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GUEST EDITORIAL

The island rule and a research agenda for studying ecogeographical patterns

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ABSTRACT

We are currently experiencing a resurgence of interest in ecogeographical rules, which describe general trends in morphology and related traits along geographical gradients. In order to develop a more comprehensive understanding of the generality and underlying causal mechanisms for these patterns, we recommend a new, more integrated research agenda. In particular, we recommend studies that simultaneously consider different clines in morphology, geographical ranges and diversity as intricately related phenomena; all being ecological, evolutionary and biogeographical responses of organisms to selection regimes that vary non-randomly over space and time, and among species with different ecological and evolutionary histories.

Keywords

Bergmann's rule, biogeography, body size, ecogeographical rules, invasive species, island biogeography, island rule, latitudinal gradients, macroecology.

INTRODUCTION

The relationship between pattern and process will always be a central focus of the natural sciences, especially for disciplines as integrative, and involving such a broad range of temporal and spatial scales, as biogeography. Among some of the most intriguing patterns in this field are ecogeographical rules, which describe general trends in morphology and related traits along geographical gradients. Included among these are the patterns ('rules') described by Bergmann (latitudinal variation in body size: Bergmann, 1847); Allen (geographical variation in appendage size: Allen, 1878); Gloger (geoclimatic variation in pelage colour: Gloger, 1883); and Jordan (latitudinal variation in vertebra number of marine fish: Jordan, 1892). A related group of patterns includes those described by macroecologists and aerographers, including Rapoport's rule (latitudinal, elevational and bathymetric clines in geographical range size: Rapoport, 1982; Stevens, 1989, 1992, 1996; Smith & Gaines, 2003); and correlations between body size and geographical range size (Brown, 1995; Blackburn & Gaston, 2003; Gaston, 2003). While few, if any, of these patterns actually merit the status of an invariant 'rule' of nature, each has the potential to identify the forces influencing the evolution and diversification of regional biotas. However, given the large and multiscale nature of these patterns, along with the challenges of conducting biogeographical studies at these scales, the search for underlying causal mechanisms influencing dynamics in traits ranging from body size of individuals to geographical range size of species may prove futile unless we develop a more integrative programme for studying what we believe are intricately related patterns.

The dynamic tension between theory and empiricism, and debates between alternative causal explanations for observed patterns, have provided some fundamental advances in our understanding of the geography of nature. These challenges and debates continue today, with the diversity of alternative explanations perhaps largely a result of differences in the systems and biota, or spatial and temporal scales, that we study. Each of these differences can provide a unique clue into causal mechanisms for some very general patterns of geographical variation of life.

A number of recent papers have reassessed the generality and causality of ecogeographical patterns. For example, some studies (Meiri *et al.*, 2004a, 2006) question the generality of Foster's (1963, 1964) island rule, which describes body-size trends in insular vertebrates; while others have confirmed it for a diversity of taxa, ecosystems and geographical regions (McNab, 2001, 2002; Anderson & Handley, 2002; Clegg & Owens, 2002; Boback, 2003; Boback & Guyer, 2003; Schmidt & Jensen, 2003, 2005; Brown *et al.*, 2004; Morwood *et al.*, 2004; Lomolino, 2005; McClain *et al.*, 2006; White & Searle, 2006). Similarly, there has been a recent resurgence of interest in other ecogeographical patterns, such as Bergmann's and Rapoport's rules, again including reports of anomalous results

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(Gaston *et al.*, 1998), as well as other studies confirming the generality of these patterns (in mammals: Ashton *et al.*, 2000; Meiri & Dayan, 2003; Meiri *et al.*, 2004b; in birds: Ashton, 2002a; Meiri & Dayan, 2003; in salamanders: Ashton, 2002b; in turtles: Ashton & Feldman, 2003; and in ants: Cushman *et al.*, 1993; Kaspari & Vargo, 1995). Rather than debating the merits of any particular papers, we use this opportunity to suggest how these independent and sometimes contradictory lines of research can be integrated into a more comprehensive, hypothesis-driven research agenda for studying ecogeographical patterns.

Here we first summarize the epistemology of the island rule as an illustrative case study. This pattern was first described by Foster (1963, 1964), but it was not labelled as a rule (and one 'with fewer exceptions than any other ecotypic rule in animals') until VanValen's papers in 1973 (Van Valen, 1973a,b: p. 35). Originally, Foster described the pattern as a tendency for different taxa (orders of mammals) to exhibit different evolutionary trends on islands, rodents tending to increase, and carnivores and ungulates tending to decrease in body size. Later, Heaney (1978), Lomolino (1985) and others reinterpreted the rule to be a graded trend from gigantism in the smaller species to dwarfism in the larger species of mammals. This recasting of the island rule reflected the heuristic tension between process and pattern, and theory and empiricism. The earliest articulation of the island rule suggested disparate evolutionary trends among mammalian orders, but this was soon found to be inconsistent with modern evolutionary theory. Rather than invoking some overriding importance of phylogenetic inertia that somehow differs among mammalian orders, the island rule (*sensu nova*) instead is inferred to reflect differences in selective pressures on islands and among species of different body size (therefore the graded trend should occur within, as well as among, mammalian orders; see explanations by Heaney, 1978; Lomolino, 1985, 2005; Adler & Levins, 1994; Adler, 1996; Marquet & Taper, 1998; McNab, 2001, 2002; Gould & MacFadden, 2004). Note, however, that the geographical context of the island rule's primary pattern is typically limited and binary: terrestrial populations occur in just two types of ecosystem, islands or mainland sites. Yet we know that islands vary in area, isolation, latitude and other characteristics that influence the abilities of organisms to colonize and maintain populations. Thus, in addition to the primary pattern, body size of insular populations of particular species should not be constant, but should vary in a non-random manner among islands and archipelagoes. These secondary or corollary patterns provide excellent opportunities to evaluate alternative explanations for the island rule, for example by testing for correlations between body size and the area, isolation and latitude of islands (see studies summarized in Table 3 of Lomolino, 2005), or equivalently by testing for dynamics in body size following range expansion and vicariance, or tectonic events, climatic fluxes and associated changes in productivity, community structure and isolation of habitats and populations (Case, 1976, 1982, 2002).

Evidence for the island rule

Until very recently, the island rule seemed to apply almost exclusively to mammals, particularly non-volant, terrestrial mammals. Early papers by Foster (1963, 1964), Heaney (1978) and Lomolino (1983, 1985) relied on a combination of their own field studies and a larger body of data collected from manual searches of museum collections and libraries. Given that these studies were conducted well before automated searches were possible, they were far from complete. Yet the diversity of species and islands comprising these data is considerable, including species ranging in size from shrews (*Sorex* spp.) to Pleistocene elephants and mammoths (e.g. *Mammuthus primigenius*), and islands ranging in area from < 1 ha to $> 500,000$ km^2. Recently these data were transcribed into digital files and re-analysed at a range of taxonomic levels (Lomolino, 2005), again confirming the generality of the island rule and, based on an updated literature review, suggesting that it applies not just to most mammals but to other vertebrates as well (database available on the Resources Page of the International Biogeography Society, http://www.biogeography.org). This does not mean that this and similar data sets are without gaps or other shortcomings; the use of modern search engines can probably increase the volume of this data set many-fold.

SETTING A RESEARCH AGENDA FOR STUDYING ECOGEOGRAPHICAL RULES

Simply expanding this or other ecogeographical data sets, however, is not as likely to contribute to a new synthesis as would a well coordinated research agenda that is based on causal hypotheses, conducted across an appropriate range of spatial and temporal scales, and designed to include the most relevant measures of dependent variables (in this case, alternative measures of body size) and optimal ranges of independent variables (e.g. trophic status, diet, ecological interactions and vagility of the species; area, isolation, species diversity, latitude, age and productivity of the islands). This would include coordinated studies that use standardized methodology and phylogenetic information, thus allowing comparisons among different groups of species and among archipelagoes (those differing in the features listed above).

If all relationships were linear, then the task of designing insightful, local- to global-scale field studies for subsequent synthesis would be relatively simple. Nonlinear relationships, however, are quiet common in ecology and biogeography, thus our studies need to be informed by theory (particularly the predicted nature of response curves that may, for example, assume polytonic, sigmoidal or asymptotic relationships; or those that include thresholds marking qualitatively different relationships between dependent and independent variables; Lomolino & Weiser, 2001; Muradian, 2001; Fahrig, 2002; Toms & Lesperance, 2003; Luck, 2005).

Just as importantly, we need to analyze existing data sets (comprising complex and heterogeneous collections of data gleaned from the literature and, ultimately, from many hundreds of field studies) with serious consideration of their limitations; for the most part, they were not designed to address the hypotheses we are now testing. For example, our understanding of the relevant characteristics of islands and species (listed above) will always be imperfect, as will our understanding of the complexity and underlying functional relationships among these variables. Even body size (the dependent variable in many ecogeographical studies) and geographical range size (the 'fundamental unit' of biogeography) can be measured in a variety of ways. Regardless of the alternative metric used, each probably exhibits a different relationship with independent variables and underlying processes, even for the same species, archipelago and geographical region.

We should also consider the possibility that these heterogeneous data sets may be unintentionally biased: they may include a limited or unrepresentative range of independent variables (e.g. based on studies of just the smallest islands, given logistical considerations, or in other cases based on data from just the largest islands, given collection biases); or they may comprise data that are complicated with confounding correlations among independent variables (e.g. in many archipelago-scale studies, island area and isolation tend to be negatively correlated). It is therefore likely that the challenges of inferring patterns and causality from such a heterogeneous collection of studies, and from a broad range of archipelagoes, regional biota and temporal and spatial scales, will contribute to both Type I errors (e.g. mistakenly declaring a body size trend to be statistically significant) and Type II errors (failing to detect the predicted pattern when it did occur; Gotelli & Ellison, 2004).

Returning to our case study of the island rule, recent studies continue to report the pattern for a growing diversity of archipelagoes and biota, most recently including such diverse species as common shrews (*Sorex araneus*) of the Scottish islands (White & Searle, 2006); mammals and birds inhabiting anthropogenically transformed landscapes in Denmark (Schmidt & Jensen, 2003, 2005); marine invertebrates in the isolated reaches of the deep sea (McClain *et al.*, 2006); Late Pleistocene hominins of Indonesia (Brown *et al.*, 2004; Morwood *et al.*, 2004); and Late Jurassic and Cretaceous sauropod dinosaurs of ancient Palearctic islands (Jianu & Weishampel, 1999; Sander *et al.*, 2006; see also Palkovacs, 2003; Millien & Damuth, 2004; Wikelski, 2005). Nevertheless, in our assessments of the generality of this and other ecogeographical rules, we should be vigilant not to dismiss or ignore seemingly anomalous findings. While they may, in some cases, be by-products of limitations of the study design and of the complexity inherent in studies of large-scale phenomena (authentic Type II errors), such exceptional patterns may actually reflect distinctive features of the system or species groups, including those associated with alternative causal explanations for ecogeographical patterns (e.g. exceptional levels of productivity, diversity, age, area or isolation of the islands; or unusual resource requirements, ecological interactions, body plans, physiology or vagility of the species).

Post hoc use of the comparative approach (in this case, comparing features of the exceptional archipelagoes and biota with those exhibiting patterns consistent with the rule in question) will continue to prove a powerful tool in biogeography. Moreover, our abilities to design and conduct field studies at local-to-global scales have now advanced to the point that such studies, if based on *a priori* consideration of causal mechanisms, can provide some fundamental insights into the geographical variation and diversification of life.

In addition to comparing clines in body size and geographical ranges among archipelagoes, biogeographical regions and biota, a new synthesis in ecological biogeography may best be achieved by making strategic, hypothesis-driven comparisons across spatial and temporal scales and levels of complexity, and by integrating insights from related (and sometimes seemingly unrelated) ecogeographical patterns (e.g. Bergmann's rule, the island rule, Vermeij's rule of predation and morphological defences, Rapoport's rule of geographical range size, and latitudinal gradients in species richness and morphological diversity; for a review of these patterns see Lomolino *et al.*, 2005: pp. 567–640).

Exploring ecogeographical rules with insights from species invasions

Perhaps most insightful among these new, more integrative research initiatives are the opportunities afforded by the many thousands of introduction 'experiments' performed by human civilizations during their advances across the globe. Each of these episodes of invasion provides an opportunity to investigate how the dynamics in one of the most fundamental characteristics of an organism – its body size – is associated with the dynamics in one of the most fundamental characteristics of a species – its geographical range. A limited, but intriguing number of studies have demonstrated that ecogeographical patterns can evolve in surprisingly short periods of time as an invasive species expands its exotic range and, as a result, experiences repeated founder events and novel selection regimes (Johnston & Selander, 1964; Huey *et al.*, 2000, 2005; Gilchrist *et al.*, 2001; Sax, 2001; Campbell & Echternacht, 2003; Fridley *et al.*, 2006; Patterson *et al.*, 2006). The converse phenomenon – changes in body size and other characteristics of individuals as the species' geographical range contracts – may prove just as insightful. We know that geographical range collapse is far from a random process, with final populations typically persisting in the most isolated reaches of the species' historical range, either along the range periphery, in montane areas or on oceanic islands (Lomolino & Channell, 1995; Channell & Lomolino, 2000a,b; see also Safriel *et al.*, 1994; Towns & Daugherty, 1994; Gaston, 2003; Laliberte & Ripple, 2004). Yet we know of no studies examining the consequences of this highly non-random pattern of range collapse on body-size variation in native or invasive species.

Similarly, studies of invasive species may provide key insights into the processes that lead to other ecogeographical patterns, particularly geographical variation in body size across latitudinal gradients and on islands. Previous work has shown that body size can change quickly in invaded regions for a variety of species, including house sparrows (*Passer domesticus*) and tree sparrows (*Spizella arborea*) in North America (Johnston & Selander, 1964; St. Louis & Barlow, 1991); brown anoles (*Anolis sagrei*) introduced to sites in central Florida (Campbell & Echternacht, 2003); and fruit flies (*Drosophila subobscura*) in North and South America, where the observed trend in body size was shown to be genetic (as opposed to a phenotypically plastic trait; Huey *et al.*, 2000, 2005).

Islands afford special opportunities to study the underlying mechanisms influencing changes in body size of invading species because of the great amount of replication that exists among these 'unnatural' experiments. Replication for these experiments exists in two forms: first, in the individual species that have been introduced to many different islands; and second, in the variety of species that have been introduced to the same islands. These experiments include at least two types of treatment: (1) different lengths of time that introduced populations have been present on islands, which allow us to examine rates of change; and (2) substantial variation in abiotic and biotic conditions found on different islands, which can inform our understanding of the causal mechanisms of change in body size. Experimental controls for these experiments also exist, in that we can compare the body size of invasives on islands with that of populations in their native range. Conversely, although much less frequently studied, insular species that invade mainland ecosystems also can provide some intriguing insights. Finally, a wealth of relevant data are available from studies of contemporary populations in native and introduced ranges, and in museum collection records, which can provide a historical record of change over space and time.

While the available records on invasive species may include gaps, collection biases and other shortcomings common to other unplanned experiments, they also offer unrivalled opportunities to advance our understanding of the processes influencing the body size of natives as well as invasives. For example, records of invasive species provide the opportunity to compare changes in body size of species varying in resource requirements (e.g. large vs. small animals; carnivores vs. herbivores; homeotherms vs. poikilotherms) and vagilities (e.g. bats and birds vs. non-volant mammals, reptiles and amphibians). They also provide us with the opportunity to examine whether rates of change vary with latitude, elevation, climate, island size, isolation, and number of potential competitors and predators. Thus, the evidence available from invasive species should help to elucidate many of the processes hypothesized to explain ecogeographical patterns in the evolution of body size.

Time-for-space substitutions in studying ecogeographical rules

As we have observed, evolution occurs not just over time, but across space as well. Studies that acknowledge this and substitute time for space provide some compelling demonstrations of the utility of reintegrating the earlier holistic, but now distinct and divergent, disciplines of evolution, biogeography and ecology (Lomolino & Heaney, 2004; Lomolino *et al.*, 2004). Climatic fluxes such as those that occurred during the Pleistocene often created a temporal series of selective regimes, equivalent in many ways to the spatial series of environments that characterize today's geographical clines (e.g. in latitude, elevation and depth). Recent studies reveal that native vertebrates often responded with evolutionary changes in body size equivalent to ecogeographical patterns in body size. For example, Millien *et al.*'s (2006) review demonstrates that, consistent with explanations for ecogeographical patterns such as Bergmann's rule, body-size evolution of vertebrates often tracks climate change over time scales of a few decades to tens of thousands of years (Pregill & Steadman, 2004). The time-for-space substitution can also prove an invaluable tool in studying evolution and the adaptive potential of species introduced onto islands, or native species that are becoming increasingly isolated in anthropogenic 'archipelagoes' of their native ecosystems. Again, Millien *et al.* (2006) have reviewed some of the evidence for rapid evolution in species introduced to islands, which includes a limited but interesting collection of studies reporting trends consistent with the island rule (including body size variation with island size, latitude, and number of potential competitors and predators). In an equally interesting set of studies of responses to fragmentation of terrestrial landscapes in Denmark, Schmidt & Jensen (2003, 2005) report that, while the body size of birds and mammals continues to track (but lag behind) rates of landscape transformation, the trajectories of changes in their body sizes are consistent with the island rule (body size increasing in relatively small species and decreasing in larger species).

RECOMMENDATIONS

The term 'ecogeographical rule' is arguably a misnomer (Mayr, 1956), as nearly all these patterns suggest not just an ecological, but also an evolutionary basis for the pattern. Exceptions are not just possible but are expected, and are likely to provide key insights in evaluating alternative explanations (for an interesting series of discussions on laws of nature and ecology see Lawton, 1999; Murray, 2000; Colyvan & Ginzburg, 2003; O'Hara, 2005). Rather than suggesting an alternative label for such patterns, instead we recommend some fundamental changes in how we study these very general phenomena. Together, these recommendations constitute a more integrated approach, and one more likely to provide a more comprehensive understanding of the underlying causal forces for these patterns.

1. Rather than just describing the patterns, our research should be designed to test causal hypotheses that attempt to explain the primary pattern, its corollaries and its exceptions.

2. We should use the comparative approach and, when possible, deconstruct (*sensu* Huston, 1994) the primary ecogeographical pattern into its component patterns for different groups of species, archipelagoes, regions, and spatial and temporal scales.

3. The research programme should be expanded to include a greater diversity of ecosystems and species and, in addition to the traditional focus on insular mammals and birds, should assess the generality and causality of these patterns among functionally different groups, including other vertebrates, invertebrates and plants.

4. Ecogeographical patterns should be mapped (displayed and explored) not just as one-dimensional clines, but as variation in body size and other characteristics across geographical templates that are two-dimensional (terrestrial systems) or three-dimensional (marine systems) (Hawkins & Diniz-Filho, 2006; Ruggiero & Hawkins, 2006).

5. Given the *post hoc* nature of many studies in ecogeography (where our ‘experiments’ are opportunistic), we should acknowledge the possibilities of both Type I and Type II errors when interpreting the results of those studies.

6. These studies should be informed by phylogenetic and phylogeographical analyses and, whenever possible, should utilize molecular markers and other techniques to reconstruct colonization histories and identify extant or extinct source populations.

7. We should capitalize on the thousands of unplanned but well chronicled introduction ‘experiments’ as opportunities to investigate simultaneously the dynamics of morphological traits and geographical range size. Among these, we include the many waves of invasions and subsequent ecological and evolutionary adaptations of *Homo sapiens*. Given the available global record on colonization by human civilizations and the substantial morphological variation among individuals and regional populations, ecogeographical studies of our own species may prove especially intriguing (Roberts, 1953, 1978; Ruff, 1994; Bindon & Baker, 1997; Brown *et al.*, 2004; Morwood *et al.*, 2004).

8. We should also assess the potential heuristic and applied value of studying changes in body size and other morphological characteristics of native species inhabiting archipelagoes of their native ecosystems that continue to dwindle in area and become increasingly more isolated. Such studies of anthropogenically fragmented biota have obvious importance for both understanding and conserving the natural character of native, but often threatened, biota (Ashley *et al.*, 2003).

9. While challenging, the most promising lines of research will be those that study simultaneously a combination of geographical clines in morphology, geographical ranges, and diversity as intricately related phenomena, all being ecological, evolutionary and biogeographical responses of organisms to selection regimes that vary non-randomly over space and time, and among species with different ecological and evolutionary histories.

10. The more integrative research agenda that we recommend should include well-coordinated studies of the spatial and temporal dynamics of body size, growth form, geographical ranges and other individual- to species-level traits of animals and plants investigated over three complementary dimensions or clines: (i) geographical gradients across the Earth’s current template, (ii) the temporal–spatial dynamics of body size in species undergoing range expansion or range collapse in recent or historical periods, and (iii) temporal clines associated with climatic fluxes of the past.

In an attempt to encourage such a research agenda, the International Biogeography Society (http://www.biogeography.org) has organized a plenary symposium – *An Integrative View of Ecogeographical ‘Rules’* – to be held at the Society’s third Biennial Conference in the Canary Islands in January 2007. The symposium will feature contributions from five distinguished scientists discussing both the generality and causality of a variety of ecogeographical patterns. These plenary talks will include a diversity of perspectives, from the physiological, behavioural, ecological and evolutionary bases of these phenomena to their expressions at regional to global scales. We are optimistic that, in addition to providing their own insightful perspectives, these speakers will stimulate new and more integrative research on these fundamental and fascinating patterns in the geographical variation of nature.

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