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update

A modelling framework to open the gates of assemblage structure

There is a known disagreement between the results of species distribution models (SDM) and those of macroecological models (MEM) of community structure. While SDM usually predict that assemblages hold more species than they actually do, MEM tend to underestimate these numbers. In a bold proposal, Guisan and Rahbek use such disagreement to provide a new framework to study (and predict) changes in assemblage structure. Building on examples of the SDM-MEM discrepancy, they propose SESAM, a modeling framework for spatially explicit species assemblage modelling.

SESAM is based on the idea of applying successive filters to account for the selection of species from the regional source pool – equivalent to the regional community advocated by Ricklefs – to the local community. Only the formation of the regional source pool from the global pool where the species are ‘produced’ in evolutionary time is missing from the framework. In successive steps Guisan and Rahbek distinguish the effects of (i) evolutionary history and dispersal, which determine the species source pool (i.e., those species that could colonize the locality in ecological time); (ii) abiotic habitat filters, which determine the presence of species within a particular landscape; and (iii) biotic filters that determine the actual composition of the local community in a given moment of time. According to SESAM, SDM can be used to model the effect of abiotic habitat filters, and MEM would provide a way of identifying the constraints to coexistence imposed by the amount of resources, productivity or habitat diversity of the locality (i.e. its carrying capacity). Which species – from those identified through SDM – are actually present in the locality will then be determined by ecological assembly rules (that within SESAM constitute the second part of the biotic filters).

It is likely that many researchers will disagree on particular methodological recommenda-

tions or on the adequacy of choosing certain terms to refer to particular processes or concepts. But, leaving apart these eventual disagreements, the simplicity and comprehensiveness of the approach proposed by Guisan and Rahbek make it hard to find conceptual cracks in their basic arguments or the hierarchy of processes they advocate. Further than its utility as a modelling framework, the integrative perspective offered by SESAM may help revive the debate on how the different determinants of the distribution and coexistence of species together give rise to the geographical patterns of diversity.

Guisan, A. & Rahbek, C. (2011) SESAM – a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography*, 38, 1433-1444. doi:10.1111/j.1365-2699.2011.02550.x

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commentary

One step closer towards disentangling competing hypotheses in macroecology

Macroecological studies of continental and global gradients are constrained to correlative approaches — including studies of so-called natural experiments — because of their large scale. Even when studies are carefully performed, strong inference may be difficult, since variation and co-variation of potential driving factors are not easily controlled. Often such macroecological data sets are characterized by strong intercorrelations among the predictor variables, so-called multicollinearity. Such problems may cripple the ability to differentiate among competing hypotheses. Nevertheless, new approaches provide greater ability for tackling these problems and progressing our understanding of what determines species diversity. These approaches include analyses that assess spatial variation in relationships, differentiate the components of species diversity, and integrate phylogenetic information into ecological studies. The recent study by Hortal et al. (2011) exemplifies an approach that combines these analytical advances and provides important progress in our understanding of species diversity patterns.

Hortal et al. (2011) are concerned with a complex and controversial, but core, question in ecology and biogeography, namely to what extent current diversity patterns are driven by current environmental conditions, notably current climate, relative to deep-time events and processes, so-called historical factors. Europe was strongly impacted by the Pleistocene glaciations, with large parts of Northern Europe covered by glaciers as late as the Last Glacial Maximum (LGM) just 21 thousand years ago. A number of recent studies have attempted to assess whether these massive past climate changes are still shaping current diversity patterns, e.g. for amphibians and reptiles (Araújo et al., 2007) and mammals (Fløjgaard et al. 2011). However, predictors describing historical factors and current climate are often strongly spatially correlated, making it difficult to tease their respective effects apart.

With their innovative, multifaceted approach, Hortal et al. (2011) have taken an important step towards overcoming such difficulties and present novel insights into the potential drivers of dung beetle diversity patterns across Europe. They used geographically weighted regression (GWR) to show that there is a remarkable geographic variability (non-stationarity) in the association of species diversity to climate variability since the LGM, indicating a stronger influence of past climate on the current diversity pattern of dung beetles in southern Europe than northern Europe. This finding for dung beetles is consistent with what Araújo et al. (2007) previously observed for other ectotherms, namely that the location of the LGM 0°C isotherm of mean annual temperature denotes a change in species composition, from small-ranged amphibians and reptiles south of the isotherm to widespread species north of the isotherm (see also Svenning et al. 2009 for a related GWR-based finding for European plants). GWR is generally useful for investigating macroecological processes where associations between drivers and patterns are likely to change in space, for example, such as in regions where the impact of past glaciations varies strongly across space (e.g. Europe).

Given that traits often show some degree of phylogenetic conservatism, phylogenetic analyses can further help us understand the physiological mechanisms involved in shaping macroecological patterns. Hortal et al. (2011) applied phylogenetic analyses to show that there was a remarkable phylogenetic difference between the southern and northern assemblages, with northern species being phylogenetically clustered, corresponding to particular cold-tolerant clades of species within the dung-beetle family studied. The deconstruction of beta diversity into its components, turnover (change in species composition) and nestedness (species richness differences) (see Baselga 2010), furthermore supported this finding as

northern assemblages also under this perspective were highly nested within the dung-beetle diversity in Southern Europe (Hortal et al. 2011), similar to earlier results for another beetle family, the Cerambycidae (Baselga, 2008). While Hortal et al. (2011) inform their interpretations with the general knowledge of the clade's temperature tolerances, direct incorporation of physiological mechanisms into explanatory analyses could further strengthen inference, as exemplified by Sinervo et al. (2010), who used physiological models to explain recent extinctions and predict future global warming impacts on lizard diversity.

While the conclusions of Hortal et al. (2011) still hinge on the strength of correlations between diversity and hypothesised predictors, investigating the study questions from the different perspectives encompassed by their multifaceted approach has strengthened inference, helping to disentangle the importance of competing hypotheses. Concerning diversity determinants, the study nevertheless has limited geographic and taxonomic scope and how much its findings can be extrapolated to other clades and regions is unknown, although some level of transferability seems likely. However, the approach of Hortal et al. (2011) has general interest to biogeographers and macroecologists because such multifaceted approaches are applicable not only to studies of other clades and regions, but also to other questions across these research fields, notably given the general problem posed by multicollinearity. For the time being, such advances are still somewhat limited by the availability of data, notably full phylogenies, but also databases on species traits needed for the development of phylogenetic and physiological models. With continual new advances in data availability we encourage macroecologists to look for new insights by deconstructing diversity patterns, investigating geographic heterogeneity and considering phylogenetic patterns and physiological mechanisms.

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Edited by Richard Field

workshop summary

State of the art and perspectives of risk assessment analysis

International workshop on methods and applications for managing biological invasions – Girona, Spain, 18th-20th April 2011

The introduction of invasive alien species (IAS) has added an additional level of complexity in the management of ecosystems (Hobbs and Humphries 1995). Given that once a non-indigenous species is established in a new region it is extremely difficult and costly to eradicate or control, recent attention has switched to developing risk assessment protocols that identify high-risk situations for species that may become established and have a negative impact in a new region. Risk analyses are systematic and comprehensive methodologies evaluate risks and uncertainties associated with the introduction/expansion of certain organisms, based on the magnitude of their possible adverse consequences and the likelihood of occurrence of these consequences (Pheloung et al. 1999). Risk assessment can thus be an important tool to avoid further invasions.

Risk assessment protocols have initially been largely developed in those parts of the world (e.g. Australia, New Zealand, South Africa) which are hit most severely by biological invasions, but a common standard of key elements of risk assessment protocols has not emerged so far. In Europe, which has substantially lagged behind in performing risk analyses for alien species, this topic has recently gained importance. This was driven by the ongoing development of an EU strategy for invasive alien species (http://www.ec.europa.eu/environment/nature/invasivealien/index_en.htm) and via EU-funded projects such as ALARM (<http://www.alarmproject.net>) and DAISIE (<http://www.europe-aliens.org>). So the time was right to evaluate to what extent risk analysis protocols may really be useful in simplifying the decision-making process that guides EU environmental policies.

The European Science Foundation (ESF) and the Agency for Management of University and Research Grants (AGAUR) of the Government of Catalonia jointly funded a workshop on methods and applications of risk assessment analysis in ma-

ning biological invasions, a meeting hosted in Girona, Spain (18th-20th April 2011). This workshop, which was co-organized by Núria Roura-Pascual, Ingolf Kühn, Wolfgang Rabitsch and Daniel Sol, brought together 21 of the world's top experts on risk analysis for biological invasion, with the overarching objective to evaluate the status quo of the field and guide the development of standard protocols for setting management priorities.

The participants presented and discussed key elements of existing risk assessment systems and their strengths and their weaknesses, and explored key future research needs. Several speakers presented the state of the art of fundamentals in risk assessment methods. Mark Burgman, the Director of the Australian Centre of Excellence for Risk Analysis (University of Melbourne), opened the workshop and used the extensive Australian experience to present fundamentals and pitfalls of risk assessment. David M. Richardson, the Deputy Director of the South African Centre of Excellence for Invasion Biology (University of Stellenbosch), highlighted recent scientific progress achieved in identifying which aspects make species invasive. Brian Leung (McGill University, Canada) outlined ways of including socio-economic assessments when analyzing the risks posed by invading species, an issue gaining increasing importance, when political decisions on IAS management are to be made. Daniel Sol (Centre for Ecological Research and Forestry Applications, Spanish National Research Council) talked about the features that make a species a successful invader, whereas Katharina Dehnen-Schmutz (University of Warwick, UK) highlighted the importance of horticulture as an entrance pathway for alien plants. Jaakko Heikkilä from MTT Agrifood Research Finland presented the results of a recent overview of current European risk analysis systems. Although objectives are similar in most cases, he found considerable differences between different approa-

ches. These presentations showed considerable progress in unravelling determinants of invasiveness and in developing methods for risk assessment, but they also pointed out that there are still many challenges.

A second set of talks was devoted to learning from experiences gained in the application of risk assessment methods. Francoise Petter from the European Plant Protection Organization (EPPO) presented the weed risk assessment system used to identify emerging plant pests in Europe (<http://www.eppo.org/QUARANTINE/quarantine.htm>), which is the most widely used risk assessment system in Europe. Piero Genovesi, the head of the IUCN SSC Invasive Species Specialist Group, presented the current status of political discussion for a more concise management of IAS in Europe. There is hope for a pan-EU risk assessment to be adopted in the coming years by the EU member states, and this political perspective has to be considered when contributing to the development of risk assessment standards. Stephan Gollasch (GoConsult) presented experiences gained in the implementation of the International Maritime Organization ballast water management convention, while Sven Bacher (University of Fribourg, Switzerland) presented the foundations of the new Swiss risk assessment method and Franz Essl (Environmental Agency, Austria) the risk analysis scheme developed for Germany and Austria (GABLIS) to prioritize management actions. These talks showed that there is substantial recent progress in Europe, but that there is a strong need for developing a unified framework for risk assessment.

Much time in the workshop was devoted to discussions and perspectives for follow-up activities. The participants selected three aspects of risk assessment that will undergo an in-depth review. These include a methodological analysis of risk

analysis, an assessment of the cost–benefit balance of risk management actions and an analysis of the linkage between risk assessment and risk management at the European level. These revisions will contribute to a better understanding of the limitations and advantages of qualitative and quantitative approaches for risk analyses, to the identification and clarification of different types of uncertainties in risk analyses, and to the assessment and cost–benefit analysis of economic costs in decision making.

This workshop on biological invasions and risk analyses has advanced dialogue and contributed to better coordination of efforts towards the development of standard protocols. This is not only important for scientific purposes, but also to implement coordinated policies and strategies aimed at reducing the effects of invasive species at the European level.

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Edited by Núria Roura-Pascual

book review

Definitive guide to China's woody plants

Atlas of woody plants in China: distribution and climate, by Fang Jingyun, Wang Zhiheng, Tang Zhiyao

2011, Springer / Higher Education Press, 2000 pp. ISBN: 978-3-642-15016-6

Price: £449.50 / \$670.00 / €499.00 (Hardcover); <http://www.springer.com/>

The sheer magnitude of the accomplishment represented by these two mammoth volumes is difficult to convey. Some descriptive information might begin to give an impression: it weighs nearly 3 kg, with over 2,000 pages and 11,427 figures. It covers the distribution of 11,405 taxa of woody plants across the entire land area of the world's third-largest country, one with more plant species than North America and Europe combined. Impressed yet? Three editors recognise 22 other contributors and 21 reviewers of focal areas. Though the plan was long in gestation, the work formally began in 2003, with no specific financial support, which fortunately came later through the National Natural Science Foundation of China, and the database was eventually completed in 2008.

The taxa are divided into 170 families and 1,175 genera, including 1,355 subspecies, based primarily on the Flora of China. There are 3,165 trees (defined as > 4 m in height), the remainder being largely woody shrubs (6,735) and vines (1,035). Cultivated plants are excluded, although this information is available elsewhere (e.g. the Vegetation Atlas of China). Pleasingly, 470 bamboo species are also incorporated, which is helpful given their importance to the dynamics of oriental forests. The most speciose genus is *Rhododendron*, its 624 species reflecting their Himalayan origins. Meanwhile, the idea of 331 *Salix* species is intimidating to those of us who still struggle with their more modest diversity in Europe. Surprisingly, only two extant endemic woody plant families occur in China: Eucommiaceae and Ginkgoaceae. Families are arranged according to the Flora of China – making this an ideal companion tome – with alphabetical order within. The family names are clearly marked at the tops of pages with thumbnails that are mostly clear examples of representative specimens. The index seems com-

prehensive and random checks suggest it to be accurate.

Data-gathering used all available sources, including floras, checklists, monographs, published articles, distribution records based on herbarium specimens, and consultation of local experts. Some judgement was applied in assessing county-level presence; while some taxa remain sporadic in their distribution, widespread species with gaps in their distribution had these filled in if it seemed that false absences were the most likely cause. Administrative units naturally vary in size and the intensity of sampling that has taken place within them, but this work represents the best possible collation of present knowledge.

What information does it contain? In the main section, six species are covered per page. Each has a distribution map which is necessarily restricted in size (5.7 x 8.2 cm). The latitudinal extent, from the southern shore of tropical Hainan, over 4,000 km northwards to the boreal border of the Amur river (*Hēilóng Jiāng* to the Chinese), is covered in under 6 cm (the islands of the South China sea are placed in an inset map). Moving from the western border at the foot of Gora Kumdandy, across the Taklimakan desert, through the Tian Shan range then on to the eastern tip by Khabarovsk, a trip of nearly 5,000 km, is accomplished in 7 cm. This degree of contraction is a necessary cost to fitting so much into the books, and the quality of printing is suitably high, though it means that the fine resolution of the underlying data is not readily accessible from reading the maps.

For each species, the atlas gives the mean and range of 13 environmental variables based on county-level averages drawn from the WorldClim website (<http://www.worldclim.org>). These include measures of temperature (mean annual, mean of the coldest and warmest months, annual biotemperature [the sum of monthly mean tem-

peratures for all those with a mean between 0–30°C], warmth and cold indices [the sum of monthly mean temperatures above and below 5°C respectively] and potential evapotranspiration), water availability (annual precipitation, precipitation in the warmest and coolest quarters of the year) and combined measures (moisture index, actual evapotranspiration, vegetative net primary productivity).

A publication of this scope carries with it a price-tag to match; at €499 it is likely that only those with a direct interest, or a particularly generous budget, will be able to afford it. Those who do will no doubt be rewarded with data that could simply not be obtained elsewhere. Perhaps this is its ultimate selling point – exclusivity. Most biogeographers would dream of access to this volume and quality of data.

It is therefore difficult, even churlish, to be critical of a publication of this scale. And yet... perhaps it is a mark of how much the landscape of science has changed that this set of volumes, which would have inspired awe when their first outline was drafted, now seems slightly dated in approach. The European publishers have no plans to make a digital or online edition available. This seems to be an enormous oversight, not simply because of the expense of the printed issues, but mainly because a searchable database from which information could be extracted would be a far more intuitive means of presentation. Of course, the dedicated researcher could trawl through each species and transcribe the information themselves, but this would test the devotion of even the most committed graduate student, while the rest of us simply don't have the time. A database exists and is described by the authors, with ac-

companying images, though it would seem to have been compiled in Chinese. The authors' website provides further details but at the time of writing it is not accessible online.

If you can afford these books then they will certainly reward you with more information than a lifetime in science could handle, though sadly not in a form that makes them readily accessible to the synthetic analyses that a biogeographer might hope to perform. I can only implore the authors and publishers to explore alternative means of publication as therein lies the potential for this work to receive the acclaim it deserves, as a landmark accomplishment that will transform our understanding of the biogeography of the Asian mainland. There is astonishing potential for visualising gradients in vegetation composition, predicting the impacts of climate change, testing for the signals of past glaciations... there is so much that could, and should, come from this work. It deserves to be used, to be cited, to be celebrated. Until the data are presented in a form that makes it possible for an international audience to extract and appreciate them, I fear these mighty tomes may gather dust, and their authors will have to wait for the plaudits which they richly deserve from a grateful worldwide community of researchers.

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Edited by Richard Field

One of the benefits open to IBS members is the opportunity to have job openings posted on the IBS blog (<http://biogeography.blogspot.com/>). If you have a position you would like to have advertised, please contact Karen Faller (faller@wisc.edu) or Michael Dawson (mdawson@ucmerced.edu) with details.

book review

A 100 million year love affair with American plants

A Natural History of the New World, by Alan Graham

2010, The University of Chicago Press, 408 pp. ISBN: 9780226306797 / 9780226306803

Price: \$110 (Hardback) / \$40 (Paperback); <http://www.press.uchicago.edu/>

I teach a class called “The Ecosystems of California”, and my students always ask the question: “Will global climate change cause trouble for California’s plant communities?” I find it impossible to give a short response, not because I doubt the grave predictions about future warming, but because many of California’s species have a long history in North America, and have already lived through ten glaciation cycles, including the recent extinction of the Pleistocene megafauna (which must have wrought major ecosystem change). Some species are old enough to have endured the massive cooling and drying that changed North America from the mostly frost-free and drought-free continent that it once was in the Eocene. On the other hand, even if non-anthropogenic climate change has offered little more than an evolutionary bump in the road when examined from a 50 million year perspective, contemporary human-mediated disruptions may be catastrophically destabilizing to ecosystems and human civilization in the short term. Thus, answering how the biota will respond to current climate changes and disturbances requires an understanding of the magnitude of the changes that have already occurred and Alan Graham’s new book provides exactly this context.

A Natural History of the New World represents a wonderful synthesis of Alan Graham’s voluminous career studying the American flora. This narrative includes detailed descriptions of plant communities of the Americas, and includes a comprehensive review of paleobotanical evidence and interpretations regarding how changes in floras have coincided with global climate changes and geological events in different biogeographic regions of the Americas over the past 100 million years.

The book opens with a very long description of all of the different biomes and vegetation types in the Americas, starting with the North Pole and

ending with Tierra del Fuego. My favorite chapter, by far, is Chapter 3, which succinctly gives the best and clearest description I have ever read of the tools used to put dates on past events. I very much enjoyed these lucid explanations of how global sea levels are reconstructed, how reversals of the earth’s magnetic field are detected, and how radiometric dating works. I will definitely use this in my undergraduate teaching. The next chapter describes the techniques that paleobotanists use to identify micro and macrofossils and also how macrofossil assemblages are used to estimate past climates. Here, I was disappointed that the explanation of leaf-margin analysis did not include any discussion of Peter Wilf and students’ work of why serrated leaf margins may be correlated with colder climates (Wilf 1997, Royer and Wilf 2006).

Graham then divides the past 100 million years into four sections: the Middle Cretaceous through the Early Eocene, the Middle Eocene through the Early Miocene, the Middle Miocene through the Pliocene, and the Pleistocene and Quaternary, to discuss how the major climatic and tectonic events have impacted the evolution and assembly of plant communities, and how and when (and why) those assemblages begin to approach recognizably modern forms. I greatly enjoyed these sections, as they provide a great review of the paleobotanical research for each time period broken down by geographic area – a synthesis of time and place that is often very difficult to piece together from other books and articles which give a more local or taxon-specific focus. The book is very well referenced throughout, a great service for readers who want to follow up on more details about particular regions and paleobotanical studies. It is indeed striking how few paleobotanical studies are published for tropical areas, and botanically megadiverse, important areas like the Amazon basin have only very few well-studied sites over large stretches of time

from the late Eocene to the middle Miocene. This middle section of the book I find to be the most valuable, because besides Graham's own monographic work in separate volumes, I can think of no other source that reviews all of the vegetational sequence over such a large time scale for the entire Americas. Willis and McElwain's (2002) *The Evolution of Plants* comes to mind, but their book is global in scope and does not provide nearly the same amount of detail regarding the fossil evidence.

My main quibble with this book is that I think it could have been organized and edited much better. The opening descriptions in Chapter 2 of the vegetation communities from pole to pole contain too many anecdotes covering completely different periods of time. The majority of this chapter as well as the "pole-to-pole" synthesis (Chapter 10) should have been integrated into Chapters 5-8, so that the reader could have learned about the changes in vegetation in one temporal sequence. There are also quite a few errors that should have been caught by an editor (p. 195: flying foxes are not related to lemurs, p. 223: *Pelluceria* actually lives on both the Pacific and Caribbean coasts in Central America (Roth and Grijalva 1991), p. 236: the Sierra Nevada achieved close to its current height by 12 million years ago (Mulch et al. 2008). Also I found the numerous historical asides and personal anecdotes distracting (although to be fair I should acknowledge here that my graduate student had the reverse reaction and really enjoyed these parts). The many links given to webpages and quotations of other people's work is a nice attempt to be comprehensive within the format of a paperback book, but I would have preferred that the author stay on topic. I say this because Alan Graham has a deep knowledge and understanding of how different plant communities have existed in the Americas – and which major geologic and climatic events were the most important in shaping American ecosys-

tems, and the many tangents detract from the main narrative.

I would recommend this book for anyone seriously interested in plant biogeography, ecology or evolution who wants to gain a better perspective on the historical events that have shaped current biotas. Considering the large amount of attention paid to global climate change recently by environmentalists, the media, and policy makers, it is critical to be able to consider changes in plant communities within the larger context of global climate change over the past 100 million years. To this end, I think that this book makes an extremely valuable contribution.

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Edited by Markus Eichhorn

book review

Fifty years of Elton

Fifty Years of Invasion Ecology: The Legacy of Charles Elton, by David M. Richardson (ed.)
2011, Wiley-Blackwell, 432 pp. ISBN: 978-1-4443-3586-6
Price: £95.00 (Hardback) / £45.00 (Paperback); <http://www.wiley.com/>

The year 1958 marked the publishing of *The Ecology of Invasions by Animals and Plants* (henceforth *EIAP*) by Charles Elton. In this book, Elton examined the introduction and subsequent success of numerous non-native species and put forth a set of hypotheses about why certain species become invasive (invasiveness) and why certain communities may be more susceptible to invasion (invasibility). Fifty years after *EIAP* was published, David Richardson organized a symposium in Stellenbosch, South Africa, that brought together 137 people from over 14 different countries to discuss how the study of biological invasions has progressed since the publication of *EIAP*. *Fifty Years of Invasion Ecology* (henceforth *Fifty Years*), edited by Richardson, grew out of that symposium and provides a comprehensive examination of what knowledge has been gleaned in the past 50 years by studying the subset of organisms that have become prolific when moved, by accident or purpose, out of their native range.

Some might find it strange for an entire book to be devoted to updates on the ideas proposed in one monograph, particularly when that monograph was written for a lay audience. Yet anyone who has read *EIAP* knows how captivating the book is, how many ideas about community invasibility were set out in it, and how the book set the groundwork for a field of biological inquiry that now generates thousands of publications per year. Whether or not Elton founded the field of invasion biology (and this is covered by a chapter by Daniel Simberloff), it is clear that *EIAP* was an “important milestone in the history of invasion ecology” (Richardson page xiii), and following up on the ideas Elton set forth and species he case-studied was a worthwhile endeavour.

The book is split into seven parts, some of which are stronger than others. The first part is one of the strongest – it provides a historical per-

spective on Elton, the field of invasion biology, and the idea of “nativeness.” The chapters in the next two parts, “Evolution and Current Dimensions of Invasion Ecology” and “New Takes on Invasion Patterns” don’t hang together as well, but I’m not sure where I would have put these chapters either. The meat of the book is called “The Nuts and Bolts of Invasion Biology,” and it is these nine chapters that people interested in determining the state of knowledge on ecological and evolutionary explanations of invasion success will be most keen to read. Almost all of the chapters cite very recent literature, including papers and books published in 2010.

The fifth part contains two chapters on “poster-child invaders”, while the penultimate part marks new directions and technologies being used to detect and evaluate the spread and impact of invasive species. This part has one of the more polemical chapters in the book, by Mark Davis. He critiques invasion ecology for relying on niche-based paradigms of community assembly and for overstating conclusions. Although this chapter is a rearrangement of one in his 2009 book *Biological Invasions*, I liked the inclusion of a chapter in *Fifty Years* that cautions against falling into the same “mess” that permeates community ecology.

The link to Elton and *EIAP* are tenuous for some chapters, but that doesn’t matter because almost every chapter provides a comprehensive, synthetic review of a topic of interest to ecologists. Interested in the state of the diversity-invasibility debate? Read chapter 10 by Jason Fridley. Interested in new techniques to detect invasive species at the point of entry? Read chapter 22 on the possibility of hand-held devices to perform DNA barcoding on the spot. In addition, several chapters discuss whether propagule pressure, the number of times and number of individuals of a species that are introduced, can ex-

plain most patterns of invasiveness equally as well as invasibility. Propagule pressure was not explicitly considered by Elton but clearly needs to be considered before invoking a niche-based paradigm of community assembly.

What would Elton say? Even with 30 chapters, each examining a different aspect of biological invasions, I felt like *Fifty Years* was missing a chapter reviewing evidence for or against the enemy-release hypothesis as well as biological control of invasive species. Elton wrote extensively about “counterpests” and the circumstances under which they may control invasive species, but this theme is not examined in *Fifty Years*. The only chapter highlighting the role of resistance by biota focuses on soil microbes, with a few examples about the effects of aboveground “natural enemies.” In addition, I would have liked to have seen more follow-up on the invasive species that Elton talked about in his book. Only two chapters incorporated this approach. James Carlton’s chapter on marine invasions updated the names of 31 of the 33 species that Elton mentioned, while the chapter by Petr Pyšek and Philip Hulme examined the current distribution of some of the animals and plants mentioned by Elton as invasive in Europe. Although many tools in population ecology have been used to try to understand the dynamics of invasive species populations, a chapter investigating individual-based and population-projection

models was also notably absent. Perhaps this was intentional, or perhaps the book, which contains 30 chapters and 432 pages in the paperback edition, was already long enough.

Some of the downsides of this edited volume are the lack of a common bibliography, variation in the strength of the chapters, and sections that contain chapters that don’t really fit together but wouldn’t fit elsewhere. Many edited volumes have these issues, and they should not be seen as unique to *Fifty Years*. With those caveats aside, the volume is a must-read for invasion biologists and would serve well in a graduate seminar on invasion biology if paired with *EIAP*. Indeed, the two books now sit side-by-side on my bookshelf.

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book review

The palm book

The Book of Palms, by Carl Friedrich Phillip von Martius [a reprint of the 240 illustrations from C. F. P. von Martius' *Historia Naturalis Palmarum*, published in installments between 1823 and 1850, with an introduction by H. Walter Lack]

2009, Taschen, 442 pp. ISBN: 978-3-8365-1779-9

Price: £99.99 (Hardback); <http://www.taschen.com/>

This is a magnificent reprint of one of the most influential books in the botanical literature, Martius' *Historia Naturalis Palmarum*, famed for its scientific accuracy and aesthetic qualities. Carl Friedrich Phillip von Martius (1795–1868) was an assistant at the Royal Bavarian Academy of Sciences when in 1817, aged 22, he was asked by Maximilian I Joseph, King of Bavaria, to join an expedition that was sent to Brazil by Franz I, Emperor of Austria. The expedition was held on the occasion of the marriage of Franz I's daughter Leopoldine to Dom Pedro, eldest son of Joao VI, King of Portugal, Brazil and the Algarve. The wedding was celebrated in Vienna on 13th May 1817, but later confirmed in Rio de Janeiro, and the 13-man natural history expedition was organized to foster relationships and increase trade between Brazil and the European kingdoms with interest in these new frontiers. The celebration in Rio was held on 6 November 1817, and following that, Martius and his zoological companion Johan Baptiste Spix set out on a 2200 km long journey to the interior of Brazil. During the journey they amassed large quantities of natural history specimens, and when Martius returned to Munich on 8th December 1820, almost four years had passed. Martius and Spix had brought back considerable collections of rocks and minerals, 350 species of birds, 130 amphibians, 116 fish, 2700 insects, 80 arachnids, 50 crustaceans and 6500 plants. The other members of the expedition had returned similar quantities to Vienna and other European museums.

Apparently being a natural historian and collector at that time was something important to the political powers. King Maximilian I Joseph made Martius and Spix Knights of the Order of Merit of the Bavarian Crown. Aged 26 Martius was elected a full member of the Royal Bavarian Academy of Sciences. At age 31 in 1826 Ludvig I, King

of Bavaria, made Martius full professor at the University of Landshut. In 1832 he became senior curator of the Botanical Institute, and in 1840 he was elected secretary of the Mathematics and Science section of the Royal Bavarian Academy of Sciences, a post which he had until his death in 1868.

From this background it is perhaps easier to understand how Martius could publish such a magnificent work on his collections from Brazil. Actually he worked on three large book projects simultaneously. One was a general account of the expedition which was published as *Reise in Brasilien in den Jahren 1817–1820* and published 1823–1831. The other was *Nova genera et species plantarum quas in itinere per Brasilian annis 1817–1820 --- suscepto colegit et descripsit*, published 1823–1826, which was a technical description of all the plants – except palms – that Martius had collected during his travels. Finally the third book project that Martius embarked on during his tenure at the Bavaria academic establishment was *Historia naturalis palmarum*, the illustrations of which are featured in the book reviewed here.

The finished version of *Historia naturalis palmarum* was made up of three volumes. But the volumes did not appear chronologically. Instead they were released in fascicles at irregular intervals. The first fascicles to appear in 1823 were from volume 2 on the American palms, and this volume was completed in 1837. This was followed by volume 3 which was completed in 1853. Volume 1 began to appear in 1831 and was completed in 1853. The publication was printed at the author's expense, and to finance that, Martius had secured that it could be sold through subscription. Those who subscribed appear on a page in the 2nd volume and include several central European royalties, and some of the famous cultural leaders

of the time, such as Goethe, who in his writing commended Martius for his contribution to humankind's understanding of the beauty of nature. The first volume is a general introduction to the palm family including sections on the structure of palms written by Hugo Mohl, a colleague to Martius at the University of Tübingen, a section on palm fossils written by Franz Unger from the University of Graz, and sections on morphology and biogeography of palms, written by Martius himself. The first volume is illustrated with 53 plates that are so detailed and precisely produced that they may serve as study objects even today. For the readers of *Frontiers of Biogeography* a World map showing the distribution and density of palm over all tropical regions may be the most interesting part. The patterns and densities shown are much in line with modern understanding, though some regions, such as the interior of Africa are white on the map, which is not surprising considering that they had not been explored at the time in the early 19th century. There are also two plates showing the New and Old Worlds, respectively, indicating the phytogeographic regions, called Imperia Floræ.

The second volume describes and illustrates palm species found only in the New World (the Americas). It includes 97 plates that either show a whole palm individual, a detail of leaves and/or reproductive structure as seen in herbarium specimens, and some landscapes that show palms in their natural habitat. These drawings are all made by Martius himself. The detail, again, is incredible and exceptionally true to what palms look like in reality.

The third volume covers palms from the Old World plus a few additional ones from the New World. The illustrations here are copied from other works on palms, but they stand out with the same beauty and accuracy as the ones illustrating the New World palms.

This book is truly breathtaking. Looking through the fantastic plates gives one the same feeling as when pressing palm specimens in the field. The structural diversity and complexity of the plants and their organs stand out and become lively in front of the reader. It is art and natural history in a splendid combination. The illustrations can be used for identifying specimens of palms without any limitation at the same time as they provide the special pleasure of seeing and disentangling the details of nature. The plates come with the original naming of the specimens that Martius provided, but for each plate the editor has generously updated the naming so all illustrations come with their modern and accepted names.

The introduction by H. Walter Lack of the Berlin Botanical Garden is nicely written and provides a thorough understanding of how this book came to exist in the first half of the 19th century. The introduction provides a wealth of detailed facts (some of which are presented above) that place the book in a historical context which enhances the pleasure of using it. The technical quality of this reprint is of a very high standard; the colouring appears to be entirely natural, the paper quality is superb with a half mat surface which make the lithographs stand out in their crisp splendour. The Taschen Book and the author of the introduction are to be congratulated on this splendid production, which comes at a very reasonable price.

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Edited by Markus Eichhorn

books noted with interest

The World's beaches: A global guide to the science of the shoreline

Orrin H. Pilkey, William J. Neal, James Andrew Graham Cooper & Joseph T. Kelley
 2011, University of California Press, 302 pp.
 \$70.00/£48.95 (Hardback), US \$29.95/£20.95 (Paperback)
 ISBN: 9780520268715 / 9780520268722
<http://www.ucpress.edu/>

Ever wonder whether you chose the wrong study system? Engagingly written and with arresting illustrations, the authors provoke jealousy of their research area with a comprehensive account of coastal geology and a global classification of beach environments. Relatively little attention is given to the biota, with characteristic plants and animals covered in short sections, though with a longer consideration of what can be learnt from sea-shells. There are no in-text references but the recommended further reading would make this an ideal primer for students or those beginning shoreline-related work. Otherwise it's perfect holiday reading for the beach.

The theory of ecology

Samuel M. Scheiner & Michael R. Willig (eds.)
 2011, The University of Chicago Press, 416 pp.
 £120.00 (Hardback), \$40.00 (Paperback)
 ISBN: 9780226736853 / 9780226736860
<http://www.press.uchicago.edu/>

The editors have assembled a Who's Who of theoretical ecologists to consider the state of the field's big ideas. Much content will directly appeal to biogeographers, including chapters on meta-communities, the Equilibrium Theory of Island Biogeography, global change and biogeographical gradients, as well as stressing linkages among areas where ideas have apparently developed independently. Each chapter opens with an instructive diagram illustrating the connections between theoretical frameworks, further stressing the continuity of the field and resolving the broader pictures. It could form the spine of a graduate ecology course or a valuable refresher for even the most experienced reader.

Markus Eichhorn

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Editorial policy for book reviews

Frontiers of Biogeography will publish in-depth reviews of recently published books (typically less than one year old) on biogeography or of interest to biogeographers, alongside a 'Noted with Interest' section providing brief details of new publications. Authors, editors or third parties are invited to suggest books for review to the Book Review Editor, Dr Markus Eichhorn, School of Biology, University Park, Nottingham NG7 2RD, United Kingdom; telephone ++44 (0)115 951 3214; e-mail markus.eichhorn@nottingham.ac.uk. We welcome offers to review books for *Frontiers of Biogeography*, but will not accept an offer to review a specific book. Anyone wishing to review books should send a brief *curriculum vitae*, description of competencies, and a statement of reviewing interests to the Book Review Editor. Reviews should be in an essay style, expressing an opinion about the value of the book, its focus and breadth, setting it in the context of recent developments within the field of study. Textbook reviews should consider their utility as resources for teaching and learning. Avoid describing the book chapter by chapter or listing typographical errors. The length should normally be 1000 words (1500 words for joint reviews of related texts) including a maximum 10 references. Authors may suggest a short heading for the review, followed by the title of the book(s), the authors/editors, publisher, publication date, price, hbk/pbk, pages, ISBN and website (where available). Figures or tables will not ordinarily be included. Authors of reviews must verify that they have not offered (and will not offer) a review of the same book to another journal, and must declare any potential conflict of interest that might interfere with their objectivity. This may form a basis for editorial decisions and such disclosures may be published. Book reviews will usually go through a light editorial review, though in some circumstances also will be considered by one or more referees.

data

Two researchers desperately seek stable 50-year-old corridors for study on conservation corridor efficacy

We seek your help in identifying 50 to 100 landscapes, anywhere in the world, that will allow us to test whether or not conservation corridors work, and to identify traits of successful corridors. In this article, we describe the criteria for a landscape to be included in our study. Please visit our website (<http://www.docorridorswork.org/>) for additional information or to suggest a site. If you know someone who might know of a site, please direct them to our website –and thank you in advance for your help.

Earth is becoming ever more fragmented by human activities, causing natural wildlife habitat to become increasingly isolated. 'Conservation corridors' are swaths of natural habitat (typically > 500 m long and > 100 m wide), preserved prior to human development of the landscape with the intended purpose of linking larger blocks of natural habitat after the surrounding landscape is converted for other uses. Conservation corridors are the most promising intervention available to land managers and conservationists to link isolated natural areas and promote demographic and genetic exchange at levels sufficient to sustain plant and animal populations. Moreover, they are the most commonly recommended conservation intervention to allow species to adapt to climate change (Heller and Zavaleta 2009). Governments and conservationists have planned many conservation corridors, and have invested millions of dollars on these plans (Wildlife Conservation Division 2010; <http://www.scwildlands.org>; <http://www.corridordesign.org/arizona>). We have been strong proponents of these corridors.

Unfortunately, we lack strong evidence that these interventions will work because most corridor research to date has studied 'structural linkages', which differ from conservation corridors in three ways. First, most research has evaluated the effectiveness of relatively short (< 100 m long) corridors (linkages), but conservation corridors are much larger. Second, most studies have defined a

corridor as any narrow swath of land connecting two habitat patches, where the patches and corridor share a land cover that is different from that of the surrounding matrix (Haddad et al. 2003). Many times, the surrounding matrix is also natural vegetation, whereas conservation corridors are proposed to be embedded in heavily human impacted landscapes (Hilty et al. 2006). Finally, most linkage studies assess corridor efficacy by documenting focal species presence or movement through the linkage (Gilbert-Norton et al. 2010). Although these are necessary components of corridor success, they do not demonstrate that the corridor enhances demographic stability or gene flow, which are ultimately what corridors are designed to do (Crooks and Sanjayan 2006). Thus, most corridor research has been conducted in the wrong landscape context, at the wrong spatial scales, and using the wrong response variables to fully gauge the utility of conservation corridors.

An ideal study design to address this knowledge gap would be a Before/After Control/Impact (BACI) study design. However, such experiments would take nearly a century, and conservation planners need information right now (Soulé and Orians 2001). To address this knowledge gap in a more timely fashion we intend to study what we call 'de facto corridors'. A *de facto* corridor is a landscape feature which structurally resembles a conservation corridor, but which may not have been explicitly designed with the intent to enhance connectivity. To identify landscapes worldwide with de facto corridors and necessary reference conditions, we need your help.

An ideal landscape for our study will be one that has a de facto corridor that is at least 500 m long and 100 m wide (small constrictions near road crossings or rivers are OK) linking two or more habitat patches embedded in a human-dominated matrix (e.g. urban, row crop agriculture, industrial forest). In addition to two patches linked by a corridor, the landscape should also

have at least one, and preferably both, of the following reference conditions: (1) completely isolated habitat patches of similar size and spaced approximately as far apart as the patches connected by the corridor, and (2) a relatively intact block of habitat large enough to allow us to collect samples at locations located as far apart as the corridor-connected patches. The landscape needs to have been in this configuration for at least 20–50 years – long enough for population demographics and gene flow to have adapted to landscape conformation (Wisdom et al. 2000, Slatkin 1993). Finally, although we are highly selective about what landscapes we will study, we will study any reptile, amphibian, mammal, flightless arthropod or sedentary bird that is found in the corridor but not in the human-dominated matrix, and we will study them on any continent.

To suggest a study site please visit our website (<http://www.docorridorswork.org/>), or email Andy at andrew.gregory@nau.edu. Our website provides more information about this project and occasional status updates. You can also follow us on Facebook at Do Corridors Work; to help publicize our study, please “Like” or “Friend” us on Facebook. Finally, anyone suggesting a study site meeting our criteria is eligible for a small finder’s fee.

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opinion

Relationship between local population density and environmental suitability estimated from occurrence data

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The spatial configuration of species' abundance has been a topic of discussion in ecology for a century (see Gaston 2003). On several occasions, the fact that abundance peaks at the centre of the geographic ranges has been reported and has even been accepted as rule of thumb (Sagarin and Gaines 2002). Assuming that local abundance is a by-product of Hutchinsonian niche processes, and that some of the most determinant variables demonstrate spatial autocorrelation and some interdependence, Brown (1984) argued that the high abundances found at the centre of the ranges of distribution are to be expected. However, the pattern is far from general (Sagarin and Gaines 2002; Gaston 2009); there are several contingent and demographic causes that may disrupt the "abundant centre" distribution hypothesis (Rapoport 1975; Brown 1984). Even when abundance truly reflects environmental suitability, given the potential complexity of the structure and geographic patterns of niches (Soberón and Nakamura 2009), violations of the single and centred environmental optimum may be the rule

rather than the exception.

Species distribution models (SDMs) have become popular in recent years, in part because of the increased availability of occurrence data in huge biological databases. Within the usual terms of "ecological niche models" or "habitat suitability models" lies the assumption that, since occurrence data reflect some parts of the niches, these methods estimate something close to the environmental suitability (herein suitability for short) of the species (Soberón and Nakamura 2009). Given that occurrence data are much easier to compile than abundance, an obvious question that arises is whether local suitability can inform us about local abundance. Curiously, few studies have directly explored this topic, and the results of the investigations of Pearce and Ferrier (2001), Nielsen et al. (2005) and Jiménez-Valverde et al. (2009) are not encouraging at all.

The study of VanDerWal et al. (2009) went a step further towards understanding the relationship between suitability and abundance. These authors suggested that the relationship between

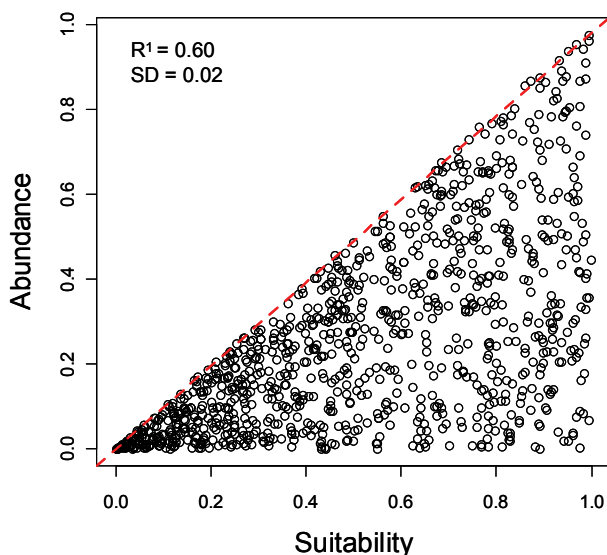


Figure 1. Idealized triangular relationship between suitability and abundance. Two vectors – one representing abundance (y) and another suitability (x) – were generated. In the case of x , 1000 values ranging between 0 and 1 were randomly extracted from a uniform distribution. In the case of y , 1000 values were also randomly extracted from a uniform distribution following the condition $0 \leq y_i \leq x_i$ ($i = \{1, \dots, 1000\}$). Linear quantile regressions were fitted to the 97.5th percentile (red dashed line). From 1000 simulations, the mean goodness-of-fit statistic for quantile regressions (R^1 ; Koenker and Machado 1999) was computed, with a value of 0.60. Analyses were done in R using the `quantreg` package (Koenker 2009).

suitability and abundance should be triangular (see Fig. 1). They reasoned that, since many factors may reduce the theoretical maximum density that a species can reach at a certain location, suitability should determine the maximum limit instead of the mean abundance. The authors modelled the distribution of 69 species of vertebrates in the Australian wet tropics region. Presence data for the species were compiled from a variety of sources and several climate and vegetation-related variables were used to fit the SDMs. The authors applied Maxent, a technique that has gained surprising popularity recently, and that uses presence and background (i.e., locations with no information about the occurrence of the focus species) data. Then they studied the relationship between suitability and abundance data derived from standardized sampling.

To test for the expected polygonal relationship, the authors argued that ordinary least square regressions were not suitable. In fact, suitability only accounted for 12% (mean) of the variation in vertebrates' mean abundance. Certainly, suitability was not a good surrogate of abundance. They applied quantile regressions (QR), which are appropriate for dealing with the unequal variation in ecological data associated with limiting variables (Cade and Noon 2003). VanDerWal and collaborators found evidence for a positive relationship between the upper limit of local abundance and suitability. Here, I want to stress four concerns.

First, the calculation of an R-squared measure (explained variance) makes little sense in a QR context (see FAQ() in Koenker 2009). While in a mean regression (ordinary least squares regression) the sum of squared residuals is minimized, in a median regression (QR fitted to the 50th percentile) what is minimized is the sum of absolute residuals. Thus, in QR, the interest is on the weighted sum of absolute residuals (R^1) as a local measure of the goodness-of-fit for a unique quantile (Koenker and Machado 1999). Second, the reported values of R^1 are not generally very large (mean value lower than 0.2), although it has to be taken into account that for an idealized perfect triangular relationship the maximum R^1 that a lin-

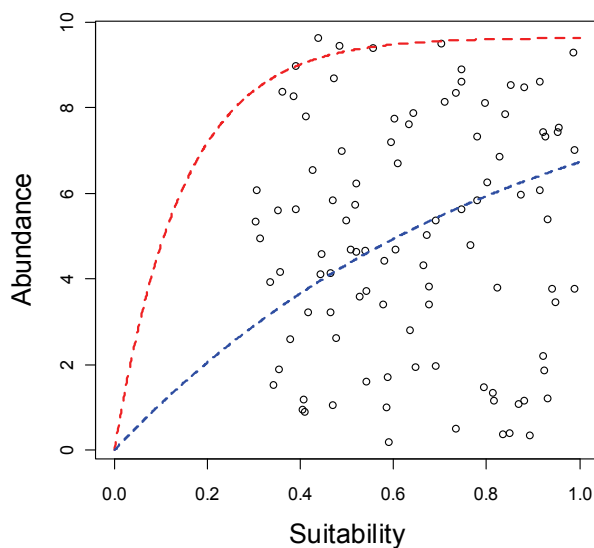


Figure 2. Naive example showing the potentially trivial results of fitting quantile regressions with a fixed (0, 0) intercept. Two uncorrelated vectors – one representing the abundance (y) and another the suitability (x) – were generated. In the case of y , 100 values ranging between 0 and 10 were randomly extracted from a uniform distribution. In the case of x , 100 values ranging between 0.3 and 1 were also randomly extracted from a uniform distribution. Nonlinear quantile regressions were fitted to the 95th (red dashed line) and 50th (blue dashed line) percentiles using the function $y = [\max(y) - \exp(-bx)]$ (in this example, $\max(y) = 10$). The parameter b was estimated as 6.84 (95th) and 1.20 (50th) and was highly significant in both cases ($p < 0.0001$). Analyses were done in R using the `quantreg` package (Koenker 2009).

ear QR fitted to the 97.5th percentile can yield is 0.60 (not 1; see Fig. 1). Third, fitting a function with a fixed intercept at point (0, 0) (as done by the authors with nonlinear QR – one of several functions fitted) may yield statistically significant but at the same time spurious results (see Fig. 2). Finally, VanDerWal and collaborators applied a threshold to convert continuous maps into presence–absence maps, and excluded locations falling below that threshold (i.e. locations with low suitability values) from the abundance–suitability regression analysis. This allowed them to avoid the inclusion of a potentially large number of zero counts in locations with very low suitability values (in which case a positive abundance–suitability relationship may be indicating good discrimination capacity of the SDMs rather than capacity to account for abundance) while still taking into ac-

count absence data within the potential range of the species. However, it would be very informative to know the extent to which the thresholding process excluded locations with very low suitability values but with non-zero species' abundance.

In any case, the fact that linear QR showed higher significant slopes in the upper percentiles, and that R^1 progressively increased, hints at the idea of a polygonal relationship. Clearly, the study of VanDerWal et al. has brought to light a new perspective in the way to approach the analysis of the "abundance–suitability" pattern. Given the difficulty of obtaining abundance data and its potential relevance in conservation practices (Brown et al. 1995), many more studies in this line of research are required to discern under which circumstances, if any, the pattern holds.

Finally, an issue that worries me about the general idea of the "abundance–suitability" pattern is that (assuming well designed sampling, yielding unbiased occurrence data), if the density of points across the grid cells is a reflection of abundance, then a positive relationship between suitability and abundance may be a trivial fact. (Note that, as is usually done in SDM studies, VanDerWal and collaborators aggregated multiple observations at the same location, which certainly helped avoid tautological relationships, but this does not invalidate my argument: I am referring to the density of points *across* the grid cells). My reasoning is that it seems justified to assume that the abundance affects the probability of detecting the species. Therefore, if the probability of detection determines the geographic density of presence points across the grid cells, is the positive relationship between local abundance and suitability that is estimated from well calibrated SDMs a revelatory pattern or just the consequence of circular reasoning?

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perspective

Musings on the Acropolis: Terminology for biogeography



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Abstract. Biogeography, like all science, is better served when its vocabulary usage is precise, organized and simple. In this light, I examine three intertwined sets of concepts concerning scale and diversity. First, I show how ‘scale’ consists of four components: sampling unit, grain, focus and extent. Using those more precise terms prevents potential ambiguities in communication. I also clear up a confusion in the usage of ‘focus’ that I promulgated in an earlier paper. Second, I explain how organizing our concepts concerning species richness relationships both disambiguates those concepts and leads to the development of new theories. Third, I explore the multitudinous ideas and terms that have collected under the general concept of ‘diversity’ and propose one scheme for simplifying current confusions. Biogeography is in a period of unification of its disparate threads of ecology, phylogeography and phylogenetics. In weaving together concepts of scale and diversity, I hope that this essay contributes to that unification.

“Rhetoric is the art of ruling the minds of men.” (Plato)

Introduction

“Sticks and stones may break my bones, but words will never hurt me.” (Child’s rhyme)

On the contrary, words matter. They solidify concepts and ensure accurate communication. Improperly used, they can obscure and sow confusion. Ecologists are notorious for inventing complex lexicons, although we are probably no worse in this regard than many other disciplines and professions. Sometimes those lexicons make meanings precise, but only if used properly. My purpose here is to examine three intertwined sets of concepts concerning scale and diversity, with a goal of making our vocabulary usage more precise, organized and simplified.

While none of this is new, our continued misuse of terminology bears its repetition. This essay was conceived while at the Fifth International Biogeography Society meeting in Crete, listening to the talks and their misuses and ambiguities of rhetoric. Having come down with the ‘flu a short time later, I spent an entire day in my hotel room writing this paper while gazing up at the Acropolis, hence the title of this piece. It is a hom-

age to those ancient Greek philosophers who gave us the foundations of our sciences.

More precise vocabulary

“It is the mark of an educated man to look for precision in each class of things just so far as the nature of the subject admits; it is evidently equally foolish to accept probable reasoning from a mathematician and to demand from a rhetorician scientific proofs.” (Aristotle, *Nicomachean Ethics*)

Biogeography deals with patterns and processes that vary in time and space from seconds to epochs and micrometers to the entire globe. In referring to these ranges of time and space, we make one of the most common vocabulary errors in our discipline by talking about differences in ‘scale.’ Because ‘scale’ has multiple components (Table 1A), the use of the word ‘scale’ is often imprecise (Dungan et al. 2002). Most often what is meant is ‘extent’ – as in, “Studies at landscape and continental scales” – and this meaning is usually, but not always, obvious in context. The other frequent meaning of ‘scale’ is ‘grain.’ It is here that the use of ‘scale’ can sow confusion.

Consider the following: “The accuracy of species richness data differs when compiled at landscape and continental scales.” That sentence

A.

Extent: the coarsest spatial or temporal dimensions that encompass all of the sampling units

Focus: the dimensions of the aggregated or summed grains

Grain: the dimensions to which data are standardized before analysis, often equal to the area, volume, or duration of the sampling unit

Sampling unit: the spatial and/or temporal dimensions of the collection unit

B.

Inventory diversity: the abundance of named objects in a specified unit or set of units

Differentiation diversity: how the composition of named objects differs among groups, i.e. units or sets of units

Pattern diversity: variation in the arrangement of groups of named objects in physical or mathematical space

Table 1. (A) The four components of scale. **(B)** The three classes of diversity; typically the objects under consideration are biological species. (Modified from Scheiner 1992; Scheiner et al. 2000).

could refer to the basic unit of analysis – the grain – or it may refer to the entire study – the extent. The causes of data inaccuracy that are being referred to in that sentence differ depending on which scale component is meant. If grain is meant, the sentence is contrasting plots within a single landscape that are typically very accurate as opposed to range maps interpolated over a latitudinal and longitudinal grid that are typically inaccurate for a given grid cell. If extent is meant, then the sentence is contrasting the less than complete coverage of plots within a landscape and the resulting inaccurate extrapolation from the samples to the entire landscape as opposed to the more accurate estimate of the total species richness of an entire continent using summed range maps. So, which of those two scales has less accurate data depends on whether one means grain or extent. Of course different particulars of data collection would alter that outcome, but you get my point.

Once we deal with data collection, two other scale components become relevant, focus and sampling unit. These components are rarely acknowledged and are typically unrecognized. We usually learn about scale by being presented with an area that has been completely gridded and sampled so that the focus is the same as the extent and the sampling unit is the same as the grain, thereby subsuming distinct concepts. In-

stead, consider an area incompletely sampled with plots and subplots; the data are averaged over subplots so that the plot is the unit of analysis (Fig. 1). Now the four scale components all differ.

A common failure is confusing focus with extent. Consider the following: “The relationship between productivity and diversity differs with the scale of the study.” That sentence could mean that the relationship changes when the extent changes from landscapes to continents, or it could mean that within a single extent, the relationship changes with increasing numbers of plots – the focus. [That sentence could also be referring to differences in grain, yet a different ambiguity.] This example may seem contrived, but I recently ran into just this type of ambiguity in a manuscript that I reviewed that was examining the effects of scale components on richness estimates. Varying grain, focus and extent all had different effects that the authors would confound by speaking of the effects of scale.

Finally, I make a *mea culpa*. When we (Scheiner et al. 2000) first defined ‘focus’ and contrasted it with ‘extent,’ our definition of the latter was the same as in Table 1A, but our usage in a hierarchical setting (e.g., Fig. 4 in Scheiner et al. 2000) confounded ‘focus’ with ‘extent’. To understand this more complex aspect of focus, consider the following instance. Assume that the sampling

units in Fig. 1 are $1/4 \text{ m}^2$ so that the grain is 1 m^2 . From these samples we calculate the mean species richness of the 15 plots. Next, we take that mean value and aggregate it with 10 other samples (say different fields scattered across a landscape) and calculate the total species richness of those data. In that landscape-level analysis, the data that make up each data point have a grain (1 m^2) and a focus (15 m^2), but the total set of data points also has a grain (1 m^2) and a focus (10 m^2). Thus, the grain and the focus of the individual data points and the aggregate data will change as the data are manipulated. Separating these scale concepts allows better communication of these manipulations. In that previous paper we, unfortunately, used ‘extent’ when referring to the focus of the analysis at the landscape level. It was only because a co-author of a recent paper (Scheiner et al. 2011) pointed out inconsistencies in my use of those terms that I saw the discrepancy in the original usage and the confusion that I had caused.

More organized vocabulary

“The chief forms of beauty are order and symmetry and definiteness, which the mathematical sciences demonstrate in a special degree.” (Aristotle, *Metaphysics*)

A fundamental relationship in ecology is that between species richness and the focus over space or time that it is measured. This relationship was

originally termed a ‘species–area curve’, and that is probably the most frequently used phrase, although ‘species–area relationship’ is also common. Several years ago (Scheiner 2003), I pointed out that this single phrase referred to a multiplicity of types of relationships differing in sampling scheme, mode of aggregation and meaning of sampling units. I attempted to tame this confusion by organizing the relationships into a typology (Table 2), which to my surprise set off a debate about which was the true species–area curve (Scheiner 2003, 2004, 2009, Gray et al. 2004a, 2004b, Dengler 2009). This is not the place to rehash that debate; see those papers and Scheiner et al. (2011) for details. From that debate, however, we can draw three lessons.

The first lesson is the importance of organizing our vocabulary. Before I proposed my typology, the multiplicity of relationships hiding within a single concept was not clearly recognized. There is emerging evidence that the form of the relationship differs in a regular way between Type IV curves and Type II and III curves (Stiles and Scheiner 2007, Chiarucci et al. 2009, Williams et al. 2009, K.A. Triantis, F. Guilhaumon & R.J. Whittaker, unpublished) in part because the different types of curves are based on different diversity metrics (Tuomisto 2010c). Having a clear way to refer to these types makes easier such discoveries.

The second lesson is the importance of words in guiding our thoughts. The problem with

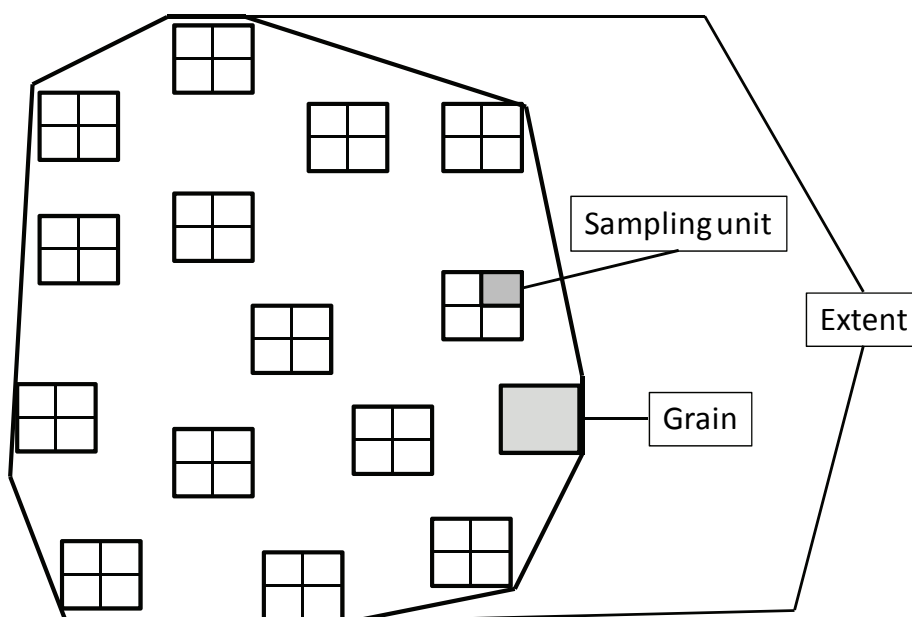


Figure 1. A sampling and analysis scheme that demonstrates the four components of scale. The data consist of surveys from an area that is sampled with scattered plots, each plot containing four subplots. The data from the subplots are aggregated at the plot level for analysis. The entire area is the extent, the sum of the sampled areas is the focus, the area of a plot is the grain, and the subplot is the sampling unit.

Type	Sampling scheme	Species density (species richness per unit area)	Construction spatially explicit	Grain	Focus	Extent
I	Nested	The number of species in a contiguous sample unit of specified size	Yes	A sample unit nested within the larger or longer one	Same as the grain	The largest or longest sampling unit
IIA	Contiguous	The number of species in a contiguous sample unit of specified size	Yes	One or more adjacent sampling units	The cumulative area or time of all sampling units	Same as the focus
IIB	Contiguous	The number of species in an aggregated sample unit of specified size	No	One or more aggregated sampling units	The cumulative area or time of all sampling units	Same as the focus
IIIA	Non-contiguous	The number of species in an aggregated sample unit of specified size	Yes	One or more neighbouring sampling units	The cumulative area or time of all sampling units	The maximum distance or time among sampling units
IIIB	Non-contiguous	The number of species in an aggregated sample unit of specified size	No	One or more aggregated sampling units	The cumulative area or time of all sampling units	The maximum distance or time among sampling units
IV	Independent units	The estimated number of species in a sample of a specified size	No	Independent space or time units	The cumulative area or time of all sampling units	The maximum distance or time among sampling units

Table 2. The six types of species richness relationships with a description of their features and scale parameters. See Table 1 for definitions of the scale components. From Scheiner et al. (2011).

the term 'species–area curve' is that the relationship could just as easily be over volume or time and 'species' is ambiguous in that it does not indicate what property of species is being measured. We (Scheiner et al. 2011) proposed substituting 'species richness relationship' (SRR), placing the emphasis on, and making explicit, the dependent variable. Although area is far and away the most common independent variable, by using our suggested term we will no longer automatically think of these relationships exclusively in terms of area. We recognize that doing so leaves the independent variable in the relationship unstated; see Scheiner et al. (2011) for a detailed explanation for this choice of terminology.

The third, and most important, lesson is that vocabulary is the precursor to concepts that are in turn the gateway to theory. Ecology is awash in theory (Scheiner and Willig 2011b), but ecologists often fail to recognize these linkages

and relationships and the resulting conceptual framework. One way to arrive at such a framework is to recognize that highly specific theories (termed 'models' in our schema) can be unified under more general theories (termed 'constitutive theories') (Scheiner and Willig 2008, 2011a). Constitutive theories are a set of propositions that act as an instruction set for building models. Formulating those propositions requires one to think deeply about the processes underlying the object of one's models. In Table 3, I codify a constitutive theory of Type II and Type III SRRs based on the set of processes outlined in Scheiner et al. (2011). [A separate theory of Type IV SRRs can be built from the equilibrium theory of island biogeography (Sax and Gaines 2011, K.A. Triantis, F. Guilhaumon & R.J. Whittaker, unpublished).] I leave to others the task of relating this theory to the current multitude of SRR models. Such an endeavour will not only help organize and synthesize those

Domain: Type II and III SRRs. The sampling units can be over space or time. The units can be contiguous or noncontiguous. The process of aggregation may or may not account for the spatial or temporal relationships of the sampling units.

Assumption: The system is at equilibrium.

Propositions for all Type II and III SRRs

1. As sampling increases to include more space or time, the number of individuals sampled may increase.
2. More individuals lead to more species.
3. As sampling increases to include more space or time, more environmental variation may be encountered.
4. If all individuals of all species are uniformly distributed, and if the sampling unit is smaller than the mean distance between individuals, then the SRR will have a positive relationship between space or time and species richness.
5. If the sampling regime encompasses large areas or long time durations, then those samples may derive from multiple species pools.

Additional propositions for spatially explicit or temporally explicit SRRs

6. Clustering in space or time of individuals of the same species will increase the rate at which species richness increases over space or time.
 7. Competition can create overdispersed distributions. Such distributions will decrease the rate at which species richness changes over space or time.
 8. The inclusion of multiple species pools will increase the rate at which species richness increases over space or time.
-

Table 3. The domain, assumption, and propositions of a constitutive theory of species richness relationships (SRRs) built from the continual aggregation of sampling units (Types II and III). See Scheiner *et al.* (2011) for a full explanation and justification of the propositions.

models clarifying assumptions and mechanisms, it will highlight other models not yet considered.

More simplified vocabulary

“Beauty of style and harmony and grace and good rhythm depend on simplicity.” (Plato, *The Republic*)

Metrics are to concepts as models are to constitutive theories. A single concept can be quantified with many metrics. Therefore, using the same word for both a concept and one of its many metrics sows confusion. We see this confusion with the concept of diversity. Blame, if such be given, needs be laid at the feet of Robert H. Whittaker, who codified diversity concepts while simultaneously using the same word for multiple metrics (Whittaker 1960), further leading us into the morass over the next decade and a half (Whittaker 1972, 1977). Thankfully, he also gave us a terminology to lead us out of that swamp.

The key is to divide diversity into three broad concepts: inventory diversity, differentiation diversity and pattern diversity (Table 1B). The first two terms were coined by Whittaker (1972), and the third by myself (Scheiner 1992), generalizing a concept first put forth by Pielou (1966). Calls for the use of this terminology have been made repeatedly (e.g. Scheiner 1992, Whittaker et al. 2001, Jurasinski et al. 2009), and done again here. One benefit of doing so is the recognition that the three diversity classes are related through a single, hierarchical framework [see Fig. 1 in both Tuomisto (2006) and Tuomisto (2010c)].

Inventory diversity, the first level of the hierarchy, is the least contentious. It consists of metrics such as species richness and the Shannon–Weiner index. However, we also have a dilemma. One way to quantify inventory diversity is by the use of numbers equivalents (Hill 1973):

where S is the number of species, p_i is the frequency of the i th species, and q is a parameter

$${}^qD = \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)}$$

that determines how species frequencies are weighed. When $q = 0$, qD is species richness. When $q = 1$, $\log({}^qD)$ is the Shannon–Weiner index. When

$q = 2$, qD is the inverse Simpson’s index.

The dilemma is that qD is called ‘diversity’, yet it is just one metric of inventory diversity. To further muddy the waters, diversity is the product of species richness and evenness, the extent to which the species within a sample have equal abundances. Diversity (measured as qD), richness and evenness are all components of inventory diversity. So, why should one component be privileged with the name ‘diversity’?

I have no real solution. The use of ‘diversity’ to reference qD and its cognates is too deeply entrenched. Ecologists have only recently moved on a regular basis to using ‘species richness’ (or ‘richness’) to distinguish that concept. All that I can offer to thread this needle is to recognize two concepts: ‘diversity *sensu lato*’ and ‘diversity *sensu strictu*’. The former is the general idea of diversity that includes all of the various types (Table 1B) as subcategories; the latter is qD . We would not actually want to use such awkward terminology, but it would allow us to be precise about which aspect of diversity we meant if not otherwise obvious from context.

We can simplify terminology related to diversity in one respect. Whittaker proposed a hierarchy of inventory diversity – point, α , γ , ϵ – depending on the extent of the sample. The problem is that those extents are vague and have been used in various ways or to mean different extents (e.g. Cody 1975, Shmida and Wilson 1985, Currie and Paquin 1987, O’Brien 1993, Whittaker et al. 2001) so that they no longer convey precise meaning. Hanna Tuomisto (2010a) wisely collapsed those into just two concepts. γ -diversity is the inventory diversity of a given sample, whatever the focus of that sample. α -diversity is the mean inventory diversity of a set of subsamples at a specified grain within a sample, again independent of any particular length, area, volume or duration. Used in this fashion, the researcher must specify the actual dimensions of any particular set of measurements, ensuring clear communication.

Differentiation diversity is the second level of the hierarchy. Rather than a dilemma, here we have a controversy; one however, that contains its own solution. The controversy comes from

Whittaker (1960) defining β -diversity five different ways, while using the same term and symbol for all of them. Which of those versions had ascendancy has waxed and waned over the years. A reviewer of the manuscript that became Scheiner (1992) insisted that I was wrong in claiming that Whittaker had defined β -diversity as the mean similarity of a set of samples; in my reply I had to quote the actual sentence from Whittaker (1972). That reviewer insisted that β -diversity was species turnover along a gradient, the prevailing concept in the 1970s and 1980s.

Today the argument is over whether the relationship between γ -diversity, α -diversity and β -diversity should be multiplicative ($D_\gamma = D_\alpha * D_\beta$) (Whittaker 1960, Jost 2006, 2007, Baselga 2010, Tuomisto 2010b) or additive ($D_\gamma = D_\alpha + D_\beta$) (MacArthur et al. 1966, Lande 1996, Crist et al. 2003, Veech and Crist 2010). The virtue of the multiplicative relationship is that it leads to D_β being the numbers equivalent of samples or communities. So, $D_\gamma = D_\alpha * D_\beta$ is interpreted as the total diversity of a set of samples (D_γ) being equal to the mean diversity per unit (D_α) times the number (equivalent) of units (D_β). Tuomisto (2010b) nicely shows the mathematical relationships among all of the concepts labelled β -diversity by Whittaker, listing some 30 different names.

We can simplify our discussion by using 'differentiation diversity' when referring to the entire concept of species variation among units, and be specific in words and symbols when referring to a particular metric (Table 2 of Tuomisto 2010b). A further reason for using the multiplicative formulation is that it leads to a simple unification of other concepts within inventory diversity – richness and evenness – with differentiation diversity (Tuomisto 2010a, pers. comm.).

Pattern diversity is the final level of the hierarchy and is the easiest to deal with because it has attracted the least attention. This concept has been labeled level-of-abstraction 3 (Tuomisto and Ruokolainen 2006) and proportional diversity (Arita et al. 2008). Currently there are few metrics, the most well known belonging to one class – nestedness (e.g. Patterson and Atmar 1986, Wright and Reeves 1992, Cook and Quinn 1998,

Wright et al. 1998). The particular metric I put forth in Scheiner (1992) – mosaic diversity – has never been further developed and is probably inferior to more recent ones (Tuomisto and Ruokolainen 2006, Arita et al. 2008). Most important is to recognize a single, unified concept, whatever its name, to clearly separate current and future metrics, and to develop a unified theory from which we can draw a better understanding of that concept.

Conclusion

"Rhetoric, it seems, is a producer of persuasion for belief, not for instruction in the matter of right and wrong." (Plato, Gorgias)

According to Homer, the Trojan War began when Eris, the goddess of strife, tossed the golden apple amidst the gods saying, "For the most beautiful one." I hope that my offering here is not such an object of discord. My goal here is not to provoke, but rather to show how a more precise, organized and simplified vocabulary can prevent confusion and advance the science of biogeography. Unification of ideas into theories begins with clarity of terminology. The building of the Parthenon on the Acropolis and the golden age of Greek philosophy occurred after the Greek city-states set aside their antagonisms and united to defeat the Persian invasion. Biogeography is seeing a similar golden age with the current unification of its disparate threads of ecology, phylogeography and phylogenetics. In weaving together concepts of scale and diversity, I hope that this essay contributes to that unification and that I am not judged to have corrupted the youth of biogeography and forced to drink from Socrates' cup.

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Edited by Joaquín Hortal

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

from the society

Looking to the future of the IBS: the 2011 IBS membership survey

The International Biogeography Society (IBS) was founded 10 years ago, with the goal of promoting biogeographical research, fostering communication among biogeographers, and increasing knowledge of and appreciation for biogeography among the general public. As a neonatal society, growth and stability were crucial: the first practical goals were to organize the first conference (held in 2003) and begin to build a membership base. Five IBS conferences have now been held, the membership has grown to 796 members representing 54 countries, an on-line IBS journal has been established (*Frontiers of Biogeography*; <http://www.biogeography.org/html/fb.html>), and the first IBS off-year conference (a young investigators conference scheduled for 23-25 September 2011 at the University of Oxford; <http://www.biogeography.org/html/Meetings/index.html>) will be held quite soon. Enthusiasm for the January 2013 IBS conference in Miami, Florida (<http://www.biogeography.org/html/Meetings/2013/index.html>) is quite high, and we may see record-high attendance. Overall, the IBS is now a strong and healthy 10-year-old.

We all recognize, of course, that we need to maintain regular communication with the members about the details of just how well the IBS is doing: where are there strengths, where are there weaknesses, and where would growth be most effective? Not long after the IBS conference on Crete in January 2011, the Board of Directors of the IBS, newly reconstituted after the meeting, was keen to look to the future immediately. We resolved to perform a survey of members and to use this opportunity to ask important questions about the biennial meetings, the role of *Frontiers of Biogeography*, the other services the society provides (or does not), and the level of enthusiasm among members for getting more involved in the society. In February, with the Crete meeting still fresh in our memory, the survey went live and IBS members were invited to respond.

Background: the IBS membership. The number of members who took the time to respond was, in itself, very encouraging. In total 285 members completed the survey, about 60% of whom had attended the meeting in Crete. Around 30% were students, 3% retired and 67% professionals. About 11% were under 30, 63% were 30–49 and 15% were 50–65; 64% of them were male and 36% female. Of the 274 people who responded, about 30% identified themselves as coming from North America, 11% from Central and South America, 18% from northern Europe, 26% from southern Europe, and 5% or less from each of Australia/New Zealand, the Middle East and Africa, and Asia. A little over 40% of the survey respondents said that the IBS was their primary professional society. The range of “other conceptual affiliations” of our members is very broad, ranging from evolutionary aspects of genetics and phylogeography, vertebrate biology (mammalogy, ornithology, etc.), systematics, botany, paleontology, and conservation biology to ecology, which was the single most-frequently mentioned topic. Clearly, geographic and conceptual breadth is a hallmark of the IBS membership.

Importance of contact from the IBS. While the danger of communication overload must always be considered, members clearly appreciate communications from the IBS. This was how many learned about the Crete meeting (58% from IBS e-mails or website). Responses to open-ended questions about making IBS better and possible web-based member benefits all highlighted the value of information flowing from the IBS to members (also among members).

The Crete meeting was deemed a success, with 77% rating the meeting as “great” or “very good”; only 0.5% rated it as “not so good”, and none as “poor”. While most respondents (72%) thought the balance between posters and oral presenta-

tions was about right, 35% preferred more concurrent oral presentations, but many expressed appreciation of the plenary approach (with not too many concurrent sessions). Respondents were nearly evenly split on preferring oral presentations from established researchers (46%) and young investigators (54%). There was much praise for the quality of the posters and the way they were taken seriously, but also recognition that the last-minute need for a change in venue in Crete imposed cramped, split rooms for the posters. Some respondents called for more workshops (on many different topics), for repeats of oversubscribed workshops, and for more time for each workshop (allowing more depth). A few people also called for an extra day to be added to the conference, to allow more time for networking, etc.

Content for future IBS meetings. Of the eleven listed symposium suggestions, all were reasonably popular, but those on species distribution models and climate refuges were most favored, followed by ‘Search for interdisciplinary congruence from the fossil record, genetics and models’. There was good support for symposia on disturbance regimes, experiments (planned, natural and accidental), the biogeography of traits and island biogeography, but also many suggestions for other topics. All of the seven workshop topics were received well, with especially strong support for “Phylogenetic analysis in macroecology” and “Spatial analysis in macroecology”. Respondents tended to think that gender, ethnicity, and geographic origin should all be considered in selecting speakers, with geographic origin clearly ranking highest among these.

Possible 2015 and 2017 meeting locations. When presented with a list of nine geographic regions where future meetings might be held, members collectively expressed a clear preference for the location of a future meeting: tropical America,

followed closely by the Czech Republic and Denmark. California, Australia/New Zealand, Hawaii, and South Africa were not far behind. The good support for the two European destinations may have been partly because more respondents were at the Crete meeting (in Europe) than not. Most who attended the Crete meeting said they would go to any of the top six locations (i.e. those listed above). Many of those who did not go to Crete (which included many respondents from North America) said they were unlikely to go to the European destinations or Australia/NZ or South Africa; they tended to prefer California or tropical America.

Meeting timing and frequency. All IBS meetings have been held in early January. While there are advantages to maintaining a consistent time for the meetings, the survey investigated the strength of interest in shifting the time. The result was ambiguous, with no clear message about a preference. Predictably, there was some tendency for those who made it to Crete to oppose different timings and those who did not make it to Crete to support them. There is interest in holding more meetings, with some calls for the main IBS meeting to be held every year, and clear support for additional IBS workshops, symposia, regional chapters, etc. This has already led to the organization of the IBS Early Career Conference in Oxford, UK, September, as mentioned earlier (<http://www.biogeography.org/html/Meetings/index.html>).

Frontiers of Biogeography. Over two-thirds of respondents regularly read the IBS on-line journal. There were many calls for more alerts about when new issues are published, and 85% said that IBS should expand/strengthen *Frontiers* because of its importance for the future of the IBS. There was also a great deal of enthusiasm about helping to edit the journal.

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/>).

Financial issues. The IBS is a young society with very limited income and very limited reserves. When asked if they would support modestly increased membership fees to expand *Frontiers* and/or provide funding for off-year conferences or workshops, over three-quarters replied affirmatively. Similarly, about three-quarters also supported increasing conference registration fees by 10% to provide funding for students or to increase international participation. About two-thirds of respondents said they are willing to donate or buy an item for an auction at future meetings, so that the proceeds could go to support IBS activities.

Training and techniques, networking, etc. Much interest was expressed in web-based activities, with more than half of respondents saying they would take part in 'on-line conferences' in chat rooms with senior biogeographers; there was also strong interest in blogs, online networking, online presentations, regular updates from the IBS, more job advertisements, online teaching resources, etc.

Volunteers. While there is much satisfaction with the IBS among the members, there is clearly room for growth. Many members stated a willingness to get involved with promoting membership, editing *Frontiers*, and organizing regional IBS chapters or off-year activities.

The results of this survey give us a fairly detailed and nuanced picture of our IBS membership: as a group, we are young, excited about our society, pleased with the conferences we have held and the journal we have established, and willing to have active involvement in expanding our programs and activities. Biogeography is clearly perceived as an exciting field of research, with great potential to make important conceptual and practical contributions to human society. As the Board of Directors of the IBS prepares for its annual administrative and planning meeting, to be held concurrently with the young investigators' conference at Oxford, this survey will provide a rich source of information and ideas on how best to direct our future growth. We would like to thank all the members who took part in this survey, those who are so supportive of our society, and particularly those so willing to give their time to help make improvements. We look to the future with considerable optimism.

Richard Field¹ & Lawrence R. Heaney²

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Job announcements

2-year postdoc position

Biodiversity and Climate Research Centre, Germany

The Biodiversity and Climate Research Centre (BiK-F; Macroecology Group) is a new interdisciplinary institute with the mission to carry out internationally outstanding research on the interactions of biodiversity and climate change on the organism level. It integrates a variety of disciplines from both natural and social sciences. The Project Area B "Biodiversity Dynamics and Climate" invites applications for the position of a Post-doctoral researcher in "Macroecology". The successful applicant will investigate the impact of climatic factors and other drivers of global change on population dynamics of organisms. We aim at trait-based, comparative analyses of long-term data sets across multiple

taxa (e.g. epizoobenthos, fish, birds, butterflies, plants) from the terrestrial, limnic and marine realm. The applicant will take responsibility in study design, statistical analyses and publication of the results in close collaboration with data owners.

The applicant should hold a Ph.D. in ecology or a related field, and have a solid background in comparative, macroecological analyses and in advanced statistical methods. Experience in analyses of species' traits and in population dynamics of organisms will be of advantage. The applicant is expected to work independently, to have an interest in a wide range of taxonomic groups, very strong oral and written communication skills and willingness to develop joint projects with multiple partners. Salary and benefits are according to

a public service position in Germany (TV-H E13). The contract shall start as soon as possible and will run for 24 months. The duty station will be Frankfurt am Main, Germany. The employer is the Senckenberg Gesellschaft für Naturforschung.

Send your application by e-mail attachment, mentioning the reference of this position (#B48a) and including a letter outlining your suitability for the post, a detailed CV, contact details of 2 referees and a selection of your most important publications before September 28th, 2011 to: Prof. Dr. h.c. V. Mosbrugger, Scientific Coordinator Biodiversity and Climate Research Centre, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany. E-mail to Service and Administration: recruiting@senckenberg.de. For scientific enquiries please write to PD Dr. Ingrid Kröncke (Ingrid.Kroencke@senckenberg.de).

3-year postdoc position

University of Azores, Portugal

The Azorean Biodiversity Group (University of Azores, Portugal) is opening a Postdoctoral position to study the dynamics of soil and canopy arthropod communities under land-use changes. The research should also improve the understanding about how land use changes have affected arthropod functional diversity and body-size frequency distribution and make projections about possible future trajectories. It is also expected to quantify the ecosystem services of arthropods in the different Land-Uses.

Applicants should hold of a PhD in Ecology, Biodiversity and Conservation, Landscape Ecology or related disciplines. We prefer candidates with publications of recognized quality and experience in spatial ecology, ecological modelling, macroecology, and R. Opportunities exist to collaborate with field ecologists both in Azores (Prof. Paulo Borges Group; <http://cita.angra.uac.pt/biodiversidade/equipa/>) and the Museum of Natural History in Madrid (Prof. Jorge Lobo Group; <http://www.biogeografia.org/>). The initial appointments are for one year and a competitive stipend (1740 €/month), and continued funding is available for an additional 2 years provided satisfactory progress. The position is available from Autumn 2011, or no later than January 2012.

Individual applications must be submitted electronically, using the web application available at: <http://www.azores.gov.pt/gra/sctr>. To apply candidates must register at the Sistema Científico e Tecnológico Regional, through the web site mentioned above. In the application form the candidate must in-

clude a copy of the PhD certificate or, in case of not having it, indicate the date of the degree, the title and the institution that conferred the degree. Despite the above, the candidate must present an authenticated copy of the PhD certificate by the time of contract signature. Incomplete application forms are excluded automatically. For enquiries contact Prof. Paulo A. V. Borges (pborges@uac.pt).

Postdoc position and PhD fellowships

Syracuse University, USA

Jason Fridley Lab (<http://plantecology.syr.edu/fridley>).

Postdoctoral associate to work on aspects of the vegetation of Eastern North America in the context of global change. Specific research objectives are flexible but will ideally take advantage of vegetation and environmental databases from Great Smoky Mountains National Park. Projects combining existing data with new field surveys of soil characteristics, plant trait data, or microclimate surveys are particularly encouraged. Other research emphases in the Fridley lab include global change impacts on grassland vegetation, comparative studies of native and invasive forest species, and biogeographic studies of successional ecosystems. The position is available as early as January 2012, and it will run for two years (annual minimum salary \$38,500, including full benefits). A PhD in ecology or related discipline is required. Preferred qualifications include evidence of strong quantitative and writing skills; statistical or GIS-based programming experience (e.g., R, GRASS-GIS); relevant field experience and taxonomic skills. Those with expertise in plant-soil relations are particularly encouraged to apply. Applicants should send a letter of interest, curriculum vitae and the names and full contact information (email and phone numbers) of three potential references to Jason Fridley (fridley@syr.edu; 315-443-3098) no later than November 1, 2011.

Two graduate (PhD) fellowships are available for students to work on aspects of the vegetation of Eastern North America in relation to global change. At least one of the fellowships will involve a comparative analysis of old field succession patterns across the Eastern U.S., using experimental and survey-based techniques in a 4-yr project with colleagues at Duke University supported by the National Science Foundation. Other research emphases in the Fridley lab include global change impacts on grassland vegetation, vegetation-environment relationships in the Southern Appalachians, and comparative studies of native and invasive species in Eastern U.S. forests. Successful applicants will join a gro-

wing plant ecology and evolution group at Syracuse University and a larger ecological community that includes SUNY-College of Environmental Science and Forestry. Fellowships are available beginning in Fall 2012 as 2-yr research assistantships, commonly used in the first and third years of graduate study; support through teaching assistantships is guaranteed in other semesters pending satisfactory progress toward the degree. Current graduate student stipends are \$25,167/yr, with

full benefits and tuition remission. Full applications to the SU Biology PhD program are due by January 31, 2012; applicants are strongly encouraged to submit a statement of interest, curriculum vitae, and GRE scores before applying to Jason Fridley (fridley@syr.edu; 315-443-3098). General information about the Biology graduate program at Syracuse is available at <http://biology.syr.edu/grad/graduate.htm>.

upcoming events

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/>

BIOLIEF 2011

2nd World Conference on Biological Invasions and Ecosystem Functioning

21-24 November 2011 – Mar del Plata, Argentina

<http://www.grieta.org.ar/biolief/>

Workshop on the Biogeography and Phylogeography of Atlantic Fishes

26-27 November 2011 – Lisbon, Portugal

http://biocongroup.eu/Workshop_Atlantic/Home.html

Annual Conference of the Society for Tropical Ecology (gtö)

Islands in land- and seascape: The challenges of fragmentation

22-25 February 2012 – Erlangen, Germany

<http://www.gtoe-conference.de/>

6th International Conference of the IBS

January 2013 – Florida, USA

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

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 and frontiersofbiogeography@gmail.com.

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news and update

update: A modelling framework to open the gates of assemblage structure, by J. Hortal	43
commentary: One step closer towards disentangling competing hypotheses in macroecology, by C. Fløjgaard & J.-C. Svenning	44
workshop summary: State of the art and perspectives of risk assessment analysis, by F. Essl	46
book review: Definitive guide to China's woody plants, by M. Eichhorn	48
book review: A 100 million year love affair with American plants, by P.V.A. Fine	50
book review: Fifty years of Elton, by S.J. DeWalt	52
book review: The palm book, by H. Balslev	54
books noted with interest	56

resources

data: Two researchers desperately seek stable 50-year-old corridors for study on conservation corridor efficacy, by P. Beier & A.J. Gregory	57
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opinion and perspectives

opinion: Relationship between local population density and environmental suitability estimated from occurrence data, by A. Jiménez-Valverde	59
perspective: Musings on the Acropolis: Terminology for biogeography, by S.M. Scheiner	62

membership corner

from the society: Looking to the future of the IBS: the 2011 IBS membership survey, by R. Field & L.R. Heaney	71
Job announcements	73
Upcoming meetings	75
