

The Concept of Taxon Invariance in Ecology: Do Diversity Patterns Vary with Changes in Taxonomic Resolution?

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Abstract Diversity patterns cannot be properly interpreted without a theory providing criteria for their evaluation. We propose a concept to prevent artificions caused by improper consideration of changes in observed patterns due to variation in taxon delimitation. Most biodiversity patterns concern assemblages of species of given higher taxon (e.g. class). Some patterns seem to be universal, e.g., body size distribution, species-abundance distribution, species-area relationship, or the relationship between diversity and energy availability. However, truly universal patterns should not change when we change taxonomic scope by focusing on subtaxa or when we merge several sister taxa together and analyze patterns in resulting higher taxon. Similarly, some patterns may not change when changing the basic unit of the study e.g., when replacing species by genera or families (or any monophyletic clades), although other patterns may not be invariant against the variation of the basic unit. In fact, there are only two possibilities: biodiversity patterns are either taxon-invariant or they vary systematically with taxonomic resolution, which would indicate some fundamental taxonomic level with interesting implications for biological processes behind those patterns. Here we develop the concept of taxon invariance of diversity patterns and apply it on the abovementioned patterns. We show that simple theoretical considerations markedly constrain the set of possible patterns, as some of them cannot be simultaneously valid for both a taxon

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and its subtaxa – frequency distributions of abundances cannot be simultaneously lognormal for a given taxon and all its subtaxa, the taxa-area relationship cannot follow a power-law for all levels of taxonomic resolution, and energy availability cannot affect diversity of all taxonomic units in the same way. Analyses of the variation in the form of biodiversity patterns with changing taxonomic resolution thus provide an extremely useful tool for revealing properties of respective patterns, their universality and logical consistency.

Keywords Abundances · Biogeography · Distributions · Macroecology · Phylogeny · Scaling · Species-energy relationship

Introduction

For many decades, ecologists have been reporting patterns concerning species assemblages defined by higher taxonomic units, typically orders, classes or phyla (Storch and Gaston 2004). Diversity patterns concern mostly numbers of species within a given higher taxon related to various factors or variables (area, latitude, productivity, temperature, heterogeneity). Macroecological patterns concerning frequency distributions of body sizes, abundances or range sizes are also based on a set of species within a higher taxon. Little is known, however, about how these patterns depend on the way the taxa are delimited. Although there were attempts to decompose some macroecological patterns into patterns for subtaxa or functional groups (e.g., Marquet et al. 2004), the changes in the form of the patterns with changing taxonomic resolution has not been systematically explored so far. The necessity to take this variation seriously emerged quite recently in the studies of diversity patterns of unicellular organisms, where uncertainties concerning appropriate taxonomic levels have led to confusion about the existence of major biogeographic and macroecological trends (Green and Bohannan 2007). Apparently, traditional taxonomic units like species and genera are not comparable between multicellular eukaryotes and microbes, which bias many patterns and even the estimates of total diversity on Earth. However, the problem is much broader.

There are two fundamental ways that taxonomic resolution can change when exploring macroecological patterns (Fig. 1). First, we can ask whether patterns that have been revealed for a set of species within a given taxon apply also for the set of species within a lower or higher taxon (of narrower or broader taxon delimitation) (Fig. 1a,b). We can call this type of variation the *taxon delimitation variation*. For instance, if we know that there is some particular frequency distribution of body sizes of species within class Aves (birds) (Fig. 2), we can ask whether the same distribution applies for species within each bird order or each bird family. More specifically, we can ask *i*) whether the distribution (or any other pattern) is exactly the same (including the parameters) for every taxon delimitation, *ii*) whether only the overall shape is retained when changing taxon delimitation, or *iii*) whether the pattern itself changes with taxon delimitation. In this example the first is apparently not true (at least because some bird orders, e.g., Falconiformes – birds of prey – have higher average body mass than is the average for all birds, so at least one parameter must vary with the clade in concern), but the second can potentially hold,

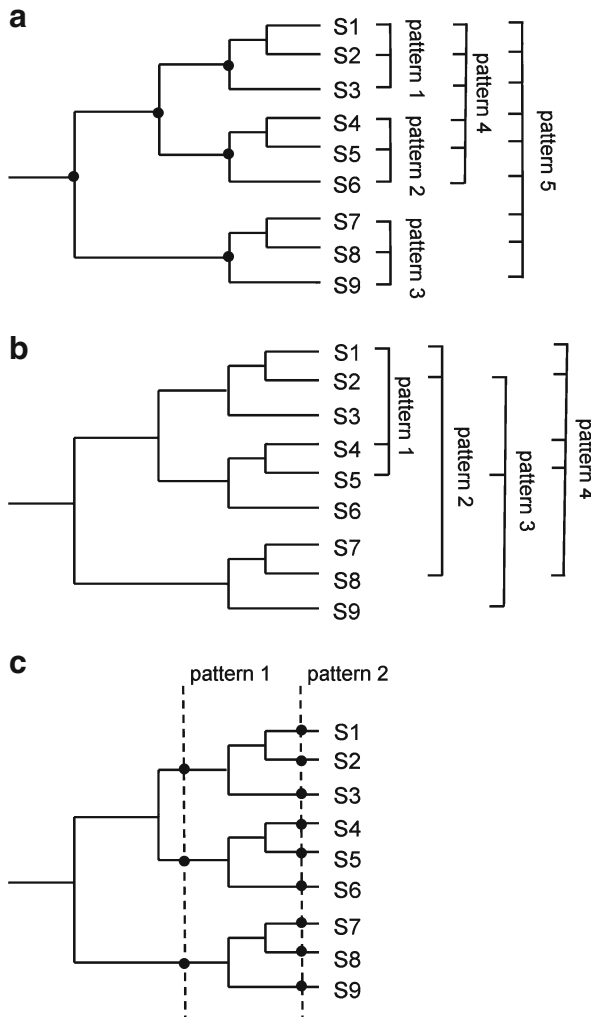


Fig. 1 Weak (a) and strong (b) principle of variation of taxon delimitation, and taxonomic unit variance (c) of a diversity pattern. The patterns observed for various taxon delimitations or units are labelled as pattern 1, pattern 2 and so on. Whereas the weak principle of taxon invariance comprises only patterns concerning monophyletic taxa, the strong principle concerns patterns comprising any set of species. The principle of taxonomic unit variance then deals with changing basic units of diversity patterns. If a pattern is taxon invariant, all the patterns follow the same rule, although their mathematical expression can differ in parameters. Otherwise, pattern 4 has to be secondarily derived from patterns 1 and 2, and so on in **a** and **b**, and pattern 2 is constrained by pattern 1 (or *vice versa*) in **c**. The S1–S9 label individual species

and it is worth exploring. Regardless, all these cases can shed light on evolutionary forces shaping body sizes, as we will show below.

The second way that taxonomic resolution can affect observed diversity patterns involves changes of the fundamental taxonomical units (Fig. 1c). We can explore how the patterns change when changing our scope from species to, e.g., genera or families (see Palmer et al. 2008, this issue). We know, for instance, that the number

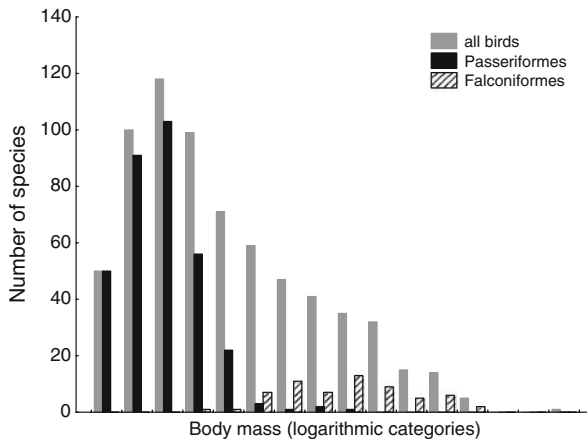


Fig. 2 The distribution of body sizes of species within a clade decomposed into the distributions for two selected subclades. This example concerns South African birds, but similar body size distribution applies for other higher taxa (e.g. mammals) as well. In this case, the overall body size distribution plotted in logarithmic scale is strongly right-skewed, but the skewness is lower in the subclades, especially in Falconiformes (birds of prey) that are mostly relatively big. The general prevalence of smaller species is to a large extent attributable to passerines (Passeriformes), which comprise mostly small birds. Note that body sizes in this example range from about 5–10 g in some passerines, to about 70 kg in ostrich (*Struthio camelus*), i.e., it spans four orders of magnitude

of species increases with the area of the study plot in a more-or-less predictable way (Rosenzweig 1995, but see Drakare et al. 2006). Does the same rule apply for numbers of genera or families? We will call the variation of the patterns that occurs when changing their taxonomic units the *unit variation*. Biologists have a tendency to assume that species are natural units of the organization of nature, whereas all the other taxa are derived and somehow arbitrary. However, although there are good reasons to consider the species level as something quite fundamental, this position has been questioned since the time of Darwin (1859). After all, all monophyletic taxa are “natural” units, as all of them share one common ancestor (Panchen 1992; Ghiselin 2005), and there is no *a-priori* reason to expect that patterns for species are fundamentally different from patterns concerning higher taxa. In accord to Darwin (1859), the same could in principle be applied for lower taxa than species (subspecies, populations, demes, or *varieties* in Darwin’s terminology). However, this is probably more complicated, because a taxon that concerns a fraction of individuals within a species does not necessarily represent a clade defined by a common ancestor.

This is related to another fundamental problem concerning the *variation of taxon delimitation*. Diversity patterns can be potentially robust against any changes of the explored set of species or, alternatively, only against changes involving natural sets, i.e., monophyletic taxa (clades). We can thus formulate the *strong principle of taxon invariance*, which states that a given macroecological pattern is invariant against any change of the set of species in concern, and the *weak principle of taxon invariance* stating that the pattern is invariant against changes in taxonomic delimitation given by the shift on the phylogenetic tree determining the node characterizing the

respective monophyletic clade (Fig. 1a,b). Although the weak principle seems to be more natural, it is probable that if a pattern is taxon invariant, it follows the strong principle, because biodiversity patterns concern mostly spatially defined assemblages, naturally comprising only a fraction of monophyletic taxa (i.e., not whole clades). The strong principle then obviously implies the weak principle.

Although the empirical ubiquity of many macroecological patterns across taxa indicates that at least some of them are more-or-less independent of taxonomic resolution, there is apparently no *a priori* theoretical reason why they should be taxon invariant. However, there are reasons why taxon invariant patterns are likely to be observed. One simply comprises our uncertainty as to the taxon delimitation or the fundamental level of description for the patterns. If we are not sure what is the appropriate taxonomic level at which the patterns should apply, and/or if there are uncertainties concerning the definition of taxa (note that many macroecological patterns have been reported using taxonomic units – e.g. orders or families – which are not comparable between plants, insects and birds), the observed general patterns are probably those which are independent of the exact taxon delimitation. Additionally, taxon invariances may reveal some fundamental symmetries in the organization of the living world or may follow from some kinds of statistical limiting processes, as we will show.

Here we will explore the consequences of variation of taxonomic resolution in four selected diversity patterns. We will demonstrate that these considerations can shed light on the relevance and logical consistency of diversity patterns and theories concerning underlying processes. In fact, these considerations may not apply only on biodiversity patterns and theories concerning them but on all ecological theory (Appendix 1). Ecology so far has relied too heavily on the assumption that the basic units of all patterns and processes are well-defined and known *a-priori*; here we show that challenging this assumption can lead to new and unexpected results.

The Distribution of Body Sizes

Body size or body weight distribution is probably the pattern in which the effect of *variation of taxon delimitation* has been most thoroughly explored. Within any taxon, most species are small, i.e., the distribution is strongly right-skewed, and this skewness is often retained even if body size is plotted on a logarithmic axis (Fig. 2). This pattern has been observed in both animals (Brown 1995) and plants (e.g., Aarssen et al. 2006), although body size distribution in plants is often less skewed than in animals, probably because of relative prevalence of tropical forest trees (e.g. Poorter et al. 2008). Body size distribution is also scale-dependent, so that the right-skewed distribution is observed at the scale of large regions and continents, and the skewness diminishes within individual communities (Brown 1995).

One theory states that the large-scale prevalence of small species can be explained by an evolutionary diversification of body sizes following a random walk in logarithmic space, constrained by a taxon-specific minimum size. This minimum represents a reflecting boundary constraining evolution of small body sizes, leading to the accumulation of species close to the boundary (McShea 1994). However, if the presence of the boundary is relevant for the taxon of concern (e.g., mammals

cannot be smaller than about 2 g because of the problems with energetic balance), the subtaxa that are far away from the boundary (e.g., mammal orders that comprise generally big animals) should not be affected by the boundary and thus we should not expect a similarly skewed body size distribution (McShea 1994). Maurer (1998) decomposed the body size distribution in birds into the distributions for various subclades, and demonstrated that the skewness is retained even in subclades that are far away from the reflecting boundary. This property of body size distribution thus seems to be taxon-invariant (in the sense of *taxon delimitation* variation), which indicates that other processes are in play (Maurer 1998). Wang (2001) further developed a methodology to partition the skewness in logarithmic body size distribution into skewness between subclades, skewness within subclades, and skewness due to changes in variance among subclades. Although so far such analyses provided mixed results, it is clear that the study of the variation of body size distribution with taxonomic delimitation has a great potential to reveal fundamental mechanisms of body size evolution.

The Species-Abundance Distribution

Within any species assemblage, most species are rare and only a few of them are abundant, the species-abundance distribution thus reveals a “hollow” curve (McGill et al. 2007). The favourite model of species-abundance distribution is the lognormal distribution (Preston 1948), and indeed, this distribution fits well most abundance data across various scales and taxa (May 1975). We can ask, however, whether the lognormal approach can hold for both the clade and all its subclades, i.e., whether the weak principle of taxon invariance applies. Assume a clade composed from two subclades. The abundance distribution of the two groups of species (whose distribution functions are Φ_1 and Φ_2) merged together obeys equality

$$\Phi(x) = \pi_1\Phi_1(x) + \pi_2\Phi_2(x), \quad (\text{SAD1})$$

where x is an abundance and π s are the proportional numbers of species in the corresponding groups. The lognormal distribution obeys

$$\Phi(x) = cx^{-1}e^{-k(\ln x - \mu)^2}, \quad (\text{SAD2})$$

where the constants c , k , and μ are real numbers. Substituting it to the equation SAD1 we get

$$cx^{-1}e^{-k(\ln x - \mu)^2} \stackrel{?}{=} \pi_1c_1x^{-1}e^{-k_1(\ln x - \mu_1)^2} + \pi_2c_2x^{-1}e^{-k_2(\ln x - \mu_2)^2}, \quad (\text{SAD3})$$

where the question mark refers to the fact that the equality may not be true for some parameters, (i.e., the equality, not the parameters, is in question). This is after simplifying

$$1 \stackrel{?}{=} \kappa_1e^{k(\ln x - \mu)^2 - k_1(\ln x - \mu_1)^2} + \kappa_2e^{k(\ln x - \mu)^2 - k_2(\ln x - \mu_2)^2}, \quad (\text{SAD4})$$

($\kappa_i = \pi_i c_i / c$). This is true only if the equality

$$-\kappa_1 \frac{d}{dx} e^{k(\ln x - \mu)^2 - k_1 (\ln x - \mu_1)^2} \stackrel{?}{=} \kappa_2 \frac{d}{dx} e^{k(\ln x - \mu)^2 - k_2 (\ln x - \mu_2)^2} \quad (\text{SAD5})$$

is met. Since all $\kappa_i > 0$, it apparently happens only if the derivatives are zero, which occurs only if all parameters k s and μ s are equal to each other and thus both distributions are identical.

Therefore, lognormal species-abundance distribution cannot hold across all taxon delimitations if the species-abundance distributions of subclades differ in parameters. The equality of parameters is unlikely because individual clades certainly vary at least in mean species' abundance. Lognormal distribution thus cannot be a proper description of species-abundance distribution for all clades at all taxonomic levels, although in principle it can apply for a particular taxon. In such a case, however, the distributions for other taxon delimitations must have different functional form (Williamson and Gaston (2005); Šizling et al., unpubl.). On the other hand, it is possible that the species-abundance distribution is actually taxon invariant (*sensu taxon delimitation invariance*), and the generally good fit of the lognormal distribution is given by the similarity of the shape between this taxon invariant distribution and the lognormal distribution.

The falsification of the weak principle of taxon invariance implies the falsification of the strong principle. Therefore, the lognormal species-abundance distribution cannot simultaneously hold for a set of species and all its mutually exclusive subsets, regardless of the delimitation of these subsets. In fact, there are only two possibilities: either the species-abundance distribution is taxon-invariant (which is not the case with the lognormal distribution) or its form changes with taxon delimitation, and thus is not a universal, clade-independent pattern. The later possibility would imply that there is a particular set of clades (i.e., some fundamental taxon delimitation) for which a given model and/or respective process applies, whereas the patterns for other clades or otherwise delimited groups are derived. The simple consideration of the variation of diversity patterns with taxon delimitation thus constrains the set of possible patterns and limits of their universality.

The Species-Area Relationship

The number of species increases with the area censused, and we can again ask whether this species-area relationship (hereafter SAR) differs between given clade and its subclades. If the SAR is well represented by the power-law, as commonly assumed (Connor and McCoy 1979; Rosenzweig 1995), we can ask whether the power-law can be retained under varying taxon delimitation regardless of taxon monophyly, i.e., we can evaluate the pattern from the perspective of the strong principle of taxon invariance. Imagine three groups of species α , β , and γ (e.g. species 1–3, 4–6, and 7–9 in Fig. 1, respectively) and assume that SARs follow power-laws for group α , merged groups α and β , and merged groups α , β and γ . The question is then whether the SAR follows a power-law for merged group α , γ , as well.

Let us formalize this problem: if all three groups α , $\alpha\beta$, and $\alpha\beta\gamma$ conform to a power-law, there are two functions of area (A), f_β and f_γ , representing SARs for the

indexed groups, so that

$$S_\alpha = c_\alpha A^{z_\alpha}, S_{\alpha\beta} = c_{\alpha\beta} A^{z_{\alpha\beta}} = c_\alpha A^{z_\alpha} + f_\beta(A), \text{ and} \tag{SAR1}$$

$$S_{\alpha\beta\gamma} = c_{\alpha\beta\gamma} A^{z_{\alpha\beta\gamma}} = c_{\alpha\beta} A^{z_{\alpha\beta}} + f_\gamma(A).$$

Now it is clear that

$$f_\gamma(A) = c_{\alpha\beta\gamma} A^{z_{\alpha\beta\gamma}} - c_{\alpha\beta} A^{z_{\alpha\beta}} \tag{SAR2}$$

and since

$$S_{\alpha\gamma} = c_\alpha A^{z_\alpha} + f_\gamma(A),$$

we get $S_{\alpha\gamma} = c_\alpha A^{z_\alpha} + c_{\alpha\beta\gamma} A^{z_{\alpha\beta\gamma}} - c_{\alpha\beta} A^{z_{\alpha\beta}}$, which obeys $S_{\alpha\gamma} = c_{\alpha\gamma} A^{z_{\alpha\gamma}}$ only if $z_\alpha = z_{\alpha\beta} = z_{\alpha\beta\gamma}$. Therefore, the strong principle of taxon invariance which states that the SAR follows a power-law for any set of species holds only if the z parameters are equal for all subsets of species. Furthermore, the weak principle would mean that the sets and subsets following the power-law comprise only monophyletic taxa. In such a case both functions f_β and f_γ follow power-law, which again implies equality of z parameters (from equation SAR1, $c_\beta A^{z_\beta} = c_{\alpha\beta} A^{z_{\alpha\beta}} - c_\alpha A^{z_\alpha}$, and $c_\gamma A^{z_\gamma} = c_{\alpha\beta\gamma} A^{z_{\alpha\beta\gamma}} - c_{\alpha\beta} A^{z_{\alpha\beta}}$). The situation is thus somehow similar to the species-abundance distribution: the pattern can be taxon-invariant (robust against varying *taxon delimitation*) only if it is the same for all taxa including the parameters. If two taxa differ in the slope of their power-law SAR, the taxon composed from these two taxa cannot follow exact power-law SAR.

How far can we go in the decomposition of a pattern in a particular clade into patterns occurring in its subclades (or how far can we move along the group-subgroup gradient if the strong taxon invariance principle applies)? Can we even go down to the level of one species? The SAR for one species does not seem to be defined, but it can be expressed as the relationship between area and the probability of species occurrence, because the sum of these probabilities is exactly equal to mean species number for given area, and so the SAR can be constructed by simple summation of these probability-area curves of individual species (Coleman 1981; Williams 1995). In line with our considerations, Lennon et al. (2002) argued that the SAR for a given taxon would follow a power-law if the individual probability-area curves were power-laws but only with equal slopes (for the proof see Šizling and Storch 2004), which is clearly unrealistic. There is an apparent logical paradox: both the SARs and the relationships between area and probability are reported to approximately follow a power-law (Kunin 1998; He and Condit 2007), and at the same time it cannot happen because addition of other power-law relationships to an assemblage revealing the power-law with a different slope pushes the resulting SAR to be more upward accelerating. The only solution of this paradox is that there must be some tiny deviation from the power-laws, the accumulation of which compensates for this upward-accelerating tendency. Once having this theoretical insight, we can realize that this cumulative deviation is due to the fact that the increase of probability of species occurrence with area is bounded by the area where probability approaches one, i.e., the probability-area relationship necessarily reveals a point of saturation (Šizling and Storch 2004; Storch et al. 2007).

Here we can furthermore explore the taxonomic *unit variation*, i.e., how the pattern changes when fundamental taxonomic units are changed. What does the

generalized taxon-area relationship look like if we take, e.g., genera or families instead of species (Fig. 3)? We should expect that the number of higher taxa will increase with area at a slower rate than the number of lower taxa (e.g., an increase in the number of species cannot always be followed by an increase in the number of genera). The slope of the genus-area or family-area relationship is thus expected to be lower than the slope of the species-area relationship. However, because the number of higher taxa cannot exceed the number of lower taxa, the taxon-area relationships for different taxonomic units cannot cross, and thus all of them cannot simultaneously follow power-laws in all scales (throughout the whole range of areas; Fig. 3).

This reasoning concerning taxonomic *unit variation* can even be extended below the species level. Each species can be considered as composed from subunits (subspecies, populations, demes) even if they are obviously not monophyletic. The most basic (indeed atomic) unit is then an individual. The average number of individuals necessary increases linearly with area, with the slope given by average population density, σ , and intercept of zero. The individual-area curve is thus a power-law with the coefficient of power, z , equal to 1 (i.e., $I = \sigma A \Rightarrow \ln I = \ln \sigma + \ln A$ where I is the number of individuals and A is area). Assuming more than one species, the number of species must always be lower than the number of individuals, so that the species-area relationship cannot follow the power-law across all areas, because otherwise it would cross the individual-area relationship (Fig. 3). The number of species must be therefore relatively lower than expected by extrapolating the power-law SAR into the areas that host only a few individuals, which has been actually reported (Hubbell 2001). This effect has traditionally been attributed to sampling effect (see also the rarefaction effect discussed by Palmer et al. 2008), as it is caused by the limitation of species numbers due to the limitation of

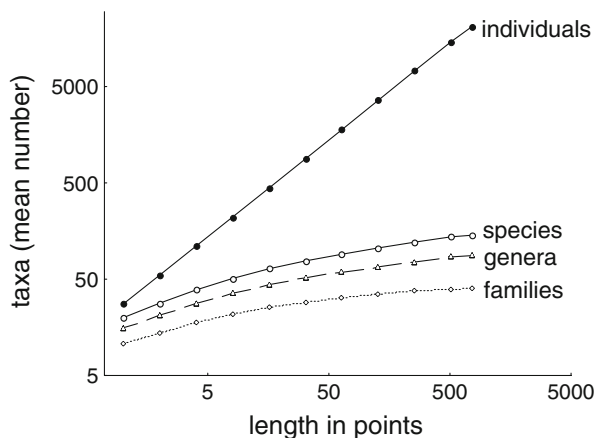


Fig. 3 The *unit variation* in the taxon-area (more precisely taxon-length) relationship in the birds of the Czech Republic, expressed as the relationship between number of consecutive mapping points and mean number of taxa from all sets of given number of points (all possible length windows). Individuals were observed on 768 points along the transect with distances between the points of about 400 m. Whereas the relationship between average number of individuals and area (length) is linear (both in arithmetic and logarithmic space), this cannot hold for other taxonomic levels, as the curves cannot cross each other, and the number of subtaxa limits possible numbers of higher taxa. Data provided by Jiří Reif and David Storch

number of individuals. However, it is a quite unusual sampling effect, as the sample of species is not a random sample from given (and always the same) distribution. Again, simple reasoning concerning the variation of the patterns with changing taxonomic resolution delimits the set of possibilities of the forms of respective pattern.

Relationship Between Energy Availability and Diversity

Spatial variation of diversity on Earth's surface has been attributed to plenty of factors, but climatic factors, namely those related to energy availability, are increasingly recognized as key diversity determinants (Hawkins et al. 2003; Currie et al. 2004). Several attempts have been made to deal with varying *taxon delimitation*, for instance by decomposing species richness patterns of large taxa and their determinants to richness patterns observed within subclades (e.g. Keil et al. 2008). Other studies actually comprised the *taxonomic unit variation* of diversity patterns, analyzing diversity variation at the level of species, genera, and higher taxa (e.g., Thomas et al. 2008). Most of these studies indicate that the rough relationship between climatic factors (or, more specifically, energy availability) and diversity is more-or-less universal and taxon invariant in both senses, i.e., it applies similarly for species richness of clades and their subclades, and it works regardless of whether one observes species or higher taxa. This is in accord with the results of studies attempting to sophisticatedly decompose spatial diversity variation to the within-clade and between-clade components (Diniz-Filho et al. 2007). Similarly as in the case of the SAR, it has been demonstrated that even an individual species probability of occurrence increases on average with energy availability, at least in birds (Bonn et al. 2004), i.e., the relationship is likely to be universal up to the species level. Therefore, the apparent taxon-invariance of the species-energy relationship can be simply attributed to the fact that all species as well as all higher taxa have a better chance to persist in an environment with higher energy availability.

The relationship between diversity and energy availability has rarely been expressed as a general quantitative law, which limits the evaluation of this pattern in terms of its sensitivity to taxon delimitation. An important exception is the theory of Allen et al. (2002), later refined by Allen et al. (2006, 2007), which relates species richness to temperature using considerations of the Metabolic Theory of Ecology (Brown et al. 2004). Allen et al. (2002) extend the energy equivalence rule (Damuth 1987), postulating that energy consumption of a species per unit area is independent of body size and temperature. Therefore, to fulfil the energy equivalence rule, species population densities of ectotherms must be lower in warmer areas in which their individual metabolic rates are higher. Further assumption of the theory is that the total number of individuals of given higher taxon (whose species richness is studied) is constant regardless of temperature. If individual species population densities in warmer areas are at the same time lower, then the total number of species has to be higher in warmer areas, exactly according to the relationship between individual metabolic rate and temperature. Apparently, this theory assumes that the processes leading to energetic equivalence vary with taxonomic delimitation:

whereas species have to conform to the energy equivalence rule, higher (further undefined) taxa do not. The problem is that there is no known mechanism based on metabolic theory which would lead to such dependence on taxonomic delimitation (Storch 2003): if higher temperature increases individual metabolic rates, we should expect the decrease of total numbers of individuals within any taxon (given constant resource supply), and there is no reason to assume that the total number of individuals remains constant whereas individual species' population densities decrease. Here, simple application of the principle of *variation in taxon delimitation* reveals logical inconsistency of the theory.

Further reformulation of the theory states that the observed increase of species numbers with temperature is due to the effect of temperature on metabolic rate and consequently all evolutionary rates including rates of molecular evolution, population diversification and speciation (Allen et al. 2006, 2007). According to the theory, the number of species should scale with temperature in the same way as metabolic rate. However, here we can apply the other principle, i.e., the *taxonomic unit variation* (similarly as in the case of the SAR), and ask whether the diversification rate driven by metabolic rate should not actually affect patterns observed at all taxonomic levels, i.e., not only species richness, but also the number of genera, families etc. Clearly, all taxonomic levels cannot scale with any environmental factor in the same way, as the rate of increase of the number of given taxonomic unit with the focal factor cannot be the same regardless of the taxonomic unit (Fig. 4). Is there any reason to assume that temperature-dependent

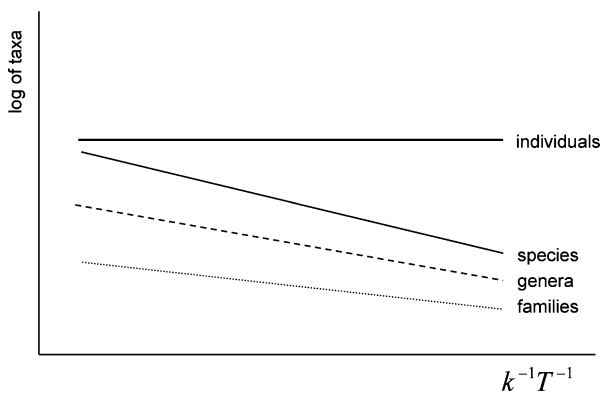


Fig. 4 Hypothetical relationship between the number of taxa and reciprocal temperature (expressed as reciprocal energy) for various taxonomic resolutions. According to the theory of Allen et al. (2002, 2006, 2007), the slope of the relationship between the logarithm of number of species and $1/(kT)$ (where k is Boltzmann constant in electron volts per absolute temperature [eV/K], and T [K] is absolute temperature) should be about 0.65 eV^{-1} , since $S \propto e^{-E/(kT)}$ where E is activation energy of metabolism, whose value is typically 0.65 eV . This theory assumes that the total number of individuals does not vary with temperature. However, it is clear that even if this theory holds for species, it cannot simultaneously predict the same slope for the relationship between $1/(kT)$ and the number of genera or families. Moreover, the total number of individuals can alternatively increase with temperature (due to increasing inflow of resources) or decrease due to increasing energy consumption by individuals. This apparently depends on the trophic level and top-down vs. bottom-up regulation of resource flow, and this necessarily affects the slopes of all the other relationships

diversification leads to the predictable effect on the number of species but not on the number of higher taxa? If so, it says something very specific about species level. Similar considerations can be applied to any other quantitative theory of spatial diversity variation.

Discussion

We have tried to demonstrate that exploration of the variation of the form of diversity patterns with changes in taxonomic resolution can shed light on the nature of the patterns, help in decisions concerning the relevance of different theories, and avoid various artifacts. Moreover, the taxon invariance principle can be used as a criterion for evaluation of consistency of various theories, as the processes assumed must always either produce taxon-invariant patterns, or must concern only some taxon delimitations or some fundamental taxonomic units, so that the patterns for other delimitations and other units have to be secondarily derived. In an extreme it is even possible that some theories are successful in predicting observed patterns only *because* they are implicitly or explicitly taxon-invariant. Hubbell's (2001) neutral theory might be so powerful in predicting general diversity patterns simply because it implicitly assumes taxon invariance, namely invariance against *unit variation* – species are only labels on individuals, and thus any higher (and potentially also lower) taxa have exactly the same properties as species and identical dynamics. Re-labelling two species and considering them as one species does not affect the dynamics, and such a re-labelling does not have any limits, as all species (actually all individuals) are ultimately identical. We can thus speculate to which extent major macroecological patterns as the species-abundance distribution or species-area relationship represent just consequences of various taxon invariances.

The question is to which extent this statement concerns also the strong principle of invariance against *taxon delimitation*, i.e., whether some diversity patterns can be derived simply from the assumption that the patterns must be robust against any changes of the set of species concerned. This assumption might seem too general for producing any patterns. However, at least the species-area relationship is apparently invariant against any delimitation of the set of species that we involve in the pattern, and the same seems to apply also in other patterns considered here. This can have a surprisingly simple explanation. It is quite probable that truly general macroecological patterns are those that are taxon invariant in the strong sense, because their generality means that the same patterns have been observed in various, mostly non-monophyletic sets of species. Almost no site is occupied by a complete monophyletic clade, and many taxa that were traditionally considered as monophyletic may be actually paraphyletic or polyphyletic (this also concerns the bird order Falconiformes used for our demonstration of the principle of *taxon delimitation variation* in body size distribution; see Hackett et al. 2008). If the patterns are regularly observed in vaguely delimited taxa, it is probable that they will be taxon invariant even in the strong sense.

The same can apply for the *taxonomic unit variation*. Even if species indeed represent the basic units of the organization of nature, this cannot lead to universal taxon non-invariance, as many evolutionary lineages are asexual, and moreover, exact delimitation of many species is notoriously difficult even in very well known taxa. In such a situation it is probable that relatively small variation in the fundamental units should not change the general patterns that have been observed regardless of the fact that species are often poorly delimited. In contrast, whereas species are cohesive units sharing ecological properties (unique ecological niche), higher taxa are not cohesive individuals (*sensu* Hennig 1966) – they are often characterized by the tendency to diversify ecologically due to interspecific competition. Changes of the patterns with varying taxonomic units are thus probable, and represent a key biological problem unexplored so far.

Another possibility how taxon invariances can emerge is due to some statistical cumulative processes such as those underlying the central limit theorem (Laplace 1812). Such processes can lead to taxon-invariant patterns for larger groups of taxonomic units by canalization of various patterns into those that are taxon invariant. This is apparently the case of the species-area relationship, as we have shown above: the relationship for large taxa is close to the power-law simply due to the accumulation of different functions for lower taxa (Šizling and Storch 2004).

The conclusion that taxon invariances in some patterns are given simply by our limitations concerning taxa delimitation or by some purely statistical process could be taken as evidence that taxon-invariant patterns are not interesting or are biologically irrelevant. However, we have demonstrated that the exploration of the variation of the patterns with changing taxonomic resolution (both *taxon delimitation* and *taxonomic unit*) is at least an extremely useful methodological tool for several purposes. First, it allows to exclude some candidate models of macroecological patterns simply by demonstrating that these models cannot be applied consistently for all taxa *i*) regardless of their delimitation, as we have shown for the lognormal model of the species-abundance distribution, or *ii*) regardless of the variation of the taxonomic unit, as we have demonstrated for the power-law model of the taxon-area relationship. This can lead to the specification of possible class of biological processes responsible for respective patterns (Šizling et al., unpubl.). Second, it can shed light on the universality of the assumed processes, as was the case of body size distribution and the relationship between diversity and energy availability, in which it can be shown that a particular process can affect only particular taxonomic levels. Third, the exploration of taxon invariance or non-invariance of some patterns can reveal interesting geometrical and mathematical connections between different patterns. These connections then constrain the set of possibilities and promote predictions of the form of the patterns, as we have shown in the case of the species-area relationship and its relation to the relationship between area and species' probability of occurrence. Last but not least, variation of observed patterns with taxonomic resolution can help us to recognize whether taxa (and which taxa) represent sensible ecological units that play a key role in the structure and dynamics of the living world.

Appendix 1 Application of the Taxon Invariance Principle in Population Dynamics

In principle, all equations of population dynamics of a three-species assemblage can be expressed as

$$x^\bullet = f_x(x, y, z); y^\bullet = f_y(x, y, z); z^\bullet = f_z(x, y, z) \tag{App1}$$

where $x, y,$ and z are population densities and the dots mark the rate of their changes in time (i.e., $x^\bullet \equiv dx/dt$). This is based on an assumption that there are exactly three clearly defined groups of individuals differing in natality, mortality and competition coefficients. However, imagine a situation in which we do not have a clear idea of what are the respective groups of species and thus we consider (either by mistake or deliberately) two of these species (e.g. y and z) as one species. The system of equations is then

$$x^\bullet = g_x(x, y + z); (y + z)^\bullet = g_y(x, y + z) \tag{App2}$$

where the g functions can, but may not differ from the f functions. Anyway, both functions g are necessarily constrained by the functions f . Then $f_x(x, y, z) \equiv_1 g_x(x, y + z)$, and $(y + z)^\bullet \equiv_2 f_y(x, y, z) + f_z(x, y, z) \equiv_1 g_y(x, y + z)$, where the equalities ‘ \equiv_1 ’ show the definitions of functions g , and ‘ \equiv_2 ’ is the mathematical constraint. There are then only two possibilities: *i*) the model of population dynamics is taxon-invariant and the g and f functions share their functional form and differ only in their parameters – i.e.,

$$g_x(x, y + z) = (\alpha + \beta x + \gamma(y + z))x, \tag{App3}$$

or *ii*) the functional forms of the g functions have to be derived from f and vice versa, depending on whether we split or merge the two population units. Population dynamics is in the latter case determined by the way how the taxonomic units are grouped, which can have profound consequence in any situation in which we are not sure about exact taxonomic delimitation of respective species or if there is hidden variation of population parameters within species that we consider to be homogeneous.

Let us have a look at the system of Lotka-Volterra equations (Volterra 1926; Lotka 1932), i.e., elementary equations of the population dynamics that can be expressed as

$$x^\bullet = (\alpha_x + \beta_x x + \gamma_x y + \delta_x z)x, \tag{App4}$$

or, alternatively, as

$$x^\bullet = (\alpha_x + \beta_x x + c_x(y + z))x + \varphi(x, y, z), \tag{App5}$$

where $\varphi = ((\gamma_x - c)y + (\delta_x - c)z)x$. The first additive term of eqn. App5 has the same functional form as the original function before merging the populations (or splitting, the reasoning is apparently symmetric), and so the additional term φ violates the taxon invariance, as equation App5 has a different functional form from eqn. App3 if φ differs from zero. However, φ can be zero for all x, y, z only if the species y and z do not differ in their parameters (i.e., if $c = \gamma_x = \delta_x$). The same can be shown for $(y + z)^\bullet$. This means that the classical Lotka-Volterra equations are not taxon invariant, i.e., their behaviour depend on taxon delimitation. In other words, if we take

two species whose parameters differ as one unit, their Lotka-Volterra dynamics is necessarily fundamentally different. Lotka-Volterra equations assume that the fundamental units (i.e., interacting populations) are well defined and *a-priori* given, which may be problematic in many cases.

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