perspective

ISSN 1948-6596

An horizon scan of biogeography

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Abstract.

The opportunity to reflect broadly on the accomplishments, prospects, and reach of a field may present itself relatively infrequently. Each biennial meeting of the International Biogeography Society showcases ideas solicited and developed largely during the preceding year, by individuals or teams from across the breadth of the discipline. Here, we highlight challenges, developments, and opportunities in biogeography from that biennial synthesis. We note the realized and potential impact of rapid data accumulation in several fields, a renaissance for inter-disciplinary research, the importance of recognizing the evolution–ecology continuum across spatial and temporal scales and at different taxonomic, phylogenetic and functional levels, and re-exploration of classical assumptions and hypotheses using new tools. However, advances are taxonomically and geographically biased, and key theoretical frameworks await tools to handle, or strategies to simplify, the biological complexity seen in empirical systems. Current threats to biodiversity require unprecedented integration of knowledge and development of predictive capacity that may enable biogeography to unite its descriptive and hypothetico-deductive branches and establish a greater role within and outside academia.

Keywords. community assembly, ecological genetics, functional diversity, multi-temporal explanations, phylogenetics, phylogeography, species distribution modeling, synthesis.

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Overview

The opportunity to reflect broadly on the accomplishments, prospects, and reach of a field may present itself relatively infrequently. The literature is voluminous, often bite-sized, and lags behind the innovations that are shaping research; ideas are seldom generated rapidly and shared instantly in easily digestible formats across the breadth of a discipline. The organized and chance discussions that accompany any disciplinary meeting provide a mechanism suited to stimulate synthesis and innovation, but modern large meetings are often difficult to navigate.

The format of the biennial meeting of the International Biogeography Society (IBS)[1] arguably provides a venue that is predisposed to reviewing and integration of the diverse disciplines that constitute, or contribute to, Biogeography. Each biennial meeting is the culmination of ~1.5 years of scoping ideas, gathering information from across the discipline, and nurturing theses that mature as synthetic symposia; these mature symposia are given added context by a dozen contributed oral and poster sessions solicited during the immediately preceding half-year. The organization of the biennial IBS meeting thus approximates multiple attributes of an 'horizon scan' (Sutherland and Woodroof 2009) in which a large portion of the community actively engages. Here, we review this ready-made panorama to highlight important developments, what is constant, seemingly perpetually in flux, or starting to change, and to explore novel and unexpected issues as well as persistent problems and trends, including matters at the margins of current thinking that may be transformative.[2]

Figure 1. A word cloud composed of biogeography-related topics extracted from draft summaries of symposia and contributed oral sessions at the 6th biennial meeting of the IBS which were compiled for this horizon scan. This figure was made using Wordle, after removing terms relating to place, taxon, or time, and all non-biogeographic words such as articles, conjunctions, prepositions, etc. The number of individual words in the analysis, n_w, totalled 122. Figures 2–4 show the complementary word clouds for terms relating to place, taxon, and relative time, thus covering the major dimensions of biogeography. A word cloud analysis was used to approximate the frequency of topics at the 6th IBS meeting while tacitly acknowledging that the semi-qualitative and derived nature of these data can only provide a general guide to the issues addressed, and relative frequencies with which they were addressed, and cannot support quantitative statistical inferences. Draft summaries, rather than the final edited versions, were used because they provided a less heavily edited representation of the meeting. Asterisks indicate root words that appeared in various forms: Analog* = analog, analogous; Compare* = comparative, comparing, comparison; Ecology* = ecology, ecological; Fossil* = fossil, fossiliferous; Paleo* = paleobiology, paleoecology (including also their English spelling versions coming from Palaeo*). Note that diverse topics may be represented in a single high-frequency (i.e. large) word such as "Area", some words or abbreviations may refer to the same concept (e.g., SDM and ENM), and many low-frequency words may have a common theme (e.g., named geologic intervals).

1 The 6th International Biogeography Society Conference – Miami, USA, 9–13 January 2013 consisted of two days of shared symposia and a day of concurrent sessions of contributed oral talks, spanned by a two-day poster session.

2 http://www.oecd.org/site/schoolingfortomorrowknowledgebase/futuresthinking/overviewofmethodologies.htm

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In this horizon scan of biogeography, we purposefully retain something of an agglomeration of views—as a perspective through our constituent compound eye. This decision is made in large part because it is informative that themes emerged more than once across symposia. Eleven summaries are presented below, ordered to assist you in finding threads and weaving your own patterns (see also Figures 1–4), before we raise some of the common and emergent themes that caught our attention.

Symposia and session summaries

Global biogeography (R. Jansson)

Phylogenies and genetic data have become a mainstay of biogeography, increasingly appearing as large-scale studies aimed at identifying general phenomena (e.g., Crisp et al. 2009, Wiens 2007). For example, comparative phylogeography of 19 ungulate taxa distributed across the savannas of sub-Saharan Africa provided highly concordant evidence for several distinct southern savanna refugia during Quaternary climatic oscillations (Eline Lorenzen and colleagues). The long-term stability of southern refuges, however, contrasts with instability in East Africa that produced complex intra- and interspecific patterns (Lorenzen et al. 2012). Comparative phylogeography of whole assemblages of species thus provides perspectives on regional histories unavailable (or at least uncertain) from single-species approaches (Hickerson et al. 2010, Dawson 2012a).

Likewise, insights into a species' history may be obtained by comparative phylogeography of the species' parasites; mitochondrial and microsatellite data of human lice (*Pediculus humanus*) indicate strong geographic structure (Martina Ascunce and colleagues). Major phylogroups of these lice evolved before the origin of modern humans, suggesting diversification on other hominids and subsequent zoonotic transfer to modern humans, or retention of diverse ancient communities during speciation of *Homo sapiens*. Current populations of human lice in the Americas mirror human host colonization; human lice diversified into North and South American clades following first human colonization of the continent with additional immigration from Europe (Ascunce et al. 2013).

Coupling phylogenetic data with growing databases of geographic occurrences and fossils offers additional possibilities. The open-source, self-updating platform SUPERSMART[3] aims to produce fossil-calibrated chronograms of plants, animals and fungi. Also, SUPERSMART applies a newly developed Bayesian meta-analysis approach, to estimate rates of speciation, extinction and migration for areas and clades (Alexandre Antonelli and colleagues). By obtaining data from GenBank, the Global Biodiversity Information Facility and fossil databases, the approach will allow testing of questions such as how and when the world's current biomes were assembled, the evolutionary significance of barriers among areas, and how different taxa and regions were affected by climate change. Another 'big data' initiative, using 22.5 million botanical observations from 760 data providers, describes diversity and abundance for all the plant species of the Americas (Brian Enquist and colleagues). A high proportion of the species are rare, having just one or a few observations. Rare species are clustered in mountainous regions, whereas the Amazon basin harbors few rare species.

The potential of coupling phylogenetic with distributional data on many species will be realized best when also integrated with matching datasets on functional relationships, for example between body size and chemical energy availability for a large dataset of marine molluscs (Craig McClain and colleagues). Based on information about 1578 species, lower food availability sets constraints on maximum size and potentially on minimum size depending on clade-specific ecology. In contrast, higher food availability promotes greater niche availability and potentially allows evolutionary innovation with regard to size (McClain et al. 2012).

Looking to the future, integrating geographic, phylogenetic and trait-based information will shed new light on old questions regarding

3 http://www.supersmart-project.org

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global-scale phenomena. As reliable global-scale data becomes available, collaborative efforts, such as SUPERSMART which integrates data from many databases and the BIEN Project[4] which tackles a specific question, are poised also to achieve conceptual integration. Paleontologists and neontologists might similarly integrate data, methods and ideas on shared questions about global phenomena to the benefit of all.

Phylogenetic biogeography (J.-P. Lessard)

Phylogenetic approaches in biogeography have in some cases largely affirmed known patterns, in other cases revealed unknown and unsuspected patterns, and in all cases enabled deeper understanding of the role of evolutionary and historical processes in shaping contemporary patterns of biodiversity. A new comprehensive map of the zoogeographic regions of the world (Ben Holt and colleagues) based on phylogenetic turnover among assemblages of vertebrates (i.e., most of the world's amphibians, birds, mammals) is highly similar to the seminal map of Wallace (1876), but nevertheless reveals, for the first time, the phylogenetic (dis)similarity among zoogeographic regions that may reflect the signature of evolutionary history on vertebrate assemblages (Holt et al. 2013).

Time-calibrated phylogenies (chronograms) permit explicit tests of alternate hypotheses in ways that were not possible before and thus can help refine explanations for broad-scale diversity gradients. Using more than one hundred published phylogenies of mammals, birds, insects and flowering plants, Jansson and colleagues tested three evolutionarily based diversity hypotheses: Tropical Niche Conservatism (TNC), Out-of-the-Tropics (OT), and differences in Diversification Rate (DR). Even though most clades originated in the tropics, clades transition from tropical to temperate climate throughout their evolutionary history, supporting the OT but not the TNC hypothesis. Differences in diversification rates between sister clades do not support the DR hypothesis of faster diversification in the tropics relative to temperate regions (Jansson et al. 2013).

Coupling chronograms with ancestral area reconstruction models addresses a core interest in biogeography. By incorporating information on historical connectivity among continents, Lagrange likelihood models (Ree et al. 2005) can more precisely estimate the history of entire clades, including the origin, movement and timing of diversification of species in a given clade. Using these techniques, the Colchicaceae, a family of flowering plant, is inferred to have originated in Cretaceous East Gondwana, diversified initially in Australia ~75 million years ago (Mya), migrated to southern Africa during the Paleocene-Eocene, and from there extended its range to southeast Asia probably through Arabia, and then to North America through Beringia (Juliana Chacón and colleagues). As the sophistication of ancestral reconstruction methods improves, so do their accuracy and power of inference. In a world-wide study of muroid rodent assemblages, a recently assembled global phylogeny allowed ancestral distributions, changes in net diversification rates, and density-dependent models of diversification to be estimated for muroid clades that colonized continental landmasses (Scott Steppan and colleagues). Whether a clade arrives first, or not, determines the initial rate of diversification. Clades that colonize first often exhibit a diversification burst, perhaps resulting from rapid adaptive radiation facilitated by unchallenged availability of diverse resources.

The role of historical factors in shaping ecological communities may be quantified by applying community phylogenetic approaches (Cavender-Bares et al. 2009) along abiotic gradients and among regions, revealing patterns of alpha- and beta-phylogenetic diversity. Community phylogenetics may be most promising if used in a biogeographic context, coupling knowledge of the evolutionary history of the study organism with the geological history of the region. For example, passerine bird communities along an elevational gradient in the Andes link spatial patterns of phylogenetic diversity to historical events. The timing of diversification of passerine clades at high elevation, which are older than clades at low elevation,

4 http://bien.nceas.ucsb.edu/bien/

corresponds with geological estimation of Andean uplift (Julie Allen and Jill Jankowski).

Whether one category of process predominantly shapes all levels of biodiversity or whether multiple scale-specific processes interact to generate emergent patterns may be key to deciphering apparently complex phylogeographic signals. Individual-based genetic data on, for example, predatory aquatic beetle assemblages sampled across Europe, allows exploration of patterns of genetic diversity across population, community and metacommunity levels (Baselga and colleagues). Equivalence in the strength of distance-decay in genetic similarity across hierarchical levels supports the general importance of neutral processes. Moreover, relationships between lineage age, lineage diversity and range size may indicate a spatio-temporal diversity continuum driven by ecologically and evolutionarily neutral processes. By switching from describing patterns of taxonomic diversity to describing patterns of (phylo) genetic diversity, biological diversity can be quantified across more levels of biological organization, thereby shedding light on predominant processes (Baselga et al. 2013).

The integration of phylogenetic approaches in classical biogeography can clarify past movements and biotic exchanges, as well as processes underlying diversification and the assembly of ecological communities. The link between phylogenetic patterns and biological processes must be made carefully (Losos 2011), but phylogenetic biogeography should deepen our understanding of the origin, distribution and maintenance of biological diversity.

Phylogeography (K.A. Marske)

Phylogeography, like other sub-disciplines in biogeography, is increasingly integrative. For example, by drawing methods and concepts from ecology, phylogeography gains capacity to understand the processes defining species' distributions and patterns shared across species. This trend toward integration is coupled with increasing adoption of hypothesis-testing methods and broadening temporal scale, including the dynamics of expanding populations and multi-temporal drivers of lineage divergence and species co-occurrence, as well as classical descriptions of glacial refugia and allelic diversity and distributions.

The opportunities for integrating phylogeography and ecology are being provided in part by classical phylogeographic systems, such as the Mississippi River discontinuity in the southeastern USA (e.g., Avise et al. 1987). In that region, a well-documented hybrid zone exists between two closely-related members of the Louisiana Iris species complex. This study system enables comparison of two ecologically similar, hybridizing species in terms of their distributions of genetic diversity throughout their ranges (Jennafer Hamlin and Michael Arnold). This situation also enables investigation of the effects of hybrid fitness, introgression and adaptive divergence on genetic structure as the two species extended their range northward along the Mississippi River.

As integrative studies increase in number, frameworks clarifying the role of phylogeography in the current convergence of ecological and evolutionary concepts (e.g., Jenkins & Ricklefs 2011) will be needed. In one such framework, phylogeography is proposed as the means to identify the processes acting between the time-scales typically studied using biogeographic and ecological methods (Katharine Marske and colleagues). Integrating comparative phylogeography and community ecology may isolate the effects of Quaternary dispersal limitation from other factors driving community assembly and beta-diversity patterns (Marske et al. in press). In principle, phylogeography can provide insights into the assembly of ecological communities, and ecology may provide context for interpreting idiosyncratic phylogeographic patterns among species (see also *The biogeography of traits*). Thus, data for 40 co-distributed Andean cloud forest bird species, as well as 130 species sampled along an elevational gradient, enable examination of the effects of range fragmentation and elevation on genetic divergence using comparative phylogeography (Andres Cuervo and Robb Brumfield). Genetic structure relative to the geographic breaks varied substantially among species, with high species

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Figure 2. Terms related to place used at the 6th IBS conference. Analysis as described in the caption to Figure 1; based on n_w = 132. "America" was associated roughly equally with North (n = 4), South (n = 3), and Central or tropical (n = 3).

pool turnover at different geographic breaks across the Andes. Genetic divergence was positively correlated with mean elevation and negatively correlated with elevational breadth, with elevational breadth counteracting the effects of geographic barriers as drivers of divergence.

Comparative phylogeography of the understory bird community from India's Western Ghats sky islands similarly informs us how species distributions and genetic divergence have been shaped by topography, paleoclimate and species' ecology (V.V. Robin and colleagues). Levels of genetic divergence ranged from deep phylogeographic breaks at ancient geographic divides to no phylogeographic breaks at all. Breaks were stronger in habitat specialists, and relatively shallow in widespread and migratory species, indicating that the evolutionary effects of vicariance and dispersal are strongly affected by species' ecology.

However, phylogeographic studies of tropical ecosystems are rare, relative to northern temperate regions (Beheregaray 2008). The aforementioned studies in the Andes and Western Ghats are thus making inroads both conceptually and geographically, and in both respects are complemented by detailed studies of single species. For example, in the Brazilian Atlantic Forest, integrated genetic analyses, phenotypic measurements, and species distribution models (SDMs) reveal strong phylogeographic structure in the absence of geographic isolation, and varying relationships between genetic divergence and phenotypic disparity across the range of a widespread lizard (Roberta Damasceno and colleagues). In this species, current and past climate gradients apparently drove divergent selection at the local scale. In the central African rainforest, comparative phylogeography of three trees with different niches—which in part addresses prior taxonomic biases in genetic studies toward light-demanding, commercially exploited species, rather than the shade tolerant species characteristic of mature rainforest—revealed three separate community genetic pools, with a north-south break across each species, evincing multiple Pleistocene forest refugia and consistent with patterns of species-level endemism (Rosalía Piñeiro and colleagues).

In spite of recent critiques (Peterson 2009, Wiens 2012), the trend for greater interdisciplinarity in phylogeography will increase its potential to generate novel insights into questions which have long interested biogeographers—the relative roles of history, species ecology, environmental conditions and adaptation in governing species distributions and driving patterns of diversification. As advances in sequencing technologies allow greater precision in estimating population divergence (Carstens et al. 2012) and examination of the role of non-neutral genetic variation in driving population structure (Lexer et al. 2013), phylogeography is likely to play a vital role in answering these classic questions.

Neotropical biogeography (A. Antonelli)

The Neotropics is a heterogeneous and extremely biodiverse region, comprising several biomes of

contrasting ecophysiological settings and evolutionary histories (Hughes et al. 2013). Many hypotheses have been proposed for these differences: species interactions, niche conservatism, dispersal ability, soil adaptations, time for speciation, energy availability and changes in the landscape (Antonelli and Sanmartín 2011). Understanding Neotropical biogeography may require revisiting these hypotheses by delving in incredible depth into complete clades to generate both new questions and new answers.

Revisiting Willis' (1922) classic hypothesis that older species have larger ranges, André Rochelle and colleagues combined a chronogram of 100+ species of mainly Neotropical plants in tribe Bignonieae (Bignoniaceae) with an extensive database of species occurrences. They found large variation in age and range sizes, and no correlation between these two variables. Similarly, a complete species-level phylogeny of Neotropical chat-tyrants (*Ochthoeca*), including samples of nearly all known populations indicates that, while even low-elevation barriers across the Andean mountains (e.g., the Táchira depression, and the Marañón and Apurimac Valleys) have played an important role in promoting genetic and often morphological differentiation, species have responded differently to those barriers (Elisa Bonaccorso and colleagues).

This complexity in lineage response may result from processes internal and external to the region. Internally, soil differences may shape diversity gradients across Amazonia. Field data from nearly 300 inventory transects in western and central Amazonia (Ecuador, Colombia, Peru and Brazil) highlighted soil cation concentration, as well as presence of a dry season, as an important influence on fern diversity (Hanna Tuomisto). However, considerable variation at different spatial scales adds to the growing view that Amazonia is not a uniform forest with gradual changes over large distances; there is high local heterogeneity in soil (ultimately derived from geological history), topography, climate and biodiversity (Malhado et al. 2013). Externally, complexity in the Neotropics may in part be a relative property given context by, or emerging from, higher latitudes. Examining the distribution of all 341 species of Neotropical bats in nine families supported the TNC hypothesis at the species level, but different patterns were evident for the 89 genera to which those species belong (Héctor Arita). Genera of bats followed a symmetrical Rapoport pattern, i.e., more genera have small ranges near the equator, whereas species showed a highly asymmetrical pattern. These differences may be attributable partly to geological history external to current species' distributions. For example, some genera traditionally believed to have originated in South America instead may have originated in North America, prior to the Great American Biotic Interchange.

Comparative phylogeography has the potential to distinguish historical biogeographic and ecological processes, but analysis of 27 widespread lineages of lowland birds indicate little common response—in time and space—to larger geoclimatic events such as the Andean uplift and Pleistocene refugia (Brian Smith and colleagues). Thus, although barriers often are associated with genetic variation, they may be playing a largely passive role in structuring this variation rather than driving diversification. Ecology, stochasticity, geographic origin, and time for speciation may instead explain the diversity and distribution of Neotropical avian patterns encountered today.

In the midst of this continental complexity, research on the existence and importance of a short-lived island chain or dry-land connection between South America and the Greater Antilles, known as the GAARlandia hypothesis (Iturralde-Vinent and MacPhee 1999) offered rare clarity. Independently assembled data from paleogeography (tectonics and stratigraphy), paleontology and dated molecular phylogenies from a variety of recent studies support both predictions of the GAARlandia model: that it facilitated the dispersal of South American animals and plants to the Greater Antilles around the Eocene/Oligocene transition (~35–32 Ma), and that the subsequent break-up of those islands led to the formation of island-endemic biotas (Roberto Alonso and colleagues).

A holistic understanding of Neotropical biogeography cannot be attained without multi-

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taxon and integrative approaches, often at the interface of ecology and evolution. Revisiting commonly held assumptions and familiar hypotheses with increasingly large data sets and novel comparative methods is raising many new questions about generally accepted patterns (see also *The biogeography of traits*).

Island biogeography (L.M. Dávalos)

The signature of geographic isolation, given time, is speciation and endemicity. The apparent inevitability of that relationship and its almost axiomatic description of contemporary oceanic island life, however, can belie complex dynamics. A true understanding of biodiversity in oceanic archipelagoes requires integration of biological and geological phenomena (Heaney 2009). Thus, endemicity is concentrated on mountains within many archipelagoes perhaps because these are the oldest sites and both ecologically and geographically isolated islands. However, endemism on the Canary Islands is concentrated at intermediate altitude in the cloud forest belt, suggesting the age of the place (e.g., a mountain top) may sometimes be less important than the age of the ecosystems; cloud forest may be older than the mountaintop ecosystem that currently occupies the Canaries, and this may explain the initially paradoxical patterns of diversity and endemism (Manuel Steinabuer and colleagues). The biogeography of other regions similarly appears to be the outcome of multiple processes, even when taxa might intuitively seem disproportionately likely to be influenced by a single mechanism, such as dispersal in volant birds. Phylogeographic analyses of White-browed Shortwing *Brachypteryx montana*, suggests range expansion from Borneo to Mindanao and then in sequence to Luzon, Palawan and Mindoro as a consequence of glacial oscillations in sea level that alternate periods of great geographic isolation with periods of island connections (Sushma Reddy and colleagues). This is consistent with earlier findings for endemic Philippine rodents (Jansa et al. 2006), but whether it is a general pattern relevant to other birds remains to be explored.

Differences among species assemblages suggest functional ecology may influence, or be influenced by, the processes of community assembly on islands. The high precipitation and temperature characteristic of the tropics, for example, result in more functionally diverse parasitoid assemblages (Ana Santos and colleagues), a pattern also reported for woody plants (Swenson et al. 2012). Rigorous tests of patterns in functional diversity, using null distributions of functional diversity built from archipelago-wide regional species pools (i.e. excluding continental biotas), however, indicate that the majority of parasitoid assemblages are functionally neither clustered nor overdispersed. Only the minority of island assemblages shows significant functional clustering consistent with structuring by dispersal filters plus conserved functional traits plus competition. Evidence for a key role for mutualism in structuring island communities is similarly mixed. Fruit–frugivore food webs from islands show no significantly greater interconnection than mainland counterparts (Kevin C. Burns). However, the result was sensitive to small sample size. Consistent with the super-generalization hypothesis, frugivores tended also to be pollinators on islands.

Changes in trophic structure form the mechanistic basis of the island rule, that island mammal populations show trends in body-size evolution on islands (Foster 1964). While recognized as a general trend for decades, the island rule has been debated intensely because few clear trends emerge after accounting for phylogenetic effects on body size (Meiri et al. 2011). The ambiguity arises, in part, also because previous critiques of the island rule had not accounted for three additional confounding effects: (1) physiological constraints on body size imposed by flight among bats, (2) the delay in evolution of optimal island body size which causes recently formed islands to be unsuitable for testing the island rule, and (3) recent anthropogenic extinctions of larger mammals on many islands. After accounting for phylogenetic relationships and these three additional effects, the island rule holds across all mammals and the threshold for an increasing or decreasing trend in body size evolution is around 1 kg (Søren Faurby and Jens-Christian Svenning).

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Figure 3. Terms related to taxa used at the 6th IBS conference. Analysis as described in the caption to Figure 1; based on n_w = 119. Asterisks indicate words that appeared in singular and plural forms.

In a first exploration of hitherto unexplored island ecosystems, the island rule, as well as the species–area relationship, appear to hold for invertebrates in island-like marine lakes (Michael Dawson and colleagues). This is consistent with long-standing evidence that island 'syndromes' are indeed general patterns that apply broadly across taxa, regions, and time periods. Comparing the diversity and distribution of current and Last Glacial Maximum bat faunas together with bathymetric inference and the fossil record shows that area reductions caused by sea level changes explained >90% of the difference between past and current species richness in the Bahamas and Greater Antilles (Liliana Dávalos and Amy Russell; Dávalos and Russell 2012). Yet, despite the success of the equilibrium theory as a null model of island biogeography, and the power of this quantitative approach, more general models are periodically sought, and sometimes formulated (Guilhaumon and colleagues; e.g., Heaney 2000, Guilhaumon et al. 2011, Rosindell and Phillimore 2011). To a first approximation, however, the equilibrium theory of island biogeography is extremely successful at explaining species richness on islands with a minimal number of parameters. More complex models incorporating geological time succeed at reducing the difference between observation and theory (Whittaker et al. 2008), and represent incremental gains toward better explaining species richness. Crucially, ecological function and interactions depend not on the richness, but on the composition of species. The time is ripe, then, for a new synthesis that moves beyond richness to other dimensions of island biogeography (Alison Boyer and colleagues).

The biogeography of traits (A.C. Algar, N.G. Swenson)

Geographical variation in species' phenotypes has long been a focus in biogeography, generating many 'rules': Bergmann's rule, Allen's rule, the island rule, Hesse's rule, Gloger's rule, and so on (e.g., Gaston et al. 2008). However, in recent years, positive feedback between efforts to assemble large trait databases (especially for plants and vertebrates) and new capabilities in mapping species' traits has opened new realms of possibility for the biogeography of traits (Swenson et al. 2012). Moving beyond simple ecogeographic 'rules,' a biogeography of traits is being pioneered that allows for unparalleled integration and testing of ecological and evolutionary hypotheses for biogeographical patterns. From a milieu of approaches and ideas crossing major taxonomic, geographical, and conceptual boundaries, three themes are emerging that situate current approaches to trait-based biogeography and, more importantly, indicate key future challenges.

(1) Integration of ecological and evolutionary process. Traits mediate ecological interactions; however, interactions can also exert selection pressures on traits. Thus, extant organisms may carry with them signals of past interactions that

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have influenced traits through evolutionary time. By combining current trait distributions with phylogenetic information, we may understand better how ecology shapes evolution and vice versa. Thus, several lines of evidence arising from phylogenetics, morphology and trophic interactions shed light on the mechanisms underlying mid-altitude diversity peaks in Himalayan birds, arguing for diversity saturation and niche filling (Trevor Price). Alternatively, linking models of trait evolution with phylogenies can reveal how ecological interactions, particularly interspecific competition, limiting similarity and character displacement, may have influenced body size evolution through evolutionary time (Folmer Bokma).

(2) The importance of understanding function. One key motivation for incorporating traits into biogeographical analyses is that they provide a more direct window into ecological interactions through space and time. However, it is insufficient to simply choose a conveniently measured trait, or one for which data can be easily gleaned from the literature (Nathan Kraft, Jonathan Losos). Demonstrating the unifying strength of traits to act as a 'common currency', two disparate study systems—terrestrial plants and Caribbean *Anolis* lizards—illustrated the importance of not taking 'function' for granted. Rather, before we can make reliable inferences about how traits mediate processes at biogeographic scales, we must understand the links between phenotype, ecology, and performance. This can only be achieved through experimental and field studies to ensure that the traits we are studying actually do what we think they do. Furthermore, Losos warned, we should also consider that the morphology-performance-ecology link might not be stationary through space or time; what applies in one biogeographic setting (e.g., islands) may not hold in others (e.g., mainland; Irschick et al. 1997, Velasco and Herrel 2007).

(3) Improving biogeographic models. The capacity of traits to link ecological and evolutionary processes in different environments suggests a potential to improve biogeographic models and hypothesis testing. By thinking beyond morphology and considering characteristics such as habitat affinity and dispersal capability, Katrin Böhning-Gaese showed traits can contribute to models of range filling and range size in birds. At the same time, morphology can be used as a proxy for ecological similarity to reveal the effects of niche incumbency on Caribbean anole distributions (Jonathan Losos; Algar et al. 2013). Integrated data on evolutionary relationships, trophic interactions and morphology could reveal processes structuring mid elevation diversity peaks in Himalayan birds (Trevor Price). In all these cases, traits allow for stronger testing of hypotheses that could not be addressed solely with data on environment and species localities or species' counts, demonstrating the potential for trait-based approaches to open the black box of biogeographical process (Nathan Swenson).

Predicting species ranges and diversity in a warmer world (A. Guisan, N.E. Zimmermann)

Projections of species ranges and biodiversity patterns into future, possibly non-analog, climates, have been dominated by correlative approaches (e.g., Engler et al. 2011, Pearman et al. 2011, Thuiller et al. 2011). Those approaches are increasingly critiqued, and more dynamic approaches to predicting species ranges increasingly advocated and used (e.g., Thuiller et al. 2008, Kearney and Porter 2009, Buckley et al. 2010, Bellard et al. 2012). The challenge is to integrate such dynamic approaches into ecologically realistic prediction tools, suitable to process larger species numbers (e.g., Dullinger et al. 2012) at macroecological scales and ultimately reconstruct communities and ecosystems (Guisan and Rahbek 2011, Nogues-Bravo and Rahbek 2011).

There is long-lasting debate about the use of mechanistic versus statistical models (Guisan and Thuiller 2005, Thuiller et al. 2008, McMahon et al. 2011). Process-based models that focus on physiologically relevant dynamics are limited by coarse taxonomic resolution, while statistical SDMs based on species occurrence data may result in spurious relationships and flawed projections under non-analog climates (Fitzpatrick and Hargrove 2009, Guisan et al. 2012; note however that non-analog climates represent a critical issue

for all modeling approaches). For the task of projecting biodiversity patterns to future centuries, many processes such as CO_2 fertilization cannot easily be accounted for within statistical SDMs. Models of the physical environment (e.g., soil moisture and evapotranspiration) plus physiological processes (e.g., phenology and drought tolerance) and demographics (establishment, growth, mortality) are at the core of process-based or dynamic biogeography models (Higgins et al. 2012, Schurr et al. 2012).

There is a range of views about how to combine different approaches to overcome the weaknesses and build on strengths of individual methods, and to provide a framework for better projecting species and biodiversity patterns under a warmer climate (Yvonne Buckley, Lauren Buckley, James Clark, Jens-Christian Svenning and Richard Pearson, Niklaus Zimmermann and Antoine Guisan). Topics appearing repeatedly included mechanistic niche models, demography, disequilibria, complex interactions, niche dynamics, and non-analog climates. Mechanistic niche models can reveal crucial information about ecophysiological constraints to ranges and demographic processes, trait variation (phenotypes), and adaptive ability across the distribution and niche of the species. Insights from SDM outputs confronted with demographic data reveal the need for population monitoring in space, and especially the need to test for relationships between habitat suitability (within the niche space) and various vital rates (growth, birth, mortality) to better estimate extinction risks. This could also allow for modeling the niche and the distribution of ontogenic stages (Bertrand et al. 2012; e.g., the regeneration niche). Studies of distributional disequilibria can clarify migration time lags (glaciation legacy) and geographic accessibility in time, and can help identify different processes affecting the leading and trailing edges of shifting ranges (e.g., through distinct migration speeds). Complex interactions between climate and biotic processes that form species' distributions may be difficult to disentangle because they act at different spatial and temporal scales, and are therefore not always easy to disentangle using statistical approaches.

All these insights reveal the same problem: across the last two decades, biogeography underwent a spectacular development of new approaches to model species distribution and within-range dynamics, but the gathering of the data needed to feed these models for many species has not followed the same trend. While very large occurrence databases have been compiled recently as a result of intergovernmental efforts (e.g., GBIF; Yesson et al. 2007), allowing presence-only SDMs to be fitted, there is to date no comparable global compilation of abundance or demographic data necessary to fit demographic or abundance models at macroecological scales. The most advanced example is the global population dynamics database (NERC Centre for Population Biology 2010; see Inchausti and Halley 2001, Knape and de Valpine 2012) including hundreds of population time series, but usually with limited number of populations, and thus limited spatial coverage, for each species. Moreover, dispersal or physiological data to develop mechanistic niche models for a large number of species are also very scarce and usually stored in separate databases with data compiled for varying numbers of taxa (Vittoz and Engler 2007).

We see here one of the greatest challenges for biogeography in the 21st Century. A promising, but partly underexplored solution would be to develop more dynamic or mechanistic models of functional groups or guilds, thus making use of the increasing trait information in databases (e.g., Kuhn et al. 2004, Statzner et al. 2007, Klimesova and de Bello 2009, Schafer et al. 2011). Yet, such shortcuts also require research on the definition of these functional groups, their distribution and frequency in natural and semi-natural landscapes and ecosystems, and their usefulness for predicting community and ecosystem properties (e.g., Dolédec et al. 1996, Shipley et al. 2006, Ackerly and Cornwell 2007). A better approach may be integration via a biodiversity and ecosystem mapping portal, such as the recently initiated Map of Life project (Jetz et al. 2012a) also incorporating dynamic data.

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Historical and paleo-biogeography (D.G. Gavin)

While it is common to separate historical and ecological biogeography, several paleo-biogeography studies have blurred this distinction. Indeed, paleobiogeography and paleoecology studies often are motivated by modern ecological questions for which the observational record is too short, while at the same time fossil records may span into the domain of historical biogeography: large-scale reorganization of biota, extinction, and evolutionary change. With historical biogeography methods increasingly being applied across a range of taxonomic, temporal, and spatial scales, and with fossil data accumulating in large data banks, more and more studies are crossing the historical–ecological divide (Jackson 2004).

Classic historical biogeography questions about the development of large-scale biodiversity patterns may extend our understanding of the lineage histories and the geographic template on which they evolve. These studies demand a synthesis across a range of data types, normally involving a combination of phylogenies, fossils, paleogeography, and paleoclimate. The TNC hypothesis (Wiens and Donoghue 2004), for example, may be addressed using community phylogenetic analyses of cold tolerance in North American forests (Bradford Hawkins and colleagues); three predictions—all upheld—relate to the central concept that cold tolerance should be strongly associated with mean angiosperm family age. All family ages were greater than 34 Mya, which is prior to the development of the modern latitudinal temperature gradient; thus cold tolerance may have developed at high elevations rather than simply at high latitudes, possibly during the early Cenozoic Rocky Mountain orogeny (Hawkins et al. in press).

The Isthmus of Panama and the Great American Biotic Interchange provides opportunity to explore reciprocal effects of tectonic processes, for example through meta-analysis of ~400 chronograms of terrestrial taxa (Christine Bacon and colleagues). The analysis shows a sharp increase in crossing rates, especially plants, at 10 Mya. This is much earlier than the generally accepted age of 3 Mya for the Isthmus of Panama. The analysis supports an early Miocene model of evolution of the Isthmus region (Bacon et al. 2013) and is consistent with a parallel analysis of marine taxa (Lessios 2008).

The role of finer-grained patterns of diversity within such macro-evolutionary patterns may always be vague, but investigations on Quaternary time scales may illuminate the realm of abiotic processes in driving patterns, for example the origin of high bird endemism in tropical dry forest of northwestern Peru (Jessica Oswald). A combination of phylogenetic divergences, paleo-SDMs, and late Pleistocene fossils (including one site dated to 16,000 years BP with 1500 bone fossils) showed that dry forest bird species had a larger distribution during the Pleistocene, with greater connectivity during the Last Glacial Maximum, suggesting that modern endemism developed relatively recently.

When and how species achieve niche stability over long time scales is an open question. Fossiliferous Late Ordovician (450 Ma) marine strata of the Cincinnati Basin contain a rich 3 million years-long record of the responses of 10 brachiopod species to a wide variety of environmental changes (Alycia Stigall; Stigall 2011, 2012). Using environmental niche models, Stigall showed greater niche evolution during and after an invasion event, mainly in the form of contraction of

Figure 4. Terms related to time used at the 6th IBS conference. Analysis as described in the caption to Figure 1; based on n_w = 130. "History" also represents the use of "historical".

niche dimensions. This suggests that niche conservatism or evolution may be related to the speed or style of environmental change. The ecological mechanisms operating through environmental changes often are investigated using pollen records. Multivariate statistical analyses of pollen records across the Midwestern United States 14000–12000 years ago showed that each site had a unique vegetational response to rapid environmental change, which contrasted with more similar responses during the subsequent early Holocene (Jacquelyn Gill and colleagues). Factors contributing to the unique responses among sites during deglaciation likely involved the geographic extent of certain tree species, the pattern of megafaunal collapse and extinction, and site factors controlling local vegetation. In another large synthesis of pollen records, the limit of semi-arid forests at the forest–steppe boundary in North China showed greater extent during early-Holocene high moisture when the monsoon was stronger than today, after which forests were displaced southward (Hongyan Liu and colleagues). This transition to steppe may have lagged behind climate changes by 2000 years and fires may have played an important role (Yin et al. in press).

Fossils in the geologic record provide the clearest and often unambiguous evidence for the presence of a taxon at a point in space and time, including places from which populations subsequently are extirpated. Fossil data organized into georeferenced databases (e.g., Neotoma, Miomap, Paleobiology Database; Uhen et al. in press) thus can facilitate comparisons and joint inferences among different data types (e.g., phylogenies and paleo-SDMs). Reciprocally, if a taxon does not form a fossil record, inferences from phylogeography about species' historical occurrences and demography have implications for understanding past environments and therefore demand comparison with environmental reconstructions from fossils and/or paleoclimate proxies. There is reason, therefore, to consider paleobiogeography methods in many aspects of biogeography.

Conservation paleontology and biogeography (E. Davis, J. McGuire)

The prospect of massive macroecological reorganization of ecosystems in the next 50 to 100 years—producing 'non-analog' communities, extirpation, and extinction—raises the question: how may knowledge of prior ecological changes inform strategies to manage future landscapes? The answers may lie in cutting-edge paleontological methods for extracting insights from past patterns and processes to inform conservation biology (Liz Hadly). We are now certain of a warmer future, with some predictions indicating we will return to temperatures of 14 Mya by the year 2100. We already have begun to feel the effects of climate change, with documented range shifts in pikas, bog lemmings, and armadillos, among others. 'Weedy' generalist species often benefit from rapid environmental change at the expense of specialist species (Blois et al. 2010). At the ecosystem scale, we see many systems that change little until they flip suddenly to new stable states, for example forests converting to grassland or desert (Barnosky et al. 2012).

Previous work has established that bird and plant community dissimilarities are linked to climate dissimilarity (Williams et al. 2001, Stralberg et al. 2009). Whether climate influences community dissimilarity in the same way across both space and time—and therefore whether one can use spatial patterns of dissimilarity to predict temporal change, or vice versa—is unknown. Fossil pollen data since the Last Glacial Maximum (LGM; from the Neotoma Paleoecology Database) indicate significant differences between spatial and temporal climate–diversity relationships (Jessica Blois and colleagues). Yet, substituting space for time performs 85% as well as using time for time. Deep-time knowledge is essential for the best predictions, although some places or periods may be better substitutes than others (Blois et al. 2013). For example, an SDM of extirpated European hyenas *Crocuta crocuta* built using only their modern distribution (limited to Africa) cannot hindcast the known LGM European distribution of hyena, probably because the SDM cannot capture the full fundamental niche (Sara Varela; Varela et al.

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2010). Subsampling the dataset with respect to climate (but not geography) improves modeling effectiveness as long as the chosen sites (which may number as few as five) broadly sample climate-space occupied by the species. These findings indicate the importance of considering climate variation, novel climatic regimes, and how they are sampled for projecting SDMs onto different climate surfaces (such as the future).

Using paleontological data to inform responses to future climate change is a clear goal of conservation paleobiogeography. It is possible to produce more precise models of ancient distributions through time – for example, Michelle Lawing used an SDM to project models of rattlesnake (*Crotalus*) species distributions onto climates interpolated between the LGM and today. She then mapped niche model characteristics onto the *Crotalus* phylogeny to interpolate paleo-niches using a Brownian model of evolution. However, similar analysis of spiny lizard (*Sceloporus*) over deeper time showed that niche models and fossil species distributions stop agreeing ~13 Mya (i.e., fossils begin appearing outside of the reconstructed range). Comparing the evolutionary rates over the last 13 Mya to projected rates for the 21st century revealed that evolutionary rates will need to be 2 to 3 orders of magnitude higher in the future (Michelle Lawing).

Paleontological and neontological timelines can be spanned by combining fossil and modern paleodemographic analyses. For example, ensemble modeling can match optimal paleoclimate and SDMs with phylogeographic lineages, including extinct lineages, based on ancient-DNA evidence. An ensemble model of American Bison (*Bison bison*) populations over the last 50,000 years showed strong support for a demographic model with population declines during two distinct phases of human hunting (Rob Guralnick and colleagues). By further focusing their study on smaller levels, they were able to distinguish among drivers of species evolution in a strong hypothesis-testing framework. The development of such frameworks for evaluating and integrating paleontological and modern data in evolution and ecology is paramount (Susanne Fritz and colleagues), particularly for understanding niche and trait evolution or for inferring extinction rates.

Conservation biology requires accurate models for projecting future responses to climate change. Fortunately, massive environmental change has occurred repeatedly through time, providing natural experiments with which to ground-truth these important modeling efforts. As with many other fields, fossil-specimen databases are being consolidated and expanded through government funding and inter-institutional cooperation. Additionally, advancements in statistical and taphonomic methods allow more effective use of fossil and ancient DNA data. As a result, historical biogeographers are harnessing the depth and breadth of the fossil record through ever-improving specimen databases to ground-truth models with paleoenvironmental reconstructions. In doing so, we are gaining unique insights into the processes that are driving biogeographic patterns and stand to better predict the responses that we might see in the future.

Biogeography of the Anthropocene (A.L. Stigall)

The impacts of human activities are clearly evident throughout every ecosystem on Earth and dominate two geologic epochs: the Holocene and the Anthropocene. The Holocene is well-established, relating to the current interglacial, whereas the Anthropocene is newly proposed to document the mark of humans on our planet and, like all formal chronostratigraphic units, must be established based on globally pervasive paleontologic criteria (Tony Barnosky). For the Anthropocene, the geographic spread of humans and invasive species will certainly be preserved in the fossil record, but archeologists, ecologists and geologists hold varying perspectives on when the Anthropocene started (Balter 2013). Barnosky argued that the best indicators are likely to be trace fossils: microplastics and roads. These would establish the base of the Anthropocene Epoch around the year 1950 CE. The Cambrian Period is similarly based on trace fossils (of trilobites), and like the Permian–Cretaceous boundary, the Anthropocene will be marked by a profound mass

extinction (Barnosky et al. 2011).

A ~1950 definition places the Holocene–Anthropocene boundary relatively recently within the time-frame of many biogeographic studies. Direct human impacts on the environment, for example, may be traceable to impacts of human habitation on fire regimes in Central African rainforests during the past 1100 years (Carolina Tovar and colleagues). Using a dozen well-dated sediment cores, a clear increase in ignition was demonstrated over the study interval, particularly in the Marantaceae forest. The charcoal surge lacked a clear spatial structure and occurred in the absence of increased local aridity, and thus provides evidence for intentional forest management practices in Africa. This is analogous to patterns reported for tropical rainforests of South America (e.g., Edwards 1986, Piperno 1994) and further bolsters the data for ecosystem modification by indigenous societies.

The onset of such changes presaged distributional shifts of taxa related to the indirect impacts of human activities including climatic warming and species invasions. Historical research, such as Alexander von Humboldt's famous Mt. Chimborazo study (von Humboldt 1805), now provide unplanned reference points for assessing change (see also Grinnell and Storer 1924 c.f. Moritz et al. 2008, Barry et al. 1995, Perry et al. 2005). Naia Moureta-Holme and colleagues sampled plant community composition every 100 m of elevation change along a series of transects to determine the present elevational distribution of plant species 210 years after von Humboldt's study. Their data reveals that Mt. Chimborazo plant species showed an average upslope elevational shift of 387m, providing clear evidence of distributional changes following Anthropocene climatic warming. Over approximately the same 200 year period, the impressive data set assembled by the PalEON project demonstrates a shift of tree species to warmer temperatures and higher precipitation in the American Midwest which was matched by shifts in community composition, pollen assemblages, and utilization of species niche space (Simon Goring and colleagues). However, it is also well appreciated that some species are unable accommodate climate change through distributional shifts (Loarie et al. 2009). Based on GIS modeling, the forecast sea level rise of 1–10 meters is predicted to impact plant species in the UNESCO world heritage site of Panama's Coiba National Park—an archipelago of several hundred small to moderate sized islands—by reducing the areal extent of individual islands by 2–100% (Kim Diver and colleagues). Certain habitats are likely to be entirely lost causing extinction of endemic species, and increased dispersal distance may further stress and possibly interrupt meta-population dynamics.

Inevitably, the fate of species may be decided not only by what happens 'at home', but also by the options that are available elsewhere. Comparing the niche space occupied by invasive species within their native and invasive ranges reveals a high degree of niche conservation between regions with analog climates (Blaise Petitpierre and colleagues; Petitpierre et al. 2012) somewhat in contrast to results from paleontological analyses (see Davis and McGuire; Stigall 2012).

Estimating species' distributional responses to changing ecosystems is an increasingly vigorous and visible area of biogeographic research. The frequency of analyses investigating niche conservatism and niche transferability in space and in time highlights the importance of disentangling the impacts of human activities, recent climate change, species invasions, and abiotic and biotic effects. Conflicting results underscore the need for developing accurate and comparable analyses. More accurate predictions rely on calibrating models of species distribution shifts and understanding patterns of evolutionary response and niche stability among taxa. Arguably, one of the best sources of calibration data comes from information about species distributions prior to anthropogenic influences on the ecosystem, which defines an important integrative research direction for biogeographers, ecologists, and evolutionary biologists.

Global change and conservation biogeography (R. Early)

The IBS meeting opened with the observation,

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originating with Wallace, that overly simplistic explanations of biogeographic patterns are unlikely to be useful (Lawrence Heaney). The same rings true of biogeographic forecasts. The complexity and idiosyncrasy of species' responses to global change was underlined by a comprehensive analysis of alpine plant range shifts (John-Arvid Grytnes and colleagues). Alpine plants are generally moving upwards, but there is no direct link to climate warming. Instead the interaction between winter precipitation and temperature appears to affect snowmelt timing, and this indirect effect appears to be the most important driver of vegetation change.

In the face of such indirect and complex climatic effects on ranges, demographic models can be used to model the effects of multiple factors on distributions (Corey Merow and colleagues). Species distributions are the outcome of survival, growth and fecundity responses to the environment, but these processes are so entwined that their individual contributions to patterns of occurrence cannot be interpreted. Measurements of these vital rates and Integral Projection Models (IPMs; Dahlgren and Ehrlén 2009, 2011) can disentangle the effects of climate, soil, and fire on a Cape Proteaceae species.

While techniques such as IPMs are effective at fine spatial resolutions, different factors drive species distributions at different scales (Luoto et al. 2007, Wisz et al. 2013). Whereas the global ranges of 15 high-risk invasive aquatic plant species were driven by mean climate conditions, their landscape-scale invasive distributions were driven by local land-use, environment and human influence (Ruth Kelly and colleagues). Thus, different range-drivers should be used to inform different aspects of invasion management. Border control and trade might be usefully informed by species' large-scale climate associations, but in-country monitoring and extermination programs should be informed by the effects of land-use and human influence.

The concern that the drivers of species' ranges might not be static, but change during range-shift, adds further complexity to the measurement of the factors that drive distributions. Indeed, evolutionary adaptation was found to facilitate range-expansion in an invasive beetle, *Leptinotarsa decemlineata* (Saija Piiroinen and colleagues). Local adaptation quickly results in clines in environmental tolerances in invasive populations. However, experimental work shows that evolutionary responses to multiple environmental stressors might not be complementary. For *L. decemlineata,* cold exposure leads to cold-adapted offspring, and appears to have assisted range-expansion at cold margins. Insecticide exposure leads to insecticide-resistant offspring. However, cold-adapted offspring are less tolerant of insecticides, which could limit expansion at the cold range-margin.

How shifts in individual species' distributions might affect (and be affected by) other species and biotic communities remains a largely open question (Gilman et al. 2010, Wisz et al. 2013). Climate-driven changes in the distributions of the global bird biota would affect functional diversity, with knock-on effects for ecosystem health (Morgane Barbet-Massin and Walter Jetz). Fuzzy logic principles in distribution modeling can be applied to predict the effects of biotic interactions on species' future distributions (Raimundo Real and colleagues) and usefully distinguish the effects of biotic interactions and the physical environment on distributions, because measurements of environmental suitability are unaffected by different prevalences of interacting species. Based on the principle that several species may coexist when the environmental conditions are favorable for all of them, fuzzy logic can predict areas of co-existence or exclusion under climate change for three types of species pairing: parapatric, symbiotic, and predator–prey (e.g., Acevedo et al. 2012).

In conclusion, management recommendations based on such in-depth analysis of biogeographic drivers indicate the maturity of conservation biogeography as a discipline. However, the real-world credibility of conservation biogeography depends on the successful application of its recommendations. This symposium yielded insights derived from single-species studies, but the great potential of biogeography is its ability to

assess global change impacts on entire biotas. Consequently, a major challenge is to link the advances in demographic, evolutionary, and community aspects of biogeography demonstrated here, to region- or biota-wide analyses. A promising technique is to apply data on species' functional characteristics to quantify impacts of changes in species' distributions or abundances on broader communities and ecosystem processes.

Existing and emerging themes

The serendipitous and 'revolutionary' natures of progress in research (e.g., Kuhn 1962) make the greatest advances in science arguably impossible to predict. However, careful consideration of expert opinion (Sutherland and Woodroof 2009) and trends in the literature (King and Pendlebury 2013) can help identify what appear to be "important developments" in areas that are "starting to change" and especially those matters that are "at the margins of current thinking [and] may be transformative"[2]. To help identify such emerging themes, we first situate biogeography among other fields and distinguish existing trends in the biogeography literature.

The place of biogeography in science

Biogeography is practiced and classified as a largely ecological and/or evolutionary—a.k.a. modern and/or historical—science (Cox and Moore 2010, Thomson Reuters[5], Figures 1, 4). A 'map of science' circa 2006 placed biogeography, as a subfield of ecology and evolution, in the context of other biological, as well as chemical, mathematical, physical, and social sciences (Rosvall and Bergstrom 2008). The strongest connections via citation from/to biogeography were internally with other ecological and evolutionary disciplines, although strong external links existed also with crop (plant) sciences, geosciences (particularly climate), microbiology, and molecular biology. Our own citation analysis in Web of Science emphasizes the connections of biogeography with ecological, evolutionary, plant, molecular, and climate sciences for the period 1999-2006, and also highlights the role of zoological studies that is masked by the classification system of Rosvall and Bergstrom (2008; see Figure 5). Together, these seven categories—in the top eight pre-2003, and top seven post-2002—accounted for ~68% of publications in biogeography during the years 1999–2006. These same top seven categories similarly accounted for two-thirds (mean 66%) of biogeography publications during 2007–2012 (Figure 5).

Existing trends in biogeography

Although, on average, the share of biogeography research in the top seven disciplines has remained fairly constant for over a decade, the relative proportions of each category has varied from period to period. Trade-offs possibly exist[6] between ecology and evolution ($r = -0.14$, $p = 0.77$), and between plant sciences and zoology ($r = -0.58$, $p = 0.17$), whereas the allied fields of genetics and molecular biology covary ($r = +0.86$, $p = 0.013$). The intuitive overlap of evolution with genetics and molecular biology (despite non-significant empirical correlations of, respectively $r = +0.46$, $p = 0.30$ and $r = +0.56$, $p = 0.19$) and the negative empirical correlations of ecology with genetics ($r = -0.83$, $p = 0.021$ [molecular biology: $r = -0.50$, $p = 0.25$]) suggest the recent wax and wane—perhaps a 'perpetual flux'—of ecology and evolution in biogeography over the duration of our analyses may be driven in part by methodological advances.

Trending down—Although the popularity of most disciplines in biogeography varies through time, and the majority are increasing in absolute terms, the past 14 years have seen overall downward trends in the relative proportions of biogeography citations in the areas of ecology (correlation of share of citations in a period

5 see archive.sciencewatch.com/about/met/fielddef/

6 Acknowledging weak statistical power we consider significance at $\alpha = 0.1$, and because addition of research categories by Thomson Reuters may influence temporal patterns we also assess trends qualitatively (e.g., ecology and evolution are not statistically negatively correlated, but visually it is obviously the case; the difference may lie in reclassifications during 2005-2006 when 10 categories were added).

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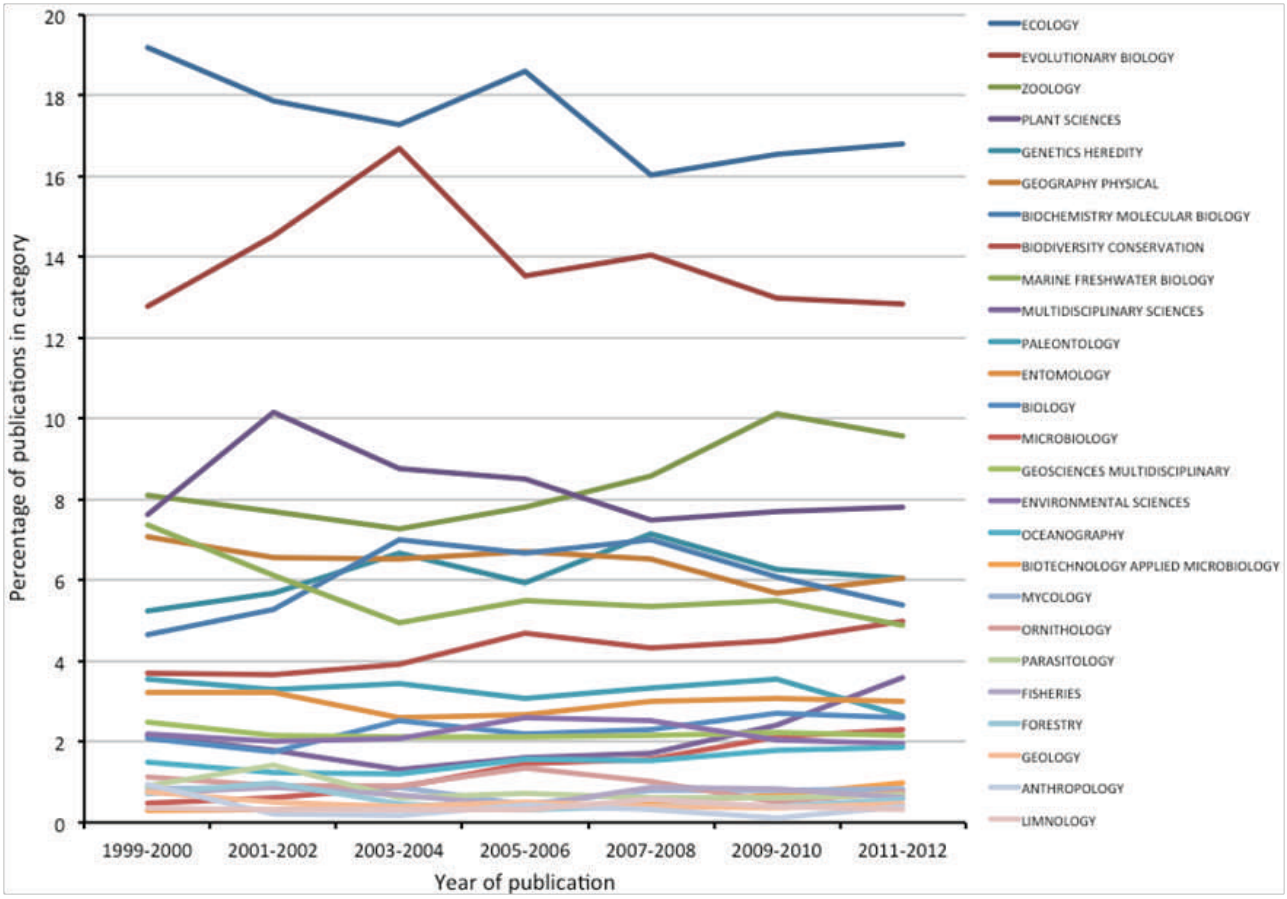

Figure 5. Percentage of biogeography publications in biennial periods since 1999 classified into each of 26 research categories per Thomson Reuters in the Web of Knowledge database. Articles were identified by the topic word search "biogeography" in the Science Citations Index–Expanded. The categories shown are the top 26 in 2011–2012 that also were recorded in all prior biennial periods. Research categories are ordered top to bottom according to their rank in 2011–2012. The number of publications in each period included in this analysis (and the percentage this represents of total biogeography publications each period) is, respectively, 1682 (97.9%), 1949 (98.4%), 2517 (98.1%), 3153 (97.7%), 3966 (97.5%), 4463 (96.7%), 4773 (94.9%). The decrease in percentage of biogeography papers represented is due to the addition of 32 new categories over the 14 year period. Other categories include agricultural disciplines, anatomy–morphology, atmospheric science, behavior, bio- and geochemistry (and other chemistry disciplines), cell biology, computational sciences, various engineering disciplines, geochemistry, infectious diseases, mathematics, physiology, remote sensing, statistics, and virology. We note that a topic word search for "biogeography" may miss biogeography-related papers that do not self-identify as biogeography, further analysis of which could itself be informative but which is beyond the scope of this study.

against number of years since start of analysis: r = -0.75; p = 0.054; change in share: -2.4%), geology (r = -0.69, p = 0.086, -0.31%), marine and freshwater biology (r = -0.74, p = 0.057, -2.5%), and physical geography (r = -0.83, p = 0.022, -1.0%). Some of these are perhaps counter-intuitive. For example, species distribution modeling is firmly in the areas of ecology and physical geography, but also is playing key, albeit debated, roles in contemporary biogeography (Figure 1; Araújo and Peterson 2012); we speculate that SDMs may in part be responsible for the recent positive trend in ecological biogeography (since 2007). Downward trends in other disciplines, however, are consistent with the generally low representation of deep-time (Figures 1, 4) and aquatic sciences (Figures 1, 2) in recent biogeography meetings.

Trending up—Overall 14-year upward trends characterize zoology (r = 0.78, p = 0.037, +1.5%), biodiversity conservation (r = 0.90, p = 0.006, +1.3%), biology (r = 0.76, p = 0.049, +0.5%), basic and applied microbiology (r = 0.99, p < 0.001, +1.8%; r = 0.87, p = 0.012, +0.7%; respectively), and oceanography (r = 0.78, p = 0.039, +0.35%). The rise in biodiversity conservation studies reflects the maturation of conservation

biogeography as a discipline since circa 2000 CE (Ladle and Whittaker 2011; see also the section *Global change and conservation biogeography*). The rise of zoology is captured in the prevalence of studies of vertebrates, particularly mammals and birds (Figure 3) often in large-scale macroecological and phylogenetic analyses (e.g., Jetz et al. 2012b) likely driven by the availability of data. The rapid growth of microbiology since 1999 doubtless has been driven in part by advances in DNA sequencing technology (Sogin et al. 2006, Reeder and Knight 2009) and in part by conceptual advances (Martiny et al. 2006); however, microbial biogeography remains under-represented at IBS meetings (Figures 1, 3). The rise of oceanographic biogeography may be tied to the rise of microbial biogeography (e.g., Sogin et al. 2006) and also to the availability of large datasets from remote sensing, biodiversity initiatives, and fisheries (e.g., Tittensor et al. 2010, Reygondeau et al. 2012) given that other aquatic sciences, including (coastal) marine research, in general are on a downward trajectory (Figure 5).

Emerging themes

Before looking for themes emerging from the proceedings of the 6th biennial meeting of the IBS, we turn to one final set of bibliographic analyses: the most recent annual analysis of 'Research Fronts' by Thomson Reuters (King and Pendlebury 2013, p.3; Table 1).

Research fronts are formed when "clusters of papers that are frequently cited together … [attain a] level of activity and coherence … with

Table 1. Research Fronts in Ecology and Environmental Sciences, and in research areas related to biogeography, for 2013 as identified by Thomson Reuters (King and Pendlebury 2013). Other research categories[7] did not contain research fronts obviously related to biogeography.

Rank	Research Fronts	Core papers	Number of citations	Mean year of Core papers
Ecology and Environmental Sciences (EES)				
1	Ocean acidification and marine ecosystems	45	3,653	2009.6
2	Biodiversity and functional ecosystems	43	3,139	2009.5
3	Mangrove forests and climate change	16	1,121	2009.5
4	Models and impacts of land-use change	18	2,318	2009.4
5	Biochar amendment techniques and effects	41	2,300	2009.4
6	Adaptive evolution in invasive species and approximate Bayesian computation	19	1,255	2009.4
7	Chytridiomycosis and large-scale amphibian population extinctions	13	1,003	2009.3
8	Pharmaceutical residues in environmental water and wastewater	50	3,815	2009.1
9	Community ecology and phylogenetic comparative biology	20	1,799	2009.1
10	Climate warming, altered thermal niches, and species impact	14	1,244	2009.1
Agricultural, plant, and animal sciences (APAS)				
1	Impact of climate change on food crops	32	1,537	2010.0
2	Comprehensive classification of fungi based on molecular evolutionary analysis	18	1,374	2010.0
6	Angiosperm phylogeny group classification	34	2,259	2009.7
Geosciences				
4	Greenland ice core chronology and the Middle to Upper Paleolithic transition	28	2,490	2009.6
6	Climate change and precipitation extremes	30	2,098	2009.5

7 see archive.sciencewatch.com/about/met/fielddef/

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the co-cited papers serving as the front's foundational 'core' … [linking] researchers working on related threads of scientific inquiry, but whose backgrounds might not suggest that they belong to the same 'invisible college'" (King and Pendlebury 2013). To a large degree, research fronts already are established areas of very active research and are therefore familiar topics, including at least eight priority areas in biogeography (Table 1: EES 2, 6, 7, 9, 10; APAS 2, 6; Geosciences 6). Several of these have a decade-long history (e.g., The Royal Society 2005) and are targeted by specific grant programs (e.g., *Ocean Acidification* and *Dimensions of Biodiversity* at the US National Science Foundation, started in 2010), large research groups (e.g., the Center for Macroecology, Evolution and Climate in Denmark), or prior IBS symposia (e.g., *Analytical Advancements in Macroecology and Biogeography*, Crete 2011; Diniz-Filho and Rahbek 2011).

To look for the most recent emerging themes we turn to the proceedings of the 6th biennial IBS meeting, contextualized by the preceding citation analyses—particularly the areas of research that may be bubbling under, or within, existing themes and yet to acquire a significant share of the published biogeography literature (see caption to Figure 5). These we consider as the potentially "important developments" in areas that are "starting to change" and may seed questions that are "at the margins of current thinking [and] may be transformative."[2] In composing, chairing, and writing about the IBS symposia, we identified at least seven such areas.

Genes, traits, and patterns of biodiversity—Interest in the biogeography of traits is as old as many ecogeographic 'rules', however studies classified as including 'anatomy–morphology' composed 0.1–0.3% of the biogeography literature in just three of the past seven biennial periods (peaking in 2001–2002). Similarly, the relationship between genes and traits has long been manipulated by agriculturalists and animal breeders among others (e.g., Real 1994). Only in the past approximately one-and-a-half decades have these two aspects been integrated directly with each other, for example in analyses of phenotype ontologies and quantitative trait loci (Mabee et al. 2007, Miles and Wayne 2008), and for <5 years have single-study designs begun to integrate genetic, trait (functional), and species diversity (Swenson 2011). Thus the combination of the geographic distribution of trait variation with known or discoverable function and genetic origin promises to link ecological and evolutionary mechanisms with environmental variation and species distributions. Mechanistic or process-based SDMs (e.g., Kearney and Porter 2009) already may link population growth and dispersal ability to heterogeneous landscapes to predict broadscale patterns of spread (e.g., Merow et al. 2011), and IPMs may link traits or trait-complexes to key emergent properties such as habitat affinity, dispersal, population density, and productivity. Compilation and publication of comprehensive trait databases for major taxonomic groups can provide the data necessary to detect process at regional, continental, and global scales. Such databases, when combined with field and experimental studies linking environment and function, position trait-based approaches at the forefront of transformations in new biogeographical models, tests and theory.

Tropical biogeography—Tropical ecosystems have long been understudied relative to northern temperate regions (Shapiro 1989, Beheregaray 2008). As such, there are long-standing questions about how processes in the regions may differ in emphasis and the extent to which processes in the tropics may drive global patterns of diversity (Antonelli and Sanmartín 2011). Strong representation of tropical studies during the IBS meeting (Figure 2) reflects in large part that tropical research has increased considerably in recent years, and thus speaks to the potential for answering some of these questions. However, increases have been uneven and challenges can remain substantial. Countries like Colombia and Brazil are rapidly gaining strength in some resource-intensive areas such as molecular phylogenetics, whereas others are lagging behind. Even within strong countries such as Brazil, rich states are investing much more

in science than poorer states (Marques 2012). The consequent unevenness that may result in environmental, genetic, trait, or species distribution databases may be exacerbated by unequal access to biological resources, which could compromise analyses in biogeography (Swenson 2013). Research infrastructure in much of the tropics remains somewhat limited relative to the opportunities at hand, diminishing potential for detailed ground-truthed long-term time-series that may be needed to understand fluctuating processes.

Marine and freshwater biogeography—Marine biogeography is a recognized subdiscipline in biogeography (Heaney and Lomolino 2009:1-2), is represented in stand-alone sessions at IBS meetings, achieves publications in leading disciplinary and general journals (e.g., Follows et al. 2007, Schils et al. 2013) but remains poorly integrated in biogeography (Dawson 2009)[8]. Underrepresentation in this horizon scan is attributable in part to absence of a symposium summary, but citation analyses indicate that 'freshwater and marine' studies have a declining share of publications in biogeography, although oceanographic studies are increasing (Figure 5). The poor integration of marine and freshwater studies into the broader biogeographic literature may be due in part to very real differences in fluid environments, in part by challenges conducting marine research, and consequently less detailed datasets than usually are available for terrestrial plants and animals (Cox and Moore 2010:28–29, 265; but see e.g., Tittensor et al. 2010, Worm and Tittensor 2011, Reygondeau et al. 2012). However, much remains to be learned about similarities and differences among aerial, freshwater, marine, and terrestrial biogeography (Dawson and Hamner 2008, Vermeij and Grosberg 2010, Webb 2012) and comparisons including marine or freshwater studies may complement how we think about terrestrial systems (Dawson 2012b) in the same way that studies of terrestrial systems continue to influence marine studies (e.g., *Island Biogeography*). Questions such as the phylogenetic and environmental distribution of traits, which are of breaking interest in terrestrial biogeography, also are being studied in the seas (McClain et al. 2012, Mirceta et al. 2013). To overcome existing barriers between subdisciplines, societies and journals need to extend their conceptual boundaries, databases must be improved, and methods must advance to include marine and freshwater taxa similar to those for terrestrial plants and vertebrates.

The challenge of integration—The challenge of assimilating or integrating information describing different datatypes, places, subdisciplines, and taxa recurs in many contexts and on many different scales. This challenge exists for process-based understanding of species distributions, predicting responses to future change, spatial-temporal transferability, and other matters including the grand goal of unified theory (e.g., Scheiner 2010). Ongoing advances in data collection and archiving, the infiltration of common data types (e.g., DNA sequences) across traditionally disparate disciplines, and the continued development of analytical tools will each chip away at existing barriers. The advent of next-generation sequencing technologies will better enable causal links to be established between the diversity and distributions of alleles, phenotypes, and environments (Gillespie 2013, Rocha et al. 2013, Figure 6). Likewise, additional frameworks to organize these data likely are also necessary and may be built, in part, on areas of study that already bridge spatial and temporal scales such as *Phylogenetic Biogeography* and *Phylogeography* (Emerson et al. 2011, Marske et al. in press). We may also find approaches to adopt from other fields such as systems biology (Levin 2010, Dawson and Hortal 2012), and we should choose natural experimental settings (Smith and Lyons 2011) in which to compete different metrics or hypotheses using standardized comparative frameworks (Chiarucci et al. 2011). Thus, studies in the history and philosophy of science could have an impact beyond their small share of the biogeography literature. For example, a better understanding of biogeogra-

8 However, organizers of the 6th IBS meeting made a conscious effort to integrate posters by concepts and themes rather than location or environment.

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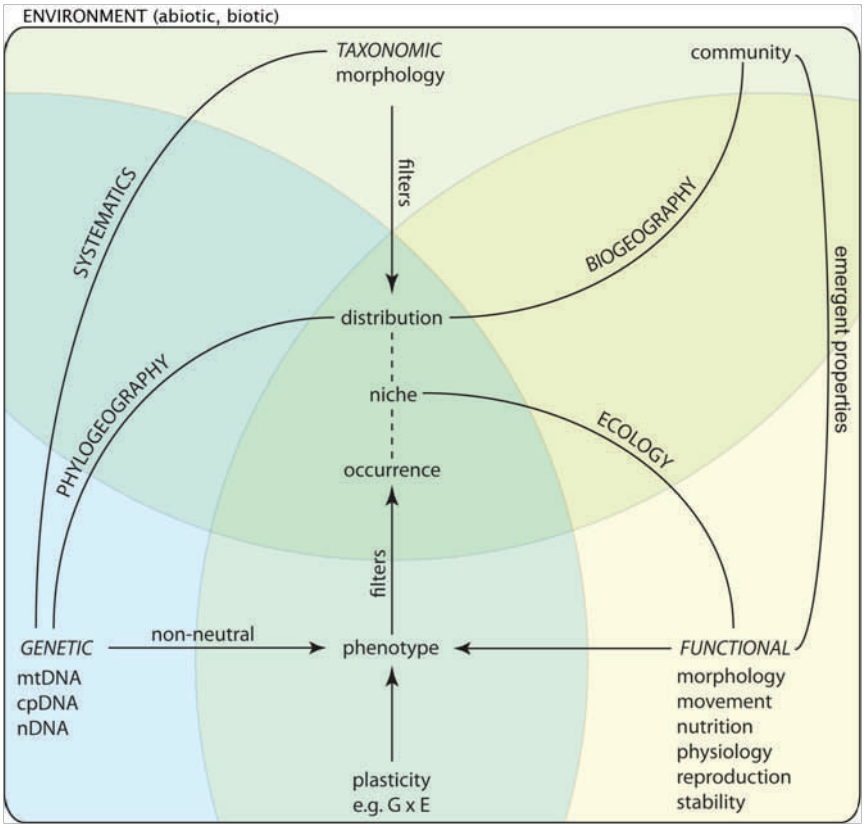

Figure 6. One possible conception of the three main components of biodiversity and their relationships to various biogeographic disciplines. The majority of investigations into the structure of biodiversity have focused on species diversity (taxonomic, green sphere), and increasingly the relationships between taxonomic and genetic diversity (blue sphere). Research on functional traits (yellow sphere) is increasingly common and interacts with genetic and taxonomic approaches. Studies simultaneously quantifying all three components generally are in the early stages of development. Figure and caption modified from NSF (2010) and Swenson (2011).

phy itself can influence how we think about the role of models (e.g., Sismondo 2000) and how we study biogeography in the future.

Challenges within integration—The grand challenge of integration is complicated by multiple sub-challenges, such as how to make sense of spatial and temporal continua. Much has been written about spatial scale dependency during the past two decades (e.g., Levin 1992, Whittaker et al. 2001, Scheiner 2011) so we will add only that it seems imperative to move to individual-based geo-referenced genetic, functional, and taxonomic data that will facilitate co-exploration of the components of biodiversity (Figure 6) across multiple levels of organization including identifying emergent patterns and processes (e.g., Clark 2010). Organisms that are mobile should be tracked temporally too, through a spatially and temporally well-described environment.

In terms of the temporal continuum, the essential evolutionary tool is clearly the chronogram, which with models of character evolution can in principle link all spatio-temporal 'locations' occupied by a lineage and integrate ecology with evolution. Such continuity between neobiologists and paleontologists may dovetail the strengths of the modern record—which is sample-rich in space and diversity—with the reciprocal strengths of the paleorecord: information on extirpated populations and extinct species. Thus, we might gain insight into micro-evolutionary processes occurring during deeper-time intervals, and greater understanding of fundamental niches of extant taxa, trait evolution (or niche conservatism), and transferability in space and/or time (Hu et al. 2009). Inferring biological processes from phylogenetic patterns, though, should be done cautiously (Losos 2011).

A key issue is how to link recent with ancient timescales. Fossils and/or geological events have long provided calibration points for rates of mutation (notwithstanding issues such as heterochrony and rate heterogeneity). However, models of nucleotide substitution under different demographic scenarios (Burridge et al. 2008, Ho et al. 2011, Crandall et al. 2012) and studies of invasive species (Darimont et al. 2009) indicate that molecular and phenotypic evolution can proceed much faster on short time-scales than is recorded in fossil records. Greater resolution of microevolutionary rates within periods of rapid change in the

paleontological record, and looking directly at ancient DNA, may help reconcile when to use fossil/geologic calibrations versus expansion-dating or perhaps suggest appropriate sliding scales, not only for conservation neo- and paleo-biologists but also for historical demographers and phylogeographers.

Model systems—Biogeography is differentiated from many other fields in lacking a model system. There arguably is no equivalent of the model organism—zebra fish, stickleback, mouse, *Anolis* lizard, or *Arabidopsis*—and the best analog of the Large Hadron Collider (as a place to study process) may be islands, but whether islands serve this purpose is debatable (Cox and Moore 2010:31). Are there places and/or (communities of) taxa that could serve such a purpose, and what new challenges and opportunities would be intrinsic to such an approach? An obvious concern would be lack of representation of place-, time-, or taxon-specific processes, but might some systems yield a worthwhile trade-off? One possibility might be to adopt organisms that already are models and also have wide geographic coverage and address many issues of concern (e.g., *Drosophila*). Other desirable attributes would include detailed genotype and phenotype databases for diverse populations coupled with an extensive historical and fossil record (e.g., *Homo;* Thomas et al. 1998) with analogues in other taxa and/or environments (e.g., Yi et al. 2010, Huerta-Sanchez et al. 2013 c.f. Mirceta et al. 2013). Recent years have seen a dramatic increase in knowledge about hominin evolution spanning many issues mentioned above (Brown et al. 2004, Perry and Dominy 2009, Callaway 2011) but biogeographic studies tend to focus on modern humans as agents of change in other species (e.g., *Biogeography of the Anthropocene* and two other symposia in this review) and less on hominins as study organisms. Conceivably, merging of hominin ecology and evolution in biogeography could further improve understanding of past impacts of humans on biodiversity, responses to global change, and predictions about the future. For macroecological and community processes, models seem likely to be drawn from the already dominant study taxa: mammals, birds and plants such as forest trees (Figure 3). In time, these infra- and inter-specific models may be integrated.

Infectious diseases—The organisms that cause infectious diseases, including microbes and parasites, provide another opportunity to integrate past and future effects at population to ecosystem levels while considering multiple species' ecologies (such as hosts including most if not all taxa in Figure 3) and timescales (e.g., those in Figure 4, divided by different generation times) within a single comparative framework. Although a symposium topic at the 4th biennial meeting of the IBS in Merida, 2009, the biogeography of disease remains a slowly breaking topic (0.07–0.36% citation share during the most recent 3 of 7 biennial periods, peaking in 2009–2010). In considering the biogeography of infectious diseases, our minds also turn to the biogeography of other symbioses in part as a subset of problems relating, say, to the niches and distributions of facultative symbionts, and effects on and of the eponymous Anthropocene species.

Concluding remarks: empiricism and theory

Biogeography has been a discipline that developed theories early but lacked the data and/or tools to test them (e.g., Hawkins 2001). These data and tools now are becoming available, and as long-standing theories are rejected, modified, or accepted, biogeography is poised for a new period of discovery. Platforms for organizing, generating and sharing knowledge (e.g., Tree of Life), some self-updating (e.g., SUPERSMART), and stand-alone software with even greater 'plug-and-play' capabilities seem an inevitable and inextricable part of the future in which phylogenetics and large datasets of genetic, distributional, or trait data become more accessible (e.g. phyloGenerator, Pearse and Purvis 2013). These tools and resources offer dizzying opportunities for cross-disciplinary or multi-faceted approaches, for which precedents already are being set. However, such automated tools carry with them great responsibility, and their obvious benefits in acceler-

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ating individual research might trade-off against the benefits of interdisciplinary collaboration. In adopting these approaches, it is incumbent upon us to understand and acknowledge the limitations of datasets which may have been compiled using methods outside of our own personal expertise; for many of the world's species, we have very little and at best highly imprecise phylogenetic, distributional, and ecological data that are insufficient for current models. Explicit conceptual and analytical frameworks, including clarification of how deviations from assumptions affect interpretation of downstream analyses, will be key.

Well-informed, collaborative, multidisciplinary biogeography is a natural progression. The fields of genetics and physics both adopted large community projects as part of a global strategy to address central questions. What would be the pillars of a unified theory of biogeography that adequately captures dynamics of neutral and non-neutral processes in interior, freshwater, marine and terrestrial microbes, invertebrates, plants, and vertebrates? Whether single large experiments are sufficient is doubtful; instead, perhaps, coordinated studies that lay the foundations for rigorous meta-analyses (e.g., Adler et al. 2011)? Equally importantly, when should biogeographers be satisfied with the answers in hand? Before beginning the human genome project, criteria were established for when the project would be considered complete (e.g., Collins et al. 2003) and 'big' physics routinely sets statistical and empirical tests based on theory to accept 'proof' (Cho 2013, Than 2013), thus enabling these fields to decide when empirical measurements or an aspect of theory are sufficiently complete to transition a majority of effort to the next endeavor. Such large projects and decisions do not negate small-scale studies in other or related fields nor signify that all work is complete, but encourage progression. A major theme throughout the 6th IBS meeting was using new approaches/data to answer existing questions, which caused some of us to wonder whether we should worry about a lack of new theory? In general, as a field, we think we are asking the 'right' questions, but perhaps this horizon scan can help identify whether biogeographers should become more ambitious.

Acknowledgments

We thank all speakers who contributed to all sessions, the IBS conference committee for their support, and Joaquin Hortal for invitation to summarize the symposium proceedings. An horizon scan was suggested by Kathy Willis during the IBS Board Meeting at the Fairchild Botanical Gardens on 8th January 2013. We thank the following sources for funding that supported work contributing to this article: the Danish National Research Foundation (for K.A. Marske), the Swedish and European Research Councils (for A. Antonelli), and the National Science Foundation (EAR-0922067 to A.L.Stigall, OCE-1241255 to M.N Dawson), Ecography (for sponsoring symposia on the biogeography of traits, conservation paleontology, and climate change), the Journal of Biogeography and its sister journals Global Biogeography and Ecology, Diversity and Distributions (for sponsoring the island biogeography symposium). We also thank C. Merow for providing references for Integral Projection Models.

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Edited by David G. Jenkins