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update

A cure for seeing double? Convergence and unification in biogeography and ecology

More perspectives are presented by *Biogeography and ecology: two views of one world* (Jenkins and Ricklefs 2011a)[1] than are enumerated in the title. This collection of ten papers targets, and reveals much about, the "converge[nce of biogeography and ecology] at intermediate spatial and temporal scales"; yet "lingering differences" hint at the challenges facing these disciplines during "the current trend towards their unification" (Ricklefs and Jenkins 2011).

Approximately twenty years ago, after decades of separation, the disciplines of biogeography and ecology found common ground spanning intermediate spatial and temporal scales, from metapopulations to regional communities (Jenkins and Ricklefs 2011b) or perhaps from assemblages to species' ranges (Guisan and Rahbek 2011, Hortal 2011, Figure 1). Macroecology (Brown 1995) played a pivotal role, providing the *raison d'être* and methodology for assembling details on individual species into broad generalizable pictures of continental diversity (Brown and Maurer 1989). As ecology reached out spatially and back in time to explain, for example, patterns of mammal body size on four major continents (Smith and Lyons 2011), so phylogenetic analyses began organizing species' traits and then intra-specific ecological variation in an evolutionary framework (Felsenstein 1985, Poulin et al. 2011). So too, the tools for distinguishing species genetically and phenotypically increased, permitting new questions about the relationships between taxonomic, phylogenetic, and functional diversity: how do the many forms of biodiversity vary spatially and temporally, how do different aspects of diversity relate across scales, and what does this tell us about community assembly and ecosystem function (Cavender-Bares et al. 2009, Davies and Buckley 2011, Emerson et al. 2011, Weiher et al. 2011. Hortal et al. 2012)? The increasing rate of publication on such issues (Cianciaruso 2011, Jenkins and Ricklefs 2011b, Smith and Lyons 2011) suggests interdisciplinary understanding of the organization of biodiversity at intermediate spatial and temporal scales is a common goal of ecologists and biogeographers helping to resolve, for example, the meaning and consequences of the niche (Chase and Myers 2011, Wiens 2011) and of diversity (Chiarucci et al. 2011).

The image of biogeography and ecology conjured up by this collection is one of many threads at the beginnings of a braid. Each paper is lightly intertwined with another on one of four topics—niche, macroecology and comparative ecology, community assembly, diversity—then wound loosely around each other within the theme (Ricklefs and Jenkins 2011). The strands are held together by only a few connections, encouraged in advance of the symposium: on average, a few cross-citations and acknowledgement of comments on earlier manuscripts. Thus, at present, the natural convergence of biogeography and ecology at intermediate spatial and temporal scales looks more like interdigitation than mutual assimilation of ideas and techniques. The challenge is, in part, overcoming the practical limitations of measuring biodiversity across multiple levels of organization and spatial scales of interest, and turning the perceptual biases dependent on grain size, spatial extent, and phylogeny into opportunities for developing scale-free formulations of biodiversity (Chiarucci et al. 2011) or scaling concepts that help merge community ecology with biogeography (Weiher et al. 2011). Overcoming this challenge may require taking the organizational model applied in this symposium one or two steps further, attracting individuals from many backgrounds to engage as interdisciplinary teams on common projects.

Whether the "trend towards … unification"

1 This August 2011 theme issue of *Philosophical Transactions of the Royal Society B* reports the proceedings of the International Biogeography Society symposium "Biogeography and Ecology: Two Lenses in One Telescope" – see http://www.biogeography.org/html/Meetings/2011/program.html

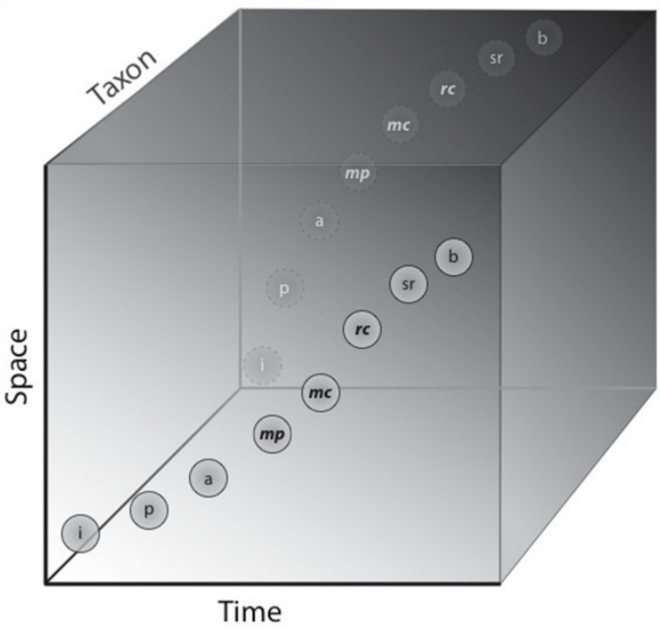

Figure 1. Studies of biogeography and ecology converge at intermediate spatial and temporal scales typical of the metapopulation (mp), metacommunity (mc) and regional community (rc), following Jenkins and Ricklefs (2011b). Other symbols represent the individual organism (i), population (p), assemblage (a), species' range/s (sr), and biota (b). Positioning in relation to the space and time axes is intended to represent approximate scale, while acknowledging there may be considerable spatial and temporal variation within and between places, times, and also among taxa. Examples of two hypothetical taxa (black text in the foreground and white in the background, representing a very simple system with respect to the taxon axis) are provided to illustrate that ecological and biogeographic processes likely have spatio-temporal relationships that vary with species' traits and biophysical interactions that do not scale linearly with organism size (e.g. Dawson & Hamner 2008 [figure 6]). Identifying natural boundaries among these scales, or the extent to which scales overlap, is a challenging research agenda that may be enabled by coordinated teams of biogeographers and ecologists (Chiarucci et al. 2011) working across scales, using new metrics such as phylobetadiversity (Emerson et al. 2011). These are fundamental challenges in how we represent, and therefore how we think about (and vice versa), the world.

of biogeography and ecology (Ricklefs and Jenkins 2011) can continue may similarly depend upon the approach. Recent efforts to develop unified theory are a little younger than macroecology (Hubbell 1997, 2001, Vellend 2005, Rosindell and Phillimore 2011) and more strongly contested (e.g. Roughgarden 2009, Fukami 2010, Clark 2012), perhaps in part because of the long history of thought surrounding idiosyncrasies in biology (Gould 1989, McIntyre 1997, Lawton 1999). Yet the truism that each extant species has an unique history of lineage and place (Lomolino et al. 2006) should not overwhelm the evidence from many natural examples of evolutionary convergences (Norris 1991, Van Valkenburgh 2007) and parallels (Elmer and Meyer 2011, Smith and Lyons 2011, Dawson 2012), nor from general theory (e.g. MacArthur and Wilson 1967) and 'rules' (e.g. Lomolino et al. 2006), that suggest natural laws (Ghiselin 1994). By broadening the scales across which some natural phenomena traditionally have been studied (see Rosindell et al. 2011) we may encompass individualism and unity within a single framework, thus avoiding the extremes of über-contingency or naturalistic theism (Gould 1989, Morris 2005), and maintaining an healthy tension that lends itself to inquisition via the logical tree of strong inference (Platt 1964). The perspectives provided by comparative biogeography and macroecology, for example, escape the overwhelmingly complicated contingency at the intermediate scales studied by community ecology (Lawton 1999).

Striking a balance between empiricism and theory also is essential. Sixty-two years ago, Albert Einstein published his conception for general unified field theory (Einstein 1950), which at the time was largely ignored but now coalesces mainstream research in fundamental physics. Einstein believed that extrapolation from phenomenological study depended too much on concepts very close to the measured experience (Van Dongen 2010:63). In biogeography and ecology, the scales at which the heterogeneity in interactions between organisms and environment manifest—and estimates of α-, β-, and γ-diversity—are affected by the grain, focus, and extent by which a particular assemblage is measured (Chiarucci et al. 2011). Because of this epistemological constraint, Einstein believed that physics needed to "apply free speculation to a much greater extent" (Van Dongen 2010:93).

Instead of looking from the viewpoints of biogeography and ecology toward their convergence at intermediate spatial and temporal scales for the source of unification, perhaps it also is necessary to stand on the common ground and look outward, occasionally to other disciplines. Systems biology, for example, is overdue for integration with ecology and evolutionary biology (Cain et al. 2008, Levin 2010) and applies advanced tools to seek natural network motifs that explain function across many scales (Alon 2007). This parallels the need for "a systems approach that integrates the relative influence of processes across a long gradient of environmental variation" (Weiher et al. 2011, also see Evans et al. 2012). Perhaps phylobetadiversity measured along continuous spatial scales provides a suitable objective criterion for delimiting communities (Emerson et al. 2011) and, with development of new statistical tools for comparative studies of "natural experiments" bridging biogeography and ecology (Smith and Lyons 2011), may contribute to better understanding of shared and unique characteristics (Langerhans and DeWitt 2004) that give shape to the natural world.

Biogeography and ecology: two views of one world reveals much about the convergence of biogeography and ecology, yet also emphasizes it is not enough that "biogeographers and ecologists study portions of the Earth in the hope that their work will help build a composite knowledge that represents the natural world" (Jenkins and Ricklefs 2011b). Rather, "the science of biodiversity badly needs a research agenda [and] … large-scale cooperative programmes" (Chiarucci et al. 2011) that merge approaches and disciplines.

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