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RESEARCH PAPER

Elevational Rapoport's rule is not pervasive on mountains

Christy M. McCain* and Kevin Bracy Knight

Department of Ecology and Evolutionary Biology and CU Museum of Natural History, University of Colorado, Boulder, CO 80309, USA

*Correspondence: Christy M. McCain, MCOL 265 UCB, University of Colorado, Boulder, CO 80309-0265, USA.
E-mail: christy.mccain@colorado.edu

ABSTRACT

Aim Elevational Rapoport's rule, proposed in 1992 by Stevens, predicts that species ranges on mountains become larger in elevational extent with increasing elevation. Here we test this prediction using 160 datasets of range size measured by maximum elevational extents for bats, birds, frogs, non-volant small mammals, reptiles, and salamanders from mountains around the globe.

Location Mountains distributed globally and spanning 36.5° S to 48.2° N.

Methods We compare three methods: (1) the Stevens method, which uses the average range size of all species within each elevational band (100-m bands); (2) the midpoint method, which uses the average range size of species whose midpoints occur in each elevational band; and (3) a quartile method that examines the distribution of only the smallest ranges (less than one-quarter of the mountain height) to see if their frequency distribution is negatively related to elevation.

Results Support for the elevational Rapoport's rule was weak across all groups of montane vertebrates. For the Stevens method, the mean r^2 value was 0.32, and strong support (positive relationship, r^2 value > 0.50) was detected in 40% of the studies, ranging from 20% for salamanders to 57% for frogs. For the midpoint method, the mean r^2 value was 0.06, and none of the datasets showed strong support. For the quartile method, the mean r^2 value was 0.26, and strong support (negative relationship, r^2 value > 0.40) was detected in 38% of the studies, ranging between 10.5% in salamanders and 58% in reptiles.

Main conclusions Across vertebrates, and within the literature for plants and invertebrates, more empirical studies find a lack of trend than the predicted trend of increasing range size with increasing elevation. Thus, elevational Rapoport's rule is not a consistently predictive pattern for understanding montane patterns in range size.

Keywords
Bats, birds, frogs, mountains, range size, reptiles, salamanders, small mammals, vertebrates.

INTRODUCTION

Understanding the factors that determine species range size distributions is becoming increasingly urgent as more climate change assessments document the heightened risk for small-ranged species (e.g. Channell & Lomolino, 2000; Sekercioglu *et al.*, 2008; La Sorte & Jetz, 2010; McCain & Colwell, 2011). Several studies have shown that the distributions of widespread, rare (small-ranged) and threatened species are not complementary, thus necessitating conservation plans to target species of various range sizes, not just hotspots of total diversity (e.g. Orme *et al.*, 2005; Grenyer *et al.*, 2006). Changes in biodiversity patterns along environmental gradients have been an emphasis of research for decades, but less effort has been applied to understanding the processes creating differences in species range sizes that underlie these diversity patterns (e.g. Anderson, 1977; Brown, 1995; Brown *et al.*, 1996; Gaston, 1996; Gaston & Blackburn, 2000). Much of the literature on range size distribution has tested Rapoport's rule (Rapoport, 1982; Stevens, 1989, 1992).

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Rapoport's rule is the positive relationship of species range sizes with increasing latitude (Stevens, 1989), elevation (Stevens, 1992) or water depth (Stevens, 1996). The latitudinal Rapoport's rule (LRR) is the most examined in the literature, including testing empirical datasets (e.g. Rohde *et al.*, 1993; Roy *et al.*, 1994; Blackburn & Gaston, 1996; Lyons & Willig, 1997; Ruggiero & Lawton, 1998; Reed, 2003; Arita *et al.*, 2005; Hausdorf, 2006), simulation modelling of the expected patterns (Colwell & Hurtt, 1994; Taylor & Gaines, 1999; Case & Taper, 2000; Arita, 2005; Stauffer & Rohde, 2006; Šizling *et al.*, 2009), and theoretical and empirical evidence for the proposed mechanisms (e.g. Rohde, 1992; Kerr, 1999; Taylor & Gaines, 1999; Gaston & Chown, 1999a; Addo-Bediako *et al.*, 2000; Parmesan *et al.*, 2005). The various reviews of the LRR to date suggest that the overall support is weak (e.g. Rohde, 1996; Gaston *et al.*, 1998; Rohde, 1999; Gaston & Chown, 1999b; Ribas & Schoereder, 2006), principally due to the high degree of variability in the fit to predictions (e.g. support: Blackburn & Gaston, 1996; Lyons & Willig, 1997; Price *et al.*, 1997; Arita *et al.*, 2005; no support: Rohde *et al.*, 1993; Roy *et al.*, 1994; Ruggiero & Lawton, 1998; Reed, 2003).

The elevational Rapoport's rule (ERR) has received less examination in the literature than the LRR, but there have also been empirical tests of its predictions (e.g. Patterson *et al.*, 1996; Pleguezuelos & Villafranca, 1997; Price *et al.*, 1997; Rahbek, 1997; Fleishman *et al.*, 1998; Ruggiero & Lawton, 1998; Nathan & Werner, 1999; Sanders, 2002; Fu *et al.*, 2004; Chatzaki *et al.*, 2005; Almeida-Neto *et al.*, 2006; Bhattarai & Vetaas, 2006; Hausdorf, 2006) and underlying theory (e.g. Rohde, 1996; Fleishman *et al.*, 1998; Gaston & Chown, 1999a; Hausdorf, 2006; Ribas & Schoereder, 2006). In the ERR, like the LRR, there is a high degree of variability in support from supportive (e.g. Patterson *et al.*, 1996; Pleguezuelos & Villafranca, 1997; Price *et al.*, 1997; Rahbek, 1997; Fleishman *et al.*, 1998; Sanders, 2002; Chatzaki *et al.*, 2005; Almeida-Neto *et al.*, 2006; Hausdorf, 2006; Ribas & Schoereder, 2006) to little or no support (e.g. Patterson *et al.*, 1996; Price *et al.*, 1997; Rahbek, 1997; Ruggiero & Lawton, 1998; Nathan & Werner, 1999; Fu *et al.*, 2004; Bhattarai & Vetaas, 2006; Hausdorf, 2006; Ribas & Schoereder, 2006). Similarly, the processes proposed to underlie the ERR (Stevens, 1992) also show a variable amount of theoretical and empirical support (Patterson *et al.*, 1996; Rohde, 1996; Rahbek, 1997; Fleishman *et al.*, 1998; Gaston & Chown, 1999a; Almeida-Neto *et al.*, 2006; Hausdorf, 2006; Colwell, 2011).

The LRR and theory of ERR both attempt to link the decrease in species richness with increasing range size along the gradients to a parallel increase in climatic variability and an influence of source–sink dynamics (*sensu* Janzen, 1967; Stevens, 1989; Rohde, 1992; Stevens, 1992; Rohde, 1996; Kerr, 1999; Gaston & Chown, 1999a). The first necessary condition of the theory is a pattern of monotonically increasing range size with latitude or elevation, which assumes at least an approximately linear relationship. This condition, and hence the theory, would be negated by a decreasing range size relationship or where the average largest or smallest ranges are not at the upper or lower ends of the gradient, respectively (e.g. a unimodal distribution). The second necessary condition is a pattern of decreasing species richness with latitude or elevation, again assuming an approximate linear relationship that would be negated by an increasing or unimodal trend in richness. The third condition of the theory is that the mechanism underlying this negative, generally linear relationship between range size and species richness is based on 'the breadth of climatic conditions organisms experience' along the gradients (Stevens, 1992, p. 893). Specifically, organisms at high latitudes (Janzen, 1967) and high elevation (Merriam, 1894; Adams *et al.*, 1920) experience greater temporal variability in temperatures and water availability (elevation), than organisms at low latitudes or elevations, and thus as a result have lower species richness (Stevens, 1989; Kerr, 1999). Stevens (1989, 1992) also adds the influence of source–sink dynamics and niche packing to the predictions of the interactions between range size and species richness along the gradients, although this has not been tested as extensively. As listed above, empirical support for the underlying mechanisms has been mixed and logical shortcomings have been noted. Specifically, if factors other than climatic variability or source–sink dynamics are more strongly linked to species richness or range size, or if datasets do not follow all of these trends but still display some of the predicted relationships, then the theory is questionable (e.g. Kerr, 1999). But as others have argued, the mechanisms are irrelevant if the range size or species richness patterns are not supported (Gaston *et al.*, 1998; Rohde, 1999; Ashton, 2001; Ribas & Schoereder, 2006). Therefore in this paper we are specifically testing the first condition of the theory: is there a positive, monotonic increase in range size with elevation?

One argument for the variability in fits to the ERR and LRR in relation to the increase in range size with latitude or elevation is that there is an array of methodological tests that have not been applied uniformly, and some methods that suffer from statistical and sampling biases (Gaston *et al.*, 1998; Ashton, 2001; Ribas & Schoereder, 2006). The appropriate measure of central tendency was raised as a potential bias, since mean range sizes used by Stevens (1989, 1992) are skewed towards the outliers in right-skewed range size distributions, whereas the median and mode are not as biased (Roy *et al.*, 1994; Gaston *et al.*, 1998). Others have argued that Stevens' method of averaging all species ranges in each elevational or latitudinal band has an inflated tendency to find positive support due to the non-independence between gradient bands and because large-ranged species are repeatedly included in means of sequential bands while small-ranged species are only included in one or a few bands (Rohde *et al.*, 1993). Thus, Rohde *et al.* (1993) advocated the midpoint method, which calculates the average (or median, mode; Roy *et al.*, 1994) of those species whose range midpoint falls within a gradient band. Using simulations, Colwell & Hurtt (1994) showed that spatial constraints (e.g. continental and montane limits) influence the spatial distribution of species ranges along latitudinal and elevational gradients that can produce reverse Rapoport effects. But they also demonstrated that sampling bias between areas of high and low diversity can produce spurious support for Rapoport's rule. Others have argued that phylogenetic non-independence may influence the level of detected support (Blackburn & Gaston, 1996; Price *et al.*, 1997). Nonetheless, in many cases where multiple methods were compared, similar support was detected among methods (e.g. Gaston *et al.*, 1998, and references therein). But more importantly, to date there is little evidence of a phylogenetic constraint on range size (Gaston, 1990; Blackburn & Gaston, 1996; Ruggiero & Lawton, 1998; Gaston & Blackburn, 2000; Diniz-Filho & Tôrres, 2002).

Here we present the first reanalysis of 160 elevational datasets of montane vertebrates vetted for sampling quality, employing standardized methodology for comparison of the major proposed ERR methods (e.g. the Stevens and midpoint methods) using both average and median range sizes. From these data, we will determine the judiciousness of focusing on Rapoport's rule in understanding elevational range size distributions based on the support for the first tenet of the theory, namely increasing range size with elevation.

MATERIALS AND METHODS

Species elevational ranges were compiled in conjunction with analyses of montane diversity for terrestrial vertebrates (McCain, 2005, 2007, 2009a,b, 2010). Elevational range data were taken directly from published articles, field guides or online distributional databases (see the above citations for more detail). Elevational range size is calculated as the maximum range extent, which assumes a species was present between its highest and lowest reported elevations on a single montane gradient. Appropriate datasets were selected based on several a priori sampling criteria (Rickart, 2001; McCain, 2005; Rahbek, 2005). A montane study was included in quantitative analyses only if sampling covered at least 70% of the elevational gradient, sampling effort was substantial and not strongly biased elevationally, and there were no strong elevational trends in wide-scale habitat disturbance (McCain, 2005, 2007, 2009a,b, 2010). After these restrictions, range sizes for each vertebrate group were included from multiple mountains for bats (12 mountains), birds (28), non-volant small mammals (40), reptiles (19), salamanders (20) and frogs (41) (see Appendix S1 in Supporting Information).

Stevens (1992) originally proposed a positive, monotonic (or generally linear) association between average range sizes within increasing bands of elevation, which has subsequently been termed the Stevens method (e.g. Fig. 1a). We compared the Stevens method with the less-biased, midpoint method (Rohde *et al.*, 1993; Roy *et al.*, 1994). The midpoint method only takes the average of those species ranges with a range midpoint that falls within that elevational band (Fig. 1c). In both sets of analyses, we compared mean and median range size data. In neither set of analyses did we use mode as a representation of central tendency, since most gradients contain too few species for a robust modal description of ranges. All analyses are conducted at a 100-m elevational grain size (e.g. 0–99.9, 100–199.9) using the extent between the lowest and highest elevational bands of a taxon's occurrence along the gradient.

Colwell & Hurtt (1994) demonstrated that spatial constraints can influence the distribution of species ranges, thus predisposing datasets to support a reverse Rapoport effect. An important point of their work was to emphasize that large-ranged species are more constrained within spatially bounded gradients than are small-ranged species (the mid-domain effect; Colwell *et al.*,

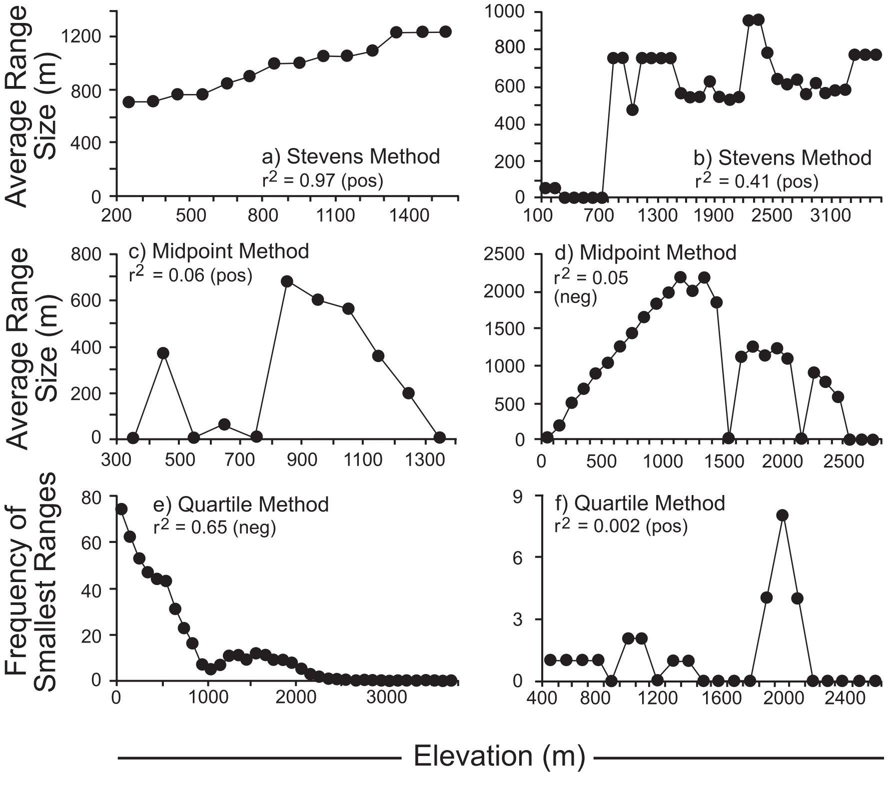

Figure 1 Empirical examples of the three methods for testing the elevational Rapoport's rule: the Stevens method with a strong (a: frogs, Smoky Mountains, USA) and a poor (b: salamanders, Oaxaca, Mexico) fit to predictions; the midpoint method with a positive (c: non-volant small mammals, Montagne d'Ambre, Madagascar) and a negative relationship (d: birds, Pyrenees, France and Spain); and the quartile method with a strong (e: reptiles, Costa Rica) and a poor fit to predictions (f: bats, Jalisco, Mexico).

2004). Thus large-ranged species can have an overriding effect on analyses of range size distributions, especially in methods repeatedly sampling large-ranged species like the Stevens method. Moreover, in the spatial context of range size distributions in Rapoport's rule, large-ranged species are less informative – they occur across both low and high elevations for the simple geometric reason that having a large range necessitates inhabiting a large range of elevations. For Rapoport's rule, the important prediction then becomes whether the small-ranged species occur randomly within the domain or differentially at low elevations, as predicted by Stevens.

To reduce the influence of the mid-domain effect, the non-independence of the Stevens method and the restrictive subsampling of the midpoint method, we propose a quartile method that focuses only on detecting whether small-ranged species are predominantly found at the lowest elevations and decrease in density with increasing elevation (example of strong support; Fig. 1e). The range-size quartiles are defined as range sizes of less than a quarter of mountain height (quartile 1 = smallest-ranged species), range sizes between a quarter and a half of mountain height (quartile 2 = small-to-medium-ranged species), range sizes between half and three-quarters of mountain height (quartile 3 = medium-to-large-ranged species), and range sizes more than three-quarters of mountain height (quartile 4 = largest-ranged species). This size delimitation was selected because it retained a sufficient number of species in each quartile, and lead to an adequate and standardized characterization of small ranges among the various mountain gradients. Various organisms have different range size distributions and numbers of species along the gradient, and this method of sorting sizes based on the mountain height leads to groupings of range sizes that are relatively uniform. For instance, just using frequency-delimited quartiles, particularly with small numbers of species, results in groupings within quartiles that can differ markedly in size just due to the need to have a quarter of the species in each quartile. Employment of size grouping for other organisms and datasets should be employed to reflect true differences in size, not just equal division of the species. Using quartile 1, we employ linear regressions to detect if the smallest ranges are clumped at the lowest elevations and decrease with increasing elevation as predicted by the ERR.

Some additional methods presented in the literature are not employed in the present analyses. One is the most-distal point method (e.g. Lyons & Willig, 1997), which has been shown to be significantly biased to a positive Rapoport effect (Nathan & Werner, 1999). Another is phylogenetic contrasts intended to reduce phylogenetic non-independence (Blackburn & Gaston, 1996; Price *et al.*, 1997; Ruggiero & Lawton, 1998), which requires species-level phylogenies for all included species. Such phylogenies do not currently exist for all the species in the included datasets (> 16,500 species). The specimen method (Almeida-Neto *et al.*, 2006), which requires species abundances within each elevational range, is also not included since abundance data are not available for the majority of the datasets. Several empirical analyses calculated species-level correlations instead of averaging by elevational bands (Fleishman *et al.*, 1998; Sanders, 2002; Ruggiero & Hawkins, 2006), but these have been used in fewer studies and are not as easily comparable with the original intent of Stevens (1989, 1992). Lastly, we did not include formal meta-analyses of effect sizes, principally due to the lack of pertinent sample size estimation for each study. The best weights for sample size in meta-analyses reflect actual strength of the results from each study (e.g. sampling effort, sampling quality). Unfortunately, a standard measure of sampling effort does not exist for these studies. A potential sample size would be the number of elevational bins, which directly correspond to the height of the mountain. Unfortunately, there is no indication in the theory or pattern of the ERR to suggest that range size should predominately increase on tall mountains rather than shorter mountains. Choosing an arbitrary sample size in order to conduct a formal meta-analysis may lead to erroneous results (Rahbek, 2005; Whittaker, 2010), and therefore is not presented here.

The distribution and average fit to the ERR predictions indicate the overall level of support determined by each method. But to further synthesize and simplify the compiled results for the 160 gradients, we chose break-off points for strong ERR support under the three methods. The Stevens and midpoint methods both test for the predicted positive, monotonic relationship of increasing range size with increasing elevation. Thus, datasets that deviate substantially from a positive, linear relationship do not support the ERR, including those trends that were decidedly curvilinear and/or highly variable in average range size among elevational bands. A monotonically increasing relationship is tested in the same manner as a linear relationship using a linear regression. Therefore, for strong support of the ERR with these two methods, we chose an r^2 value of 0.50 or greater. We chose this as our cut-off for several reasons. First and most importantly, effect sizes below this value indicate substantial nonlinearity and often unimodal relationships (e.g. Fig. 1; see also McCain & Sanders, 2010). Second, for regression analyses along gradients with variable numbers of data points, the comparison of probabilities (*P*-values) is known to be a biased indicator of significance (Colwell *et al.*, 2004). Third, for similar regression studies of predicted relationships with elevational species richness and abiotic factors using the same underlying data as here, the strong relationships averaged r^2 values considerably higher than 0.50, usually between 0.70–0.90. (McCain, 2005, 2007, 2009a, 2010). So in this synthetic, macroecological context, effect sizes below 0.50 tend to be on the poorer side as predictor variables. The stringency for strong support for the quartile method was lowered to include r^2 values > 0.40, due to a lower importance of a linear trend and due to the small sample sizes within the quartiles.

RESULTS

Vertebrate elevational extents along the 160 montane gradients were extremely heterogeneous, as evident in the results for all three ERR methodologies (Fig. 1). The results using the mean and the median for the representation of central tendency in range sizes were nearly identical for both the Stevens method and the midpoint method (Stevens, $r = 0.99$, $P < 0.0001$; midpoint, $r = 0.97$, $P < 0.0001$). Therefore, we present only the results for mean range sizes. Using Stevens' methodology, relationships between range size and elevation varied from positive relationships with a maximum r^2 value of 0.98 to negative relationships with a maximum r^2 value of 0.91. The distribution of r^2 values was bimodal with the peaks centred at zero and 0.70 (Fig. 2a), and an average fit of 0.32. A similar distribution was detected for each vertebrate group individually (Appendix S2). Thus using the strong fit criterion (positive relationship, $r^2 \geq 0.50$), among each of the vertebrate groups the majority of datasets (60%) did not demonstrate strong support for the ERR using the Stevens method (Fig. 3a). The midpoint method uniformly found no support for the ERR among vertebrates along the elevational gradients (Fig. 2b, Appendix S2). All r^2 values fell between 0.05 for positive relationships and 0.35 for negative relationships with a unimodal peak in r^2 values around the average fit of 0.06 (negative relationship). Therefore, no datasets demonstrated strong support for the ERR using the midpoint method. As can be noted in Fig. 1(c, d), due to the small number of species along each gradient, many elevational bands had no species whose midpoint fell within the band. This created many zeros in the midpoint analyses.

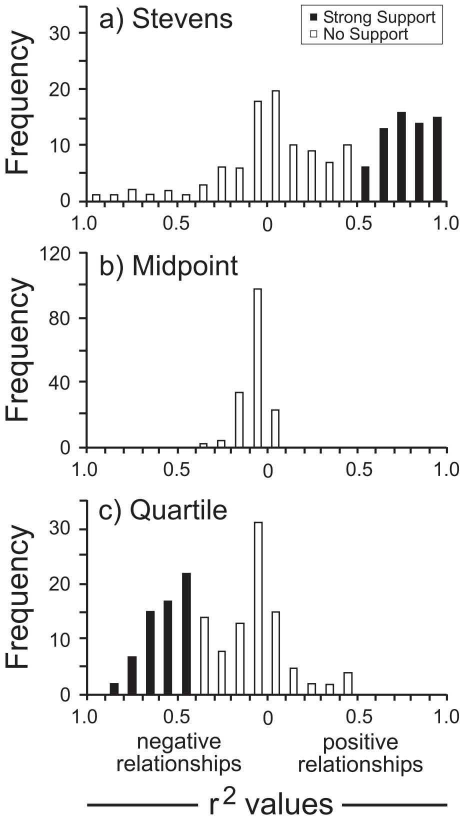

Figure 2 Linear regression r^2 values for positive and negative relationships between range size and elevation combined for all vertebrate groups ($n = 160$). Black bars indicate strong support for the predictions of the elevational Rapoport's rule using (a) the Stevens method, (b) the midpoint method, and (c) the quartile method. See Appendix S2 for results by taxonomic group.

Both the Stevens and the midpoint methods can detect a positive, reverse or lack of an ERR trend due to an overriding effect of large-ranged species, which occur across a broad swath of the elevational gradient. Using the quartile method, the smallest ranges (quartile 1) were highly variable in linear regression fits to the predicted relationship of decreasing frequency with increasing elevation, ranging from a positive relationship between quartile 1 ranges and elevation with an r^2 value of 0.50 to a negative relationship with an r^2 value of 0.86. The distribution of r^2 values was bimodal with the peaks centred at 0.10 and 0.50 (both negative relationships), and an average fit of 0.26 (negative; Fig. 2c). A similar distribution was detected for each vertebrate group individually (Appendix S2). When comparing the strong support for the ERR ($r^2 > 0.40$) using quartiles among vertebrate groups, again the majority of datasets (62%) failed to demonstrate strong support for the ERR (Fig. 3b).

Stevens (1992) suggested that locally sampled elevational transects (alpha-scale data) would be stronger tests of the ERR than regional elevational compilations (gamma-scale data). We compared this expectation and found mixed results among the three methodologies. A comparison of local and regional elevational data using the Stevens method revealed stronger ERR support for the regional data (mean $r^2 = 0.42$) than local data (mean $r^2 = 0.11$) (Mann–Whitney U, $Z = -3.42$, $P = 0.0006$), contrary to Stevens' prediction. A comparison within the midpoint method was also significant (Mann–Whitney U, $Z = 4.85$, $P < 0.0001$), but less meaningful due to the overall poor and opposite ERR trends (local: mean $r^2 = 0.02$; regional: mean $r^2 =$

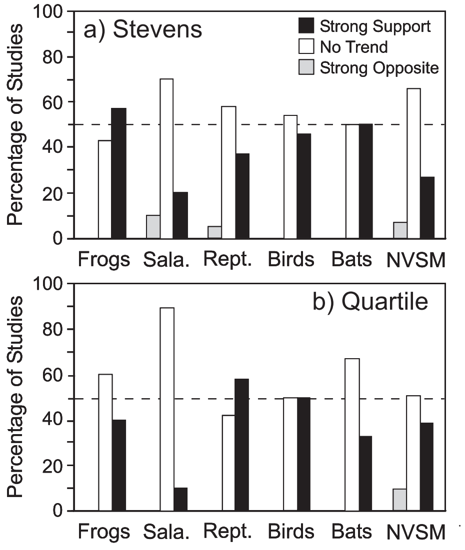

Figure 3 Support for the elevational Rapoport's rule for terrestrial vertebrate groups [frogs, salamanders, reptiles, birds, bats and non-volant small mammals (NVSM)] using (a) the Stevens method and (b) the quartile method. The dashed lines indicate 50% of studies. The quartile method uses only the smallest ranges (quartile 1, less then a quarter of mountain height) to detect a decreasing abundance of small ranges with increasing elevation.

0.08). Finally, the quartile method found no significant differences in fit between local and regional datasets (Mann–Whitney *U*, $Z = 0.13$, $P = 0.90$).

It has been suggested that the LRR is supported strongly only at high northern latitudes (i.e. > 23° N; Rohde *et al.*, 1993). We tested whether ERR fits were higher for mountains above and below 23° N latitude and detected significantly stronger fits at the higher latitudes using the Stevens method (Mann–Whitney *U*, $Z = 1.68$, $P = 0.0467$; high-latitude average $r^2 = 0.41$, low = 0.25), but no trend using the quartile method [Mann–Whitney *U*, $Z = -0.39$, $P = 0.6504$; high = 0.20 (negative); low = 0.21 (negative)] and a significant difference using the midpoint method but opposite to the ERR predicted trends [Mann–Whitney *U*, $Z = 2.83$, $P = 0.0023$; high = 0.02 (negative); low = 0.07 (negative)]. Across all latitudes, the ERR fits do not show any clear association (Stevens: $r = 0.06$, $P = 0.3364$; quartile: $r = -0.06$, $P = 0.4293$).

DISCUSSION

In 1992, Stevens used eight datasets (four tree, one insect, one herpetofauna and two bird studies) showing an increase in average range size with increasing elevation to propose his elevational Rapoport's Rule (ERR). That same paper examined two vertebrate datasets (one bird, one herpetofauna study), which did not show the predicted ERR relationship. Since that time, there have been many additional empirical tests for various taxonomic groups (e.g. Patterson *et al.*, 1996; Rohde, 1996; Pleguezuelos & Villafranca, 1997; Price *et al.*, 1997; Rahbek, 1997; Fleishman *et al.*, 1998; Ruggiero & Lawton, 1998; Nathan & Werner, 1999; Gaston & Chown, 1999a; Sanders, 2002; Fu *et al.*, 2004; Chatzaki *et al.*, 2005; Almeida-Neto *et al.*, 2006; Bhattarai & Vetaas, 2006; Hausdorf, 2006; Ribas & Schoereder, 2006; Brehm *et al.*, 2007). But the split support for the ERR remains, and the onus is now to show that the rule applies more often than expected randomly (e.g. Gaston *et al.*, 1998; Ashton, 2001; Ribas & Schoereder, 2006). In total, comparing all three standardized methods for 160 vertebrate datasets we demonstrate that the ERR is detected on average in 26% of cases.

Could this lack of support for the ERR be methodological? Both measures of central tendency resulted in virtually identical results. We compared three statistical methodologies: the Stevens method, which suffers from spatial non-independence and biased contributions from ranges of different sizes; the midpoint method, which corrects for spatial non-independence and emphasizes large ranges but is restrictive in subsampling, especially for datasets with few species; and the quartile method, which corrects for the mid-domain effect (stronger constraints on large ranges) potentially present in both the Stevens and the midpoint methods. All three methods detected support for the ERR in fewer than 50% of the cases. The least restrictive Stevens method detected the highest level of support for the ERR (40%), and the most restrictive midpoint method detected the lowest level of support for the ERR (0%). Regardless of which methodology one prefers, overall support for the ERR among montane vertebrates is weak.

Alternatively, could the lack of support for the ERR be due to data quality? No biological data are without error and that is certainly the case with the 160 studies included here as well. As Colwell & Hurtt (1994) pointed out, a lack of sufficient sampling in the highly diverse regions of gradients can lead to spurious support for Rapoport's rule. But the critical error would need to lead to systematic bias, and we tried to vet these data to only those with robust sampling without elevational biases (e.g. Rickart, 2001; Nogués-Bravo *et al.*, 2008; McCain, 2009b). Additionally, we found no consistent spatial scale bias (e.g. Stevens, 1992), as local transects and regional transects both revealed low support for the ERR across methods. A within-mountain scale could influence ERR fits, for instance the number of elevational bins used per mountain, for example between a 500-m scale (e.g. Stevens, 1992) and a 100-m scale (herein). At the coarsest scale, comparing the average range sizes within the lowest third of the mountain and the highest third of the mountain, there is a strong tendency to have larger ranges in the highest third of the mountain for all these vertebrate groups except salamanders (McCain, 2009b; using most of the same datasets). But this scale is not a strong test of the ERR, because the original ERR proposal was that there was a linear increase in range size with elevation and a bimodal test does not include any linear indication. In fact, the average maximum and minimum range sizes can occur at any elevation within the lower and upper thirds of mountains. Specifically, curvilinear relationships can still be common and are as depicted in the 100-m scale analyses presented here (e.g. Fig. 1).

Could the lack of support for the ERR be due to the focus on vertebrates? We have presented comprehensive results for terrestrial vertebrates. To date there is only one study for montane fish (Fu *et al.*, 2004), which detected no support for the ERR. Nonetheless, terrestrial vertebrates may not be indicative of patterns in the more species-rich invertebrates and plants. To assess this taxonomic effect, we reviewed the literature for ERR tests of invertebrates and plants (Appendix S3). These datasets could not be standardized for methodology (e.g. Wolf, 1993; Sanders, 2002; Almeida-Neto *et al.*, 2006; Brehm *et al.*, 2007) or for sampling, and only a portion published the statistical values for the ERR. Therefore, three categories of support were delineated: (1) 'support' which included either strong support with a test statistic > 0.50 or no statistic given but positive support noted; (2) 'minimal support' which included a test statistic between 0.10 and 0.40; and (3) 'no support' which included a test statistic of < 0.10, a negative or opposite relationship, or a notation of no support for the ERR. In accordance with the vertebrate studies, the invertebrate and plant studies also found highly variable ERR results with overall less than 50% of the studies detecting support except for trees (Fig. 4). No support for the ERR was detected in 64% of insect studies or in 57% of other invertebrates (e.g. spiders, land snails) and non-tree plants. In contrast, tree studies predominantly detected support for the ERR (83%). This could be indicative of an ERR trend, but suffers from low sample size ($n = 6$) and four of these were from the original paper (Stevens, 1992). Additionally, one of the papers Stevens included on Costa Rican trees was shown to have a spurious

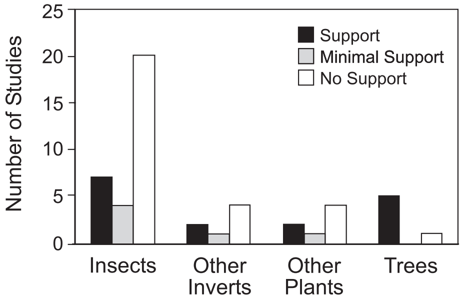

Figure 4 Support for the elevational Rapoport's rule (ERR) for insects, other invertebrates, non-tree plants and trees assessed from a literature review. The categories of support are (1) 'support' which included either strong support with a test statistic > 0.50 or positive support noted; (2) 'minimal support' which included test statistic between 0.10 and 0.40; and (3) 'no support' which included a test statistic < 0.10, a negative or opposite relationship, or a notation of no ERR support.

Rapoport effect due to sampling biases (Colwell & Hurtt, 1994, pp. 591–592). Overall, support for the ERR among non-vertebrate organisms combined still averaged only 41%.

Could the lack of a strong ERR pattern be a result of truncated climatic gradients on mountains? For example, if the mountains do not extend through sufficient ecological space (temperature zonation), then species may not have adequate space to display the appropriate range size or resulting range size distributions on the mountain. One problem with this hypothesis is that the earth only contains mountains of certain heights and distributions, so biogeographic reality dictates that for the predictions of the ERR to be relevant it needs to be displayed on existing mountains. But beyond that limitation, if the ecological span of the montane gradient is critical for detecting positive support for the ERR, then higher mountains should have stronger ERR fits than less high ones. With the vertebrate data, we found no predictive pattern between mountain height and strength of fit to ERR predictions (Stevens: $r^2 = 0.003$, slope = 0.00, $P = 0.524$; midpoint: $r^2 = 0.11$, slope = 0.00, $P < 0.001$; quartile: $r^2 = 0.06$, slope = –0.0001, $P = 0.002$; see Appendix S4 for figures). Thus, at least with the mountains and groups studied here, mountain height and thus the span of the ecological gradient, does not appear to be indicative of a better test of ERR predictions.

Overall these results indicate that the ERR is not a very predictive theory for the distribution of the range sizes or organisms on mountains, and in fact it may be misleading for it to be so emphasized in the literature. As stated by Stevens (1992), "if no tendency for altitudinal range to vary with elevation is found, then the current explanation for the latitudinal Rapoport's rule and its potential influence on local species richness is somehow flawed". The time has come to move beyond the simple idea that range size increases with elevation and apply a more nuanced approach to understanding the variation in range size distributions within mountains. We suggest three avenues of analyses that may provide interesting insights: the biogeographic context of range sizes; species-specific correlates of range size; and ecological and evolutionary correlates of range size, across gradients. Range sizes of organisms fluctuate over long temporal scales between speciation and extinction (Rabinowitz, 1981; Gaston, 2003), and undoubtedly have sequentially expanded and shrunk in response to glacial and interglacial periods (e.g. Jackson & Overpeck, 2000; Colwell & Rangel, 2010). Varying levels of stability and change may influence montane range size distributions in predictable ways (e.g. Dynesius & Jansson, 2000). Species-specific correlates with range size, for example body size, abundance distributions, habitat specificity, taxon age, could also provide insight into mountain distributions of range size (e.g. Brown, 1995; Gaston, 2003). Lastly, the often-tested ecological correlates (temperature, precipitation, productivity, area) across gradients of species richness could also be examined for influences on range size distributions, for example testing the influences of environmental productivity and niche packing, which would predict smaller range sizes in areas of the highest productivity. This vast field of possibilities for examining montane range sizes in more ecological and evolutionary detail is an open frontier waiting on interest, empirical data, and modelling.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Details of 160 vertebrate elevational gradients used in analyses.
Appendix S2 Summary figures of analyses of the elevational Rapoport's rule per vertebrate group.
Appendix S3 Details and citations for papers used in review of the elevational Rapoport's rule for invertebrates and plants.
Appendix S4 Figures of analyses to detect relationship between mountain height and elevational Rapoport's rule fits.

BIOSKETCHES

Christy McCain is an Assistant Professor in the Department of Ecology and Evolutionary Biology and Curator of Vertebrates in the Museum of Natural History at the University of Colorado at Boulder. She did her post-graduate work in mammalian ecology at the University of Kansas and post-doctoral work in ecology at the National Center for Ecological Analysis and Synthesis. Christy is an ecologist focusing on large-scale ecological patterns with particular emphasis on species richness, abundance and distribution patterns along ecological gradients. She is also interested in null models, ecological modelling of species ranges, montane biogeography, climate change and theoretical and empirical aspects of the causes and maintenance of species diversity.

Kevin Bracy Knight is a PhD student in Christy McCain's lab at the University of Colorado at Boulder, and is interested in community ecology, GIS and global change biology.

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