

What's on the horizon for macroecology?

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Over the last two decades, macroecology – the analysis of large-scale, multi-species ecological patterns and processes – has established itself as a major line of biological research. Analyses of statistical links between environmental variables and biotic responses have long and successfully been employed as a main approach, but new developments are due to be utilized. Scanning the horizon of macroecology, we identified four challenges that will probably play a major role in the future. We support our claims by examples and bibliographic analyses. 1) Integrating the past into macroecological analyses, e.g. by using paleontological or phylogenetic information or by applying methods from historical biogeography, will sharpen our understanding of the underlying reasons for contemporary patterns. 2) Explicit consideration of the local processes that lead to the observed larger-scale patterns is necessary to understand the fine-grain variability found in nature, and will enable better prediction of future patterns (e.g. under environmental change conditions). 3) Macroecology is dependent on large-scale, high quality data from a broad spectrum of taxa and regions. More available data sources need to be tapped and new, small-grain large-extent data need to be collected. 4) Although macroecology already lead to mainstreaming cutting-edge statistical analysis techniques, we find that more sophisticated methods are needed to account for the biases inherent to sampling at large scale. Bayesian methods may be particularly suitable to address these challenges. To continue the vigorous development of the macroecological research agenda, it is time to address these challenges and to avoid becoming too complacent with current achievements.

The unparalleled rise of large-scale ecology as a newly recognized field in biology over the last two decades warrants a reflection on its current state and future development. Since the term ‘macroecology’ was coined by Brown and Maurer (1989), the subject has moved from the fringes to the center of ecological thinking and journals that emphasize macroecology have caught up with the top-tier ecological journals (Fig. 1).

Macroecology investigates patterns of ecological systems that emerge at large spatial or temporal scales. Following Brown's wordplay (1995), macroecology uses ‘macroscopes’ to step away from the objects, just as other fields of biology use microscopes to get closer to them. Such distance to the raw data facilitates the recognition of general patterns. Among the recurrent themes of macroecology are latitudinal

gradients in species richness (Hawkins et al. 2007), metabolic scaling theory (West and Brown 2005, Capellini et al. 2010), range size distributions (Svenning and Skov 2004, Beck et al. 2006) and phylogenetic relationships (Capellini et al. 2010, Wiens et al. 2010). A common thread in many current studies is the use of species distribution data linked to phylogenies (Winter et al. 2009, Cadotte et al. 2010), range size (McPherson et al. 2004, Morin and Chuine 2006), network theory (Cumming et al. 2010), or analyses of species richness patterns (Adler et al. 2005).

Still, macroecology faces several methodological shortcomings that need to be overcome to successfully advance large-scale ecological research. Now is a good moment in the discipline's development to evaluate where macroecology is standing, and to point out some burning issues that will be

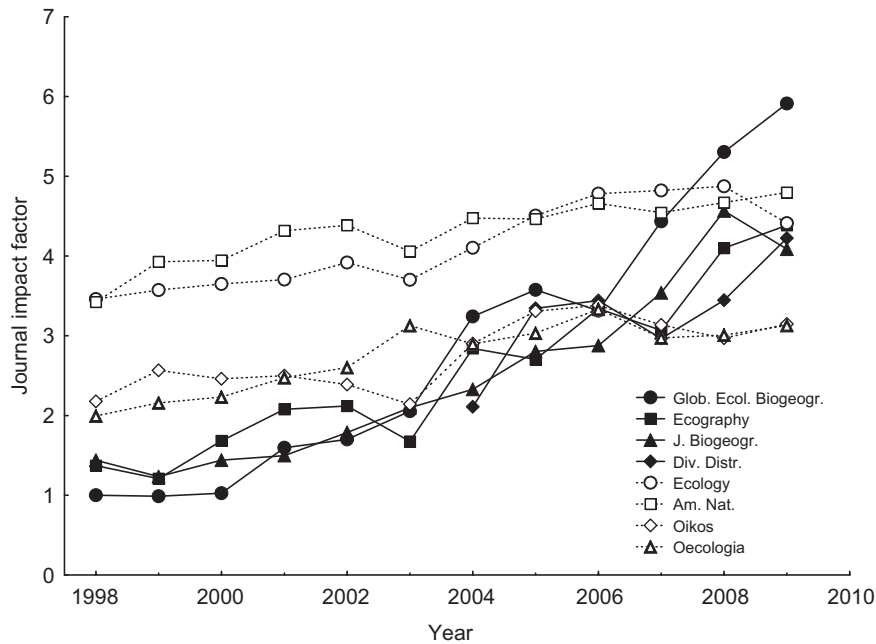


Figure 1. Impact factors (ISI Web of Science, < www.isiknowledge.com >) of four journals with a strong focus on macroecology (filled symbols), in comparison to four established general ecology journals (open symbols) for the same time period. Impact factors are an index of citation frequency of articles from a journal in relation to the number of articles published in the journal.

relevant to the discipline's further growth. In this paper, we elaborate on four topics within macroecology as particularly important to many in the research community: 1) the role of biogeographic and Earth history, 2) the importance of processes in understanding patterns, 3) issues of data availability, and 4) advances in statistical analysis. We identify the major challenges in each of these fields, and we discuss potential solutions. Our account does not aim at reviewing the literature in an exhaustive manner; instead we focus on general problems and promising positive examples.

Throwing light on the shadows of the past: the role of history in macroecological patterns

Macroecology aims at explaining biotic patterns predominantly by using current environmental conditions. However, there are temporal contingencies in ecological systems due to past fluctuations of environmental conditions (e.g. climatic changes, plate tectonics) and organisms' phylogenetic history that affect, e.g. trait distributions (Jablonski 2008, Wiens et al. 2010). Historical signals are thus an inherent component of current species distributions and other objects of macroecological investigation, and ignoring these 'shadows of the past' could lead to erroneous findings. This is especially true if historical patterns are collinear with current conditions (Hortal et al. 2011). Indeed, some authors have argued that prominent topics in macroecology, such as the latitudinal biodiversity gradient, can only be understood by following a top-down hierarchy of filters from the historical, evolutionary effects on regional species pools to the mechanisms that determine species occurrence at the community scale, and not vice versa (Ricklefs 2004, Wiens and

Donoghue 2004). Additionally, more recent historical events such as anthropogenic impacts on ecosystems may heavily distort patterns observed in recent data (Kelt and Meyer 2009, see also Hermy and Verheyen 2007).

We see three main avenues for integrating historical information into the macroecological research agenda: 1) using paleo-data on species distributions, climate, land-cover, etc., 2) considering phylogenetic relatedness of taxa, and 3) integrating analytical approaches from historical biogeography.

1) Incorporating paleo-data into macroecological analyses is conceptually relatively straightforward. Fossil time series can be used to investigate the temporal variation of macroecological patterns (e.g. the latitudinal species richness gradient: Jablonski et al. 2006, Powell 2007) or trait variation in extinct communities (e.g. prior to human impact: Erwin 2008). For plants, pollen records provide useful information about past species distributions and abundances (Theuerkauf and Joosten 2009) and properties of past communities (Odgaard 1999, Bush et al. 2004). However, there are substantial data limitations and a considerable bias towards well-fossilizing taxa (Foote and Sepkoski 1999). Paleo-data can also be reconstructions of past abiotic (e.g. climatic) or biotic (e.g. vegetation type) conditions, which can be used to understand historical effects on past and current species distributions (e.g. dispersal-related lags in colonization after Pleistocene climate fluctuations; Montoya et al. 2007, Svenning and Skov 2007) or on patterns of species richness or endemism (Dynesius and Jansson 2000, Jansson and Davies 2008). However, this approach can involve subtle circularity if paleodistributions of one taxon are the basis of climatic reconstruction, which is then used to model other species' distributions (Svenning et al. 2011).

Hind-casting of species distributions based on reconstructions of past climates by techniques of ‘ecological niche modeling’ (Elith and Leathwick 2009), in particular, is an increasingly employed method with great potential, but also many pitfalls (Nogues-Bravo 2009, Svenning et al. 2011). Such approaches are seen as particularly useful in combination with phylogeography (see below) as they can provide information on past scenarios of distribution, hence the preconditions of speciation events (e.g. allopatry of populations), that can then be tested against phylogenetic reconstructions.

Species distribution models and analyses of geographic patterns of species richness and endemism may profit from novel ways to quantify the degree and pattern of past climate fluctuations and the potential that landscapes (and seascapes) offer for species to track such changes (Loarie et al. 2009, Sandel et al. 2011) or to provide microrefugia (Rull 2009).

2) The integration of phylogenetic information into macroecological analyses is encouraged by the increasing availability of comprehensive phylogenies (Bininda-Emonds 2004, Wiens and Donoghue 2004, Davies et al. 2008). Many different approaches have been taken to incorporate these data into macroecological analyses. They range from phylogenetically informed analyses of trait correlations or deconstructions of spatial patterns into different phylogenetic lineages or systematic groups (Marquet et al. 2004, Beck and Kitching 2009) to more complex calculations of phylogenetic diversity or phylogenetic structure in space (Hawkins et al. 2007, Davies et al. 2008).

Comparing the relatedness of coexisting taxa to the phylogeny of the regionally available pool (i.e. whether coexisting communities indicate phylogenetic overdispersion and clustering) has yielded interesting results in community ecology (Webb et al. 2002). Theoretical expectations have been formulated regarding the patterns of phylogenetic composition and trait similarity that may be expected under various geographical and ecological scenarios (Emerson and Gillespie 2008, Cavender-Bares et al. 2009). Techniques of incorporating such ‘local’ phylogenetic measures into larger-scale macroecological analyses are currently being devised (Graham and Fine 2008, Kühn et al. 2009, Dormann et al. 2010, Kissling et al. 2012). We think this is a very promising approach to be developed and applied.

Explicitly analyzing the link between phylogenies and emergent traits (such as niche dimensions) that affect distributions is another approach that may considerably advance our understanding of the relevance of the past for the patterns observed today (Hof et al. 2010, Wiens et al. 2010). Phylogeography, the analysis of (mainly intraspecific) molecular phylogenies in a spatial context (Avice 2009), may be particularly useful to macroecology in the context of providing independent tests for geographic range scenarios from past distribution modeling (see above). However, data and techniques from phylogeography – be it intra- or interspecific – may also benefit a potential revival of cladistic biogeography, as outlined below.

3) Integrating classical historical biogeographical approaches with macroecology is a third, rarely utilized approach. Cladistic biogeography uses the phylogeny of taxa occurring in a region to infer historical events that shaped their evolution. Area cladograms, depicting the relatedness

of regions with respect to speciation of an investigated taxon (Morrone 2009), might reflect the evolutionary relevant geographic history of regions (e.g. vicariance events). These patterns can be tested and verified against other taxa. The designation of biogeographic regions, for example, can be the outcome of such historical analyses, going beyond current faunistic or floristic similarities (Kreft and Jetz 2010). Broad biogeographical regionalizations have been included in macroecological analysis to investigate regional historical effects (Kreft and Jetz 2007, Hof et al. 2008). A drawback of such analyses is that historical effects are likely to leave their mark at much finer spatial scales. For instance, a biogeographical region like the Afrotropics contains many sub-regions that are assembled from different species pools with different evolutionary histories. Indeed, many finer-scaled, hierarchical biogeographic classifications are available in the literature for many regions and taxonomic groups (de Klerk et al. 2002, Kreft and Jetz 2010, Rueda et al. 2010) that may provide useful geographic templates to investigate regional effects. We suggest that these data should be utilized more and that the approach be expanded to fit the extent and resolution of macroecological analyses (i.e. having small regions, such as islands or grid cells, at the tips of area cladograms; Fig. 2). Existing information from phylogenies or supertrees (Bininda-Emonds 2004, Bininda-Emonds et al. 2007) should also continue to be exploited more for cladistic biogeographic analyses. Advances in historical inference and methodology are being made and may lead to accelerating the construction of area cladograms (Linder 2001, Donoghue and Moore 2003). Knowledge of evolutionary history in grid cells would allow mapping and incorporating the historical homogeneity of cells as a continuous variable in macroecological modeling, facilitating much finer-scaled and robust partitioning of current vs historical effects on response variables.

Integrating phylogenetic and distributional data into a place-based history could be achieved by a transfer of available techniques of accounting for phylogenetic contingencies in interspecific comparative studies (Fig. 2; Freckleton et al. 2002). Clearly, it will require some effort to assemble the relevant data (or to collect new data where necessary), and to devise and assess analytical procedures that best integrate them into analyses. If successful, however, this would represent a major advance in bridging the conceptual and methodological gaps between the aggregation levels of ecology, macroecology, and historical biogeography.

Putting processes into macroecology

Macroecology has proven very successful in describing general patterns, but ultimately this is not sufficient if we cannot infer causalities (Dormann 2007, Kearney and Porter 2009). It is a long-standing issue in ecology to understand the processes behind patterns (West and Brown 2005), even more so as this is a prerequisite for reliable future predictions of impacts of climate and land-use change and for the development of mitigation and adaptation strategies. Ecological processes and mechanisms have long been investigated much more thoroughly on the community scale (Supplementary material Appendix 1). On a macroecological

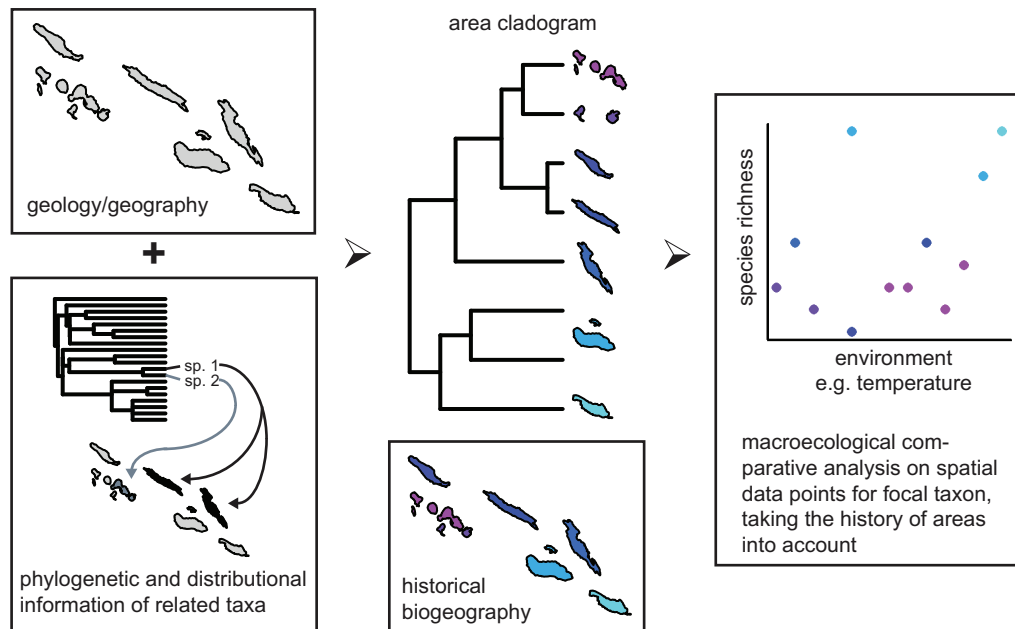


Figure 2. Integration of historical biogeography into macroecological research using area cladograms and comparative methods. We illustrate an island chain here, but the approach could be similarly applied to grid cells. The macroecological question addressed as an example is the relationship of species richness for a taxon of interest with environmental correlates, such as temperature (right panel). In order to integrate the historical biogeography of the region, we propose building an area cladogram (middle panel) from information (left panel) on phylogenies and distributions of taxa (ideally, many taxa should be used). This area cladogram can then be integrated by applying phylogenetic comparative methods to the spatial data points of the macroecological analysis, i.e. the relationship of richness vs temperature can be assessed controlling for area history as illustrated by the color of the data points (right panel).

scale this is more challenging not only because of practical limitations (e.g. the difficulties of large-scale experiments), but also because some mechanisms are likely to act differently at community and at macro-scales.

The path to a better understanding of the processes behind macro-scale patterns may be analyses of the scale-dependencies of relationships, or the collection of standardized experimental data on local processes over large spatial extents (Passy 2008, Hendriks et al. 2009). Formulating multiple, testable predictions from hypotheses aids the differentiation between mechanisms that lead to similar patterns (Currie et al. 2004, McGill et al. 2006).

To disentangle causalities for emergent patterns, the application of process-based simulation models to derive null expectations for large-scale patterns (Zurell et al. 2009, Gotelli et al. 2010) seems more promising than current statistical approaches (e.g. path analysis), but it is challenging due to difficulties of their parameterization (Hodges 2010, Lele 2010). Recently, modelers have started to develop individual-based, spatially-explicit approaches to test large-scale patterns (Zurell et al. 2009, Buchmann et al. 2011). Models that include macroecological mechanisms, such as dispersal limitation and evolutionary origins, have been developed to predict biogeographic patterns (Gotelli et al. 2009). Species distribution models have begun to incorporate dispersal limitation into future predictions using realistic dispersal variables (Engler and Guisan 2009).

Another challenge is that interspecific competition may influence distribution ranges (see e.g. Ritchie et al. 2009 for a recent example). Consumer-resource or biotic interactions

are increasingly included in species distribution models, and such models yield improved results compared to the more simplistic ones (Heikkinen et al. 2007, Schweiger et al. 2008). Still, these analyses are correlative, and a better model fit with a potential competitor included may simply indicate that both have related environmental niches, not that they actually interact. In other words, species distribution models usually do not include ecological assembly rules that could account for biotic interactions (Guisan and Rahbek 2011). However, approaches that incorporate this kind of information are already being developed, such as functional and phylogenetic approaches and their combination: 1) functional traits link species occurrence to the environmental factors that govern occurrence (Díaz et al. 2004); 2) phylogeny takes into account that today's communities are a product of not only recent but also evolutionary processes (Gerhold et al. 2008). Hence, by considering function and phylogeny in concert, we can link environment and history to better understand underlying community assembly processes on small scales as well as on large scales, such as species richness gradients. Moreover, to disentangle effects of environmental filters from effects of biotic interactions, analyses of phylogenetic diversity and trait conservatism within lineages were already proving useful (Cavender-Bares et al. 2009). Besides function and phylogeny, data on population size or abundance were already identified as key variables for better linking many ecological processes and patterns (Evans et al. 2008, Cadotte et al. 2010, Beck et al. 2011). These parameters could easily be implemented in the approaches described above.

Integrating all parameters that potentially affect community assembly into one macroecological framework might be achieved by combining existing methods, such as recently proposed by Guisan and Rahbek (2011). In their SESAM approach (spatially explicit species assemblage modeling), they account for both abiotic and biotic filters by combining species source pools and ecological assembly rules with macroecological modeling and species distribution modeling. However, Guisan and Rahbek (2011) admit that ecological assembly rules, which are the key to explaining biotic interactions in SESAM, are at best available at local scales (for some taxa in some regions), but missing at large scales. However, patterns and processes can change across scales, as shown, for example, by Belmaker and Jetz (2011) for richness-environment associations. Consequently, macroecological research needs more spatially resolved data at small-grain scale, but covering large spatial extents (see section Data: deficits and solutions) to increase the feasibility of scaling up pattern-process relationships from small to large scales.

There seems to be an interesting parallel between current directions in understanding patterns in macroecology and history of advancement in understanding of patterns of population dynamics. Research on population dynamics started with simple, top-down, non-spatial and non-individual-based models. This has changed dramatically in recent decades, as more detailed knowledge on the importance of effects of underlying processes such as individual behavior has been gathered (Grimm et al. 2005). Based on these findings, the use of bottom-up approaches advanced the ability to predict future population dynamics considerably. This may be true for macroecology as well. With the advancement of data quality, statistical methods, and macroecological theory, we will be increasingly able to move beyond describing patterns towards including and testing the processes behind them, particularly dispersal and biotic interactions.

Data: deficits and solutions

It was more than a decade ago that Wilson (2000) expressed the need for a global assessment of all aspects of biodiversity, a ‘map of biodiversity’. But even for species richness of well-studied groups, this goal has not been achieved. Moreover, missing data on species traits, distributions and phylogenetic relatedness make it difficult to thoroughly assess global biodiversity patterns and underlying processes. Although a range of automated assessment frameworks were developed in recent years to handle large data sets, to link different data sources and to create large phylogenies (Guralnick and Hill 2009), macroecological analyses still suffer from large uncertainties and gaps in the raw data. Specifically, macroecological research until now has largely been driven by data already available, revealing two major shortcomings: 1) limited coverage of biomes, taxa and spatial scales, and 2) insufficient or unknown data quality. We warn against the common practice of accepting published data as unquestioned truth: by citing a data source, the suitability of these data for the question at hand is often taken for granted (Robertson et al. 2010), in marked contrast to reviewer skepticism on researchers’ own data.

Most macroecological studies focus on few taxa (Fig. 3). While mammals and birds are vastly overrepresented in studies, and all other vertebrates as well as vascular plants are reasonably well studied, macroecological studies on invertebrates, non-vascular plants, and fungi are scarce. Until now, the majority of macroecological studies deal with terrestrial taxa (Fig. 4), despite the fact that a large number of phylogenetic lineages are restricted to, or predominantly occur in, the marine realm (Witman and Roy 2009). It is not surprising that Europe and North America are the best studied continents, while more diverse tropical regions, particularly Asia or Africa, are heavily underrepresented (Fig. 4).

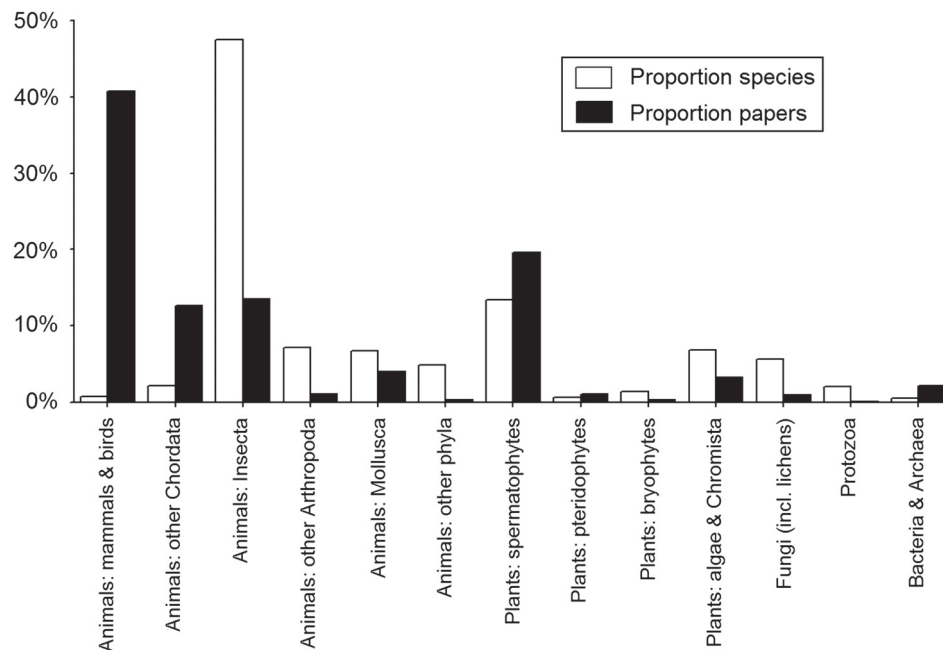


Figure 3. Distribution of macroecological papers in ISI Web of Science (3 April 2010) regarding major taxa. The bar chart depicts the proportion of papers in relation to the proportion of described species of the respective lineage (for details on the literature search see Supplementary material Appendix 2).

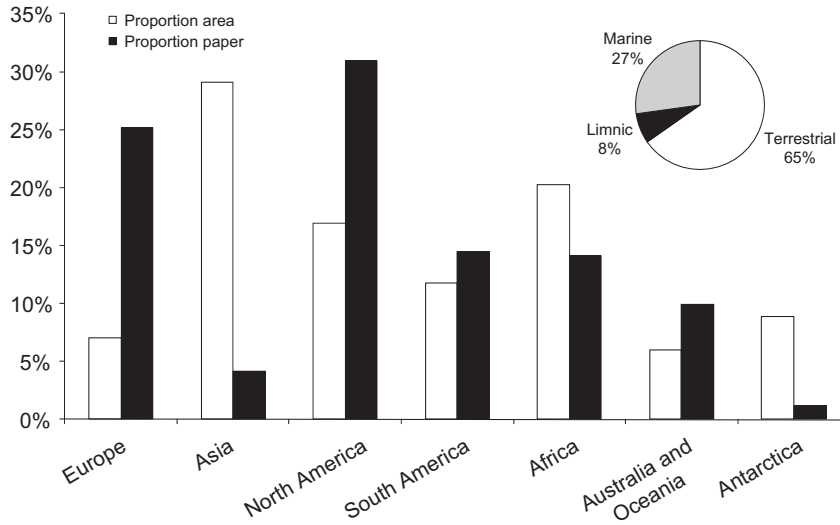


Figure 4. Distribution of macroecological papers in ISI Web of Science (3 April 2010) regarding terrestrial, limnic, and marine habitats (pie chart). The bar chart depicts the geographic distribution of the terrestrial studies to continents and relates this to the proportional surface of each continent (for details on the literature search, see Supplementary material Appendix 3).

Generally, ecologists acknowledge that ecological processes act at different spatial scales (Turner and Tjørve 2005), and thus the patterns detected and their underlying processes will normally be scale-dependent (Willig et al. 2003). ‘Scale’ refers to both ‘extent’ and ‘grain’ (Shmida and Wilson 1985, Rahbek 2005). While macroecology essentially considers large extent, this can be combined with coarse or fine grain. However, data at large extent derived from distribution atlases, as they are typically applied in macroecology, primarily have large grain sizes (Robertson et al. 2010). Hence, studies with a small grain but covering a large spatial extent are extremely scarce (Fig. 5). Therefore, up to now the

macroecological perception is dominated by biodiversity patterns and inferences about underlying drivers at large grain sizes ($\geq 100 \text{ km}^2$), and there is a wide-spread believe in the scale invariance of these findings (Rahbek 2005). This is astonishing as even early macroecological works demonstrated that, among relatively similar, large grain sizes, results might nonetheless vary significantly (Kaufman and Willig 1998, Rahbek and Graves 2001). More recently, comprehensive reviews have demonstrated that the differences increase when medium or small grain sizes are included (Rahbek 2005, Field et al. 2008). While considering coarse-grained data might be sufficient for

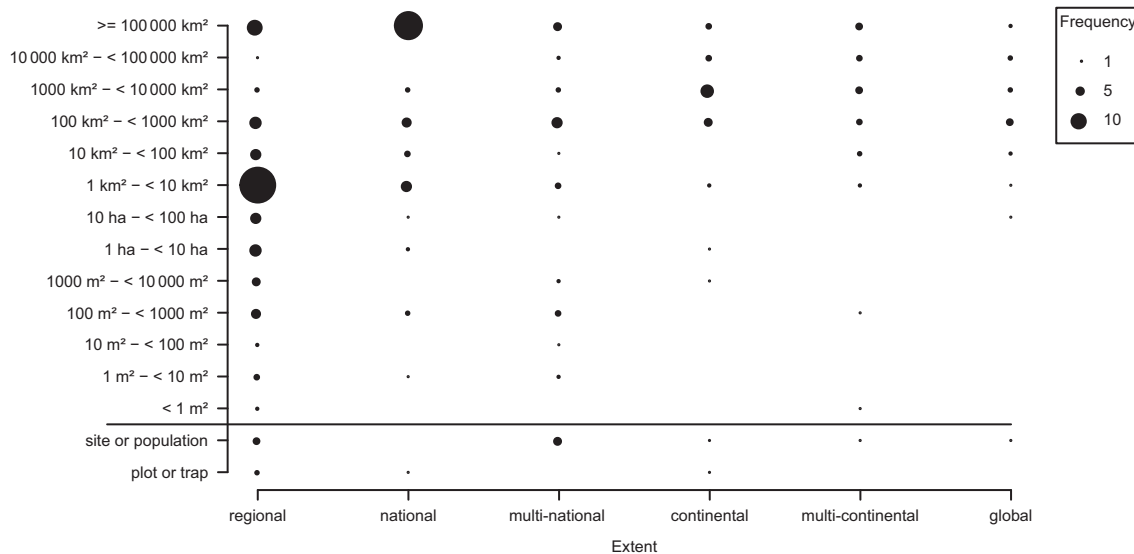


Figure 5. Extent and grain sizes used in macroecological studies published between 2007 and 2009 (for details on the literature search see Supplementary material Appendix 4). Dot size represents the number of studies conducted for a given extent and grain size. Dot size varies continuously; the legend shows frequencies 1, 5, and 10 for orientation. Studies that did not use a defined grid but sampled single sites, populations, or traps are given separately in the two bottom rows.

explaining processes that act at large scales (e.g. climate, plate tectonics, orogenesis), we suggest that fine-grained macroecological data could open new avenues in understanding the imprint of small-scale processes (e.g. dispersal, niches, species interactions) on patterns at large scale, particularly across steep environmental gradients. Moreover, the emergent pattern of scale-dependencies (Willig et al. 2003, Drakare et al. 2006) in itself might be an interesting topic of macroecological research, which could deepen our theoretical understanding (Rahbek 2005).

Macroecological data, including species distribution data, often lack information about data quality and uncertainty (Rocchini et al. 2011), which in turn increases model uncertainty: different levels of data quality can have significant effects on model predictions and ecological inference (Dormann et al. 2008). Data uncertainties may already result from the use of different species nomenclature (Jansen and Dengler 2010). These problems are inherent to aggregating and comparing data from different sources. For trait analyses, ignoring intraspecific variation and its impact on correlations especially across large scales and climatic gradients can be problematic (Jenouvrier et al. 2009, Albert et al. 2010), but trait values are often available only as averages per species.

We suggest not waiting passively for better data that fill the highlighted gaps, but actively stimulating field inventories with statistically sound, highly standardized field methods. In many regions of the world research and monitoring initiatives are active in this direction, but they often lack methodological rigor, international standardization or the awareness which data types are most urgently needed. By emphasizing the need for standardization and proposing appropriate multi-purpose monitoring schemes (Dengler 2009), macroecologists could have a hand in making the data from such monitoring schemes more useful without increasing the overall effort. An outstanding positive example is the Swiss Biodiversity Monitoring program (Hintermann et al. 2000); other positive examples are the Biodiversity Observatories of BIOTA Africa (Jürgens et al. 2012) and the Large Forest Dynamics Plots of CTFS (<www.ctfs.si.edu/>). All three examples combine large spatial extent with small spatial grain, which could bring macroecology closer to the processes behind patterns. Based on the BIOTA Observatory data, Schmiechel et al. (2010) could, for example, show that the inter-biome diversity patterns of vascular plants at grain sizes of 100 m² or 1 km² are not necessarily consistent with those found at large grain sizes (Barthlott et al. 2005).

However, macroecologists could also make better use of existing data. These are often scattered in different places or not accessible through the internet. Not only museums but also universities, administrative agencies and citizen science programs collect valuable ecological information (Edwards et al. 2000, Dengler et al. 2011). Mobilizing these data (which in many cases will require their digitization) would vastly increase the pool of available data, especially for poorly known taxa and for small grain sizes. We see an urgent need for establishing and strengthening cooperation between macroecology and bioinformatics in order to facilitate data finding and sharing among a large number of researchers and institutions.

Various online databases aim at making available large amounts of data, e.g. on biodiversity and distribution (Global Index of Vegetation-Plot Databases, <www.givd.info/>; Global Biodiversity Information Facility, <www.gbif.org/>), phylogenetic or trait data of whole taxonomic groups (mammals: YouTheria, <www.utheria.org/>; plants: TRY, <www.try-db.org/>), DNA barcoding data (BOLD, <www.barcodinglife.com/>), or nomenclature (Taxonomic Name Resolution Service for plants, <<http://tnrs.iplantcollaborative.org/>>). Recent initiatives aim at creating central databases (Guralnick and Hill 2009, Reichman et al. 2011, Jetz et al. 2012), e.g. TreeBase (<www.treebase.org/>), DataOne (<www.dataone.org/>) or Map of Life (<www.mappinglife.org/>). They will significantly decrease the amount of time for finding data and simplify data management for publication (Whitlock 2011).

Further tasks on the horizon: analytical methods for macroecology

Macroecology has become a pacemaker in introducing advanced statistical methods to ecology and related disciplines. Combined with the increase in computing power this has greatly increased the complexity of statistical applications in ecology (Heisey et al. 2010). We have progressed considerably in meeting the methodological challenges in macroecology that were pointed out 15 yr ago by Blackburn and Gaston (1998). While early analyses, for example, were based on simple tools such as ordinary least square regressions, it has now become standard to account for spatial and phylogenetic contingencies in data, to apply appropriate null-models, to consider scale-dependency of results, and to appropriately treat non-linear relationships. Spatial autocorrelation, in particular, has received a lot of attention as a methodological issue (Dormann et al. 2007, Beale et al. 2010), although there is considerable controversy whether this attention has led to ecological advances (Bini et al. 2009, Hawkins 2012). Other issues remain, such as the need for better data and a better understanding of the causality of processes (see above).

However, a major impediment that still waits to be broadly acknowledged and addressed is that macroecological data result from two hierarchical processes: the underlying stochastic processes in nature and the stochastic sampling process generating observations. This relates to the 'missing species' and 'artefacts' problem in Blackburn and Gaston (1998) – sampling can never be perfect and may always introduce a bias. However, this is especially true if the data were actually not sampled for the purpose at hand, but represent, e.g. compilations of local field studies, taxonomic and museum collections, etc. If we are to learn from such data about the 'real' processes, we need methods that can adequately account for both stochastic components. Spatially and taxonomically biased undersampling has been pointed out (Graham et al. 2004, Rondinini et al. 2006, Boakes et al. 2010), but this can be only the beginning of tackling the problem.

Many statistical analyses in macroecology face three challenges, which perhaps can be addressed simultaneously most successfully in a Bayesian framework: 1) data bias (e.g. due

to detection probabilities, sampling effort); 2) correlated but causally clearly hierarchical predictors (e.g. temperature decreasing with altitude, but the former directly affecting plant and insect growth, while the latter is only an indirect variable *sensu* Austin 2002); and 3) quantification of prediction uncertainty when combining these two issues with classical modeling methods (e.g. spatial GLMs). The methodological objective, under a hierarchical Bayesian framework, is to represent the observed data (be it presence-absence or abundances) as a random variable emanating from processes at several hierarchical levels. For example, Latimer et al. (2006) used a Bayesian approach to embrace spatial autocorrelation and spatially variable detection probabilities when analyzing presence-absence data (see also Meyer et al. 2011).

A second common problem is collinearity among ecological predictors, which Shipley (2002) argues is most satisfactorily embraced through structural equation modeling. Representing not only alternative explanations but also detection probabilities and perhaps different data sets to inform different parts of a mechanistic model, as well, is beyond the capabilities of any current off-the-shelf software. If interactions are likely to influence a species' distribution, then other interacting species may also need to be represented in the model; many species may remain undetected but still affect the abundance of target species and thus have to be modelled 'without data' (as done in Ovaskainen and Soininen 2011). When species are additionally assumed to interact non-homogeneously in time and/or space, a high level of statistical sophistication is required (Bierman et al. 2010, Cressie and Wikle 2011).

Although multi-level or hierarchical models can be coded in a frequentist framework (e.g. in mixed models; Zuur et al. 2009), it can be argued that Bayesian approaches are more transparent since they lay open the mechanisms modeled as well as the sampling processes (Royle and Dorazio 2008).

Fundamentally, however, the point is not whether Bayesian methods are needed to code ecological and sampling processes satisfactorily, but that incorporating these processes into statistical analyses promises to further our ecological understanding (Clark and Gelfand 2006). It was through a (non-Bayesian) fitting of a population model that Schooler et al. (2011) were able to explain biological control success, while Pagel and Schurr (2012) used a Bayesian framework for solving a similar problem based on demographic modeling. Knowing the system well enough to propose (several) population models and having the data and statistical tools to choose among them is the central methodological challenge.

Conclusions

We have highlighted challenges and potential solutions in four areas crucial for the future development of macroecology: the roles of history and underlying processes, and the need for better data and more appropriate analytical methods. Here, we have pointed out the main current problems and possible solutions. Without these, we shall not be able to maintain the successful abstraction and generalization of ecological understanding from large data sets that is macroecology.

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Supplementary material (Appendix E7364 at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.