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Introduction

Biogeography and ecology: two views of one world

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Both biogeography and ecology seek to understand the processes that determine patterns in nature, but do so at different spatial and temporal scales. The two disciplines were not always so different, and are recently converging again at regional spatial scales and broad temporal scales. In order to avoid confusion and to hasten progress at the converging margins of each discipline, the following papers were presented at a symposium in the International Biogeography Society's 2011 meeting, and are now published in this issue of the *Philosophical Transactions of the Royal Society B*. In a novel approach, groups of authors were paired to represent biogeographic and ecological perspectives on each of four topics: niche, comparative ecology and macroecology, community assembly, and diversity. Collectively, this compilation identifies points of agreement and disagreement between the two views on these central topics, and points to future research directions that may build on agreements and reconcile differences. We conclude this compilation with an overview on the integration of biogeography and ecology.

Keywords: biogeography; ecology; regional; spatial scale; temporal scale

1. INTRODUCTION

An unassisted human eye has not seen the full Earth since 1972, when astronauts on the last Apollo mission to the Moon used a handheld camera to photograph the Earth. Only 25 people have had a first-hand opportunity for such a distant 'blue marble' view, but so many of us are familiar with that famous image that we fail to reflect on how rare and recent this perspective is in the human experience. More routinely, 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 (as in the cubist interpretation of the blue marble on the cover of this issue). As the human population expands toward seven billion, some would argue that we are in a race to understand the natural world if we are to keep some of it intact, let alone support all those people and mitigate our collective 'footprint'. It is time to assemble a strong composite view of the natural world.

But different fragmentary views of nature necessarily lead to different perspectives on its patterns and processes. And disciplines that use different perspectives will naturally develop disparate concepts of the natural world. Biogeography and ecology have historically focused on different spatial and temporal

scales, but that is changing as each discipline has grown, and as new technologies and access to information have accelerated. Biogeographers and ecologists increasingly rely on an ever-changing spectrum of technologies aimed at diverse spatial and temporal scales to extend their understanding beyond immediate, personal experience. At one end of the spectrum are satellites, computers and software that enable sophisticated models representing complex processes and patterns at regional to global spatial and temporal scales. At the other end of the spectrum is the nearly astronomical growth of information on the molecular basis of life; consider that only approximately 60 years elapsed between the discovery that DNA encodes genetic information and the advent of high-throughput sequencing of the Neandertal genome [1]. Linnaeus, Darwin and Wallace would be impressed.

In this issue, we consider two different views of the same world—views that share a common beginning but that have since diverged owing to different emphases and perspectives. This compilation addresses four topics at the interface between biogeography and ecology (niche, macroecology and comparative ecology, community assembly, and diversity) as a means to better understand the differences between the two disciplines and to seek meaningful connections, or at least to identify differences remaining to be bridged. We believe this task is timely and important because biogeography and ecology are starting to converge at intermediate spatial and temporal scales, in part because technologies permit it and in part because perspectives have expanded.

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One contribution of 10 to a Theme Issue 'Biogeography and ecology: two views of one world'.

Table 1. Contrasts between biogeography and ecology. Descriptors of each discipline are acknowledged to be stereotypical categorizations having many exceptions. Ecology here refers to modern organismal, population and community ecology, and sets aside ecosystem and global ecology as operating at a different hierarchical level that is more focused on biogeochemistry and energetics (e.g. carbon cycles) than organisms and populations *per se*.

attribute	biogeography	ecology
spatial scales	global to regional	regional to local
temporal scales	millions to thousands of years	generation times to population cycles
fundamental units of study	clades, species, ranges, distributions	individuals, populations, communities
fundamental processes of interest	speciation, extinction, range expansion or contraction	abiotic and biotic interactions that affect density or distribution
adjectives describing fundamental methods	descriptive, correlative, phylogenetic	experimental, correlative, replicated
example questions	what geological events best explain clade distributions? why are species distributed as they are? where has speciation or extinction occurred, and when?	why do populations increase or decrease? how do species interact, and does that change with environmental context? what factors best correlate with species diversity?

2. BIOGEOGRAPHY AND ECOLOGY PARTING

The histories of ecology and biogeography are beyond the scope of this brief introduction. We simply note the long-time segregation between these disciplines that is reflected in the different approaches of biogeography and ecology, and that explains the need for a discussion of their recent integration, exemplified by the contributions to this issue. Biogeography and ecology were not always so clearly distinguished [2,3]; diverging scales of interest apparently contributed in part to their subsequent specialization, while rapid advances in technologies and exponential growth in scientific information enable re-annealing, much as in other sciences [4].

A discipline ‘crystallizes’ [2] when persons identify themselves as being part of that discipline and collectively this event is denoted by formalized groups such as professional societies and journals. Persons studying natural biological systems once described themselves as naturalists, as evidenced by the American Society of Naturalists (ASN), founded in 1883. That society and its journal *The American Naturalist* remain important, but few academic biologists call themselves naturalists these days; instead, most of us have adopted more specialized labels. The partitioning of organismal biology roughly coincided with the Apollo missions, molecular biology and the advent of field experimental ecology, exemplified by Joseph Connell’s seminal work on interactions of intertidal organisms [5]. Of course, experiments were a part of the laboratory biologist’s toolkit much earlier, including investigations into the growth and regulation of populations [2,6]. Experimental agriculture also preceded by decades the advent of widespread experimentation in field ecology [7]. At larger scales in time and space, ecosystem ecologists were concerned with accounting for energy flows and element cycling in ecological systems [8], but without detailed accounting of population dynamics or organism activities. We focus here on the part of ecology that addresses the distribution and abundance of organisms.

Many organismal biologists also worked on patterns and processes at spatio-temporal scales beyond those typically addressed by ecologists. These individuals may have been members of the Society for the Study of Evolution (founded 1946), but were not clearly self-described as biogeographers despite that discipline’s origins in the 1800s. The delayed formalization of biogeography was related to the slow acceptance of plate tectonic theory, which finally occurred in the early 1960s [3]. Biogeography did not have its own institutional home until the *Journal of Biogeography* began publication in 1974 and, in 2000, when both the International Biogeography Society and the American Geophysical Union’s Biogeosciences Section were founded. Thus, the ‘crystallization’ of biogeography lagged behind that of ecology, though the discipline began early and its growth has accelerated in recent years.

Biogeography and ecology continue to explore the world from different perspectives, reflecting each discipline’s history, particularly the distinction between observational and experimental approaches, and the different scales of relevant patterns and processes (table 1). In general, biogeography addresses evolutionary, climatic and geological processes (e.g. plate tectonics) to explain the distribution of diversity over the surface of the Earth and across its oceans. Biogeography remains primarily descriptive, but modern approaches incorporating phylogenetic (historical) information endeavour to test hypotheses about underlying processes (e.g. cladistic biogeography). The challenges of space and time in biogeographic research have also engendered sophisticated analytical approaches related to mapping (e.g. geographical information systems), spatial relationships [9,10] and large-scale patterns in the diversity of organism traits and biological diversity, known as macroecology [11,12]. The advent of molecular techniques and rapid computation in recent decades has helped make biogeography increasingly quantitative, statistical and inferential. In contrast, ecology primarily focuses on adaptive evolution, population processes, and abiotic and species interactions, to explain coexistence of

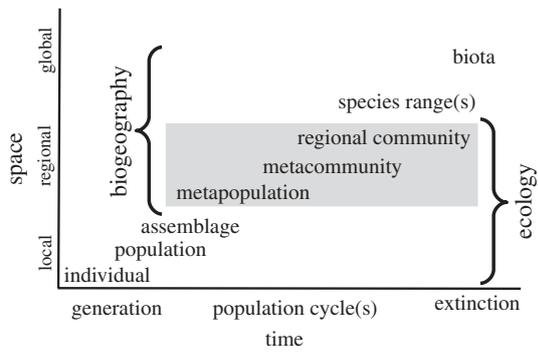


Figure 1. Biogeography and ecology intersect at regional spatial scales and broad temporal scales.

species in local areas. Modern ecology gains its inferential power inherently by its reliance on experimentation and statistical models (plus advances in computation), but does so within restricted spatial scale and temporal extent. As such, the two disciplines represent recently overlapping ends of a spatio-temporal gradient in our views of the natural world and how it works (figure 1).

3. BIOGEOGRAPHY AND ECOLOGY CONVERGING

During recent years, shared technologies and approaches have provided biogeography and ecology an opportunity to converge upon topics of mutual interest and at spatial and temporal scales relevant to both disciplines (figure 1). The overlap between the disciplines is rapidly increasing, as evidenced by the faster growth of papers described by both disciplines compared with papers identifying themselves as belonging to one or the other discipline (figure 2). In addition, it is worth noting that the number of biogeography papers has increased exponentially since 1990, whereas experimental ecology papers are increasing linearly. To be clear, papers that intersect the two fields are fewer than the sum of papers in either field (figure 2 inset), but the exponential rate of increase (figure 2) of intersecting papers and the rising prominence of journals, such as *Ecography* and *Global Ecology and Biogeography*, reflect the shift towards work conducted at the intersection of biogeography and ecology.

Biogeography addresses patterns and processes at large spatial and temporal scales, and naturally ranges from regional to global in spatial breadth. Within that breadth, different approaches exist. For example, historical biogeography uses phylogenetic and geological information to infer long-term and large-distance patterns in distribution of clades, including extinct species. Ecological biogeography considers distribution of extant species as a function of modern conditions (e.g. climate, latitude, etc.). Both historical and ecological approaches are relevant to understand species distributions and predict future changes.

The shift in ecology towards spatial and temporal scales beyond local habitats is a direct outcome of multiple changes in recent decades, especially a paradigm shift away from a locally based balance-of-nature viewpoint towards a dynamic mixture of local and regional

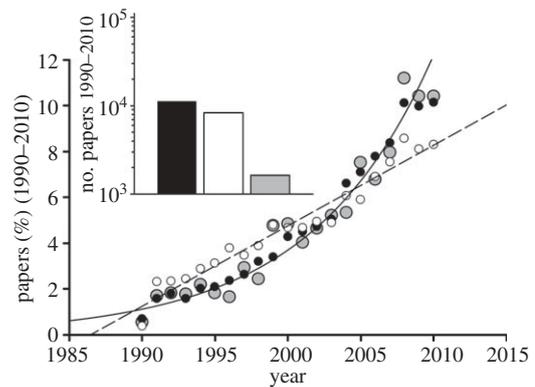


Figure 2. The growth of papers in biogeography (black circles), experimental ecology (white circles) and papers in the union of biogeography and ecology (grey circles). Data are expressed as per cent of the papers published in each set between 1990 and 2010. Papers at the intersection of biogeography and ecology are far less numerous than in either biogeography or experimental ecology (inset), but papers at the intersection of biogeography and ecology are growing exponentially. Data were obtained from the ISI Web of Science database using Boolean search terms 'biogeography NOT ecology' (black bar), 'experimental ecology' (white bar) and 'biogeography AND ecology' (grey bar). Experimental ecology was used as an indicator of local-scale ecology.

mechanisms as drivers of species diversity [13–15]. Along the way, integrative topics such as source–sink relationships, landscape ecology, metapopulations, metacommunities and regional communities have attracted much interest [16–20] and will continue to serve as mesoscale bridges between biogeography and ecology. Regional spatial scales at the convergence of ecology and biogeography correspond to intermediate timescales that are also considered relevant to ecology and evolution [21]. Another notable emphasis uniting biogeography and ecology is the increasing use of phylogenetic information, which further brings an evolutionary and historical dimension to research on diversity and distributions (e.g. [22–26]); we expect that this approach will continue to grow as phylogenetic information and regional-scale research continue to expand.

The convergence of biogeography and ecology is a relatively recent phenomenon (e.g. [13,14,20]) and was the motivation for the symposium upon which the papers in the present issue are based. We see that convergence as an intellectually exciting and practically essential direction for future research, and we hope that these contributions will help bridge the gap by discussing concepts, language and approaches that are relevant to both disciplines. Our hope is that these contributions will promote greater sharing of concepts and language, as well as methods between ecology and biogeography. Conceptual and linguistic coherence between biogeography and ecology is essential to each discipline because the most challenging issues for both lie in processes and patterns at regional scales. Fundamental theory and concepts in ecology need to be tested for generality at regional scales, just as ideas from biogeography must also be tested at smaller scales to find the margins of generality. The union between biogeography and ecology also

informs applied research because many of the effects of local processes (e.g. habitat fragmentation, pollution) and global processes (e.g. climate change) will be addressed at intermediate, regional scales and must translate to those scales. The topics addressed here are representative of the intersections between biogeography and ecology, but some topics, such as metapopulations and metacommunities, are not discussed because others have provided recent excellent summaries [18,19,27]. Moreover, evolution implicitly permeates both disciplines, as exemplified by the four topics discussed here.

The papers in this issue reflect a novel approach to organizing contributions. We asked paired sets of authors to represent each of the four topics from either a biogeographic or an ecological perspective, and to communicate with each other about their contributions well in advance of a symposium, held during the International Biogeography Society meeting in Heraklion, Crete (7–11 January 2011). The symposium was entitled ‘Biogeography and Ecology: Two Lenses in One Telescope’. Authors were asked to address their counterpart’s perspective on their topic as much as possible, with the hope that bridges might begin to form between disciplines, or at least that chasms might become more evident. The four topics chosen as the focus of discussion in this issue are:

- Niche—variously an individual’s and a species’ place in nature—is a concept central to both biogeography and ecology but for different reasons. John Wiens [28] reviews niche as a driver of biogeographic patterns, but argues that relatively little is known about the niche at the biogeography–ecology interface. Jonathan Chase and Jonathan Myers [29] review the rich history of deterministic niche theory, and its recent counterpart, neutral theory, which is based on stochastic processes. They then approach the biogeography–ecology intersection by considering beta diversity and its potential message for these major themes.
- Macroecology and Comparative Ecology—macroecology is often associated with biogeography because it addresses broad biological patterns and processes among taxa. Felisa Smith and Kathleen Lyons [30] explain the new discipline of macroecology and then demonstrate an application with mammalian body size distributions as an ecologically relevant pattern across biogeographic space and time. Modern comparative ecology is focused on detailed differences and similarities among taxa, but unlike some other ecological disciplines, it is based partly on phylogenetic relationships among those taxa. Robert Poulin *et al.* [31] illustrate this approach with two parasite clades while also addressing biogeographical and ecological themes not often tackled with phylogenetically based comparative methods.
- Community Assembly—Biogeographic analyses of community assembly address large spatial temporal scales (e.g. post-Pleistocene) and rely on phylogenetic information. Brent Emerson *et al.* [32] summarize that approach and suggest what the next generation of community analyses might bring, based on rich molecular data produced by next-generation sequencing of otherwise challenging organisms, such as

collembolans. In contrast, ecological community assembly has often dwelled on the role of dispersal, niche-based habitat filters and neutral processes that affect community structure. Evan Weiher *et al.* [33] summarize that work and argue that trait-based approaches, rather than a customary focus on species composition, are a key to a better understanding of community assembly among multiple sites.

- Diversity—Variety is central to much of what we value in natural systems, and it has been measured in many ways. Jonathan Davies and Lauren Buckley [34] describe phylogenetic diversity as a way to incorporate evolutionary diversification in measures that are more nuanced than simple richness, and which reveal features important to conservation policies. They then illustrate the value of phylogenetic diversity by analysing global patterns of mammalian phylogenetic diversity to reveal novel patterns that may guide conservation policies. Ecology has a long history of interest in diversity, and thus a long list of ecological diversity measures. Alessandro Chiarucci, Giovanni Bacaro and Samuel Scheiner [35] make sense of this diversity of measures according to their central traits, and discuss the challenges in reconciling measures based on richness, abundance and phylogeny.

We conclude this issue with comments on the integration of biogeography and ecology, addressing each of the four main topics, as well as other topics that affect the convergence of biogeography and ecology (language, data and analyses; scale and perspective; biogeographic patterns; phylogenetic approaches; species sorting and niche partitioning; local/regional saturation; and diversification of regional biotas) [36]. We consider these topics (among others) to be relevant to future progress at the intersection of biogeography and ecology. We also expect that research in these directions will help to develop the evolutionary basis that underlies and should unite historically different views of the natural world.

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