



# frontiers of biogeography

vol. 3, nº 1 - june 2011



the scientific magazine of the  
**International Biogeography Society**

ISSN 1948-6596 – freely available at <http://www.biogeography.org/>

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volume 3, issue 1 - June 2011

ISSN 1948-6596

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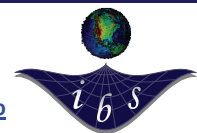
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**cover:** View of a “*campo húmido*” (wet grassland) with some *buriti* palm trees, taken from the Jardim de Maytreia viewpoint, Parque Nacional da Chapada dos Veadeiros, Goiás, Brazil. *Picture by Ana M.C. Santos*

## Advancing *Frontiers*, with a retrospective

The first issue of a new volume of *Frontiers of Biogeography*, following soon after a Biennial meeting of the *International Biogeography Society (IBS)*, provides a timely opportunity to take stock of achievements and to chart the new course for the journal. We aim to do this in two installments: first a brief retrospective herein, followed by a prospective in the next issue.

*Frontiers of Biogeography* is now seven issues, and not quite two years, old (the first issue was published in September 2009). During this period, we have maintained an average of over 30 pages per issue of diverse content, including opinions and perspectives, book reviews, news and comment on the current literature, and updates for the *IBS* membership. That level of output, although small by the standards of an established journal, is a testament to the support of *IBS* members in submitting articles and a dedicated editorial team. We take this opportunity to thank this team of editors, who are listed inside the cover of all the issues of the journal. Many of them are early-career scientists with a great enthusiasm for our subject: key members of the next generation of leading biogeographers. It is great to have such dynamic, motivated people involved.

A key part of our mission is inherited from the antecedent *IBS Newsletter*: to abet communication among all the members of *IBS*. The membership corner remains a pillar of that mission, in partnership with the *IBS* blog, facebook, and twitter sites. We have been able to bring some of the latest content from the diverse biogeography literature to your laptop, including discussion of topics in the peer-reviewed literature. With the Wiley–Blackwell biogeography journals discontinuing their book reviews about four years ago, *Frontiers* is now the place to look for reviews of, and information about, books in our field; the recent appointment of Markus Eichhorn as Book Reviews Editor has made this a strong feature of the journal. We also bring early delivery of ideas gestating within the minds of a series of highly regarded interviewees; the interview with Robert E. Ricklefs in this issue brings up to date the series on Alfred

Russel Wallace Award winners.

In this vein, the current issue again engages with some of the very latest in biogeography in a series of reports from the 5<sup>th</sup> Biennial International Conference of the *IBS*, convened in Heraklion, Crete. Each report provides a summary of cutting-edge topics within the field, but we suggest there are gems hidden in these reports that emerge most clearly when reading the entire issue's contents in quick succession, regardless of speciality. Several common themes spring out. To choose just two examples, the importance of body size (see the summaries of the *Two Lenses*, *Hot Topics*, and *Marine Biogeography* symposia) and the role of ecology in species distributions (*Two Lenses* and *Marine Biogeography* symposia) have a large presence across nominally distant disciplines. Additionally, the *Conservation Biology* and *Palaeoecology* summaries explicitly draw links between symposia. These glimpses of transversality are evidence that, by bringing together biogeographers from different areas of research, the *IBS* meetings are facilitating a multidisciplinary exchange from which conceptual syntheses can emerge. But also, reading the book reviews and interview, we are led to consider the merits of practising biogeography in different ways: focusing on place, question or taxon, using shallow sampling with great breadth or sampling intensely with depth. In this issue we have the added opportunity of viewing one symposium through the eyes of both the organizers and two student attendees (fittingly, this is the *Two Lenses* symposium on biogeography and ecology). The diversity of points of view, conceptual and methodological approaches and research topics provided by these discussions, in print, represents the vitality of the meeting, the society and the discipline they seek to represent.

Thus, as *IBS* continues to establish itself as a scientific society, *Frontiers of Biogeography* also is evolving to take on a broader role in communicating biogeography. Our long-standing series of contributed opinion and perspective articles (now highlighted on the *Frontiers of Biogeography*

homepage) is providing a venue for conceptual developments in biogeography; we particularly encourage you to consider submitting papers like these. Importantly, these articles published in *Frontiers of Biogeography* (or previously in the *IBS Newsletter*) are already being cited in the mainstream literature (e.g. see Hawkins & DeVries 2009, Beck & Sieber 2010, Morales-Castilla et al. 2011, Peterson 2011), a quickly accomplished objective test of quality for any nascent journal.

Michael N Dawson<sup>1</sup>, Richard Field<sup>2</sup> & Joaquín Hortal<sup>3</sup>

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## Keynote speakers

### Lawrence Heaney

- Oceanic Island Biogeography: Emerging Perspectives and Questions

### Michael Dawson

- Advances in Marine Biogeography

### Catherine Graham

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### Ken Feeley

- Advances in Understanding the Niches and Distributions of Species

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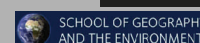
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symposium summary — organizer's perspective

## Biogeography and ecology: two lenses in one telescope

A symposium at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

Biogeography and ecology had common roots in natural history but have been largely separate disciplines for decades, as evidenced by their distinct journals and professional societies. A dichotomous key to the disciplines might separate biogeography and modern ecology as explicitly historical and ahistorical, respectively (McIntosh 1985, Lomolino et al. 2010). In addition, experimental ecology has necessarily focused on local-scale processes and patterns that operate over relatively short time intervals, whereas biogeography has typically focused on processes and patterns that operate over long time intervals and larger spatial scales. Thus, biogeography and ecology may be considered at first glance to be very different views of nature.

In spite of their divergent histories, biogeography and ecology are increasingly converging on intermediate spatial and temporal scales, as evidenced by theoretical and empirical research on metapopulations, metacommunities, regional communities, and evolutionary ecology (e.g. Ricklefs and Schluter 1993, Hanski and Gaggioti 2004, Holyoak et al. 2005, Emerson and Gillespie 2008, Ricklefs 2007, 2008, Cavender-Bares et al. 2009). This convergence has resulted from the maturation and extension of each discipline and from increasing attention to global climate change and its effects at regional scales. As the temporal and spatial scales of biogeographical and ecological concepts increasingly overlap, the two disciplines risk developing separate conceptual imagery, jargon, and expectations for the same natural phenomena. If biogeography and ecology are to inform the conservation and management of nature amidst the simultaneous pressures of 7-plus billion people and global climate change, these disciplines must speak the same language to talk about common concepts. To extend the visual metaphor of the Symposium title, the two lenses of biogeography and ecology need to be aligned to form one telescope through which we receive clear and accurate conceptual images of the natural world and human

impacts.

As part of the 5<sup>th</sup> International Biogeography Society meeting in Crete (7–11 January 2011), a symposium was convened entitled “Biogeography and ecology: Two lenses in one telescope”. Speakers were organized in pairs: one ecologist and one biogeographer were each assigned to a topic and asked to converse with each other in advance of the Symposium. After an introduction by David Jenkins outlining the background of the Symposium, four topics relevant to both disciplines were addressed by the eight speakers; niche, comparative ecology/macro-ecology, community assembly, and diversity.

Jonathan Chase addressed core issues with a summary of ecological niche concepts and suggested that divergent ecological and biogeographic views of niche might be regarded as ‘MacArthur's Paradox’ (Robert MacArthur contributed mightily to both ecological niche and island biogeography theory). Dr. Chase also explained more recent extensions of ecological niche research, including neutral theory and the use of null models to distinguish niche-based and stochastic processes driving community structure. John Wiens then considered the niche concept at biogeographic scales (e.g. species ranges), and noted that abiotic tolerances have been prominent in biogeography while biotic interactions remain relatively unstudied as drivers of large-scale distribution. Dr. Wiens also argued that biogeography should incorporate species' ecology and niche into explanations for species distributions.

Phylogeny is explicit in much of biogeography, but not often in ecology. However, Robert Poulin emphasized the benefit of a phylogenetic context and consideration of ecological traits (e.g. niche breadth) to modern comparative ecology. Dr. Poulin's research on parasites highlighted the intersection between ecology and biogeography when he described the interaction of host specificity, life cycle, and host mobility as factors affecting

parasite communities across spatial scales. In contrast to that detail-oriented approach, Felisa Smith championed macroecology as a broad, phenomenological approach to general patterns at large temporal and spatial scales. Dr. Smith highlighted the prominent role that mammal body size has played in macroecology to reveal common patterns across continents and through evolutionary time.

Community assembly has a long and sometimes acrimonious history in ecology, including recent disagreements over neutral and niche-based processes. Evan Weiher summarized community assembly from an ecological view, and emphasized that a mechanistic understanding of species traits, particularly in combination with phylogenetic analyses of communities, will better advance community assembly theory. Brent Emerson discussed the value of a phylogenetic approach to community assembly, focusing on the application of high-throughput sequencing to understanding diversity in communities of cryptic organisms, such as Collembola.

Diversity is a fundamental measure of ecological and biogeographic pattern. Alessandro Chiarucci summarized the diverse methods used by ecologists to quantify diversity, and the ongoing challenges in measuring diversity for conservation applications and at biogeographic spatial scales. He emphasized the need for spatially explicit, large-scale programs using standardized methods, efforts that require multinational collaborations. Jonathan Davies discussed phylogenetic diversity (PD), which goes beyond ecological diversity measures (e.g. species richness) to include phylogenetic relationships among species in a clade. Dr. Davies used analyses of terrestrial mammals to show that PD adds an evolutionary dimension to diversity-based conservation approaches, producing better-informed regional conservation strategies.

Robert Ricklefs wrapped up the Symposium with an overview that tied together the four themes discussed by the speakers, and related similarities and differences among biogeography and ecology to their separate terminologies and traditions, focal scales for data collection and analyses, and different applications of history

(recorded in phylogenies and biogeographic patterns). Recent research at the interface between biogeography and ecology, often conducted at regional scales, suggests that the two disciplines can be connected through evolution and other large-scale processes, which filter down to the local scale. Dr. Ricklefs suggested that these processes might include coevolutionary interactions between species and their pathogens, which might influence regional distributions of species on spatial scales that lie between ecology and biogeography.

Naturalists followed different traditions as biogeography and ecology were separated, deconstructed, and then re-built from the component parts. The processes of re-assembly have progressed far enough that the two disciplines once again interact. The symposium “Biogeography and ecology: Two lenses in one telescope” highlighted points at which biogeography and ecology are already exchanging ideas (e.g. modern comparative ecology and macroecology are each phylogenetically based), as well as subjects where ecology and biogeography are just beginning to converge (e.g. niche concepts, measures of diversity). Much recent progress has also been made in phylogenetic community assembly (e.g. Emerson and Gillespie 2008, Cavender-Bares et al. 2009) which also serves to join the otherwise divergent disciplines. Evolutionary history (as represented in phylogeny) and ecological traits will continue to be important for research on questions of niche, community assembly, regional diversity, and macroecological comparisons, which span the intersection of biogeography and ecology. The Symposium will be published in a forthcoming issue of the *Philosophical Transactions of the Royal Society, B* and hopefully will contribute to aligning the biogeography and ecology lenses. We look forward to watching and participating in this potential alignment—it is an exciting time to be a biogeographer and/or ecologist.

David G. Jenkins<sup>1</sup> & Robert E. Ricklefs<sup>2</sup>

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Edited by Michael N Dawson

[symposium summary — a perspective from two delegates](#)

## Biogeography and ecology: two lenses in one telescope

A symposium at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

The heterogeneous distribution of life on Earth is a ubiquitous pattern, but knowledge about causal factors remains elusive. Questions regarding this pattern have been traditionally addressed with different approaches, namely historic (biogeographical) vs. contemporary (ecological). Often, these perspectives were considered separate since each recognized different processes responsible for biological diversity, geography and history on one side and ecological interactions and climate on the other. This created a chasm between ecology and biogeography that remained from the maturation of ecology during the 1960's until recent years (Wiens and Donoghue 2004). Recognition of scale as an object of study instead of a nuisance in ecological studies (Wiens 1989) and the broadening perspective of ecological systems being influenced by both biogeographical and ecological contexts (Ricklefs and Schluter 1993) paved the way to acknowledge the interaction of regional effects on local patterns and vice versa. Consequently, the development of new concepts and disciplines (e.g. neutral theory, macroecology), along with analytical techniques and data availability (e.g. phylogenetic reconstruction), have helped bridge the gap towards a com-

prehensive understanding of biodiversity patterns. As an example of such bridging, Dave Jenkins and Bob Ricklefs convened a symposium during the 5<sup>th</sup> IBS meeting, in Crete, Greece, that showed progress in this direction. Here, we give a brief overview of this Symposium through the lenses of two biogeographers in-training.

A major constraint to the evaluation of the effect of biogeographic factors in local communities is the lack of manipulative ways to address their influence. Null modelling approaches have provided a framework to distinguish potential processes involved in community assembly when experiments are not possible. Jon Chase presented an example of combining these approaches with actual experiments. He showed that integration of null models and controlled experiments under a regional perspective aids in disentangling the relative effects of niche and stochastic processes in biogeography. His results of experiments in freshwater ponds reveal the effect of niche-based processes in lower productivity systems and stochastic processes (i.e. drift) at higher productivities. In the same vein, Evan Weiher presented results of a unique large-scale experiment evaluating the relative influence of dif-

ferent factors in community assembly. Through the analysis of functional parameters, Weiher found support for biotic interactions as important processes in shaping community functional traits, indicating that traits, beside phylogenetics, are necessary for understanding the mechanistic structure of communities.

Morphological or functional traits are obvious candidates for examining the relationship between species characteristics and their ecological and biogeographic patterns. A trait that has been favoured for its obvious ecological and evolutionary importance is body size. Felisa Smith presented the current knowledge regarding past and present body-size patterns in mammals from a macroecological perspective. Her presentation showed how such patterns have changed through time in different continents and the potential effect of human intervention in shaping them. Her approach emphasized the need to integrate different perspectives (e.g. reproductive physiology) at large geographic and taxonomic scales in the search for general patterns and processes across space and time. The assessment of such biodiversity patterns has relied mostly on species richness as the standard metric (as response variable). In his presentation, Alessandro Chiarucci argued that standardized methods to assess and monitor biodiversity applicable to both ecological and biogeographical perspectives are actually lacking. He suggested a solution based on improving data gathering, basically following an *“ecological lens across units typical to biogeographical studies”*.

An important contribution in merging ecology and biogeography has been the application of the niche concept (ecology driven), in the study of biogeographic patterns (history driven). John J. Wiens showed that the niche concept has profound effects on our understanding of biodiversity patterns. Wiens suggested that niches influence biogeographic patterns mainly through limits on dispersal determined by ecological conditions. He also presented examples combining large-scale biogeography, ecological traits and phylogenies that illustrate the combination of ecological and biogeographical perspectives. The basic premise behind niche influence on biogeography is that

environmental preferences between closely related species are similar as a result of phylogenetic conservatism. Such influence of phylogeny has also been acknowledged in the assessment of aggregate statistical patterns mainly in relation to statistical (non) independence of species and how to control for it. Robert Poulin presented an excellent example considering this influence in comparative analyses. He showed how controlling for phylogenetic influences helps reveal geographic patterns in species traits, such as range size and niche breadth. This highlights the importance of obtaining and incorporating phylogenetic information to the study of biodiversity patterns in space and time. The recent increase in availability of phylogenetic information, mediated by technological and analytical advancements, has fostered its use at a range of scales from individual organisms and populations to species assemblages and regional biotas—adding an evolutionary dimension in pattern description and explanation. The contributions by Brent Emerson and Jonathan Davies illustrated this fact. Brent Emerson showed how new techniques in molecular sequencing allow description of species relationships, which in turn facilitates a detailed inspection of assembly patterns. His framework offers a way to connect phylogeography, biogeography and community assembly and has wide applicability. Likewise, Jonathan Davies presented results from incorporating evolutionary hypotheses (particular phylogenies) to explain contemporary patterns of geographic variation in species richness. By contrasting phylogenetic diversity and species richness, Davies showed how distinct regions might hold similar species numbers but still differ in their phylogenetic diversity. This, he argued, can inform about the historical aspect of biodiversity, a feature that has recently gained importance in conservation goals.

Overall, the series of contributions presented at this Symposium represents an step towards the integration of biogeography and ecology to increase our understanding of biodiversity patterns. Although such steps have come mostly (but not exclusively) from the ecological side towards biogeography, they have certainly clarified

the intrinsic relationship between both disciplines and have shown how they are, indeed, two lenses in one telescope.

### Fabricio Villalobos<sup>1</sup> & Omid Paknia<sup>2</sup>

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Edited by Matthew J. Heard

### symposium summary

## Mediterranean biogeography: where history meets ecology across scales

A symposium at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

The Mediterranean Basin looks almost designed as a model system for biogeographical research. It is a semi-closed sea offering coast to three continents and 24 countries, with a marine surface area of some 2,500,000 km<sup>2</sup>, a maximum depth of 5,121 m, and a coastline of 46,500 km. 24,600 km of this coastline belong to the 11,879 Mediterranean islands, 243 of which host permanent human populations. Even though there has been some disagreement on the precise definition of what constitutes the terrestrial Mediterranean Region, the dominant view includes some 2,300,000 km<sup>2</sup> of land around the basin (Blondel et al. 2010).

An important aspect of the Mediterranean Region is its long history of human presence that spans several millennia, with agriculture being practiced in the region for approximately 10,000 years, and the sequential rise and fall of many important civilizations, especially during the past 5,000 years. Another crucial feature is the intensive tectonic activity caused by the subsidence of the African plate beneath the European plate, and the strong east-west pressures to Asia Minor exerted by the Arabian plate. The palaeogeography of the Mediterranean Region is also complex, and highly marked by the Messinian Salinity Crisis. During this key event the Gibraltar strait closed

and the Mediterranean Sea was reduced to a series of saline lakes for some 630,000 years (5.96–5.33 Ma), leading to large-scale changes in both marine and terrestrial biota. The unique combination of geological and climatic factors has led to the development of a characteristic and highly diverse biota, as reflected by the inclusion of the Mediterranean among the most important biodiversity hotspots. The vast biotic diversity and the complexity of processes shaping Mediterranean biodiversity are reflected also in the diversity of approaches to the biogeography of the region, a small sample of which were covered in this Symposium.

Hans Peter Comes from the Paris-Lodron University of Salzburg (Austria) explored processes of plant speciation in the Mediterranean, contrasting patterns of adaptive and non-adaptive radiations. Ecological speciation plays an important role in Mediterranean plant radiations, both old and young, with radiation often accompanied by niche differentiation amongst lineage members. Nevertheless, at least one case of purported 'non-adaptive radiation' in plants has been suggested, with mutation and genetic drift being the primary factors causing divergence of populations occupying ecologically similar habitats: the *Nigella*

*arvensis* complex in the Aegean. *Nigella* phylogeny reveals rapid radiation in the Pleistocene, starting from the central Aegean and proceeding to the periphery. The speciation rate accelerated during the late Quaternary due to range fragmentation triggered by sea-level changes in the Holocene. Genetic drift is in this case shown to be a major cause of differentiation and development of post-mating reproductive isolation among lineages, i.e. suggesting non-adaptive radiation.

Chronis T. Tzedakis from University College of London (UK) built on his recent paper (Tzedakis 2009) and the work by Médail and Diadema (2009) to focus on the role of glacial refugia as both 'museums', conserving plant diversity during glacial periods, and 'cradles', producing new diversity due to their long persistence, in contrast to previous beliefs. He presented detailed and new data on climatic changes during the Pleistocene that, when combined with palaeogeographic reconstructions, show that glacial refugia around the Mediterranean could have persisted for long periods of time, allowing for extensive diversification of several taxa. These refugia thereby offer a mechanism for the Mediterranean as a source of diversity for temperate Europe.

Oliver Rackham (Cambridge University, UK), focused on the role played by humans and their activities in the distribution of Mediterranean plants, especially the endemics on the many islands of the Aegean. Various aspects of human history and prehistory, such as the extermination of native mammals, the introduction of domestic animals and plants, as well as exotic wild plants and animals from the mainland, and the various uses of endemic plants by humans, have affected modern plant distributions. Rackham provided a comprehensive view on past and present human impacts on the environment of Mediterranean islands, addressing also possible future threats to island endemics, including those from the globalization of plant diseases and/or global warming.

Rocío Santos-Gally and colleagues from the Universidad de Sevilla (Spain) reported on the phylogeography of mountain and lowland groups of the plant genus *Narcissus*. The ancestor of *Narcissus* originated in the Iberian Peninsula far earlier than the onset of the Mediterranean climate.

Then, it expanded its range, colonizing several mountain ranges in northern Africa. Three key historical events in *Narcissus* diversification are recognized: the Messinian Salinity Crisis, tectonic shifts of the Alboran Domain, and the establishment of the Mediterranean climate, followed by repeated glaciations.

The presence of early humans in the Mediterranean coast during the Plio-Pleistocene, as revealed *inter alia* by findings at Gibraltar Rock, was discussed by Clive Finlayson from the Gibraltar Museum, who emphasized the time dimension in biogeographic studies. Finlayson focused on the biogeographic significance of the successive fragmentation of the once extensive and continuous 'mid-latitude belt', a temperate/subtropical zone of savannahs and wetlands between 30° and 50° N, whose western end is formed by the Mediterranean basin. The break-up of this belt during the late Tertiary led to the diversification and expansion of species adapted to rocky and arid habitats. Early hominids exploited the new opportunities in a process that provides important clues to the occupation of Europe by the genus *Homo*, as well as to the evolution of modern Mediterranean biota.

Maria Rita Palombo from Università di Roma 'La Sapienza' (Italy) used evidence from fossils of animals living on western Mediterranean islands to provide a detailed overview of the palaeogeography of this region. The Western Mediterranean basin, with an age of some 30 Myr, has always hosted a high level of biodiversity including numerous remarkable island endemics, mostly reflecting repeated events of isolation and connection of insular and mainland areas. Land mammal fossils offer substantial information for the reconstruction of the complex history of the Western Mediterranean. The progressive depletion of endemic mammals during the Holocene was linked to the interplay of climate change and human impacts.

An important feature of the Mediterranean region is its strong environmental and geographic heterogeneity at all spatial scales, from the very local to the regional. This environmental and geographic complexity has not only been a key driver of Mediterranean biodiversity, but also resulted in

a similarly high heterogeneity in the research approaches to Mediterranean biogeography. In addition to the lectures described above, more than 35 poster contributions addressed various aspects of both marine and terrestrial Mediterranean biogeography, ranging from phylogeographic analyses to studies of fossil faunas and floras. Thus, one take home-message from this Symposium is that the Mediterranean can be also designated as a 'hotspot of biogeographic research'.

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Edited by Joaquín Hortal

## symposium summary

# New perspectives on comparative phylogeography: novel integrative approaches and challenges

A symposium at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

Phylogeographic inference reveals that many species, as recognized by current taxonomy, are comprised of multiple genetically divergent lineages that are morphologically cryptic yet represent terminal branches on the tree of life and are relevant to understanding evolutionary processes in relation to environmental change (Avice 2000, 2008). Comparative phylogeography endeavors to reveal how whole communities or assemblages become structured into co-distributed sets of divergent lineages by shared responses to past environmental changes as well as histories that are unique to specific species. In so doing, comparative phylogeography makes the link between traditionally separate ecological and evolutionary processes thereby leading to ecosystem-level understanding about how climate change and geography interact with aspects of species ecology and natural history to drive geographic patterns in biodiversity, community assembly and natural selection. The symposium “New perspectives on comparative phylogeography: Novel integrative ap-

proaches and challenges” brought together researchers who are using multi-taxa phylogeographic data sets to answer these questions while allowing the idiosyncrasies of particular systems to guide specific questions, hypotheses being tested and level of detail at which inference can be made.

Highlighting that conservation is one of the most pressing applications for comparative phylogeography, Moritz et al. demonstrated how divergent lineages within species can inform land resource management strategies. Spatial bioclimatic modeling and phylogeographic inference across wide assemblages in tropical Australia and coastal Brazil strongly demonstrate that non-adaptive and allopatric divergence can drive species diversification and that narrow-range phylogeographic lineages will be concentrated in climatically stable landscapes (Schneider et al. 1998; Carnaval et al. 2009). This result aligns with emerging consensus on the need to protect present climatic refugia in the context of rapid global

warming. Thus, not only do we now have the means to predict these areas that harbor narrow range endemics, we can then protect this prevalent component of biological diversity (Moritz 2002).

In the context of island biogeography across major Pacific archipelagoes, Gillespie et al. used multiple lineages of animals and plants from remote Pacific islands to test hypotheses about determinates of island colonization. Wind and storm patterns, ocean currents, and migratory routes provide sufficient information to formulate, comparative phylogeographic hypotheses of island colonization by (1) rafting over water, (2) attachment to migratory birds, or (3) aerial dispersal. Differentiable predictions based on these three dispersal mechanisms are that (1) rafting will lead to sequential stepping stone colonization, (2) bird vector dispersal will lead to colonization along migratory routes, and (3) wind dispersal will lead to colonization of remote sites directly from a mainland source if there is a good match between the mainland and island habitats. Generally speaking all three mechanisms of long distance dispersal, (ocean currents, winds and bird vectors) interact with the biotic forces of selection and competition in the islands which then lead to observed patterns of island biodiversity.

In a similar vein, Riginos demonstrated that the magnitude of egg dispersal potential in benthic fishes globally predicts population subdivision and taxonomic diversity at the family level (Riginos et al. 2011). In this case, the tools from landscape genetics are used to statistically evaluate how coastline features, geographic distance and transitions between biogeographic regions can potentially drive population subdivision and ultimately biodiversity. While landscape genetics makes use of space explicitly, doing so within a model-based coalescent framework has not been possible beyond spatial approximations. In this light, Baird describes a method of connecting the spatial ecological parameter 'effective density' with 'effective population size', an important population genetic parameter used in standard coalescent population genetic inference (Baird and Santos 2010). To illustrate, a coalescent

model based on Kimura's stepping stone model was presented and applied to recent range expansion of the cane toad (Estoup et al. 2010). As spatial coalescent methods become mature technology, applications to make inferences across spatially co-distributed species using multi-taxa models will drive comparative phylogeography to a new level.

Moving beyond well-studied biogeographic regions and groups, Reynolds et al. focused on the biogeographic inference of ectomycorrhizal truffles while Ramakrishnan et al. were interested in the biogeographic drivers of regional diversity in the Indian subcontinent. Using phylogenetic data, Reynolds et al. demonstrated, contrary to expectations for low dispersing taxa (truffles are dispersed only by mammalian mycophagists attracted to their scent), that frequent long-distance dispersal expands the known geographic ranges of common Northern Hemisphere species. Ramakrishnan et al. demonstrated that, unlike many other regions, strong physical barriers are absent within the Indian subcontinent, and with its relatively small area, most mammalian groups are present due to recent colonization. Given these factors, phylogeographic patterns are hypothesized to be driven by species' ecology, as shown in seven mammal taxa that include cats and primates (Mukherjee et al. 2010; Robin et al. 2010). Following this general prediction, Ramakrishnan et al. found that habitat preference drives phylogeographic patterns as does body size and differences in sex-biased dispersal for some groups. Although the Indian subcontinent is tropical, like temperate zones it was heavily impacted by Pleistocene glaciations due to the surrounding Himalayas, and expectedly, the authors do find genetic signatures of post-Pleistocene population expansions in some groups.

In conclusion, we look forward to expansion of the novel and traditional approaches presented in this Symposium. As this field matures and becomes fully integrated with ecological fields that make use of GIS technologies and rapidly improving global databases, comparative phylogeography will become a major tool for identifying climatic refugia for conservation in the context of

rapid global warming. In so doing, comparative phylogeographic inference will increasingly be able to predict and identify climatically stable landscapes that harbor divergent lineages below the species level.

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Edited by Michael N Dawson

## symposium summary

# Analytical advancements in macroecology and biogeography

A symposium at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

Macroecology analyzes patterns and processes of biological diversity at broad scales, both in space and time, based on an integration of distinct fields of ecology, physiology, behavioural sciences, evolution and biogeography. Common definitions of macroecology (e.g., Brown 1995, Gaston & Blackburn 2000) emphasize two sets of contrasting issues: “patterns and processes” and “scale”. In that context, we can ask not only how ecological and evolutionary processes at local scales—such as selection, drift, dispersal and competition—affect individuals and populations, but also how they may lead to geographic range dynamics

(extinction, contraction and fragmentation) at the species level. We can then contemplate how the patterns derived from ecological and evolutionary processes may shape broad-scale patterns of diversity, and also how other emergent processes or properties contribute to diversity patterns.

To achieve this synthetic, integrative view, and understand the roles of different processes and emergent properties at distinct scales, it is important to think about which methods could be used. The continuous development of computing capacity and increasing data generation allow ever more sophisticated analyses, enabling novel in-

sights into macroecological and biodiversity patterns. These methodological developments are interesting for biogeography and macroecology mainly from a theoretical perspective. To answer complex questions and test hypotheses using large data sets, we might find use for complex analytical tools developed or used in other research fields of ecology and evolutionary biology, or science in general. Bringing together researchers with different backgrounds and working with different methods that may be potentially useful for macroecologists and biogeographers was the main purpose of the symposium on *Analytical Advancements in Macroecology and Biogeography*.

The symposium started with Andy Purvis (Imperial College at Silwood Park, UK) showing how new macroevolutionary approaches and phylogenetic comparative methods can be projected into geographical space and used to test niche conservatism, which he illustrated with global data on mammals and amphibians (e.g., Olalla-Tárraga et al. in press). Pedro Peres-Neto (University of Montreal, Canada) followed the same trend of unifying the analytical frameworks for geographical and evolutionary processes. He showed many simulation results, comparing methods for dealing with spatial and phylogenetic autocorrelation, contrasting Moran's eigenvector methods (see Griffith & Peres-Neto 2006) with generalized least-squares approaches. His talk was followed by Robert Colwell (University of Connecticut, USA) and Thiago F. Rangel (Universidade Federal de Goiás, Brazil) who showed how mid-domain models, originally developed as null models for macroecological patterns in species richness, could be expanded into mechanistic models that account for the roles of various processes causing latitudinal and altitudinal gradients in species richness (e.g., Colwell & Rangel 2010).

At a finer evolutionary scale, Albert Phillimore (Imperial College at Silwood Park, UK) showed how quantitative models of geographic and temporal variation within a species can be used to study adaptive processes at broad geographical scales, providing an interesting link between quantitative genetics and macroecology (Phillimore et al. 2010). Next, Marcel Cardillo

(Australian National University, Australia) presented an analysis of phylogenetic diversity and structure of Carnivora assemblages (Cardillo 2011). Finally, Richard Ree (Field Museum of Natural History, USA) provided models for analyzing speciation, extinction and range dynamics using phylogenies (e.g., Ree & Sanmartín 2009).

Each speaker provided a fresh perspective on methods that were developed in different fields in recent years and which are useful for answering a variety of questions in macroecology. It is important to note that some of the methods and procedures are still under development, and their application to new problems will require more research and deeper evaluation of statistical properties and computational facilities. This is certainly a stimulus to young as well as older researchers and many exciting advances and insightful applications may be expected in the years to come. There seems to be a clear trend towards using tools that simultaneously evaluate phylogenetic and geographical patterns, adopting an explicit definition of macroecology and biogeography as ways to deal with processes underlying species' dynamics in space and time.

In that context, the recent paper by Jonathan B. Losos on the limitations of phylogenies in comparative biology is a reminder to us all that patterns are not to be confused with processes (Losos 2011), and that while a new tool provides exciting new insights it may not necessarily be the best way to hammer an old nail. Also, methodological advances are not a substitute for conceptual and theoretical development. The symposium speakers insightfully illustrated how new methods can aid conceptual advances, via better-defined questions, hypotheses and predictions.

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Edited by Joaquín Hortal

## symposium summary

# Marine biogeography

A contributed session at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

How does life in the sea compare or contrast with life in or above its land, lakes, rivers, and streams? By asking questions about geographic patterns of marine speciation (Renema, Tellier et al., Tyberghein et al.), how well landscape metrics describe saltwater systems (Wedding et al.), and how patterns of human use impact the marine biota (Davidson et al., Tittensor and Worm), one might begin to intuit some answers.

Willem Renema's study of the distinctive *Cycloclypeus*, the largest living benthic foraminifera (10–12 cm diameter), which occupies a very well characterized niche on tropical coral reefs, provides a well-constrained fossil series, of a quality rare in any realm, for examining patterns and rates of speciation. He found that long-distance dispersal events from the Indo-West Pacific culminate in extinction in the Mediterranean, and that morphological disparity increases regionally but not globally during the Middle Miocene following range contraction and re-expansion. The region of speciation may vary among taxa, even if speciation is contemporaneous. These results suggest patterns of marine species diversity can be influ-

enced by local 'species pumps' (that is, vacuum pumps drawing species in, rather than pressure pumps pushing species outward) causing regional dispersal and diversification, and that evolutionary ecological dynamics of at least some taxa may play out as a series of taxon cycles.

Florence Tellier and colleagues also found evidence of geographically variable evolutionary dynamics along the intertidal rocky shore of the southeastern Pacific. Their comparative phylogeographic study of two low-dispersal co-distributed species, an isopod (*Excirologa hirsuticauda*) and a kelp (*Lessonia nigrescens*), revealed genetic discontinuities in both taxa at 30°S, with sub-groups—possibly cryptic species—of one or the other species either side of this well-known biogeographic filter. Their inference is that concordant phylogeographic patterns may arise from significant environmental factors such as vicariance mediated by oceanography. Yet, secondary discontinuities that are geographically incongruent exist in these taxa: at 27°S for the kelp and 33°S for the isopod. Transplant and laboratory experiments with the kelp suggested at least some of

this genetic structure is due to local adaptation, with differences among kelp populations in their tolerance of desiccation and high heat. Differentiation of secondary sexual characteristics in the isopod suggest reproductive isolation and maybe sexual selection may contribute to, or result from, local adaptation in the isopod.

Lennert Tyberghein and colleagues (Tyberghein et al. 2011) described the new tool Bio-ORACLE (Ocean Rasters for Analysis of CLimate and Environment) that should help determine environmental factors to which populations may be locally or regionally adapted. Bio-ORACLE brings together 23 geophysical, biotic, and climatic rasters at ~9 km<sup>2</sup> resolution in a format intended to be easier to use than the existing detailed yet disparate datasets (such as those available for download from the National Oceanic and Atmospheric Administration [NOAA]). The dataset was illustrated by maximum entropy species distribution modeling of genetic variation in two seaweed genera: *Halimeda* and *Codium fragile*. The environmental correlates for *Halimeda* suggest origin in warm water and evolution of one clade into cooler waters. Their findings with *C. fragile* are reported in *Global Ecology and Biogeography* (Verbruggen et al. 2009). A major challenge remains gathering reliable empirical data for near-shore environments—where the organisms in the seminal marine studies of Joseph Connell, Paul Dayton, Robert Paine, Peter Sale, Terry Hughes and others live—which Bio-ORACLE currently interpolates.

Lisa Wedding and colleagues examined some of these coastal processes that may influence species diversity at a very fine scale. Particularly, they focused on understanding processes that lead to diversity in a particular place, for which the first task was to establish a method for gathering large datasets. Wedding et al. demonstrated that Light Detection and Ranging (LIDAR) is an effective and accurate way to increase geographic coverage with resolution comparable to traditional time-intensive underwater surveys. The rugosity of coral reefs, as measured by the finest resolution possible with LIDAR is proportional to rugosity measured by experienced divers. Moreover, these fine-resolution LIDAR estimates

of rugosity are significantly correlated with fish diversity at all scales. Thus, there is potential for these nearshore GIS-like tools to be integrated with the offshore data of Tyberghein and colleagues. When this level of integration becomes routine, and we can regularly work with marine datasets approaching the size and resolution of terrestrial datasets, we will be one step closer to understanding how marine systems compare and contrast with those in other realms.

Reaching the level of integration of information, including biological characteristics, that will enable prediction of the consequences of global change is a priority that unites aerial, freshwater, marine, and terrestrial research during a time of intense global change (Barnosky et al. 2011). The final two talks of the marine biogeography session both addressed anthropic challenges facing the natural environment. Ana Davidson and colleagues took on the challenge of developing a predictive and spatially explicit model for determinants of global extinction risk in marine mammals. Using random forest models, they were able to predict extinction risk with 90% accuracy. The four major predictors (of high risk) were, in order of descending importance, the speed of life-history (slow), group size (small), geographic range (small), and body mass (large). Including extrinsic environmental factors did not improve performance of the model greatly. Polar bears (*Ursus maritimus*), for example, have the slowest life-history for their body size of any mammal (marine or terrestrial) and so are predicted to be among the most endangered mammals with the least potential for recovery if threats are removed. In general, high productivity marine coastal regions, i.e. those about which we have most biological data and least environmental data, are where most marine mammals are at risk. Yet the large predatory fishes that roam the high oceans have not escaped unscathed. Intense fishing pressure has decreased the abundance and diversity of large marine animals. Derek Tittensor and Boris Worm asked whether these animals have also experienced changes in range. Their sampling data, derived from commercial fisheries data, are substantial: logbook data from Japanese fisheries alone since 1950, for example, provide billions of

sample points (hooks) and hundreds of millions of observations (fish caught). By stitching together several such datasets, and after correcting for variability in the data such as geographically unevenly distributed effort, Tittensor and Worm were able to detect changes in range. They found generally similar patterns across the Atlantic, Indian, and Pacific oceans, showing an apparent effect of life-history. Fishes that grew more slowly and to larger size and spawned in aggregations, such as the bluefin tuna (*Thunnus thynnus* and *T. orientalis*), showed decreases in range size; the range of *Thunnus thynnus* has contracted almost entirely from the South Atlantic, and populations are fractioning in the Pacific. In contrast, fishes that grow faster to smaller maximum size, such as the albacore tuna (*Thunnus alalunga*) generally have shown no change or an increase in range. Whether changing ocean climate or exploitation provide a more likely explanation is currently under investigation. Thus, we find consensus in the results of Davidson et al. and Tittensor and Worm in predicting, if human activities don't change, an ecological extinction of the marine megafauna that echoes the extinction of the terrestrial megafauna from the Americas thousands of years ago. While in many ways we are beginning to see

parallels between marine and terrestrial systems, it would be heartening to see a difference in this respect.

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Edited by Chris Burridge

## symposium summary

### Palaeoecology

A contributed session at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

The IBS meeting is rapidly emerging as a critical meeting for those interested in paleobiogeography, and in particular for those interested in how past and present biogeographic patterns are shaped by the intersection of past environmental changes with ecological and evolutionary processes. Paleoeecology was well represented at the Crete meeting, with 25 abstracts submitted, a packed oral session, and many cross-cutting talks. Several general themes emerged from the talks in the paleoecology session.

One running theme was species niches and their shifting manifestation over time in response to new species interactions and environmental conditions. Alycia Stigall (“Using ecological niche

modeling to evaluate niche stability in deep time”) applied GARP and Maxent analyses to Late Ordovician brachiopod species to show that niche conservatism decreased during and after a major invasion event (the Richmondian Invasion), suggesting that species responded to invasion pressure. Jack Williams and co-authors (“Apparent niche shifts and no-analogue climates in eastern North America during the Late Quaternary”) tackled the problem of reconstructing ‘truncated’ niches, i.e. species’ fundamental niches for portions of environmental space that do not exist at present, showing that different starting assumptions resulted in very different reconstructions of species fundamental niches, and hence very different pre-

dictions for the late-Pleistocene no-analog climates by species distribution models. This problem of reconstructing truncated niches was echoed in a talk by Ken Feeley in the global change oral session (“Extinction risks of Amazonian plants”), who developed a separate method for reconstructing the niche breadth of South American plant species for future climates warmer than any at present.

A second running theme was the effects of glacial-interglacial climate changes on past and current species distributions. Dan Gavin and Erin Herring (“Reconstructing a putative cryptic northern mesic refugia”) reviewed the evidence for and against a northern mesic full-glacial refugia in the interior montane cedar-hemlock forests of northern Idaho and eastern British Columbia. Phylogeographic data suggest that this area was a full-glacial refugium for amphibians and plant species, yet fossil pollen records suggest that mesic forests formed in only the last 3000 years and niche models driven by paleoclimatic simulations also suggest unfavorable conditions for mesic taxa. This apparent paradox remains to be reconciled. Kristine Westergaard and co-authors (“Glacial survival may matter after all”) presented convincing molecular evidence that some arctic-alpine plants must have survived on nunataks and other small refugia in formerly ice-covered portions of northern Europe, Svalbard, and eastern Greenland.

A related third theme was the ability of species to keep up with climate change. Rachid Cheddadi (“Revisiting Reid’s Paradox by integrating genetic and topographic information: *Abies alba* (Mill.) – a case study”), used a combination of late-Quaternary fossil pollen data, topographic data, and current haplotype distributions to revise estimates of post-glacial colonization migration rates for *Abies alba*. His estimates of 50 to 150 m/year are substantially lower than earlier pollen-based estimates. In a related talk from the global-change session, Sandel et al. (“Climate change velocity since the Last Glacial Maximum and its impor-

tance”) computed the velocity of climate change between the last glacial maximum and present and showed that a) the contemporary diversity of small-ranged species was negatively correlated with climate velocity and b) post-glacial climate velocity was a better (negative) predictor of small-ranged species than contemporary climate variables.

Not quite fitting into this neat 1-2-3 arrangement of themes, and thus extra-interesting, was the paper by Mariana Munguía-Carrara and co-authors (“Differential dispersal response of mammals during the Great American Interchange”) who applied niche models to test hypotheses about why the Great American Interchange was so asymmetrical, with more North American species invading southward than South American species heading north. They found that North American species had a larger area of potentially suitable climates in South America than vice versa, and that successful colonizers tended to have a shorter migration distance to new climates.

As can be seen from the above, the talks in the paleoecology session tended to have a strong but not exclusive emphasis on late-Quaternary timescales and on climate-driven dynamics. This was counterbalanced by other talks at the meeting that had a strong phylogenetic emphasis and often emphasized evolutionary processes operating at longer timescales. Overall, these talks reinforced my growing impression that IBS offers an increasingly essential meeting place for the international community of paleoecologists, evolutionary biologists, macroecologists, and others studying biological dynamics at broad spatiotemporal scales.

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You can find information about the **International Biogeography Society** at <http://www.biogeography.org/>, find job offers and information on upcoming events at the **IBS blog** (<http://biogeography.blogspot.com/>), and contact with other biogeographers at the **IBS facebook group** (<http://www.facebook.com/group.php?gid=6908354463>) and the **IBS twitter channel** (<https://twitter.com/biogeography>).

## symposium summary

## Conservation biogeography

A contributed session at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

Theory and analyses developed in biogeography can provide new and valuable insights into how to conserve diversity, especially in an era of increased human degradation of both terrestrial and aquatic ecosystems, coincident with climate change (Whittaker et al. 2005). Inspired by increasing research in the field, and by Richard Ladle and Rob Whittaker's new edited book 'Conservation Biogeography' (2011), the *International Biogeography Society* devoted a contributed session to conservation biogeography at its fifth biennial conference. The session covered six related themes: biotic homogenization, invasive species, agricultural ecology, disease ecology, reserve design and communicating conservation biogeography to the general public. Climate change, also an important theme in conservation biogeography, was discussed in its own contributed paper session.

In the first talk, Martin Winter and colleagues evaluated the extent to which invasive species lead to homogenization of species, traits and phylogenetic composition of vascular plants and vertebrates in North America and Europe. Their analyses considerably extend current work which has mostly been conducted at the species level and has not evaluated all three levels of diversity simultaneously. They found that all three levels of diversity were influenced by non-native species, and communities within and among the two regions are becoming increasingly similar. Nonetheless, climatic differences and geographic distance between North America and Europe still seem to limit homogenization. Also on the theme of invasions, Alejandro Ordonez (and co-author Olf Han) evaluated how patterns of species and functional trait distribution of co-occurring native plants varied across a nested series of spatial scales. Their analyses revealed the importance of both trait-based environmental filtering and local-scale factors on the distribution of invasive species.

George Roderick and colleagues contributed a different perspective on the topic of community assembly. They used a series of case studies of crops and their herbivorous pests and natural enemies to uncover patterns of assembly of co-occurring species in the Mediterranean. They found that some herbivores and their natural enemies were already present in the region before crop domestication, while others were associated with subsequent movements of domesticated crops into the region, both early and more recent. The variety of mechanisms by which pests of crop plants moved into the Mediterranean highlights the complexity of the origins of these multispecies interactions, and the challenges associated with conserving—the earliest known—native diversity. Harris Nyeema (with co-author Robert Dunn) also evaluated multispecies interactions and the diversity of co-occurring species, in their study of carnivores and their parasites. They modeled host-parasite associations to explore the consequences of loss of carnivore diversity (29 species) in North America on zoonoses (i.e., diseases transmitted between humans and wildlife) and the implications for parasite diversity and conservation. They showed that the loss of carnivores was a potential human and wildlife health risk, and a concern for parasite conservation because it increased the overall proportion of zoonotic parasites (relative to non-zoonotic parasites) and parasite homogeneity.

Lira-Noriega, Villalobos and colleagues presented a method to simultaneously analyze species richness and range size to identify distinctive assemblages of species. Distinctive assemblages are both species rich and harbour small-ranged species, the combination of which is not always included in conservation assessments. They found that distinct assemblages are poorly represented within the Mexican national reserve system, and thus these tools have clear conservation value.

The final talk in the session, presented by Leticia Ochoa-Ochoa, used the golden toad story (*Bufo periglenes*) as a case study to evaluate how some science stories influence the media, and peoples' resulting perception of biodiversity loss. She and her colleagues explored the emergence of the words "biodiversity crisis," in the media from the 1987 to 1992, and suggest that the toad was instrumental in shifting society's perception of biodiversity loss. More broadly, they emphasized that conservation biogeographers (and conservation biologists in general) know little about how the media perceives their work and the impact it could have on societal views towards the conservation of biological diversity.

In summary, these talks touched on many of the themes and challenges to conservation biogeography outlined by Ladle and Whittaker (2011). A critical challenge is to implement and

disseminate the new knowledge and tools to conservation practitioners and the public.

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Edited by Michael N Dawson

## symposium summary

# Hot topics in biogeography and ecology

A contributed session at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

The "hot topics" session of the Meeting of the International Biogeography Society (IBS) aimed to highlight new developments and ideas in the field of biogeography. While there was no predetermined theme linking the presentations, several topics were raised by several presentations during the session. For example, it was apparent that molecular data have become increasingly instrumental to furthering our understanding of biogeography, including distribution patterns, dispersal routes, historic events, ecological trait variation and community assembly. In addition, multidisciplinary studies (e.g. drawing data from ecology, morphology, climatology, geology, species distributions and molecular phylogenies) employing recent methodological advances were shown to provide a deeper understanding of several long-standing questions in biogeography and macroecology. Here, we summarize the presentations that made up the session and attempt to highlight their significance.

In recent years it has become increasingly apparent that long-distance dispersal events are responsible for the disjunct distributions of many organismal groups (de Queiroz 2005). What have been less explored are the factors that facilitate such dispersal—and subsequent colonization—events. Peter Linder and colleagues used a dated phylogeny of danthonioid grasses to infer their long-distance dispersal routes. This allowed them to explore the effects of factors such as dispersal distance, prevailing wind direction, the nature of dispersal routes and the age of source areas on the probability of long-distance colonization events, of which the age was the main explanatory factor.

The field of community phylogenetics (Webb et al. 2002) has provided novel tools to recover patterns in ecology and species distribution. Employing such tools, Catherine Graham and colleagues presented their work on patterns of morphological variation in hummingbirds across

an elevational gradient from tropical lowlands to the high Andes. Building on their previous work (Graham et al. 2009), they combined phylogenetic, morphological and ecological data to discover that traits vary with elevation and that environmental filtering is particularly strong at high altitudes. Furthermore, they provided evidence that traits vary evenly across the elevational gradient, pointing to niche differentiation.

Daniel Kissling and co-authors combined phylogenetic with global distribution data of the palm family to assess the degree of phylogenetic clustering (higher relatedness than expected from random) within geographic regions (Webb et al. 2002). At this large spatial scale they observed spatial heterogeneity in phylogenetic clustering and could therefore identify areas where palms have undergone radiations, though they also concluded that clustering was scale dependent.

Carina Hoorn and colleagues also used a multi-disciplinary approach to address one of the most persistent objectives of macroecology: to elucidate the drivers of species richness patterns from a mechanistic perspective. By linking geologic events and their consequences for climatic changes to the patterns of diversification across a range of taxa, Hoorn et al. proposed explanations as to why the Amazon is the most species-rich area of the world (see Hoorn et al. 2010). Evidence suggests that the uplift of the Andes was responsible for much of the current Amazonian biodiversity, as it shaped the greater region by changing climatic patterns, water courses and local habitat mosaics.

David Storch and colleagues tackled species richness variation from another perspective. Geometric models were employed (Šizling et al. 2009) to test Rapoport's rule (which states that geographic extents of species decline from high to low latitudes) and Stevens' principle (species' environmental tolerances increase with latitude), which attempts to explain Rapoport's rule (Stevens 1989). They tested whether latitudinal clines in range size could be simulated under different biological (Stevens' principle) and geometric (including geographic barriers to ranges) constraints. Simulations indicated that, while

Rapoport's rule could be generated under various conditions, Stevens' principle resulted in a reversed Rapoport's rule. This work provides insights into evaluating the role of species tolerances and dispersal boundaries on diversity patterns.

Finally, Sofia Silva presented an assessment of longitudinal distribution patterns of vertebrates of the Atlantic forest, one of the most species-rich biodiversity hotspots. Compiling distribution data from the literature, she and her team confirmed the presence of a longitudinal distribution pattern in the Atlantic forest, but a more complex one than previously thought. Using a technique that draws tracks linking occurrence data, they found support for currently recognized hotspots of endemism and uncovered previously overlooked hotspots. Their study demonstrates the underlying complexity of the biogeographic history of biomes (Carnaval et al. 2009), which should be taken into account when making decisions about their conservation.

The "hot topics" session illustrated how new methods, simulations, and collation of data from across disciplines continues to advance our understanding of biogeography. It will be interesting to see how the field has advanced when the next IBS meeting happens in Miami in 2013.

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Edited by Matthew J. Heard

### symposium summary

## Climate change biogeography

A contributed session at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

Anthropogenic climate change and its realized and potential impacts on biodiversity represent the kind of large-scale complex phenomena for which the integrative broad-scale view of biogeography is especially useful. This was well exemplified at the 5<sup>th</sup> IBS conference's contributed papers session on "climate change biogeography". Earth's climate has exhibited marked changes and fluctuations in the past, and several studies (B. Sandel et al., Aarhus University; G. Rodriguez-Castañeda et al., Umeå University) provided deep-time perspectives on climate-change impacts on biodiversity, showing that the location and extent of long-term climatically stable areas have left strong imprints in current large-scale species diversity patterns. An important implication of these studies is that much species diversity may depend on climatic stability. Linked to this several studies addressed the complexity of ecological responses to current and expected climate change, showing that tree-lines may recede despite a warming climate, due to the interacting effects of fire and dispersal limitation (C.D. Brown and J.F. Johnstone, University of Saskatchewan), and that different ecological groups of closely related species may exhibit deviating responses to climate change, e.g. due to differential dispersal abilities and contingent differential lags in their responses

to climate change (C. Hof et al., University of Copenhagen). Finally, several studies highlighted the potentially critical losses due to 21<sup>st</sup> century climate change of not just species diversity, but also of unique evolutionary lineages within species (E. Vázquez-Domínguez et al., Universidad Autónoma de México). Even more worrying is the risk of wholesale loss of biodiversity from Amazonia, one of Earth's most biodiverse regions (K.J. Feeley et al., Florida International University). Together the studies presented not only illustrate how progress in our understanding of climate-change impacts on biodiversity is being provided by biogeographical research, but also illustrate how the field is rapidly advancing by creative development and application of sophisticated modeling approaches that integrate ecology, physical geography, and genetics.

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Edited by Dan Gavin

## symposium summary

## Island biogeography

A contributed session at the 5th International Biogeography Society Conference – Heraklion, Greece, 7–11 January 2011

It is now almost 50 years since the publication of Robert H. MacArthur and Edward O. Wilson's 1963 paper, *An Equilibrium Theory of Insular Zoogeography* which led to their famous book, *The Theory of Island Biogeography* (MacArthur and Wilson 1967). These publications were instrumental in a switch from a static, historically oriented biogeography, based in the direct interpretation of the data collected in the field, to a 'dynamic' equilibrium paradigm, based on a synthetic approach to biogeographical processes.

By their nature, the processes underlying biogeographic distributions and evolution on (remote) islands occur on large scales of time and space and remain among the most difficult to study and understand. Although some of the topics emphasized by MacArthur and Wilson still remain relatively unexplored, recent advances in island theory demonstrate that we are moving towards a new synthesis, identifying and incorporating aspects of the island systems that were not considered in the past. All the talks in the island biogeography session pointed in this direction.

One of the first lessons taught to us by Wallace, decades before MacArthur and Wilson, is that comparisons among different archipelagos and biogeographic regions of the globe can offer significant insights and increase our understanding of the processes regulating biodiversity across time and space (see Wallace 1887). Daniel Carstensen and colleagues compared the biogeographical patterns of birds in Wallacea and the West Indies, adopting a network approach to detect biogeographical modules (i.e. sub-regions of islands compartmentalized on the basis of a common avifauna) and the roles of each island according to its spatial location and the topology of the geographical network. They discussed the relative importance of island features and species richness on the local and regional fauna of the two biogeographical regions. Similarly, Silvia Aranda and co-workers compared, within the framework

of the *Theory of Island Biogeography*, the effects of area, isolation, geological age and climate on bryophyte species richness on Macaronesian Islands. They provided evidence that, in addition to area, it is necessary to quantify other variables that are also critical for the establishment of biodiversity and at the same time have high explanatory power (such as island age and climate), if we are to build up a more predictive science of species richness variation across island systems.

However, island area remains the most powerful single variable in explaining variation in the number of species occupying an island and the species–area relationship (SAR) is one of ecology's few laws. Even and Kathleen Tjørve showed that we should consider with caution the common assumption that the power law of Arrhenius is appropriate for both sample-area (mainland) SARs and isolate (island) SARs. Especially regarding isolate SARs, they argue that the form of the relationship is actually sigmoid when the finest scales are included. Based on this assumption, they proposed a new species–area model and presented results from different archipelagos and taxa.

Fifty years ago E.O. Wilson, studying Melanesian ants, coined the term 'taxon cycle' to describe 'the inferred cyclical evolution of species [of Melanesian ants], from the ability to live in marginal habitats and disperse widely, to preference for more central, species-rich habitats with an associated loss of dispersal ability, and back again' (Wilson 1961). However, the taxon cycle has, until recently, been difficult to test (see Ricklefs and Bermingham 2002). Evan Economo and Eli Sarnat evaluated taxon cycle predictions with a new dataset on habitat distributions of the entire Fijian ant fauna and a community phylogeny for one of the genera present in that archipelago. They provided evidence that as lineages progress to higher levels of endemism, they undergo shifts from marginal to interior primary habitats, from ecological generalism to specialization, and from

high to low population density, consistent with one of the major predictions of the taxon cycle.

One of major driving forces considered in the taxon cycle and most importantly in the *Theory of Island Biogeography* is (natural) extinction. The extinctions caused directly and indirectly by humans colonizing isolated islands of the globe have been dramatic (Steadman 2006). Alison Boyer and Walter Jetz quantified the distribution of functional diversity, a major component of biological diversity, in 45 pre-historic island bird communities of the Pacific and documented its reduction via species extinctions over the past 3,500 years. They concluded that the loss of functional diversity in the system under study is highly predictable from the pre-extinction composition of communities, with island age and isolation being less important determinants.

One of the major challenges for the *Theory of Island Biogeography* has been understanding the origin of the diversity patterns on oceanic islands. The conceptual model of MacArthur and Wilson (1967) has been less successful and is arguably less complete when applied to oceanic island systems. Although they already recognized that on the more remote islands increasing proportions of the biota are the result of *in situ* evolutionary change, they chose to focus on the immigration–extinction dynamics for simplicity. The recognition of this shortfall has led to the introduction of new theories (e.g. Whittaker et al. 2008) but other challenges remain, such as species–abundance distributions on islands. James Rosindell and Albert Phillimore presented a new unified model of island biogeography (Rosindell and Phillimore 2011), based on the neutral theory of biodiversity and biogeography (Hubbell 2001), aiming to tackle these major issues. Most of their model’s predictions are consistent with a broad range of patterns in empirical data and existing theory. This integration of classic island biogeography with neutral theory provides a critical addition to the existing theoretical framework for describing and understanding the evolutionary biogeography of oceanic islands.

It is an exciting era for island biographers; it is now more obvious than ever that no theory is

an island. We are moving towards refining existing theories, introducing new ones and eventually new syntheses. I hope that, in the next IBS meeting in Miami (2013), held 100 years after the passing of Alfred Russel Wallace, and 50 years after the publication of MacArthur and Wilson’s (1963) seminal article, island biogeographers will be able to celebrate new theories; *we still have some of the Cretan spirit, raki, left...*

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Edited by Joaquín Hortal

## book review

## Bread, butter and marmite

Climate change impacts on freshwater ecosystems, by Martin Kernan, Richard W. Battarbee and Brian R. Moss (eds.)

Wiley–Blackwell, 2010, 328 pp. ISBN: 978-1405179133

Price: £45 (Hardback)

<http://www.wiley.co.uk/>

This book summarizes the outputs of Euro-limpacs, a major European Union (EU)-funded project which investigated the impact of global change on freshwater ecosystems. As the title of the book suggests, the focus is on assessing the impacts of climate change on lakes, rivers and wetlands. However, the breadth of the material covered here is greater. The book aims to quantify and model past and recent climatic impacts on freshwater ecosystems, but also to predict the consequences of future change. The book also covers the numerous problems such as contamination with pollutants and structural modifications that will influence potential responses of inland waters to climate change. The pervasive nature of such problems means that they must be considered in order to give useful insights into future climate impacts. The material covered thus more truly concerns global and environmental change than simply climate change. The scope of the project acknowledges the importance of considering processes at a catchment scale and thus some of the material considers how terrestrial responses translate into changes in water bodies. The policy implications for the work are also considered, with chapters covering implications for existing legislation (with a focus on the EU Water Framework Directive) and ideas for translating science into policy.

As might be expected of an EU-funded project, the majority of the work within this book concerns research in Europe. The geographical context is important because there is great diversity in climatic conditions across Europe which opens up possibilities for research (e.g. spatial comparisons), but also increases the challenge of mitigating and adapting to future change. Europe also has a long history of human disturbance, with some areas being intensely affected by anthropo-

genic change and others being relatively pristine. There are also barriers to dispersal of organisms across parts of Europe that will influence how species ranges adapt to climate change. The context in which climate change is being dealt with therefore varies spatially. Thus, although there has been a marked growth in research on climatic impacts on freshwater globally, there are good reasons to focus on Europe. As might be expected, European studies are placed into context by reference to literature from other geographical regions.

This book should attract a broad readership because of the range of subject matter covered. In contrast to similar books (e.g. George 2009) it deals with rivers, lakes and wetlands and therefore should appeal to a wider spectrum of freshwater scientists. It acknowledges the importance of anthropogenic stressors in chapters on hydrology and morphology (Chapter 4), eutrophication (Chapter 6), acid deposition (Chapter 7) and persistent organic pollutants and mercury (Chapter 8) and so should be of interest to researchers in these fields.

One of the interesting aspects of this book is that it includes a diverse array of methodological approaches. The scientific studies presented use long-term monitoring programmes, spatial surveys, palaeolimnology, experiments (from microcosm to ecosystem scale) and various modelling approaches across a broad range of scales. There are also chapters that may interest social scientists concerned with policy development and implementation (e.g. Chapter 11 – “Tools for better decision making: bridges from science to policy”). This combination of material creates a book that facilitates the cross-fertilization of ideas among subject areas and disciplines.

The presentation of this book is stylish, with

plenty of clear colour diagrams that would lend themselves well to undergraduate teaching. However, it is probably pitched at a level most appropriate to postgraduate students, expert practitioners, academic researchers, or to undergraduates doing research projects. There is good cross-referencing and linkage among chapters and thus, in contrast to some edited books, this reads like a coherent piece of work rather than a collection of individual chapters. One of the stand-out features of this book, though, is that the 'bread-and-butter' chapters are crowned with the final chapter ("What of the future?") written in uniquely flamboyant style by Brian Moss. This provocative chapter pools the thoughts and experience of experts in the field to take the reader on a journey through the climatic ecozones of Europe to imagine what the future will be like. The settings for this chapter are the River Erehwomos in the arctic/boreal ecozone, the River Gutflave in mid-continental latitudes, the island of Hibscotia representing peninsulas and islands and the River Graecerina in the Mediterranean region. The resulting chapter is limnological marmite. The descriptions of the future focus largely on the nega-

tive impacts of future warming and are likely to antagonise those optimists who advocate technological innovation as the answer to climate warming. However, the material in this chapter builds on a sound scientific base and when considered in the context of the error margins of some numerical models, there is no reason to consider that these models of the imagination are any less realistic a scenario. Whether you agree with the interpretation or not, this is a fun approach to science that makes the book all the more enjoyable.

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Edited by Markus Eichhorn

### book review

## A truly colourful inter-continental tropical kaleidoscope

Tropical Rain Forests – An Ecological and Biogeographical Comparison (second edition), by Richard T. Corlett and Richard B. Primack

Wiley-Blackwell, 2011, 336 pp. ISBN: 978-1-4443-3255-1

Price: £55.00 (Hardback) / £34.95 (Paperback)

<http://www.wiley.co.uk/>

On Sunday 21 October 1492, Christopher Columbus wrote of the Caribbean Island that he calls "Cabo de Isleo" that

"The trees are of many kinds, each with its own fruits, and all have a marvellous scent. It grieves me extremely that I cannot identify them, for I am certain that they are all valuable".

Columbus was no botanist but he paid attention to plants —he was keen to find the Asian spice trees he had promised to his sponsors. His diaries show his recognition that the plants of the West Indies were different to those in Africa and Europe.

As Columbus was aware, forest communities differ depending on their continental context. Far from being uniform formations, where valued resources known from one location such as the nutmeg, cinnamon and cloves of Asia can be anticipated in similar settings elsewhere, forests are diverse and their communities differ markedly with location. Observations from one site may or may not apply to another. Seeking Asian spice plants in Caribbean forests only seemed reasonable while these islands were judged to be Asia.

While few actually set out to argue that all tropical forests are similar it is often a default as-

sumption. How frequently do we see research conclusions from one region applied unquestioningly to another? It is common and each is a possible error. Every tropical region has its own characteristics and we generalise at our peril. In *Tropical Rain Forests* the authors explore and summarise many differences among the rain forests of Africa, the Americas, Madagascar, New Guinea (and Australia) and Southeast Asia. They also consider a host of island forests.

The authors stated in the preface to the first edition that they hoped that their readers

“will come away with an appreciation that our planet is host to not one monolithic tract of rain forest, but many unique tropical rain forest habitats, all worthy of study and protection.”

It was a simple idea and they succeeded with style. Now they are back with more. This second edition is extensively updated throughout — indeed it is a substantially different book to the first. It is available as a paperback. It includes a new chapter on island ecosystems. There are now even more illustrations and the entire book is printed in colour.

The book's nine chapters focus on the global setting and history, plants, primates, vertebrate carnivores and plant eaters, birds, fruit bats and gliding vertebrates, insects, island forests, and threats (“the future”). Chapters are packed with examples and most conclude by posing intriguing questions and offering suggestions for comparative studies.

The book offers a well-judged balance between many details of natural history and more general ecological summaries. I enjoyed the stimulating selection of facts and ideas. It is hard to capture the flavour, but by opening the book at random and browsing for a moment I can offer some illustrations. One example (p. 155) concerns the dietary overlap and complementary diversity patterns of parrots and squirrels—is it perhaps that a high diversity of one necessitates a low diversity for the other? Another (p. 172) notes that Madagascar's bizarre aye-aye (*Daubentonia madagascariensis*)—a wood excavating lemur—and New Guinea's striped possums (*Dactylopsila* spp., also excavators but marsupials) occur in re-

gions lacking woodpeckers. Is this a coincidence? Want some more? OK, let us compare the manner in which different regions' fruit bats feed (p 189): only the paleotropical pteropodids regularly spit out fibrous material after prolonged chewing—the neotropical phyllostomids are more likely to swallow seeds. But apparently such differences cannot explain (p. 193) the low reliance of Asian pioneer vegetation on bat dispersal when compared to otherwise similar American vegetation—when neotropical pioneers have been introduced to Asia they are effectively spread by Asia's pteropodid bats. Another? The close relationship between oil gathering bees and oil providing Malpighiaceae plants is entirely neotropical—though these plants have colonised the paleotropics these species have adopted other pollinators and no longer provide oils (p. 231).

Yes there are minor quibbles. For example, one or two graphics lack adequate explanation, e.g. in Figure 9.6 we remain uncertain what is meant by the distance that an “edge effect” penetrates, as no clarifications are provided (perhaps more importantly given the book's theme the idea that such patterns may differ with location and among continents also remains unexplored). A few more references to link key facts to sources would have been welcome too. I'd also have preferred more consideration of variations within continents and what these might tell us—but of course that would have required a substantially larger book. Perhaps the third edition...

In summary: this is a fascinating book. I enjoyed it, I learned from it and I recommend it. It will be of value to academics, researchers and students, and, due to its accessible style and illustrations, it will appeal to many others too. Columbus would have found it helpful—but over half a millennium later so might many of us.

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Edited by Markus Eichhorn

## book review

## The ecology of place

The Ecology of Place, by Ian Billick and Mary V Price (eds.)

University of Chicago Press, 2011, 512 pp. ISBN: 0-226-05043-2

Price: US \$120 (Hardback) / US \$45 (Paperback)

<http://www.press.uchicago.edu/>

As a long-term student of the ecosystems of South Sinai, I have come to appreciate myself the immense value of being in for the long haul. The new insights brought by just working there every year constantly amaze me. The first 15 years were pure biology, but more and more I appreciate the subtle contributions that the Bedu have made in renewing, enhancing and maintaining the mountain ecosystem. In fact, I have gradually come to believe that maintaining Bedouin traditional practices is the single most vital action required to conserve its arid and punishing landscape. So it isn't hard to convince me of the value of the 'ecology of place', the aim of this book.

What is the value to ecological science of long-term studies of one particular location? The 75th birthday of the Rocky Mountain Biological Station in Colorado created an opportunity to reflect on the contribution that such studies have made, and their position in ecological science in general. Edited collations of papers are always a risk, but here the book succeeds in its aim remarkably well, making it well worth reading.

Biological scientists adopt one or more of three main modes of working: studying questions, taxa or places. Proponents of each mode deride the others, often in the most vitriolic manner. Question-driven science has had the upper hand for the last 20-30 years, and in particular the purse-strings of grant makers, enabling them to cast whole groups of researchers into the wilderness. It's a game of power, not science. Those who study taxa are mere 'stamp collectors'; those who study places are merely 'monitoring', or doing science that shows 'intellectual weakness', a mere 'inductive boiling of hypotheses, with too little effort to place the work in a more general ecological context' (Peckarsky et al. chapter). In this way the eradication of taxonomy and systematics as an intellectually respectable discipline in the UK has

been achieved.

Whether a hypothetico-deductive (H-D) approach actually is more productive, and really does move a discipline forward more quickly, is a question crying out for an answer. Biology needs definitively to junk its 'physics-envy', and embrace the idea—virtually unacknowledged until recently—that it is a fundamentally different kind of science from others because of the importance of contingency, variability and history. Nearly all of its theories are exemplar-based attempts at generalising based on very limited sampling of the biological universe. Is it really better to work in a top-down mode, the H-D testing of theory? Or in a bottom-up mode, searching for broad generalisations from studying units, either taxa or places? It isn't clear to me that either has logical primacy, and I know of no evidence from biology that either is a quicker mode of progression.

Ecologists in particular seem to spend a good deal of time and effort navel-gazing about the alleged slow progress we are making. There is no shortage of suggested solutions: we suffer from "weakness of method: there is too much natural history; there is too little natural history; we need more experiments; we should be looking for patterns; we should be studying mechanisms; we should be integrating; we should be using strong inference and rigorous hypothesis-testing; we do too much hypothesis-testing and not enough model-fitting; there is too much theory; there is too little theory, or theory of the wrong sort" (p. 2 of the book).

We forget that we are studying the difficult questions of Nature. Physics, molecular biology, genetics, physiology—all are simple sciences relative to the study of ecological communities. How organisms perform in Nature is so contingent, variability so essential to the result, it is hard to see pattern and mechanism. The role of chance is large. The role of history is very large. Thus ecology is either

as simple as any other discipline but for our stupidity in not looking at problems in the correct way, or it is a different kind of science altogether from those hitherto considered by nearly all philosophers of science.

This book suggests that the long-term study of a single system, the *ecology of place* represents a third mode of study to the top-down H-D and bottom-up study of units. I am not convinced it is different from the latter mode. The addition of 'long-term' is not the issue, since many biologists spend their lives studying in great depth a single question, or a single taxon, or indeed, a single place. Surely there are two axes here: the type of study (question, taxon, place) and mode (short-term studies of many units to obtain breadth, long-term study of a single unit to obtain depth). In terms of community ecology, macroecology is an example of the former mode, and the *ecology of place* the latter. The book is written by North Americans about the study of American places. It is a pity to have such a narrow focus, and the attempt is made to claim the whole topic as an American invention stemming from Aldo Leopold. Well, this is news to most European ecologists, where long-term studies of particular places have been the norm rather than a novelty for a very long time.

Nevertheless, the contributions are remarkably good. The unitary purpose of the book creates a thought-provoking and stimulating read, with an entirely convincing message of the fertility and importance of the ecology of place to the science. Chapters are divided into five sections: the history of the idea; the insights gained; the development of local models; the generalisations that emerge; and encouragement to build capacity. All contributing are interesting, with some really excellent, heuristic and thoughtful explorations of the various aspects of the topic.

Sharon Kingsland writes beautifully on the history of the *ecology of place*, tied up as it is with the establishment of field stations. The claim is that after Darwin and the voyage of the Beagle, British and European biologists resolutely retired to the laboratory with their field-collected specimens, leaving the establishment of true field-

based research to the North Americans. She documents the interesting theory of Margalef, who thought that ideas could be traced to the influence of the places whose study gave rise to them. Thus desert ecologists emphasized the role of the weather; Alpine ecologists, the plant communities; Scandinavian ecologists, population biology; and ecologists working in the American Midwest, the idea of succession.

Ronald Pulliam and Nickolas Waser's very thoughtful article asks whether there are ecological invariants, using the fundamental niche as an example. Like Vincent Dethier's failed attempts to iron out neurophysiological variation in a feeding blowfly to use invariant responses as a baseline, Pulliam and Waser show just how difficult it is to establish anything invariant about species and communities.

A masterful summary of work done over more than 30 years on Darwin's finches on islands in the Galapagos by Peter and Rosemary Grant shows how exceptionally useful deep long-term study of one place can be. The results are not at all parochial, but on the contrary, illuminate and advance important generalities of evolutionary ecology. In particular, the rare events only picked up by such long-term dedication turn out to be vital structuring elements of the whole system.

Another exceptional contribution by Stephen Hubbell documents the series of hypotheses tested in his 29 years of studies on Barro Colorado Island about how tree species coexist. In this case the study was planned as long-term because the longevity of many tropical trees made it likely that mechanisms of coexistence might only be evident over several decades. Interestingly, the tree composition on the 50-ha plot turned out to be far more dynamic than anyone had imagined.

These are but a sample of the excellent set of contributions, drawn together by insightful and valuable prefaces to each section, and a final summary, by the editors. The volume is timely because of the lamentable state of field stations in Europe, casualties of government cut-backs and the bean-counting culture that knows the price of all but the value of nothing. The hope is that books like this will renew confidence in field sta-

tions, and underline the value of their outputs in long-term field studies. These might restore them to their rightful place in the ecological pantheon, places where students can learn to appreciate the insights they offer, and hence maintain them.

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Edited by Markus Eichhorn

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## book review

# Macro-ecology of the world's savannas

Ecosystem function in savannas: measurement and modelling at landscape to global scales, by Michael J. Hill and Niall P. Hanan (eds.)

CRC Press, 2010, 623 pp. ISBN: 978-1-4398047-0-4

Price: US\$159.95 (Hardback)

<http://www.crcpress.com/>

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A quarter of a century has passed since the 'legacy work' of Tucker and collaborators (e.g. Tucker et al. 1985) characterizing the spatio-temporal dynamics of vegetation using temporal series of NDVI data from the NOAA AVHRR sensor, notably over the Sahel region. In the meantime, thanks to advances in Earth Observation (EO), an impressive array of technologies and methods has emerged, multiplying the number of biological and physical variables that can be measured, mapped and monitored over broader spatial and temporal scales than ever before. Progress comes from the development of new sensors, but also thanks to numerous initiatives aiming at facilitating data accessibility, the most recent of which is the launch of the Google Earth Engine© platform.

Therefore, although a number of books exist on savanna ecology, the time is definitely ripe for a general survey of where we are, after these crucial developments, in our understanding and monitoring capacity of savanna ecosystems. This is what Hill and Hanan, along with an impressive team of renowned contributors, have achieved in this volume, notably by bringing together different communities working respectively on field measurement, remote sensing assessment and modelling of savanna structure, dynamics and biogeochemical fluxes at landscape to global scales.

A central question, which continues to stimulate the scientific community, concerns the determinants of tree–grass coexistence in savannas. Mainstream hypotheses are reviewed

(chapters 2 and 13), such as bottleneck models, in which perturbation by fire, herbivory or drought tend to reduce tree density, as opposed to the so-called Walter niche-separation hypothesis, according to which trees are maintained by access to deeper soil resources. Of course, real mechanisms are a great deal more complex, and a number of feedbacks and interactions between plants (facilitation and competition), and with grazers or browsers, are detailed. We could further argue that the question itself of 'tree–grass coexistence' might be stated in over-simplified terms, because not all tree and shrub species, for instance, show the same dynamics and strategies with regard to fires and herbivory (see e.g. Beckage et al. 2009).

Given the number of variables interacting in different soil and climate contexts (well presented in chapter one), and the spatial and temporal scales involved, it is clear that empirical/experimental approaches are difficult to implement. The combination of 'natural experiment' approaches with modelling studies is therefore a good way forward. In the former, one investigates multiple correlations and interactions between biological variables and potential physical drivers, through space and time, using EO data; in the latter, these correlations can be tested in 'controlled' conditions *in silico*.

This brings us back to the technological developments of remote sensors. In a synthetic table (table 27.2), the authors list a range of biophysical variables that can be estimated at different reso-

lutions and extents, from detailed 3D structure using new LiDAR, radar and hyper-spectral optical technologies at landscape scales, to fractional canopy cover and fire history at broader scales and extents. Chapter 8 illustrates quite well the exciting possibilities offered by active sensors, including ground- and air-based LiDAR, for instance to obtain reliable biomass estimates. I cannot resist citing another recently published application (Levick et al. 2010), in which airborne LiDAR was used to map the spatial distribution and sizes of termite nests, an important factor in savanna ecology.

Linking these remotely sensed data to field measurements may yield impressive results, despite the difficulty of matching scales —especially for low resolution data. This is illustrated by the link found in chapter 4 between MODIS-derived fPAR (absorbed fraction of the photosynthetically active radiation) and carbon fluxes measured at an eddy covariance site in the Kruger park; or in chapter 11 by the relationships found for fractional canopy cover between (field) densiometer measurements of the tree canopy cover, airborne LiDAR-derived estimates and a parameter inversion using Landsat and JERS-1 backscatter data.

The importance of using spatially explicit approaches, is emphasised throughout the book. Table 14.1 for instance, lists some of the major spatial processes in savannas, together with their scale and effects. I strongly agree with this vision, but I would have appreciated some more emphasis on the possible ways to quantify the spatial structure of vegetation (in terms of scales of patchiness for instance), or to model how heterogeneous structures may emerge endogenously, within a given catenal, edaphic, or climatic context. In that respect, the potential of very high resolution (metric) optical imagery should be highlighted. Indeed, the hindsight provided by aerial surveys starting in the middle of the 20<sup>th</sup> century and the recent release of confidential digitised spy satellite (Corona) imagery, along with the current development of space-borne digital sensors (Ikonos, Quickbird, GeoEye, SPOT) provide splendid sources of information for the dynamics of savanna structure (e.g. Laliberte et al. 2004, Barbier et al. 2006, Deblauwe et al. in press).

A large portion of the book covers the modelling of savanna dynamics and biogeochemical fluxes at various scales and using varying modelling frameworks. A crucial point is of course how to integrate field and remote sensing data within these models. However, despite the potential of EO data to establish cross-scale links, the authors deplore that most of the time EO data are still predominantly used to define basic land-cover categories, whereas their potential for obtaining quantitative estimates of biophysical variables remains largely underutilized. This certainly justifies the desire, expressed in this book, to build bridges across disciplines.

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Edited by Markus Eichhorn

## books noted with interest

***Driven to extinction: the impact of climate change on biodiversity***

Richard Pearson

2011, Sterling Publishing, 264 pp.

US \$22.95 (Hardback) ISBN: 1-4027-7223-8

<http://www.sterlingpublishing.com/catalog?isbn=9781402772238>

A primer on one of the most contentious topics in modern ecology, drawn from the scientific literature, and aiming to take a balanced view. Written in a light style with short, easy-to-read chapters, this would make an ideal inspiration for young scientists, or serve to convince a sceptical friend. Although the detail presented is not sufficient for use as a textbook, full references are given in footnotes, while photos illustrate many of the organisms presented. It should act as an effective counter to misinformation elsewhere and includes an insightful discussion of the difficulty of communicating science both accurately and effectively.

***Ecology (2nd edition)***

Michael L. Cain, William D. Bowman and Sally D. Hacker

2011, Sinauer, 648 pp.

\$119.95 (Hardback) ISBN: 978-0-87893-445-4

[sites.sinauer.com/ecology2e](http://sites.sinauer.com/ecology2e)

Though there is currently a glut of ecology textbooks on the market, this remains my personal favourite, largely due to its superior coverage of processes at the community, ecosystem and biome levels, and therefore particularly appropriate for biogeographers. Written in an accessible style that stresses key concepts, and filled with colourful illustrations, this will appeal to students and instructors alike. Unsurprisingly given the authorship, a large proportion of the examples are North American, though the range of life forms covered is admirably broad. A plethora of student exercises are available in the book or on the companion website. Highly recommended.

Markus Eichhorn

Book Review Editor.

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## Interview with Robert E. Ricklefs, recipient of the 2011 Alfred Russel Wallace award

by Rosemary G. Gillespie

Division of Organisms and Environment, University of California at Berkeley, USA

**Rosemary Gillespie:** You started working on islands as a new graduate student. Why islands?

**Robert E. Ricklefs:** When I arrived at the University of Pennsylvania to begin graduate studies with Robert MacArthur, he and Ed Wilson had just published their seminal paper in *Evolution* on the “theory of insular zoogeography.” It was only natural that I turned my attention to islands—and birds because I had for years been an avid bird-watcher, as was MacArthur; the West Indies because James Bond at the Academy of Natural Sciences of Philadelphia had published a distributional checklist. I quickly developed a scheme postulating changes in bird distributions in the islands similar to Wilson’s “taxon cycle,” but MacArthur felt that historical hypotheses were untestable and discouraged further work. I slipped in some observations of bird distributions on the island of Jamaica one summer, which resulted in a 1970 publication, but did not return to the topic until I had become an Assistant Professor at Penn., and began a collaboration with George Cox, a superb ecologist and naturalist at San Diego State University. My doctoral thesis at Penn. addressed issues in bird life histories—nothing on community ecology or biogeography.

**RG:** You began your career in the 1960s, following in the footsteps of Hutchinson and MacArthur, and at a time when the ideas of Lotka and Volterra were highlighted, competitive exclusion was a new and important topic, along with related themes of niche specialization, ecological sorting, limiting similarity, and community saturation. How important were these in shaping your ideas and the field of biogeography in general?

**RER:** One had to be impressed by the power of competition, and other types of interactions, revealed in experimental studies. Most ecologists brought up in the Hutchinsonian tradition be-

lieved in niches and in resource limitation. These properties of systems were the basis for character displacement, density compensation, and other ecological and evolutionary phenomena. So, all these elements fit together well. Community saturation was perhaps the weakest aspect of the developing theory, as this was difficult to demonstrate experimentally in natural systems, and similar environments in different regions sometimes supported very different numbers of species. The degree to which species interactions constrained species ranges and probabilities of establishment following dispersal were harder to judge, although some ideas about biogeography, such as Jared Diamond’s checkerboard distribution patterns, had an essentially ecological foundation.

**RG:** The 1960s were also the early days of plate tectonics, and the start of panbiogeography, cladistics and vicariance/dispersal debates. How much interaction did you see between these fields? How did they inform one another? How did discussions with the different players affect your thinking?

**RER:** As an ecologist, these developments had relatively little influence on me. Ecologists were relatively indifferent to phylogenetics (as opposed to evolution) at the time, and to any kind of historical explanation, although we were very much interested in adaptive radiation, convergent evolution, character displacement, and evolutionary ecology. From my perspective, the debates concerning panbiogeography, cladistics, and vicariance/dispersal were peripheral issues, and the kind of biogeography involved in these debates seemed to have little connection to ecology. These were historical/geographical issues, and were not discussed widely among ecologists.

Similarly, ‘island biogeography’ was considered as distinct from ‘community ecology’. The

perception was that islands just didn't have enough species for ecological limitations on diversity to play a major role. The ecological space on islands wasn't saturated with species. Rather it was colonization limitation and area-dependent extinction that prevented the buildup of a lot of species. Islands were regarded as quite different from mainland continental areas. Moreover, MacArthur wanted ecology to have a quantitatively rational basis; he was very oriented towards understanding predictable processes. Considering these fields separately allowed them to develop in their own logical frameworks.

**RG:** Was there an active shift that really started the integration between island biogeography and evolutionary biology?

**RER:** One really has to go back to David Lack and the Galapagos finches. His book (*Darwin's Finches*) is very explicit about character displacement, mechanisms of diversification on islands, and how species partitioned resources. People tend to forget about his major contributions. Lack's themes were picked up by Peter and Rosemary Grant in their seminal work on *Geospiza*, and on it went from there. Likewise, the *Anolis* studies grew out of the Ernst Williams' group at Harvard. Williams had a lot of foresight, with much emphasis on morphology and taxonomy, even if not in a phylogenetic framework. So that was around, especially in the general context of adaptive radiation.

**RG:** What about phylogenetics being applied to vicariance, and the ordering of the break-up of the continents?

**RER:** That happened later —mid 1980s or 1990s, in particular, when it became possible to date events. The integration of these different fields can really be thought of as a large, braided river, with channels separating and reconnecting the way that areas of research branch apart and come

together again in new combinations of ideas and approaches.

**RG:** You made several trips to the Caribbean early in your career. How important were these field trips in shaping your ideas. What advice would you give to beginning graduate students in terms of the importance and role of field work in developing projects and ideas?

**RER:** For ecologists, there is no substitute for working in the field —not just for gathering data, but also for developing 'insight' into natural systems, and making observations that challenge the views one has of nature. Perhaps biogeographers are more able to work solely from maps, but without the ecological dimension of space one can miss out on the transforming effect of environment on species and their distributions. I share the concern of many of the older generation of biogeographers that the increasing use of large-scale datasets and focus on computer-intensive data analysis is drawing students and young investigators away from the more time-consuming fieldwork. I also wonder whether the focus of macroecological studies on place —often latitude–longitude grid cells— is diverting attention from species distributions and ultimately might detract from the integration of ecology and biogeography.

**RG:** It seems that the early field excursion to Jamaica was very important in the development of your ideas. Would you recommend such an intensive field experience for beginning graduate students today?

**RER:** It's very difficult for students now, because the kinds of pressures they experience are much different than in earlier times. Having to produce 4-5 high-profile papers out of one's doctoral and postdoctoral years is a pretty high bar. So students feel a lot of pressure to publish results quickly, which is not entirely compatible with de-

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tailed field observation and the development of expertise with a given taxon. Having too little time to master a group of organisms or the ecology and geography of a region can deprive a student of valuable insight.

**RG:** So maybe one of the important things for students to do is develop mastery of one taxon.

**RER:** Yes, it's helpful, but often not easy to achieve. Some institutions have maintained their emphasis in organismal biology, with courses tied to collections and taught by people that curate those collections. But many have let go of this side of the organism-oriented curriculum in favour of equally important training in genetics, population biology, and other more experimental and analytical sides of biology.

**RG:** Over the years, you have collaborated with many people working in diverse areas, starting in the early days with Henry Hespenheide, Reed Hainsworth, George Cox, and others. What advice would you give to others, and especially students, as to the importance of building collaborations?

**RER:** Beyond being, for me, one of the most pleasurable aspects of science, collaborations are very important in developing broader perspectives and fostering integration and synthesis. Of course, there are the practical considerations that a single person cannot do everything and so collaboration brings complementary expertise together. The most successful and satisfying collaborations occur when researchers challenge each other to integrate their approaches—to find the commonalities in their different concepts of biological systems.

**RG:** You have a long-held interest in how communities develop in the context of regional processes. How have your ideas changed over the years?

**RER:** Starting out as an ecologist with a strong interest in island biogeography, particularly in the context of MacArthur and Wilson's equilibrium theory, I have always had a strong sense of the

impact of regional processes on localized ecological systems. Many other ecologists at the same time had similar perspectives, but from the 1960s through the 1980s, historical explanations were out of favour as being untestable and perhaps even unscientific for that reason. I was able to return to island biogeography 20 years after my initial work with George Cox, with the development of phylogeographic and phylogenetic analyses, and this allowed me and my collaborator Eldredge Bermingham to place distributional events on a time scale and test such time-dependent ideas as the taxon cycle hypothesis.

**RG:** You wrote the first version of the *Ecology* text early on. Where did you see the need at the time?

**RER:** The book was a major undertaking. In 1972 and 1973, 6 or 7 new ecology texts were published, largely as a reaction to the absence of population and evolutionary perspectives in the ecology texts available at the time. In ecosystem ecology, there was Eugene Odum's text—the text I used as an undergrad. But even that was primarily descriptive and not particularly quantitative, with little emphasis on formulating testable hypotheses in ecology. So people were reacting to this—ecology was becoming much more quantitative, much more scientific, much more process oriented, with a strong emphasis on adaptation, that is, evolutionary ecology.

**RG:** You have seen many significant developments in the field of biogeography over the years. What do you see as the major “game-changers” in the context of conceptual breakthroughs? Clearly the *Equilibrium Theory* was important. What other ideas stand out?

**RER:** Certainly the development of modern phylogenetic analysis has to have been the major game changer during the past decades. Placing a time scale and directionality on evolutionary divergences allowed one to infer areas of origin, directions and timing of major dispersal events, and to distinguish, in many cases, between vicariance and long-distance dispersal. Growing availability of palaeoclimate reconstructions and long

fossil series have also greatly strengthened our empirical foundations for interpreting the history and geography of life. Increasing data on distributions and improved analytic capacities are shaping many aspects of biogeography at the present time, although one might also lament the balancing decline of support for basic taxonomic and systematic research required to ensure data quality and to provide a context for determining the biogeographic implications of these data.

**RG:** There has been a lot of recent attention on community phylogenetics —ecological sorting, filtering, and niche modelling. Where do you see this going?

**RER:** This line of research has been productive, but often tells us little that we didn't already know in a less formalized context. Niche modelling has been used to look at changes in distribution under climate change scenarios and whether or not introduced species can spread. The problem is that one doesn't know ahead of time whether an introduced species can spread through conditions that are outside its range back home. So what is the appropriate distribution model for that species? How much is the distribution of that species back home controlled by factors that are unrelated to climate, but rather reflect interactions with other species? We really don't have a good handle on that. Moreover, in addition to climate, other factors such as soil and habitat structure, are important components. So progress will need to wait until we get a better handle on what the niche of a species is.

**RG:** What do you see are going to be the major exciting developments in the context of ecological/ evolutionary theory in biogeography?

**RER:** I would go back all the way to Ed Wilson and some of his contemporaries. What they considered important was the biogeography of species. At the moment we are hung up on the ecology and biogeography of places. We decompose regions into lat/long, grid cells, cataloguing what occurs in a particular place, rather than focusing on where a particular species occurs. So while en-

vironmental niche modelling and related approaches address species distributions, ecologists and many macroecologists focus on the local fitting of species into assemblages, rather than how populations of species are distributed and fit together in regional landscapes. So the integration of what species are doing individually, and what whole communities of species are doing in large regions, is ripe for development. I think that a focus on species populations as the fundamental units of ecology, evolutionary biology, and biogeography provides a natural direction for biogeography in the future.

**RG:** So how do we get there?

**RER:** Part of it may be giving up the place-oriented perspective that we have for research on certain types of questions. Islands are one thing — discrete, self contained. Quite different from setting down grid squares in South America, where it is better to look at distributions of species within these large regions and start to develop hypotheses as to why different species are distributed in different ways. Work has started, but in the context of trying to integrate all the species in a large area —their distributions, evolutionary history, interactions— we have a long way to go.

**RG:** How important do you think are the recent ideas that have come out of comparative phylogenetic and phylogeographic analyses of diversification?

**RER:** These models deal with evolution within phylogenies rather than evolution within communities or regions. Adding the additional layers of complexity is a challenge. Even defining the problems remains to be done in a useful way. The reality is that the diversity of species, and their geographic and ecological distributions within regions, unfold over evolutionary time. Do we have to tackle it at this level of complexity to really understand it? I suspect we do to achieve a fundamental understanding of what's going on. So how do we package this in such a way as to get all of that complexity and history and geography and evolutionary adaptation into a study system that is simple enough to get a handle on? Islands give

us advantages as they are discrete and not terribly diverse; and archipelagoes are very instructive because of their propensity to support species diversification. Whether we can scale up from these simpler systems is not clear, but it is a place to start.

**RG:** The argument has been made that the genomic era and the ability to sequence everything cheaply will allow us to answer many of these questions.

**RER:** I think that high throughput sequencing might make life even more confusing and challenging! Finally we will begin to understand the total diversity of ecological systems. And what is all this doing, and how is it maintained? We can generate hundreds or thousands of cytochrome b sequences or cytochrome oxidase I sequences from soil in a small patch of habitat, each representing a unique type of organism, with its own ecological role and history and distribution. It's obviously an important step towards characterizing diversity and distributions, but how will we generate new insights from such data.

**RG:** What would you recommend for students starting out in the field if they want to do something new and different?

**RER:** I would emphasize the importance of making connections across different traditions and areas of biology. Achieving integration and breadth is hard for students. We don't foster it enough in our academic structure, as departments are often divided and academic traditions confined. And it's often hard to master more than one area. But I feel that I have benefited from having a curiosity about many things —not unlike a stamp collector's curiosity! I find interest in almost anything. So I have pursued a lot of different issues in ecology and biogeography, which has enabled me to draw connections. I undoubtedly have sacrificed depth in some of my work, but it has allowed me to be more integrative and to pull disparate things together.

**RG:** Why do you think the public should care about (and fund) research in biogeography?

**RER:** I would certainly emphasize the commonly repeated social benefits of science in general: satisfying a deeply felt need to understand the world around us; providing information to help predict the consequences of global climate change, to help manage populations of economic importance and conservation concern, and to predict the emergence and spread of pathogens. Beyond these considerations, science is a defining aspect of our culture and civilization, and its practice in the context of a wide variety of phenomena, including the evolution and distribution of life on Earth, helps to maintain a certain level of analytical competence in society as a whole. Our success depends in large part on coming to rational conclusions and making informed decisions based on data. Of course, all scientists do this in the practice of their profession, but biogeographers uniquely work with evolutionary and ecological processes on global scales of time and space, maintaining valuable traditions within our culture.

*Interview held the 16<sup>th</sup> of March of 2011*

*Robert E. Ricklefs is the Curators' Professor of Biology at the Department of Biology, University of Missouri at St. Louis, USA*

Your participation in **frontiers of biogeography** is encouraged. Please send us your articles, comments and/or reviews, as well as pictures, drawings and/or cartoons. We are also open to suggestions on content and/or structure.

Please check <http://www.biogeography.org/html/fb.html> for more information, or contact us at [ibs@mncn.csic.es](mailto:ibs@mncn.csic.es) and [frontiersofbiogeography@gmail.com](mailto:frontiersofbiogeography@gmail.com).

## BIOSKETCH: Robert E. Ricklefs

I grew up close to nature in coastal central California and was fortunate to have teachers and other mentors who encouraged my interest in wildlife. Margaret Moody introduced me to bird watching as a child; Merton Hinshaw and Vern Yadon, Curators of the Pacific Grove Natural History Museum, were always patient answering my questions about natural history; several grad students and postdocs at the Hopkins Marine Station, who also taught in my school, opened my eyes to the marine world. I had an idyllic childhood! As a Biology major at Stanford University in the early 1960s, I was further exposed to wonderful mentoring, especially from Richard Holm and grad student John Lawrence, and a number of exceptional teachers, including several who inspired former Wallace Awardee John Briggs when he was a grad student in that department 10 years earlier.

As I was looking around for graduate schools in 1963, Paul Ehrlich, a young assistant professor at the time, advised me to head east to the University of Pennsylvania and Robert H. MacArthur. First-hand exposure to the exciting developments in population biology, evolutionary ecology and island biogeography in the mid-1960s set the course for the rest of my career. MacArthur left for Princeton in 1965, and I finished my doctorate at Penn. in 1967 under the supportive mentorship of W. John Smith. A post-doctoral year at the Smithsonian Tropical Research Institute in Panama, with Neal Smith, Stan Rand and Mike Robinson, prepared me well enough to return to Penn. as an assistant professor (MacArthur's replacement!).

My 27 years on the faculty at Penn. involved building a small but distinguished ecology program, writing two text-books (*Ecology*, 1973; *The Economy of Nature*, 1976), and developing research programs in island biogeography and the evolutionary and physiological ecology of avian life histories. Through this period, enjoyable and productive collaborations developed with George Cox, Matthias Starck, Joe Williams, Biff Bermingham and Dolph Schluter, among others, and with many outstanding graduate students. In 1995, so that my wife, Susanne Renner, and I could enjoy positions in the same institution, I moved to the University of Missouri-St. Louis, which has an outstanding program in tropical ecology. The past 16 years at UMSL have produced a further maturation of my research program, which has both returned to earlier research interests in island biogeography and turned in new directions towards fundamental issues in community ecology, including the influence of pathogens on the distribution and abundance of populations, the topic of my Wallace Award essay.

Looking back, one can always regret certain decisions and missed opportunities, but I have no complaints whatsoever. The profession, my students and colleagues, and my family have consistently provided inspiration and support, enough to keep me excited by, and engaged in, scientific inquiry into the natural world.



Picture courtesy of Robert E. Ricklefs

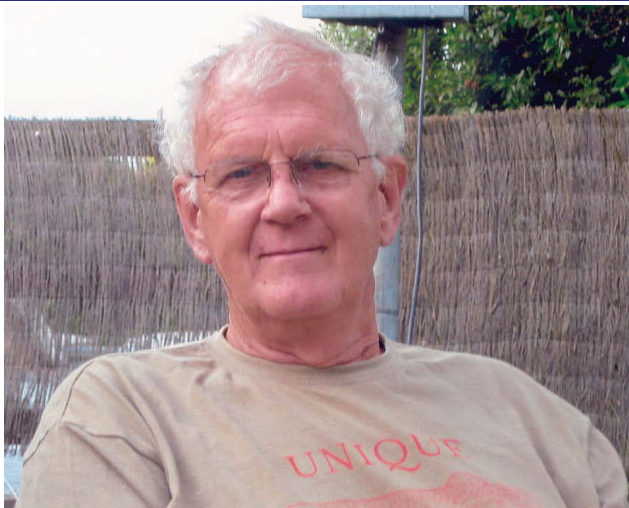
## obituary

## Bob McDowall (September 1939 - February 2011): a key contributor to our understanding of Southern Hemisphere biogeography and the significance of marine dispersal

It is with great sadness that I report the loss of Dr Robert ("Bob") Montgomery McDowall, on February 19<sup>th</sup>, 2011. Bob was a key figure in the study of Southern Hemisphere biogeography and marine dispersal.

After a childhood of fishing and freshwater activities with his parents, both of whom were also scientists, Bob completed a MSc on the ecology of redfin bully (*Gobiomorphus huttoni*) at Victoria University, Wellington, in 1962. Bob subsequently joined the Fisheries Laboratory of the New Zealand Marine Department in 1963, studying *Galaxias maculatus*, the dominant contributor to the New Zealand whitebait fishery, and a species that probably ignited his interest in biogeography, much as its distribution had earlier intrigued the likes of Charles Darwin. Bob was soon awarded a National Research Fellowship to study overseas, and started a PhD on galaxiid systematics at Harvard University in 1965, in an environment that included some of the foremost evolutionary biologists (Mayr) and biogeographers (Darlington) of the time. Bob completed his PhD in 3 years, a timeframe to be much admired even in this age, which enabled him to return to New Zealand via Chile—for galaxiid collections, of course! Back in New Zealand, Bob became New Zealand's foremost freshwater fisheries scientist, outlasting the names of several Government departments, prior to "retiring" from the National Institute of Water and Atmosphere Research (NIWA) in March 2000. However, like many a great scientist, retirement freed Bob from administrative burdens such that he was able to focus entirely on research.

While predominantly employed as a fisheries biologist, Bob somehow managed to regularly publish biogeographic research. In this context, Bob focussed on the Southern Hemisphere "Gondwanan" distribution of galaxiid fishes, and also the influence of diadromy (migration between the ocean and freshwaters) on species distributions. In the period following the acceptance



The late Bob McDowall in December 2010.  
Picture by Ainslie McDowall

of plate tectonics, Bob was a dominant protagonist for the retention of oceanic dispersal as a valid biogeographic hypothesis (McDowall 1978), particularly in taxa such as his diadromous *Galaxias maculatus*, where conspecific populations broadly occupy temperate lowland catchments throughout the Southern Hemisphere, and larvae have been recorded 100's of km out to sea (McDowall et al. 1975). Bob argued his point against several notable opponents within the discipline: Nelson, Rosen, Platnick, Croizat. Much subsequent research has supported Bob's position on oceanic dispersal, with many examples from terrestrial, freshwater, and nearshore marine faunas and floras (McDowall 2002; Sanmartín and Ronquist 2004; de Queiroz 2005). But while Bob could easily be considered a strong proponent of oceanic dispersal, it perhaps best reflects his attention to balanced approaches of scientific inquiry, and in recent correspondence he was keen to highlight that Gondwanan vicariance should not be forgotten (fearing that the pendulum was now swinging too far the other way).

Bob was a frenetic publisher, with (at last count) 267 scientific papers and 232 reports and popular articles. His papers spanned a variety of journals, including those not immediately within

his training (e.g. Bob brought his knowledge of diadromy to bear on molecular diversity of Nearctic and Palearctic fishes; McDowall 1999). His 12 books include the definitive *New Zealand Freshwater Fishes - A Natural History and Guide* (1990), and he also edited a similar book on the southeast Australian freshwater fish fauna: *Freshwater Fishes of Southeastern Australia* (1994). Bob performed editorial duties for several journals, including *Journal of Biogeography*, and his impact in the scientific field was apparent as early as 1984, when he was made a Fellow of the New Zealand Royal Society.

Bob is survived by his wife Ainslie, children Stephen and Susan, and two grandchildren.

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**Don Jellyman**

Freshwater Fisheries, NIWA, New Zealand

Edited by Joaquín Hortal



*Bob McDowall catching galaxiids, small freshwater fishes, to show to other members of the New Zealand Conservation Authority during a visit to the Chatham Islands in mid 2010. Picture by Brian Stephenson*

from the members

## On the biogeography of biogeographers

Biogeography is concerned with “*the study at all possible scales of analysis of the distribution of life across space, and how, through time, it has changed*” (Whittaker et al. 2005). It is a long established field of research, with its roots in the early nineteenth century. Recently, the fifth IBS International Meeting was held in Irakleion, Crete, where the latest scientific research in relation to biogeography was presented by biogeographers from around the world. The list of topics covered in this conference was comprehensive: there were four symposia covering Mediterranean biogeography, comparative phylogeography, biogeography and ecology, and analytical advancements in macroecology and biogeography; and six sessions with contributed papers on island biogeography, climate change biogeography, conservation biogeography, palaeoecology, marine biogeography and hot topics in biogeography. Overall, there were 63 talks and 271 poster presentations covering a wide range of biogeographical topics.

However I noticed that the geographical origin of the attendees of the conference was less diverse: the majority were from the US and Europe and I was surprised to see only a few researchers from South America and Asia and practically none from Africa. In a relatively advanced field such as biogeography, concerned with distribution patterns, I found it slightly ironic that the diversity of the biogeographers at this meeting was relatively low. Out of the total of 334 contributions at the meeting, nearly 60 percent of the authors came from a European institution and 26 percent from North American ones, whereas 7 percent of the first authors came from Central and South America, just about 5 percent from Asia, 2 percent from Oceania, and only 0.3 percent from Africa. So I wondered: where were our colleagues from these regions?

I wanted to know whether the low proportion of researchers from outside of Europe and North America at the IBS meeting is representative for the wider academic biogeography community, so I investigated recent contributions pub-

lished in the four main biogeography journals. I looked up all articles published during 2010 in *Journal of Biogeography*, *Global Ecology and Biogeography*, *Diversity and Distributions* and *Ecography*, and counted and classified them into six geographical regions according to the United Nations Statistics Division (2010) composition of macrogeographical regions based on the first mentioned affiliation of the first author of the paper. I considered a total of 490 papers in these four journals and found that 45 percent had a first author affiliated with an institution in Europe, 29 percent had a first author from North America, nearly 13 percent from Oceania, just about 5 percent from Asia, 4 percent from Central and South America, and only 4 percent from Africa.

The fact that the proportion of Europeans was relatively high at the conference is logical since the conference was being held in Europe and thus easier to attend for researchers based in this part of the world. The opposite is true for biogeographers from Oceania, who were underrepresented, probably because of the large distance they had to travel to attend the conference. However, considering these minor differences, the geographical distribution of the biogeographers attending the conference seems to correspond with the distribution of those publishing in the four journals. Thus, it would be fair to say that the biogeographers at the IBS meeting were fairly representative of the wider publishing biogeography community in terms of their geographical origin.

There are of course various factors contributing to the observed patterns, and I will refrain from attempting to explain them. Moreover, the manner in which I classified the publications does not acknowledge the contribution from co-authors affiliated with institutions outside of Europe and North America, which is likely to hide a wider international participation. Nevertheless, it is interesting to be aware of the geographical distribution of biogeography researchers and encourage further participation and contributions from underrepresented regions. For example, it

might be worthwhile to increase the number of invited speakers from these regions at future IBS meetings. Another way of increasing the diversity of biogeographers at the meetings and facilitating the integration and collaboration of international biogeography researchers is to assist researchers from these regions to attend the meetings by offering special travel grants<sup>1</sup>. I believe it would certainly enrich the IBS meetings if the diversity of the participating biogeographers would be increased.

Seline S. Meijer

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UCD Forestry, Agriculture & Food Science Centre, University College Dublin, Ireland. e-mail: [s.meijer@cgiar.org](mailto:s.meijer@cgiar.org);  
<http://www.ucd.ie/agfoodvet/ucdforestry/>

Edited by Joaquín Hortal

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1. *Note from the editor*. The IBS supports the attendance to its biennial meetings of researchers from developing countries, as well as of many students worldwide, by means of travel grants. The number of grants awarded each year is unfortunately determined by the limited funds available. Due to this, a program started last year raised funds from senior biogeographers who volunteered to sponsor student travel grants. If you are willing to contribute in this or similar initiatives, please contact Karen Faller at [biogeography.ibs@gmail.com](mailto:biogeography.ibs@gmail.com), or make a direct donation through the IBS webpage, <http://www.biogeography.org/>.

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## Job announcements

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### 2-year postdoc position

#### University of Lund, Sweden

Ecosystem Modelling & Biodiversity Studies Group, <http://www.nateko.lu.se/embers/>. Project "Simulating species and functional group responses to climate change, based on the mechanistic modelling of habitat change, population dynamics and dispersal". The objective will be to develop a generic methodology that may be applied to many species or functional groups, and to demonstrate this for one or two specific species, chosen from the Swedish bird monitoring database among species already demonstrated or suspected to be showing a response to climate change in terms of their distribution and abundance. Relevant habitat factors, or proxies for these, e.g. vegetation type, will be identified and simulated through vegetation modelling. Changes in the spatial configuration of habitat elements will be analysed using landscape ecological approaches as input to modelling

of the population dynamics and dispersal of the target species. Advanced statistical methods will be employed for the comparison of observed species distributions with simulated distribution and abundance in space and time.

Qualifications: PhD in Ecology or similar with particular expertise in landscape ecology. Strong statistical and computing skills including demonstrated programming ability are required. The successful candidate will have a good publication record and excellent written and spoken English.

Applications including a full CV and a covering letter highlighting the applicant's skills and relevance to the advertised position should be made on-line system at: <http://www.lunduniversity.lu.se/about-lund-university/jobs> where this vacancy (NPA 2011/271) is displayed. For further information please contact: Martin Sykes, Professor of Plant Ecology ([Martin.Sykes@nateko.lu.se](mailto:Martin.Sykes@nateko.lu.se); Phone +46 46-2229298). Closing date: 30<sup>th</sup> June 2011; Start date: 2011-10-01 or as soon as possible.

Did you know that any member of the IBS may raise an issue or appeal a decision of the governing Board of Directors by placing a matter before the Board of Directors for discussion?

If there is a matter you would like discussed at the next Board meeting, write to the society's Secretary (check current list of officers at <http://www.biogeography.org/>).

**Postdoctoral position in theoretical ecology****McGill University, Canada**

I am seeking a postdoc to help me develop integrative theory at the interface between ecosystem ecology and community or evolutionary ecology. More details on current research interests in my lab can be found on <http://www.biology.mcgill.ca/faculty/loreau/>. Applicants should (1) have obtained their PhD during the last five years, (2) have strong quantitative or mathematical skills, and (3) develop an independent research project. The position is available for one year but will be renewable.

Review of applications will continue until the position is filled. To apply, e-mail a letter of application, a CV, a statement of research interests and arrange to have e-mailed three letters of recommendation to me: Michel Loreau, Professor and Canada Research Chair in Theoretical Ecology, Department of Biology, McGill University. e-mail: [michel.loreau@mcgill.ca](mailto:michel.loreau@mcgill.ca); Phone: 514-398-3778.

**3-year postdoc position****School of Biological and Chemical Sciences, Queen Mary, University of London**

Full time position starting in October 2011 or as soon as possible thereafter. A postdoctoral applicant is sought with an interest in ecological modelling. The successful applicant will be developing coupled, process-based, models of ecological systems under the supervision of Professor M.R. Evans (QMUL). Candidates should hold a PhD in a relevant area of ecology or computer science or have equivalent experience. Training can also be given where needed and there will be opportunities to attend international conferences.

Further details and an application form can be obtained from the Human Resources website on: <http://www.hr.qmul.ac.uk/vacancies> (reference number 11144/KK). For further information about the School, please see <http://www.sbcs.qmul.ac.uk>. Informal enquiries can also be made to Professor. M.R. Evans at [m.r.evans@exeter.ac.uk](mailto:m.r.evans@exeter.ac.uk). The closing date for applications is 23rd June 2011 at 4.00pm. Interviews will be held 12th July 2011.

**Upcoming events****8th Biennial Conference of the Systematics Association**

4-8 July 2011 – Belfast, UK

<http://www.systass.org/>

**Vlth European Congress of Mammalogy**

19-23 July 2011 – Paris, France

<http://www.alphavisa.com/ecm2011/>

**3rd International Conference on Climate Change****Impacts and responses**

21-22 July 2011 – Rio de Janeiro, Brazil

<http://www.Climate-Conference.com>

**XVIII International Botanical Congress**

23-30 July 2011 – Melbourne, Australia

<http://www.ibt2011.com/>

**Ecological Society of America 96<sup>th</sup> Annual Meeting**

7-12 August 2011 – Austin, TX, USA

<http://www.esa.org/meetings/>

**Conference on Frontiers in Historical Ecology**

30 August-2 September 2011 – Birmensdorf, Switzerland

[http://www.wsl.ch/frontiers\\_historical\\_ecology](http://www.wsl.ch/frontiers_historical_ecology)

**European Society for Evolutionary Biology Meeting**

20-25 August 2011 – Tuebingen, Germany

<http://www.eseb2011.de/>

**GfÖ 2011****British Ecological Society**

5-9 September 2011 – Oldenburg, Germany

<http://www.gfoe-2011.de/>

If you want to announce a meeting, event or job offer that could be of interest for (some) biogeographers, or you want to make a call for manuscripts or talks, please contact us at [ibs@mncn.csic.es](mailto:ibs@mncn.csic.es) and [frontiersofbiogeography@gmail.com](mailto:frontiersofbiogeography@gmail.com).

### **BES Annual Meeting**

**41st Annual Meeting of the Ecological Society of Germany, Austria and Switzerland**

12-14 September 2011 – Sheffield, UK

<http://www.britishecologicalsociety.org/meetings/>

### **Biodiversity Institute Symposium**

**Conservation beyond protected areas**

21-22 September 2011 – Oxford, UK

<http://www.biodiversity.ox.ac.uk/>

### **IBS Early Career Conference**

**Advances in Biogeography**

23-25 September 2011 – Oxford, UK

<http://www.biogeography.org/html/Meetings/>

### **12th EEF Congress**

**European Ecological Federation**

25-29 September 2011 – Ávila, Spain

<http://www.eefcongress2011.eu/>

### **6th International Conference of the International Biogeography Society**

January 2013 – Florida, USA

<http://www.biogeography.org/>

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We gratefully acknowledge Evolutionary Ecology, Ltd. and Mike Rosenzweig in particular for the advice on copyright matters.

# frontiers of biogeography

the scientific magazine of the International Biogeography Society

volume 3, issue 1 - June 2011

ISSN 1948-6596

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