

0 What's on the horizon for macroecology? 53

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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

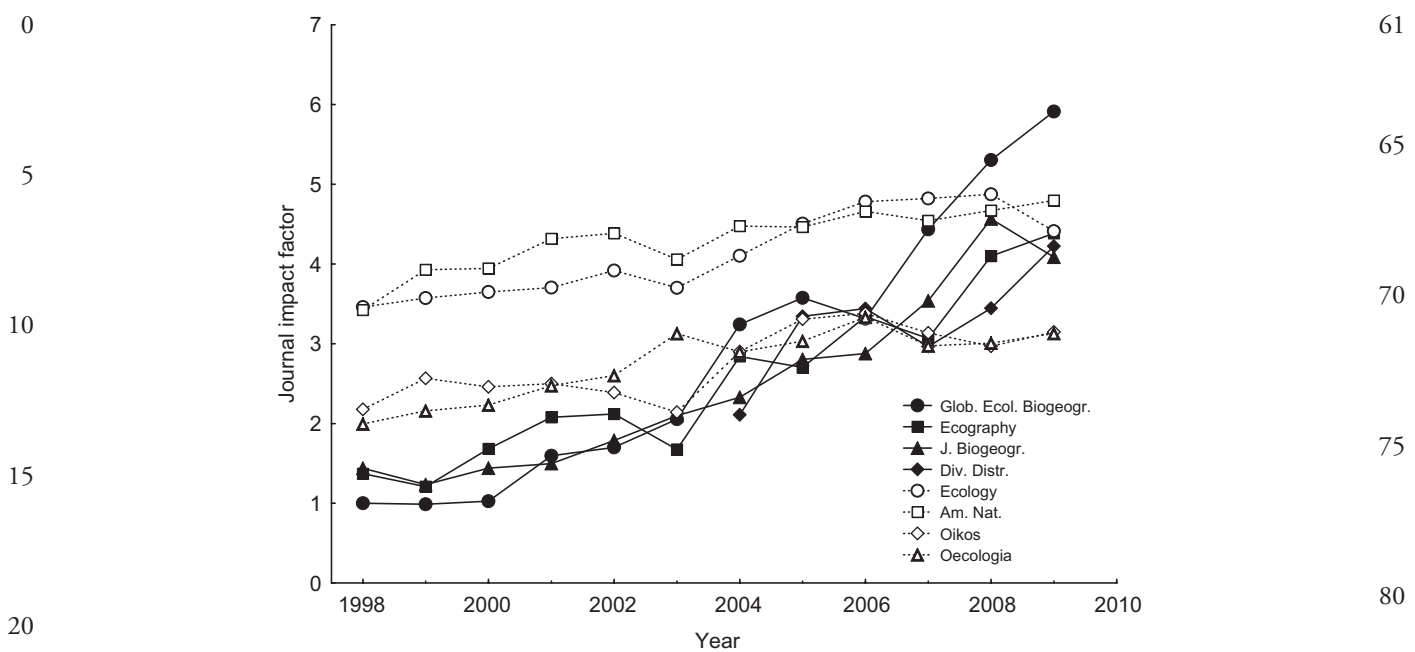


Figure 1. Impact factors (ISI Web of Science, < www.isiknowledge.com >) of four journals with a strong focus on macroecology (filled symbols), in comparison to four established general ecology journals (open symbols) for the same time period. Impact factors are an index of citation frequency of articles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

0 Hind-casting of species distributions based on recon- 61
 10 structions of past climates by techniques of ‘ecological niche 62
 15 modeling’ (Elith and Leathwick 2009), in particular, is an 63
 20 increasingly employed method with great potential, but also 64
 25 many pitfalls (Nogues-Bravo 2009, Svenning et al. 2011). 65
 30 Such approaches are seen as particularly useful in combi- 66
 35 nation with phylogeography (see below) as they can pro- 67
 40 vide information on past scenarios of distribution, hence 68
 45 the preconditions of speciation events (e.g. allopatry of 69
 50 populations), that can then be tested against phylogenetic 70
 55 reconstructions. 71
 60 Species distribution models and analyses of geographic 72
 65 patterns of species richness and endemism may profit from 73
 70 novel ways to quantify the degree and pattern of past climate 74
 75 fluctuations and the potential that landscapes (and seas- 76
 80 capes) offer for species to track such changes (Loarie et al. 2009, 77
 85 Sandel et al. 2011) or to provide microrefugia (Rull 2009). 78
 90 2) The integration of phylogenetic information into 79
 95 macroecological analyses is encouraged by the increasing 80
 100 availability of comprehensive phylogenies (Bininda-Emonds 81
 105 2004, Wiens and Donoghue 2004, Davies et al. 2008). 82
 110 Many different approaches have been taken to incorporate 83
 115 these data into macroecological analyses. They range from 84
 120 phylogenetically informed analyses of trait correlations or 85
 125 deconstructions of spatial patterns into different phyloge- 86
 130 netic lineages or systematic groups (Marquet et al. 2004, 87
 135 Beck and Kitching 2009) to more complex calculations of 88
 140 phylogenetic diversity or phylogenetic structure in space 89
 145 (Hawkins et al. 2007, Davies et al. 2008). 90
 150 Comparing the relatedness of coexisting taxa to the phy- 91
 155 logeny of the regionally available pool (i.e. whether coexist- 92
 160 ing communities indicate phylogenetic overdispersion and 93
 165 clustering) has yielded interesting results in community 94
 170 ecology (Webb et al. 2002). Theoretical expectations have 95
 175 been formulated regarding the patterns of phylogenetic 96
 180 composition and trait similarity that may be expected under 97
 185 various geographical and ecological scenarios (Emerson and 98
 190 Gillespie 2008, Cavender-Bares et al. 2009). Techniques of 99
 195 incorporating such ‘local’ phylogenetic measures into larger- 100
 200 scale macroecological analyses are currently being devised 101
 205 (Graham and Fine 2008, Kühn et al. 2009, Dormann et al. 102
 210 2010, Kissling et al. 2012). We think this is a very promising 103
 215 approach to be developed and applied. 104
 220 Explicitly analyzing the link between phylogenies and 105
 225 emergent traits (such as niche dimensions) that affect distri- 106
 230 butions is another approach that may considerably advance 107
 235 our understanding of the relevance of the past for the pat- 108
 240 terns observed today (Hof et al. 2010, Wiens et al. 2010). 109
 245 Phylogeography, the analysis of (mainly intraspecific) mole- 110
 250 cular phylogenies in a spatial context (Avice 2009), may be 111
 255 particularly useful to macroecology in the context of provid- 112
 260 ing independent tests for geographic range scenarios from 113
 265 past distribution modeling (see above). However, data and 114
 270 techniques from phylogeography – be it intra- or interspe- 115
 275 cific – may also benefit a potential revival of cladistic bioge- 116
 280 ography, as outlined below. 117
 285 3) Integrating classical historical biogeographical 118
 290 approaches with macroecology is a third, rarely utilized 119
 295 approach. Cladistic biogeography uses the phylogeny of taxa 120
 300 occurring in a region to infer historical events that shaped 121
 305 their evolution. Area cladograms, depicting the relatedness 122

of regions with respect to speciation of an investigated taxon 61
 (Morrone 2009), might reflect the evolutionary relevant 62
 geographic history of regions (e.g. vicariance events). These 63
 patterns can be tested and verified against other taxa. The 64
 designation of biogeographic regions, for example, can be 65
 the outcome of such historical analyses, going beyond 66
 current faunistic or floristic similarities (Kreft and Jetz 67
 2010). Broad biogeographical regionalizations have been 68
 included in macroecological analysis to investigate regional 69
 historical effects (Kreft and Jetz 2007, Hof et al. 2008). A 70
 drawback of such analyses is that historical effects are likely 71
 to leave their mark at much finer spatial scales. For instance, 72
 a biogeographical region like the Afrotropics contains many 73
 sub-regions that are assembled from different species pools 74
 with different evolutionary histories. Indeed, many finer- 75
 scaled, hierarchical biogeographic classifications are avail- 76
 able in the literature for many regions and taxonomic groups 77
 (de Klerk et al. 2002, Kreft and Jetz 2010, Rueda et al. 78
 2010) that may provide useful geographic templates to inves- 79
 tigate regional effects. We suggest that these data should be 80
 utilized more and that the approach be expanded to fit the 81
 extent and resolution of macroecological analyses (i.e. hav- 82
 ing small regions, such as islands or grid cells, at the tips 83
 of area cladograms; Fig. 2). Existing information from phy- 84
 logenies or supertrees (Bininda-Emonds 2004, Bininda- 85
 Emonds et al. 2007) should also continue to be exploited 86
 more for cladistic biogeographic analyses. Advances in his- 87
 torical inference and methodology are being made and may 88
 lead to accelerating the construction of area cladograms 89
 (Linder 2001, Donoghue and Moore 2003). Knowledge 90
 of evolutionary history in grid cells would allow mapping 91
 and incorporating the historical homogeneity of cells as a 92
 continuous variable in macroecological modeling, facilitat- 93
 ing much finer-scaled and robust partitioning of current vs 94
 historical effects on response variables. 95
 Integrating phylogenetic and distributional data into a 96
 place-based history could be achieved by a transfer of avail- 97
 able techniques of accounting for phylogenetic contingen- 98
 cies in interspecific comparative studies (Fig. 2; Freckleton 99
 et al. 2002). Clearly, it will require some effort to assemble 100
 the relevant data (or to collect new data where necessary), 101
 and to devise and assess analytical procedures that best inte- 102
 grate them into analyses. If successful, however, this would 103
 represent a major advance in bridging the conceptual and 104
 methodological gaps between the aggregation levels of ecol- 105
 ogy, macroecology, and historical biogeography. 106

Putting processes into macroecology 110

Macroecology has proven very successful in describing 111
 general patterns, but ultimately this is not sufficient if 112
 we cannot infer causalities (Dormann 2007, Kearney and 113
 Porter 2009). It is a long-standing issue in ecology to under- 114
 stand the processes behind patterns (West and Brown 2005), 115
 even more so as this is a prerequisite for reliable future 116
 predictions of impacts of climate and land-use change and 117
 for the development of mitigation and adaptation strate- 118
 gies. Ecological processes and mechanisms have long been 119
 investigated much more thoroughly on the community scale 120
 (Supplementary material Appendix 1). On a macroecological 121

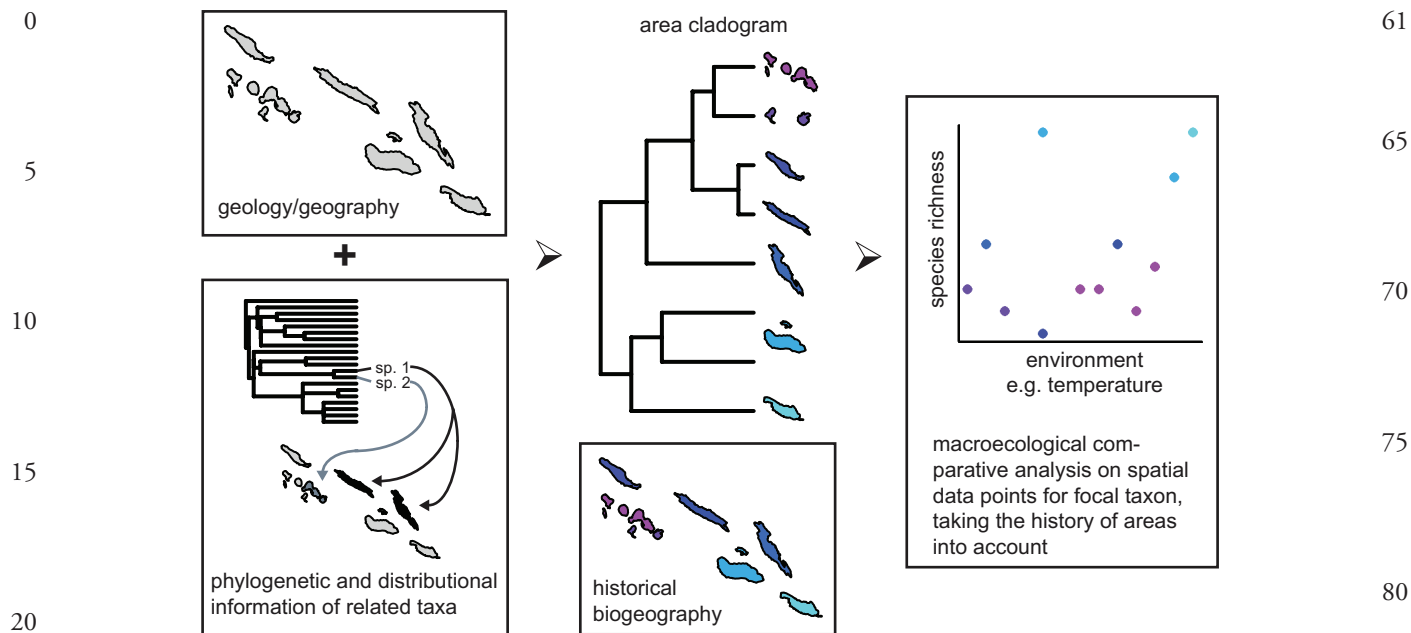


Figure 2. Integration of historical biogeography into macroecological research using area cladograms and comparative methods. We illustrate an island chain here, but the approach could be similarly applied to grid cells. The macroecological question addressed as an example is the relationship of species 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 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.

0 Integrating all parameters that potentially affect commu-
 nity 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),
 5 they account for both abiotic and biotic filters by combining
 species source pools and ecological assembly rules with mac-
 roecological modeling and species distribution modeling.
 However, Guisan and Rahbek (2011) admit that ecological
 assembly rules, which are the key to explaining biotic interac-
 10 tions 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
 15 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.

20 There seems to be an interesting parallel between current
 directions in understanding patterns in macroecology and
 history of advancement in understanding of patterns of pop-
 ulation dynamics. Research on population dynamics started
 with simple, top-down, non-spatial and non-individual-
 based models. This has changed dramatically in recent
 25 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 find-
 ings, the use of bottom-up approaches advanced the abil-
 ity to predict future population dynamics considerably. This
 30 may be true for macroecology as well. With the advancement
 of data quality, statistical methods, and macroecological the-
 ory, we will be increasingly able to move beyond describing
 patterns towards including and testing the processes behind
 them, particularly dispersal and biotic interactions.

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-
 65 studied groups, this goal has not been achieved. Moreover,
 missing data on species traits, distributions and phyloge-
 netic relatedness make it difficult to thoroughly assess global
 biodiversity patterns and underlying processes. Although a
 range of automated assessment frameworks were developed
 70 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 uncer-
 tainties and gaps in the raw data. Specifically, macroecologi-
 cal research until now has largely been driven by data already
 75 available, revealing two major shortcomings: 1) limited
 coverage of biomes, taxa and spatial scales, and 2) insuffi-
 cient or unknown data quality. We warn against the com-
 mon practice of accepting published data as unquestioned
 truth: by citing a data source, the suitability of these data for
 80 the question at hand is often taken for granted (Robertson
 et al. 2010), in marked contrast to reviewer skepticism on
 researchers’ own data.

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

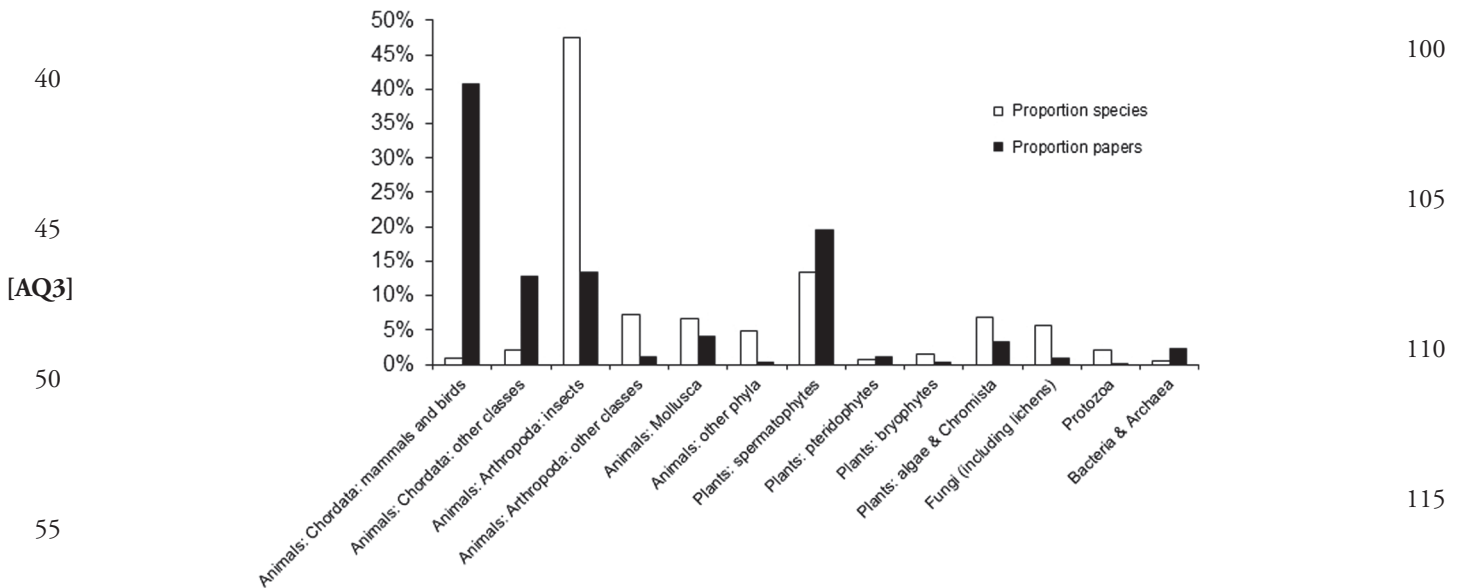


Figure 3. Distribution of macroecological papers in ISI Web of Science (3 April 2010) regarding major taxa. The bar chart depicts the proportion of papers in relation to the proportion of described species of the respective lineage (for details on the literature search see Supplementary material Appendix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

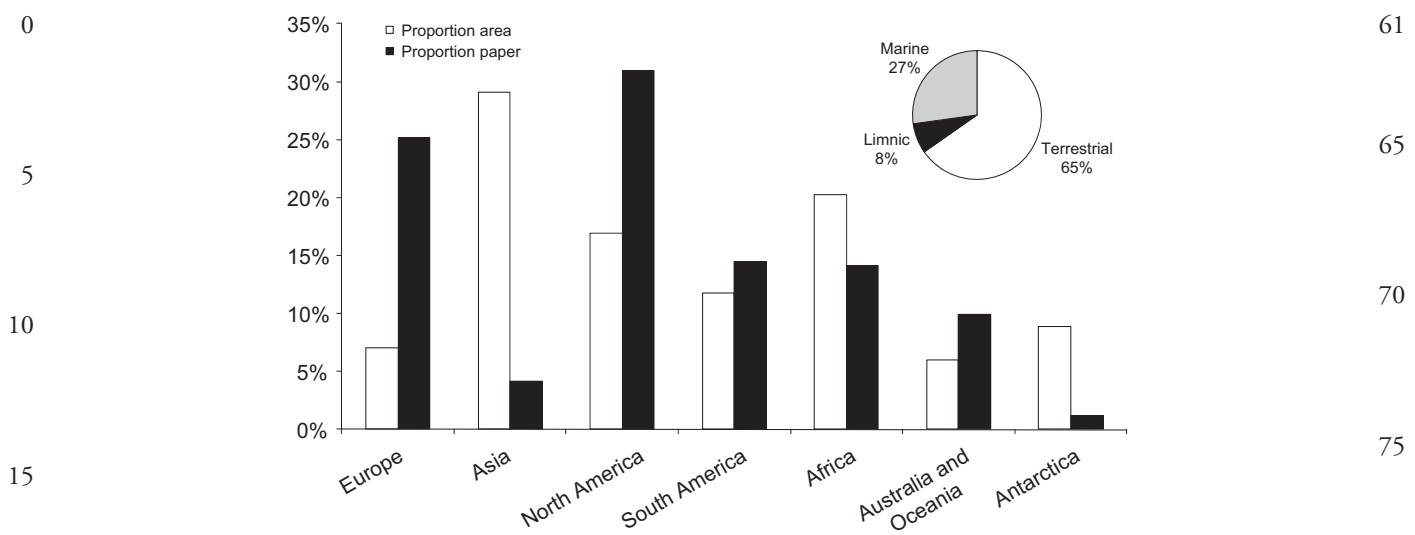


Figure 4. Distribution of macroecological papers in ISI Web of Science (3 April 2010) regarding terrestrial, limnic, and marine habitats (pie chart). The bar chart depicts the geographic distribution of the terrestrial studies to continents and relates this to the proportional surface of each continent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

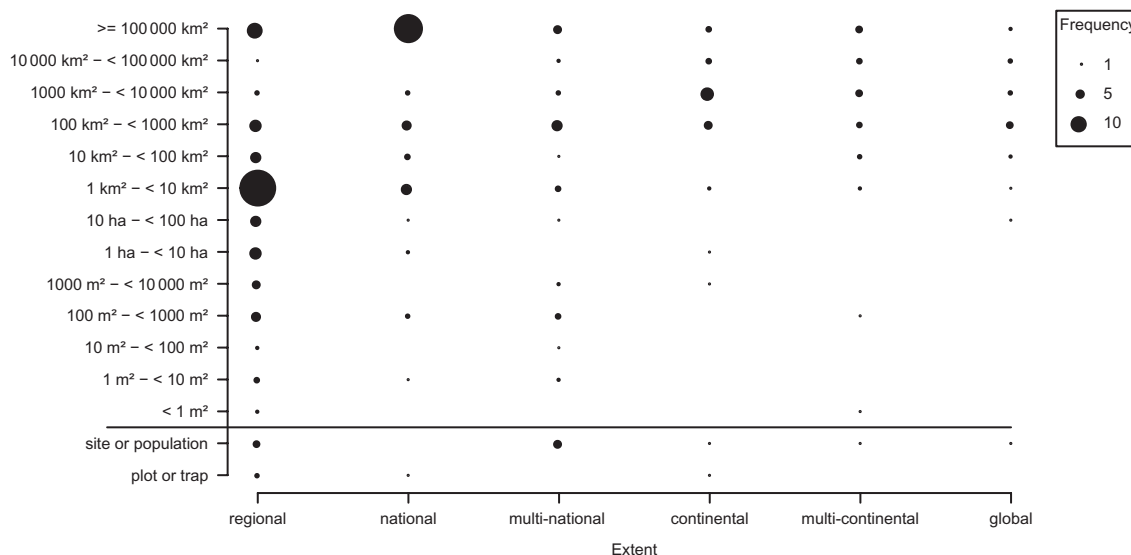


Figure 5. Extent and grain sizes used in macroecological studies published between 2007 and 2009 (for details on the literature search see Supplementary material Appendix 4). Dot size represents the number of studies conducted for a given extent and grain size. Dot size varies continuously; the legend 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.

0 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).

10 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.

25 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).

45 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 years 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

0 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
5 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
10 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).

[AQ2] 15 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
20 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
25 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
30 (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
35 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
40 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
45 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.

50 Conclusions

We have highlighted challenges and potential solutions in
four areas crucial for the future development of macroecology:
55 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
60 large data sets that is macroecology.

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