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Species' borders: a unifying theme in ecology

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Biologists have long been fascinated by species' borders, and with good reason. Understanding the ecological and evolutionary dynamics of species' borders may prove to be the key that unlocks new understanding across a wide range of biological phenomena. After all, geographic range limits are a point of entry into understanding the ecological niche and threshold responses to environmental change. Elucidating patterns of gene flow to, and returning from, peripheral populations can provide important insights into the nature of adaptation, speciation and coevolution. Species' borders form natural laboratories for the study of the spatial structure of species interactions. Comparative studies from the center to the margin of species' ranges allow us to explore species' demographic responses along gradients of increasing environmental stress. Range dynamics further permit investigation into invasion dynamics and represent bellwethers for a changing climate. This set of papers explores ecological and evolutionary dynamics of species' borders from diverse empirical and theoretical perspectives.

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All species are distributed in space – but within limits (Lawton et al. 1994, Brown and Lomolino 1998, 1999). Understanding the factors shaping species' ranges is a central question in both ecology (e.g. the study of invasions, Mack et al. 2000) and evolutionary biology (e.g. interpreting faunal responses to large-scale environmental fluctuations, Graham et al. 1996). In their classic study of island biogeography, Robert MacArthur and E.O. Wilson prophetically concluded that "... future [biogeographic] theory will concentrate on the boundaries of species ranges as they are encountered on ecologically uniform or continuously varying terrain (p. 182, MacArthur and Wilson 1967)". In subsequent years a burgeoning literature has developed, both on empirical and theoretical fronts, concerned with species' borders. Indeed, there has been an explosion of interest in this area in the last few years. Part of this resurgence surely reflects the development of technologically sophisticated tools, such as GIS and computational devices such as neural network and artificial intelligence models (Peterson 2003, Thuiller 2003). Part also reflects an increasing appreciation of space and spatial processes across the ecological and evolutionary sciences. Part also surely is driven by the practical urgency of comprehending and responding to our rapidly changing world. Many crucial applied issues, such as understanding the spatial responses of species to climate change (Parmesan and Yohe 2003, Root et al. 2003), or predicting the extent of impact of introduced species (Peterson 2003), or assessing the impact of land use change on the distribution of endangered species (Channell and Lomolino 2000), lead naturally to a close scrutiny of processes at range margins.

This collection of papers stems from a working group at the National Center for Ecological Analysis and Synthesis (Univ. of California, Santa Barbara, CA USA). The aim of this working group was to develop elements of a conceptual framework for understanding

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the manifest diversity in species ranges. The papers combine synthesis and review with presentation of new material and questions. At a broad level, range limits must arise because of the interplay of birth, death, and dispersal processes in space. At times, a range limit may have an obvious cause (e.g. the margin of the ocean marks a precise limit for a huge variety of terrestrial and marine organisms). But in other cases, range limits arise along smooth gradients without obvious environmental discontinuities. Some species borders are highly unstable, others seem quite stable; some are geometrically simple, others have a fractal-like complexity. Analyzing these patterns requires a deep understanding of how adaptive evolution, demographic processes, and interspecific interactions play out across space.

The starting point of any investigation of a species' border is to characterize with precision the border in terms of spatial patterns on a map. Fortin et al. survey statistical methodologies that are useful in characterizing the sharpness and shape of species distributional limits, and in comparative analyses. Holt et al. then provide an overview of theoretical approaches to single species' borders, emphasizing the importance of non-equilibrial perspectives, metapopulation dynamics along gradients, and the potential for quasi-stable range limits in homogeneous environments. Case et al. place single species' ranges in the broader context of interspecific interactions, community organization, and coevolutionary dynamics. Ecological communities arise in the first place because species' ranges overlap; conversely, local interactions and metacommunity dynamics can define range limits. Quo et al. take a comparative approach, using simulation models to examine contrasting effects of different dispersal modalities on species' ranges. Finally, Parmesan et al. provide a broad, synoptic overview of empirical approaches to range limits. They define key issues faced by empiricists examining the mechanistic causes of range boundaries, and highlight a set of broad hypotheses regarding comparisons among systems.

Overall, these papers summarize many facets of our current understanding of the ecology and evolution of species' borders, outline recent methodological advances, and identify key issues which need to be addressed in future studies. These papers collectively provide many of the elements of an emerging conceptual framework that will permit ecologists a firmer basis for quantifying, comparing, and ultimately understanding the great diversity that exists amongst species in their geographical ecologies. In the remainder of this introductory piece, we focus on some perspectives and questions that transcend the foci of this set of papers.

We feel that analyses of species' biogeographic range limits are quintessentially integrative intellectual exercises, in that understanding range limits requires one to draw on many of the core concepts of ecology and evolution. Gaston (2003) has recently reviewed the biogeography of range limits, and notes that there are three broad questions which must be addressed to understand range limits. First, what are the abiotic and biotic factors which mechanistically prevent further spread? Second, how is the impact of these factors made manifest in terms of population dynamics? Finally, what are the genetic underpinnings of species' responses to factors determining range limits?

The range of a species is clearly influenced in a major way by its ecological niche, defined as that set of environmental conditions, resources, and so on, which permit populations to persist without immigration. However, the problem of species' ranges is more complicated than just characterizing species' niches, and for several reasons. Given dispersal, ranges extend into habitats beyond niche limits because recurrent immigration sustains 'sink' populations at locations where conditions are outside the niche (Pulliam 2000). Conversely, a species may be absent from habitats where it might be expected to persist because of historical accidents and dispersal barriers, Allee effects, and the stochastic vagaries of extinction dynamics. Moreover, a species' niche is not fixed; the Darwinian paradigm, after all, is that species adapt to their environments. Sometimes a species' range as a whole can change, for instance because evolved plastic responses spread across a broad geographical range, or because local populations develop adaptations to spatially localized selection regimes, or because dispersal syndromes evolve. Evolutionary processes can lead to either range expansion or shrinkage (Kirkpatrick and Barton 1997, Holt 2003). Yet the paleoecological record suggests that species can be quite conservative in their basic ecological niches (Bradshaw 1991). What forces prevent adaptation to conditions at the edge of species' ranges, and how do evolutionary dynamics influence the overall shape and dynamics of species' ranges? Moreover, species' distributions cannot ultimately be understood in isolation; because of interactions such as competition and predation, species influence each other's ranges, both positively and negatively, over both ecological and evolutionary time-scales. Interactions among species can either confine ranges (e.g. competitive exclusion) or permit range expansion (e.g. facilitation). Gaston (2003) sketches many plausible examples of range limitation due to interspecific interactions, and emphasizes the importance of interactions among multiple factors in understanding range limits.

There are many important challenges remaining in the study of species' range limits. Many sophisticated distributional models (Thuiller 2003, Peterson 2003, Fortin et al. this issue) are essentially static (elaborations of the basic concept of 'climate-matching'). Ultimately, one should aim for developing fully dynamic models, describing the parameters and functional forms of spatially explicit population dynamic models (Maurer and Taper 2002, Holt et al. this issue), and linking these to computational and statistical predictive models. A particularly intriguing challenge is to link models of species' ranges to processes happening at different levels.

For instance, the role of intraspecific genetic variation and evolutionary processes in determining range limits is still poorly understood. An old idea in evolutionary biology is that species can exhibit a kind of self-limitation in their geographical distributions, if gene flow via dispersal from numerically abundant central populations 'swamps' adaptation to marginal conditions (Mayr 1963, Kirkpatrick and Barton 1997). Yet dispersal can also facilitate local adaptive evolution, if genetic variation is limited in local populations (Bradshaw 1991) and gene flow permits enhancement of local pools of variation (Gomulkiewicz et al. 1999, Barton 2001). Whether or not gene flow among natural populations primarily restricts range limits, or facilitates range expansion, is an important and poorly understood question (Butlin et al. 2003).

Another important direction is placing this question about the microevolutionary dynamics of range limits into a broad community context. Case and Taper (2000 Case et al. this issue) provide an important step in this direction, by showing that interspecific competition can greatly expand the impact of gene flow as a factor limiting species' ranges. In general, it is difficult to explain observed patterns of conservatism in species' ecological niches (which to a rough approximation determine many aspects of range limits, Peterson 2003), without considering interactions among species sorting out in spatially heterogenous environments (Ackerly 2003). Analyses of range limits thus should begin to consider the dynamics of entire metacommunities – sets of local communities linked by the dispersal of their constituent species (Holyoak et al. in press). This is a large and challenging task.

It seems clear to us that understanding the intrinsically multifaceted nature of species' borders requires a truly interdisciplinary approach. To understand any given range limit (e.g. the lark sparrow example explored in the Fortin et al. paper) in any detail and depth requires the integration of a wide spectrum of biological and earth science understanding, ranging from GIS database analyses, to demographic models of sources and sinks, to evolutionary interpretations of local adaptation and dispersal syndromes, to an appreciation of the influence of interactions such as competition and predation. The tools, concepts, and theories synthesized in these papers provide an indication of the range of perspectives that may need to be brought to bear in addressing any particular example of a range limit. As noted in Parmesan et al. (this issue), there is increasing urgency in developing a sophisticated understanding of the mechanistic underpinnings and dynamical patterns of range limits, given the looming threats posed by shifting climates, habitat degradation, and the unceasing rain of exotic species being transported around the globe. Ecology is becoming an increasingly interdisciplinary field, both in its applied and basic dimensions. We hope that this set of papers will help focus attention on the emerging theme of species' borders as a unifying locus for ecological and evolutionary studies, and that we are on the threshold of fulfilling MacArthur and Wilson's prophetic prediction.

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