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cover: Looking northward from Mill Creek, California (35° 59.00' N 121° 29.52' W), where the land meets the sea.

news

Bern Convention group of experts on European island biological diversity: an international network to preserve island biodiversity

The Council of Europe (Bern Convention) promoted the first Meeting of a group of Experts on Island Biological Diversity, a meeting hosted by the Government of Canary Islands at Tenerife (1-3 October 2009) and organized by Eladio Fernández-Galiano.

A group of about 30 experts on European Islands discussed during two days the priorities for the conservation of a unique patrimony, the island biotas. The aim of this first meeting was threefold: 1) create a network of experts on island biodiversity; 2) discuss the problems that affect specifically island biodiversity; and 3) identify priorities for action and proposals to the Standing Committee to the Bern Convention.

A report prepared by Jorge Fernández Orueta and presented by Eladio Fernández-Galiano listed the potential lines of work on islands, the most relevant being: the lack of an inventory of European islands (but see the GIN – Global Island Network, <http://www.globalislands.net/index.php>); need to inventory the island protected areas; assessment of island biodiversity (islands contribute significantly towards global biodiversity; 10 out of the 34 biodiversity hotspots defined by Conservation International are islands); impact of Invasive Alien Species (IAS); impact of climate change; sustainability of medium and small size islands; oil-spills and other seaborne pollution risks; coordination mechanisms for a network of experts.

The presence of representatives of the Governments of Canary Islands, Azores and Madeira in most of the discussions gave some relevance to the event since it could help the implantation of local policies in conservation management

Kate Brown, representing the Convention on Biological Diversity (CBD) presented the Global Island Partnership (GLISPA <http://www.cbd.int/island/glispa.shtml>) that “assists islands in addressing one of the world’s greatest challenges: to conserve and utilize the invaluable island natural

resources that support people, cultures, and livelihoods in their island homes around the world”. She provided an example of a capacity building network in Pacific islands.

Olivier Tyack and Margarita Astrálaga representing IUCN outlined the reasons of IUCN to cooperate with this Group of Experts on Islands: there is much to conserve; much to learn; and much to save! IUCN will contribute influencing policy and institutions.

M^a Mar G. Villagarcía described the NET-BIOME initiative, an European support to biodiversity research on Islands (including Pacific tropical French islands), that will launch in 2010 a call for research projects within the field of tropical and subtropical research on islands.

Experts of several countries presented the problems that affect specifically island biodiversity on Azores, Madeira and Canary Islands (Macaronesia), Balearic Islands, Cyprus, Italian islands, North Atlantic and Baltic islands (Sweden, Norway, United Kingdom), Iceland and Arctic. In most of the cases the main problems are global warming, habitat destruction, pollution and IAS.

José Luis Martín Esquivel (Canary Islands Conservation Bureau) described the impressive biodiversity of Canary Islands and presented the ATLANTIS database, that allows the study of spatial distribution of species in a small scale (500x500 m) in the Macaronesian islands.

Antonio Machado (Observatorio Ambiental Granadilla) from Canary Islands described in detail the main problems that affect specifically island biodiversity, stressing the fact that the red-listing categories of IUCN cannot be applied to islands, a fact that was reinforced by José Luis Martín Esquivel and Paulo Borges (University of Azores, Azorean Biodiversity Group) that called for an international consensus and a complete revision of IUCN red-listing categories creating new evaluation tools for both islands and invertebrates.

Paulo Borges (University of Azores, Azorean Biodiversity Group), described the Azorean Biodiversity Portal (<http://www.azoresbiportal.angra.uac.pt/>) and highlighted the importance of science communication for the general public, putting island biodiversity on the web. He also explained the importance of standardized studies and monitoring of island ecosystems using Long Term Ecological Studies (LTER).

Frederico Cardigos (representing the Azorean and Madeiran Governments) affirmed that along the whole processes of governance and nature conservation policies, it is assumed that public perception is of great importance and has a considerable impact on the way politicians react. In addition he presented the plan of the Azorean Government for the management of both terrestrial and marine environments.

António Machado referred that the task is immense and complex, and that as an island decreases in size and its distance to the mainland increases (isolation), its ecological vulnerability also increases, the data is scarcer, and there is insufficient local technical capacity and lack of political commitment.

IAS on Islands were discussed by Juan Luis Rodríguez Luengo (Canary Islands) that presented the TOP100 Macaronesian initiative, Piero Genovesi (Italy) that presented the ISSG (Invasive Species Specialist Group), Lucilla Carnevali that presented the database on IAS in European Islands and Sarah Brunel (EPPO), that talked on Biosecurity in Islands – Using Plant health instrument to control IAS. Invasive species were considered the

most important problem to the conservation of the native island biota and ecosystems.

By the end of the meeting the Priorities for action and Proposals to the Standing Committee of the Bern Convention were discussed under the coordination of Eladio Fernández-Galiano. Suggestions included: EU legislation dedicated to IAS on islands; portfolio of biodiversity on islands; manual of best practices; establishing working groups (climate change; IAS; IUCN criteria revision adapted to islands and invertebrates; communication improvement); for the parties – special attention to natural systems on islands promoting initiatives of biodiversity information gathering.

A major challenge of this group of Experts on Island Biological Diversity is to influence the policy-makers, managers and general public on the importance of putting special resources for the conservation of island biota and ecosystems, maintaining also a sustainable life for island human populations.

The solid experience and knowledge in island ecosystems of most of the experts that participated in this meeting, together with the commitment of local politicians is a strong indicator that the goals of this meeting will be entirely achieved, and that we will create an international network of expertise in island studies.

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update

Decomposing beta diversity

Baselga (2009) proposes a creative analysis to decompose patterns of beta diversity into effects of nestedness and species turnover. This kind of approach moves us closer to distinguishing different mechanisms that can contribute to observed measures of beta diversity. Two additional considerations will help to improve this analysis.

First, more effort should be devoted to carefully exploring the statistical performance of

this index with artificial data sets that have specified amounts of randomness and structure. The analyses presented in Figures 2 and 3 are an excellent start, but we need an expanded analysis of different kinds of benchmark matrices to evaluate the potential for Type I errors (incorrectly rejecting a true null hypothesis) and Type II errors (incorrectly accepting a false null hypothesis). These kinds of tests are challenging because they

require a careful consideration of exactly what constitutes a "random" and a "structured" matrix with respect to species nesting and spatial turnover. But they should be conducted before attempting a meta-analysis of published empirical matrices.

Second, this index, like most other measures of nestedness and beta diversity, assumes that island censuses are complete and there are no undetected species. Anne Chao and colleagues have recently modified classic similarity indices to take into account undetected shared species. The presence of undetected species biases the unmodified indices towards underestimating shared species (and hence over-estimating beta diversity). It is not yet clear how serious of a problem this is for Baselga's (2009) proposed partition.

Baselga (2009) has made an innovative contribution that deserves further exploration.

Baselga, A. (2009) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, doi:10.1111/j.1466-8238.2009.00490.x.

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Edited by Thiago F. Rangel

update

Of refugia and colonization, an innovative use of biogeography for climate studies

A beautiful sight in Glacier National Park is found along the Trail of the Cedars, a stand of western red cedar (*Thuja plicata*) replete with mossy rocks and cold running waters. This tree, and western hemlock (*Tsuga heterophylla*), are emblematic of the northern coastal temperate rainforests of the western US and Canada. However, they are also found over 160 kilometers to the east, across a large expanse of sagebrush steppe, on the western flank of the Rocky Mountains. This well known disjunct rainforest distribution is the subject of a new biogeographic study titled, "The coastal-disjunct mesic flora in the inland Pacific Northwest of USA and Canada: refugia, dispersal and disequilibrium" by Daniel Gavin, professor of Geography at the University of Oregon. Dr Gavin analyzed the patterns of biodiversity between the coastal populations and northern and southern interior populations of 67 vascular plant species, all components of the temperate rainforest group. He used the biogeographic patterns to explore the possible interactions between species richness, climate change, and glaciation. The study examines how species richness varies with climate; how distribution patterns may have been affected by

glaciated *versus* un-glaciated areas in the interior; and whether life history characteristics such as seed dispersal mode and growth habit help explain the current extent of the species analyzed.

Dr. Gavin mapped each plant's range distribution to 50x50 km grid cells using a variety of reference materials. He then examined patterns of species richness, according to life history characteristics and climate as defined in the PRISM data sets. The study used regression models of species richness as a function of Actual Evapotranspiration (AET) in the coastal regions (most mesic and specious) to develop expected levels of species richness for the AET of more recently suitable interior regions. This permitted regional quantification of the level of disequilibrium from expected species richness, an indication of incomplete colonization by the regional flora. The northern interior was most in disequilibrium, indicating that many species have yet to disperse into the area. Since several sources of colonizers exist, the implication is that some plant species may have a difficult time dispersing into newly suitable habitats across a fragmented landscape under future climate change.

The pattern-based analysis provided an opportunity to test a variety of dispersal and refugia scenarios that have been proposed for the Pacific Northwest, because it has three categorical areas: coastal non-glaciated, southern interior non-glaciated, and northern interior glaciated. Species with the highest dispersal capacity had the largest ranges and were more likely to have dispersed to the northern interior glaciated (recently unglaciated) zone. The study also found that the northern interior zone had been colonized by species from both the coast and from further south in the interior. Less dispersive capable species showed more restricted range, including six endemic species from Idaho, which had not moved to the north.

This last finding led the author to conclude that plant characteristics are likely an important component in the effort to determine what species may be able to successfully shift range across

a fragmented landscape under future climate change. The author points to the importance of including phylogeographies in future work, but has done a remarkable job of identifying vulnerabilities of plant species to climate change using more traditional biogeographic techniques.

Gavin, D.G. (2009) The coastal-disjunct mesic flora in the inland Pacific Northwest of USA and Canada: refugia, dispersal and disequilibrium. *Diversity and Distributions*, 15, 972-982.

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update

More uncertainty with BIOMOD

Species distribution modeling (SDM) has grown in importance over the last decade to become a powerful tool in conservation planning, global change forecasting, ecological hypothesis testing, and characterization of niche properties in phylogenetic analyses. Many scientists have contributed to the conceptual, statistical and technical development of this field. While I believe that further development has asymptoted in many domains of SDM research, it is clear that BIOMOD is a significant contribution.

A decade ago, we faced numerous uncertainties and limitations in building SDMs. Few statistical techniques were available and no comparative studies existed. Generalized Linear Models were a standard method, and key issues included how best to fit response shapes, how to evaluate competing models, and what statistical methods to use to get “the best model” of a target species. Climate change projections were usually established by simply adding 2-4°C to annual mean temperature maps, and “the best model” was then projected into the future. BIOMOD, in its

first version of 2003, was a huge step forward. It included four different statistical methods to model hundreds of species automatically. Further, it used a simple method to identify the model that best fit the general trend among the resulting models.

At the same time modeling and forecasting of a range of scenarios, including the assessment of projection uncertainty, became an important aspect of research on climate change impacts. This has dramatically increased the demand for model building, model averaging, ensemble forecasting, and analysis of complex output. We are no longer interested in identifying “the best model”, but rather the mean and variation of models – currently and when projected to the future.

Ensemble forecasting is so complex that most of us will only include a fraction of the possible uncertainty sources when modeling potential climate change effects upon species distribution patterns. Over the last 6 years BIOMOD has been developed, improved, and extended. It now offers

the capacity to deal with numerous statistical models, ranges of initial conditions, different climate projections, and many more effects. Personally, I never liked the idea of automatically processing hundreds of species without careful consideration of predictor sets with regard to a specific species. However, I will now use BIOMOD even for single species projections, simply because the general framework makes ensemble forecasting so easy for us. And if one chooses to use only a few carefully chosen predictors, then BIOMOD can successfully process many species simultaneously.

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M.B. (2009) BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, 32, 369-373.

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Edited by Thiago F. Rangel

commentary

Geographic patterns of establishment success among exotic bird populations

Human-mediated species invasions are a major component of global environmental change and there remains a pressing need to understand the mechanisms by which a species becomes invasive. With this in mind, the key stage in the invasion pathway (*sensu* Williamson and Brown 1986) is species establishment. It is at this stage, when a species has been transported outside its native geographic range and released in a novel recipient environment, that a species either fails or succeeds to establish an exotic population. However, while much attention has been focussed on what species-level traits determine establishment success in exotic bird populations (Blackburn et al. 2009), relatively less research has concerned the role of location-level variables.

The most obvious reason for this relative 'lack of research' is that in most cases, comparative analyses have consisted of large datasets of good quality records of different species to single specific locations (e.g. Hawaii, Moulton et al. 2001; Australia, Duncan et al. 2001; New Zealand, Duncan et al. 2006) rather than repeated introductions of the same species to multiple locations. Bird species are conspicuous elements of the environment and their distribution and abundance have attracted considerable research attention in the discipline of biogeography (e.g. Gaston and Blackburn 2000). It is therefore somewhat surprising that autecological studies of exotic birds have received disproportionately limited research attention within invasion biology (Pyšek et al. 2008).

A recent article in the *Journal of Biogeography* (Strubbe and Matthysen 2009), provides a timely example of a study that addresses this bias.

Diederik Strubbe and Erik Matthysen compiled data on the introductions and establishment success of two parakeet species (ring-necked *Psittacula krameri* and monk *Myiopsitta monachus* parakeets) across their exotic European distribution. In doing so, the authors provide one of the first comparative biogeographic studies to test environment-level features of establishment success among exotic birds. In total, 181 introduction events were used for their analysis in the exotic range. In their native ranges, parakeet occurrence was estimated using the presence-only method MAXENT (Phillips et al. 2006). For both parakeet species, individually, their establishment success in Europe was 53%. Data from environmental and climatological variables were used to test the relative influence of alternative 'climate-matching' and 'human-activity' hypotheses. The authors found that parakeet establishment success was greater in areas of more dense human population settlement and, both in the native and exotic ranges, their distribution was associated with a smaller number of annual frost days. Further examination revealed that both species were equally sensitive to frost in their exotic range, the majority of failed introductions occurring in regions with more than 50 frost days per year. Human activity can influence establishment success both indirectly, through habitat modification and provision

of resources (e.g. supplementary food and breeding sites), and directly by increasing the local introduction effort. Interestingly, Strubbe and Matthysen (2009) found that after controlling for the number of parakeets released during the first introduction event, human population density was still an important predictor of establishment success.

If environmental change continues in mainland Europe, as is likely for the considerable future, then local geographic features such as climate warming and increased urbanization may act to increase the probability of establishment success for the parakeet species even further. Strubbe and Matthysen (2009) only included in their analyses exotic parakeet populations that were introduced before the year 2000, evidenced breeding in the 2007 breeding season, and had not indicated a population crash in recent years. The authors note that the exotic parakeet populations range in size (and distribution) between a few individuals and many thousands. In many cases, the time since introduction will explain the differences in population size. In others, features of the biotic and abiotic environment will likely be responsible for influencing whether a population, once established, continues to grow and spread. The spread of exotic bird populations has attracted considerably less empirical and comparative investigation than any other stage of the invasion pathway. Although in the past biological invasions have been modelled in relatively simple terms using parameter sparse models (Hastings et al. 2005), this approach does not offer insight into the individual processes influencing population expansion. It is clear that as data on the differences in the distribution of exotic bird populations become available the features that influence their variability in growth and spread will be of considerable future importance in studies of invasion biogeography.

Strubbe and Matthysen (2009) note that the large dataset available to them for analysis was, at least in part, facilitated by the particular conspicuousness of the parakeet species and the large number of amateur bird watchers living and visiting in mainland Europe. Few exotic species are similarly conspicuous or well distributed, and future studies of this kind will only be possible with accurate data on introduction events and the concerted monitoring of exotic populations across a wide range of habitats and regions.

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Edited by Frank A. La Sorte

commentary

Colonization of the arctic archipelago Svalbard

We have more knowledge on colonization to the Arctic Archipelago of Svalbard than to any other arctic region. Previous analyses include the only native terrestrial mammals, reindeer (Flagstad and Røed 2003) and arctic fox (Dalen et al. 2005), the only fresh water fish, arctic charr (Brunner et al. 2001), several *Daphnia* species (Weider et al. 1999), the moth *Plutella xylostella* (Coulson et al. 2002), and many vascular plant species (Brochmann et al. 2003, Alsos et al. 2007). Recently, also the colonization routes for the only resident terrestrial bird, the Svalbard rock ptarmigan (*Lagopus muta* ssp. *Hyperborea*, Figure 1) have been analysed (Sahlman et al. 2009).

Svalbard represents an ideal model system for studying colonization for several reasons. It was almost entirely glaciated during the last glacial maximum 20,000 years before the present (Landvik et al. 1998, Landvik et al. 2003) and thus glacial survival can mainly be ruled out as explanation for the presence of species. Fossil evidence indicates sparse arctic vegetation from 10,000

years B.P. (Birks et al. 1994), which thus gives the maximum time frame for colonization events. It is geographically isolated, and the distances to nearest lands are 470 to northeast Greenland, 650 km to N Norway, 870 km to Novaya Zemlya, and 240 to the high arctic archipelago Frans Josef Land.

The Svalbard rock ptarmigan, *L. muta* ssp. *hyperborea*, is restricted to Svalbard and Frans Josef Land. It belongs to the large rock ptarmigan species complex (*Lagopus muta*) which originated in Beringia (Lucchini et al. 2001), and now consists of up to 30 different subspecies which are found throughout the circumpolar region as well as in many temperate alpine regions (Storch 2007). The Svalbard rock ptarmigan is commonly seen from March to October, but it is a puzzle where they spend the winter, as the dark polar night makes visual observations difficult. Rock ptarmigan in other regions have seasonal migrations of up to 500 km (arctic Russia) or 1,000 km (coastal Greenland). It is assumed that Svalbard rock ptarmigans stay in Svalbard during winter, possibly



Figure 1. The Svalbard rock ptarmigan (*Lagopus mutus* ssp. *hyperboreus*) colonized Svalbard from Russia or Greenland according to a recent study (Sahlman et al. 2009). Photo: Bjørn Erik Sandbakk.

feeding below the bird cliffs (Kovacs and Lydersen 2006). However, it has also been claimed that they migrate and, recently, satellite transmitters have been fitted to eight individuals in order to elucidate this question (<http://svalbardrype.npolar.no/en/index.html>).

In their paper titled 'Island in the ice: colonization routes for rock ptarmigan to the Svalbard archipelago', Sahlman, Segelbacher and Höglund (2009) present molecular data on rock ptarmigan, having genotyped populations from Svalbard, W Greenland, Iceland, Scandinavia and Taymyr for 12 microsatellite loci. In addition, they sequenced the mitochondrial control region (mtCR). The sequences represent a nice expansion of previous studies mainly from the Nearctic and the Bering region e.g. (Holder et al. 1999, Holder et al. 2004), and the sequences were aligned with all previously identified sequences available in Genbank. They thereby fill in a gap in the circumpolar phylogeography of rock ptarmigans.

On a circumpolar scale, populations from Svalbard, Taymyr and W Greenland were closely related to other arctic populations, whereas populations in Scandinavia and the Pyrenees are most differentiated from all other populations. The Scandinavian populations were also differentiated from the arctic populations based on the microsatellite data. Thus, Scandinavia could be ruled out as a source region for Svalbard rock ptarmigan (Sahlman et al. 2009). It is striking how few of the species analysed so far show a colonization route from Scandinavia to Svalbard (Brochmann et al. 2003, Alsos et al. 2007), suggesting that the open ocean between these regions constitutes a larger dispersal barrier than the sea-ice covered oceans between Svalbard, NW Greenland and Russia, although the distance to Russia is longer. This emphasizes that we should be cautious with assuming a northward migration due to current climate warming. One has to look for both likely dispersal barriers and dispersal bridges, as this might strongly modify the migratory route of the species.

It remains uncertain whether rock ptarmigan colonized Svalbard from east or west, but as Svalbard and Taymyr populations had one haplotype in common, an eastern colonization route is slightly more likely (Sahlman et al. 2009). These colonization routes are not mutually exclusive as, for example, has been shown for several plant species that most likely colonized Svalbard from

several source areas (Alsos et al. 2007). To answer this question for Svalbard rock ptarmigan, samples from East Greenland should be included, as different subspecies have been found in different parts of Greenland (Holder et al. 2004). Also, more and better quality samples are needed from north-western Russia. For all studies addressing the phylogeography of arctic species, it is a challenge to obtain good samples from Russia. The feather obtained from Taymyr by Sahlman et al. (2009) gave poor genotyping success. This is a pity, as this turned out to be the most likely source area. More predictable condition for field work in Russia as well as easier transfer of samples would not only greatly improve our knowledge on the Russian part of the arctic, but also shed more light on the biogeography, ecology and systematics of the arctic region in general.

The most common haplotype found in Svalbard rock ptarmigan was also the most widespread one, and it was placed in the center of the haplotype network. This is a striking similarity to what has been observed in the circumpolar bird-dispersed species *Vaccinium uliginosum* (Alsos et al. 2005, Eidesen et al. 2007). In the purple saxifrage, *Saxifraga oppositifolia*, too, only the most widespread haplotypes were found in Svalbard (Abbott et al. 2000). A possible explanation for this is that Svalbard was colonized from long distance, and just by chance the most frequent haplotypes are most likely to survive and establish a local population.

Both the sequence data and the microsatellite data showed lower levels of genetic diversity in Svalbard than in other regions. This suggests that a strong genetic bottleneck has occurred in the past (Sahlman et al. 2009). In arctic vascular plants, a similar bottleneck is seen in rather thermophilous species but not in species well adapted to the local climate conditions (Alsos et al. 2007). Whether the bottleneck occurred during colonization, or was due to some other processes later on, is unknown. Even though hunting pressure has been extreme for other Svalbard animals, and has almost lead to their extinction, the Svalbard rock ptarmigan most probably has not been hunted that much (Løvenskiold 1964).

Based on the accumulating phylogeographical studies of arctic species, there is a good potential to study immigration routes also to other arctic and subarctic archipelagoes. Especially good datasets exist for the North Atlantic regions,

where meta-analyses of existing data could indicate migration routes to Iceland and Greenland. For rock ptarmigan, additional samples from east Greenland would be needed to answer this question. The data also allows exploring for differences in colonization routes for different functional groups. For example, while birds might disperse plants, the presence of plants might determine if any occasional dispersed birds will survive and be able to establish a population. Thus, having data on many different organisms, as we are now compiling for Svalbard, will open up new research perspectives.

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commentary

A Darwinian approach to community ecology

In *A Darwinian approach to plant ecology* the late John Harper argued that evolution should be the conceptual basis for all plant ecology (Harper 1967). Quoting extensively from the *Origin of Species*, and taking examples from ecological restoration, interspecific competition and life-histories, his thesis was that evolution is central to understanding the diversity of adaptations and interactions in plants. Forty-odd years later this vision is playing out with the availability of information on the evolutionary history of species allowing ecologists to explore the links between evolution and ecology in ever more imaginative and detailed ways. In a new synthesis of our current understanding of the links between evolutionary theory and community ecology, Cavender-Bares and colleagues present a compelling case that community ecology has been revolutionised in the past 10 years through advances in phylogenetics and the application of evolutionary ideas. They argue that evolution is central to understanding interactions between species, the diversity of life histories and in deciding between competing hypotheses for species diversity.

Evolution and community assembly

Communities are vague entities at best (Ricklefs 2008) and the processes driving community composition are varied. On the one hand communities may be assembled primarily through migration, for example when habitat is cleared and a community is formed through immigration. On the other, if a community is allowed to develop and essentially left undisturbed for a long period, species will evolve *in situ*. This division is as old as ecology itself, reflecting the difference between Clements' and Gleason's theories on communities. The 'modern synthesis' for community ecology (e.g. for recent reviews see Ricklefs 2008, 2009, Vellend 2010) is that the species present within an area are determined by the relative balance of four processes: speciation, extinction, dispersal and ecological sorting. Traditional community ecology has put a great deal of emphasis on ecological sorting in a narrow sense, particularly focussing on the details of processes and interactions at the micro scale. However as Ricklefs (2009) succinctly puts it, "*The presence of shrub X*

might exclude herb Y from a 1-m² study plot, but much is left unexplained, including why X and Y are there is the first place". Historical factors must play a huge role in determining the composition of a community, through biogeography, speciation and adaptation. The imprint of these historical processes can be untangled if we know the phylogeny of the species present.

What can phylogeny tell us?

Phylogeny can tell us about the degree to which various historical factors shape the distribution of traits and diversity. It is straightforward to statistically test whether differences in species traits (specifically those which relate to niches) scale with phylogenetic distance or not. The expectation is that nearer to the tips of a phylogeny, species would be more divergent if niche processes are important, particularly character displacement. On the other hand, at larger scales phylogenetic niche conservatism should mean that larger clades are reasonably distinct.

Phylogeny will also be informative about the species that we might expect to co-occur. For example, competition at small scales will determine which species co-occur. Such processes may occur on scales of even a few metres. On the other hand at intermediate spatial scales we would expect to see phylogenetic clustering: as a consequence of its biogeographic history a group will be restricted to a given area.

Of course these predictions are only the expectation under one scenario: in practice other factors could operate. For instance, if species are highly mobile they would be expected to show less of an imprint of evolutionary history on their traits and phylogeography as they will show less spatial clustering and be adapted across a wider range of habitats. Modern phylogenetic comparative approaches allow a suite of patterns of diversity of traits and diversity to be modelled and tested.

When we look at small scales the composition of species within a community will reflect the interplay between the effects occurring at all of these scales as well as the outcome of ecological sorting. Biogeography and history determine the pool of species that can form a community. Then

interactions, the environment and micro-evolution combine to determine the traits of the species that are drawn from this pool in a given area.

The distribution of traits and species with respect to phylogeny exhibit a variety of patterns including clustering, randomness and overdispersion. Clustering of traits is where species from only those clades with specific adaptations can persist in the community; randomness is where species are drawn apparently at random with respect to their traits and phylogenetic position, most likely because the determinants of community composition are complex; and overdispersion occurs where traits leading to successful establishment are distributed throughout a phylogeny. By examining the phylogenetic distribution of traits and their dispersion it is possible to distinguish different types of processes driving species traits and community membership.

A key assumption is that phylogeny is a good reflection of evolutionary history: this includes the relationship between species (the topology of the phylogeny) and evolutionary distances (branch lengths). There are a number of reasons why the phylogeny might not accurately reflect history, or it is frequently the case that there is uncertainty such that different phylogenies are equally as well supported. Moreover, it is important not to regard the incorporation of phylogeny as an end in itself: phylogenies need to be used along with an explicit hypothesis-testing framework. This is a strong point made by Cavender-Bares et al. (e.g. see their figure 4 for an example of how this can be done).

Challenges and opportunities

The revolution in the availability of phylogenetic information has had enormous impacts in evolution and ecology, and the review by Cavender-Bares et al. shows how this has impacted on community ecology. Indeed, major advances continue to happen: for example, recent weeks have seen the first publication of a phylogeny for an entire tropical tree community (the famous Barro Colo-

rado Island study site) assembled from DNA barcodes (Kress et al. 2009). The ease with which we can now assemble evolutionary histories of groups of species is quite remarkable.

The challenges lie in exploiting this information and Cavender-Bares and colleagues point out that there are several areas where much remains to be done. For example, there are increasingly sophisticated models linking traits to community assembly (e.g. Purves et al. 2008) but there are challenges in linking these models to evolution and predicting how traits will evolve and relate to phylogeny. Simple niche-filling models have been developed for adaptive radiations (Price 1997, Freckleton and Harvey 2006), however this area is in its infancy.

Importantly this work is starting to tell us about the degree to which traits predicting community assembly are phylogenetically constrained, that is the degree to which historical factors drive community composition or, equivalently, the degree to which species within communities are ecologically labile. In the face of climate and environmental change this will inform us about which systems and which species are likely to respond – or not – to these changes, and the potential for evolutionary compensation.

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symposium summary

The importance of being small: does size matter in biogeography?

One-day symposium at Systematics, the First BioSyst conference – Leiden, The Netherlands, 13th August 2009

Since the 18th century, scientific expeditions in remote places have discovered new species and even new orders and new classes of macro-organisms with limited distribution. In contrast, scientists have discovered that microscopic organisms found in remote places could be mostly ascribed to taxa already known in their home countries. This idea was encapsulated by Beijerinck (1913) and Baas-Becking (1934), and became known as the 'everything is everywhere' (EisE) hypothesis: micro-organisms are globally distributed due to their potential for long-range dispersal (Kellogg and Griffin 2006) and large abundances (Finlay 2002). The assumption that organisms smaller than 2 mm are cosmopolitan in their distribution is best supported when species are defined using traditional taxonomy based on morphological characters. However, the EisE hypothesis has been challenged recently as molecular evidence has revealed a high degree of cryptic diversity, restricted dispersal and phylogeographic patterns in a variety of microscopic organisms, including both prokaryotes and eukaryotes (e.g. Martiny et al. 2006, Green et al. 2008).

The recent debate on the EisE hypothesis began after the contributions by Finlay and Fenchel (e.g. Finlay and Clarke 1999, Finlay 2002, Fenchel and Finlay 2004), and different research groups are currently trying to test its reliability on different model organisms. Thus, it was considered timely to organize a full-day symposium on this topic, and that was held during the BioSyst meeting in Leiden, a joint conference of all the

European systematics associations.

The current debate on the EisE hypothesis divides scientists in two major groups (Whitfield 2005). One group follows the EisE hypothesis in its original form, assuming that species differences in samples from different areas occur because of environmental differences, and not because of restricted dispersal. Thus, 'everything is everywhere, but the environment selects' is considered the rule for micro-organisms. The other group proposes that traditional taxonomy of microscopic organisms based only on morphological characters is not able to resolve their actual diversity, and cosmopolitan ranges therefore result from misidentification and lumping of spatially isolated lineages. Thus, cosmopolitanism is considered an exception in micro-organisms, as it is in macro-organisms.

It has been suggested that the EisE hypothesis incorporating environmental selection may be difficult to falsify because of unmeasured aspects of the environment that differ consistently among regions (Foissner 2006). However, if we assume a dense sample of equivalent habitats across sampling regions, the hypothesis makes clear predictions about genotype distributions. If EisE is the rule, the degree of genetic relatedness between two individuals should be independent of the geographical distance between them. Conversely, if EisE does not hold true, spatially explicit models should work in the same way as they do for macro-organisms, and genetic diversity should be related to geographical distances by a classical

distance–decay relationship. On the other hand, it has been proposed that the EisE hypothesis should be dismissed, as it is not a testable hypothesis at all.

During the symposium we discussed results gathered from different taxa, including thermophilic bacteria, ciliates, amoeboid protists, diatoms, green algae, cacti-associated yeasts, and also macro-fungi, mosses and small aquatic animals. We had an overview of the variety of methods currently used to obtain large amounts of additional empirical evidence, especially performing Next Generation Sequencing of environmental samples. Different theoretical approaches from the biological properties in common between micro-organisms and from simulations were presented, deepening our understanding of the processes involved but with a caveat: similar patterns may mask very different processes. Things may not be so easy as expected. For example, geographic patterns with genetically more similar organisms in nearer areas may be obtained from theoretical models that both contrast and support the EisE hypothesis.

One of the main messages from the symposium is that generalizations may be dangerous and misleading, as different taxa respond in different ways to the same habitat. Biological properties other than size (e.g., dormancy) indeed influence the patterns of distribution of organisms. Thus, further work needs to be undertaken to gather more data.

Moreover, micro-organisms are becoming a highly suitable model in other fields of biology. One example is the application in conservation biology that has come from the research that the EisE hypothesis has stimulated (Brodie et al. 2009), including how different organisms respond to the same habitat. Another application is in experimental biogeography; using small organisms in mesocosm experiments to test predictions from theories in biogeography is an exciting new frontier.

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congress summary

EMAPI 10: Bridging approaches to plant invasions

10th International Conference on the Ecology and Management of Alien Plant Invasions (EMAPI 10) – Stellenbosch, South Africa, 23-27th August 2009

“Invasion biology” has developed considerably in the 17 years since the first meeting on the Ecology and Management of Alien Plant Invasions (EMAPI) in 1992. Biological invasions provide a broad umbrella under which an increasingly wide variety of interdisciplinary studies are conducted. Nowhere was this more clearly illustrated than at this year’s EMAPI 10 conference hosted by the Centre of Excellence for Invasion Biology in Stellenbosch, South Africa. The 31 sessions covered a broad spectrum of topics from understanding ecological and evolutionary mechanisms driving invasions, predicting future invasion patterns and dynamics, to designing and implementing effective management strategies. More than 230 presenters and attendants came from all continents to discuss the state of the art of invasion ecology and management.

Until now invasion biology has to a large extent been concerned with identifying general patterns and processes, for example particular plant traits or natural enemy release, to explain why, and ultimately to aid in predicting which taxa become invasive (Richardson and Pysek 2006). Some novel approaches to these problems were discussed during the conference such as the use of altitudinal gradients to tease apart the relative roles of climate, habitat and anthropogenic influences as drivers of invasion using multi-scale, multi-regional comparisons (Pauchard et al. 2009). The conference also reflected the growing importance of an evolutionary perspective. Indeed, a large proportion of the more theoretical presentations addressed evolutionary questions using molecular approaches, for example to reconstruct invasion pathways and assess levels of genetic variation in introduced populations. There was also recognition that climate change will impact patterns of invasion and community invasibility. Several studies used niche modelling approaches to predict some of these changes, but apart from a presentation by Bruce Osborne few attempts to

experimentally assess synergistic impacts of climate change and invasion were presented. Despite the advances, there was generally a lack of presentations which tested or introduced novel theory and mechanisms of invasion. To an extent this might reflect the difficulty of making broad generalisations across invasions. This might also represent a shift towards the use of plant invasions as tools to address basic ecological and evolutionary questions (e.g. Sax et al. 2007), for example the evolution of species range margins or breeding systems, rather than as a research topic in its own right.

Although theory and management of invasions are usually treated separately in the literature, EMAPI meetings have always provided a platform for discussion of the interaction between science and application. One of the main points discussed in the meeting was to what extent we should worry about controlling invasive species in countries with lower resources and where other conservation issues seem to be more urgent (Nuñez and Pauchard 2009). However, plenary addresses by Arne Witt and Sue Milton emphasised the negative impacts of invasive species on human livelihood in sub-Saharan Africa, for example as a drain on scarce water resources. This is also the message of the South African “Working for Water” programme (<http://www.dwaf.gov.za/wfw/>) which employs annually approximately 20,000 people from underprivileged sectors of society in the control of invasive species. As noted by David Richardson, the chief-organizer, this meeting included a large number of managers coming from many developing countries of Africa. This unique opportunity to share experiences between scientists and practitioners should be encouraged in all scientific meetings, especially when dealing directly with conservation themes.

Another important message we can extract from the meeting is the need to clarify the goals and implications of our management actions.

There seems to be in some cases an excessive prejudice against non-native species, reflected in the language we use (e.g. “enemy”, “invader”), which might sometimes have beneficial ecological properties, for example when used for remediation of ecosystems damaged by mining or industrial activities (Dye et al. 2008). Rather than focusing so much on controlling invasive species, we should aim to restore native ecosystems, a task that requires much more effort than just the eradication of particular species. The implications of controlling invasive species go far beyond their ecosystem effects and include complex social aspects. How we communicate to society the need for management of invasive species and the restoration of biodiversity and ecosystem services is a crucial task not only for managers, but also for scientists. This was explicitly addressed in a symposium specifically focussed on pine invasions; no matter how much research is done on the invasion of pines, little progress can be made if we do not convince the key stakeholders about the implications of such invasions and the need for control.

EMAPI meetings as well as other invasion biology meetings should serve to advance our understanding about the implications of invasive species in conserving biodiversity and ecosystem services. However, only three sessions at the conference dealt explicitly with impacts of alien plants on native species richness, multitrophic interactions and ecosystem functioning. This reflects some concerns, voiced at the meeting for example by Marcel Rejmánek, that statements about the impacts of plant invasions are often based on very limited data. It is therefore crucial for the credibility of the discipline and to convince policy makers of the need for management action that this imbalance is addressed. The future challenge of invasion biology and future EMAPI conferences therefore remains to bridge the gap between theory and the application of effective management.

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Your pictures can be the cover of the next **Frontiers of Biogeography** issue. If you have photos or artwork related to biogeography that could make a great cover send them to ibs@mncn.csic.es or frontiersofbiogeography@gmail.com. The best pictures received will be the cover of forthcoming issues (in the case of pictures in landscape layout, an excerpt will be used). We will also consider pictures for the inside of the journal.

book review

A book for our time

Spatial Conservation Prioritization — Quantitative Methods and Computational Tools, by Atte Moilanen, Kerrie A. Wilson and Hugh Possingham

Oxford University Press, Oxford, 2009, 328 pp. ISBN 978-0-19-954777-7

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

"Spatial Conservation Prioritization" is a remarkable book about a remarkable field. In it, the editors have assembled a quiet manifesto for a new kind of conservation biology - or rather for the universal adoption of the last decade's mathematical developments in conservation planning. I say a quiet manifesto because in spite of an absolutely pressing need for conservation organizations worldwide to wake up and smell this particular methodological coffee, this is not an evangelistic book and the contents are left to stand on their obvious merits.

In a nutshell, Moilanen et al. present a series of chapters written by researchers at the forefront of the field, detailing the various ways in which precise spatial questions can be asked and answered with optimization techniques from the wider field of operations research. A reasonable amount of theory is introduced, and introduced well for the non-specialist: something to be commended as the specialist primary literature on the subject is sparse and difficult to approach. This is particularly true of the three excellent chapters dealing with the mathematical formulation of spatial choice problems, the linear programming techniques used to solve them, and the heuristics to those solutions which are used most frequently in current practice. As the concluding chapter says, this is most familiar to readers in the context of "which nature reserve to buy next?" given a goal and some available resources, but in reality can be extended to most stages of the conservation planning process.

These extensions are covered in detail in several chapters which look at recent advances in ways to increase the realism of the program to be solved: integrating population viability analysis, how to optimize for maintenance of metapopulation and landscape dynamics, how to deal with uncertainty, dynamism in habitat and in the future

distributions of species. The book then proceeds with a series of chapters introducing (with examples) four of the most well-known software packages for heuristic spatial solutions: Marxan, Zonation, C-plan and ConsNet, before concluding with a best practice chapter on interacting with the other parts of the planning process and an intriguing future prospects wrap-up by the editors.

That's not to say the book is free from problems. Chapters with a heavy policy basis are in places pretty turgid going, and this might limit the utility of the book in undergraduate teaching. And to me one glaring omission is anything on the ability of spatial conservation planning to transcend the biological boundaries within and between spatial scales and levels of organization. There are good chapters on planning approaches at the level of the metapopulation, the community and the region, but nothing about how to cross-link such analyses into a holistic plan (see Cabeza et al. 2010 for an excellent example). These are, though, small gripes, in the face of the wider benefits of the approaches set out in the book. And these are, frankly, enormous.

Implicit in the use of actual or heuristic optimization is the use of a quantity to optimize - i.e. what it is *exactly* that we as conservation biologists are actually trying to do? If this process, the mathematical formulation of a goal in a programmatically tractable form, can become the *de facto* first step in any conservation process, then a number of things would begin to happen.

First, and most obviously, individual conservation decisions can take advantage of the techniques (as described in the book) to make the best use of resources whilst being assured that they are achieving their goals. If a particular outcome can be had with less land, less money, shorter borders or less antagonism, not only does that particular project work better, but more opportuni-

ties for action become viable. Furthermore, the case for public, governmental or private support is put on a better footing as the amount of guesswork and number of rules of thumb is reduced, and the business case improves.

Second, the arguments within the conservation community about alternative strategies, diversity metrics, prioritization schemes and all the other baggage in which action gets bogged down, become themselves more tractable. We can ask how different in practice the solutions are when a particular conservation decision is optimized for one group of organisms over another, or one measure of diversity over another. We can also determine how much it will actually cost to reconcile different priorities. I recently heard the head of science policy at a major NGO say that he saw the organization's business as being the preservation of species and not interspecific diversity. My concern is not with the decision itself, but that it is made without data: a choice amongst species necessarily produces some value of diversity. In fact, conservation action with one goal will achieve some performance against all goals, so why make a choice about how to conserve before knowing that you have to? And conversely, what is the cost of our preconceptions if different goals have very different solutions? Involving optimality gives us at the very least a more nuanced view of the decision process, and a quantitative basis for our opinions. In an increasingly data-rich world, if we're going to make decisions, they may as well be wise ones.

Perhaps most importantly, by doing conservation through optimality we would be doing it in the same language as (for want of a better term) our opponents. An open, transparent system with an explicit goal for conservation allows the integration of conservation goals into the same optimality frameworks businesses use to decide their activities and governments use to apportion resource use. The fear of compromise in many conservation strategies is paralytic: genuine conflict for habitat is clearly widespread and where it exists the conservation battles need to be fought as strongly as possible, but some conflict is clearly illusory. Each case where human activities and

conservation success can coexist is vitally important for involving biodiversity preservation in wider society, where too often the conservation argument is seen as anti-business, anti-wealth and anti-development. But without integration under a systematic framework such situations cannot be seen beforehand, and every fight is entered into blind.

The problem, of course, with setting an explicit quantitative public criterion for conservation success is that conservation failure becomes public and easy to measure. Once committed to, conservation schemes quickly become inviolate, and do in proportion to their profile and worth. This is a wider issue for the conservation community to deal with, but incorporating spatial and wider systematic planning concepts into high profile schemes at the beginning, and using the scientific review process for its intended purpose would mitigate the problem.

For me, then, the single most important thing in this book isn't actually written down in it anywhere. It's an excellent summary of the state of the art and should make spatial prioritization a standard part of any conservationist's training. But by doing so, it might shift the baseline for all conservation decisions firmly into the quantitative, and into the rational. And that would be good for all of us.

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thesis abstract

Potential impacts of climate change on the distribution of freshwater fishes in French streams and uncertainty of projections

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Climate change and its impact on biodiversity are receiving increasing attention from scientists and people managing natural ecosystems. Recent modifications of climate have induced diverse functional (e.g. phenology, physiology) and structural (e.g. species distribution shifts, range contraction, local extinctions) responses among organisms (Walther et al. 2002). Given the projections of future climate change, these responses are expected to continue throughout the 21st century and climate change could thus have major consequences on species and assemblages. A common approach to project the potential impacts of environmental changes on the distribution of biodiversity is the use of species distribution models (SDM) (e.g. Thuiller 2003). These correlative models first relate the present-day species distribution to a set of climate and other environmental descriptors. Then, the application of scenarios of future climate changes provides predictions of the habitats potentially suitable in the future for the species. In spite of their widespread use, a growing concern has emerged for the variability in the predicted impacts by such models due to the methodological decisions taken during the modeling process (Thuiller 2004). Improvements in the accuracy of predictions combined with an estimation of the uncertainty inherent to those predictions are thus urgently needed.

Among freshwater ecosystems, stream fish have no physiological ability to regulate their body temperature and could therefore be very sensitive to climate warming, especially cold-stenotherm fish such as salmonid species. Stream fish also have to cope with hydrological variability of streams and strong anthropogenic pressures (e.g. habitat loss, stream fragmentation). In addition,

they have limited dispersal ability within hydrographic networks in which they currently live. Yet their response to current and future climate change has been poorly documented and few studies have used SDM to assess the potential consequences of the on-going climate change on freshwater fish species distribution, especially in European streams.

In that context, the aim of my PhD thesis was to assess the potential impacts of climate change on fish in French streams, mainly on species distribution and assemblages' structure. I used fish data provided by the Office National de l'Eau et des Milieux Aquatiques (ONEMA), the institution in charge of the protection and conservation of freshwater ecosystems in France. These data were combined with climate and environmental descriptors through the use of correlative statistical modeling. As my goal was to provide reliable estimates of the future impacts of climate change on stream fish, I have considered recent criticisms (e.g. choice of statistical method, pure bioclimatic models) of species distribution models by justifying each step and optimizing the use of such models. In all, five papers are derived from my PhD work. The first three papers set the bases for the building of the models by considering the uncertainty in predictions, while the latest two assess the impacts of climate change on stream fish species and assemblages.

In stream fish ecology, many studies have been conducted to identify the environmental drivers structuring fish assemblages (reviewed in Matthews 1998). It appears that fish species distribution and structure of fish assemblages are determined by a complex interplay of biotic, abiotic and spatial factors (Jackson et al. 2001). Disentan-

gling the relative effect of climate versus the one of non-climatic factors (i.e. habitat, topography) on the distribution of fish species was thus of the utmost importance before assessing the potential consequences of changing climate. This issue was addressed in a first study (Buisson et al. 2008a) in which we modeled the spatial distribution of 28 fish species within a river network (the Adour-Garonne watershed) according to a set of climatic and non-climatic factors. Applying both statistical approaches (hierarchical partitioning and generalized additive models), we found that a combination of both thermal variables (mean temperature) and variables describing the local habitat and the position within the river network (upstream-downstream gradient) was important to explain the current distribution of fish species. This result showed that distribution models for stream fish species should combine both climate and other environmental descriptors and not be restricted to the climate envelope, especially at the regional scale (Pearson and Dawson 2003). We also found that the predictive performances of the GAM were high (on average, AUC = 0.85) indicating that the studied climate and physical factors were relevant to predict fish species distribution. However, fish species responded differently to the environmental factors highlighting the need of a species-specific modeling approach to predict species responses to environmental changes.

During the last few decades, a large number of statistical methods modeling species distributions have been developed. Recent studies have highlighted that the predictive performance and predictions of species distributions vary depending upon the method implemented. The emerging recommendation is to combine the outputs of several statistical methods in an ensemble modeling framework and to explore the range of resulting predictions with consensus approaches (Araujo and New 2007; Marmion et al. 2009). It has also been emphasized that species' ecological characteristics may influence the outputs of SDM (McPherson and Jetz 2007), but no studies have addressed the potential relationship between species ecological attributes and the results of ensemble modeling and consensus approaches.

We explored the usefulness of ensemble modeling approaches and tested whether the outputs of consensus models were influenced by the range of species along four environmental gradients (Grenouillet et al. 2009). Eight single statistical methods were computed to predict the current distribution of 35 stream fish species in France and then, we combined the whole predictions ensemble using the average value. Overall, we found that the predictions from single statistical methods were roughly consistent (proportion of consensus between 69.7 and 94.1% depending on species) with the exception of predictions at the edge of the recorded species distributions. However, single methods had consistently lower predictive performances than the average model, which was in accordance with some other recent studies (e.g. Marmion et al. 2009). The improvements in the accuracy of single methods by the average model were higher for species with smaller ranges along the four environmental gradients. In addition, more consensual and accurate predictions of current distribution were achieved for species with small thermal or elevation ranges validating the common hypothesis that specialist species yield models with higher accuracy than generalist ones (e.g. Luoto et al. 2005). Thus, these results strengthen the usefulness of ensemble modeling and consensus approaches and caution against the use of single modeling techniques, especially for species with large environmental ranges.

In the study described above, it has been confirmed that the statistical method may greatly influence the predictive performances and the predictions of the current distribution of species. Other studies have shown predictions to be sensitive to other methodological decisions such as model parameterization, model selection or data characteristics as well (Heikkinen et al. 2006). When projecting the potential distribution of species under future climate change, additional sources of variability arise with the use of climate change scenarios projected by a variety of General Circulation Models (GCM). Measuring the uncertainty in the projections of future distribution and quantifying the relative contribution of different

uncertainty factors thus appear to be crucial issues to enhance the confidence placed in those projections.

In Buisson et al. (2009), we focused on the variability in future projections of climate change impacts on stream fish species and assemblages arising from four uncertainty factors: initial dataset, statistical method, GCM and greenhouse gas emission scenario. Several modalities of these four uncertainty sources were combined in an ensemble forecasting framework resulting in 8400 different projections. We found that the projected future impacts of climate change on fish species and assemblages were highly variable. The choice of the statistical method was the main source of uncertainty, resulting in more variability in projections than the GCM and emission scenarios, especially for short-term projections, and thus corroborating the results of recent studies (e.g. Thuiller 2004). Moreover, the variability in projections was spatially structured, indicating that the projected impacts of climate change in some particular geographical areas should be considered with great caution. Like in Grenouillet et al. (2009), these results emphasize that combining the outputs from several sources of uncertainty, especially different statistical methods, in ensemble approaches would help to enhance the reliability of projected future impacts. This would allow management and conservation decisions to be taken with awareness of the inherent uncertainty in projections.

Based on the results of the aforementioned studies, we lastly estimated the potential impacts of future climate change on fish species in French streams. The potential consequences of climate change were projected to the end of the 21st century at the levels of fish species distribution (Buisson et al. 2008b) and fish assemblages' diversity, composition and similarity by overlapping individual predictions obtained from multiple species distribution models (Ferrier and Guisan 2006: 'predict first, assemble later' strategy) (Buisson and Grenouillet 2009).

We found that most fish species occurring in French streams could be sensitive to future climate modifications. Only a few cold-water species

(i.e. brown trout, bullhead) could experience a strong reduction in the number of suitable sites, and thus restrict their distribution to the most upstream sections of river networks. For instance, the brown trout could reduce its range by 75.9%. In contrast, many cool- and warm-water fish species (e.g. barbel, European chub) could colonize newly suitable habitats and expand their range by migrating to sites located in most upstream sections of watersheds. These results were consistent with those obtained in previous studies conducted mainly in North America, which predicted a decrease in salmonids distribution but more contrasted responses for cool- and warm-water species (e.g. Mohseni et al. 2003). We also found that the projected changes in individual species distributions could lead to reshuffling of fish assemblages (i.e. change in assemblages' composition) both at the taxonomic and functional levels. For instance, at least half of the current pool of fish species could be changed in about two-thirds of the studied assemblages. The local fish species richness and trait diversity could increase (e.g. on average + 9.2 species per site in 2080) in parallel with a global fish species and trait homogenization (e.g. increase in similarity index from 0.25 to 0.51). All of those projected impacts could be remarkably different depending on the assemblages' location in France and on the position along the upstream-downstream gradient. Upstream assemblages could be more sensitive to the forecasted climate change than downstream assemblages. Most of our results corroborate the trends that have recently been observed in freshwater fish and other taxa in response to the recent climate modifications: increase in species richness (e.g. Daufresne and Boët 2007), assemblages becoming dominated by southern species having warm-temperature requirements (e.g. Daufresne et al. 2004) and biotic homogenization (e.g. Jurasinski and Kreyling 2007). Therefore, these findings indicate that the changes in the structure of fish assemblages which have already been observed would continue and could even become more pronounced with the forthcoming climate change.

However, in spite of the numerous methodological issues considered in this PhD work to project the most reliable estimates of those impacts, they may only be viewed as potential impacts. Indeed, many factors could hinder those projections to occur (Pearson and Dawson 2003) such as the natural and physical barriers to displacements (e.g. fragmentation), the limited dispersal ability of species, the interactions between species or the physiological and behavioural adjustments (e.g. phenological changes) in response to climate modifications instead of shifts in species distribution. Therefore, future research is needed to refine the projected impacts of climate change on stream fish presented here in order to provide more realistic projections to aquatic biodiversity managers.

In conclusion, my PhD thesis brings new insights for the understanding of stream fish species distribution in France and expected consequences of climate change. Overall, fish could be affected by climate modifications both at the species and assemblages levels. More fish species could expand their range than reduce it, but this finding does not mean that climate change will not have deleterious effects on fish assemblages and aquatic ecosystems functioning. This work thus provides biodiversity managers and conservationists with a basis to take efficient preservation measures, but it also raises interesting issues concerning the choice of biodiversity metrics (e.g. local vs. global diversity) and actions to prioritize (e.g. conservation of the most vulnerable species). In addition, methodological developments considered in this PhD are an important contribution to the improvements of projections by statistical models of species distribution through the use of ensemble forecasting and consensus approaches. They also allow a better understanding of the inherent uncertainty and stress the need for providing projected impacts of climate change in combination with an assessment of their uncertainty to increase the relevance of those forecasts.

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thesis abstract

Understanding the evolutionary radiation of the mega-diverse Monkey Beetle fauna (Scarabaeidae: Hopliini) of South Africa

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South Africa is the global centre of diversification for monkey beetles (Scarabaeidae: Hopliini). 69 % of the world fauna occur here, with 98% of the 1040 South African species and 80% of the South African genera being national endemics. This thesis was the first analysis of the regional distribution patterns, and the processes underlying the generation of the mega-diverse monkey beetle fauna of South Africa. Specifically, the aims of the thesis were to:

1. Identify hotspots of richness and endemism, and to explore the relationship between area and richness.
2. Compare centres of endemism of monkey beetles with those of other faunal and floral taxa, and to investigate patterns of biogeographic congruence.
3. Explore the role of local environmental factors (rainfall, temperature, habitat heterogeneity, host plant diversity) as explanatory variables of regional richness patterns of monkey beetles.

4. Model spatial turnover (beta diversity) in beetle community composition as a function of environmental (rainfall, temperature, altitude, soil fertility) and plant (host species, vegetation types, and bioregions) variables.
5. Describe and quantify patterns of sexual dimorphism and putative sexually selected traits and investigate the role of sexual selection in the generation of species richness.

Methodological procedures followed current and newly-developed analytical techniques used in the fields of biogeography, spatial ecology, and evolutionary biology. A key first methodological step was the compilation of a geo-referenced presence-only dataset from field observations, museum collections, and taxonomic revisions. This comprised 6959 unique point locality records which were analysed within a geographical information system (GIS). This allowed portraying of the spatial variation in richness and endemism across local and regional habitats.

Within South Africa, and particularly within the global hotspots of the Cape Floristic Region and Succulent Karoo, biogeographic congruence of patterns of richness and diversification across faunal and floral groups has not yet been investigated. This was the first study to use modern analytical methods to delimit centres of endemism and diversification (areas of historical biogeographic significance) of a South African insect taxon. Monkey beetle centres of endemism were delimited using an Integrated Weighting technique (a technique which sought consensus from different weighting and clustering algorithms) (Linder 2001, Bradshaw 2009), in conjunction with GIS interrogation, and then spatially matched to other faunal (Carcasson 1964, Endrödy-Younga 1978) and floral biogeographic (van Wyk and Smith 2001, Goldblatt and Manning 2002, Born et al. 2007) centres to search for congruence.

Shifting focus away from historical biogeographic perspectives and towards contemporary ecological variables, localised regression techniques (geographically weighted regression; Fotheringham et al. 2002) were used to relate regional beetle richness patterns to smaller scale environmental explanatory variables (rainfall, temperature, habitat heterogeneity, host plant diversity). Furthermore, generalised dissimilarity models (Ferrier et al. 2007) were used more specifically to explore species compositional dissimilarity (beta diversity) as a function of environmental (rainfall, temperature, altitude, soil fertility) and plant (host species diversity, vegetation habitat categories) variables, at regional (quarter degree grid cells; presence-only data) and field site (presence/absence data from winter-rainfall field survey sites) scales.

Finally, an additional shift in focus was made, away from ecological perspectives, exploring the potential role of sexual selection in influencing rates of speciation of monkey beetles (Ritchie 2007). Leg and colour sexual dimorphism was measured across two beetle feeding guilds: Embedders (relatively sessile beetles feeding embedded in the capitulum of disk-shaped flowers) and Non-embedders (highly mobile beetles feeding on a wider range of flower shapes). In addition,

the proportions of sexually dimorphic species (as based on a point scoring system) were calculated for each genus and related to its species richness.

Key results from this thesis highlighted the exceptional levels of richness and endemism of South African monkey beetles and the importance of the region as a primary centre of diversification for these pollinators. More specifically, hotspots of richness and endemism for South African monkey beetles were concentrated within the winter-rainfall biomes (Fynbos and Succulent Karoo). Based on slope and intercept values from species-area curves (Rosenzweig 1995), the winter-rainfall biomes accumulated species significantly faster per unit area, and showed higher richness per unit habitat area than summer-rainfall biomes, arguing for their evolutionary importance as centres of adaptive radiation. For these biomes, the exceptional diversity of monkey beetles was matched by congruent patterns of insect diversity across a range of disparate taxonomic groups, highlighting the importance of this region as a centre of adaptive radiation (Hesse 1969, Gess 1992, Whitehead and Steiner 2001, Kuhlmann 2005, Barraclough 2006). Furthermore, the patterns of endemism of the beetles showed concordance with phytogeographical centres, suggesting possible co-evolutionary histories between plants and insects, particularly since many of the species-rich insect groups are closely associated with plants and flowers. This congruent pattern was also suggestive of parallel responses of fauna and flora to historical climatic and geological events (Stuckenberg 1998).

Retrieval of a number of well-defined centres of endemism within the winter-rainfall regions allowed historical biogeographic insights into this biodiversity hotspot. In broad congruence with previously delimited zoogeographic zones, such as those delimited intuitively by early historical biogeographers for butterflies (Carcasson 1964) and beetles (Endrödy-Younga 1978), monkey beetle distribution patterns were divided into distinct western and eastern zones, as shown from the primary split of a hierarchical cluster analysis (using presence data of genera) into two

distinct clusters at the > 5% similarity (i.e. 95% dissimilarity) level. The western zone showed high monkey beetle species richness, endemism and concentrations of lineage diversifications, conforming to a pattern described for several other insect groups (Tjeder 1967, Mansell 1985, Kuhlmann 2005). Furthermore, the large number of range-restricted beetle taxa and local endemics highlights the uniqueness of the winter-rainfall region and reinforces the suggestion of the existence of a distinct Cape Faunal Zone (Endrödy-Younga 1978, Picker and Samways 1996). Of the eighteen centres of endemism that were delimited across South Africa, the largest were located in the winter-rainfall, western regions, and showed the highest levels of endemism and species richness, with species richness strongly correlated with endemism, thus further supporting this region as a centre of diversification. Across this western region, the fairly good spatial congruence with plant and other insect biogeographic centres highlights the presence of possible shared centres of diversification across taxonomic groups. In contrast, the eastern, predominantly summer-rainfall region showed lower richness values, and fewer endemic species. The eastern zone retrieved for monkey beetles was seen to be less zoogeographically distinct compared to the western zone, sharing Afrotropical elements with southern and central African regions (Lawrence 1952). Key historical processes associated with the two distinctive biogeographic patterns were inferred to comprise geographical fragmentation of populations as a result of palaeoclimatic change and geomorphic evolution (Cowling and Proches 2005, Cowling et al. 2009). Such factors are postulated to promote allopatric speciation through vicariant events and vicariant speciation in the Cape Mountain system has been proposed for various insect and invertebrate taxa (Endrödy-Younga 1988, Wishart and Day 2002, Prendini 2005). Studies have estimated that palaeoclimatic change has isolated various montane insect populations within the Fynbos Biome for at least 4 million years (Wishart and Day 2002). The role of historical processes and their relation to high levels of cladogenesis and endemism as observed in the Fynbos and Succulent Ka-

roo biomes would need to be considered in order to fully explain monkey beetle diversity and distribution patterns. The need for phylogenetic data was highlighted in this study, as this would allow a deeper understanding of the evolution of the monkey beetle fauna and provide a means of testing the hypotheses for the observed patterns of cladogenesis and endemism. Furthermore, the possibility of dating lineage diversifications would allow cladogenetic events to be related to the geological and climatic evolutionary history of the winter vs. summer-rainfall regions of South Africa. Results from macroecological analyses of beetle distributional and richness data showed host plant richness is generally an important predictor of regional beetle richness; however, the predictive power of explanatory variables (host plant diversity, rainfall, temperature, habitat heterogeneity) varied geographically (strong spatial non-stationarity), and was fundamentally different between areas classed as winter, summer, and non-seasonal-rainfall. The spatial variation of environmental and plant variables as predictors of beetle richness highlighted the necessity of using modelling techniques that can relate regional richness patterns with smaller scale variations in host plant diversity, rainfall, temperature and habitat heterogeneity (see also Foody 2004).

Spatial turnover (beta diversity) at field site and regional scales was strongly correlated with environmental and plant variables, with environment being the stronger predictor. Plant variables recorded contrasting results, with variables associated with habitat heterogeneity of vegetation types being of greater importance, whereas turnover of plant species was seen to be a weak predictor. Plant species were less important because most monkey beetles are generalist feeders and thus do not perceive landscape heterogeneity at the level of plant species occurrence. In contrast, habitat heterogeneity (steep edaphic factors and floristic gradients) provided habitats for a wider range of feeding guilds, and therefore was associated with increased turnover. Interestingly, geographic distance between site pairs explained minimal amounts of species turnover at both data scales (< 1%). Complete species turnover (100%

compositional dissimilarity of beetle communities) was recorded within very short distances, and beyond this asymptote increasing geographical distance had no effect on turnover. This finding was explained by the steep ecological and environmental gradients, combined with poor dispersal abilities (through habitat fidelity) of some monkey beetles. Steep environmental gradients in rainfall seasonality, concentration and annual rainfall, as well as altitude, were all important factors in explaining turnover. These factors reflect extensive ecological gradients (niche width and diversity), which promote species turnover, either through habitat specialisation or divergence as a result of limited gene flow (Latimer et al. 2005). Overall, the findings associated with turnover patterns for monkey beetles were in contrast with patterns seen in other Mediterranean and arid systems (e.g. Potts et al. 2003), and are probably related to the unusually steep environmental gradients associated with South Africa's Mediterranean regions. Furthermore, interesting contrasts with other biodiversity hotspots, such as tropical rainforests (see Novotny et al. 2007), were noted in that high alpha diversity was matched by high beta diversity indicating that locally co-existing beetle species do not represent a large proportion of the regional species pool.

The study also showed that the processes explaining richness in beetles are not necessarily the same as those for plants, even when plant and beetle taxa are closely linked, through, for example, pollination. Moreover, cladogenesis in monkey beetles may be independent and separate from processes driving diversification in individual host plants, because their generalist feeding habits and vagility allow them to perceive the landscape not at a plant species level but at a coarser grain, such as vegetation types.

Despite the increased power of geographically weighted models over models that assume static relationships between richness and explanatory variables across the whole region, the ecological models developed here did not fully account for variation in species diversity. A key finding was that sexual selection may be an important driver of diversification and speciation in monkey

beetles, highlighting the need to look beyond ecological determinants of richness patterns. The prevalence of pronounced sexual dimorphism suggests that strong sexual selection pressures may be an important driving force of speciation, and thus, an additional explanatory factor in species diversity. Sexual selection was shown to be an important variable explaining clade richness and diversification. Striking and highly divergent secondary sexual traits (hind leg and colour) were features of a high percentage of species (64.3% were sexually hind leg dimorphic, 84.9% sexually colour dimorphic). Dimorphism patterns were strongly linked to feeding guild (Embedders and Non-embedders) and mating system (aggressive male-male combat with prolonged mate guarding in the former vs. non-aggressive combat, with limited mate guarding in the latter). Leg dimorphism was almost exclusively associated with Embedders: the evidence of clear sexual hind leg dimorphism, plus positive allometry of hind leg traits suggests that the hind legs of Embedder species are under strong sexual selection forces. In contrast, colour dimorphism occurred in equally high frequencies across both guilds. Contrasting patterns were seen when relating number of species found within a genus and the proportion of sexually dimorphic species. The proportion of leg dimorphic species within a genus was not related to its species richness. A significant positive relationship was, however, seen between the proportion of colour dimorphic species within a genus and its species richness, with speciose genera showing a myriad of striking colour dimorphic patterns. Thus, the prevalence of sexual dimorphism in monkey beetles suggests that strong sexual selection pressures may be an important driving force of speciation and diversifications.

Tapping the wealth of insect data awaiting collation from natural history collections would greatly improve the understanding of zoogeographic patterns and faunal zones in South Africa. Moreover, the use of insect data in conservation planning has been hampered by a lack of available data, but the results of this study suggest that obtaining such data is of high priority; firstly because monkey beetle richness and levels of en-

endemism were exceptionally high, and secondly because processes relating to the evolution and maintenance of plant and insect richness and turnover patterns can differ, even for insects dependent on plants. Thus, conservation planning needs to be more inclusive in its use of such data.

There is currently little knowledge of the physiological requirements of adult monkey beetles, and even less about their larvae, which may have entirely different ecological requirements because of the contrast in feeding habits between the two stages of the life cycle (pollen feeder vs. detritivore, respectively) and mobility. These requirements, together with ecophysiological parameters of adults (e.g. temperate montane vs. arid-adapted species) could be used profitably to further investigate fine scale distributions within the monkey beetles.

Finally, the role of sexual selection may hold the key to explain elevated levels of speciation, unrelated to host plant diversity. Phylogenetic data being assimilated at present will allow a deeper understanding of the evolution of the group and provide a means of testing the hypothesis that sexual selection has promoted rates of speciation by allowing accurate sister taxa comparisons.

Papers in preparation

Five manuscripts are currently in preparation from the thesis; one manuscript for each of the chapters/key aims of the thesis. Additional analyses undertaken subsequent to the completion of this thesis explore compositional dissimilarities in beetle communities, with plant compositional dissimilarities having also now been modelled, using the same environmental variables used in the beetle model, and using beetle turnover as an explanatory variable. This was done to contrast the varying degrees of influence that dissimilarity in pollinator communities have on host plant communities, and the influence that dissimilarities of host plant communities have on beetle species composition.

Availability of thesis

A print copy of the thesis is available from the University of Cape Town library (www.lib.uct.ac.za); or a PDF copy is available at request from the author.

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New Book: Systematics, Evolution & Biogeography of Compositae

V. A. Funk., A. Susanna, T. Stuessy & R. Bayer (eds)

The Compositae are the largest family of flowering plants with ca. 25,000 species. Until recently the classification has remained largely unchanged since the 1800's. This volume is based on the latest phylogeny for the family and each clade is examined by the experts (morphological & molecular). Nearly every group is based on a color coded biogeographic tree and the concluding chapter shows the movement of the extant members around the globe. The book has 44 chapters, 80 authors, 1000 pages (200 in color) and is available for \$110 at compositaebook@gmail.com. All proceeds go to the International Association for Plant Taxonomy (<http://www.botanik.univie.ac.at/iapt/>).



Trans-realm biogeography: an immergent inter-face¹

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Introduction

In his influential paper on geographic speciation in sea urchins and jellyfishes, Ernst Mayr (1954:16) concluded that “marine animals agree in [their] pattern of variation and distribution completely with terrestrial animals.” Yet the sentiment that “it is useless to think of [the sea] as we think of the terrestrial world” (Hardy 1962), i.e. that marine and terrestrial realms are fundamentally different, has remained commonplace (e.g. Smetacek and Pollehne 1986, Secord 2003). The persistence of this bipolar abstraction of the natural world is troubling. Aquatic, atmospheric, and terrestrial systems can be tightly coupled such that an almost Gaian perspective is needed to meet the challenges of climate change (Menge et al. 2009) yet perceived irrelevance of research from different realms maintains the barriers to multi-disciplinary understanding that slow scientific progress.

Background

The perception of a vital difference between marine and terrestrial environments, which echoes terrestrial human bias (Smetacek and Pollehne 1986, Hamner 1988, Dawson and Hamner 2008) and ancient Greek natural philosophy, has been propagated in part by the balkanization of 20th century scientific infrastructure (Steele 1995, Sarkar 2005, Stergiou and Browman 2005).

Heaney and Lomolino (2009:1-2), for example, noted during their editorial in the first issue of this magazine that “marine and terrestrial biogeography [have been] discussed in different journals using different terminology”. This lack of meme flow afflicts many relevant disciplines. Menge et al. (2009) bemoaned the lack of cross-referencing between papers in ecological journals serving primarily marine or primarily terrestrial audiences. In journals that do cater to both audiences, such as *Journal of Biogeography*, papers are generally either marine or terrestrial, and rarely link realms². When marine and terrestrial systems have been discussed together, the environments often are contrasted as having “fundamental differences” (e.g. Steele 1985, Smetacek and Pollehne 1986, Hamner 1988, Thomson and Gilligan 2002, Carr et al. 2003, Lourie and Vincent 2004, Halley 2005). Such a radical position, which implies at least two kinds of ecology, two kinds of evolution, etcetera, is not supported by any empirical study nor enshrined in any biological theory. Dawson and Hamner (2008) thus proposed that conceptual integration of marine and terrestrial natural history was awaiting only development of a compelling quantitative comparative framework.

A suitable quantitative comparative framework might be provided by expanding Aleyev's (1977:1) “biohydrodynamic conception of life” in which fluid mechanics provides a suite of tools for comparing the aerial and aqueous fluid environ-

1. ‘*Immergent*’, a play on ideas, is defined in the Oxford English Dictionary as either “Not merging into something else” or “Erroneous spelling of ‘*emergent*’, in sense ‘Unexpectedly arising’, ‘urgent’.”

2. A search of Thompson's Web of Science on 15 November 2009 was conducted for articles containing the topic words ‘marine’, ‘terrestrial’, or ‘marine and terrestrial’ published in the *Journal of Biogeography*. All titles, and the abstract of papers with ambiguous titles, were read before final categorization. Articles categorized as ‘marine’ ($n \approx 119$) or ‘terrestrial’ ($n \approx 139$) outnumbered those that discussed ‘marine and terrestrial’ ($n \approx 4$) issues; a total of 2842 records for the *Journal of Biogeography* were recovered, of which 2558 referred to neither “marine” nor “terrestrial” in the fields included in the topic search.

ments of organisms, whether they fly or float or swim, are rooted in the soil, emerge from sediment, or attach to rock (Dawson and Hamner 2008). This biohydrodynamic approach could be used, for example, to estimate, from basic physical principles, whether propagules might 'drift' as far in the sea or atmosphere depending on their size, shape, and density relative to the surrounding fluid or be able to realize philopatry (Dawson and Hamner 2008). Another quantitative comparative framework might contextualize population dynamics and therefore demographic evolutionary processes in terms of the colors (i.e. frequency spectra) and magnitudes of temporal variation in the respective environments (Vasseur and Yodzis 2004). For example, the rates and extents of change in environmental conditions might be used to standardize comparisons of the wax and wane of populations, responses to climate change, or the duration, net diversification interval, and time for speciation of marine and terrestrial species (Coyne and Orr 2004, Table 12.1) and would compliment the more common geospatial focus on the impact of habitat variation in limiting species' ranges.

Dawson and Hamner (2008) suggested these frameworks could be applied, to improve on the existing tendency to intuit the importance of biological differences by qualitatively contrasting organisms in dissimilar physical contexts, in two ways:

1. by quantifying physically dissimilar settings (e.g. marine pelagic with marine coastal benthic) and the respective biological differences in marine and terrestrial realms to establish statistical correlations, and/or
2. to compare marine and terrestrial organisms in environmental settings that were quantitatively similar (e.g. aerial vs. marine plankton with similar Reynolds number, or organisms inhabiting terrestrial vs. marine islands; see also Dawson et al. 2009).

These macro-ecological approaches are yet to be explored empirically. Instead, here, I apply the tradition of thought experiments, testing these

proposals using five papers³ that were unavailable to Dawson and Hamner (2008).

Recent case studies

Latitudinal gradients in diversity (Roy and Goldberg 2007)

In a cogent argument for integrating biogeographic and macro-evolutionary processes when studying latitudinal gradients, Roy and Goldberg (2007) emphasized the potential for dispersal, rather than origination and extinction, to drive patterns of diversity and differences in the mean age of biotas. The potential influence of dispersal, an evolutionary mechanism that has captivated marine biologists for much of the last 30 years (Riddle et al. 2008), led Roy and Goldberg (2007) to pose the question, "are marine and terrestrial diversity gradients driven by different processes?"

Their preliminary answer, based on comparison of avian taxa and marine mollusks which are two of the best studied taxa in their respective environments, was that "the nature of macro-evolutionary and biogeographic processes may differ between terrestrial and marine diversity gradients" (Roy and Goldberg, 2007:S71). For birds, which diversified less rapidly and are on average younger taxa in extratropical latitudes than in the tropics, the primary processes establishing the latitudinal gradient were inferred to be either [1] higher extinction in extratropical regions or [2] time-inhomogenous processes, such as selective extinctions and dispersal of taxa into the extratropics. Both inferences differed from that for marine molluscs: preferential origination in the tropics followed by expansion of geographic ranges into high latitude macroevolutionary sinks. The difference was posited to result from Pleistocene glacial cycles that resulted in "total habitat destruction" and extinction of species restricted to those areas on land but manifested largely as temperature and circulation changes in the ocean that are not strongly linked with global extinction of marine species.

Roy and Goldberg (2007) briefly contrasted terrestrial and marine systems in two additional

3. Publications were located using the Web of Science keyword search "marine AND terrestrial AND freshwater" limited to publications from 2006 to 2009 with additional papers drawn from the citation lists therein.

ways. First, they contrasted the colours of variation, noting that variation in the terrestrial environment is typically 'white' (i.e. random) whereas variation in the marine environment is typically reddened (i.e. auto-correlated). Consequently, for example, population level responses to marine environmental change should include boom-bust cycles of greater magnitude more often resulting in extirpation. Second, they emphasized that "long-distance larval dispersal and recolonization dynamics", considered a key determinant of ecological and biogeographic patterns by marine ecologists, has "virtually no analogue in terrestrial animal ecology". They concluded these "difference[s] in the nature of the [terrestrial and marine] habitats" may explain the "difference between marine and terrestrial groups in the timing, magnitude, and nature of putative extinctions" (Roy and Goldberg 2007:S81) and, therefore, the subsequent sources - origination and/or dispersal - of the modern biotas.

These additional comparisons provide a simple segue to Dawson and Hamner (2008). We showed that although the predominant colours of variation do differ between realms, there is more overlap than generally acknowledged. For example, coastal terrestrial environments are reddened by virtue of their proximity to the sea (Vasseur and Yodzis 2004), and on long time-scales the ocean-atmosphere circulation is tightly coupled (Steele 1995). Similarly, we argued, drawing heavily on data presented by Kinlan and Gaines (2003), that although marine taxa may on average disperse farther than terrestrial taxa, there also are short-dispersing marine taxa and far-dispersing terrestrial taxa; soil-dwelling aerially-dispersed microbes are an example of the latter. Furthermore, from the standpoint of our 'thought experiment', Roy and Goldberg (2007) make three notable caveats. First, Roy and Goldberg (2007) excluded shallow sea basins before stating that marine systems experienced only changes in temperature and circulation with glacial cycles. Yet, like high-latitude intertidal zones scoured by glaciers, the shallow sea basins, continental shelves, and other subtidal areas currently immersed by less than ca. 120 m of ocean, were once inter-

glacial marine habitat that was totally destroyed during Pleistocene glacial periods. In these cases, both the magnitude and frequency of environmental variation were comparable between marine and high latitude (or altitude) terrestrial environments. Second, Roy and Goldberg (2007) note that evidence for Pleistocene glacial extinctions of terrestrial groups is indirect due to the lack of a well-preserved fossil record; this would also be the case for shallow-water invertebrates that inhabited the aforementioned 0 m to -120 m depth range and had restricted ranges. Thus, the true level of extirpation also is unknown for these taxa, an issue exacerbated by the prevalence of cryptic species (e.g. Bickford et al. 2007, Oliver et al. 2009) and shorter-than-assumed dispersal in marine environments. Third, Roy and Goldberg (2007) acknowledge that differences in macroevolutionary and biogeographic dynamics of terrestrial birds and marine molluscs are phylogenetically incomplete evidence that such dynamics differ in important ways between the land and the sea.

What might constitute good evidence that macroevolutionary and biogeographic dynamics do (or do not) differ between land and sea? Perhaps, studies of the following? The biotas of [a] areas in each realm whose habitats were completely destroyed or [b] areas in each realm whose habitats were modified. For example, perhaps shallow-water tropical basins and high-altitude tropical regions; the biota's of both likely shifted to greater depths or lower altitudes during glacial advance, and vice versa during glacial retreat, but did not necessarily shift many degrees of latitude or longitude near the equator (e.g. Floeter et al. 2008). Another approach would be to compare [c] taxa from each realm whose life-histories are more similar than birds and molluscs. For example, certain categories of terrestrial plants and marine animals (Palumbi 1992).

Roy and Goldberg (2007:S82) concluded that "[s]olving the problem will require using ... information and analytical methods in a consistent manner across different clades within the framework of quantitative models that include both macroevolutionary and biogeographic processes." Moreover, until such comparisons of ter-

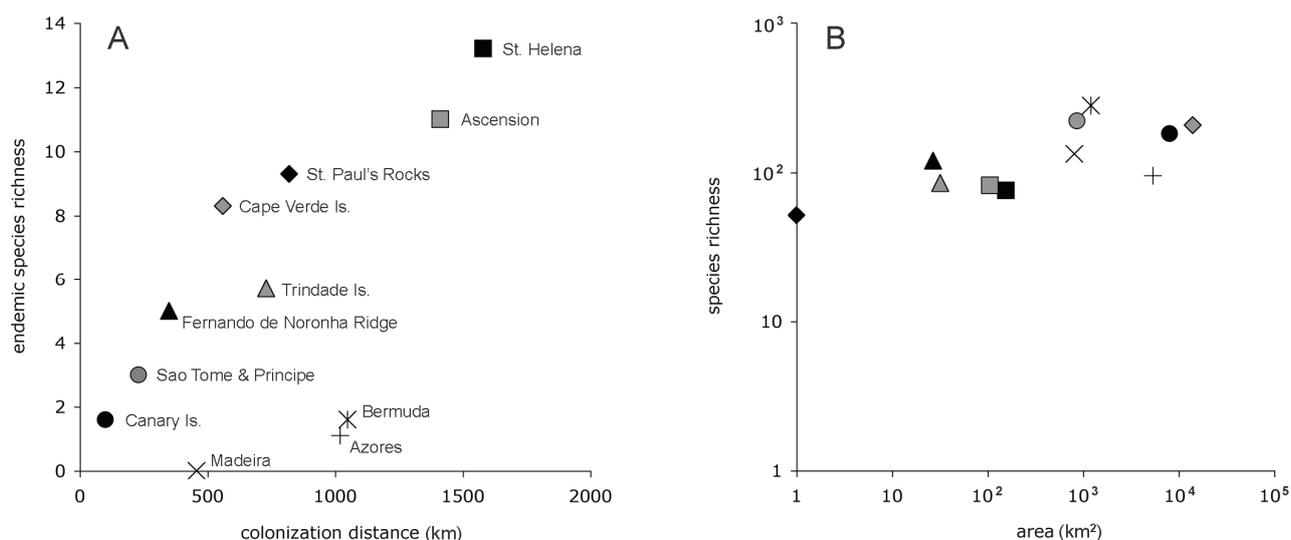


Figure 1. Spatial patterns of species diversity in Atlantic reef fishes inhabiting islands and archipelagoes (data from Floeter et al. 2008, Table 4). **(A)** The number of endemic species plotted against the colonization distance, calculated as the mean distance of an island or archipelago from the nearest mainland and nearest reef habitat. **(B)** The number of species, S , plotted as a function of island or archipelago area, A . $S = 1.755A^{0.1322}$, $R^2 = 0.5167$, $p = 0.013$. Symbols in panel B are as labelled in panel A.

restrial-like with marine-like are done, along with quantifying the biological-environmental differences that may correlate with the impact of different drivers of latitudinal patterns, it is premature to conclude that the nature of macroevolution and biogeographic processes differ between land and sea.

Island evolution (Floeter et al. 2008)

Although many zoogeographic descriptions have reported endemic marine species from oceanic islands (e.g. Randall 1998, Robertson 2001; see also Dawson and Hamner 2005) there has been a long tradition of excluding island theory (e.g. MacArthur and Wilson 1967, Rosenzweig 1995) from marine biogeography and vice versa (see Dawson and Hamner 2008)⁴. The recent phylogenetic analysis of Atlantic fishes by Floeter et al. (2008) provides additional evidence that marine species may evolve on islands and show familiar patterns of increasing endemism in more isolated locations and higher species richness where habitat availability is greater (Fig. 1). The Mid-Atlantic Ridge islands of Ascension and St. Helena, for example,

together harbour 111 reef fish species of which 29 are endemic. Atlantic reef fish species distributions, though, result from the interaction of colonization distances and routes, area (or diversity) of habitat, and island age and history (Floeter et al. 2008). Low endemism on Bermuda, the Canary islands, and other high-latitude islands is inferred to result from Pleistocene glaciation and recent colonization with little time for subsequent speciation (N.B. see discussion of processes influencing bird diversity in Roy and Goldberg [2007]). Intermediate levels of endemism at São Tomé and Príncipe, Fernando de Noronha Ridge and Trindade Island result from close proximity and/or stepping-stone connections to continental margins. High endemism on the Cape Verde islands may be related to isolation from the mainland, high habitat heterogeneity, and maintenance of warm surrounding waters during glacial maxima (Floeter et al. 2008). Exploring the underlying incidence functions may thus enable more explicit quantitative comparison with the adjacent emergent terrestrial habitat.

4. David Starr Jordan, the first President of Stanford University and arguably the father of American Ichthyology, wrote a letter to Robert Evans Snodgrass, before the Hopkins-Stanford Galapagos expedition of 1898-1899 in which he opined that "The archipelago does not appear to offer a good laboratory for researching the impact of isolation, because the barren islands do not harbor many isolated fish pools." Yet 11.7% of the 300 species of reef fishes in the Galapagos are endemic (Allen 2008).

Island ecology (Martins et al. 2008)

With recognition that marine biotas, like terrestrial biotas, of oceanic islands may show endemism, there is growing effort to explore and expand the reach of marine island ecology. Martins et al. (2008) sampled 12 taxa, distributed in the low or middle or high zones of the intertidal rocky shore using an hierarchical sample design in which quadrats were nested within zones, within sites, within islands of the Azorean archipelago. They hypothesized that high dispersal of marine taxa would result in population and community dynamics being influenced more by regional processes than by within-island processes. Indeed, larger-scale (i.e. island-scale) dynamics were evident in the lower-shore (i.e. more marine-influenced) communities, less prevalent in mid-shore communities, and statistically absent from high-shore sites. Martins et al. (2008) concluded that “along the vertical gradient of emersion, there is a trend for a decreasing influence of larger-scale processes with increasing shore height ... [which may be] the result of differences in the dispersal ability between the lower-shore, algal-dominated assemblages ... and the higher-shore, animal-dominated communities” and noted the importance of variance in the immediate environment on population dynamics. These results illustrate two points. [a] In the same way that variation in coastal terrestrial environments is ‘reddened’ by their proximity to the ocean, the reciprocal is also true; variation in marine intertidal environments is ‘whitened’ by their proximity to land. [b] Even over small distances, it is important to quantify variation in both the environment and biota when comparing sea and land. Measurements on the same scale will lead to differences (Gray et al. 2006, Webb et al. 2009) which should be ascribed to the mechanisms directly influencing those differences as opposed to simply ‘marine’ or ‘terrestrial’ categories.

Effects of species diversity on temporal stability (Jiang and Pu 2009)

As an example of the need to ascribe differences to mechanisms rather than to realm, Jiang and Pu

(2009) showed that aquatic (freshwater and marine) communities and populations generally are more temporally stable than their terrestrial counterparts. The greater stability, however, is not attributable to the physical environment – perhaps because the marine studies included small intertidal rockpools (e.g. Romanuk and Kolasa 2004) in which physical variation is whitened by atmospheric influence – but rather to the multitrophic nature of the aquatic communities versus the unithrophic terrestrial communities considered (Jiang and Pu 2009)⁵.

Microbial community assembly (Horner-Devine et al. 2007, Fuhrman 2009)

Analyses of metagenomic data describing the microbial world hint at ‘universal’ biogeographic patterns. There is growing evidence for microbial taxa-area relationships from aquatic and soil samples with ‘z-values’ (which describe the sensitivity of species richness to area [Whittaker and Fernández-Palacios 2006:81]) similar to those measured in macrobiota, and for microbial distance-decay relationships which indicate mechanisms acting with different relative strengths at different depths in the sea (Fuhrman 2009). Both results support our thought experiment. On the other hand, Fuhrman (2009) concludes that the evidence for microbial latitudinal gradients is mixed between land and sea, perhaps due to different scales of spatial environmental heterogeneity or to the small number (three) of available studies. The largest meta-analysis to date, relevant to our question, is a meta-analysis of 124 microbial datasets (Horner-Devine et al. 2007) that found a majority (56%) of studies describe non-random patterns of species occurrences suggesting assembly ‘rules’. These patterns, which may be due to competitive exclusion, filtering by habitats, or geographic speciation, are trans-realm; the measure of species segregation showed a statistically similar standardized effect size across freshwater, marine, soil, and sediment habitats.

5. Jiang & Pu (2009:657) also note that variation may be polychromatic: “natural communities may oscillate synchronously at one timescale and asynchronously at another timescale, likely a result of the operation of different mechanisms at different scales.”

Box 1. Areas in which a trans-realm perspective may advance biogeography

Reciprocal illumination may occur in several ways, of which some possible examples are provided below, including what a marine perspective may lend to global biogeography (1-3), how marine biogeography may benefit from looking more at terrestrial biogeography (4-6), and synergistic effects at their interface (7-10).

1. Dispersal. Studies of dispersal have preoccupied marine biogeographers for 30 years. Coupled biophysical models are now commonly used to explore larval dispersal (e.g. Cowen et al. 2000, 2006, Dawson et al. 2005, Galindo et al. 2006, Follows et al. 2007). A comparable initiative in atmospheric modeling of aerial (or water-borne) propagules is lacking from studies of terrestrial and freshwater taxa.

2. Cryptic speciation. Studying how cryptic species are distributed has a long history in the seas (e.g. Knowlton et al. 1993). Ten percent of metazoan morphospecies contain cryptic species (Pfenniger and Schwenk 2007) and the proportion may be much higher in marine taxa (Dawson 2004, Bickford et al. 2007, Oliver et al. 2009). Circa 55% of California coastal marine taxa have cryptic north-south phylogeographic lineages (Dawson 2001). Discovering how cryptic species are distributed phylogenetically and geographically is essential for understanding biodiversity and evolutionary mechanisms influencing biogeography and requires comprehensive biogeocoding initiatives (Cunningham 2009).

3. Life-histories. Understanding the influence of life-history, and particularly larval mode, on the ability of organisms to disperse has been a major focus of marine molecular ecology (e.g. Crisp 1978, Palumbi 1992, Bohanek 1999). Terrestrial organisms also have diverse life-histories, for example that influence successional community assembly (Whittaker and Fernández-Palacios 2006), and a full understanding of the effect of life-history on dispersal (or retention) and biogeography demands comparison of the full continuum of life-history strategies across diverse physical environments.

4. Natural selection and local adaptation. The focus of marine ecology on dispersal displaced much attention away from natural selection and local adaptation. Rich theory, and a multitude of examples, developed primarily for terrestrial taxa should be applied increasingly in marine settings.

5. Techniques. Analytical techniques emerge primarily from terrestrial studies. Application and development of analyses for marine taxa will promote better mechanistic understanding across a broader suite of environments (e.g. Roy and Goldberg 2007).

6. Island biogeography. The theory of island biogeography, and extensions thereof, have been absent from studies of marine systems for almost 40 years; their reincorporation is overdue.

7. Marine and terrestrial (and freshwater) environments interact at the coast. Many taxa live at, or cross, this margin (e.g. anadromous and catadromous organisms, mangroves, shorebirds). These taxa may tell us about differences and commonalities between freshwater, marine, and terrestrial biogeography.

8. Generation-corrected frequency spectra. Frequency spectra are presented in terms of absolute time (e.g. months, Vasseur and Yodzis 2004), but organisms' life-spans differ dramatically. Demographic and evolutionary effects of environmental variation depend on their duration relative to generation time. Frequency spectra measured in generation times will promote appropriate biophysical comparison of marine and terrestrial systems.

9. Constraints. Comparison of physically similar environments in different realms may reveal vacant niches and evolutionary constraints that influence biogeographic patterns.

10. Trans-realm comparative phylogeography. Statistical and comparative phylogeography (e.g. Knowles 2004, Hickerson et al. 2007) have become mainstays of biogeography, revealing shared biogeographic histories including glacial refugia (Maggs et al. 2008), post-glacial recolonization routes (e.g. Taberlet et al. 1998), cryptic historical filters (Riddle et al. 2000), and elucidating evolutionary mechanisms (Hickerson and Meyer 2008) within realms. Few studies have integrated across realms (but see Riginos 2005), although statistical comparative techniques would similarly enable quantitative comparisons, or contrasts, of biogeographic patterns and mechanisms among clades with shared evolutionary histories where they are co-distributed (e.g. across Pacific islands) or interdigitated (e.g. marine and terrestrial taxa in Beringia). Difficulties of mounting inter-realm biogeographic analyses are substantial, beginning with acquiring the necessary geographically large-scale and densely sampled biotic inventories, particularly from marine habitats. Maritime regions where existing marine and terrestrial phylogeographic and biogeographic studies might easily be enriched include southeast and southwest USA, Baja California, southeast Australia, and the North Atlantic (e.g. Avise 1992, O'Hara and Poore 2000, Wares & Cunningham 2002, Blanchette et al. 2008, Ayre et al. 2009, Pelc et al. 2009).

Prospective

These five studies provide a surprisingly consistent picture of the state of comparative inter-realm biogeography. Studies often make a priori divisions between marine and terrestrial environments (e.g. Horner-Devine et al. 2007, Roy and Goldberg 2007, Jiang and Pu 2009). Oftentimes, the comparisons involve multiple potential sources of variation, only some of which are ascribed to the marine and terrestrial experimental groups (e.g. Roy and Goldberg 2007). Yet, differences between the realms are not supported (e.g. Horner-Devine et al. 2007) or can be explained by trophic, biogeographic, macroevolutionary, or life-history traits that are not necessarily realm-specific (e.g. Roy and Goldberg 2007, Floeter et al. 2008, Jiang and Pu 2009). The results of our thought experiment therefore generally support the contention that “marine and terrestrial biogeography ... have a great deal in common and will provide reciprocal illumination in many respects” (Heaney and Lomolino 2009, see also Dawson and Hamner 2008; Box 1).

To achieve reciprocal illumination, we must break down the boundaries currently separating sub-disciplines of biogeography (Lomolino and Heaney 2004) practised by different people using almost entirely different scientific infrastructure (Steele 1995, Sarkar 2005; see also Stergiou and Browman 2005). When inventing derivative terms such as ‘riverscape’ and ‘seascape’ that superficially equate environments, we might also imagine a truly inclusive vocabulary that is applicable trans-realm. While supporting detailed within-realm studies as chapters in books (e.g. Lomolino and Heaney 2004), articles in journals (see footnote 1), sections in articles (e.g. Riddle et al. 2008), and symposia at conferences (e.g. the 3rd Biennial meeting of the International Biogeography Society), we should increasingly foster cross-realm multi-disciplinary treatments (e.g. Briggs 1995, Lomolino et al. 2006, Dawson and Hamner 2008; Box 1). The degree to which integration of freshwater, marine, and terrestrial biogeography gives way to their assimilation will depend on the extent to which a ‘seagrass roots’ community-up approach can align with a new or re-organized

scientific infrastructure (see Menge et al. 2009). For the first time in over 50 years, we – biogeographers, *Frontiers of Biogeography*, and the International Biogeography Society – may have the potential to cross this major frontier.

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Edited by Chris Burridge and Joaquín Hortal

from the society

A new membership manager for the IBS

As some of you may have already noted due to some recent email activity, I am the new Manager of Membership Services for the International Biogeography Society. My background is in biology, including as a fish and wildlife consultant and an evolution research technician in a University setting; and have always felt that there's never enough cross-over contact between people working in different fields that are essentially trying to understand and conserve the worlds' biota. So I am very excited to be working for IBS.

In my new role with IBS, I am looking forward to making membership services more personable, more accessible, and easier to follow. To that end, I will be working on changing some things in the coming months including making membership renewal clearer, and streamlining access to journal benefits. I appreciate your patience, as many of these things will be works in progress for a while.

If you are not yet a member but are interested in becoming one, either to have access to member benefits such as free online access to Blackwell's biogeography journals (see <http://www.biogeography.org/> for full benefits) or to

become more involved with the world of biogeography, please feel free to contact me with questions or check out the IBS website.

If you believe you are a member but have not heard from me already via email, please check that we have your current email address on file by either logging onto the system yourself through the "Member" tab on www.biogeography.org, or by contacting me at faller@wisc.edu.

If you have any questions, suggestions or concerns about your membership or services provided by IBS, I would love to hear from you. I'm also happy to try and answer any general questions you may have, or direct you to appropriate people within the IBS board.

Keep an eye out for future emails about changes to the system, and about the upcoming meeting in Iraklion, Crete in January 2011. I'm looking forward to working with you!

Karen Faller

Manager of Membership Services

from the society

Nomination of IBS officers

The Nomination Committee is now receiving suggestions for Officers and Members-at-Large for the 2010 election. IBS has four positions to fill: President, VP for Conferences, and two Directors-at-Large.

Please submit your suggestions no later than 15 January 2010 to both José Alexandre Felizola Diniz Filho (jafdinizfilho@gmail.com, diniz@icb.ufg.br) and Ella Vazquez (evazquez@ecologia.unam.mx). For each nomination please supply the name, address, email, and a brief description on why you think this person would be a good candidate for the position.

The Constitution states that the Past President (Vicki Funk) and the two Directors-at-Large (Vazquez & Diniz-Filho) are members of the committee. In addition, the President has added Larry Heaney (President elect) as a member.

All of our offices are critical to the functioning of our society so we ask that you spend some time thinking about who would be good at the various jobs and willing to spend the time.

Many thanks,

Vicki Funk

Past President

Did you know that by submission of a petition signed by at least twenty-five voting members of the Society, members may request that an item proposed by a member of the Society during the Governing Board of Directors meeting will be voted on as an initiative by the full Society membership by electronic mail ballot? The results of any such ballots shall be reported to the membership.

IBS-sponsored events

Conservation biogeography: Integrating biogeography and conservation science in a changing world

The UNESCO is holding an *International Year of Biodiversity Biodiversity Science-Policy Conference* in Paris during 25-29 January 2010. As part hereof, a conference session dealing with the theme: 'Conservation Biogeography: Integrating Biogeography and Conservation Science in A Changing World', will be held, in association with the International Biogeography Society, on day 2 of the Conference, 26 January 2010 (Conveners Robert J. Whittaker and Jens-Christian Svenning).

The International Biogeography Society

The International Biogeography Society (IBS) was founded as a non-profit organization in 2000 with the following mission:

- Foster communication and collaboration between biogeographers in disparate academic fields - scientists who would otherwise have little opportunity for substantive interaction and collaboration.
- Increase both the awareness and interests of the scientific community and the lay public in the contributions of biogeographers.
- Promote the training and education of biogeographers so that they may develop sound strategies for studying and conserving the world's biota.

Further information available at: <http://www.biogeography.org/>.

Remit of the Conservation Biogeography Symposium

Conservation Biogeography has been defined as "the application of biogeographical principles, theories, and analyses, being those concerned with the distributional dynamics of taxa individually and collectively, to problems concerning the conservation of biodiversity". It is thus a sub-field of conservation science and of the discipline of biogeography, being concerned with pattern and process over large extents of space (and time), and the insights this subject brings to understand-

ing patterns of biodiversity and the processes that threaten biodiversity in the 21st century. Conservation Biogeography can contribute to understanding the impacts of habitat loss, climate change, biotic homogenization, and other drivers of biotic change, while also contributing to conservation solutions, and especially to strategic conservation planning.

The aim of the Conservation Biogeography session is to link biogeographic theory and practice to improve the conservation and sustainable and equitable use of biodiversity – the three main objectives of the CBD. The session will feature a series of prominent biogeographic scientists who will speak on how the long-term, large-scale perspectives provided by the various subfields of biogeography, which collectively provide crucial insights for biodiversity conservation and management:

- Robert J. Whittaker (University of Oxford) "Conservation biogeography: assessment and prospect"
- Jens-Christian Svenning (Aarhus University) "Historical biogeography: implications of long-term macro-scale biodiversity dynamics for conservation"
- Kathy Willis (University of Oxford) "Long-term ecology and conservation science"
- Sara Lourie (McGill University) "Marine conservation biogeography"
- Wilhelm Barthlott (University of Bonn) "Global assessments of plant species richness and endemism: implications for conservation in a changing world"
- Miguel Araújo (CSIC, National Museum of Natural Sciences, Madrid) "Spatial conservation planning and climate change"
- Richard Pearson (American Museum of Natural History) "Predicting species distributional shifts and extinction risk under climate change"
- Josh Donlan (Advanced Conservation Strategies) "Rewilding"

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>).

from the members

Re-unite Gondwanaland!

Impressions from the 4th international conference of the International Biogeographical Society at Mérida, Mexico, 8-12th January 2009

The very ambitious demand above was written with 50 cm large flaming letters in the Geodepartment of the University of Copenhagen, in the roaring seventies, on the wall in the gangway between the section of palaeontology and that of tectonics. I suppose somebody felt that good old geology had been torn by suboceanic lava flows, and longed back to former unity.

As a green researcher in those days, with interest in organismal biology (biodiversity had not been coined as a term yet), I felt that my discipline became torn too. The rift was between the taxonomical bookkeeping and the ecological wilderness and often much sharper terms were used to express mutual disregard.

When biodiversity in the beginning of the nineties became an issue of interest (for once in this sequence: first politically, then scientifically), I and several others hoped that now taxonomy and ecology could converge again but that did not happen, at least in the circles where I was. Instead, the field of biodiversity became a battle ground where taxonomists and ecologists fought intensively for grants, and accordingly the tone between the parts became more and more garish.

Biogeography existed as a term (or two terms: phytogeography and zoogeography) but encompassed an array of disparate disciplines:

- description of distribution patterns of plants and animals leading up to biogeographical regions and realms,
- historical biogeography focusing on a long term temporal scale,
- ecological biogeography with an autoecological approach to understanding of what determines species distribution,
- vegetation (or community) geography trying to define supraspecific ecological units and to explain their distribution,
- panbiogeography – the biogeography based on the paradigm of vicariance
- island biogeography where species are numbers rather than individual entities
- macroecology where species numbers become dots in graphs or colours on maps

Even though there were contacts between actors on this scene and even if media like *Ecography* and *Journal of Biogeography* existed, there was no common forum for biogeographers before 2000 when the International Biogeographical Society was founded. The foremost paragraph of the mission statement was the following: “Foster communication and collaboration between biogeographers in disparate academic fields – scientists who would otherwise have little opportunity for substantive interaction and collaboration.”

How did the 4th International Conference in Merida live up to this purpose? To judge from the titles of the symposia one should not expect sound healing of the ruptures between the disparate academic fields. The topics were (**bold typing** is my invention):

1. Pattern and Process at Biogeographic **Boundaries**
2. The Biogeography of **Disease**
3. Biogeographic **Disjunctions** between Asia and North America
4. **Extinction** Biogeography

The boldfaced terms do really not forebode unification or strengthening, but as the lectures proceeded it became evident that they represent potential fields for syntheses rather than black holes where biogeographic pattern and process vanish.

The speakers were excellent, the coherence between lectures within the symposia fine, and the scientific level high without being so sophisticated that part of the audience was disconnected. As a result there was only little seeping away from the lectures even at times where people got tired, hungry or overwhelmed by jetlag.

Without reducing the quality of the other three symposia I wish to point out the talks in the extinction symposium. It was an oratorical fireworks. We almost felt the late-Permian suffocation, we were almost shattered from the impact in the Chicxulub crater, and we almost heard the roar of the last mammoth and the swan-song of the giant Hawaiian goose.

But the clou of the conference was still to come. John C. Avise was granted the Alfred Russel Wallace Award and rewarded us with a brilliant talk on his field: phylogeography. It was a masterly review of molecular phylogenetic methods and their advantages and limitations, and the potential in biogeographical studies. I heard many of the participants afterwards express that they wished they had had this introduction to the field as the first point of the conference, or even better, years ago.

I especially appreciated the perspectives he outlined for biogeography as a unified discipline. He envisioned the ecological continent with its landscapes of microevolution, demography, population dynamics, ethology and ecological interactions on one side, and the taxonomical continent on the other side with historical geography, palaeontology, phylogenetics and sytematics as landscape elements. He urged for a reunion of these two continents and proposed phylogeography as stepping stones that might develop to a land bridge.

Let us give it a try. Let us reunite these continents. It should be more likely to happen than the reunion of Gondwanaland.

Apart from the invited speakers there were a lot of short talks in the three concurrent sessions. The ones I heard were inspired and inspiring. But it is annoying that you have to miss two third of the talks. It is a recurring problem at all conferences that could be overcome by one additional day. I do not understand that people that invest plenty of money and fuel to attend conferences cannot also set aside the time to fully enjoy the outcome of the investments.

The poster presentations were as always interesting. I enjoyed the diversity. The spatial scale was from biogeography of your teeth to global distributions. Imagine that a visit to the dentist may have as sincere effect in a small universe as a Chicxulub impact on global scale! The presented interpretations of the discipline of biogeography certainly verify the formulation in the mission statement that it encompasses disparate academic fields. This is not a rebuke: it is better

that way than the situation where posters are just echoes of mainstream interests. The poster sessions were so well frequented that it sometimes was almost too crowded. The authors should take that as the best proof that they did a good job.

The excursions gave good glimpses of the attractions of Yucatan : amazingly flat landscapes, marvellous white beaches, cenotes and caves, a rich bird life and at last but not at least magnificent remains of Mayan cities. I stayed for a couple of additional days so I visited all excursion targets. Everybody should have done the same: it was worth it.

Merida proved to be a lively and hospitable city. It was unproblematic to walk around and a lot to observe in the close neighbourhood and in the vibrating centre. The hotel served appropriately as a hosting organisation – my only complaint is that it was meaningless that even hardy Scandinavians like me should suffer from the refrigerator climate in the lectures hall!

The last comment must be a large bouquet of roses to the organizing committee. I am sure that there is score of anonymous helpers but I am also sure that that Ella Vázquez-Domínguez really deserves to be the one who receives the bouquet. She was just everywhere, smiling, helpful, competent and charming. Thank you, Ella. If we really want to reunite Gondwanaland, she should be in the action committee.

IBS seems to like dramatic events. Last conference was on the edge of mega-landslides in Tenerife, this one was in the Chicxulub impact area, and the next one will be on Crete close to Santorin where a mega-eruption destroyed most of the Minoan culture. Hope to see you all there among the ruins.

Henning Adersen

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<http://www1.bio.ku.dk/>

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.

from the members

Alan Graham awarded for his career

Alan Graham received the Asa Gray Award from the American Society of Plant Taxonomists (ASPT) and the Botanical Society of America's (BSA) Merit Award at their annual meetings in Snowbird, Utah, 2009. They were in recognition of 'his lifetime of perceptive study by which he laid the foundations for our concepts about the origins and history of tropical vegetation, greatly advanced the field of vegetation history, and the way in which we

should understand present distributions.' The awards were, in part, to commemorate publication later this year of *Late Cretaceous and Cenozoic History of Latin American Vegetation and Terrestrial Environments* (Missouri Botanical Garden Press, 2009).

See <http://www.mobot.org/mobot/research/curators/graham.shtml> for more information on Alan Graham's work.

Job announcements

Postdoctoral position

Landscape Ecology Group, Dept. Ecology and Environmental Science, Umeå University

One **postdoctoral position** on effects of climate changes on the biodiversity of protected areas in the Barents region. The project has three major goals: (1) to assess whether the network of protected areas can conserve its species and ecosystem types, (2) to identify the major gaps in terms of providing stepping-stones or migration routes between reserves, and in representing natural variation, (3) to evaluate the economic consequences of alternative conservation strategies aiming at representing biodiversity. The position will start as soon as possible and last for about 20 months. For further information, contact prof. Christer Nilsson (christer.nilsson@emg.umu.se) or associate prof. Roland Jansson (roland.jansson@emg.umu.se).

The complete application should be sent to jobb@umu.se (marked with the reference 315-1076-09 as subject) or to the Registrar, Umeå University, SE-901 87 Umeå, Sweden to arrive January 7, 2010 at the latest. For more information see www.emg.umu.se/en.

Lecturer in Plant Ecology

Lund University

A position of a Tenure-track Lecturer in Plant Ecology within the Department of Ecology is now being advertised. See full details at <http://www.planteco.lu.se/lecturer091123.pdf>.

1 Postdoctoral and 2 PhD positions

Jetz Lab, Dept. of Ecology and Evolutionary Biology (EEB), Yale University

One **2-3 year postdoctoral position** in Biodiversity Science and Informatics is available starting between January and July 2010. We are looking for an expert in the analysis, management, and visualization of large quantities of spatial (and phylogenetic) biodiversity data. One specific research opportunity is an assessment of the fate of East African terrestrial vertebrates under climate change. Please email short letter of interest, C.V., and the names and contact details of three referees (ideally all combined in one pdf) to walter.jetz@yale.edu – subject line: Biodiversity Postdoc.

Up to **two fully-funded PhD positions** in Ecology, Biogeography and Conservation are available starting Fall 2010. We are interested in students with research experience who are excited about interdisciplinary work spanning a range of ecological scales. Applicants should have a strong interest in combining theory, data analysis and modeling, and potentially fieldwork to address questions in Community ecology, Community phylogenetics, Geographical ecology, Movement ecology, Biodiversity science, Biogeography, and Global change ecology. See <http://www.yale.edu/eeb/grad/index.htm> and <http://www.yale.edu/graduate-school/admissions/index.html>.

A complete description of the applications is available at the IBS blog (<http://biogeography.blogspot.com/>). See <http://www.yale.edu/jetz> for further information.

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.

5 Postdoctoral, 2 PhD and 1 Science Officer positions

BioFresh - Biodiversity of Freshwater Ecosystems – several European institutions

BioFresh is a large, integrative EU-funded 4-year project aiming to build a public freshwater biodiversity information platform, provide spatially-explicit information on the status and trends of freshwater biodiversity and its ecosystem services, and predict future responses of freshwater biodiversity and its services to climate and socioeconomic pressures. Eight positions are offered in total:

1 PhD-position — Climate Change on Lake Ecosystems Based on Long-Term Records — Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany (IGB, www.igb-berlin.de) (contact: adrian@igb-berlin.de, tockner@igb-berlin.de)

1 PostDoc-Position — Global Change Impacts on Freshwater Biodiversity — IGB (contact: tockner@igb-berlin.de; freyhof@igb-berlin.de)

1 PostDoc-Position — Ecosystem Modeling — Swiss Federal Institute for Aquatic Science and Technology (www.eawag.ch) (contact: gessner@eawag.ch)

1 PostDoc-Position — Effects of Global Change on Freshwater Biodiversity Patterns — University of Barcelona, Spain (contact: bonada@ub.edu)

1 PhD-position — Groundwater Biodiversity Patterns and Trends — Université Claude Bernard Lyon 1, Ecolo-

gie des Hydrosystèmes Fluviaux, France (contact: ma-lard@univ-lyon1.fr, christophe.douady@univ-lyon1.fr)

1 PostDoc-Position — Determinants of Freshwater Diversity and Impact of Human Disturbance — University Toulouse 3, France (<http://www.edb.ups-tlse.fr/>) (contact: brosse@cict.fr)

1 PostDoc-Position — Freshwater Macroecology — Museum of Natural History in Paris, France (contact: oberdorf@mnhn.fr)

1 Science Officer — Establishing a web portal that will provide free and open access to relevant data sources and bioinformatics tools — Royal Belgian Institute of Natural Sciences (contact: hendrik.segers@natural-sciences.be)

A complete description of the applications is available at the IBS blog (<http://biogeography.blogspot.com/>).

Postdoctoral Position

Carleton University

A postdoctoral position in Spatial Ecological Modelling is available at Carleton University. The objective of the research is to build a set of hypotheses that predict the spatial scale over which landscape structure affects population dynamics. The position is available for up to three years, beginning April 2010, at a salary commensurate with an NSERC PDF. enquiries: lenore_fahrig@carleton.ca.

Upcoming events

UNESCO IYB Biodiversity Science-Policy Conference

Session on Conservation Biogeography in association with the IBS

25-29 January 2010 – Paris, France

<http://www.unesco.org/en/biodiversity>

SAFARI Symposium

Remote Sensing and Fisheries

15-17 February 2010 – Kochi, India

<http://www.geosafari.org/kochi>

VI Southern Connection Congress

Gondwana reunited: a southern perspective for a changing world

15-19 February 2010 – Bariloche, Argentina

<http://www.sccongress2010.com.ar/>

9th Meeting on Vegetation Databases

Vegetation databases and climate change

24-26 February 2010 – Hamburg, Germany

<http://www.botanik.uni-greifswald.de/>

2010 AAG Annual Meeting

Association of American Geographers

14-18 April 2010 – Washington DC, USA

<http://www.aag.org/annualmeetings/>

19th Workshop of the European Vegetation Survey

Flora, vegetation, environment and landuse at large scale

29 April - 2 May 2010 – Pécs, Hungary

<http://www.obki.hu/evs/>

The Evolution of Pacific Biota

20-22 May 2010 – Honolulu, Hawaii, USA

<http://www.pacificscience.org/meetings.html>**7th European Dry Grassland Meeting****Succession, restoration and management of dry grasslands**

28-31 May 2010 – Smolenice, Slovak Republic

<http://www.edgg.org>**GeoMed 2010****2nd International Geography Symposium**

2-5 June 2010 – Antalya, Turkey

<http://web.deu.edu.tr/geomed2010>**95th ESA Annual Meeting****Ecological Society of America**

1-6 August 2010 – Pittsburgh, USA

<http://www.esa.org/pittsburgh/>**25th International Ornithological Congress**

22-28 August 2010 – Campos do Jordão, Brasil

<http://www.ib.usp.br/25ioc/>**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/>**5th International Conference of the International Biogeography Society**

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/>**XVIII International Botanical Congress**

23-30 July 2011 – Melbourne, Australia

<http://www.abc2011.com/>**frontiers of biogeography copyright notice**

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