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BIODIVERSITY VIEWPOINTS

Are ecological and evolutionary rules being dismissed prematurely?

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Abstract. Recently, it has been suggested that the group of patterns known as the ecological and evolutionary rules are invalid and only of interest historically. Here, I briefly review evidence for the four most prominent patterns: Bergmann's rule, Cope's rule, Rapoport's rule, and the latitudinal gradient in species richness. Although more comprehensive reviews exist for these patterns, the purpose of this paper is to highlight recent work illustrating the validity of each pattern, to question the conclusion that these patterns are only of historical interest, and to briefly explore possible connections between each of these patterns. I also recommend that meta-analytical techniques, a group of statistical methods rarely used in ecology and evolution, need to be incorporated in future tests of general trends.

Key words. Ecological rules, evolutionary rules, Bergmann's rule, Rapoport's rule, Cope's rule, species diversity gradient.

INTRODUCTION

A general goal of science is to document broad patterns and understand the mechanisms that generate those patterns (MacArthur, 1972). This is particularly true for the fields of ecology and evolution. In fact, ecology has been described as 'the study of patterns in nature, how those patterns came to be, how they change in space and time, why some are more fragile than others (Kingsland, 1995).' Documenting and understanding the processes that generate broad patterns in ecology and evolution are important steps towards understanding biodiversity.

Recently, a group of patterns in ecology and evolution, the ecological and evolutionary rules, have been called into question (Geist, 1987; Gould, 1997; Gaston *et al.*, 1998a). Clearly, many 'rules' have been proposed without the necessary supporting evidence. However, there appears to be an attitude in recent literature suggesting that the study of ecological and evolutionary rules is of primarily historical interest, and that many of the proposed patterns are invalid (e.g. Gould, 1997; Gaston *et al.*, 1998a). For instance, Gaston *et al.* (1998a, p. 70) wrote:

> The list of evolutionary and ecological 'rules' and 'laws' is brief, and primarily of historical rather than current interest. Of those that have been postulated, most have subsequently proven not to exhibit the generality which was initially claimed, or have been found to be artifactual (e.g. Bergmann's Rule, Cope's Rule ...).

However, the studies cited by Gaston *et al.* (1998a) to substantiate their argument that these rules are invalid and primarily of historical interest are problematic. In particular, none of the references they cite for Bergmann's rule (Geist, 1987; Currie & Fritz, 1993; Hawkins & Lawton, 1995) reviewed general intraspecific patterns of body size variation for endothermic vertebrates,

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the common definition of Bergmann's rule (Rensch, 1938; Mayr, 1956). Rather, they concern arguments about the mechanisms responsible for Bergmann's rule (Geist, 1987), interspecific patterns for a group of ectothermic organisms (Hawkins & Lawton, 1995), or interspecific patterns based on unclear methodology and taxonomic sampling (Currie & Fritz, 1993). Additionally, the one study cited by Gaston *et al.* (1998a) to dismiss Cope's rule (Jablonski, 1997) has itself been criticized (Alroy, 1998a). Further, showing that Cope's rule does not hold over a relatively short period for one group of animals (Jablonski, 1997) does not imply that it does not hold over longer periods or for other groups. Thus, the dismissal of these two rules, and possibly other rules as well, appears premature.

Here, I briefly review recent research that has increased our understanding of the validity and breadth of four such patterns: Bergmann's rule, Cope's rule, Rapoport's rule, and the latitudinal gradient in species diversity. I chose these four patterns because they are the most prominent of the ecological and evolutionary rules and there are intriguing possible connections between them. My intention here is not to comprehensively review the massive amount of literature on these four patterns, but rather to highlight recent studies that show support for each of these patterns in contrast to recent views presented in the literature (e.g. Gould, 1997; Gaston *et al.*, 1998a). Because all of these patterns have some level of support, they deserve explanation, and are therefore of current interest. However, I do not discuss specific processes to account for any of the trends. This is intentional because I think it is important to first solidly document any pattern before attempting to explain the pattern, and each of these patterns requires further documentation. I conclude by suggesting future research that is greatly needed and exploring the interrelatedness of these patterns.

PATTERNS

Bergmann's rule, as currently defined, states that there is a general intraspecific trend, in endothermic vertebrates, towards larger size in cooler environments (Rensch, 1938; Mayr, 1956, 1963). Although Bergmann's rule was supported by earlier work (Rensch, 1936), it has recently been questioned and/or dismissed (Geist, 1987; Gould, 1997; Gaston *et al.*, 1998a; Blackburn *et al.*, 1999) based primarily on one review of mammals (McNab, 1971). Yet, the studies of both Rensch (1936) and McNab (1971) suffer methodological flaws (McNab, 1971; Ashton *et al.*, 2000). Specifically, Rensch's (1936) review is based on subspecies comparisons, which are at best crude approximations of population level variation; McNab's (1971) data were analysed in a manner that decreased statistical power, possibly failing to detect patterns of body size that actually existed (see Ashton *et al.*, 2000 for discussion). The most extensive review of body size variation in mammals found broad support for Bergmann's rule (latitude: 78/110 species; temperature: 48/64 species; Ashton *et al.*, 2000), and recent analyses have also found broad support for the pattern for birds (latitude: 72/100 species; mean environmental temperature: 20/22 species; Ashton, 2001; also see James, 1970; Zink & Remsen, 1986). There has been much debate over whether ectotherms show general intraspecific patterns of size variation in relation to latitude or temperature (e.g. Van Voorhies, 1996; Mousseau, 1997; Blackburn *et al.*, 1999). The only extensive study for a large group of ectotherms found support for a Bergmann's rule-like trend in turtles (latitude: 19/23 species; mean environmental temperature: 14/15 species), but the inverse of such a trend in squamate reptiles ('lizards' and snakes; latitude: 60/82 species; mean environmental temperature: 36/53 species) (Ashton, 2001). Thus, Bergmann's rule is valid for endothermic vertebrates; however, whether there is a general size trend for all ectotherms awaits further study.

In addition to debate over whether ectotherms and endotherms show similar patterns of intraspecific size variation, it has also been debated whether interspecific patterns of body size variation occur with latitude, particularly among groups of insects (Cushman *et al.*, 1993; Barlow, 1994; Hawkins & Lawton, 1995; Hawkins, 1995). Recently, it has been suggested that Bergmann's rule be defined as 'the tendency for a positive association between the body mass of species in a monophyletic higher taxon and the latitude inhabited by those species', and that the intraspecific formulation be renamed 'James's rule' (Blackburn *et al.*, 1999). The rationale for the proposed change in the current definition of

Bergmann's rule is to reflect the exact writings of Bergmann, translated in James (1970), showing that Bergmann was discussing interspecific patterns. However, the intraspecific definition of Bergmann's rule is clearly the currently accepted version and arguments have been presented that the between-species variation that Bergmann was discussing was actually intraspecific variation (Mayr, 1956). Therefore, it appears prudent to continue to refer to the intraspecific pattern as Bergmann's rule, and instead either refer to the interspecific pattern as the 'interspecific Bergmann's rule pattern' or possibly give it some other name (or no name at all). The reason it is important to distinguish the intraspecific from interspecific pattern is that the patterns need not be the same at both biological levels. Regardless of the name given these patterns, it is clear that general intraspecific patterns of size variation relative to latitude or temperature do exist (Ashton *et al.*, 2000). It is now important to further test for size patterns, both intraspecific and interspecific, in additional groups of animals.

Broadly defined, Cope's rule is a general tendency for size to show an evolutionary increase over time (Rensch, 1948; Jablonski, 1996). However, it is important to separate within-lineage trends from between-lineage trends because they may have different responsible processes (Alroy, 1998a). Additionally, Cope's rule is usually attributed to the selective advantages of large body size (Rensch, 1960; Stanley, 1973; Brown & Maurer, 1986), suggesting that the common formulation of Cope's rule is with respect to within-lineage trends. As with Bergmann's rule, it has been suggested that this trend should be renamed (Polly, 1998). Yet, as Alroy (1998b) has pointed out, retaining the name 'Cope's rule' acknowledges Cope's substantial influence on this topic.

McKinney (1990) briefly reviewed studies of temporal size changes, both cladogenetic (between lineage) and anagenetic (within lineage). He reported that for anagenetic comparisons, 92 studies showed a size increase over time, while 28 studies either found no trend or the opposite trend. In contrast, cladogenetic size increases ($n = 6$) were no more common than decreases ($n = 6$). Upon further examination, McKinney (1990) found that size increases were reported for almost every anagenetic study that sampled over 1 million years or more. In contrast, studies of shorter duration most often reported size decreases. This suggests that both the level of analysis (within or between lineages), and the duration of analysis, influence the presence of any size trends on a temporal scale. In fact, these two factors may explain variation in the results of recent studies. For instance, most recent studies have failed to support Cope's rule (e.g. Jablonski, 1996, 1997), leading to the assertion that Cope's rule is a psychological artefact (Gould, 1997). However, these studies have several methodological problems, mainly because of sampling over a relatively short time period and not analysing ancestor–descendant pairs (Alroy, 1998a). The most recent and comprehensive analysis of within-lineage body size evolution for any group found broad support for Cope's rule in mammals (Alroy, 1998a). Analyses of size trends in other groups, using similar methods, are greatly needed in order to ascertain the breadth of Cope's rule.

Rapoport's rule, a general positive relationship between the latitudinal extent of an organism's geographical range size and latitude, is probably the most recently named ecological rule (Stevens, 1989). Stevens (1992, 1996) has subsequently suggested that Rapoport's rule also holds over elevational and bathymetric gradients, as well as potentially over many other environmental gradients. Stevens' methods have been criticized in two ways. First, because species-range size distributions tend to be skewed, Stevens' use of the mean as a measure of central tendency may be inappropriate (Roy *et al.*, 1994). Second, Steven's method uses samples that are not spatially independent (Rohde *et al.*, 1993). However, the results of analyses using Stevens' method, and alternative methods that avoid these problems, tend to recover the same patterns (Gaston *et al.*, 1998a).

Gaston *et al.* (1998a) recently reviewed the available literature on Rapoport's rule, but it is difficult to evaluate the taxonomic generality of the rule because several studies with conflicting results are presented for the same group of organisms (e.g. birds; see Gaston *et al.*, 1998a, table 1). Rapoport's rule does seem to hold at higher northern latitudes for most studies, whereas it does not appear to hold in marine environments or in the Southern Hemisphere. To explain the lack of Rapoport's rule in marine environments, Stevens (1996) suggested that bathymetric gradients must be taken into account because they may confound latitudinal patterns. Whether or not Rapoport's rule occurs in the Southern Hemisphere requires further study because only five studies have been performed in that region (Gaston *et al.*, 1998a). Re-examination of the data presented by Stevens (1989) shows that the trend occurs north of 35° N latitude, which is consistent with the conclusion that Rapoport's rule is a regional phenomenon (Rohde & Heap, 1996; Rohde, 1996; Gaston *et al.*, 1998a; Gaston & Chown, 1999). Subsequent studies have found additional support for Rapoport's rule as a regional phenomenon (Ruggiero & Lawton, 1998; Santelices & Marquet, 1998; Hecnar, 1999). Yet, this conclusion is tentative because only three (Cowlishaw & Hacker, 1998), and possibly none (Gaston *et al.*, 1998b), of the studies included by Gaston *et al.* (1998a) may be free from the problems of spatial non-independence, phylogenetic non-independence and boundedness. It is clear that standard methods for analysing patterns of range size variation need to be developed to allow comparison among studies (Gaston *et al.*, 1998b). Based on the available evidence, it is premature to either accept or dismiss Rapoport's rule.

Why has Rapoport's rule become so well known if its validity is so deeply questioned? The answer lies in Stevens's (1989) suggestion that Rapoport's rule might cause the latitudinal gradient in species diversity, 'the major, unexplained pattern in natural history' (R. E. Ricklefs, p. 527 of Lewin, 1989). However, in order to explain the pattern of species diversity, range size variation must be concordant with the latitudinal gradient of diversity; a fact that has been demonstrated for some (e.g. Santelices & Marquet, 1998) but not all groups (e.g. Blackburn & Gaston, 1996; Roy *et al.*, 1998). In addition, tests of Rapoport's rule as an explanation for patterns of species diversity have yielded conflicting results (e.g. Kolasa *et al.*, 1998; Kerr, 1999; Taylor & Gaines, 1999; Addo-Bediako *et al.*, 2000).

The negative correlation between species diversity and latitude is known as the latitudinal gradient in species diversity (or richness). This trend is well documented (Dobzhansky, 1950; Hutchinson, 1959; Fischer, 1960; Simpson, 1964; MacArthur, 1965; Pianka, 1966; Arnold, 1972; MacArthur, 1972; Stevens, 1989; Rosenzweig, 1995; Gaston, 1996; Brown & Lomolino, 1998; Rohde, 1999), and certainly many studies have tested for this pattern. In fact, because the pattern appears to be nearly universal, it has been suggested that a common explanation exists (e.g. Pianka, 1966). However, the universality and the details of the pattern are not clear. Previous reviews (e.g. Rosenzweig, 1995; Gaston, 1996; Brown & Lomolino, 1998; Rohde, 1999) list some examples for and against the trend, but it would be preferable to have an exhaustive summary of studies of latitudinal variation in species diversity. Such a review would allow examination of the overall strength, breadth and variation of any trends. Additionally, groups for which data are not available can be identified and studies directed to obtain information for those groups. It is clear that all latitudinal species diversity gradients are not the same; some appear gradual, whereas others show more abrupt changes (e.g. Roy *et al.*, 1994; Rosenzweig, 1995; Roy *et al.*, 1998; Santelices & Marquet, 1998; Roy *et al.*, 2000). This variation in the nature of latitudinal patterns of species diversity suggests multiple causes of such gradients. A quantitative summary of the various studies on this subject is greatly needed.

CONCLUSIONS

Are ecological and evolutionary patterns solely of historical interest? I strongly argue that they are not. In fact, some of the best 'known' patterns have only recently been extensively tested (e.g. Alroy, 1998a; Ashton *et al.*, 2000). The number of publications on Rapoport's rule provides additional evidence that ecological and evolutionary patterns are very much of current interest. For instance, a quick search of an online database showed that Stevens's (1989) paper has been cited 183 times, 24 times in the year 2000 alone, a substantial recent influence for a topic that is supposedly of primarily historical interest.

The recognition of patterns should not be discouraged, as long as the necessary data are presented. Two issues might have contributed to the current trend of rejecting patterns despite evidence supporting such patterns. First, these patterns have traditionally been labelled rules or laws. Such labels suggest universal or nearly universal applicability. However, the usual criterion for the validity of such a trend is that it holds in greater than 50% of instances. Lawton (1999) proposed terminology that may be more consistent with the perception of these trends. He suggested that we label these trends as general patterns, and refer to the underlying processes as rules or laws. Regardless of the terminology, it is important to recognize that presenting data for a handful of species (e.g. Geist, 1987) does not invalidate a general trend. Second, it is crucial to separate data relevant to the pattern itself from data evaluating mechanisms proposed to account for such a trend (Mayr, 1963) because the same pattern can be generated from different processes (Lawton, 1999).

It is important to recognize general patterns in ecology and evolution because shared patterns suggest common causality. Further, studying these patterns and their causes can help explain fundamental questions about biodiversity. For instance, understanding the processes that generate the four patterns discussed above can greatly improve our knowledge of how biodiversity is generated and structured within communities. At the same time, it is critical to recognize the value of studying the exceptions to general rules. In fact, our understanding of a general pattern can be improved by explaining why such exceptions occur.

Whatever we call these four patterns (e.g. Niemela *et al.*, 1991; Polly, 1998; Blackburn *et al.*, 1999) and whether they are named as rules or not (Lawton, 1999), the trends are valid at some level. All patterns deserve further investigation because very few methodologically appropriate studies exist, the available studies are biased regionally or taxonomically, or a comprehensive summary of the evidence has not been published (Cowlishaw & Hacker, 1998; Gaston & Blackburn, 1999). Meta-analytical techniques are necessary to test for general patterns in ecology and evolution (Arnqvist & Wooster, 1995). However, these techniques are just beginning to be used in these fields and issues that confound meta-analyses (e.g. publication bias; Palmer, 1999) are only beginning to be explored. These techniques would be particularly useful in assessing the generality of ecological and evolutionary patterns. I argue, as previous authors have (e.g. Gaston & Blackburn, 1999), that much research on basic patterns remains to be done before we can move on to testing hypotheses to explain these patterns. Dismissing ecological and evolutionary rules without presenting enough data to evaluate them is premature.

I have presented a brief review of these four patterns together because, first, they are the best known and, second, the potential interrelatedness among these patterns is intriguing. For instance, Blackburn & Gaston (1996) tested for spatial patterns in body size, species diversity and range size for species of birds in the New World. Their study found concordant latitudinal patterns of body size variation (i.e. interspecific Bergmann's rule) and species diversity. In fact, the inverse correlation between body size and species diversity was stronger than the relationship between either variable and latitude. The relationship between body size, or species diversity, and range size is much weaker. This suggests that patterns of species diversity and body size are more closely tied than either is to range size, and thus may share a common explanation (Blackburn & Gaston, 1996). In addition, Bergmann's rule and Cope's rule may be related. It is possible that the mechanisms, related to temperature, driving size variation on a spatial scale (i.e. Bergmann's rule) also might drive Cope's rule within lineages, at least during certain periods. For example, Smith *et al.* (1995) showed that body size for a species of woodrat was negatively related to environmental temperature over both the contemporary spatial scale and a temporal scale. The interrelationships, and possible uniting explanations, of these four patterns deserve further study.

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