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perspective

A second horizon scan of biogeography: Golden ages, Midas touches, and the Red Queen

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Abstract. Are we entering a new 'Golden Age' of biogeography, with continued development of infrastructure and ideas? We highlight recent developments, and the challenges and opportunities they bring, in light of the snapshot provided by the 7th biennial meeting of the International Biogeography Society (IBS 2015). We summarize themes in and across 15 symposia using narrative analysis and word clouds, which we complement with recent publication trends and 'research fronts'. We find that biogeography is still strongly defined by core sub-disciplines that reflect its origins in botanical, zoological (particularly bird and mammal), and geographic (e.g., island, montane) studies of the 1800s. That core is being enriched by large datasets (e.g. of environmental variables, 'omics', species' occurrences, traits) and new techniques (e.g., advances in genetics, remote sensing, modeling) that promote studies with

increasing detail and at increasing scales; disciplinary breadth is being diversified (e.g., by developments in paleobiogeography and microbiology) and integrated through the transfer of approaches and sharing of theory (e.g., spatial modeling and phylogenetics in evolutionary–ecological contexts). Yet some sub-disciplines remain on the fringe (e.g., marine biogeography, deep-time paleobiogeography), new horizons and new theory may be overshadowed by popular techniques (e.g., species distribution modelling), and hypotheses, data, and analyses may each be wanting. Trends in publication suggest a shift away from traditional biogeography journals to multidisciplinary or open access journals. Thus, there are currently many opportunities and challenges as biogeography increasingly addresses human impacts on, and stewardship of, the planet (e.g., Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services). As in the past, biogeographers doubtless will continue to be engaged by new data and methods in exploring the nexus between biology and geography for decades into the future. But golden ages come and go, and they need not touch every domain in a discipline nor affect subdisciplines at the same time; moreover, what appears to be a Golden Age may sometimes have an undesirable 'Midas touch'. Contexts within and outwith biogeography—e.g., methods, knowledge, climate, biodiversity, politics—are continually changing, and at times it can be challenging to establish or maintain relevance. In so many races with the Red Queen, we suggest that biogeography will enjoy greatest success if we also increasingly engage with the epistemology of our discipline.

Contents

Introduction

Biogeography is an evolving (e.g., Whittaker 2014) centuries-old discipline (e.g., von Humboldt and Bonpland 1807; Darwin 1859; Wallace 1881). This is the second horizon scan in a series intended to report, track, and understand recent changes in biogeography. Specifically, these horizon scans are intended to distinguish important developments and trends, novel and unexpected issues, and matters at the margins of current thinking that may be transformative; by contrast, they also highlight what is constant or seemingly in perpetual flux, and persistent problems (Dawson et al. 2013; see also OECD[1]).

The first horizon scan, which emerged from the 6th Biennial meeting of the International Biogeography Society (IBS) in 2013, noted benefits in biogeography accruing from rapid data accumulation, new tools, a renaissance of interdisciplinarity, including integration across the evolution–ecology continuum (i.e., across spatial, temporal, taxonomic, phylogenetic, and functional scales), and their application in re-examining classical assumptions and hypotheses (Dawson et al. 2013). We also noted that advances were taxonomically and geographically biased, and that key theoretical frameworks still awaited tools to handle, or strategies to simplify, the complexity of empirical systems. Meeting these challenges, we thought, might enable biogeography's descriptive and theoretical branches to be united, establishing a greater role within and outside academia, for example in conservation biogeography and mitigating threats to biodiversity. In the past few years, we have seen, for example, greater involvement of IBS in the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES; Opgenoorth and Faith 2014), publications in the highest profile general science journals applying new tools to old questions (e.g., Holt et al. 2013, Helmus et al. 2014, van Kleunen et al. 2015), and recognition of a new golden age in island biogeography (Fernández-Palacios et al. 2015, Santos et al 2016).

This second horizon scan is again coupled with a snapshot of a biennial meeting of the IBS[2] (see Gavin et al. 2014; herein G14), thus approximating multiple attributes of an 'horizon scan' (Sutherland and Woodroof 2009) that actively engaged a large portion of the community (see Dawson et al. 2013). This article might be read profitably from beginning to end or by dipping into sections of particular interest. We first present 15 summaries that highlight the content and outcomes of symposia and sessions at the IBS meeting (see also Figures 1–5) before raising some of the common and emergent themes that caught our attention. We also consider how the publishing landscape is evolving and shaping biogeography (or vice versa). We ask whether trends suggested by the first horizon scan are continuing to progress, or whether they are being replaced by other trends. In answering those questions, we contemplate perceived strengths of biogeography, potential weaknesses, and persistent challenges, and consider what the future may hold for the discipline. As a metaphor, following Fernández-Palacios et al. (2015), we ask whether we may be entering a new 'Golden Age' not just for island biogeography but for biogeography in general; we also consider whether such successes can have a 'Midas touch' in the mythical sense, i.e. when apparently fabulous short-term benefits have very undesirable longer-term outcomes.

Symposia and session summaries

Adaptation, migration, persistence, extinction: New insights from past climate changes (F. Rodríguez-Sánchez & D. Nogués-Bravo)

Climate change is one of the major threats to biodiversity. The range of biodiversity responses is well known: persist locally (e.g., in refugia), migrate to more suitable places, change phenotypically (through plasticity or evolutionary adaptation), change abundance, or go extinct. Yet we are still struggling to predict which response(s) will be more likely across different taxa and in different circumstances. Looking into the past can improve

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Figure 1. A word cloud composed of biogeography-related topics extracted from 521 abstracts submitted for symposia and contributed oral sessions at the 7th biennial meeting of the IBS (see Gavin et al. 2014 [G14]). This figure was made using Wordle[3], after removing terms relating to place (see Figure 2), taxon (see Figure 3), or time (see Figure 4), and all non-biogeographic words such as articles, conjunctions, prepositions, acronyms and most units of measurement (see Figure 5), etc. The number of individual words remaining in the analysis, n_w, totalled 7,565. The word cloud analysis is used to approximate the frequency of topics at the 7th IBS meeting while tacitly acknowledging that the semi-qualitative and derived nature of these data can provide only a general guide to the relative frequencies with which topics were addressed. The size of a word is proportional to the number of abstracts in which the word occurred. All abstracts, rather than the subset that were accepted, were used because they arguably provided a less biased representation of the topics that interest the biogeography community. Asterisks indicate root words that appeared in various forms, for example, Biodivers* = biodiverse, biodiversity. Note that diverse topics may be represented in a single high-frequency word such as "Area", some words may form phrases (e.g., [species] distribution model[ling]). The word "Species" was excluded from this analysis but was present in 451 of the 521 abstracts. The most common term ("Distribution*") in the analysis occurred in 226 abstracts; the least common term in the analysis occurred in only one abstract.

our understanding and predictive ability (see also _Paleobiogeography_, _Climate-change biogeography_). How did biodiversity respond to past climate changes? And which factors (if any) could explain the outcome in retrospect? How do biotic interactions affect species responses?

The fossil record has provided invaluable evidence about long-term _in situ_ persistence of populations — even in periods of remarkable climate change — as well as migration (both fast and slow; e.g., Lyford et al. 2003). There are also cases of extinction that may be associated with environmental change (e.g., Jackson and Weng 1999). Yet

generalization of responses (in a theoretical-predictive framework) beyond particular case studies is proving elusive, perhaps still due to limited availability of evidence and responses often being individualistic. Greater interdisciplinary engagement and epistemological rigor, together with deeper consideration of taphonomy and natural history, could help paleoecology move forward (Jackson, G14 p.15)[4]. Molecular data and phylogenetic studies also provide invaluable information about macroevolutionary responses to climate change (Condamine et al. 2013). New phylogenetic methods allow clade diversification and

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3 http://www.wordle.net/
4 Where names only are given with page numbers, we are referring to a talk or session for which an abstract can be found in the IBS 2015 Conference Program (herein "G14"), http://escholarship.org/uc/item/5kk8703h

trait evolution to be related to environmental change (Morlon, G14 p.15; Moen and Morlon 2014).

Among the five different biotic responses to past climate change, evolutionary adaptation is probably the least well known. This is largely due to a lack of long time-series of phenotypic and genotypic change through one or more periods of gradual or abrupt environmental change. Resurrection ecology—using ancestors from egg- or seed-banks in transgenerational experiments (Kerfoot et al. 1999)—in combination with spatially-replicated high-resolution temporal reconstruction of past environments shows great potential to fill this gap (Orsini et al. 2013). It is now possible to resurrect individuals of some species (e.g., cladocerans) and to associate observed phenotypes to changes in the genotype or the environment. However, fully exploiting information from the past will require new integrative frameworks. New modeling methods are able to integrate multiple paleo-data, such as macrofossils, microfossils, and ancient DNA, that improve reconstructions, forecasts of species range dynamics, and biodiversity scenarios (Fordham et al. 2014). Taken together, these approaches hold great promise to enhance our current understanding of past biotic responses to climate change (e.g., Moritz and Agudo 2013), which in turn will improve our ability to anticipate future biodiversity dynamics in the Anthropocene.

Return to Table of Contents

Tracking changes from space: Advances of remote sensing in biogeography (A.F. Cord, K.S. He & M.-N. Tuanmu)

Biogeographers and ecologists have long strived to understand the spatial patterns and temporal dynamics of biotas. Geospatial tools developed for biogeography and macroecology enhance monitoring and prediction of species distributions and their changes in space and time (e.g., *Modelling species and ecosystems*). In this age of rapid rates of biodiversity losses and species extinctions, such knowledge has become essential for biodiversity management and conservation. Particularly, the ability to process large volumes of satellite image-ry has allowed us to derive complete spatial coverages of the earth surface with finer resolution, and repeated coverage of field sites has enabled studies of temporal dynamics and change. Novel analytical techniques, increasing computational capacity, enhanced sensor fusion and networking capability, and free access to satellite data (Turner 2014) have made remote sensing one of the most powerful approaches, in terms of time and costs and advances, for observing key biogeographic patterns.

However, remotely sensed data remain underused in biogeography despite their potential for hypothesis testing and exploration of general biogeographic patterns. Especially underused are tools that capture novel biotic and abiotic indicators of land surface, such as very high resolution multispectral and hyperspectral sensors, active radar, and LiDAR. Novel products of these technologies include 30 m forest cover, 30 m land cover, high-resolution mapping of soil moisture (NASA-SMAP), cloud cover at 1 km resolution, and UV-B radiation derived from NASA's Ozone Monitoring Instrument (He et al. 2015). Such datasets provide the opportunity to more deeply understand biodiversity patterns by incorporating water, energy, and carbon-cycle processes into biodiversity modeling (e.g., *Global functional diversity in a data-rich era*). These empirical remote-sensed predictors provide more reliable signals than spatially interpolated layers and avoid inflated spatial autocorrelation, leading to higher model accuracy (Jetz, G14 p. 18). Further, new fusion technology combines information from multiple sensors to increase the quality of data by using complementary information derived from sensors with different spectral, spatial, and temporal resolutions (Asner et al. 2012, Torabzadeh et al. 2014). These developments have been significantly improving characterization of biodiversity patterns (Rocchini, G14 p.17) and paving the road for developing more robust and reliable models for predicting species' distributions (He et al. 2015), estimating biodiversity (Wallis and colleagues, G14 p.17), assessing invasion risks (Bradley, G14 p.18), and evaluating habitat suitability (Tuanmu and Jetz 2014).

Figure 2. Terms related to place that appeared commonly in abstracts submitted for the 7th IBS biennial meeting. Analysis as described in the caption to Figure 1; based on n_w = 1793. Asterisks indicate the word also occurred in plural or other form (e.g., "America*" represents "North …", "Central …", and "South America" as well as the "Americas"; "Ocean*" includes all and any oceans; and so on). The most common term ("Region*") in the analysis occurred in 144 abstracts; the least common term in the analysis occurred once. "MontaneMountain*" represents occurrences of "montane" or "mountain*" which were often used synonymously but are not captured by a single meaningful string of letters.

At the same time, it is important to note the limitations of remote sensing in biogeography research. For example, remote sensing of biogeographic patterns will always be limited to detection—e.g. of biophysical traits, such as build, texture, chemical composition, and shape of objects—based on spectral signature (Schmidtlein, G14 p.18). The temporal window is usually restricted to the last several decades. It is also crucial to estimate and communicate the uncertainties associated with remotely sensed datasets, including maps of ignorance (Rocchini et al. 2013). Full advantage of remote sensing data will not be realized for biogeography, until we also have (1) joint data analysis including the creation of sensor networks and improved interoperability between remotely sensed information and *in situ* biological data collections, (2) ecologically meaningful predictors and application of cross-scale approaches, and (3) targeted coordination of field campaigns and the acquisition of remote sensing data (Turner, G14 p.17).

Return to Table of Contents

Paleobiogeography: The importance of fossil data to biogeography past, present, and future (A.L. Stigall & C.E. Myers)

The importance of analyzing and understanding biogeographic patterns of fossil taxa is increasingly appreciated, not only because they describe paleodistributions and paleoniches, but also because fossil data may provide unique perspectives that enhance biogeographic analyses and our understanding of the general principles behind biogeographic processes. Perspectives from the 'shallow' parts of the fossil record are reasonably widely acknowledged (e.g., *Climate-change biogeography*, *Quaternary legacies*), while the contributions from 'deep time' are just beginning to emerge. In part, the temporal extension of paleontological contributions is due to greater appreciation of the richness and adequacy of the fossil record for many types of biogeographic investigation. Data for certain fossil taxa are as complete as the data available for modern taxa in many respects (Benton et al. 2001). Examples of the rich data available in Paleozoic through Cenozoic strata abound (Stigall, Servais, Kiessling, Badgley, G14 pp.19–20) and in most cases, similar methods can be used to analyze fossil and modern datasets (Denk, Meseguer, G14 p.20). For example, novel uses of fossil data in ecological niche modeling (ENM) and phylogenetic biogeographic analyses show that the rate and type of environmental change directly impacts mode of speciation and the relative degree of niche stability and niche occupation exhibited by species (e.g., Stigall 2014,

Myers et al. 2015). Further, paleogeographic information is useful to constrain paleobiogeographic maps, biodiversity pumps, migration pathways, and oceanographic patterns as far back as the early Paleozoic (Harper and Servias 2013). For example, Kiessling (G14 p.19) identified biogeographic controls of Mesozoic and Cenozoic marine provinciality based on analysis of 1.3 million biogeographic occurrence points acquired from the Paleobiology Database[5].

Another emerging theme is the value added (extra to that added by 'shallow time', see *New insights from past climate changes*) when 'deep' fossil data are incorporated into modern analyses of ecology and biogeography. For example, data from Eocene and Miocene fossils resolved outstanding biogeographic hypotheses surrounding the migration and distribution of Northern European trees (Denk et al. 2002). Integrating fossil occurrence data, phylogenetic biogeography, and ENMs, Meseguer et al. (2015) combined geological connectivity with ENM-predicted ecological connectivity to construct a comprehensive biogeographic history of *Hypericum* over the past 50 million years. Their analysis revealed that regional extinctions contributed to poor performance of biogeographic models using only modern taxa. Similarly, analyses of Neogene mammalian communities demonstrated the importance of environmental changes (e.g., sea-level oscillations) in determining the accessibility of dispersal corridors within environmentally and tectonically active regions, and consequent impact on biogeographic patterns of species richness (e.g., Badgley 2010).

There is much to be gained from both independent and combined analyses of fossil and modern taxa. The added value of multiscale analyses improves our understanding of biogeographic patterns in a diversity of taxa across a broad temporal spectrum – nearly the entire Phanerozoic Era. Consequently, it is crucial that we expand communication and collaboration among modern- and paleo-biogeographers.

Return to Table of Contents

Global functional diversity in a data-rich era (B. Reu & M. Mahecha)

The functional characteristics of plant species, such as their morphological, physiological, or life history traits are a result of adaptation to environmental conditions, biotic interactions, and other eco-evolutionary processes. However, local to regional trait prevalences and variability (i.e., functional diversity) not only reflect responses of organisms to external constraints, but also determine the functioning of ecosystems (Hooper et al. 2012). This raises the question of how to establish a functional biogeography that reveals the role of biological diversity in the functioning of the Earth system (Reichstein et al. 2014). One promising avenue is today's unprecedented data availability. Researchers are investigating various elements underlying functional biodiversity gradients, including plant traits across the globe (Kattge et al. 2011), species occurrences (e.g., using GBIF) and plant distributions (e.g., using Map of Life). This view can be complemented at the same time using global maps of ecosystem functions estimated from integrating station and satellite remote sensing data, such as on gross primary productivity or water use by vegetation (Reichstein et al. 2014; also see *Tracking changes from space*).

A fundamental element of addressing research questions in a data-rich era is to apply cautionary statistical approaches avoiding artifacts in (spatial) data analytics. For example, inference may be limited when comparisons naively rely on spatially contiguous data-sources (Hawkins, G14 p.23). By contrast, there also can be unrealized potential in macroecological data, for example for understanding plant pollination systems across Europe, their drivers (Helm, G14 p.21), and their crucial role in functioning ecosystems. Such approaches may clarify how functional diversity underpins niche processes and challenge the central role of competition (Ricklefs, G14 p.21). Given that biological evolution and historical events determine contemporary patterns of functional diversity, we need to know more about how legacies affect current ecosystem functioning and how a

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[5] http://www.paleodb.org

loss of biodiversity may translate into future ecosystem functioning (Ordonez, G14 p.21). Historical drivers of contemporaneous functional diversity of tree species, for example, affect the productivity across modern European forests (Ruiz Benito et al. 2014). The ultimate goal of exploring data on functional diversity and ecosystem functioning, then, has to be gaining knowledge that can be built into models with predictive capabilities. A new generation of mechanistic models that aim to predict emerging functional diversity patterns may open novel investigations of the link between functional diversity, its drivers and effects on ecosystems, and biogeochemical cycles (Scheiter et al. 2013).

To achieve such a synthesis, though, we are still partly lacking sufficiently well-knit theoretical, experimental, and observational approaches. More effort is needed to exploit the opportunities offered by increasing data availability to improve understanding of how functional diversity affects ecosystem functioning across scales.

[Return to Table of Contents]

Island biogeography (M. Steinbauer)

Island biogeography has again become a stimulating research field with exciting developments and conceptual advances (Fernández-Palacios et al. 2015; Santos et al. 2016). This invigoration is reflected in a new and very successful conference series on Island Biology[6], with the second hosted in the Azores in July 2016 by the newly formed Society for Island Biology and several open initiatives for more intense scientific communication and exchange (like the Global Island Plant Conservation Network[7] or the Island Biology Interest Group[8]). The renewal also is reflected in the emergence of core topics in island biogeography as components of general biogeographic discussions (and vice versa).

One topic, for example, is a long-standing aim of island biogeography — the formal integration of ecological and evolutionary processes into a coherent framework — that has made considera-

ble advances in recent years. Islands are cradles of evolution and probably the best places to understand evolutionary patterns and underlying mechanisms. One of the central questions is whether the evolution of traits is largely idiosyncratic, as in the example of Sulawesi's murid rodent fauna (Esselstyn and colleagues, G14 p.28). Alternatively, convergent (directional/adaptive) evolution may prevail as could be shown for "spiny-leg" spiders on different Hawaiian Islands (Brewer et al. 2015). The temperate ancestry of many Hawaiian taxa that have evolved into (sub) tropical climates, exemplifies that the environmental niche of species can change considerably, a result questioning niche conservatism (Price and Wagner, G14 p.28). Evolutionary pathways are further influenced by dispersal characteristics, which cause systematic differences in phylogenetic structure of island assemblages among taxonomic groups such as angiosperms, ferns, and palms (Weigelt et al. 2015). Fundamental questions, such as why some lineages are more diverse than others, the influence of environment and history and chance on evolutionary processes, and the contribution of different modes of speciation to richness patterns will remain a central focus of island biogeography and of biogeography in general.

A second topic that is stimulating research, on and off islands, is how to better integrate changing environments into existing theories of island biogeography and the increasing awareness of non-equilibrium dynamics. This includes, but is not restricted to, the ontogeny of islands (Whittaker et al. 2007), sea-level fluctuations (Fernández-Palacios et al. 2016) and the temporal dimension of geographic isolation (Papadopoulou and Knowles, G14 p.28). Changing environments in turn elicit consideration of context-dependent adaptations, for example in reaction to changing trophic interactions (Novosolov et al. 2015). The transfer of novel concepts to other isolated systems such as habitat islands (Whittaker and colleagues, G14 p.29) or pumice rafts (Velasquez, G14 p.27) will promote exploration of the bounds

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6 http://www.islandbiology2016.uac.pt/
7 https://www.bgci.org/where-we-work/islandsnetwork/
8 http://www.aeet.org/Island_Biology_Interest_Group_IBIG_309_p.htm (in Spanish): see also http://escholarship.org/uc/item/7h9394np

of island biogeography and its integration with biogeography in general. Active connection with community ecology and succession theory (considering differences in temporal dimensions) are at the forefront of island biogeography, as is the integration of functional ecology (Warren et al. 2015, Santos et al. 2016). Island biogeography is increasingly an integrative field where several different disciplines exchange ideas and advance our understanding of nature.

Return to Table of Contents

Climate-change biogeography (J. Blois)

An age-old pursuit in biogeography is trying to understand associations between climate and biodiversity as well as the particular mechanisms or processes underlying those associations. This pursuit now transcends taxa (Figure 3), time-scales (see *New insights from past climate changes*, *Paleobiogeography*), approaches, and disciplines (Figure 1), and studies in climate-change biogeography reflect this diversity.

Climate impacts on species have been detected in the past and the present, and are expected in the future, and climate itself is experienced by species at many different timescales. At the shortest scale, that of individual events and their transient or seasonal impacts, migratory birds responded to extreme warming in March 2012, which was associated with subsequent decreases in productivity during the breeding season (La Sorte et al. 2014). La Sorte (p.103) reported that several species showed increased occurrences during warming, but generally no negative consequences of the event were detected in subsequent seasons. At the other end of the timescale, climate change likely affected evolutionary processes; elevated extinction rates were related to the Mid-Miocene Climatic Optimum in Indian geckos (Agarwal and Karanth 2015). Patterns at both scales might be associated with niche breadth, and Myers and colleagues (p.31) used simulations to show that the number of environments in which a species existed was the primary control on speciation and extinction, with dispersal ability only a minor component. Furthermore, evolutionary processes are likely to be affected by

climate change in the future, with both immediate practical implications and long-term effects of changing evolutionary processes. González-Orozco and colleagues (p.31) demonstrated that such climate impacts would influence phylogenetic lineages and the evolutionary potential of species (e.g., Mishler et al. 2014). Likewise, by first modeling then projecting temporally the climate envelope of *Aedes albopictus*, a vector for dengue, Jaeschke and colleagues (p.32) found that risk of disease transmission may increase in the future because of warming climates, fewer constraints on egg survival, and shorter incubation periods at higher temperatures.

Despite such advances, theoretical and technical questions about quantification of climate change and attribution of biodiversity responses remain. In simulations, even medium levels of population variability caused inaccurate detection of abundance or range-shift responses to climate change (McCain and colleagues, G14 p.30). Although many of the mammal species previously found to have experienced range shifts (e.g., McCain and King 2014) are generally species that experience lower population variability, so their inferred responses to climate change are likely to be correct, population variability should be accounted for in future attribution studies. Another question persists around whether the spatial and temporal relationships between climate and abundance in birds are interchangeable. Despite previous work showing that relevant climate variables are consistent in predicting bird species distributions across space and time (Barbet-Massin and Jetz 2014), the effectiveness of space-for-time substitution (i.e., using a climate–abundance model built on spatial patterns to predict temporal patterns of bird abundance) was poor.

Taken together, one fruitful area of research that emerges is determining how climate-change responses link across timescales — under what conditions are short-term climate events important and are there particular types or durations of climate change that will translate into lasting impacts on ecological and evolutionary processes? Despite decades of research, there are

Figure 3. Terms related to taxa that appeared commonly in abstracts submitted for the 7th IBS biennial meeting. Analysis as described in the caption to Figure 1; based on n_w = 1189. Asterisks indicate the word also occurred in plural or other form (e.g., "Aves*" represents also the use of "Bird" and "Birds"; Flora includes "Floras" and "Floristic"). The most common term ("Plant*") in the analysis occurred in 131 abstracts; the least common term in the analysis occurred once. As noted in Figure 1, the word "Species" was excluded from this analysis but was present in 451 of the 521 abstracts.

still unresolved questions about attribution and detection of climate-change impacts.

[Return to Table of Contents](#)

Gradients, range limits, and beta diversity (C. Beierkuhnlein)

Species richness is an important attribute of ecosystems and communities, but describes only a subset of the biodiversity attributes needed to understand spatial gradients at large scales. Species' traits and our limited taxonomic knowledge substantially influence estimates of alpha-diversity and thus interpretation of patterns and processes. In recent years, moreover, various approaches and diverging views on beta diversity have developed, adding methodological and terminological confusion (Chase, G14 p.33; see also Jurasinski et al. 2009, Tuomisto 2010). Yet even if there is no "true" single measure for beta-diversity, we still need to be able to quantify dissimilarity in species and traits between ecological units and to relate these compositional data to ecosystem functioning.

Beyond the classic sampling problem of grain and extent, which is far from being solved

when spatial gradients are investigated (Steinbauer et al. 2012; see also *[Biodiversity hotspots](#)*), spatial patterns of biodiversity are manifest in qualitative, quantitative, and functional traits. Recently, using phylogenetic diversity (PD) as a measure for the relatedness of taxa in communities has become widely applied for large data sets (e.g., Nunes et al. 2015), which makes sense only if it can be disentangled from mere species richness (Nipperess and Matsen 2013). Multidimensional niche similarity between species pairs can be tested (Nunes, G14 p.34) and may indicate both species richness and diversity of functions.

A related, fundamental, challenge also remains in detecting the limits of species pools. Drivers of species pools—such as geographic area, evolutionary age, and immigration and diversification—are scale dependent. Thus, answers to the fundamental question of whether current ecological constraints are placing upper limits on regional diversity also may be scale dependent (Cornell 2013). In this context, the climatic drivers of variation in diversity are badly understood. The Metabolic Theory of Ecology (Brown et al. 2004) is fo-

cused on energy, but the role of water availability and its interaction with energy should receive more attention (Vetaas, G14 p.36). Answers may be possible using novel probabilistic approaches that are emerging to identify how different dispersal and environmental constraints influence species pool size and compositional turnover (Karger, G14 p.35).

In addressing these challenges, perhaps in the guise of searching for a grand unifying theory in compositional biogeography, we may find more common ground through practical approaches such as the design of nature reserves (Tjørve, G14 p.33) and increasing availability and application of "big data" (Chiarucci, G14 p.34).

[Return to Table of Contents](#)

Conservation biogeography (J.C. Axmacher)

Conserving global species richness and associated genetic resources is an overarching aim uniting many fields of biogeography. Aspects of 'conservation biogeography' therefore are also addressed elsewhere in this paper (e.g., *Biodiversity hotspots*, *Climate-change biogeography*, *Global functional diversity in a data-rich era*, and *Gradients, range limits, and beta diversity*). Three of these appear particularly relevant in the context of this horizon scan: functional traits, large-scale patterns, and climate change.

Growing interest in species' roles in ecosystem functioning and the provision of ecosystem services (Diaz et al. 2013) means that analysis of the geography of species' traits increasingly complements research into patterns of species richness. A study of tropical coral reef fishes has revealed high concentrations in certain traits, including specific size ranges, activity periods, mobility, and activity periods, and schooling patterns. Simultaneously, many 'rare' traits are represented by single species (Mouillot et al. 2014). Globally, spatial fish trait turnover appears particularly pronounced in the Atlantic realm (Villeger and colleagues, G14 p.40). In tropical forest birds, distinct trait variations indicate shifts from competition- to colonization-dependent communities with decreasing size of forest habitat fragments (Ulrich and colleagues, G14 p.40). Placing functional traits

into a phylogenetic context could prove instrumental in evaluating intrinsic extinction risks in mammal species (Dobrovolski and colleagues, G14 p.42), including for species listed as data deficient.

Meta-analyses of large-scale distribution and diversity patterns—using species distribution data increasingly available in our 'big data' era—are replete with potential problems and biases, while also showing great potential. Despite detailed data on vertebrates, regional socioeconomic constraints, and available local expertise often remaining unevenly distributed or generally inadequate (Meyer and colleagues, G14 p.152), links between large-scale species richness and environmental factors can highlight conservation priority areas at least for well-known taxa. Yet, data-rich analyses raise methodological concerns, with uses of different measures of land-use intensity measures potentially altering the modeled associations between intensive agriculture and the diversity in endemic vertebrate taxa (Kehoe and colleagues, G14 p.41).

Species' responses to climate change also are multifaceted. Species' ability to evade predicted temperature rises through migration commonly are limited by natural boundaries (Burrows et al. 2014) and habitat fragmentation by roads, cities and agricultural areas across the USA (McGuire and colleagues, G14 p.41). Often, species will need active help to track predicted climate change, with new migration corridors providing one potential solution.

These cases exemplify substantial progress in our discipline through increasingly available 'big data' on vascular plant and vertebrate species distributions and traits in combination with advances in data processing and analysis. Simultaneously, they indicate two substantial gaps. The needs of ~95% of known animal species, including virtually all invertebrates, are currently significantly underrepresented in our field. Additionally, the divide between conservation biogeographers, who are using increasingly sophisticated analytical methods and models, and the conservation practitioners and politicians addressing conservation issues on a daily basis, appears to be widening. A strong engagement of our community in IPBES

(Opgenoorth and Faith 2013) could represent a possible solution to these issues.

Modeling species and ecosystems (F. Rodríguez-Sánchez)

Species distribution modeling (SDM) has been a burgeoning field in the last decade, and it continues to be so. In the last few years many new approaches have been developed attempting to account for biotic interactions, dispersal limitation, intraspecific variation in climatic tolerances, as well as uncertainty and biases in species' distributions and climate data. While species' distribution data remain too limited for many taxa, calling for strengthening field data collection and aggregation (Meyer and colleagues, G14 p.152), improved high-resolution climate and land-cover layers of global extent are being derived from remote sensing (see *Tracking changes from space*), which can greatly improve accuracy of SDM projections.

One promising way to overcome data limitations is exploiting phylogenetic information to model data-deficient species based on better known taxa (Morales-Castilla and colleagues, G14 p.43; Jetz and Freckleton 2015). Indeed, great advances have occurred in incorporating species co-occurrence patterns to better model single taxa, species assemblages or even entire biomes: from joint SDMs (Wharton et al. 2015) to community models (D'Amen et al. 2015), to global vegetation models (DGVMs; Scheiter et al. 2013). Further, Petr Keil and colleagues (Keil et al. 2013, Keil and Jetz 2014) have developed hierarchical Bayesian models to downscale species' distributions and species richness to fine spatial resolutions, which bring the relatively coarse data often available much closer to the local scales most useful for ecological research and management.

Thus, we have seen great progress in the last two years, and there are signs that the explosion of new methods and data will continue in coming years. There is a fast-growing collection of R packages that facilitate the incorporation of these new approaches into ecological modelers' toolboxes. Yet the rate of proliferation of new

Figure 4. Terms related to time that appeared commonly in abstracts submitted for the 7th IBS biennial meeting. Analysis as described in the caption to Figure 1; based on n_w = 820. Asterisks indicate the word also occurred in plural or other form (e.g., "Histor*" represents the use of "history", "historic", and "historical"). The most common term ("Histor*") in the analysis occurred in 114 abstracts; the least common term in the analysis occurred twice. The ratio of terms relating to Pleistocene and earlier times versus Holocene and later times (excluding the "future") is approximately 11:9.

methods is also a challenge, and comparative benchmarking studies become strongly needed to try to find out their respective strengths and weaknesses. Results from multi-model comparisons are encouraging in the sense that some models (or model ensembles) perform consistently well and can be trusted in most situations (Naimi and colleagues, G14 p.44; Zurell and colleagues, G14 p.45 [Zurell et al. 2016]). But at the same time no model consistently outperforms the others (Qiao et al. 2015): all have trade-offs, which calls for thoughtful consideration of the particularities of each study before choosing any of the available approaches.

Return to Table of Contents

Phylogeography (A. Papadopoulou)

Phylogeography is experiencing a transformation. Rapid advances in sources of data and analytical tools, as well as increasing integration with other subdisciplines, are opening up new opportunities to address fundamental questions in biogeographic research that seemed unattainable a few years ago.

In the era of high-throughput genomic sequencing, phylogeographers are seeking the most efficient and inexpensive protocols for obtaining thousands of orthologous loci from the genomes of non-model organisms and moving away from the limitations of the traditional phylogeographic markers and the use of gene-trees (McCormack et al. 2013). One such protocol, the ultraconserved elements (UCEs) strategy of sequence capture, originally developed for deep-level phylogenomics, is now also applied to phylogeographic timescales (Smith et al. 2014) and allows reconstruction of highly resolved species-trees for cryptic species complexes and recent island radiations such as that of lizards in Southeast Asia (Brown, G14 p.47).

Whole-genome sequencing approaches are also being adopted for refining specific phylogeographic questions, especially questions related to adaptation. A combined approach of whole-genome sequencing with thermal tolerance experiments and traditional markers from historical specimens (Krehenwinkel and colleagues, G14 p.46) demonstrates how the Northern European range expansion of a wasp spider was enabled by a climatic niche shift, associated with a recent genome-wide admixture of Eastern and Western Palearctic lineages, which presumably provided the genetic material for rapid climatic adaptation (Krehenwinkel and Tautz 2013).

Further insights into the key challenge of understanding demographic responses to climate change are provided by reconstructing past population dynamics using ancient DNA of Holarctic mammals (Florez-Rodriguez and colleagues), where taxon-specific differences in demographic trends are associated with ecological traits. Moreover, testing alternative paleodemographic scenarios by integrating Ecological Niche Modelling with Approximate Bayesian Computation can help elucidate the extent of niche conservatism in Palearctic bats and predict future losses of genetic diversity due to climate change and habitat loss (Razgour et al. 2013, 2015).

Another major theme is the use of molecular phylogenies for understanding how biogeographic and/or ecological processes drive diversification patterns in biodiversity hotspots (see also *Biodiversity hotspots*). Within this context, the Philippines archipelago offers a model island system for studying the evolutionary processes of diversification (Brown et al. 2013), with the example of the plant genus *Ixora* showing how several dispersal and vicariance events have led to multiple independent radiations within the archipelago (Banag and colleagues, G14 p.47). Both biogeographic and ecological processes are important for the diversification of neotropical ferns, where a combination of migration events across the continent and ecological adaptation to different soil types within Amazonia drive speciation patterns (Tuomisto and colleagues, G14 p.48).

While such model systems will continue to play a major role in biogeographic research, it remains to be seen how the unprecedented resolution offered by genomic data and increasingly integrative analytical approaches will transform the way we think about phylogeography in the near future.

Return to Table of Contents

Quaternary legacies (D. Gavin)

The patterns of biodiversity on the planet today are the result of past events that have occurred across all time scales (e.g., *Paleobiogeography*, *Climate-change biogeography*, *Invasions*), but the climate and sea-level changes of the Quaternary and Holocene have left a particularly distinct signature. The colder (and often drier) period of the Last Glacial Maximum (LGM), and glacial episodes prior to it, caused the contraction of temperate taxa into smaller geographic ranges (refugia), and now modern patterns of endemism, disjunction, and co-distribution can be traced to such refugia (e.g., Hultén 1937; Braun 1955). New studies of fossil records and genetics are continuing to amass primary data to help reveal the significance of the Quaternary glacial cycles on modern biodiversity.

A classic example of Pleistocene refugia is the contraction of temperate-adapted species into southern Europe during glacial episodes. European beech is a well-studied species for which genetics, fossil records, and paleodistribution models all point to refugia in southern Europe and possibly in the Carpathian Mountains. However, the rich herbaceous diversity associated with beech forests has not received similar attention: the fossil record of these species is sparse, there are few phylogeographic studies, and the spatial pattern of beech-habitat taxa has not been thoroughly studied. New data from the vegetation plots of the Braun-Blanquet Project now reveal that a large diversity of narrowly distributed herbaceous species cluster closely to the refugia locations for European beech (Willner and colleagues, G14 p.51).

While many warm-adapted species had restricted distributions during the LGM, many cold-adapted species were more widespread in the past and persist in modern-day refugia. Most likely, a diverse mixture of temperate and boreal-adapted species existed during the LGM in the Carpathian Mountains of east-central Europe, for which the southern Siberian mountains (Russian Altai) provide a good modern analog (Chytry and colleagues, G14 p.50). Including several components of the biota (vegetation, mammals, and terrestrial snails) and using the environmental niches of modern pollen to suggest the distributions of analogous conditions in the past greatly narrows the interpretation of glacial environments (Magyari et al. 2014).

Growing databases of fossil records[9] are fueling a renaissance of paleobiogeography. For example, within mountainous regions characterized by sky islands, Late Pleistocene vegetation change provides a dynamic context for island-biogeographic processes. Detailed pollen records from the Andes show substantial elevation change in ecotones through time, resulting in changing connectivity and island sizes for the cold-shrub biome (Flantua and colleagues, G14 p.49). Although this biome is now at only 5% of its most common Pleistocene extent, there have been few known extinctions. Similarly, although abrupt climate changes of the Younger Dryas cannot be excluded as a major contributing cause of the North American megafaunal extinction, combining paleoecological and archeological databases shows substantial intervals between the times of human first occurrences and megafaunal last occurrences, suggesting sufficient duration for humans to contribute to megafaunal extinction (Davis and colleagues, G14 p.49).

While the cause of the North American megafaunal extinction remains contentious, the event provides an opportunity to study the community-composition consequences of the loss of large consumers and predators. A detailed 20,000-year record of mammal assemblages from a cave in Texas reveals high turnover during both extinction and climate change, changes in species associations, and changes in the body-size distribution (Smith and colleagues, G14 p.50). Detailed records from single sites may also help identify extinctions that otherwise would have been left undetected. Ancient DNA from a small jawbone of a rodent evinces the Holocene extinction of a clade in the genus *Ototylomys* (Gutiérrez-García and colleagues, G14 p.49; Gutiérrez-García et al. 2014). Taken together, these studies reveal how the Quaternary provides rich context for understanding

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9 e.g., Neotoma Paleoecology Database, www.neotomadb.org; Latin American Pollen Database.

processes of extinction, persistence, and adaptation.

Invasions (B. Bradley)

Invasion ecology has long suffered from biases in geography (with Africa and Asia underrepresented) and taxonomy (Pyšek et al. 2008; see also *Conservation biogeography*, Figures 2, 3). But, spatial analyses of invasion are following the broader trend in biogeography towards compiling more consistent, broad-scale datasets (e.g., *Quaternary legacies*). By turning many smaller datasets into 'big data', invasion biogeography may soon overcome some of these biases and identify novel invasion patterns at regional to global scales.

Although lists of non-native flora have been assembled globally (Randall 2012), these data are not spatially explicit. A new global database of establishment of over 11,000 alien plant species, called the Global Naturalized Alien Floras (GloNAF; van Kleunen et al. 2015), identifies non-native species richness at national or sub-national levels. Winter and colleagues (p.54) highlight the importance of temperate Asia as a primary donor of alien species to the global pool.

At regional scales, invasive species occurrence records are biased by differences in monitoring and reporting. Forest Inventory and Analysis (FIA) plots highlight invasion patterns using a more consistent spatial dataset (Oswalt et al. 2015). Fei and colleagues (p.195) showed that invasions initially colonize via long-distance leaps across human population centers and only later infill their range. This pattern is consistent with recent findings that invasive plants are widely dispersed across their invaded range, but have low range infilling compared to natives (Bradley et al. 2015).

Studies of marine invasions are underrepresented in invasion ecology. Analysis of non-native tunicate establishment across 11 sites of coastal South Africa showed expanded range and abundance of non-native tunicates over 50 years (Rius et al. 2014). Rius and colleagues (p.54) compiled novel broad-scale datasets on seawater temperatures and shipping volume from historical shipping records, to identify important predictors of marine invasion.

Big datasets describing the distribution of invasive species and spatial predictors of invasion are time intensive to compile but are critical for overcoming the geographical and taxonomic biases that pervade invasion ecology (Pyšek et al. 2008). Ongoing analyses of regional and global datasets will continue to uncover important invasion patterns, which are essential for identifying risk and improving broad-scale management.

Latitudinal biodiversity gradients (R. Jansson)

The understanding of latitudinal diversity gradients has advanced rapidly during the last decade as more geographic and phylogenetic data and
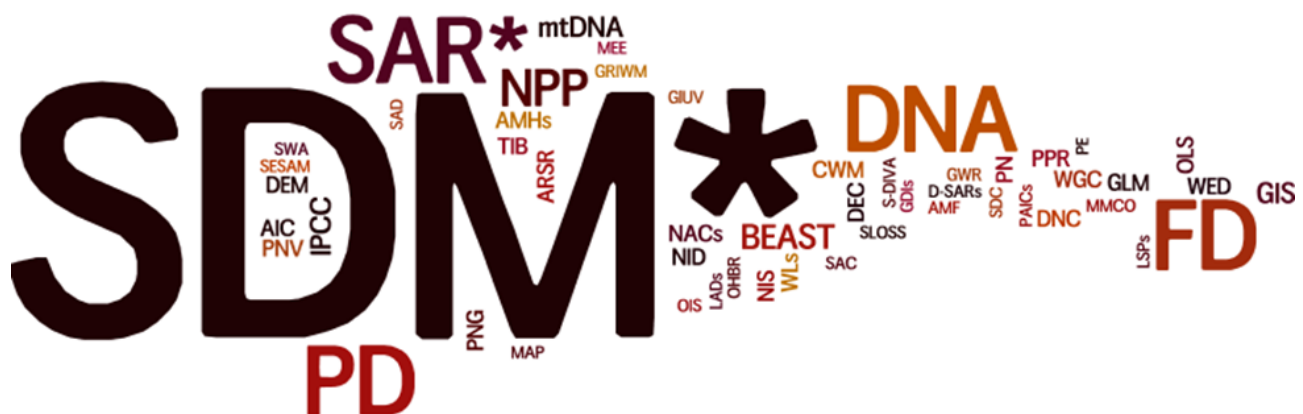
Figure 5. Abbreviations appearing commonly in abstracts submitted for the 7th IBS biennial meeting. Analysis as described in the caption to Figure 1; based on n_w = 325. Acronyms that occurred in fewer than three abstracts were excluded from the analyses. Asterisks indicate the word also occurred in plural form. The most common term ("SDM*") in the analysis occurred in 60 abstracts; the least common term in the analysis occurred in three abstracts. Comparison with Figures 1–3 emphasizes key topics considered during the 7th IBS biennial meeting.

methods have become available (see also *Gradients, range limits, and beta diversity*). Integrating these approaches is key, for example, in revealing that while two major clades of passerine birds in the New World both peaked in diversity in the tropics, they arrived there along different evolutionary trajectories (Kennedy, G14 p.56). The Suboscines colonized over 40 Mya and first diversified in tropical South America, with more derived species found at progressively higher latitudes, whereas the Oscines entered through North America much later, with more derived groups having progressively more southern ranges, and a burst of diversification when reaching the Andes and the Amazon (Kennedy et al. 2014).

A contentious issue in the mechanisms behind species richness gradients is whether species richness is set by processes limiting the number of locally coexisting species, or whether species richness is simply the sum of species tolerating environmental conditions in an area (Boucher-Lalonde et al. 2014). Based on the tolerances to mean and maximum temperature and precipitation of each mammal species in the New World, many more species were expected to co-occur in grid cells with higher mean annual temperature. A shortfall in the number of co-occurring species indicates top-down control of species number per grid cell, or that many species are constrained by variables other than temperature and precipitation (Boucher-Lalonde, G14 p.57). These other variables may include history and biotic interactions, as the relatedness of species co-occurring within the geographic range of a focal species, measured as the "phylogenetic field metric", shows that co-occurring mammals were phylogenetically clustered in the New World, but overdispersed (i.e., co-occurring species were distantly related) in the Old World (Villalobos et al. 2013), consistent with the findings of Davies and Buckley (2012). Fruitful insights may be gained by comparing gradients in latitude and elevation; not only do organisms perceive mountain passes to be higher in the tropics because of lower climatic tolerance (Janzen 1967), but there is also a latitudinal gradient in the absolute height of mountain ranges (Steinbauer and colleagues, G14 p. 56; Steinbauer et al. 2016).

These factors interact with increasing plant endemism with elevation to contribute to high plant species richness at low latitudes. Steinbauer and colleagues also speculated that the opportunities for population isolation offered by mountain ranges might elevate tropical speciation rates.

In most clades, the high proportion of species occupying tropical latitudes can be explained by one or a combination of three factors: tropical origins, high speciation and low extinction rates (e.g., Wiens and Donoghue 2004, Rolland et al. 2012), but explaining why origination and diversification rates are higher in the tropics is a future challenge. Moreover, the frequency of lineages expanding their ranges to new latitudinal zones varies among clades (Jablonski et al. 2013, Kennedy et al. 2014), but the nature of this variation and its potential causes require much further study.

Return to Table of Contents

Biodiversity hotspots (J. Dengler)

Myers (1988) defined "biodiversity hotspots" originally as those areas that are exceptional in concentration of species, levels of endemism, and degrees of threat. Myers et al. (2000) then specified that, to qualify as a "biodiversity hotspot", an area must contain at least 1,500 vascular plant species as endemics. However, this definition lacks reference to a grain size and thus ignores the well-known fact that endemic richness, like total richness, increases with area, but with an exponent of the power law larger than unity (Storch et al. 2012). Despite this oversight, "hotspots" became popular in biogeography, and the term risks becoming a mere buzzword to label study areas 'interesting' irrespective of whether they meet specific criteria.

One positive exception was a comprehensive biogeographic analysis of a large vascular plant family (Cactaceae), including high-resolution diversity maps for two grain sizes (100 km² and 2,500 km²; Barthlott and colleagues, G14 p.203). Analyzing these data for all species and for narrow-ranged species allowed the authors to delimit biodiversity hotspots consistently and without bias. Other studies making meaningful contributions showed that often diversity patterns (and

thus hotspots) of major taxa are discordant (Axmacher, G14 p.58), which renders the frequent concentration of biodiversity research to terrestrial vertebrates and vascular plants problematic. Such conflicts may be resolved in part by multiple metrics of geodiversity that can explain where hotspots of biodiversity occur (Sejmonsbergen, G14 p.59).

Fifteen years after Myers et al. (2000), the biodiversity hotspots discussion is in clear need of terminological and methodological refinement. For example, biodiversity rankings or hotspot selections based on such fundamentally flawed approaches as ignoring area when comparing diversity of differently-sized entities or dividing richness by area (as happens frequently, even in high-rank journals) should be abandoned. It has long been established in biogeography that practically all diversity components scale with area and do so in a non-linear manner. The aim thus should be to establish global average diversity-area regressions and to identify hotspots as those geographic units of any size that show the biggest positive deviations (residuals in log space) from the average, as proposed by Bykov (1979) for the fraction of endemics and by Hobohm (2003) for the richness of species and endemics. This is a non-trivial task because of the limited and biased availability of data for most taxa, the strong differences in regression functions between ecozones (Gerstner et al. 2014) and the scale-dependence of their slopes (Storch et al. 2012). Deriving such global regressions would allow transparent, gradual ranking of areas of any size along a gradual scale from "very cold" to "very hot" for the different components of diversity in various taxa. Even then it might happen that one area is a hotspot for one grain size but not for another; for example, Wilson et al. (2012) demonstrated that for areas smaller than 100 m² some temperate grasslands are hotter hotspots for vascular plants than tropical rainforests. Resolving these issues is of paramount importance to both 'basic' and 'applied' biogeographic disciplines (e.g., *Conservation biogeography*, *Latitudinal biodiversity gradients*, and *Gradients, range limits, and beta diversity*).

The Grand Subject (L. Heaney)

Biogeography is practiced on an impressive array of phenomena (e.g., see the preceding symposium summaries); but there is great merit in recognizing both the types of data that we do collect, analyze, and interpret, and those that we do not. An impressive example of the latter is the virtual absence of attention given to one of the most pervasive aspects of the natural (and anthropogenic) sphere: the sound-scape (Lomolino et al. 2015). Personal experience leads us all to immediately accept that different habitats and environments have distinctive auditory components, yet almost no research has been conducted on this topic, leaving a new and intrinsically appealing broad topic for study by biogeographers.

The scale at which we choose to study any phenomenon may influence the result we measure. While geographic scale is widely recognized as an important factor in the outcome of analyses of evolution and ecology, much less attention has been paid to the equally critical impact of phylogenetic scale (Graham and colleagues, G14 p.52; e.g., Graham et al. 2016). It has become increasingly apparent that, within limited phylogenetic scales, patterns (and correlations) are often different, sometimes opposite, from those that are evident at larger phylogenetic scales; analyses that explicitly investigate phenomena on multiple phylogenetic scales may be crucial. As robust phylogenies become increasingly available, such analyses should contribute increasingly important perspectives on the geography of nature.

Nonetheless, as data increase and methods accommodate studies of different scales, we will benefit from being frank about problems with especially popular analyses (e.g., De Camargo and Currie 2015). From the perspective of the long-serving Editor in Chief of *Global Ecology and Biogeography*, David Currie (G14 p.52) believes that macroecology often is beset by weak inference. The problems include the development of hypotheses that are weakly supported by statistical analyses; over-emphasis on P-values and under-emphasis of correlation (r or equivalent) values; and the rarity with which the resulting hypotheses are subsequently tested. These are great challeng-

es for all biogeographers, calling for critical self-assessment by authors and heightened attention by reviewers and editors.

A topic of great concern to all biogeographers is the incompleteness of our knowledge about the extent and distribution of biodiversity, and the existence of geographical bias in the knowledge gap (e.g., Hortal et al. 2015). As discussed by Hortal and colleagues (G14 p.52), novel ways exist to conceptualize our ignorance (a nec-

essary but necessarily difficult proposition), and some novel analytical approaches to investigate the spatial and temporal distribution of these biases are available. Biases and ignorance surely are among the most frequently encountered impediments to biogeographic research, and—only in part because they are the flip-side of opportunity—are deserving of much additional attention.

Return to Table of Contents
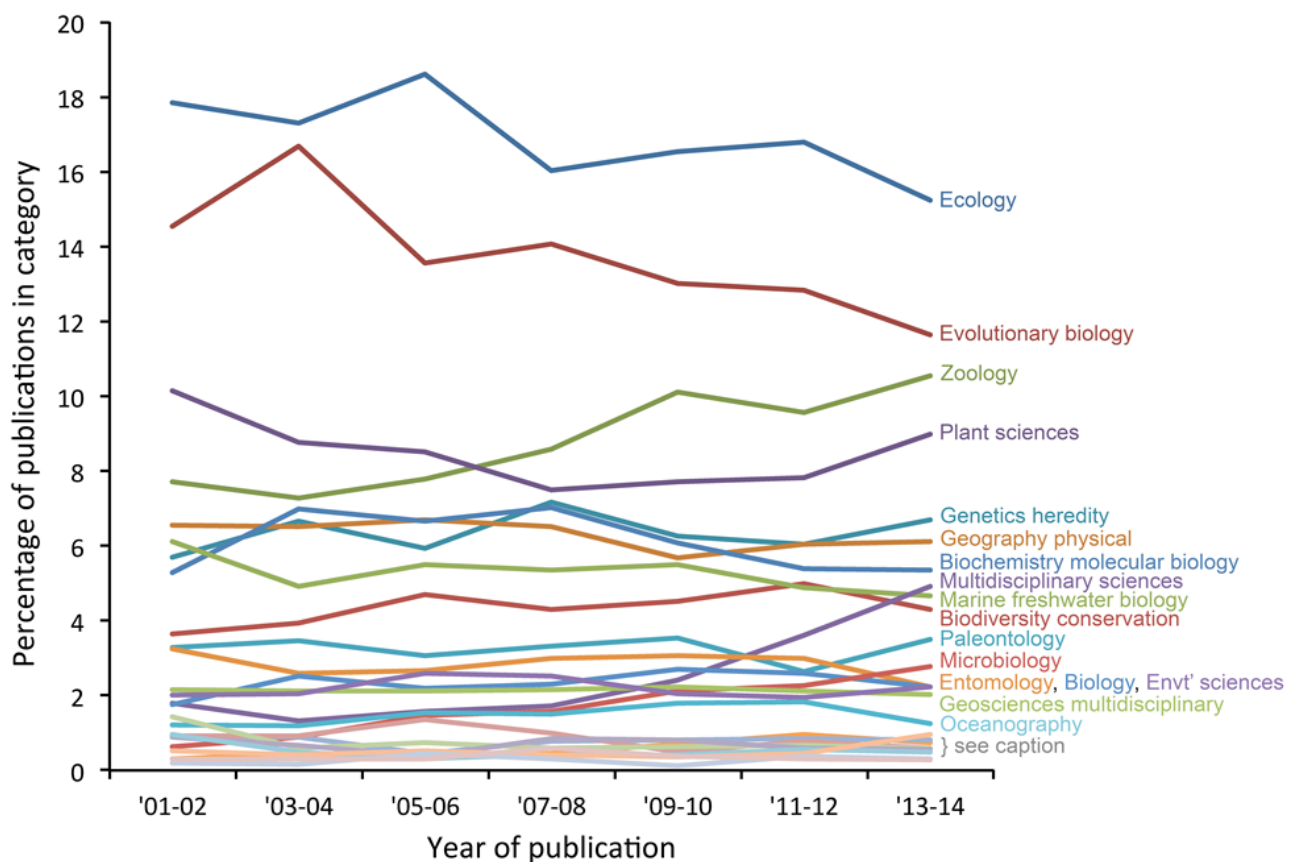
Figure 6. Percentage of biogeography publications in biennial periods since 2000 classified into each of 26 research categories by Thomson Reuters in the Web of Knowledge database. Articles were identified by the topic word search "biogeography" in the Science Citations Index–Expanded database. The categories shown are those present in the same analysis for the first horizon scan of biogeography (Dawson et al. 2013) and represent the top 26 categories in 2011–2012 that also were recorded in all prior biennial periods. The least frequent nine categories from more to less common, are: geology, mycology, biotechnology applied microbiology, ornithology, parasitology, fisheries, forestry, anthropology, limnology. The analysis for 2013–2014 includes 4588 papers published as of 30 November 2014 (more recent analysis is not possible because Thomson Reuters subsequently changed their research categories, e.g., lumping Environmental Sciences and Ecology). The number of publications in each preceding biennial period (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%) (Dawson et al. 2013). Note that categories are journal-level metrics, not article-level metrics. Simply for context, the four main biogeography journals are categorized as follows: *Diversity and Distributions* = biodiversity conservation & ecology; *Ecography* = biodiversity conservation & ecology; *Global Ecology and Biogeography* = geography (physical) & ecology; *Journal of Biogeography* = geography (physical) & ecology.

Synthesis

Emerging themes

This horizon scan of biogeography is only the second, following just two years after the first. Hence, changes in the discipline, and potential causes, are challenging to discern. Nonetheless, we explore and call attention to apparent developments and trends, novel and unexpected issues, and matters at the margins of biogeography. Our goal is to illustrate what is constant, trending, or in perpetual flux and which, together, present a suite of opportunities and challenges. We consider three principal lines of evidence: narratives and word clouds summarizing the 2015 IBS symposia and meeting (Figures 1–5), recent publication trends in biogeography (Figure 6), and identification of 'research fronts' (Table 1). In the context of our horizon scan, several key questions arise, for which the answers are often elusive. These questions include: Which current trends may represent emerging disciplinary themes? What data or research questions are driving these trends? Do any trends foretell a long-term change in the discipline, for better or for worse (or both)?

The place of biogeography in science: evidence from IBS symposia – Biogeography is practiced and classified as a largely ecological and/or evolutionary science (Rosvall and Bergstrom 2008, Cox and Moore 2010, Thomson Reuters[10]). Studies of current or recent 'ecological' phenomena outnumber deeper 'evolutionary'—phylogenetic and paleontological—timescales (see the symposium summaries, also Figures 1, 6); however, the bias toward neontology has been less obvious at recent IBS meetings (Dawson et al. 2013; Figure 4) than in the discipline as a whole. Several areas of investigation are actively exploring intersections between these traditionally disparate timescales (see e.g., *Climate-change biogeography*, *Island biogeography*, and *Phylogeography*). Likewise, paleobiology, including anthropology, is taking on multiple roles and ages ('deep' *Paleobiogeography* and 'shallow' *Quaternary legacies*). Biogeography

is still characterized in large part by its traditional affinities with zoology, plant sciences, genetics (and molecular biology), and physical geography, reflecting the original (circa 1892) definition of the discipline—the "branch of biology that deals with the geographical distribution of plants and animals" (Oxford English Dictionary)[11]. However, importantly, these categories are increasingly integrated, as within studies of biotic interactions, traits and functional diversity, and properties of ecosystems (see e.g., *Global functional diversity in a data-rich era*, *Modelling species and ecosystems*, *Quaternary legacies*, *Conservation biogeography*, and *Tracking changes from space*). Traditional disciplinary temporal and taxonomic boundaries within the discipline are being overcome, as are limitations on the spatial resolution and geographic range considered in analyses (see e.g., *Tracking changes from space*). Thus while the place of biogeography in science has in large part been relatively unchanged for more than 120 years, 'grand challenges' of critical importance for humanity have forced the discipline's evolution; therefore, one might best view biogeography's position as adapting and advancing with its surroundings, perhaps like the Red Queen running just to keep up, and becoming increasingly interdisciplinary as a result.

Existing publication trends in biogeography – The seven core categories of biogeography—botanical, ecological, evolutionary, genetic & molecular, geographic, zoological (Figure 6)—have been among the eight most well-represented categories since 2000 and the top seven post-2002[12]. However, there has been a small, consistent decrease in the representation of journals in these categories. Together, they accounted for ~68% of biogeography publications between 1999–2006, ~66% between 2007–2012, and ~65% in 2013–2014 (Figure 6; Dawson et al. 2013). This trend does not represent a decrease in the number of 'biogeography' papers being published overall – as in most disciplines, more papers in biogeography

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10 see archive.sciencewatch.com/about/met/fielddef/
11 http://www.oed.com/view/Entry/19209?redirectedFrom=biogeography#eid
12 The start-point of analyses was arbitrarily chosen to coincide with the establishment of IBS (Dawson et al. 2013).

are being published every year (Dawson et al. 2013; Whittaker 2014). Rather, the trend appears to represent a shift in the distribution of biogeography papers among core areas and into non-core categories.

The slight downward trend is being driven primarily by substantial decreases (~5%) in the categories of ecological and evolutionary biogeography, which are being offset largely by an increase (~3%) in zoology. Given that five of the seven core categories likely have defined the discipline of biogeography since its inception, we might not think too much of meanderings such as the recent rise and fall of molecular biology or the recent fall and rise of plant sciences (Figure 6); such 'perpetual flux' may reflect categorization of the journals in which articles are published as well as the topics of the underlying studies. However, to the extent that journal-level and article-level metrics are concordant, with each other and with patterns in other datasets (e.g., Figures 1–3), these changes in the practice of biogeography should interest us. They may be associated with changes in natural phenomena, funding cycles, public interest, ground-breaking discoveries, or more. Moreover, small changes necessarily presage (but may not ineluctably become) major changes. For example, genetics and molecular biology, which must have been absent in the 1890s when the term "biogeography" was coined, now represent 12% of biogeography publications, reflecting such significant changes as the 1940's *Modern Synthesis* in evolutionary biology (Mayr and Provine 1998) and the origin and emergence of phylogeography in the early 1980s through 1990s (Avise 2000, Riddle et al. 2008, Whittaker 2014).

Of the overall long-term trends (2000–2012) noted in the first horizon scan (Dawson et al. 2013), six continued in the same direction in 2013–2014. Decreasing trends for ecology, evolutionary biology, and marine and freshwater biology persisted; increasing trends for plant sciences, zoology, and microbiology endured. A small and recent increase is seen for geology (+0.6% since 2009-2010), which reflects increased analysis of 'deep time' paleobiogeography. By far the strongest new trend, expected but not yet observed in 2013, is the rapid rise of multidisciplinary sciences (+3.6% since 2003-2004 [+2.8% since 2000]; Figure 6; see also Whittaker 2014), which mirrors an emphasis of almost all IBS sessions on increasing interdisciplinarity.

To explore the rise in inter/multidisciplinarity, we plotted the frequency of "biogeography" papers in four of the most recognized, including the most high-profile multidisciplinary journals (Figure 7). While biogeography papers in the two highest-impact multidisciplinary journals (*Nature*, *Science*) have been fewer than the 15-year average in recent years (e.g. being below average in 2/3rds – 3/4ths of the past 4–6 years), the number of biogeography papers in *PNAS* has been consistently higher since 2008. The bibliographic pattern of multidisciplinarity may, however, be driven primarily by *PLoS ONE*, beginning in 2006. The ascendancy of *PLoS ONE* raises the question of whether the trend in 'multidisciplinary' publications is in fact an artifact of biogeographers being motivated more by the rewards of open access publishing than by traditional biogeography publications. Indeed, *PLoS ONE*, like the higher impact 'multidisciplinary' journals, actually includes many papers that fall neatly within disciplinary boundaries. Conversely, multidisciplinary work often appears in disciplinary journals. An explicit trade-off between *PLoS ONE* and the traditional journals is suggested by the contemporaneous flattening-out of the number of papers published in *Journal of Biogeography* since circa 2007 (see Whittaker 2014) although establishing cause-and-effect may be challenging.

Research fronts – The third and final type of evidence, considered for identifying emerging themes, is the recent analysis of 'research fronts' by Thomson Reuters, in association with the National Science Library, Chinese Academy of Sciences (JRCETA 2014; Table 1). Research fronts form when "clusters of papers that are frequently cited together … [attain a] level of activity and coherence … with the co-cited papers serving as the front's foundational 'core' … [linking] researchers

Table 1. Research Fronts for 2014 in Ecology and Environmental Sciences and in research areas related to biogeography, as identified by the Joint Research Center of Emerging Technology Analysis established by Thomson Reuters and the National Science Library, Chinese Academy of Sciences (JRCETA 2014). Other research categories in their analysis (i.e., clinical medicine, biological sciences, chemistry & materials science, physics, astronomy and astrophysics, and mathematics & computer science & engineering) did not include any 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	Drought- and heat-induced tree mortality	21	1,889	2011.3
2	Shifting plant phenology in response to global change	15	1,154	2010.1
3	Effects of ocean acidification on marine ecosystems	24	2,186	2009.8
4	Predicting species potential distributions with Maxent	36	5,614	2009.6
5	Diversification rates and adaptive radiation	28	2,554	2009.4
6	Landscape genetic studies	13	1,077	2009.4
7	Biochar amendment impacts environment	19	1,538	2009.3
8	Ecological communities of ammonia-oxidizing archaea and bacteria	30	3,865	2009.2
9	Plant-animal mutualistic networks	11	1,176	2009.2
10	Stable isotope ecology	12	1,654	2009.1
Agricultural, plant, and animal sciences (APAS)				
8	Analysis of rhizosphere fungal communities using DNA sequencing	22	1,040	2010.6
10	Biological control of invasive crop pests using predators	14	953	2010.5
Geosciences				
6	Application of regional climate models in the prediction of surface temperature and precipitation and studies on model optimization	14	1,086	2010.2
Social sciences				
8	Early *Homo* origins and evolution	29	1,149	2010.6

working on related threads of scientific inquiry" (King and Pendlebury 2013). Consideration of research fronts complements [evidence from the IBS symposia](#) and recent [publication trends of "biogeography"](#)—which largely provide perspectives relating subdisciplines to each other within biogeography—by providing a non-biogeographer's perspective on the relative contributions of biogeography among related fields. Analyses of recent trending papers also are available from BioOne[13] and Scopus[14], although these analyses tend to emphasize single articles over whole disciplines.

Biogeographic research fronts by definition fall primarily in the Ecology and Environmental Sciences (EES) section, but also can be found in Agricultural, Plant, and Animal Sciences (APAS), Geosciences, and Social Sciences sections of Thomson Reuters (Table 1). Apart from the topics of the research fronts themselves, perhaps one of the more interesting observations is that seven of the ten 2014 'research fronts' relate to core papers with a mean year of publication (2009) that is similar to the publication year of core papers for research fronts identified for 2013. Three of the 2014 research fronts are variations on 2013 research fronts—*climate change*, *ocean acidification*, and *species distribution modeling*—which include some of the least and most common topics in IBS symposia and in the biogeography litera-

ture. Furthermore, as we noted in 2013, to a large degree, these research 'fronts' already are established areas of very active research (whether or not within biogeography), familiar topics with up to a decade-long history, and targeted by specific grant programs, large research groups, or prior IBS symposia. Species distribution modeling (SDM), for example, dates to the 1980s (Booth et al. 2014), gained significant traction in the late 1990s (e.g., Peterson et al. 1999), the currently most popular software was introduced a decade ago (Phillips et al. 2004), and SDMs have been the single most well-represented approach at the last two biennial meetings of the IBS (Dawson et al. 2013; Figure 5). Chronologically younger biogeographic research fronts tend not to be in the EES core, but in applied biogeography in the categories of APAS, Geosciences, and Social Sciences (Table 1) and often related to species interactions. Similarly, four of the six biogeographic papers in the 40 most-viewed articles indexed by BioOne addressed applied issues: the Anthropocene, climate change, invasive species, and rates of extinction (and map to symposia such as *Climate-change biogeography*, *Conservation biogeography*, and *Invasions*). Biogeographic research did not, however, feature as a leading discipline in the report by Scopus despite inclusion of subject areas such as *Agricultural and Biological Sciences* and *Environmental Science* (Halevi and Moed 2014).

Emerging themes: synthesis — The best candidates for emerging themes might conceivably be novel topics that are somewhat disproportionately well-represented at IBS meetings relative to the recent literature, that represent a relatively small percentage of publications but demonstrate an upward trajectory and are bubbling under or just in the top 10 research fronts. Candidates meeting two of these three criteria include: *human biogeography* (i.e., dispersal and evolution of *Homo*), *data-rich methods* (e.g., genomics, remote sensing), *functional ecology*, *geology*, *microbial ecology*, and *multidisciplinary sciences*. A number of these topics resemble those also identified as emerging themes in 2013, including *genetic-functional biodiversity*, *tropical biogeography*, *marine and freshwater biogeography*, *integrative bio-*

geography, *model systems*, and *infectious diseases*. At the time, we also considered humans as a potentially important component of several topics, not least human biogeography, often now captured under the topic *Anthropocene*. The appearance of such topics as phenological shifts, adaptive radiation, and human evolution in Thomson Reuters' 2014 research fronts, and the increasing share of publications on microbial ecology and multidisciplinary sciences, suggests that several of these topics are indeed significant emerging trends. However, some topics (e.g., microbiology and anthropology), tend to be published in their own disciplinary journals and discussed at specialist conferences, rather than being in the 'big four' biogeography journals or at the biennial IBS meetings.

Opportunities

Emerging trends offer exciting opportunities, perhaps particularly for early career biogeographers yet to settle on their major research topics. So too, potentially, do long-standing underdeveloped areas of study (e.g. paleobiogeography), especially for those who already have these as research foci. In either context, biogeography of practically any non-plant and non-vertebrate (especially non-avian and non-mammalian) organism—particularly but not exclusively those living in freshwater, marine, or tropical terrestrial environments—would increase the diversity of biogeography and address known taxonomic and geographic biases (see *Conservation biogeography*, *Invasions*, Figures 2, 3). Further, by increasing the spatiotemporal and taxonomic context in biogeographic investigations, we might also accelerate the recognition of patterns and processes that unite or differentiate levels of organization (Vellend 2005, 2010, Vellend and Geber 2005, Vellend and Orrock 2009, Emerson et al. 2009, Jenkins and Ricklefs 2011, Ricklefs and Jenkins 2011), taxa (Green and Bohannan 2006, Martiny et al. 2006, Axmacher et al. 2011), and places (Halley 2005, Vermeij and Grosberg 2010, Hachich et al. 2015, Dawson et al. 2016).

Comparative, integrative endeavors will benefit greatly from data collected synchronously

at multiple places on multiple spatial and temporal scales including long-term datasets, as emphasized by almost all of the IBS symposium summaries, above. Such data will also directly address the long-standing challenge of understanding spatial scales (Levin 1992, Scheiner 2011) and likewise clarify how processes scale across time (Steele 1985, Steele and Henderson 1994, Steele 1995) and therefore across phylogenies (Graham et al. 2012). Beyond casually incorporating fossils as an additional time-dependent datatype, long-term 'ecological' studies can link individual life-spans and demography with the intergenerational time-scales of population genetics (D'Aloia et al. 2015), paleoecological studies may use indirect proxies for conditions impacting ancestors of modern taxa in the geologic past (e.g., Stigall 2014, Myers et al. 2015), and phylogenetic biogeography places modern ecological and distributional patterns in their historical evolutionary context (e.g., Quintero et al. 2015).

The potential for 'big data' and technological developments to better unify biogeography by adequately capturing dynamics of neutral and non-neutral processes across diverse places, taxa, and times was recognized in the first horizon scan, and again in the majority of symposium summaries above. We speculated (Dawson et al. 2013) that the greatest potential lies in developing rigorous meta-analyses (e.g., Adler et al. 2011) rather than single global analyses; meta-analyses again emerged as a fruitful pursuit, if cautiously employed, in this second horizon scan. The advantage in meta-analyses remains in part because detailed instrumental ecological data are often lacking and only gatherable by time- and people-intensive methods; new domain-specific databases and depositories can leverage the value of multiple such datasets (e.g., *Quaternary legacies*, *Invasions*; Kattge et al. 2014). Concomitantly, if meta-analyses are a goal, we reiterate the opportunity for teams to establish shared approaches and criteria for assessing when empirical measurements or an aspect of theory are sufficiently complete to move on to the next endeavor. As trends of increasing data and changing technology continue, there also is value in explicitly address-

ing the structure of biogeographic knowledge and how to advance the discipline epistemologically, for example through increased coherence of concepts (Cottee-Jones and Whittaker 2012; see also *Biodiversity hotspots*) and new theory.

Challenges

In the first horizon scan, we pondered whether we should be worried about a lack of questions arising from new biogeographic theory. Our concern emerged from an emphasis throughout the 6th IBS meeting on using new approaches to answer existing questions. While new theory is evolving in some disciplines (e.g., island biogeography: Whittaker et al. 2008, Rosindell and Phillimore 2011), we surmise again, on the basis of threads running through multiple symposia at the 7th IBS meeting, that on the whole biogeography currently is being driven more by techniques and expansion of data streams, particularly oriented toward questions about current and future change, than by new theory (but see, e.g., Whittaker 2014). Although new techniques and data are essential for resolving recalcitrant problems (Andrew et al. 2013) and questions about unprecedented circumstances may generate unprecedented answers, we look cautiously at the rapid adoption and dominance of a subset of methods if they do not also usher in new perspectives and commensurate advances in theory early in their development. Filling in detail within an existing body of knowledge through technological advances, new data, or new compilations of data, can be invaluable. Nonetheless, the true gains for a field become elusive if applied routinely, for the nth time, divorced from theory or contradicting assumptions; in such circumstances "normal science"—the time-consuming and less illustrious work of filling-in details of existing theory—cannot as easily fulfill its essential implicit function of accruing contradictions to the prevailing paradigm that lead ultimately to "scientific revolutions" (Kuhn 1962). Thus, like others before us, we wonder, for example, about the dominance (Figures 1, 5; Table 1; see also Dawson et al. 2013) and rigor (e.g., Araújo and Peterson 2012) of species distribution modeling, particularly as applied routinely to mod-
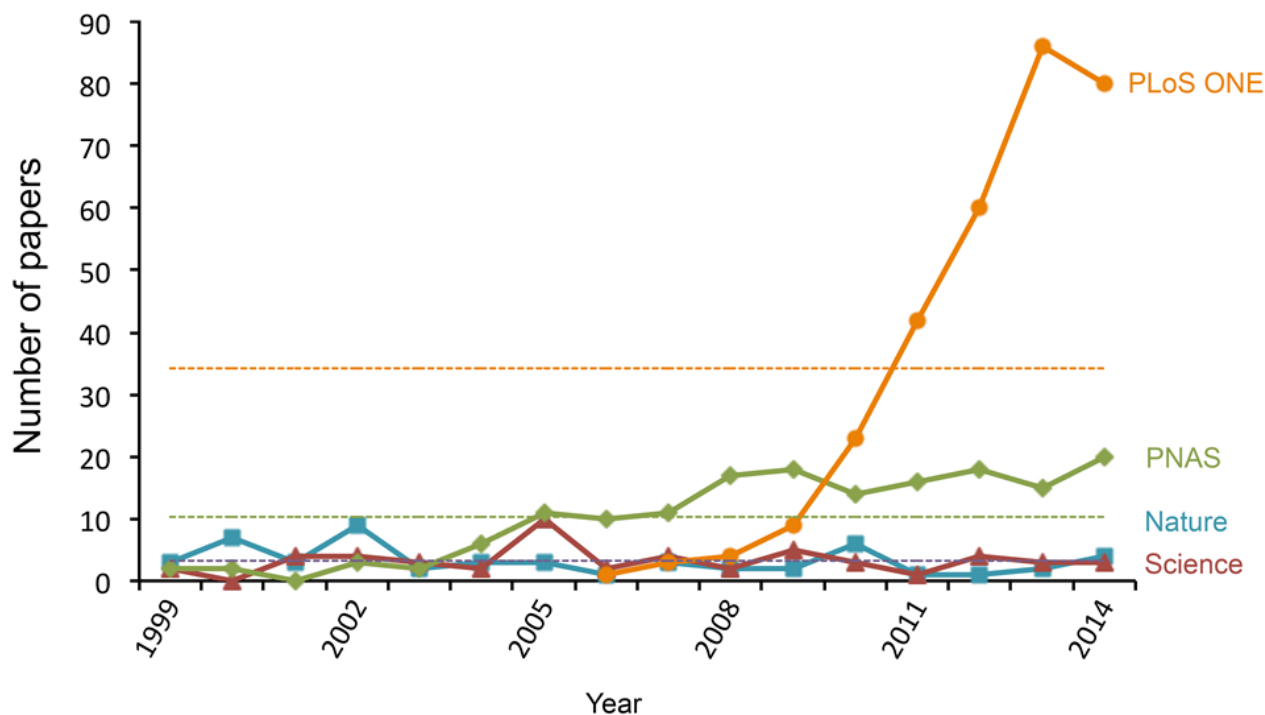
Figure 7. Number of biogeography papers published in four of the most recognized "multidisciplinary sciences" publications, as categorized by Thomson Reuters, annually since 1999, per the Web of Knowledge database (solid lines). Horizontal dashed lines show the long-term mean number of articles per year per journal for the 15 year period analyzed. Articles were identified by the topic word search "biogeography" in the Science Citations Index–Expanded, 13 September 2015.

ern data and climate forecasts. We would identify the same shortfall in the discipline from any subdiscipline that becomes reliant on a small subset of approaches (e.g., Moore et al. 2016) or has limited remit, such as single locus or single species phylogeography. Yet we also recognize that such approaches can be re-invigorated by new tools or in novel combinations (e.g., Razgour et al. 2013; Myers et al. 2015; Riddle 2016). Periods of rapid advance interrupted by durations of consolidation, which may appear to be stagnation relative to the preceding period or to faster advancing fields, are a long-standing characteristic of the sciences (Kuhn 1962) including biogeography (Cox et al. 2016 – Ch. 1). The challenge that every subdiscipline might hope to face sooner or later is how to capitalize on achievements without falling victim to its own success: how to make a golden age without succumbing to the mythical 'Midas touch'.

Concluding remarks: Golden ages, Midas touches, Red Queens

As biogeographers who have practiced our discipline for between one and four decades, we are impressed by biogeography's progress in the last 10 years, certainly the last 20 years, and ever more so the farther one looks back in time. Nonetheless, progress has been heterochronous within and between fields, and we believe reflection on that variation can provide insights into the practice of the discipline. As practitioners of biogeography, we are interested in what is driving research trends, and what, in sum, emerging themes and challenges may reveal about the future of the discipline.

Advances in many areas are being accelerated by technology, for example data-rich methods such as functional diversity benefit from satellite-based observations (Ustin and Gamon 2010). Microbial biogeography benefits from data-rich genomics and environmental sensors but also is increasingly being shaped by adapting existing theory (Green and Bohannan 2006, Martiny et al. 2006). Advances in biodiversity, paleobiogeography, and invasion biology are being powered by the gathering of many local-scale observations into continental- to global-scale data repositories. Other areas—such as human biogeography—are being driven by many new discoveries (Berger et

al. 2015) and by genomics using ancient DNA (Prüfer et al. 2014). Biogeography, in general, may be driven by molecular phylogenetics, climate change, advances in ecoinformatics, social dynamics, and publication technology (Ladle et al. 2015; see also Beck et al. 2012). In sum, there is progress on many fronts, and emerging upward trends are driven by a mix of opportunity, available data, expectations, interest or perceived need, and theory.

But progress is uneven. Are static or decreasing trends, then, reciprocally driven by too few discoveries, insufficient data, low expectations or disinterest, and lack of theory? Possibly yes: relatively. For example, invertebrates and marine systems have long been under-represented in biogeographic conferences, databases, journals, and theory relative to vertebrate, plant, and terrestrial systems (e.g., *Conservation biology*, *Invasions*, Figures 2, 3, 6; Dawson 2016). Such under-representation of a taxon or a field is not new and has many causes (Cox et al. 2016 – Ch.1) but alone is an insufficient explanation for all observed trends. For example, the apparent decreasing trend of biogeography in ecological and evolutionary journals (Figure 6) is occurring despite biodiversity and climate change being among the most pressing problems globally, "eco–evo" studies invigorating both ecologists and evolutionists (Schoener 2011), and evolution being one of the most theoretically rich disciplines in biology. Rather, in this case, a reasonable portion of the ~5% decrease in ecology and evolutionary biology categories over the study period seems to have been replaced by a ~3% increase in multidisciplinary studies (Figure 6), which might be consistent also with an increase in mean number of authors per paper in biogeography (Whittaker 2014), an emphasis on interdisciplinarity in IBS symposia, and is perhaps a reflection on greater appreciation of the complexity and integration of natural systems.

If that is the case, then has this multidisciplinarity increased the quality of biogeographic science, in line with the proposition that "collaborations produce some of the highest quality science" (Uzzi et al. 2013, Grayson and Pincock 2015)? To return to the metaphor posed in the Introduction: might we be entering a new 'Golden Age' not just for island biogeography (Fernández-Palacios et al. 2015) but for biogeography in general?

We believe the evidence is mixed. For example, consider the increase in "multidisciplinarity" as one dimension of the perceived influence of biogeography (Figure 7). If one assumes that publications in journals such as *Nature*, *Proceedings of the National Academy of Sciences of the USA* (*PNAS*), and *Science* represent 'quality'—these journals are, for example, among those in the new Nature Index[15] although there is an important case for prioritizing article-level metrics[16]—then, arguably, the story is ambiguous. In recent years, the number of biogeography papers in the two highest impact multidisciplinary journals (*Nature*, *Science*) have been fewer than the 15-year average, but the number in *PNAS* has been consistently higher since 2008. Perhaps a certain amount of excitement about biogeographic discoveries has ebbed since a heyday in the early 2000s, but given way, overall, to a more predictable and consistent stream of 'high-quality' papers in mid-to-high level general interest journals. However, the publication trend in multidisciplinarity may primarily be an artifact of open access publishing (*Publication trends*) and related pressures. Changes in the models for scientific publication, measures of scientific impact, career prospects, and other consequential matters are interlinked, complex, and playing out in current time (Bergstrom and Bergstrom 2006, Dawson 2014, Whittaker 2014, Vale 2015, Geman and Geman 2016).

These perspectives, like concerns about poorly developed hypotheses with ill-matched analyses or about insufficient and biased data (see *Conservation biogeography*, *Modelling species and ecosystems*, *Invasions*, *The Grand Subject*), can leave one chastened or heartened; they are challenges and opportunities. We live in a rapidly

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15 See *Altrimetric* scored papers at http://www.natureindex.com/, accessed 16 November 2015.
16 See http://www.ascb.org/dora/, accessed 14 January 2016.

changing world, with environments and biodiversity changing around us as we write; there is urgency and timeliness to our mission as biogeographers. Yet a new 'Golden Age' may be elusive if increasing infrastructure such as data, databases, and analytical tools—providing a seeming wealth of riches—is not accompanied also by changes in the way we conceptualize biogeography. Such circumstances risk drowning a field in a flood of minor 'discoveries', but when creative explanatory science is re-emphasized "there is no lack of frontiers" (Geman and Geman 2016). We need to continue all possible efforts to make biogeographic research as rigorous as possible, to choose wisely among the many options in the great new vistas that are opening for study, and to develop concomitant theory. *The Grand Subject* doubtless will keep biogeographers fully engaged for generations to come. The question, perhaps, is how also to keep non-biogeographers—public, politicians, practitioners and others—engaged with our discipline as circumstances change around us, and fields wax and remain (or wane). Pause to think, Red Queens, then run!

Online supplementary information. 521 abstracts submitted for the 7th International Biogeography Society meeting, 2015, made available for alternative text analyses, and the word cloud input for Figures 1–5.

Acknowledgements

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