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Quality of basic data and method to identify shape affect richness–altitude relationships in meta-analysis

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Abstract. We compiled 109 species richness–altitude (SRA) relationships in arthropods to test the hypothesis that identification of shape and robustness of pattern are contingent on the selection of studies included in meta-analysis. We used attributes of their sampling design to distinguish three subsets of data according to stringent, intermediate, and lax selection criteria. We tested (1) whether uncertainty over identification of shape increases as the criteria of inclusion of studies relaxes and (2) whether studies that conform to stringent selection criteria show robustness in SRA patterns to variation in method used to identify shape. We identified the shape of each SRA relationship using statistical and visual methods; data sets that suggested several shapes as equally likely were sorted out by consensus. Arthropods suggested multiple forms in the SRA relationship, with predominance of hump-shaped patterns in the stringent subset. Uncertainty over identification of shape increased after application of intermediate and lax selection criteria. The method of analysis interacted with the quality of basic data to influence the relative distribution of patterns. We concluded that the gathering of large quantities of data is insufficient and that critical evaluation of literature is crucial to infer with confidence the general shape of ecological patterns in meta-analysis.

Key words: arthropods; elevation gradient; hump-shaped pattern; meta-analysis; monotonic decreasing pattern; sampling design; species diversity.

Introduction

The perception of ecological patterns in meta-analysis is susceptible to being influenced by eventual misclassifications of studies or potential biases in the statistical procedures followed to detect the pattern (e.g., Whittaker and Heegaard 2003, Whittaker 2010 and references therein). The common approach of conducting extensive primary analysis of data from previous authors has contributed contradictory conclusions about the form of relevant patterns in ecology. For example, it has been suggested that artefactual mechanisms associated with the way data are extracted, analyzed, manipulated, and contextualized in different research syntheses may account for the form of the species richness–productivity relationship, sometimes leading to an overestimation of the frequency of hump-shaped patterns (Whittaker 2010 and references therein). This has led to the idea that a profound change in the criteria being used to select studies for research synthesis in ecology, and deep consideration of methods used to detect pattern is needed (Whittaker 2010). Nonetheless, the extent to which variation in the selection criteria of studies may influence the perception of patterns in ecological meta-analysis has not been explored systematically. In the present study, we used a comprehensive compilation of species richness–altitude (SRA) relationships in arthropods as an example to address this issue.

The shape of the SRA relationship is a controversial issue. Although, in the past, the altitudinal species richness gradient was often thought as a monotonically decreasing pattern homologous to the latitudinal diversity gradient (e.g., MacArthur 1972, Lawton et al. 1987, Brown and Lomolino 1998), recent evidence suggests that a hump-shaped pattern, with a peak in species richness at mid-elevations, or even multiple forms, may be more typical (Rahbek 1995, 1997, 2005, McCain 2007, 2009, Nogués-Bravo et al. 2008). Less frequently, patterns show a low altitude plateau of higher species richness (Janzen et al. 1976, Lods-Crozet et al. 2001), an altitudinal increase in species richness (Turner and Broadhead 1974, Sanders et al. 2003), or follow a U-

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shape (Ribeiro et al. 1998). Such multiple forms in the SRA relationship question the universality of the altitudinal diversity gradient. Here, we compiled SRA relationships from different parts of the world to test the hypothesis that identification of SRA patterns depends upon the quality of original studies included in meta-analysis and the method used to identify shape. We tested the predictions that (1) uncertainty over identification of shape increases as the criteria used to include a study into the analysis becomes more lax, and (2) studies that conform to stringent selection criteria show robust altitudinal richness patterns with respect to variation in method used to identify shape. The selection of published studies used to create different subsets of data has been useful to examine the effects of scale, sampling, and areal standardization on SRA patterns (Rahbek 2005). Our study will show that the use of different methods to identify SRA shapes interacts with the quality of basic data to influence the relative distribution of patterns.

A caveat is needed about the approach adopted in the present study, which used data from mountains in different parts of the world to compare the relative frequency of SRA patterns, but without disentangling the role of different environmental drivers on shape. Data collected along altitudinal gradients reflect the combined effect of general climatic and geophysical changes with altitude and regional phenomena (e.g., history and isolation of mountain biota; see Plate 1); hence, it has been suggested that the lack of a "standard mountain" complicates the interpretation of discrepancy between findings from different altitudinal gradients by different researchers if only "altitude" is taken into account as explanatory variable (Körner 2007). Nonetheless, throughout the present study altitude was not considered the driving factor for species richness, but just the template for our meta-analysis. Our purpose here was to evaluate the extent to which decisions taken by researchers at the time of data compilation and assignment of gradients to different shapes may complicate detection of robust patterns in meta-analysis; confidence in the identification of shape is needed before any attempt to identify underlying drivers of SRA relationships is made.

METHODS

Selection of data

We carried out a literature search through Zoological Record and Scopus (*available online*).[2,3] We used altitud* or elevation* *and* richness or diversity as key words. Asterisks are used to substitute for any other character or characters in the search string. For instance, search terms such as altitud* would return any word that begins with "altitud," such as altitude and altitudinal. We searched for papers with any of the first two words [altitud* or elevation*] *and* any of the second two words [richness or diversity]. Additional papers were obtained by examining the references of original articles. We selected all papers that reported data on the richness of arthropod species for at least five different elevations. To reduce the so-called "file drawer problem" (Rosenthal 1979, Csada et al. 1996), we selected studies that were originally designed to test the SRA relationship along with others that were not specifically designed for this purpose. We included gradients provided they reported data on raw species richness (neither rarefied nor transformed) for each altitude. For a few studies where data on richness were not available, we estimated local richness at each altitude based on confirmed (i.e., not interpolated) presence of species. To overcome the problem of pseudo-replication, we selected papers from the same author/s provided they worked with different data sets, and we analyzed richness data from different years in the same location only if they were from different sampling points. When a study combined data on local richness estimations from several mountains to describe a regional altitude–richness relationship, we selected data on the local altitudinal gradients and discarded values at regional scale. When a study reported richness–altitude data of subordinate taxa (e.g., subfamilies) within a higher taxonomic level (e.g., family), we separately analyzed the data on each subordinate taxon and discarded the values reported at higher taxonomic level. Our selection process resulted in a working list of 75 studies with altitude–richness data on 109 altitudinal gradients (see Appendix A). Data only published in graphic form were digitized using DataThief II 1.1.0 (Tummers 2006; *available online*).[4] Our last search was in December 2007, and papers published since then were not included in our study.

Criteria used to classify gradients into different subsets of data

We classified each altitudinal gradient with respect to four variables that allowed their subsequent inclusion into different subsets of data (see Appendix A: Table A1). For each study, we recorded three factors involving sampling design (points 1–3) and one involving the impacts of human presence (point 4): (1) Proportion of gradient sampled. McCain (2009) proposed that analysis of SRA relationships should be based on studies that cover at least 70% of the total mountain range. (2) Sampling standardization. We recorded the presence of standardized or equal sampling effort across different altitudes, which are known

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[2] ⟨http://thomsonreuters.com/products_services/science/science_products/a-z/zoological_record⟩

[3] ⟨http://www.scopus.com/home.url⟩

[4] ⟨http://datathief.org/⟩

to influence the SRA patterns (Rahbek 2005). (3) Number of sampling points. Whittaker (2010) adopted a 10-data point minimum as suitable to discriminate between linear and unimodal form in the species richness–productivity relationship. (4) We recorded the presence of anthropogenic disturbance as a potential confounding variable of the SRA relationship. Whittaker (2010) argued that the study design should not involve potential confounding variables of the tested ecological relationship.

We assigned each gradient to a different subset of data according to the following criteria: (1) stringent ($\geq$70% of the gradient sampled, standardized or equal sampling effort across different altitudes, and $\geq$10 sampling points); (2) intermediate (standardized or equal sampling effort along with one of two other possible conditions [either the proportion of gradient sampled was $>$50% and the number of sampling points was $<$10, or the number of sampling points was $\geq$10, but the proportion of gradient sampled was $<$70%]); and (3) lax (studies that involved unstandardized or unequal sampling effort across different altitudes and/or showed evidence of anthropogenic disturbance as a potential confounding variable; if standardized sampling effort was applied, then they had $<$10 sampling points and $<$50% of gradient sampled).

Most of the studies included in our analysis were field studies that sampled arthropods at very local grain sizes using different sampling methods; there were only a few studies that used collection data from museums or distributional information from maps (see Appendix A: Table A1). After classification of studies into the three subsets, we confirmed that the stringent subset of data encompassed gradients of $\sim$1890 ± 760 m of mean altitude extent (mean ± SD) and $\sim$129 ± 45 m of mean inter-site resolution (i.e., mean distance between sampling points), with a greater proportion of studies at the landscape scale (i.e., linear distance between the two most extreme points $>$30 km) rather than at local scales (i.e., distance between the two most extreme points $<$30 km): 62% vs. 38%, respectively. The intermediate subset of data encompassed gradients of $\sim$1537 ± 668 m of mean altitude extent, $\sim$221 ± 134 m of mean inter-site resolution, and a greater percentage of studies at local (71%) than at landscape scale (29%). The lax subset of data encompassed gradients of $\sim$1490 ± 808 m of mean altitude extent, $\sim$238 ± 137 m of mean inter-site resolution, and similar percentage of studies at landscape and local scale.

Identification of patterns

We analyzed 109 altitude–richness gradients by two methods: (1) a standard protocol that allowed the statistical description of pattern (hereafter referred as "statistical method") and (2) visual examination of shape ("visual method"). Our purpose here was primary descriptive, and we used standard statistical or visual methods to account for the shape of altitudinal richness gradients (e.g., Rowe and Lidgard 2009 for a similar approach).

Statistical method.—For each data set, we regressed data of richness (y) on altitude (x) to evaluate the likelihood of the data given four different models. Model 1: a simple linear SRA relationship ($y = a + bx$, where a is the intercept and b is the slope) that described a monotonic decreasing (DEC) or increasing pattern (INC), depending on the sign of the slope. Model 2: a nonlinear SRA relationship of the form $y = a + bx^2$, which described a low-plateau pattern (L-PL; rather constant high richness at low altitudes followed by a decrease in richness) when $b < 0$. Model 3: of the form $y = a + bx + cx^2$, with a is the intercept, and b and c are regression coefficients, which, depending upon the sign of c coefficient, described a hump-shaped pattern (H-SH; $c < 0$), or U-shaped pattern (U-SH; $c > 0$). Model 4: the only-intercept model ($y = a$) that evaluated the lack of altitudinal pattern (NP). For each data set assigned to H-SH, we further checked that the maximum richness fell within the range of altitudes encompassed by the data. The statistical method allowed the detection of other forms in the SRA relationship (e.g., J-shaped or L-shaped patterns) that we maintained in a single category (OTH).

To find the best explanatory model, i.e., for assignment of each data set to a different pattern, we used the Akaike's information criterion corrected for small samples (AIC_c; Burnham and Anderson 2002, Diniz-Filho et al. 2008), which allowed ordering the four models fitted to each data set from best to worst. We considered the model having the minimum AIC_c as the best model supported by the data. We estimated the size of the increments of information loss (Δi) for each model compared to the estimated best model ($\Delta i = \text{AIC}_{ci} - \text{AIC}_{\text{cmin}}$); models having $\Delta i > 2$ of the best model were considered to have considerable less support (Burnham and Anderson 2002, Diniz-Filho et al. 2008). Models that had a $\Delta i < 2$ of the best model were considered equally likely for a particular data set; in this case, we assigned support to each SRA pattern involved, in equal proportions, dividing 1 by the total number of SRA patterns supported.

Visual method.—For each data set, we elaborated a scatter plot of the variation of richness as a function of altitude for visual identification of shape: monotonic decreasing (DEC), monotonic increasing (INC), hump-shaped (H-SH), U-shaped (U-SH), and low-plateau (L-PL). To minimize the inherent subjectivity of this method, we followed McCain (2009)'s criteria for assignment of SRA relationships into different patterns. We defined DEC and INC as those patterns in which species richness, respectively, declined or increased monotonically with elevation. H-SH was a unimodal

PLATE 1. Panoramic view of a temperate mountain region in northern Patagonia, showing an example of the kind of environmental changes that occur with altitude. Photo credit: V. Werenkraut.

pattern that has a richness peak at intermediate altitudes with 25% or more species than at the base or top of the mountain (i.e., the so called "mid-elevation peak" by McCain 2009). A L-PL pattern had >300 m of consecutively high richness at the mountain base and thereafter decreasing species richness (see McCain 2009 for further details and other possible forms). Data sets that suggested no clear SRA relationship were assigned to NP, and other different forms were included in OTH.

We looked for a consensus between the visual and statistical methods to identify the final shape of each data set; datasets showing lack of consensus were labeled as "contradictory" (CONT).

To further evaluate uncertainty over identification of shape, we square root-transformed the coefficients of determination (R^2) from the ordinary least squares (OLS) regressions to obtain correlation coefficients (r) (e.g. Hillebrand 2004), which were transformed to an effect size (z_r, Fisher's z-transformation; Hedges and Olkin 1985). We estimated a common measure of effect size for the stringent, intermediate, and lax subsets of data, taking into account that the nonsystematic variance of estimates of effect size was inversely proportional to the sample size of the gradients on which estimates were based (Hedges and Olkin 1985). Combination of linear and quadratic terms in meta-analysis requires that all the study-specific regressions have been fitted with the same number of terms (K. Mergensen and J. Gurevitch, *personal communication*). Hence, we conducted this analysis separately for each SRA pattern (H-SH, DEC, and L-PL). We performed all the analyses using R software (R Development Core Team 2009).

Close examination of patterns in our whole data set, after consensus, showed that, although the relative frequency of the most abundant patterns (H-SH, DEC, L-PL) was independent of taxonomy (permutation-based Fisher-Freeman Halton test for small-sample categorical data [FI] = 20.16, df = 18, $P = 0.19$), there was an association with climate (FI = 30.87, df = 24, $P = 0.02$), and biogeography (FI = 23.03, df = 12, $P = 0.003$) (see also Appendix B: Fig. B1). We tested these associations in the three subsets of data to elucidate the extent to which taxonomy, climate, and biogeography might influence changes in the relative proportions of SRA patterns after our data manipulation. These analyses were conducted using StatXact-6 (2003).

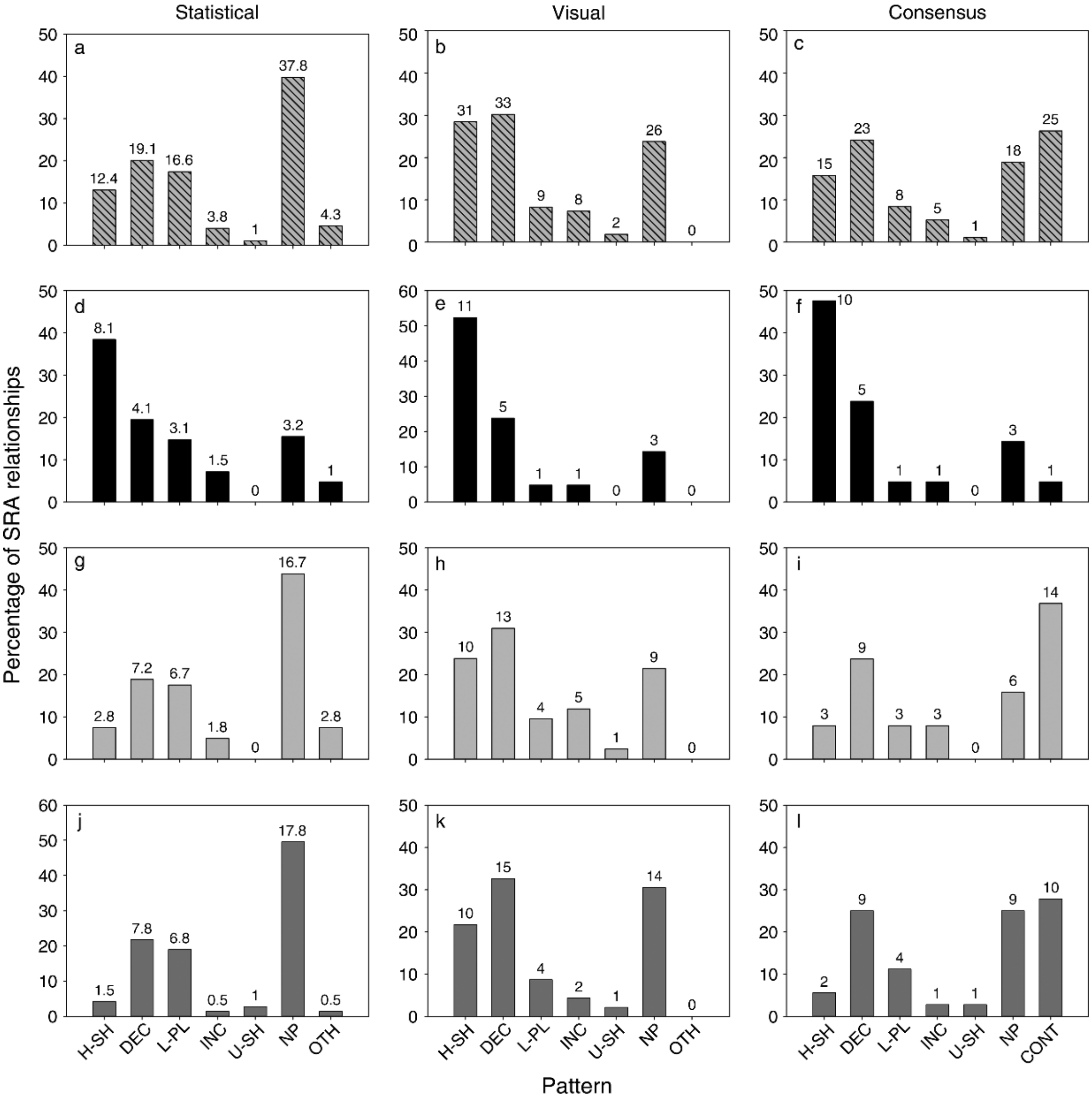

FIG. 1. Relative frequency distributions of SRA (species richness–altitude) patterns observed in subsets of the worldwide arthropod data: (a–c) whole data set; (d–f) stringent subset; (g–i) intermediate subset; and (j–l) lax subset. The patterns were analyzed by statistical and visual methods and by consensus. Abbreviations are: H-SH, hump-shaped; DEC, monotonic decreasing; L-PL, low-plateau; INC, monotonic increasing; U-SH, U-shaped; NP, no pattern; OTH, other patterns; and CONT, contradictory. Numbers above bars are sample sizes. Studies with a low number of sampling points ($N = 5$) were not analyzed by the statistical method.

RESULTS

The total of 109 SRA relationships taken together showed differences in the proportional representation of different forms between the two methods of analysis, and consensus (Fig. 1a–c). The statistical method suggested lack of pattern in ~40% of the data sets (NP; Fig. 1a). DEC and L-PL had a similar (~20%) proportional representation, followed by H-SH (~13) (Fig. 1a). The visual method half-decreased the proportional representation of NP and L-PL, and increased considerably the proportional representation of H-SH and DEC (Fig. 1b). The consensus suggested DEC was the most abundant SRA relationship, followed by H-SH, and L-PL became rarer; ~20% out of the total data sets remained as NP, and ~25% showed no consensus (CONT; Fig. 1c).

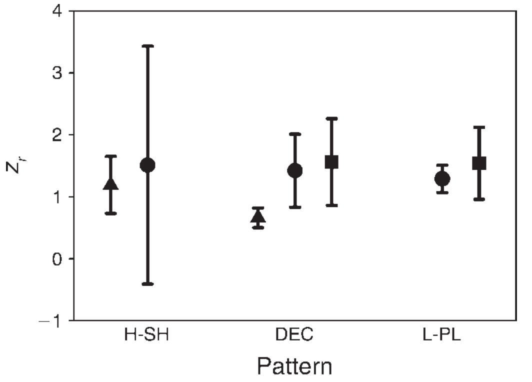

FIG. 2. Effect of relaxing the selection criteria of studies, from stringent (triangles), to intermediate (circles), and lax (squares), over uncertainty (shown as 95% confidence intervals) in the estimation of a common effect size (z_r, Fisher's z-transformation) for H-SH (hump-shaped), DEC (monotonic decreasing), and L-PL (low-plateau) patterns.

The stringent criteria of inclusion of SRA data came up with a subset of 21 data sets that showed a consistent order in the relative importance of the most abundant SRA patterns throughout both methods of analysis and consensus (HS-H > DEC > L-PL; Fig. 1d–f). The percentage representation of H-SH rather increased, and L-PL decreased with the visual method and consensus, compared to the statistical method (Fig. 1d–f). The percentage representation of NP, and moreover of CONT, was lower than in the whole data set (compare Fig. 1c, f).

Relaxing the selection of SRA data, came up with two data subsets of 42 (intermediate subset) and 46 (lax subset) SRA relationships. The relative frequency distribution of different SRA patterns in both subsets largely followed the observed in the whole data set by all methods of analysis (compare Fig. 1a–c and g–l). The statistical method showed the highest percentage of NP (Fig. 1j, k). The visual method somewhat decreased the percentage of L-PL and NP, which increased the percentage of H-SH and of DEC (Fig. 1h, k). The consensus confirmed the predominance of DEC, although there was a high percentage of NP and CONT (Fig. 1l). INC and U-SH patterns were rare throughout (Fig. 1j–l).

After controlling for differences in sample size, we further confirmed that relaxing the selection of SRA data increased uncertainty in the estimation of the magnitude of SRA relationships (Fig. 2).

There was no association of shape with taxonomy or climate after our data manipulation (Table 1, Appendix B: Figs. B2 and B3), but a significant biogeographical relationship was evident in the stringent subset (Table 1), which suggested that H-SH patterns were recorded only in the Nearctic and Paleartic regions, whereas DEC were more frequent in the Neotropics (Appendix B: Fig. B4).

DISCUSSION

Our manipulation of SRA relationships into different subsets of data showed that the quality of basic data selected for meta-analysis is crucial to reliable identify shape (see Whittaker 2010 for discussion). We confirmed the two predictions proposed at the outset of the present study. In general, uncertainty over identification of shape increased as the criteria of inclusion of studies into the analysis became more lax; studies that conformed to stringent selection criteria showed robustness in the SRA patterns to variation in method used to identify shape. Rahbek (2005) demonstrated that decisions concerning the analytical design of individual studies can completely turn around the statistical outcome related to the shape of the SRA pattern (but see Rowe and Lidgard 2009). Our study showed how these effects could also interact with two methods (statistical and visual) used to identify shape to affect the overall relative frequency distributions of SRA patterns.

The total SRA relationships taken together suggested the predominance of monotonic decreasing patterns after consensus. However, the application of stringent selection criteria confirmed the predominance of hump-shaped patterns over monotonic decreasing ones. In general, the relative frequency of patterns in the whole data set paralleled those found in the intermediate and lax subsets, which taken together represented >80% of the SRA relationships in our study. Changes in the proportional representation of shapes after data manipulation were not associated with climate and taxonomy, although we found an association with biogeography in the stringent subset. This association suggested a

TABLE 1. Tests of association between the relative distribution of frequencies of the three most abundant patterns (hump-shaped, monotonic decreasing, and low-plateau) of arthropod distribution after consensus and taxonomy, climate, and biogeography.

	Stringent			Intermediate			Lax		
Test of association	FI	df	*P*	FI	df	*P*	FI	df	*P*
Taxa × SRA pattern	13.648	10	0.117	11.086	12	0.826	14.080	14	0.706
Climatic region × SRA pattern	15.425	12	0.179	15.534	14	0.157	14.333	16	0.987
Biogeographic region × SRA pattern	13.810	6	0.003	9.356	8	0.271	11.346	12	0.818

Notes: Abbreviations are: FI, permutation-based Fisher-Freeman-Halton statistic; df, degrees of freedom; *P*, probability level; SRA, species richness–altitude relationship. See *Methods* for descriptions of the stringent, intermediate, and lax selection criteria.

tendency for H-SH to be most frequently found in the Nearctic and Palearctic regions, which complicated interpretation. Nonetheless, whereas H-SH represented 30% out of the total Palearctic + Nearctic (taken together) SRA relationships in the whole data set, its representation rose to 77% in the stringent subset. Also, the proportional representation of Neartic + Palearctic regions increased by a factor of 1.25 in the stringent subset, whereas the proportional representation of H-SH patterns increased by a factor of 3. Thus, in spite of the biogeographic association, the substantial change in the proportional representation of different shapes shown in the stringent subset can be hardly considered as merely the consequence of the presence of Nearctic and Palearctic SRA relationships.

One effect of relaxing the selection criteria of inclusion of SRA relationships, from stringent to intermediate and lax, was to increase the proportional representation of monotonic decreasing patterns. This suggested that reducing the sampling effort in individual studies, i.e., either by lowering the number of sampling points, or by reducing the proportion of the gradient sampled, may favor the perception of monotonic decreasing patterns, and this could alter the relative distribution of different SRA patterns. Variation in sampling effort has been previously found to affect other macroecological relationships (e.g., body size–abundance relationships; Griffiths 1998). Examined within the context of SRA relationships, the reduction of the number of sampling points, or the proportion of gradient sampled, may be associated with effects of spatial scale known to affect the analysis of species diversity patterns (Lyons and Willig 1999, 2002, Rahbek and Graves 2000, Whittaker et al. 2001), and specifically, of altitudinal richness gradients (e.g., Rahbek 2005, Jankowski and Weyhenmeyer 2006, Nogués-Bravo et al. 2008, Sanders et al. 2009). We showed the higher frequency of occurrence of hump-shaped patterns in the stringent subset of data, which encompassed studies that involved greater sampling effort, and spanned over longer altitudinal extents than the intermediate and lax subsets. On the other hand, all hump-shaped patterns in the stringent subset came up from studies performed at landscape scale within the Palearctic and Nearctic regions. Given the low number of observations in our stringent data set, all these effects deserve further attention in future studies.

Another consequence of our data manipulation was increasing uncertainty in the identification of pattern using the intermediate and lax subsets of data, and also, after controlling for differences in sample size, uncertainty over estimation of the magnitude of SRA relationships increased with the relaxation of criteria of inclusion of data. The occurrence of no pattern (NP) was greater in the intermediate and lax subsets of data rather than in the stringent subset, especially for the statistical method. For the lax and intermediate subsets, the statistical method was more conservative in the detection of pattern, and suggested a higher proportion of NP rather than the visual method. The visual method and the consensus helped in sorting out NP data sets into recognizable shapes; however, a considerable proportion of data sets suggesting no pattern or contradictory information remained. The stringent subset had less average inter-site resolution, which implies that a greater effect of spatial autocorrelation in this data set might contribute to decrease uncertainty about detection of shape. There are a number of attributes in the design of studies that composed the intermediate and lax subsets that may complicate the detection of pattern, including less and/or unstandardized sampling effort, and increased inter-site resolution that promotes an increase in the scattering of data. However, a proportion (~15%) of data sets in the stringent subset also showed no pattern. This suggests that the presence of idiosyncratic variation in the SRA relationships might be rather common in arthropods.

Our study showed that the use of different methods to identify SRA shapes indeed interacts with the quality of basic data to influence the relative distribution of patterns. Only the stringent subset of data revealed a consistent order in the relative importance of different SRA shapes that was robust to variation in method of analysis. Too few SRA relationships remained in the stringent subset as to infer general conclusions on the extremely highly diverse arthropods. However, the consistency in the outcome in the stringent subset makes reasonable to infer the existence of multiple SRA forms, with the predominance of hump-shaped patterns over monotonic decreasing ones, along with the presence of considerable idiosyncratic variation. Had we based our interpretation on the whole data set this would have led to a different conclusion about the predominant patterns in arthropods. We conclude that decisions followed to gather the data and the method we use to infer SRA relationships (visually or statistically) both may influence our perception of the relative frequency of predominant shapes, and not necessarily the largest data set is the best for meta-analysis.

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APPENDIX A

Details of the papers used as basic data (*Ecological Archives* E092-021-A1).

APPENDIX B

Relative frequencies distributions of SRA relationships observed in different taxa and in different climatic and biogeographic regions (*Ecological Archives* E092-021-A2).