



There's more to macroecology than meets the eye

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ABSTRACT

Macroecology sits at the junction of, and can contribute to, the fields of ecology, biogeography, palaeontology and macroevolution, using a broad range of approaches to tackle a diverse set of questions. Here, we argue that there is more to macroecology than mapping, and that while they are potentially useful, maps are insufficient to assess macroecological pattern and process. The true nature of pattern can only be assessed, and competing hypotheses about process can only be disentangled, by adopting a statistical approach, and it is this that has been key to the development of macroecology as a respected and rigorous scientific discipline.

Keywords

Geographical ecology, macroecology, mapping, Rapoport's rule, spatial autocorrelation, statistics.

INTRODUCTION

In a recent issue of *Global Ecology and Biogeography*, Ruggiero and Hawkins (2006) note the debt that the development of macroecology owes to Robert MacArthur and his book *Geographical Ecology* (MacArthur, 1972). However, they go on to suggest that macroecology has taken a 'deleterious detour' from these roots in that the geographical perspective has been lost, citing decreasing numbers of maps in more recently published books on the subject. They suggest that macroecology has instead adopted a statistical approach to ecology, often with an 'individual species focus' and the application of comparative analysis to explore pattern, and favouring scattergrams over maps. They argue that this 'non-geographical' approach provides no information on the location of species, and hence that the spatial environmental effects underlying species distribution and diversity cannot be assessed. Further, they argue that most processes studied by macroecologists are geographical, even if they cannot depict them on a map, and so call for a return to the basics and a greater emphasis on mapping. We think that Ruggiero and Hawkins significantly misrepresent the situation with regard to macroecology, and here we present an alternative view on the importance of mapping in this discipline.

MACROECOLOGY IS MORE THAN GEOGRAPHICAL ECOLOGY

The field of macroecology does indeed owe a debt to the work of MacArthur (see Blackburn & Gaston, 2003a; Brown *et al.*, 2003), but macroecology is more than geographical ecology. Blackburn

& Gaston (2002) paraphrased Brown (1995) in describing macroecology as 'a way of studying relationships between organisms and their environment that involves characterizing and explaining statistical patterns of abundance, distribution, and diversity, exploring the domain where ecology, biogeography, palaeontology and macroevolution come together'. Marquet (2002) summarized macroecology as the search for general and invariant principles underlying the diversity and variability of ecological systems. Rather more broadly, Brown *et al.* (2003) identified a perspective on macroecology that was concerned with the patterns and processes revealed by the statistical distributions of variables among large collections of equivalent 'ecological particles', such as individual organisms within species or species within communities and biogeographical regions. Thus, it should be clear that 'geographical ecology' is but one facet of macroecology.

Nevertheless, some see that facet as the dominant one. Ruggiero & Hawkins (2006) contend that 'most questions asked by macroecologists are geographical, even if they do not express them on a map' because 'the evolutionary process is always embedded within a geographical context, and the evolution of form is not independent of time and location'. This last statement may be correct, but it is also unhelpful. One could logically go further and conclude from it that all of evolution (and indeed ecology) is geographical. Yet, it is clear that much of the study of evolution and ecology progresses perfectly well without considering the geographical perspective at all. We suspect that the attempt to define most of macroecology as geographical has more to do with specific than general research agendas within the field.

Many of the concerns of macroecology cannot easily, or sensibly, be represented on a map. Brown (1995) was the first to present

a vision of macroecology as a broad research programme. Amongst his explicit aims were to introduce geographical and historical perspectives to ecology, but also ecological perspectives to the history and composition of regional and continental biotas. He recognized the geographical perspective as one of several within the field. Gaston & Blackburn (2000) attempted to review what were then perceived to be the main concerns of macroecology, and to begin to draw connections between them. Amongst the issues they addressed were the interspecific frequency distributions of abundance, range size and body size, the bivariate interspecific relationships between these variables, spatial variation in species richness (latitudinal, longitudinal, altitudinal) and in the distribution of abundance, range size and body size, nestedness in community composition, beta diversity, local–regional richness associations, temporal dynamics in speciation and extinction, and species–area relationships. The symposium volume on macroecology (Blackburn & Gaston, 2003b) that includes the chapter with Brown *et al.*'s (2003) definition also has chapters on the ecological and evolutionary implications of the scaling of vascular networks (Enquist, 2003), models of niche apportionment (Nee, 2003), the relationship between life history, population dynamics and extinction risk (Reynolds, 2003), macroecology and palaeobiology (Jablonski *et al.*, 2003), whether speciation rates are influenced by body size (Purvis *et al.*, 2003), and whether diversification is driven by key innovations (Vogler & Ribera, 2003). Thus, macroecology has not drifted from geographical ecology or biogeography, but has charted its own course, in directions that have been appropriate to its search for general and invariant principles underlying ecology. Maps are a valid way to present some of the patterns of macroecology, and can obviously help understand several of the concerns just listed. Nevertheless, mapping is by no means the dominant way or the only way, and in many cases it is not even an appropriate way.

In fact, much of the historical provision of maps was associated with a marked paucity of any analysis of those data (e.g. Simpson, 1964; Cook, 1969; MacArthur, 1972), so that without the statistical perspective little progress towards an understanding of mechanism was made. Arguably, that may have contributed to large-scale ecology languishing in the 1970s as it was eclipsed by the strides made by experimental approaches to ecology (Gaston & Blackburn, 1999; Brown *et al.*, 2003). While there may indeed be a historical decline in the proportion of figures published in 'macroecology' texts that are maps, that decline seems to us to be correlated with an increase in the amount of evidence provided in those texts about the statistical reality of the geographical patterns being discussed, and with an increase in the level of understanding of macroecological patterns and their determinants.

Even where macroecology can be mapped, maps are only the first step on the path to understanding. They illustrate patterns, and may indeed provide clues about process, and so the provision of more maps may well be desirable. That said, it is important to recognize that many authors (ourselves included) will have mapped their data as part of a study, without necessarily always publishing those maps. Moreover, rigorous assessment of mechanism will only come from the application of statistical approaches to

the data that underlie the map. Many macroecological analyses that do not use maps relate the ecological and evolutionary traits of species in local assemblages to various environmental factors. It is the statistics of these relationships that ultimately indicate whether or which spatial environmental effects are concluded to underlie species distribution and diversity, and the presentation or otherwise of maps does not preclude appreciation or assessment of such effects. Nor does provision of maps guarantee that spatial statistics will be applied, or applied appropriately. Of course, the same can be said of bivariate scatterplots, which will be more misleading by dint of their inability to depict spatial autocorrelation, but that does not alter our point: maps are not crucial to answering the questions being addressed (e.g. Turner & Hawkins, 2004), and clearly neither authors nor referees have seen the lack of maps in publications as an impediment to understanding macroecological patterns.

RAPOPORT'S RULE AS AN ILLUSTRATION

An example of a macroecological pattern that can be mapped, but for which mapping is only one approach to understanding pattern and process, is spatial variation in geographical range sizes. This is sometimes termed 'Rapoport's rule', although the term was originally coined by Stevens (1989) to designate the positive correlation he observed when plotting the average latitudinal range size of a group of organisms inhabiting a given latitude against latitude (following Rapoport's (1982) explicit exploration of latitudinal effects). Perhaps unsurprisingly in the circumstances, the most common method of studying Rapoport's rule is to plot a measure of range size vs. latitude (e.g. Ruggiero, 1994). The next most common is analysis across multiple species (e.g. Hawkins, 1995), while few studies have mapped range size variation (but see Orme *et al.* (2006) for the global map for birds). Although Rapoport's rule was originally framed in terms of average range sizes across latitudinal bands, the rationale behind Stevens's (1989) analysis was that range size variation was an outcome of the same process as the latitudinal species richness gradient, and hence that it could shed light on the cause of this latter pattern. This suggests that if true, tests of the association between species richness and range size can be made using other spatial dimensions, such as longitude (e.g. Graves & Rahbek, 2005), altitude (e.g. Stevens, 1992) or depth (e.g. Smith & Gaines, 2003), or even directly, though we note that the last of these is surprisingly rare (but see Orme *et al.*, 2006). An explicitly geographical approach to range size variation would undoubtedly present a useful perspective on pattern in this case.

Nevertheless, even here it is not fundamentally necessary to map range size variation to study or to understand it. Most of the early advances in understanding this pattern, while arguably limited, did not make use of maps. Moreover, other approaches to spatial variation in range sizes provide different, and equally useful, perspectives. For example, as noted above, range size variation has also been assessed in terms of interspecific comparisons. This approach is conceptually quite different from a mapping approach, as it considers not the mean (or median, minimum or maximum) range size of assemblages of coexisting

species, but rather addresses (implicitly or explicitly) how the relationship between range size and range position evolves along a phylogeny. The latter is a departure from Rapoport's rule as originally formulated (Stevens, 1989), but is no less valid a way of exploring variation in range size. The difference between the two approaches means that we would not expect them necessarily to give the same answer, for example if a tendency towards large ranges in certain regions was due to the absence of higher taxa with a propensity towards restricted ranges, rather than repeated correlated evolution across a phylogeny. Maps do not reveal the evolutionary history underlying patterns such as Rapoport's rule.

Ruggiero & Hawkins (2006) concede that the evolutionary processes underlying patterns of association between ecological traits are indeed difficult to map, but use the point to argue that the problem is that currently available techniques are insufficient. We agree that it would be very useful to have access to techniques that allow spatial and phylogenetic autocorrelations to be integrated into a single model for the evolution of ecological associations. However, to use that lack as a stick with which to beat the use of those techniques that are currently available is unfair and unjustified. As we have already noted, there are other macroecological questions than just the mappable ones, and the available phylogenetically independent methods (e.g. independent contrasts or generalized least squares) have long been useful tools for investigating them. We would also note that even mappable patterns arise through the interaction of species characteristics with the environment, and hence modelling the evolution of those characteristics with the methods that are available is both reasonable and logical (see also Freckleton *et al.*, 2003). Modern phylogenetic comparative methods can and have been used to track the evolution of ecological associations across phylogenies, and indeed the problem has been less the utility of the methods than actually getting ecologists to use them (Harvey *et al.*, 1995; Harvey, 1996).

While maps clearly have their uses, it is important to remember that they can also be deceiving. It is well known that most people (including many ecologists) carry a completely false impression of global geography in their heads, through familiarity with map projections (e.g. Mercator) that were useful for crossing oceans, but not for providing a sense of the relative size of land masses. Equal areas on maps do not always translate into equal areas on the planet's surface, which can distort presentations of associated biological patterns. Mapped patterns can also give an artificial sense of relationships for the variables that they express, as the eye likes to see pattern regardless of whether it truly exists. For example, Orme *et al.* (2006) present a map of range size variation in birds of the world, but do not analyse the likely determinants of that variation. Nevertheless, visual inspection of the map clearly suggests that, aside from islands, small range sizes are located particularly in the tropical Andes. However, we are aware of other situations from our own work in which such visible associations have been misleading: by drawing attention to the peaks (or troughs) in the geographical distribution of a variable, maps have in fact highlighted outliers at the expense of more general geographical relationships. Thus, the

maps themselves may distract from details that would be more apparent were the data presented in a different manner. Maps may also bias subsequent tests of mechanism towards the 'obvious' answer, when other ways of plotting the information would enable the patterns that appear to occur in the map to be investigated more closely. That perception of pattern and process is influenced by the method of analysis clearly works both ways.

In the case of bird range sizes, there are several possible answers. One is that, globally, small ranges are associated with islands and, for continental species, with high elevational variation in areas of high ambient energy. But, as we noted above, it is only through analysis of the data underlying the maps that any such association can be identified, and other equally plausible mechanisms (such as the effects of productive energy or habitat diversity) ruled out.

CONCLUSIONS

Scientific disciplines almost always evolve in unpredictable directions, but the unpredictability does not mean that the evolution is not comprehensible with the benefit of hindsight. Fields develop as data, the techniques to analyse them, and the machinery to run those analyses, become available. Historically, the presentation and robust statistical analyses of large-scale spatial relationships in ecology would have been hindered by the paucity of appropriate distributional data sets, the difficulty of producing publication-quality maps from the data that were available, a lack of understanding of the techniques necessary for spatial analysis, and the limited computing power available to implement such analyses (indeed, computing power remains a limitation on robust spatial analyses of large data sets). Now that these shortcomings have largely been rectified, and it is possible to map global patterns in species geographical distributions and perform spatially explicit analyses on them, it is still unfair to criticise workers in the past for doing the best they could with the tools then available.

Even so, maps are no more than a tool themselves, and indeed on their own they are insufficient to assess macroecological pattern and process. Whether or not maps are presented, the true nature of pattern can only be assessed, and competing hypotheses about process can only be disentangled, by adopting a statistical approach. We contend that the statistical perspective has not been a 'deleterious detour', but rather key to the development of macroecology as a respected and rigorous scientific discipline. Visualization is important in science, but ultimately there is a limit to what can be learnt from looking at pictures.

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