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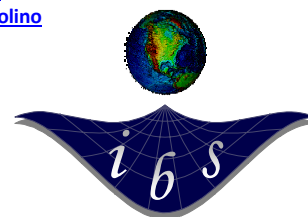
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cover: Mammal remains at Kruger National Park, South Africa. Picture courtesy of Aristides Moustakas.

commentary

Scale-dependence of spatial patterns of insect distribution and abundance

The most recent issue of *Ecography* (February 2010) contained eight papers devoted to patterns in the distributions and abundance of insects, and to the dependence of these patterns on spatial scale.

It has been known for some time that our perception of patterns of biodiversity, and the relative importance of the factors that determine these patterns, vary with the spatial scale considered (Whittaker et al. 2001). However, as Hortal et al. (2010) point out in their introduction to the *Ecography* special issue, most previous analyses have focused on species richness patterns, not on the distributions of individual species. Furthermore, in these previous studies, as in conservation and ecology research more generally (Clark and May 2002), there has been strong bias towards vertebrate animals and plants: in a meta-analysis of 394 studies of species richness patterns across different spatial scales (Field et al. 2009), only 68 focused on insects. The growing number of macro-ecology studies that do focus on insects is probably a reflection of increasing knowledge about the distributions of these species. In relation to the number of species they represent, insects are still massively under-sampled (Newbold 2010), but there are now nearly 15 million geo-referenced distribution records for insects in the Global Biodiversity Information Facility database (<http://www.gbif.org>), spread across all continents except Antarctica.

Covering a wide range of taxa, geographical regions and methodologies, these papers together make an important contribution to our understanding of patterns of insect biodiversity at different spatial scales.

Scale-dependence in the drivers of biodiversity patterns

The different studies in this special issue considered patterns of insect distribution and abundance at a wide range of scales. This is reflected in

the different factors identified as important in explaining observed patterns and in the different methods used for analysis.

Several of the studies considered very broad (country-level or continental) scales, successfully using species distribution models with climate variables to explain distribution patterns (Lobo et al. 2010, Kriticos and Leriche 2010, Warren et al. 2010, Soberón 2010). At finer scales, other factors emerge as more important. In agricultural fields in the UK, arthropods showed patterns of co-occurrence that suggest an effect of biotic interactions (Bell et al. 2010). At small scales, micro-climate and topography are also important. In a national park in Hawaii, the extent of an Argentine ant (*Linepithema humile*) invasion was modelled better using microclimate data than landscape-level climate variables (Hartley et al. 2010), and a metapopulation model for the silver-spotted skipper butterfly (*Hesperia comma*) in Britain suggested that as the global climate warms, the ability to inhabit more northerly-facing aspects with warmer micro-climates is allowing faster rates of range expansion (Wilson et al. 2010).

Although it has been suggested several times that multi-scale models with different sets of drivers would help to better understand diversity patterns (e.g. Mackey and Lindenmayer 2001) and to make better predictions of species' responses to environmental change (Randin et al. 2009), this approach remains relatively rare in practice (but see e.g. Anderson et al. 2007). The marked variation with scale in the relative importance of different explanatory variables, and the decline in the importance of landscape-level climate variables at the finer resolutions, lends weight to the argument for including factors such as biotic interactions, habitat, and microclimate into models in a multi-scale framework.

Several of the studies explicitly tested the effect of spatial scale on the conclusions drawn from biogeographical analyses (Cabeza et al. 2010,

Hui et al. 2010, Kriticos and Leriche 2010).

Mar Cabeza and colleagues (Cabeza et al. 2010) presented a very interesting study looking at the outcome of systematic conservation planning exercises for butterflies in Finland at three spatial scales. The relative importance of areas was assessed using different methods at each of the scales: species distribution models with climate variables at the national scale, relating abundance to habitat variables at the regional scale, and using metapopulation models at an even finer (landscape) scale. Each of the three approaches revealed something different regarding the relative importance of areas for conservation, highlighting the advantages of a multi-scale approach.

On the other hand, distribution and abundance patterns can sometimes be explained successfully in spite of the scale-dependency of patterns. For two insect species in Australia, distribution models developed with climate data at different resolutions were very similar overall (Kriticos and Leriche 2010). However, in this case the aim was always to explain the same broad-scale distribution data, and climate variables were generally sufficient. If the aim is to explain fine-scale distribution patterns, then models developed with coarse-scale climate variables might well be inadequate.

If the factors that determine the occurrence of species at fine scales are themselves correlated with coarse-scale climate patterns, then models based on the latter might be able to explain the finer-scale patterns. Jorge Soberón (Soberón 2010) showed that this is the case by simulating a species distribution, determined at large scales by climate but with an effect of competition at finer resolutions. Distribution models based on climate variables were able to explain the simulated distribution at a coarse resolution very well, supporting the use of such models for estimating the current distribution of species. Nevertheless, this highlights the importance of choosing explanatory variables carefully when the aim of the model is predictive. A model that appears to explain current distributions will not necessarily capture the real response to the environment (Austin 2007).

Data issues

Although our knowledge of the distribution of species is increasing rapidly, data remain scarce, patchy and biased for many taxa, especially for insects (Newbold 2010). Two of the studies in the special issue considered data availability, specifically the lack of data on species absence, and how it affects our ability to model the distributions of insect species (Lobo et al. 2010, Soberón 2010).

Species distribution models often require data on species absence as well as data on species presence, but a record of species absence can occur for a number of reasons: unsuitable environment, inability of the species to disperse to an area, or failure to detect a present species (Lobo et al. 2010). For an Iberian dung beetle, modelled distributions were markedly different depending on the type of absence data used (Lobo et al. 2010). Grid cells with no presence record were divided into three types of 'absences': those in environmentally suitable areas (estimated using an exploratory model, with a technique that requires only presence data) and within the observed extent of occurrence of the species were assumed to be unrecorded owing to inadequate sampling; those in environmentally-suitable areas, but outside of the extent of occurrence, were assumed to be unoccupied as a result of other factors, such as interactions among species or dispersal limitation; grid cells that were not within the initial modelled distribution were assumed to be genuinely environmentally unsuitable.

For modelling the distribution of the short-horned Baronia butterfly (*Baronia brevicornis*) in Mexico, Jorge Soberón (Soberón 2010) took a different approach to dealing with a lack of data on species absence, modelling the potential distribution using a simple climate envelope approach and then assuming that the butterfly is only able to disperse to those ecoregions in which it has been observed. This idea is a very promising one, although assessing whether the models really capture the distribution better will require evaluation with independent data, since the refined models by definition fit the data used to train them better than unrefined models.

These two studies highlight the importance of having clear objectives when modelling the distribution of species: whether one is interested in modelling actual distributions versus potential distributions, or in predicting distributions under new conditions versus explaining current distributions, will strongly affect the appropriate choice of data and methods.

Data on the abundance of insect species are even more scarce than data on the occurrence of species. Gösta Nachman and Michael Borregaard (Nachman and Borregaard 2010) adopt an interesting solution to this problem, using a spatially implicit model of the proportions of patches inhabited by either or both of a spider mite (*Tetranychus urticae*) and its predator (*Phytoseiulus persimilis*) to help understand the population dynamics of the system where spatially explicit data on abundance are lacking.

Conclusions

The papers in this special issue of *Ecography* show how far we have come in understanding spatial patterns in the occurrence and abundance of insects. They also demonstrate techniques for making use of the incomplete and patchy spatial data on insects. Importantly, they also show how different the factors that shape observed patterns can be depending on the spatial scale considered. A proper understanding of the distributions of species will require models that incorporate as many of these different factors as possible at the appropriate scale.

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Edited by Jan Beck

symposium summary

Introduced conifer invasions in South America: an update

One-day symposium at 6th Southern Connection Congress – Bariloche, Argentina, 16th February 2010

Species in the family Pinaceae are currently among the most widely distributed trees in the world. Although almost exclusively native to the northern hemisphere, many species have been introduced and widely planted throughout the southern hemisphere. Introduced conifers have been mainly used for plantation forestry, amenity, shelter and erosion control, and in the last few decades a number of species have become increasingly invasive. On February 16th, 2010, we held a symposium entitled “*Pine Invasion In South America: Patterns, Process, and lessons to be learned*” during the 6th Southern Connection Congress in Bariloche, Argentina (<http://www.sccongress2010.com.ar>). The symposium was organized by the Southern Hemisphere Network on Conifer Invasion (SHNCI), a group of concerned scientists working on conifer invasions in the southern hemisphere (details in Richardson et al. 2008). Speakers from different parts of the world, especially the Southern Hemisphere, shared their research experiences and presented studies on the ecology and management of invasive conifers. The aim of this note is to highlight the key ideas presented and discussed at the meeting on the study and management of conifer invasions in South America.

An introduction by Dan Simberloff et al. suggested that there are few problems more unique to the southern hemisphere, specifically to

parts of the former Gondwanaland, than introduced conifer invasion. Pinaceae native to the northern hemisphere have been widely planted in the last few decades. Today the invasion of these species is occurring outside managed areas, and is expected to increase in the next decades. Given the ecological and economic impacts that invasive conifers can produce, a better understanding is essential if they are to be most cost-effectively controlled and managed in the future (Simberloff et al. 2010).

History, Patterns & Processes

A better understanding of the history and the current status of conifer invasions in South America is urgently needed. For Chile, Aníbal Pauchard et al. described how the Chilean government and forestry companies began massive reforestation programs during the late 20th century, using fast-growing conifer species to stop soil degradation, even in protected areas. Commercial *Pinus radiata* plantations began in the late 1960s and boomed in the 1980s. In southern areas, other species such as *Pinus sylvestris*, *P. ponderosa*, *P. contorta* and *Pseudotsuga menziesii* were also planted and are now becoming invasive, especially *P. contorta* (Langdon et al. 2010).

Pine invasions have been used as a model for understanding plant invasions (Richardson 2006) and South America provides exciting new

opportunities for furthering this research. For Central Chile, Ramiro Bustamante et al. indicated that the availability of light, regardless of other local and landscape attributes, is probably the main driver of *P. radiata* invasion in fragmented *Nothofagus* forests. Pines fail to establish in the interior of closed canopy forests but become abundant when the canopy cover is reduced significantly. Consequently, management to prevent pine invasion should be focused on the conservation of continuous canopies in remnant forests. In forests of Argentina, Martin Nuñez et al. tested different factors that limit the invasion of Pinaceae on Isla Victoria, Nahuel Huapi National Park. They found that intense seed predation and the lack of proper mycorrhizal fungi may be limiting the invasion of exotic plants, while deer herbivory seems to have a positive effect on the invasion, by reducing the competitive abilities of native species. Propagule pressure and the intrinsic invasiveness of certain species appear to play lesser roles in these invasions. On the same island, María Andrea Relva et al. tested whether exotic herbivores (deer) promote the invasion of exotic conifers. They suggested that the animal type (domestic vs. wild), intensity of herbivory, and local plant community (forest vs. non forest) can be key factors in determining the type of response (facilitation or inhibition). These results, together with those gathered from other continents, show that the response of invasive conifers to exotic herbivores is highly context-dependent, but that some general response patterns do exist (Relva et al. 2010).

Impacts and Management

Invasive conifers have caused important changes in natural communities (Simberloff et al. 2010). In Patagonia, several pine species including species with adaptations to cope with (and regenerate vigorously after) fire, have been planted in areas that were formerly treeless. Estela Raffaele et al. studied the establishment of pines after fires in 17 sites where pine plantations had been burnt between 1985 and 2002 in the Argentinean northern Patagonia. They found high levels of invasion both inside the burnt plantations and in native areas around them, and concluded that there is a risk

that pines will increase fire regime intensity and frequency in Patagonia, creating a positive feedback between invasion and wildfires.

To date, there has been little control of introduced conifer invasions in South America, and international experience could guide efforts to control them in the region. New Zealand is a leading country in strategies to control invasions. Nick Ledgard described a project aimed at improving spread risk assessment and mapping, the determination of cost-effective means for controlling wilding conifers, the assessment of vegetation successions associated with conifer management, and improving public awareness of wilding spread and its control. The project, supported by the South Island Wilding Conifer Management Group, has produced a wilding risk assessment decision support system, maps of wilding-affected areas, a wilding control manual and several academic and non-academic papers and articles which are available to the public via their website (www.wildingconifers.org.nz). A synergic association between those affected by conifer spread and specialist researchers has proved to be a successful means of improving the ecological understanding of wilding spread, risk assessment, control techniques and awareness.

The future: taking control

Based on the history of conifers introduced elsewhere in the southern hemisphere, and current reports from within South America, it is likely that invasions in that continent will increase in number and size. Large-scale conifer plantings began about 50–80 years later in South America than in Australia, New Zealand, and South Africa. It is likely to be a similar story for reports of invasion and subsequent impacts, such as replacement of non-forests areas by conifer forests, modifications of hydrological and fire regimes, changes in soil nutrients, and alterations in above-ground and below-ground biotic communities. A number of these effects have already been recorded in different parts of South America. There are large areas planted with exotic conifers in Chile, Argentina and Brazil and many of these are growing rapidly and producing large quantities of seeds. In spite of

this negative scenario, governments continue to give public subsidies to stimulate pine plantations. Regulations for conifer invasion in other parts of the southern hemisphere are being enforced by legislation, which has yet to be introduced to South America. The conditions in a country such as New Zealand seem to be quite different from those in South America, where there are many challenges to establishing successful control strategies – these are mainly due to lack of awareness and economic resources (Nuñez & Pauchard 2010). However, based on discussion at the symposium, we are confident that local research and the experiences gained from areas with more expertise and history on invasions can be used to develop programs and legislation to mitigate introduced conifer invasions in South America. The commitment of private and public agencies as well as the education of people will be critical to achieving these objectives.

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book review

An integrative overview on alpine habitats

The Biology of Alpine Habitats, by Laszlo Nagy & Georg Grabherr
Oxford University Press, 2009, 336 pp. ISBN13: 978-0-19-856703-5
<http://www.oup.com/>

Mountains, and specifically alpine habitats, are fragile and extremely sensitive to perturbations, because of intense gravity effects on flows of energy and materials. As a consequence, they are highly exposed to global change impacts. Understanding the abiotic and biotic patterns and processes involved in alpine habitats is not only of utmost importance for researchers interested in mountain regions, but also for those looking to gain deeper insights in current biological debates, such as the effects of nutrient limitations on species diversity, dispersal/colonization dynamics and niche space filling, the changing nature of species interactions in harsh habitats, or impacts of global change in “nowhere to go” habitats. Nagy and Grabherr’s *The Biology of Alpine Habitats* deals, among others, with those topics and it is a neat inspection of the upper part of mountains, their constituent elements and the challenges that they face under global change.

The book is organized in eleven chapters. The first part (chapters 1, 2, and 3) focuses on defining alpine habitats, describing the different mountain regions across the globe from high latitudes to the tropics, and also the distribution of the main abiotic and biotic factors along elevational gradients. The second part of the book (chapters from 4 to 8) describes the main abiotic factors constituting alpine habitats, such as energy, climate, landforms, hydrology and soils, and the relation of these factors to alpine communities. These first two parts of the book provide the necessary foundations to discuss global change impacts on climate, nitrogen deposition and land uses in alpine habitats, and to offer a brief summary on conservation issues (chapters 9 and 10).

The way the authors frame and organise the book provides the reader with the chance to surf smoothly across the key elements constituting alpine habitats and the relationships between these elements. This easy-to-follow flow also con-

tinues when it comes to integrate the variety of spatial and temporal scales in which the drivers shaping current alpine habitats operate: from explanations of the evolutionary and biogeographic processes behind the formation of alpine floras and their traits, to the role of species interactions and their specific abilities in the colonization of new areas. This journey across scales allows Nagy and Grabherr to integrate knowledge that belongs to disciplines such as geology, climatology, biogeography, community ecology or eco-physiology. Their definition of ecological communities (“...*net outcome of all biotic interaction and abiotic constraints in a given location at a given time, with a given background of history, species pool*”) illustrates the integrative perspective in which this book is framed.

The role of historical biogeographic processes to explain the formation of alpine floras and current alpine biodiversity patterns is explicitly discussed in Chapter 7. Readers will find that the authors highlight how biogeographical disciplines such as phylogeography (Box 7.1) are of utmost interest for linking past dynamics and structure of alpine populations with current biodiversity patterns. An excellent idea was to devote the last part of this chapter to the adaptation and survival of alpine organisms. In doing this, the authors recognise the evolutionary foundations of issues that have been often perceived as pure ecological phenomena, such as eco-physiology or reproduction (adaptations to alpine existence across different time scales are summarized in Fig 7.12). This integration of evolutionary and ecological aspects in a biogeographical framework to better understand adaptation and survival abilities of alpine habitats provides a robust venue to better discuss future responses of alpine biodiversity to global change.

In summary, *The Biology of Alpine Habitats*, which is part of the Habitat Series published by Oxford University Press, intends to provide stu-

dents and scientists embarking on alpine research with an integrative overview on alpine habitats. The book largely fulfils this aim, providing clear descriptions of relevant theories and hypotheses, describing general and broad patterns in alpine habitats across different mountains of the world but at the same time highlighting regional or local deviations from these global trends, and offering significant supplementary information to the text in the form of pictures, plots, graphs and tables. There are some issues that would need more work, such as a better integration of animal assemblages in alpine habitats (the book mainly focuses on plant communities), or a deeper explanation of future climate impacts in alpine biodiversity. Also, and although the text flows smoothly, there are some parts of the chapters that are embedded without a logical connection to their previous or following parts. One of these parts, for example, is devoted to species richness and the applicability of the theory of island biogeography to the alpine zones of the mountains, which ap-

pears between a pure descriptive introduction to the biogeography of the different mountain regions and a section on the evolution of alpine organisms. However, these are just minor issues and the book by Nagy and Grabherr is highly recommended for its exhaustive and integrative provision of current knowledge on alpine habitats.

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Edited by Joaquín Hortal

book review

All islands in a large nutshell

Encyclopedia of Islands, by Rosemary G. Gillespie and David A. Clague (eds)

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This beautiful book starts with a very bold claim: “The *Encyclopedia of Islands* is a comprehensive, complete, and authoritative reference dealing with all of the physical and biological aspects of islands and island habitats” (p. xxix – the first sentence of Guide to the Encyclopedia, which opens the book after the contents and contributor listings). Similarly, on the book’s website Jonathan Losos is quoted as saying that the book “is a comprehensive compendium of all topics related to islands and the science conducted on them.” I cannot agree with such hyperbole, which represents a near-unachievable ideal. Nor, it seems, do the authors themselves agree: “The *Encyclopedia* functions as ingress into a body of research only summarized herein” (p.xxx). Even so, and despite its faults, I do recommend this book to anyone with any sort of interest in islands.

At £65 or US\$95 the book is expensive for a coffee-table volume, but good value for an academic work of its size and publication quality. So which is it? I am not sure. The back cover (see also “Description” on the website) also suggests confusion over the intended role: “This essential, one-stop resource... will introduce island science to a wide audience and spur further research on some of the planet’s most fascinating habitats.” The Guide to the Encyclopedia says the book provides “a broad overview of the current state of knowledge... intended for students as well as the interested general public” (p. xxix), but later on same page: “The articles... are all intended for the interested general public.” The book is largely jargon-free and technical terms are not over-used; most of those that are used are defined in a 30-page Glossary, with over 900 terms, which is itself a

useful resource.

The emphasis on the interested general public seems to be responsible for what I regard as the book's biggest weakness: failure to cite sources. A decision was clearly made, by the editors or the publishers, to instruct contributors to provide short lists of further reading, mostly textbooks and review articles, but no in-text citations or accompanying reference lists. So it is nearly impossible for readers to establish the source of much of the information presented. This is extremely annoying, severely reduces the book's value as a reference and effectively represents plagiarism. It seriously compromises stated aims to guide readers "to the vast literature on island science" (p. xxxi). It is also a bad example to students. I find it very annoying when writing contributions to similar compendia, under similar rules: at universities we sweat blood to get our students to cite their sources and reference properly, sometimes punishing them severely for plagiarism, only to direct them to our own published work in which these rules are broken. I wish this practice of forcing authors not to cite their sources would stop. I think the general public is able to cope with the concept of sources being cited and should not be patronised in this way. If publishers insist on trying to 'de-clutter' the text (by prohibiting in-text citations) to maximise readability then there are ways of doing so that retain the key information. A good example is Bill Bryson's excellent *A Short History of Nearly Everything*.

There is much that is good about the book. It is well presented and illustrated: though the quality and quantity of illustration varies between articles, most of the abundance of photos, maps and drawings are very high in quality. Coverage is nearest to complete for biological and geological aspects of islands, although the treatment of biogeography is not very satisfying: the heading "Biogeography" is simply used to group together the "Biology" articles for all the first-category islands (see next paragraph). I like the broad definition of 'island' as "any discrete habitat isolated from other habitats by inhospitable surroundings." Thirty island types, each covered in a dedi-

cated article, include organic falls on the ocean floor and a separate entry for whale falls, seamounts, cold seeps, *Lophelia* oases and mountain-tops (colourfully termed "Sky Islands"). Even the most knowledgeable reader will surely learn something by browsing through these articles, and those on other types such as Kīpuka, Makatea, Motu and Pantepui. Islands are considered from a pleasing range of viewpoints: headings under which articles are listed include various categories of 'true' islands (see next paragraph); island types; concepts relating to ecology and evolution, geology, oceanography and climatology; notable plants and animals; "Human Impact"; and "History and Pre-history". Perhaps the most useful pages of all are the "Contents by subject area" (pp. xi-xiv), which elucidate not only the organisation of the book, but also some of the aims and philosophy behind it, putting the reader on more-or-less the same wavelength as the editors.

From my own reading of the book, 'true' islands and archipelagos seem to fall into five categories. First, principal ones (my term). Each of these has two full articles, one each on the geology and the biology: Antarctic Islands, Antilles, Arctic Islands, Canary Islands, Californian Channel Islands, Fiji, French Polynesia, Galápagos Islands, Great Barrier Reef Islands, Greek Islands, Hawaiian Islands, Indonesia, Japan's Islands, Macquarie, Marianas, Mascarene Islands, New Caledonia, New Guinea, New Zealand, Philippines, Samoa, Solomon Islands, Taiwan. One could argue about the circumscription of some of these in political units rather than biogeographic ones (especially in the Wallacean region), but more importantly I question the validity of this list as the implied most important islands on the planet. While all these islands are clearly globally significant, do some of them (such as Fiji, Samoa, Californian Channel Islands) really deserve this top status when Madagascar, for example, does not? The second category is those islands listed under the heading "Important Islands", each with one article of its own. These islands range from Madagascar to Warming Island (off Greenland), and the Cook Islands to Cozumel (off Mexico). Third, some islands have articles to themselves, but are listed

under the heading “History and Pre-history” (Barro Colorado Island, Tierra del Fuego, Pitcairn, Midway and Tatoosh – note the bias toward the Americas). Fourth are islands mentioned somewhere, but without articles devoted to them or their archipelago. These are quite well indexed at the end of the book, though errors can cause hindrance, such as when I was looking for mention of the British island Lundy: this is incorrectly indexed as “Lunday”. (Also the island of Great Britain is labelled “Britain”.) Finally come the islands with no mention anywhere in the book. Surprise omissions include the Bay Islands of Honduras, to which there are regular, direct international flights from Italy.

Some of the world’s most significant islands, by any standards, such as Greenland (stated as the world’s largest island), Sulawesi and Sumatra, only get only very short sub-sections in articles on major archipelagos (Arctic Islands, Indonesia). Meanwhile, Wizard Island (a tiny island in Crater Lake, Oregon, USA), Fernando de Noronha (a small archipelago off Brazil), Rottneest (a small holiday island in Western Australia with little terrestrial ecosystem left), among other surprising choices, have full articles to themselves, under the heading “Important Islands”. It is also odd that Borneo gets its own article while Sumatra, Java and Sulawesi do not and all of these islands are covered under “Indonesia”.

The list of 300 contributors reads a bit like a hall of fame of people who research islands. Most contributors have only one article, a few have two and only Rosemary Gillespie has three. This appears to be a genuine attempt to get buy-in from as many places as possible. Certainly the contributors come from all around the world, and both the content and the author list are, at first sight at least, reassuringly global in coverage. Closer inspection, however, reveals considerable bias towards North America (particularly) and Europe. In terms of contributors, nearly half of the 300 people listed have North American institutional addresses and only a quarter are not listed as working in Europe or North America. Institutional addresses all end with the country, except for those in the USA, where this appears to have been

deemed unnecessary. I was confused for a moment by Dennis Geist’s entry: “University of Idaho, Moscow”. Twenty-six of the 300 contributors are from Hawaii! Hawaii also illustrates bias in the contents. The disappointing article by Mueller-Dombois entitled “Vegetation”, for example, would be better named “the vegetation of Hawaii”. In the “Lava Tubes” article by Kauahikaua *et al.*, the Kīlauea volcano is mentioned, with no indication of where in the world it is, nor is it listed in the Index; you are simply expected to know that it is in Hawaii. Reading through the book, you soon learn to default to the USA if information to the contrary is not provided. One can find other types of bias: of the 24 articles listed under “Plants and Animals”, only two are on plants (orchids and silverswords) while 14 are on vertebrates. The two on plants bring me back to the Hawaii bias: while silverswords are interesting, and, as Baldwin’s article makes clear, certainly a good example of insular adaptive radiation, does this endemic Hawaiian group really deserve an article to itself when, for example, figs and mangroves do not? I was disappointed that these plants, and the concept of keystone species, got such short shrift.

Having so many contributors must make it hard to achieve coherence. The editors seem to have tried to ensure longer articles are organised in a standard way, by topic, but the flow is hindered by errant entries, such as Cody’s article “Baja California: Offshore Islands”. Most featured archipelagos have maps, but some don’t (e.g. Madeira). The index is useful but not perfect (why separate entries for “fig trees” and “*Ficus*?”), with bold font used (rather inconsistently) to indicate dedicated articles. Another potentially useful feature is the “Encyclopedia website”, proudly proclaimed on p. xxx: “[it] provides a list of articles, the contributors, several sample articles, published reviews...”, with a promise that “The content of the site will evolve with the addition of new information”. So far, this seems to be a wasted resource. At the time of submission of this review (May 2010), nine months after the listed publication date of the book, I can find no list of articles, nothing about the contributors (just three lines on the editors), only one sample article and

just six soundbites of 'review', which appear to have been selected purely for publicity. Personally, I would prefer to see some attempt at balance here; the book is good enough to stand constructive criticism on its website.

Overall, despite its faults, this book contains many fascinating, informative and sometimes insightful articles, which together make both a useful reference and a fine addition to a coffee table. Most readers should, like me, happily spend hours flicking from one article to another, learning something while celebrating the wonderful diversity that is the world's islands. If you are thinking of treating yourself to something a little indulgent, you could do a lot worse than the *Encyclopedia of Islands*.

thesis abstract

In search of the forest primeval: data-driven approaches to mapping historic vegetation

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Introduction

The current biogeographic patterns in a given area are not only the product of contemporary environmental factors, such as climate, topography, and edaphic conditions, but historical factors as well, including anthropogenic disturbance regimes. In North America, for instance, much of the native temperate forest and grassland has been modified in the time since European settlement as a result of intensive human activity (e.g. Forman 1998). Since past human activities can influence biotic patterns for many years (Dupouey et al. 2002), interpretation of biogeographic phenomena without explicit consideration of human influence may lead to erroneous conclusions.

To better understand the influence of these disturbance regimes on ecosystem structure and function, researchers are increasingly using historical data to construct baselines from which subsequent changes in biogeographic patterns can be measured (e.g. Shutler and Hoagland 2004;

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Fritschle 2008). Among the datasets that have been extensively used in such reconstructions are the Public Land Survey (PLS) field notes, witness tree records, and plat maps (i.e. survey map of tracts of land) (Wang 2005). Public Land Survey records provide one of the few quantitative records of pre- and early-European vegetation in much of the western United States. These data have been used to evaluate vegetation dynamics (DeWeese et al. 2007), composition and structure of historical forest and woodland communities (Anderson and Anderson 1975), species-environment interactions (Wang 2007), and distribution and abundance of individual species (Wang & Larsen 2006).

Despite their widespread adoption, PLS data are fraught with limitations, among them bias in tree selection (Bourdo 1956), taxonomic uncertainty (Mladenoff et al. 2002), and the coarse sampling methods employed by surveyors (He et al. 2007). Nonetheless, the data of the PLS

have richly contributed to our understanding of past ecological conditions and use of these and similar datasets in biogeographic reconstructions is likely to continue. The challenge for current researchers, then, is to develop novel approaches to overcome some of the limitations and improve the robustness of these data for use in ecological analysis (e.g. Mladenoff et al. 2002, Wang and Larsen 2006; He et al. 2007).

Aims and methods

My PhD research is built upon the broad supposition that evaluation of current biogeographic patterns must be predicated on antecedent conditions, typically prior to widespread anthropogenic disturbance regimes. In a narrow sense, my dissertation focuses on land use, land cover, and woody plant compositional changes in the Arbuckle Mountains of south-central Oklahoma during a period of rapid demographic change (circa 1870 to 1898). In this regard, the research seeks to provide insight into the ecological processes of habitat fragmentation, woody plant encroachment, and so-called mesophication that are believed to have occurred subsequent to the historical period under investigation.

In a broader context, this research is an evaluation of how anthropogenic alterations in landscape patterns and processes may affect the distributions of individual woody plant taxa. Though the datasets utilized in this research are unique to the region, the methods employed in this study should be transferable to other areas of interest. Additionally, the patterns and processes under investigation are not unique to the region under investigation. The results, therefore, should be placed within the context of anthropogenic change that has occurred throughout the eastern deciduous forests of North America, particularly in the western cross timbers, in the period following European settlement.

In order to accomplish these goals, my dissertation is divided into two broad research themes. The first employs repeat PLS data from the 1870s and 1890s, respectively, to quantify changes in landscape structure, woody taxa assemblages, and anthropogenic markers in the

study area during this period of rapid demographic transition. The present-day state of Oklahoma, U.S.A., is unique in that the U.S. General Land Office (GLO) conducted two separate Public Land Surveys in a portion of the state during a relatively short time span (Hoagland 2006). Beginning in the early 1870s, the GLO surveyed all lands of the Chickasaw Nation in what was then Indian Territory (Gibson 1981). In 1895, the United States Congress appropriated funds for the survey of all tribal lands in Indian territory, including those lands that had been previously surveyed in the 1870s (Gibson 1981).

Part of the resurveyed area includes a portion of the state that is characterized by a mosaic of forest, woodland, and grassland vegetation known collectively as the cross timbers (Hoagland et al. 1999). During the past century, a combination of land use practices and fire suppression is believed to have contributed to increased woody plant abundance in former grasslands in the region (Hoagland and Johnson 2001) and may have led to increases woody plant densities in woodlands and forests (i.e. so-called mesophication) (Engle et al. 2006). Moreover, there is evidence of widespread habitat fragmentation in the area resulting from various land use practices (Hoagland and Johnson 2001; Shutler and Hoagland 2004).

The goal of this portion of the research was to utilize the repeat PLS data to evaluate the biological consequences of various anthropogenic activities. Specifically, I quantified landscape structure and associated woody plant assemblages at two discrete points in time, one corresponding to pre-European settlement, the other following European settlement. The analyses involved the quantification of habitat fragmentation, analysis of changes in the distribution and composition of woody plant species, and comparisons of structural differences in arborescent habitats between the two survey periods.

I databased all PLS witness tree records in the study area for the two survey periods and plotted the location of individual witness tree records using conventional GIS techniques. Additionally, I digitized all PLS plat map data for the study area, creating GIS layers for land cover types

and anthropogenic markers, such as structures and transportation networks (see Fagin and Hoagland 2002 for a discussion of GLO survey methods). I calculated the spatial association between individual tree taxa and environmental covariates to test the null hypothesis of no differences in species composition in the different environmental units between the two survey periods. A rejection of the null hypothesis would indicate that other factors (e.g. anthropogenic) contributed to distributional differences. I calculated average distance to recorded trees, density, and basal area at each survey point for each survey period and tested for significant differences between the survey years. I also used calculated stem density values and universal kriging to create continuous density surfaces for each survey period to characterize the differences in dominant arborescent community types.

The second broad research theme utilizes a Bayesian method known as weights-of-evidence (WofE) to address the problem of coarse sampling structure of PLS records (tree data were only collected along section lines at 0.8 km (0.5 mi) intervals). Several attempts have been made to convert discrete PLS point data into continuous surfaces using kriging and other interpolation methods (e.g. Wang and Larsen 2006; Wang 2007). While these methods may adequately represent the spatial patterns of individual species over large areas (Wang and Larsen 2006), these methods typically fail to consider the numerous environmental covariates, such as edaphic conditions and topographic position, which can influence the distribution of individual species at finer scales. A more statistically rigorous method calls for combining species–environment relationships to estimate the areal extent of individual species from point data (He et al. 2007).

Weights-of-evidence is a discrete, data-driven multivariate method based on a log-linear form of Bayes' rule. Weights-of-evidence is used to measure the spatial association between maps of independent environmental variables and dependent variable point data (Bonham-Carter et al. 1989). Weights-of evidence modeling proceeds in several phases: development of a spatial data-

base, extracting predictive evidence for the phenomena under investigation, calculating weights for each predictive map (evidential layer), combining weights for each evidential layer, and model validation (Kemp et al. 1999). In my models, the dependent variables were individual woody taxon occurrences estimated from PLS witness tree records. I selected six wood plant taxa (*Quercus stellata*, *Q. marilandica*, *Q. velutina*, *Carya texana*, *C. illinoensis*, and *Juniperus* spp.) to model, based on their historical or subsequent importance within the study area. For the independent variables, I selected five environmental factors known to influence the distribution of the selected taxa and that were available at both the spatial and temporal scale under investigation. The covariates selected were substrate (parent material), soil type, elevation, moisture availability (derived from slope and aspect), and historical land cover. I ran six different models, one for each of the taxa under investigation, to estimate the historical posterior probability of occurrence of each taxon under investigation. I validated each model using a split-sample approach, in which the occurrences of each taxon were divided into two randomly generated sets, a model building set and a validation set (Carranza and Hale 2000). For a complete discussion of the WofE method, see Bonham-Carter et al. (1989).

Results

The main results of my dissertation will be presented in several forthcoming publications. The first paper, currently under review, focuses on the use of WofE modeling of PLS data. A second paper, currently in preparation, will compare the land cover and woody plant compositional changes in the Arbuckle Mountains between the two survey periods. Additional papers will compare the present-day Arbuckle landscape to historic conditions and explore alternative methods to WofE to model PLS data to finer resolutions. Finally, this research belongs to a larger body of past and ongoing research on the historic vegetation of Oklahoma (e.g. Shutler and Hoagland 2004; Hoagland 2006).

The core findings of this research are: 1. The landscape of the Arbuckle Mountains became increasingly fragmented during the 27 years between the two surveys as large scale agriculture became ubiquitous in the region; 2. Changes in stand composition between the two survey are concurrent with anthropogenic disturbance regimes; 3. Analyses of changes in density between the two surveys indicate that the cross timbers of the Arbuckle Mountains were denser immediately prior to European settlement than in the period following settlement, while data from both survey periods tend to confirm that the present-day cross timbers are denser than historic times; and 4. The WoFE method adequately estimated the posterior probabilities of *Q. stellata*, *Q. marilandica*, *C. texana*, and *Juniperus* spp., but underpredicted posterior probabilities for *C. illinoensis* and *Q. velutina*.

Discussion

The land cover change documented in the study area between the two surveys corresponds to a period of rapid demographic shift and is primarily due to land clearance for agriculture, transportation networks, and anthropogenic structures. The changes in stand composition between the two surveys imply that these anthropogenic disturbance regimes may be responsible for shifts in biogeographic patterns. However, these changes may also be related to taxonomic uncertainties in the historical datasets rather than actual changes in community dominance.

Despite several inherent limitations, the weights-of-evidence method proved to be a statistically valid method to map individual taxon distributions at finer resolutions than afforded from traditional methods of mapping PLS data. Weights-of-evidence belongs to a growing body of research techniques that can be used to predict species distribution from point occurrence data (see Elith et al. 2006 for reviews of similar methods). While my results indicate that WoFE may also be used to create probabilistic maps of the historic distribution of certain woody plant taxa from PLS data, several other methods, such as weighted logistic regression (Agterberg et al.

1993) or the Dempster-Shaefer (Yager and Liu 2008) may better handle issues arising from uncertainty in historical datasets and missing data.

Conclusion

Within the last decade, there has been an increase in the use of PLS data in ecological analysis (Fagin and Hoagland 2002; Wang 2005). As use of these data becomes more commonplace, the need to properly place the significance of historical biogeographic patterns in the context of the contemporary landscape becomes essential. Moreover, the need to map these data to finer resolutions to truly elucidate changes in biogeographic patterns increases. My research analyzed the degree and direction of changes in woody plant abundance since historic times in the Arbuckle Mountains, Oklahoma. However, the methods utilized and the findings thereof are applicable to a wide range of biogeographic studies.

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Edited by Richard Field

The *Ecography* special Issue on the 4th IBS Meeting is now out

Ecography is publishing in July a special issue with a selection of contributions that arose from the 4th IBS International Meeting (Mérida, Mexico, 2009). The special IBS issue has 22 papers, plus and editorial by David Nogués-Bravo and Carsten Rahbek, representing the diversity of current biogeographical research. Classic biogeographical topics such as diversification, extinction and migrations are examined in the light of new data, approaches and different angles, encompassing scales from the molecular to the macroecological.

The special IBS issue is already available at *Ecography* webpage: <http://www.wiley.com/bw/journal.asp?ref=0906-7590>

opinion

Habitat data resolution and the detection of species interactions

In a recent paper, Gotelli et al. (2010) presented evidence for competition structuring in the bird assemblages of Denmark at two spatial scales (5 and 10 km grid cells). They used whole-matrix null models to show that ecologically similar species co-occurred less than expected by chance. As these species had similar habitat preferences they concluded that species interactions must have created the mutually exclusive distributions of the birds. This led them to suggest that species interactions should be included in environmental niche models for predicting species occupancy.

Whilst the methodology presented in the paper is sound, we have some doubts about the conclusions. As acknowledged by Gotelli et al. (2010), spatially segregated distributions can be formed either by species interactions, e.g., competitive exclusion, or by species having distinct habitat preferences. The probability of detecting habitat differences is directly related to the resolution of available habitat data; at low resolutions it is unlikely that habitat differences within a guild of similar species will be detected. For example, two species may both live in forests, but if the species require different types of forest they will not overlap. This difference in habitat preference will not be detected unless habitat types are more finely defined than "forest". Gotelli et al. (2010) only recognize 12 habitat types in Denmark, but we believe that birds are likely to have more specific habitat preferences. If so, the spatial segregation of species may reflect the distribution of microhabitats rather than competitive interactions.

Ecologists are increasingly recognizing that the importance of ecological mechanisms changes according to the scale of observation. Similarly, the apparent importance of species interactions at macroecological scales will be contingent on habitat resolution. Broad habitat designations will al-

ways overestimate the importance of species interactions. However, at fine enough resolutions we are bound to conclude that patterns are due to habitat partitioning. Unfortunately, the only way to truly detect competition is to perform manipulative experiments in the field or lab. Even then it is hard to separate the importance of present-day competition from the "ghost of competition past". Given that manipulative experiments are impossible at large scales, should we consider biological interactions in niche models as proposed by Gotelli et al. (2010)? We believe that the resolution of habitat data should influence such decisions. An environmental niche model using coarse habitat designations may indeed need to incorporate species interactions to predict species occupancy. However, a similar model using finer-grained habitat designations may not.

Gotelli N.J., Graves G.R., & Rahbek C. (2010) Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences USA*, 107, 5030-5035.

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Learning new tricks from old trees: revisiting the savanna question

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Introduction

Savannas are ecosystems comprising of a mixture of woody species (trees and bushes), grasses and forbs. They cover about a fifth of the global land surface and about half of the area of Africa, Australia and South America (Scholes and Archer 1997, Sankaran et al. 2004). Savannas are characterized by a continuous grass understorey and a discontinuous tree layer. A savanna, where trees and grasses co-dominate (often referred to as co-existence), may be viewed as an intermediate ecosystem between grassland (grass dominance) and forest (tree dominance). Tree-grass ratios vary widely in savannas, with higher precipitation usually leading to a more continuous tree layer (Sankaran et al. 2005). However, tree canopies in mesic savannas are still discontinuous enough, with significant understorey grass biomass for the system to be characterised as a savanna and not forest. There are several different savanna ecoregions worldwide, each containing different subsets of species and displaying substantial variation in physical and structural attributes (Scholes and Archer 1997, House et al. 2003). In this paper, we focus primarily on tropical and subtropical savannas, although some of the conclusions might be valid for a broader extent of savannas.

Until the early 1990s, it was generally believed that trees and grasses coexist because of a separation of rooting niches (Scholes and Archer 1997). This idea was based on Walter's (1939) two-layer hypothesis, a version of niche separa-

tion theory (Walker et al. 1981). According to this theory, water is the limiting factor for woody species as well as grasses. It was assumed that grasses were the better competitors for topsoil moisture (usually < 30 cm, depending on soil properties), but because woody species could develop deeper roots they were able to persist by exploiting subsoil resources (usually > 30 cm). Topsoil is usually defined by its fast reaction to climatic regimes, getting wet during light rain, drying out with a few days of sunshine (Knoop and Walker 1985). The two-layer theory has been verified by field experiments which reported that in the Nylsvlei savanna (South Africa) grasses reduced the supply of water to the trees (Knoop and Walker 1985). Furthermore, subsoil competition between the trees, probably for water but possibly also for nutrients, was reported (Smith and Goodman 1986). Several studies have concluded that savanna stability is based on the two-layer theory (e.g. Knoop and Walker 1985, Skarpe 1990).

There is a growing body of literature that questions the validity of the two-layer theory. A number of field studies have reported facilitative effects of trees on grass biomass, where grass biomass is greater below tree canopies rather than away from trees (e.g. Belsky et al. 1989). Among others, Ludwig et al. (2004) reported a field experiment where the two-layer theory is inappropriate. More specifically, according to Ludwig et al. (2004) "prevention of tree-grass interactions

through root trenching led to increased soil water content indicating that trees took up more water from the topsoil than they exuded via hydraulic lift. [...] grasses which competed with trees used a greater proportion of deep water compared with grasses in trenched plots. Grasses therefore used hydraulically lifted water provided by trees, or took up deep soil water directly by growing deeper roots when competition with trees occurred". This means that rooting niche separation fails to generally explain savanna tree–grass co-dominance in this system. Further, in ecosystems (e.g. Kalahari and Namibia) where soil was too shallow to allow for a two-soil layer differentiation, trees and grasses coexisted (Hipondoka et al. 2003, Wiegand et al. 2005).

As the niche separation theory was inappropriate in several cases, new theories were proposed to explain savanna stability and wood plant–grass co-dominance. One such influential theory is the demographic bottleneck theory which suggests that savannas are unstable systems that are constantly perturbed by disturbances such as fire, herbivory and climatic variability (Jeltsch et al. 2000, Higgins et al. 2000). Ideally, in the absence of such disturbances, a savanna would turn into woodland (forest) or into grassland (Scholes and Archer 1997, Jeltsch et al. 2000). Demographic bottleneck models take life stages explicitly into account and emphasize the role of disturbances and climatic variability in limiting tree establishment and growth in arid areas, and preventing tree dominance in mesic areas (Jeltsch et al. 2000, Higgins et al. 2000, Sankaran et al. 2004). Fire is typically considered to be the most important driver limiting tree dominance in mesic areas, thereby maintaining the system as a savanna (Jeltsch et al. 2000, Higgins et al. 2000, Sankaran et al. 2004, Bond 2008). In contrast, in arid savannas, the primary demographic bottlenecks for woody species are germination and seedling establishment (Higgins et al. 2000). Here, tree recruitment is pulsed in time following stochastic rainfall patterns. The fact that trees are long-lived enables them to persist, and 'store' reproductive potential, over periods when precipitation is sufficient only for grass and not for tree

germination (Higgins et al. 2000). There are several savanna ecosystems where there are many gaps in tree canopy cover but no germination; in such places the lack of germination is due to the absence of consecutive days with sufficient soil moisture rather than to the absence of gaps. Fewer consecutive days and lower soil moisture appears sufficient for grass persistence but not bush or tree germination (Noe 2002).

Bush encroachment

A common phenomenon in savannas is the increased dominance of woody species, often referred to as bush encroachment (Ward 2009). In Africa, the phenomenon is often associated with bushes such as *Acacia mellifera*, *A. karroo*, *A. nilotica*, *Dichrostachys cinerea* and *Grewia flava* which suppress grasses (Ward 2009). While the problem may be more acute in arid savannas with heavy grazing, the increase of savanna woody species is a more "global" savanna phenomenon observed in African (e.g. Hudak and Wessman 2001, Britz and Ward 2007), American (e.g. Archer 1989), and Australian (e.g. Burrows et al. 1990) savannas. This increase of woody species is a serious problem in savannas because many herbaceous plants are suppressed or lost, and as a result, biodiversity is decreased. Furthermore, domestic livestock is unable to pass through such places (Scholes and Archer 1997).

There have been attempts to explain the causes of bush encroachment. Experimental studies carried out in savannas at higher rainfall found evidence that competition from relatively shallow-rooted grasses for water reduced the growth of relatively deep-rooted trees (Kraaij and Ward 2006 for seedlings; Knoop and Walker 1985 for adult trees), and evidence that trees competed with each other, plausibly for water (Smith and Goodman 1986). It has also been reported that the cover of some shrub species was increased only in the most heavily grazed areas (Skarpe 1990). There was evidence that the species which did increase (*Acacia mellifera* and *Grewia flava*) had a lot of shallow roots, which must suffer direct competition from grasses in an ungrazed system. The conclusion drawn was that in a mini-

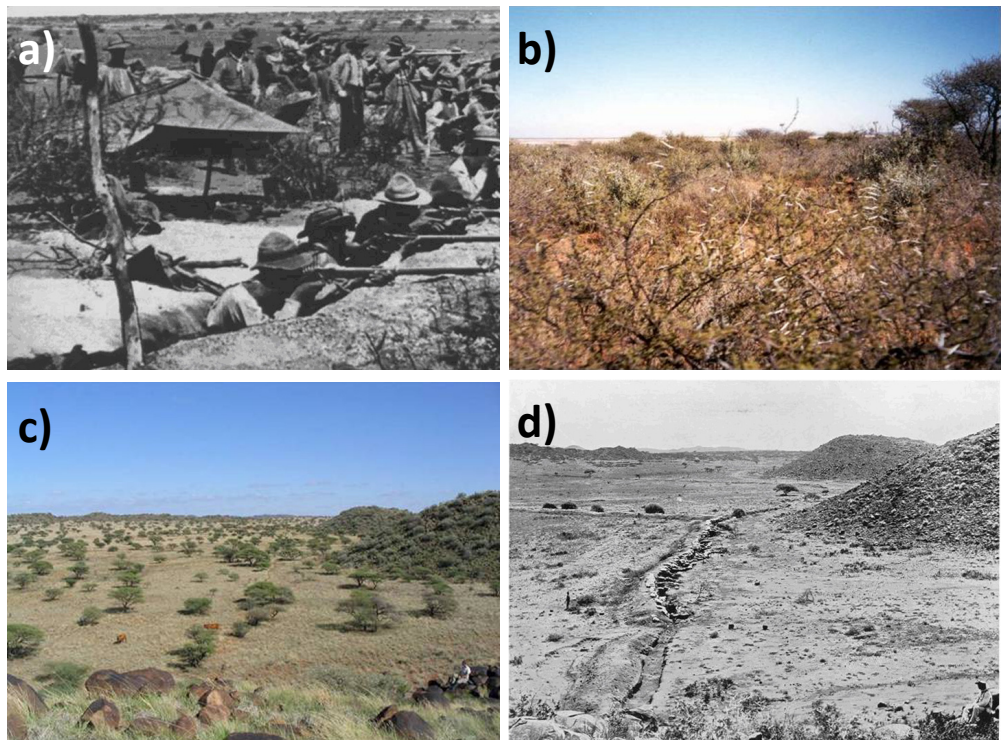
mally grazed system these shrubs and the grasses can coexist despite having most of their roots in the upper soil (Skarpe 1990). That has led to the conclusion that the increase in cover of certain relatively shallow-rooted shrub species seen in heavily grazed dry savannas on both deeper and shallower soils is primarily a result of an increase in soil water content that is due to the absence of competition with grass roots. However, the co-dominance of tall shrubs with grasses on shallow soils shows that, with certain combinations of species, co-dominance is not dependent on root stratification and thus grasses are not better competitors in shallow soil layers. While this does not mean that when root stratification occurs it makes no contribution to the maintenance of co-dominance, the validity of this explanation is limited because it fails to explain the increase of woody species in areas with shallow soils (Hipondoka et al. 2003, Wiegand et al. 2005), or in areas with little grazing (Hipondoka et al. 2003).

A second alternative theory attempting to explain the increase of woody thorny species was based on the evidence that increasing levels of global CO₂ favour the growth of trees and bushes which are C₃ species rather than grasses which are mainly C₄ species (Knapp 1993, Ward 2010). Spe-

cifically, it was found that different responses in stomatal conductance between C₃ and C₄ species during periods of sunlight variability resulted in a twice as rapid rate of change in the C₃ species (Knapp 1993). C₃ plants have a metabolic pathway which is more energy efficient, and if water is plentiful, the stomata can stay open and let in more CO₂. However, carbon losses through photorespiration are high. Thus, elevated levels of CO₂ would be expected to increase the abundance of C₃ species as carbon availability levels would increase. However, the validity of this theory was significantly reduced by the findings of Archer et al. (1995), reporting an autogenic succession of an open savanna to an encroached one (Fig. 1). Nonetheless, there is expected to be a greater increase in the net photosynthetic rate of C₃ plants (which are usually trees) than C₄ plants (Wolfe and Erickson 1993). An additional factor that may be important is that higher levels of CO₂ may reduce transpiration rates of grasses, which results in deeper percolation of water and, consequently, greater growth rates of trees.

Other theories combining fire with low atmospheric CO₂ (Bond et al. 2003) and resource ratios have been proposed (Ward 2010). However, they have not been verified with field studies.

Figure 1. Photographs taken at Magersfontein battlefield, South Africa in (a) 1899 and (b) 2001. The Boer soldiers massacred the British, but today they would not have been able to do so because of *Acacia tortilis* encroachment. (c) Panoramic view of the battlefield. The trees in the foreground are *Acacia tortilis*. The hillside in the distance is covered with the encroaching *Tarchonanthus camphoratus* in 2005 (d) but was not in 1899. The area is now bush encroached in spite of the absence of heavy grazing. This is an example of autogenic succession of an open savanna to an encroached one (see also Archer et al. 1995).



Patch dynamics

The driving forces of savanna ecology are mainly unknown. Furthermore, the reported increase in density of woody species in savannas is not well understood. Scientists writing about co-dominance in savannas prior to the 1990s did not write specifically about the issue of scale. However they might have had a scale at which they worked, e.g. the scale of the individual tree or tall shrub or tussock grass, and that scale was taken for granted. It was recorded that many tall shrub species in savanna have many of their roots in the same layer as the grasses, and are thus differentiated from the taller *Acacia* tree species such as *A. tortilis* and *A. erioloba* (Smith and Goodman 1986, 1987). Moreover, it was established that an analogy existed for gap-demanding and shade-tolerant tree species in forest; dominant *Acacia* species were found not to be able to recruit under themselves, but various broad-leaved shrubs (both deciduous and evergreen) did so, and thus self-thinning would occur (Smith and Goodman 1986, 1987). The work on bottlenecks summarized by Higgins et al. (2000) represented the next logical stage in analysis.

Currently, researchers are thinking about dynamics at larger scales, facilitated by models, palaeoecological research (see also Gavin 2010), and technological advances of remote-sensing which allow encapsulating a larger temporal and spatial extent of savannas. There are some field studies that have already suggested that, over large spatial scales, savannas may undergo cycles between grassland and woodland (e.g. Dublin et al. 1990), but the phenomenon of cyclical transitions was not examined across several spatial scales. Using simulation models alternative stable states have been reported as well (e.g. Rietkerk and van de Koppel 1997). With the aid of remote sensing, vegetation patches have been increasingly reported in several ecosystems including savannas (Rietkerk and van de Koppel 2008).

Recently, Gillson (2004a, 2004b) and Wiegand et al. (2005, 2006) developed the idea that savannas are hierarchical patch dynamic systems. Scale is a fundamental problem in ecology because different processes occur at different scales

and are linked to patterns at other larger scales (Levin 1992). In patch dynamics, it is assumed that the landscape consists of distinct patches of variable size and that in every patch the same cyclical succession progresses (Meyer et al. 2007). Successional states may vary in duration and occur spatially asynchronously. The proportion of each state is approximately constant at a landscape scale. As a result, at large spatial scales an equilibrium can persist, although at smaller scales non-equilibrium dynamics occur (Levin 1992, Meyer et al. 2007). Most theories trying to explain savanna tree–grass co-dominance did not explicitly state the scale of their applicability (Gillson 2004a).

According to the patch dynamics theory, savannas are patch-dynamic systems composed of many patches in different states of transition between grassy and woody dominance. In arid savannas, key factors for patches are rainfall, which is highly variable in space and time, and intra-specific tree competition. According to the savanna patch dynamics theory, bush encroachment is part of a cyclical succession between open savanna and woody dominance (Wiegand et al. 2006). The conversion from a patch of open savanna to a bush-encroached area is initiated by the spatial and temporal overlap of several (localized) rainfall events sufficient for germination and establishment of woody species (trees and bushes). With time, growth and self-thinning of the species that are present will transform the bush-encroached area into a mature woody species stand (of the same species identity) and eventually into open savanna again (Wiegand et al. 2006). Patchiness is sustained because of the local rarity (and patchiness) of rainfall sufficient for germination of woody plants, as well as by plant–soil interactions. According to this theory, there is spatial and temporal variation in savannas. Temporally, a specific patch will pass through an encroached phase and sequentially to a more open savanna, until it is encroached again. Spatially, when a savanna is viewed at a specific time step, there are some encroached patches, while some other patches comprise of an open savanna (for a detailed description, see Wiegand et al. 2006).

This process is, to an extent, similar to the gap-generation phase in forests: in some forests, both temperate and tropical, most turnover is through the replacement of single adults which either fall and make gaps or die *in situ* and do not make canopy gaps. The analogy to savanna dynamics at the scale of individual trees was observed by Belsky and Canham (1994). In other forests the predominant pattern is for groups of trees (regardless of size) to die and be replaced at a given time. The patch dynamic approach at larger scales as described by Wiegand et al. (2006) is similar to the second option: individual trees and tall shrubs in patches defined at the scale of a group of adult trees pass through the various stages of regeneration at the same time because of the precipitation-driven germination of several seedlings in the same year and low seedling germination during several drier years. However, it is important to note that in savannas the key bottleneck is not gaps, as it is in forests, because savanna tree canopies tend not to overlap.

Synthesis

Thus, there are now three types of theories for tree–grass co-dominance in savannas: niche separation (Walter’s two-layer hypothesis, Walter 1939), demographic bottlenecks (Higgins et al. 2000, Jeltsch et al. 2000), and patch dynamics (Gillson 2004a, Gillson 2004b, Wiegand et al. 2006). All of these vary in terms of the mechanisms and the scales over which they predict tree–grass co-dominance or persistence. The theories also differ in terms of the conditions under which they predict bush encroachment should occur. The niche separation theory (Walter’s two-layer theory), even if the evidence for and against root partitioning is equivocal, does in fact predict encroachment under heavy grazing. Higgins et al. (2000) model suggests that it is the occurrence of unusually wet years which allows trees to escape the demographic bottleneck and establish in arid and semi-arid sites, i.e. bush encroachment is driven by climatic variability in the form of wet years. Finally, the patch dynamics theory suggests that it is a natural cyclic phenomenon in space and time, and thus bush encroachment is a standard

part of patch dynamics rather than a special case. In some ways, the patch dynamics theory can be seen as a spatial extension of the Higgins et al. (2000) model, again invoking rainfall characteristics to explain bush encroachment and persistence of both life forms in space. Ultimately, in order to differentiate between these alternative theories, there is a need for long-term data on savanna plant demography. Long-term remotely-sensed images (Fig. 2) provide a promising approach for understanding tree demography over long time frames.

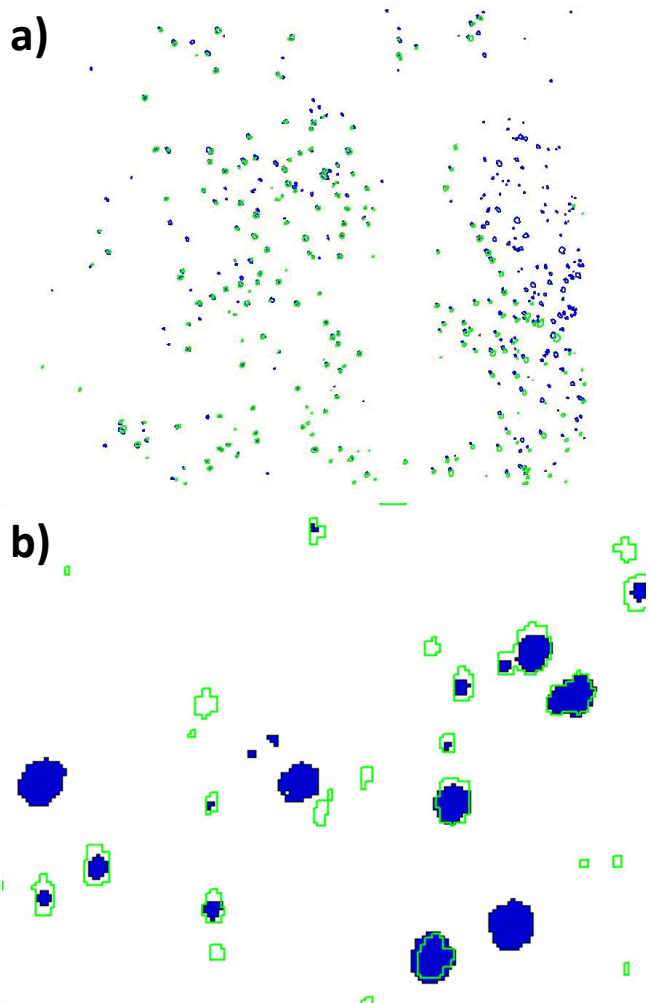


Figure 2. (a) Example of processed aerial photos of a savanna near Kimberley, South Africa. All objects are trees and their X,Y coordinates and projected canopy surface area are known. (b) Detail of processing of a time series of aerial photos. Trees as seen in the 1940 aerial photo are in blue while trees present in the 1964 aerial photo are in green. Trees are individually followed through time and recruitment, death, and canopy growth increments can be detected, c.f. Moustakas et al. (2006).

The next logical step in future analysis after patches have been detected will then be 'How do the patches arise?' If they can be shown not to depend on patchiness in the soil layer, or limited dispersal capabilities or systematic patchiness in the incidence of factors causing death of trees (e.g. fungi or insect herbivores), then it becomes a question of building a bridge between self-organized patchiness, catastrophic shifts that are due to grazing, fire or climate (Rietkerk and van de Koppel 1997, Rietkerk and van de Koppel 2008, Beckage et al. 2009) and patch dynamics using field data. In that case the limits of irreversible vegetation changes due to grazing, fire, and climatic change need to be assessed.

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Edited by Dan Gavin

Call for papers: The "Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea" editors welcome survey and review papers for a first volume of this new book series. The series will be dedicated to the taxonomy and systematic of plants and animals as well as biogeographical, ecological and conservation research of the region of Indo-Australian transition. Volumes will be published on a regular base every 2-4 years.

The main geographical focus of the current issue is Wallacea and New Guinea, that is Sulawesi, Lesser Sunda Islands (also known as Nusa Tenggara), the Moluccas, New Guinea (including Raja Ampat, Bismarck and Louisiade archipelagoes), and the Solomon Islands. Revisional works may also cover wider geographical regions with main focus on above mentioned area.

Please indicate your intention to submit a paper to the chief editor, Dmitry Telnov (e-mail: anthicus@gmail.com), including the title of the paper, author(s) names, and abstract. Authors' guidelines and further information can be found on the website <http://leb.daba.lv/book>, or requested by e-mail. Deadlines: Intent to Submit: August 1, 2010; Full Version: March 1, 2011; Decision Date: May 1, 2011; Final Review: July 1, 2011

from the society

The forthcoming 5th IBS International Meeting (Irakleion, Crete, Greece 7–11 January 2011) is almost here

Two years after a successful meeting in Mérida, Mexico, the 5th biennial meeting of the Society is going to be held in Irakleion, Crete, Greece, from 7th to 11th January 2011. Registration will open by the end of August, so start preparing your abstracts and your luggage for this journey to the southeastern corner of Europe. The meeting venue seems custom-made for biogeography, with its thousands of islands, the fragmented landscape, a geographic position on the borderline of three continents, and the long history of human activities. In addition, the historical significance and natural attractions of Greece, and Crete in particular, will be waiting for you, so there is no excuse to miss this meeting.

The scientific part, as in all previous meetings, is more than appealing, with four main symposia taking place during two days of the meeting, and six sessions with contributed papers during the third day. The four symposia are:

1. *Mediterranean biogeography: where history meets ecology across scales* (organizers: Spyros Sfenthourakis & Rémy Petit). The Mediterranean is a highly species-rich and complex biogeographic region. It has a complex tectonic and environmental history, hosts numerous islands, exhibits strong topographic diversity, and has experienced the impacts of human civilization for more than 8 millennia. This symposium explores novel perspectives on Mediterranean biogeography across spatial and temporal scales.

2. *Comparative phylogeography: new perspectives, integrative approaches & challenges* (organizers: Ana Carnaval & Mike Hickerson). This symposium will explore how innovative, integrative studies are expanding the boundaries of classic comparative phylogeography, while discussing novel methodological alternatives to circumvent

current and foreseen challenges in the field. Among the topics covered are new insights into suture zones and island community assembly and novel approaches employing genomics, spatial information systems, climate modeling, community-scale DNA barcoding, etc.

3. *Biogeography and ecology: two lenses in one telescope* (organizers: Dave Jenkins & Bob Ricklefs). Biogeography focuses on large scales, while much of ecology uses the opposite end of the telescope to focus on many of the same patterns and processes at small scales. Despite historical separation, each discipline is now expanding its spatial and temporal scales towards the other: this symposium will match a biogeographer and an ecologist on each of four key topics of shared interest (niche, comparative/macro-ecology, community assembly, and diversity) to seek alignment of the two perspectives.

4. *Analytical advancements in macroecology and biogeography* (organizers: Alexandre Diniz-Filho & Carsten Rahbek). The continuous development of computing capacity and increasing data generation allow ever more sophisticated analyses, enabling novel insights about biodiversity patterns. This development depends upon continuous input from other fields in terms of methods and theory. This symposium presents new advancements in spatial analyses, phylogenetic reconstruction, and computer simulation modelling.

The contributed papers' sessions will cover subjects like island biogeography, conservation biogeography, marine biogeography, climate change biogeography, palaeoecology, and other hot topics.

Another important event will take place on the last day of the congress, when Bob Ricklefs

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

will receive the Wallace Award and give his keynote lecture, in what will be one of the main highlights of the meeting.

On the day before the meeting starts officially, three workshops will be offered, on *Spatial Analysis in Macroecology* (see <http://www.ecoevol.ufg.br/sam/>), *Phylogenetic Analysis in Macroecology* (up to 40 participants each), and *Communicating biogeography* (up to 20 participants).

For those not attending the workshops, and for those staying one day after the meeting, there are exciting possible destinations to choose for full day or half-day excursions around Crete. Of course, accompanying persons will have additional opportunities to visit interesting places during the meeting.

A brief presentation of possible excursions may provide some general idea of what to expect:

a) *Lassithi Plateau - "Dikteon" Cave - Kera Monastery*. The Lassithi Plateau is one of the few areas in the Mediterranean with permanent inhabitants at an altitude >800 m. "Dikteon cave", where Zeus was born, is also located there. The place is described as 'the plateau of 10,000 windmills'. Originally, the locally constructed windmills made their appearance in the valley at the end of the 1800s. During the 1950s, about 4,000 of the structures offered invaluable assistance to local farmers. Exiting the Lassithi Plateau and heading towards Irakleion, there's an area by the village of Kera, where 24 stone flour mills, dating back to the 1800s, once stood. They operated until the end of WW II, but today most are in various stages of ruin, with only three restored so far. Just beyond this area is the "Kera" Monastery, famous for its beautiful frescoes.

b) *Knossos Archaeological site and "Archanes" traditional village*. Knossos, also known as the Labyrinth or Knossos Palace, is the largest Bronze Age archaeological site on Crete and probably the

ceremonial and political centre of the Minoan civilization and culture. It is also a tourist destination today, as it is near the main city of Irakleion and has been substantially restored by archaeologist Arthur Evans. Archanes also hosts an archaeological site of ancient Minoan settlement in central Crete. The discovery of ancient roads leading from Archanes to a variety of nearby and more distant locations, indicate that Archanes was an important hub in the region during Minoan times. Archanes was probably a summer palace for the Knossos kings.

c) *"Anogia" Traditional village - Ideon cave*. Anogia is a municipality in the Rethymno Prefecture. The original settlement was probably founded by villagers from Axos, at the location where the Minoan city Axos was situated. It is located at an altitude of 740m up the north face of the mountain Psiloreitis, very close to the stunning Nida Plateau and the Ideon cave, where Zeus grew up, according to mythology.

The social events during the meeting will offer a strong taste of Crete and Greece.

Information on both the scientific and the social parts of the meeting is available at the website of IBS (www.biogeography.org), and will be regularly updated, so please return to this website every now and then.

Spyros Sfenthourakis

Local Organizing Committee of the 2011 IBS meeting

Jens-Christian Svenning

V. P. for Conferences

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

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

Job announcements

Postdoctoral Researcher in Macroecology Biodiversity and Climate Research Centre (BiK-F), Goethe-University Frankfurt am Main, Germany

The postdoc will investigate the impact of climatic factors and/or land-use on the macroecology of vertebrates (birds or large mammals). The focus will be on the macroecological and/or macroevolutionary analysis of the ecological niches and geographic ranges of vertebrates, including the impact of climate and land-use change on the ranges of large mammals, the macroevolution of climatic niches in birds or the inclusion of dispersal or biotic interactions in species distribution models of vertebrates.

The applicant should hold a PhD in ecology or a related field, and have a strong background in macroecological or macroevolutionary analyses of large data sets, advanced statistical analyses (e.g. species distribution modeling) and an interest in birds or mammals. He or she is expected to develop joint research projects, write funding proposals, engage in the supervision of Ph.D. and masters students, and contribute to teaching. A solid publication record, good written and oral communication skills, and the willingness to develop collaborations within the working group and the center as a whole are required.

Salary and benefits are according to a public service position in Germany (TV-H E 13). The contract shall start as soon as possible and will initially be restricted to 3 years, with a possible extension to further 3 years subject to performance. The employer is the Senckenberg Gesellschaft für Naturforschung.

Please send your application by e-mail, mentioning the reference of this position (#B20) 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 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 Finances: recruiting@senckenberg.de. For scientific enquiries please write to Prof. Dr. K. Böhning-Gaese (e-mail: katrin.boehning-gaese@senckenberg.de).

Interdisciplinary postdoc position on Geospatial Informatics

Aarhus University, Denmark

An interdisciplinary Post Doc position is available starting August 2010 or later. The responsibilities include work on geospatial problems on the boundary between computer science and biology, more specifically between algorithms and ecology/biodiversity, using modern detailed (and thus massive) topographic data in a computationally efficient way for various global-change-relevant modeling applications, including fine-resolution topography-derived variables on a global scale, as well as local- and global-scale flooding scenario modeling and impact assessment. Modest teaching responsibilities may also be required.

The Post Doc will be affiliated to the Danish National Research Foundation Center MADALGO (Center for Massive Data Algorithmics, - www.madalgo.au.dk) under the supervision of computer science Prof. Lars Arge (person.au.dk/en/large@cs), but will also work extensively with researchers in the Ecoinformatics & Biodiversity group at the Department of Biological Sciences under the supervision of Prof. Jens-Christian Svenning (person.au.dk/en/svenning@biology). Applications are welcomed from computer science researchers with skills in the design, analysis and implementation of algorithms (preferably also with I/O-efficient algorithms), as well as from geoinformatics or biology researchers with skills in ecoinformatics, GIS, and programming. Researchers with interdisciplinary research experience will be preferred. Applicants should use the application form available at www.madalgo.au.dk. Applications will be considered until the position is filled. For further information contact Professor Lars Arge at large@madalgo.au.dk or Professor Jens-Christian Svenning at svenning@biology.au.dk.

One of the benefits open to IBS members is the opportunity to have job openings posted on the biogeography.org website. 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.

3-year PhD assistantship in plant evolution and biogeography

University of Zurich, Switzerland

Origin and evolution of island endemics in the Mediterranean Region. Our first studies on Rutaceae, Araceae and Boraginaceae used chloroplast DNA sequences and geological data to reconstruct the temporal and spatial frameworks for the origin of plants endemic to the continental fragment islands of Corsica and Sardinia and the oceanic islands of the Canarian archipelago. Some of the open questions include: i) Are species in the selected Mediterranean groups monophyletic? ii) What are the origins of the polyploid species? iii) Is there variation of ploidy levels within species? iv) Was island colonization associated with a shift of the ecological niche? The successful applicant will choose one or more of these plant families to: generate

flow cytometry data aimed at determining ploidy levels; generate nuclear DNA sequences and infer species trees; incorporate ecological data to investigate issues of niche conservatism vs. niche evolution in the selected groups.

Experience in molecular, phylogenetic and flow-cytometry methods and/or ecological niche modeling will be highly valued in the selection process. Excellent knowledge of the English language, written and oral, required. Familiarity with additional European languages (especially Spanish) would be useful for fieldwork in the Mediterranean Region. The position will be open until a suitable candidate is selected, with starting date no later than February 1, 2011. For full job description, please contact Prof. Elena Conti (ContiElena@access.uzh.ch), Dr. Barbara Keller (barbara.keller@systbot.uzh.ch) or Frau Corinne Burlet (corinne.burlet@systbot.uzh.ch).

Upcoming events

2nd International Conference on Climate Change: Impacts and Responses

8-10 July 2010 – Brisbane, Queensland, Australia

<http://on-climate.com/conference/>

EDIT Summer School of Modern Taxonomy

European Distributed Institute of Taxonomy

17 July - 1 August 2010 – Madeira, Portugal

<http://www.atbi.eu/summerschool/node/183>

Plant Biology 2010

Joint Annual Meeting of the American Society of Plant Biologists and the Canadian Society of Plant Physiologists

30 July - 5 August 2010 – Montreal, Canada

<http://www.aspb.org/pb-2010/>

95th ESA Annual Meeting

Ecological Society of America

1-6 August 2010 – Pittsburgh, USA

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

II Conference on Biodiversity of the Guiana Shield

1-4 August 2010 – Amapá, Macapá, Brazil

<http://www.ufpa.br/naea/>

25th International Ornithological Congress

22-28 August 2010 – Campos do Jordão, Brasil

<http://www.ib.usp.br/25ioc/>

Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖe)

30 August - 3 September 2010 – Giessen, Germany

<http://www.gfoe-giessen-2010.de/>

FOSS4G 2010

Conference on Geospatial Free and Open Source Software

6-9 September 2010 – Barcelona, Spain

<http://2010.foss4g.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.

BES Annual Meeting 2010

British Ecological Society

7-9 September 2010 – Leeds, UK

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

VI Spanish congress of biogeography

7-11 September 2010 – Alicante, Spain

<http://web.ua.es/es/vi-congreso-biogeografia/>

Global Change and the World's Mountains

26-30 September 2010 – Perth, Scotland, UK

<http://www.perth.uhi.ac.uk/mountainstudies/2010>

AfricaFOSSGIS 2010

Free and Open Source GIS software and its application and development in Africa

27-29 September 2010 – Johannesburg, South Africa

<http://afossgis.org/>

Hydrology Conference 2010

The Changing Physical and Social Environment: Hydro-logic Impacts and Feedbacks

11-13 October 2010 – San Diego, California, USA

<http://www.hydrologyconference.com>

BIOME 2010 Biodiversity Meeting

21-22 October 2010 – Virac, Catanduanes, Philippines

<http://pacifictech.multiply.com/>

International Conference on Biodiversity and Climate Change

17-19 November 2010 – Manila, Philippines

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

5th International Conference of the International Biogeography Society

7-11 January 2011 – Crete, Greece

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

Neogene park – Vertebrate migration in the Mediterranean and Paratethys

1-3 March 2011 – Scontrone, Italy

<http://www.comune.scontrone.aq.it/>

Spatial Statistics 2011

Mapping Global Change

23-25 March 2011 – Enschede, The Netherlands

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

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