causes of species range limits. Population-genetics theory predicts that range boundaries can be limited solely by gene flow when local variation and adaptation to 'marginal conditions' at the range edges is swamped by gene flow from the abundant center, where populations experience 'optimal conditions' [47,48]. Given that increasing numbers of studies show non-abundant center population patterns, is it then possible that dense edge populations, or the cumulative effects of multiple populations situated across a large range edge, could swamp central populations through gene flow from the range edge? Such questions support the argument that there remains a substantial chasm between theoretical predictions about genetic diversity and data from the field [38,49]. In fact, recent empirical work finds evidence for either higher genetic diversity at the edges or higher diversity at range centers [16,18]. Vucetich and Waite [17] made some progress in determining the causes of this diversity with analyses suggesting that variability in migration rates could explain different patterns of relative diversity. Indeed, newer theoretical work shows that variation in migration affects relative fitness of marginal versus central populations strongly [50].

The need for more large-scale descriptive ecology

After decades of advances in experimental ecology, observational approaches to hypothesis testing are not at the forefront of the field and are often considered 'less rigorous' than experimental approaches [51]. When addressing larger-scale problems, however, we are still 'observation limited'. Moreover, as the studies of spatial variability reviewed here suggest, findings from even the most carefully controlled experiments conducted at a given

site with a species range might not be relevant to other parts of the range. As concern about species responses to climate warming increases and degradation of natural populations becomes more widespread, interest in basic monitoring of populations to establish baseline conditions has increased [52,53]. Yet, little is known currently about reproductive behaviors, microhabitat requirements, population trajectories and a suite of other crucial ecological characteristics across entire species ranges [37]. Fortunately, advances in technology, including remote sensing and biophysical monitoring [19], ecological physiology [54,55], and molecular genetics [17,38] and genomics [56], are rapidly enhancing our ability to assay population and individual patterns across large spatial scales, rather than continuing to rely on untested assumptions about geographical patterns. Moving beyond assumptions creates an opportunity to bring new rigor to the emerging field of macroecology, provides strong tests of potential 'unifying theories' [57,58] in macroecology, and offers new insight into fundamental ecological and evolutionary processes.

Acknowledgements

This paper benefited greatly from the support of the Andrew W. Mellon Foundation and the David and Lucile Packard Foundation. This is contribution number 216 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans funded primarily by the Gordon and Betty Moore Foundation and David and Lucile Packard Foundation.

References

- Hengeveld, R. and Haek, J. (1982) The distribution of abundance. I. Measurements. *J. Biogeogr.* 9, 303–316
- Guo, Q. *et al.* (2005) Spatial-temporal population dynamics across species range: from centre to margin. *Oikos* 108, 47–57
- Sagarin, R. and Gaines, S. (2002) The 'abundant centre' distribution: to what extent is it a biogeographic rule? *Ecol. Lett.* 5, 137–147
- Gaston, K.J. (2003) *The Structure and Dynamics of Geographic Ranges*, Oxford University Press
- Stevens, R.D. *et al.* (2004) Comparative community ecology of bats from eastern Paraguay: taxonomic, ecological, and biogeographic perspectives. *J. Mammal.* 85, 698–707
- Brewer, A.M. and Gaston, K.J. (2002) The geographical range structure of the holly leaf-miner. I. Population density. *J. Anim. Ecol.* 71, 99–111
- McGeoch, M.A. and Price, P.W. (2004) Spatial abundance structures in an assemblage of gall-forming sawflies. *J. Anim. Ecol.* 73, 506–516
- Herlihy, C.R. and 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
- Kluth, C. and Bruelheide, H. (2005) Central and peripheral *Hornungia petraea* populations: patterns and dynamics. *J. Ecol.* 93, 584–595
- Bas, C. *et al.* (2005) Population structure of the South American estuarine crab, *Chasmagnathus granulatus* (Brachyura: Varunidae) near the southern limit of its geographical distribution: comparison with northern populations. *Hydrobiologia* 537, 217–228
- Defeo, O. and Cardoso, R.S. (2004) Latitudinal patterns in abundance and life-history traits of the mole crab *Emerita brasiliensis* on South American sandy beaches. *Div. Distrib.* 10, 89–98
- Gilman, S. (2005) A test of Brown's principle in the intertidal limpet *Collisella scabra* (Gould, 1846). *J. Biogeogr.* 32, 1583–1589
- Murphy, H.T. *et al.* (2006) Distribution of abundance across the range in eastern North American trees. *Glob. Ecol. Biogeogr.* 15, 63–71
- Jump, A.S. and Woodward, F.I. (2003) Seed production and population density decline approaching the range-edge of *Cirsium* species. *New Phytol.* 160, 349–358
- Sorte, C.J.B. and 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
- Williams, C.K. *et al.* (2003) Population dynamics across geographical ranges: time-series analyses of three small game species. *Ecology* 84, 2654–2667
- Vucetich, J.A. and Waite, T.A. (2003) Spatial patterns of demography and genetic processes across the 'species' range: null hypotheses for landscape conservation genetics. *Cons. For. Genet.* 4, 639–645
- Hampe, A. and Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* 8, 461–467
- Helmuth, B. *et al.* (2005) Biophysics, physiological ecology and climate change: does mechanism matter? *Annu. Rev. Physiol.* 67, 177–201
- Caughley, D. *et al.* (1988) The edge of the range. *J. Anim. Ecol.* 57, 771–785
- Gaylord, B. and Gaines, S.D. (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* 155, 769–789
- Carter, R.N. and Prince, S.D. (1981) Epidemic models used to explain biogeographical distribution limits. *Nature* 293, 644–645
- Welch, D.W. *et al.* (1995) Upper thermal limits on the oceanic distribution of Pacific salmon (*Oncorhynchus spp.*) in the spring. *Can. J. Fish. Aquat. Sci.* 52, 489–503
- Blackburn, T.M. and Gaston, K.J. (2003) Introduction: why macroecology? In *Macroecology: Concepts and Consequences* (Blackburn, T.M. and Gaston, K.J., eds), pp. 1–14, Blackwell
- Garrido, B. *et al.* (2003) Regional differences in land use affect population performance of the threatened insectivorous plant *Drosophyllum lusitanicum* (Droseraceae). *Div. Distrib.* 9, 335–350
- Helmuth, B. *et al.* (2002) Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298, 1015–1017
- Harley, C.D.G. and Helmuth, B.S.T. (2003) Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnol. Oceanogr.* 48, 1498–1508
- Sagarin, R.D. and Somero, G.N. (2006) Complex patterns of heat-shock protein 70 expression across the southern biogeographic ranges of the intertidal mussel *Mytilus californianus* and snail *Nucella ostrina*. *J. Biogeogr.* 33, 622–630
- Santamaria, L. *et al.* (2003) Plant performance across latitude: the role of plasticity and local adaptation in an aquatic plant. *Ecology* 84, 2454–2461
- Busch, J.W. (2005) The evolution of self-compatibility in geographically peripheral populations of *Leavenworthia alabamica* (Brassicaceae). *Am. J. Bot.* 92, 1503–1512
- Watkinson, A.R. *et al.* (2003) Macroecology and microecology: linking large-scale patterns of abundance to population process. In *Macroecology: Concepts and Consequences* (Blackburn, T.M. and Gaston, K.J., eds), pp. 256–273, Blackwell
- Kluth, C. and Bruelheide, H. (2005) Effects of range position, inter-annual variation and density on demographic transition rates of *Hornungia petraea* populations. *Oecologia* 145, 382–393
- Davis, A.J. *et al.* (1998) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *J. Anim. Ecol.* 67, 600–612
- Garcia, D. *et al.* (2000) Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. *J. Ecol.* 88, 436–446
- Hernandez-Alcantara, P. and Solis-Weiss, V. (2005) Seasonal variations of the Spionida (Palpata: Canalipalpata) in the sublittoral zone of the Gulf of California. *Mar. Ecol.* 26, 273–285
- Sanford, E. (1999) Regulation of keystone predation by small changes in ocean temperature. *Science* 283, 2095–2097
- Parmesan, C. *et al.* (2005) Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* 108, 58–75
- Garner, T. *et al.* (2004) Genetic diversity across a vertebrate 'species' range: a test of the central-peripheral hypothesis. *Mol. Ecol.* 13, 1047–1053
- Parmesan, C. *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399, 579–583
- Rodriguez, A. and Dlibes, M. (2004) Patterns and causes of non-natural mortality in the Iberian lynx during a 40-year period of range contraction. *Biol. Cons.* 118, 151–161
- Medail, F. *et al.* (2002) Comparative analysis of biological and ecological differentiation of *Anemone palmata* L. (Ranunculaceae) in the western Mediterranean (France and Spain): an assessment of rarity and population persistence. *Bot. J. Linn. Soc.* 140, 95–114

- 42 Klok, C.J. *et al.* (2003) The geographical range structure of the holly leaf-miner. III. Cold hardiness physiology. *Func. Ecol.* 17, 858–868
- 43 Brewer, A.M. and Gaston, K.J. (2003) The geographical range structure of the holly leaf-miner. II. Demographic rates. *J. Anim. Ecol.* 72, 82–93
- 44 Defeo, O. and McLachlan, A. (2005) Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. *Mar. Ecol. Prog. Ser.* 295, 1–20
- 45 Zacherl, D. *et al.* (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
- 46 Clarke, A. (2003) Costs and consequences of evolutionary temperature adaptation. *Trends Ecol. Evol.* 18, 573–581
- 47 Case, T.J. and Taper, M.L. (2000) Interspecific competition, environmental gradients, gene flow, and the coevolution of 'species' borders. *Am. Nat.* 155, 583–605
- 48 Kirkpatrick, M. and Barton, N.H. (1997) Evolution of a 'species' range. *Am. Nat.* 150, 1–23
- 49 Butlin, R.K. *et al.* (2003) Genetics and the boundaries of 'species' distributions. In *Macroecology: Concepts and Consequences* (Blackburn, T.M. and Gaston, K.J., eds), pp. 274–295, Blackwell
- 50 Alleaume-Benharira, M. *et al.* (2006) Geographical patterns of adaptation within a 'species' range: interactions between drift and gene flow. *J. Evol. Biol.* 19, 203–215
- 51 Francis, R.C. and Hare, S.R. (1994) Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. *Fish. Oceanogr.* 3, 279–291
- 52 Dayton, P.K. *et al.* (1998) Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol. Appl.* 8, 309–322
- 53 Sagarin, R. (2001) Historical studies of species responses to climate change: promises and pitfalls. In *Wildlife Responses to Climate Change* (Schneider, S. and Root, T., eds), pp. 127–164, Island Press
- 54 Sorte, C.J.B. and Hofmann, G.E. (2005) Thermotolerance and heat shock protein expression in Northeastern Pacific *Nucella* species with different biogeographical ranges. *Mar. Biol.* 146, 985–993
- 55 Dahlhoff, E.P. (2004) Biochemical indicators of stress and metabolism: applications for marine ecological studies. *Annu. Rev. Physiol.* 66, 183–207
- 56 Hofmann, G.E. *et al.* (2005) Genomics-fueled approaches to current challenges in marine ecology. *Trends Ecol. Evol.* 20, 305–311
- 57 McGill, B. and Collins, C. (2003) A unified theory for macroecology based on spatial patterns of abundance. *Ecol. Evol. Res.* 5, 469–492
- 58 Bell, G. (2001) Neutral macroecology. *Science* 293, 2413–2418
- 59 Brown, J.H. (1984) On the relationship between abundance and distribution of species. *Am. Nat.* 124, 255–279
- 60 Sagarin, R. and Gaines, S. (2002) Geographical abundance distributions of coastal invertebrates: using 1-dimensional ranges to test biogeographic hypotheses. *J. Biogeogr.* 29, 985–998
- 61 Ceballos, G. and Ehrlich, P.R. (2002) Mammal population losses and the extinction crises. *Science* 296, 904–907
- 62 Channell, R. and Lomolino, M.V. (2000) Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *J. Biogeogr.* 27, 169–179
- 63 Lonhart, S. and Tupen, J.W. (2001) New range records of 12 marine invertebrates: the role of El Niño and other mechanisms in Southern and Central California. *Bull. South. Calif. Acad. Sci.* 100, 238–248
- 64 Rehmeier, R.L. *et al.* (2005) Long-term study of abundance of the Hispid cotton rat in native tallgrass prairie. *J. Mammal.* 86, 670–676
- 65 Roy, K. (2001) Analyzing temporal trends in regional diversity: a biogeographic perspective. *Paleobiology* 27, 631–645
- 66 Sagarin, R.D. *et al.* (1999) Climate related changes in an intertidal community over short and long time scales. *Ecol. Monogr.* 69, 465–490
- 67 Murray, B.R. and Lepschi, B.J. (2004) Are locally rare species abundant elsewhere in their geographical range? *Aust. Ecol.* 29, 287–293

Articles of Interest in other *Current Opinion* and *Trends* Journals

- M.J. Wargo and D.A. Hogan (2006) Fungal-bacterial interactions: a mixed bag of mingling microbes. *Curr. Opin. Microbiol.* doi:10.1016/j.mib.2006.06.001
- K-H. Kogel *et al.* (2006) Endophyte or parasite - what decides? *Curr. Opin. Plant Biol.* doi:10.1016/j.pbi.2006.05.001
- U. Paszkowski (2006) Mutualism and parasitism: the yin and yang of plant symbioses. *Curr. Opin. Plant Biol.* doi:10.1016/j.pbi.2006.05.008
- E.B. Holub (2006) Evolution of parasitic symbioses between plants and filamentous microorganisms. *Curr. Opin. Plant Biol.* doi:10.1016/j.pbi.2006.05.011
- L. Chittka and N.E. Raine (2006) Recognition of flowers by pollinators. *Curr. Opin. Plant Biol.* doi:10.1016/j.pbi.2006.05.002
- J-W. Bae and Y-H. Park (2006) Homogeneous versus heterogeneous probes for microbial ecological microarrays. *Trends Biotechnol.* doi:10.1016/j.tibtech.2006.04.010
- P.L. Bhalla (2006) Genetic engineering of wheat - current challenges and opportunities. *Trends Biotechnol.* doi:10.1016/j.tibtech.2006.04.008
- A.C. Courville *et al.* (2006) Bayesian theories of conditioning in a changing world. *Trends Cogn. Sci.* doi:10.1016/j.tics.2006.05.004
- N. Chater and C.D. Manning (2006) Probabilistic models of language processing and acquisition. *Trends Cogn. Sci.* doi:10.1016/j.tics.2006.05.006
- S. Biswas and J.M. Akey (2006) Genomic insights into positive selection. *Trends Genet.* doi:10.1016/j.tig.2006.06.005
- Y. Gilad *et al.* (2006) Natural selection on gene expression. *Trends Genet.* doi:10.1016/j.tig.2006.06.002
- Jinling Huang and Johann Peter Gogarten (2006) Ancient horizontal gene transfer can benefit phylogenetic reconstruction. *Trends Genet.* doi:10.1016/j.tig.2006.05.004
- B. Dujon (2006) Yeasts illustrate the molecular mechanisms of eukaryotic genome evolution. *Trends Genet.* doi:10.1016/j.tig.2006.05.007
- A.Z. Worden *et al.* (2006) In-depth analyses of marine microbial community genomics. *Trends Microbiol.* doi:10.1016/j.tim.2006.06.008
- G. Dehaene-Lambertz *et al.* (2006) Nature and nurture in language acquisition: anatomical and functional brain-imaging studies in infants. *Trends Neurosci.* doi:10.1016/j.tins.2006.05.011
- D.S. Manoli *et al.* (2006) Blueprints for behavior: genetic specification of neural circuitry for innate behaviors. *Trends Neurosci.* doi:10.1016/j.tins.2006.06.006
- H. Sandermann (2006) Plant biotechnology: ecological case studies on herbicide resistance. *Trends Plant Sci.* doi:10.1016/j.tplants.2006.05.004