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Using Museum Collections to Estimate Diversity Patterns along Geographical Gradients

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Abstract Quantifying species-richness patterns along geographical gradients (typically latitude and elevation) has a long history in ecology and can be based on more-or-less complete censuses from a specified area (plot sampling), selective collection within a specified area (e.g. museum collections), or general information about species distributions (e.g. observations of extremes along the gradient, distribution maps). All these approaches require complete sampling to give the true richness in an area, but the richness pattern (i.e., the relative changes in richness along the gradient) may be estimated without complete sampling, although equal sampling between areas is necessary. This is relatively easy to do for fine-scale plot sampling, but rarely easy for other types of data. For data extracted from museum collections, a correct perception of the species richness pattern therefore depends on post-sampling treatment of data. Two commonly applied techniques for quantifying species richness patterns with these types of data are discussed, namely interpolation of species ranges and rarefaction. Such treatment may correct for unequal sampling in some instances, but may in other cases introduce artificial patterns. With incomplete sampling interpolation introduces an artificial humped pattern and rarefaction requires similar species abundance distributions to make unbiased comparisons among samples. One must therefore be cautious when applying these methods for estimating species richness patterns along geographical gradients.

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Introduction

Studies of broad-scale geographical gradients in species richness have been a central topic in ecology and biogeography for centuries. Since the discovery of the existence of latitudinal patterns of species richness over 200 years ago, numerous broad-scale diversity patterns have been described (Brown and Lomolino 1998; Gaston and Blackburn 2000; Hillebrand 2004). Recently, interest in altitudinal richness patterns has also increased. This is partly due to the anticipation that altitudinal gradients will provide renewed insight into latitudinal richness patterns (Brown 2001). Altitudinal gradients also offer a unique opportunity to compare transects in different regions, and searching for similarities and differences in diversity patterns among regions (Rahbek 2005; Grytnes and McCain 2007; Körner 2007).

Quantification of richness patterns along geographical gradients are commonly based on non-standardized collections of data. It can be based on more-or-less complete censuses from a specified area (plot sampling), a more-or-less random collection of individuals within an area (e.g. museum collections), or more-or-less correct information about species distributions (e.g. observations of extremes along the gradient or distribution maps). The latter is, in turn, often based on information from collections and depends on the quality of these collections. For studies of broad-scale gradients in species richness it is often inappropriate to use plot sampling, at least when plots are so small that complete sampling is possible. In these cases it will be difficult to separate local factors from regional and historical factors. A possible exception to this is local altitudinal transects where the whole study area is within the same region and differences in historical factors are minimal (Grytnes 2003).

Museum collections contain a rich source of information for macroecologists and biogeographers. When using museum collections to estimate a species-richness pattern, the observed pattern may be quite sensitive to the intensity of sampling, and museum collections are typically unequally distributed along the gradient studied. There may be many reasons why one area is more sampled than another area, the most obvious being accessibility of the area. This must be accounted for before presenting a species-richness pattern based on museum collections. Species-richness patterns along geographical gradients are typically estimated either by interpolation of species ranges between observed extremes (Grytnes and Vetaas 2002; McCain 2005; Romdal et al. 2005) or by rarefaction (Wolf and Alejandro 2003; McClain and Etter 2005; Grytnes and Beaman 2006; Brehm et al. 2007). Some studies also use different estimators, like Chao, ACE, Jacknife, etc. to estimate the true species richness in an area (Wolf and Alejandro 2003; Andrew and Hughes 2004; Brehm et al. 2007).

The focus of this paper is how the treatment and quality of museum collections, or similar data, may influence species-richness patterns and sometimes create artifictions in species-richness patterns (Palmer et al. 2008). By species-richness pattern we mean the relative number of species between a set of samples, typically between different intervals along a latitudinal or altitudinal gradient. It is not then necessary to obtain the absolute species richness in each sample. Examples of

empirical data resembling museum collections include point observations in the field where each observation is georeferenced or related to a specific placement along the geographical gradient. For simplicity we refer to all these type of samples as museum collections in the current paper.

Interpolation

One common way to account for sampling intensity when studying species richness along geographical gradients is to assume that each species is present at all intervals or sampling stations between the extremes observed (range interpolation). This method has been used extensively, both in studies of altitudinal richness pattern (Grytnes and Vetaas 2002; Vetaas and Grytnes 2002; Bhattarai et al. 2004; Grau et al. 2007), and along latitudinal gradients (Hillebrand 2004; Romdal et al. 2005). Hillebrand (2004) did a meta-analysis of latitudinal species-richness patterns and characterized one-third of the patterns as being based on species ranges. It has previously been demonstrated that interpolation will create an artificial hump in species richness along the elevational gradient if sampling is incomplete (Grytnes and Vetaas 2002). The hump arises because the endpoints only consists of observed species at that elevation, while sampling points in the middle of the gradient will have observed species at that elevation plus species found above and below. As one moves further from the endpoints there will be a higher probability of finding species above and below, thereby creating a humped curve (Grytnes and Vetaas 2002). Here we will look closer at how interpolation of species ranges affects diversity patterns and evaluate the sensitivity of this method to incomplete sampling and how this depends on species-range sizes. For simplicity, we will focus on one-dimensional geographical gradients. Although the points discussed are also valid for two-dimensional patterns in species richness, they are not directly transferable to two dimensions. For two-dimensional gradients these points have also been partly discussed in several other studies (Hurlbert and White 2005; Graham and Hijmans 2006; Hurlbert and Jetz 2007; La Sorte and Hawkins 2007; McPherson and Jetz 2007).

Two assumptions must be made for the species-richness pattern based on interpolated ranges to be correct. First, the species are actually present in all the cells (bands, intervals, or other sample units) between the extremes. Second, no specimen is found beyond the observed extremes, i.e., that the observed extremes correspond to the real extremes. The first assumption may be violated in several ways. A species can be absent in a sampling unit between the extremes due to, for example, species interactions or lack of suitable environment in the sampling unit, and observed extremes can be the result of a rare dispersal event. The second assumption will be violated if the sampling is incomplete, so that the correct extreme occurrences of the species distributions have not been recorded.

To illustrate some points on the effect of interpolating species ranges to quantify species-richness patterns along geographical gradients we did some simulations. The simulations were done in the same way as in Grytnes and Vetaas (2002). We simulated a geographical domain from 0 to 1 and divided this into 100 intervals. The endpoints of the domain correspond to the observation limits. Species-range sizes were randomly selected from a uniform distribution with minimum range size of

zero and maximum range size set to either 1.0 (potentially covering the whole domain) or 0.3, to illustrate how smaller range sizes affect the pattern. The species ranges were placed along the domain by randomly selecting a potential midpoint. This potential midpoint can also be found outside the domain as long as the maximum range size can reach the domain. This means that with a maximum range size of 1, the potential midpoint is distributed between -0.5 and 1.5. A constant species-richness pattern is simulated by having an equal probability for the potential midpoint for each point between these extremes. At each of the 100 intervals in the domain, species were randomly assigned as "observed" or "not observed" using a binomial randomization with a given probability for each species that have their range overlapping the interval. To explore the effects of more-or-less complete sampling the probability of finding a species was set to either 0.2 or 0.8. After doing this "sampling", the species ranges were interpolated and the new "observed" ranges were found (see Grytnes and Vetaas (2002) for more details on these simulations). For each analysis we simulated 1,000 species initially and the number of species with interpolated ranges overlapping each interval was counted. To reduce the noise in the simulated species-richness pattern we increased the number of species simulated to 5000 when maximum range was set to 0.3. To standardize between the different analyses, the number of species found in each interval relative to the number of species that could have been found with a complete sampling is given. Each analysis was repeated 100 times and average relative species richness in each interval is presented.

Incomplete sampling is often the argument for interpolation in the first place, and some simple simulations presented in Fig. 1 demonstrate that interpolation may be an effective way of accounting for gaps in sampling. In these simulations a rather large gap with poor sampling is assumed. Figure 1 also demonstrates that interpolation becomes less effective at accounting for sampling differences when species have smaller range sizes. In Fig. 1 it is assumed that 11 intervals have a lower sampling intensity than the rest. If only one interval had a low sampling intensity (10% of species found) and the remaining intervals in the domain had almost complete sampling (80% of species found) it would decrease interpolated species richness from 99% of true richness down to 95.5% of true richness when species are allowed to have range sizes up to 1. This would be, in most cases, a negligible difference compared to the trend in true species richness along the domain, or the random variation in species richness due to other factors. Interpolation would then be an effective way of masking differences in sampling intensity. With shorter range sizes (maximum 0.3) the interpolated species richness for the interval with lower sampling intensity is 85% of true richness.

Although interpolation often corrects for undersampling in parts of the sampled gradient, the correction will be uneven along the gradient the sampling is incomplete, causing an artificially humped richness pattern. This is because observations of species extremes are always based on observations of species occurrences within a certain area or geographical range. This area could, for example, be limited by political or natural borders, the end-points of altitudinal gradients (sea level and mountain top), or other practical limits for a study area. In the case of altitudinal and latitudinal gradients, the observation limits often coincide with the hard boundaries of the gradient (Colwell et al. 2004), but this is not necessarily so. To make a clear distinction between hard boundaries and the effect of

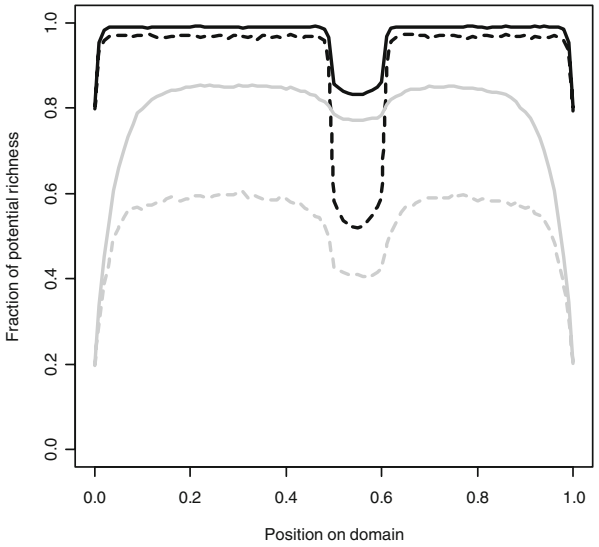

Fig. 1 Illustration of the effectiveness of using interpolation. A section between 0.5 and 0.6 along the domain is assumed to have a lower sampling intensity (10% of species present are sampled) than the remaining parts of the domain. Outside this section it is assumed that either 80% (*black lines*) or 20% (*grey lines*) of the species is sampled. Because the domain is divided into 100 intervals there is a gap of 11 intervals (including 0.5 and 0.6) with low sampling intensity. The effect of interpolation varies with the range sizes of species. If species have larger range sizes (uniformly distributed between 0 and 1 relative to the extent of the domain) interpolation accounts relatively well for sampling differences (*unbroken line*). With smaller ranges (uniformly distributed between 0 and 0.3) interpolation is not very efficient at accounting for sampling differences (*broken line*). See text for further details about the simulations

limits on interpolation, we refer to the latter as "observation limits". These observation limits refer to the extent of the geographical gradient or area from where the observed extremes are reported. Limits of observation restrict the study area for the richness pattern. In most studies hard boundaries coincide with the observation limits, which, in turn, commonly coincide with the study area of the species-richness pattern. It is, however, important to separate the observation limits from hard boundaries to see what is affecting species-richness patterns when using the interpolation method. Henceforth we use the term "interpolation effect" to refer to the effect of interpolation of species ranges on observed species-richness patterns in the presence of observation limits in combination with violating one (or two) of the assumptions mentioned above.

Grytnes and Vetaas (2002) demonstrated how the interpolation effect may create a humped species-richness pattern by violation of the second assumption. We here extend on this by investigating how differences in sampling intensity and range distributions in combination can affect the observed pattern.

The total species richness (STOT) in a sampling unit (i) based on interpolation is:

$$STOT_i = SOBS_i + SINT_i,$$

where $SOBS_i$ equals the number of species observed in the target sampling unit and $SINT_i$ is the number of species not observed in the sampling unit but are interpolated

to be present in the target sampling unit. $SINT_i$ is dependent on having species observed both above and below the target unit, whereas $SOBS_i$ is not. To illustrate the artifact we made some simple simulations assuming that *i*) there are no trends in species richness along the gradient studied; *ii*) species richness is incompletely sampled along the gradient; and *iii*) the sampling error is the same along the whole gradient. With incomplete sampling, $SOBS_i$ will be similar for all samples but $SINT_i$ will be dissimilar along the gradient. At the extreme ends of the gradient, $SINT_i$ will be zero as no observations are made beyond the extreme points and adding species by interpolation is therefore impossible. The probability of finding an interpolated species increases as more samples are found between the extreme points and the target sampling unit (i). This will create a humped pattern of $SINT_i$ and because $SOBS_i$ has no trend, $STOT_i$ will follow $SINT_i$. The exact shape of SINT (and therefore also STOT) along the gradient depends on the probability of finding a species and on the distribution of the species ranges. Figure 2 illustrates that a humped relationship is observed when using interpolation of species ranges and incomplete sampling even though the true species-richness pattern is without any trend along the domain. The humped pattern is a result of underestimation of species richness at the extremes, because these extreme points have only the observed species richness, and in Fig. 2 this corresponds to the fraction of species observed, i.e., 0.2 and 0.8 respectively. It is also evident from these simulations that when range sizes are larger the effect of interpolation on the species-richness pattern is larger. However, the observed species richness is closer to the true species richness in the middle of the domain. This is because larger

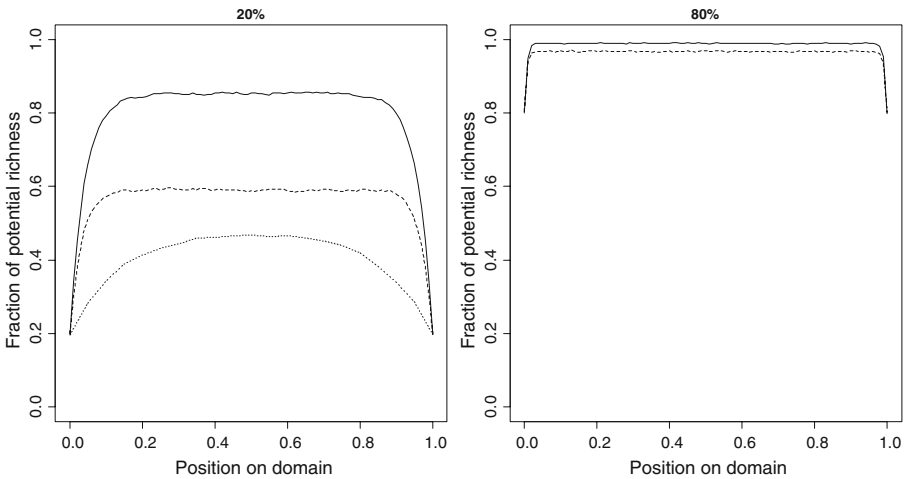

Fig. 2 Illustrations of the effect of interpolation method with different range distributions and different sampling efficiencies. When the sampling is poor (probability of finding a species is 0.2; left), interpolation affects the pattern more with larger maximum range size (*unbroken line*) than for smaller maximum range size (*broken line*). When sampling is relatively complete (probability of finding a species is 0.8; right) the interpolation effect is relatively small and almost independent of the maximum range sizes. The lower *dotted line* in the left panel represents the pattern when the domain is divided into 20 intervals. In this case the richness pattern is affected by interpolation in the entire domain

range sizes result in an increased probability of adding a species by interpolation, and thereby finding a larger portion of the true species richness in the middle. With smaller range sizes many species will be entirely missed in the domain. With small range sizes and a sampling probability of 0.8 there is hardly any effect of interpolation on the species-richness pattern; only the extreme points show a weak tendency to have lower species richness.

In these simulations we divided the observational domain in 100 sampling intervals. For the 20% sampling efficiency the outermost ten intervals were affected by the interpolation. With fewer intervals a larger part of the domain will be affected. If only 20 intervals were constructed and we again assumed that 20% of the species was found in each interval the entire domain would be affected by the artifictions introduced by interpolation (Fig. **2** left; *dotted line*).

Accounting for the biasing effect of interpolation is difficult if we do not know how exhaustive the sampling has been. It may be possible to crudely estimate the effect of interpolation if we assume that sampling was equal along the domain, but as mentioned above this is often not the case for museum collections. However, in many cases the richness pattern is so strong, and variation due to other random effects so large, that a gap in sampling at a certain interval may not be visible when interpolation is used (cf. Fig. **1**). If there is a trend, i.e., decreasing sampling efficiency with higher altitude or latitude, interpolation will not be an efficient way of accounting for differences in sampling. The best solution is probably to avoid using the interpolation method whenever possible. In some cases interpolation will, however, be the only option. It is then important to be aware of the artificial pattern that might result. If interpolation is used to estimate a species-richness pattern along a geographical gradient, one should consider discarding the richness estimates towards the observation limits. How large a part needs to be discarded depends on how well the sampling has been done and on the range sizes of the species. Vetaas and Grytnes (2002) excluded the upper and lower 1,000 m when studying altitudinal species-richness patterns in the Nepalese Himalaya before correlating the observed species richness to any explanatory factors. This was based on the simulations done in Grytnes and Vetaas (2002), which showed that the interpolation effect influences the altitudinal richness pattern in the first and last 1,000 m along the Himalayan altitudinal gradient. The simulations were based on collections of only 20% of the species at each altitude interval, which was considered to be a worse scenario than would typically be achieved in a survey.

The effect of interpolation may be mistaken for a Mid-Domain Effect (MDE) (Colwell and Hurtt 1994; Zapata et al. 2003; Colwell et al. 2004). The MDE is commonly investigated using interpolated ranges, both in the empirical pattern and in the creation of randomization tests for the MDE, and it may therefore be difficult to separate the MDE from the interpolation effect in many cases. Dunn et al. (2006) suggest a way to account for the effect of interpolation when information about presences within the intervals between the range endpoints is available. This is done by randomly assigning absences to intermediate intervals in the randomly placed range to match the fill of the empirical range. In this way the inflation of species richness that is due to interpolation of species ranges is avoided and the MDE can be separated from the interpolation effect (Colwell 2008).

Rarefaction

Rarefaction is a way of estimating the species-richness pattern along a gradient if detailed knowledge about the distribution of specimens along the gradient is available. Such information is becoming readily available as more museum collections are digitized and made publicly available (e.g. at Global Biodiversity Information Facility: www.gbif.org). Rarefaction generates the expected species richness in a given subsample of the total number of individuals randomly drawn from a large pool of individuals (Sanders 1968; Hurlbert 1971; Gotelli and Colwell 2001). An analytical solution for rarefaction, based on hypergeometric distribution, has been suggested (Hurlbert 1971; Heck et al. 1975). Rarefaction can be used both at individual level and at sample level, but because the focus here is on museum collections we discuss only individual-based rarefaction (sensu Gotelli and Colwell 2001). This method has been used to explore species-richness patterns along gradients with museum collections in recent studies (Wolf and Alejandro 2003; Grytnes and Beaman 2006). Softwares available for doing rarefaction include EcoSim (Gotelli and Entsminger 2007), EstimateS (Colwell 2005) and the vegan package in R (http://vegan.r-forge.r-project.org/). The latter was used for doing the rarefaction analyses in this paper.

A rarefaction curve (a curve describing how richness varies with number of specimens included in the rarefied sample) depends both on the richness of the assemblage and on the evenness of the abundance between species (Fager 1972; Olszewski 2004). Museum collections are not random samples of the assemblages. Common species are generally undersampled and rare species tend to be over-sampled in museum collections compared to abundances observed in natural communities. Museum collections may also have other biases, such as expertise and interests of local taxonomists, avoidance of difficult groups, higher collection intensity of conspicuous groups, etc. Information about evenness based on museum collections is therefore rarely of interest because it is not related to the original assemblage. Because rarefaction is dependent on the species-abundance distribution (SAD) of the species in the collections (Fager 1972; Olszewski 2004), the SAD should be equal between the different samples to be compared for rarefaction to work as an unbiased estimate of species-richness patterns (note that here we refer to richness pattern and not to estimation of true species richness in an area). To be an unbiased estimator of true species richness in a natural community the sample must be a random representation of the community (Gotelli and Colwell 2001). This is also important when rarefaction or accumulation curves are used to estimate total species richness in an area by extrapolation (Colwell and Coddington 1994). Museum collections are therefore not well suited to estimate total species richness using extrapolation.

We provide a range of simulations to illustrate how the SAD influences the rarefaction curves based on "communities" with one of three SADs. The first community mimics a natural community with a lognormal abundance distribution with mean (log abundances) = 4, and s.d. (log abundances) = 2. The selected values for the parameters of this lognormal distribution are chosen based on inspection of a data set of beetles and spiders from Finse in southern Norway (Ottesen 1996; Hauge and Ottesen 2002), trees on Barro Colorado Island (Condit et al. 2002), and other

data sets. The second community mimics an abundance distribution found in a museum collection with a lognormal abundance distribution with mean (log abundances) = 0.8, and s.d. (log abundances) = 1.2. The selected values for the parameters of the lognormal distribution are chosen based on inspection of several museum collections, e.g. the vascular plant data from Mount Kinabalu used in Grytnes and Beaman (2006), plants in Taiwan and the Fungal database from Danish Mycological Society (both the two latter datasets were accessed through GBIF data portal, http://data.gbif.org/datasets/). In the case of museum collections, a distribution with a more peaked distribution than a lognormal distribution could probably make a better fit to the empirical data. However, it is only used here to illustrate how differences in SAD affect the rarefaction curve, and the main point is that museum data will have a more equal abundance distribution than random data from a natural community. A third community is added for comparison assuming a much more equal abundance between species than the lognormal distributions using a normal distribution of species abundances with mean = exp(4), and s.d. = 10. Each of the three communities was simulated with two different species pools, one with 100 species, and another with 200 species. From each of these six communities we randomly picked 10,000 individuals with the given SAD as probability for selecting a species, simulating a rather extensive sampling of the total pool of individuals available. From these 10,000 individuals we constructed a rarefaction curve for between 50 and 1,000 individuals. Note that some of the rare species in the lognormal distribution from the "natural community" were not "sampled" among the 10,000 individuals resulting in different richness among the 10,000 individuals between the three communities. Accounting for this by sampling from a larger pool of species, such that this community had 100 or 200 species among the 10,000 individuals, had only a minor effect on the results and did not change the conclusions.

The results of the simulations are shown in Fig. 3. This figure demonstrates that rarefaction curves are clearly affected by differences in SAD as shown previously by Fager (1972) and Olszewski (2004). More equal abundances between species result in a steeper rarefaction curve and it relatively quickly reaches an asymptotic level. This means that with a small sample from an assemblage with relatively equal abundances between species we will overestimate species richness relative to an assemblage with a broader dispersion of the SAD (compare the dotted line (equal abundances) with the unbroken line (very unequal abundances) of the same colour in Fig. 3). In the simulated assemblages used, it is only at above approximately 850 individuals where the assemblage with 200 species of the "natural community" of very unequal abundances is estimated to have more species than the assemblage with 100 species and equal abundances (Fig. 3).

Additional simulations were tried varying the mean and standard deviation of the lognormal distribution for SAD. These simulations revealed that the mean of the lognormal distribution had no effect on the rarefaction curves, but the dispersion (or standard deviation of the SAD) had a large effect. This is not surprising as changing the mean does not affect the relative abundance of species but only the absolute values. When using rarefaction to compare species richness along geographical gradients it is therefore important that the standard deviation of the SAD is approximately equal, whereas the average abundance does not matter. However, it is

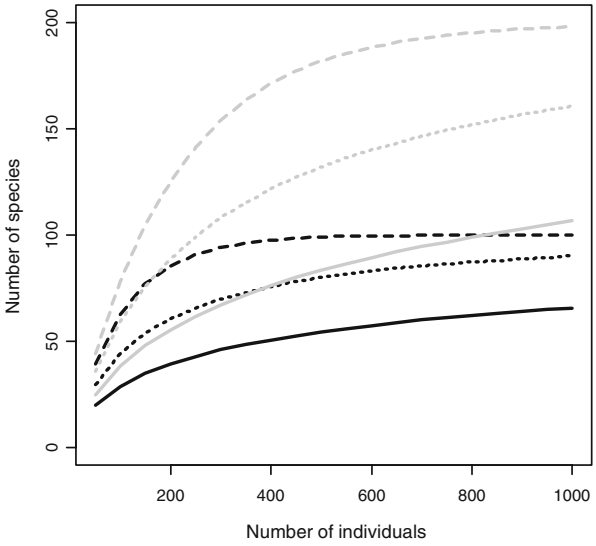

Fig. 3 Results of the rarefaction of species richness from three different Species-Abundance Distributions (SADs). *Solid lines* – lognormal distribution with mean(log abundances) = 4 and s.d. (log abundances) = 2; *dashed lines* – lognormal distribution with mean(log abundances) = 0.8 and s.d. (log abundances) = 1.2; and *dotted lines* – normal distribution with mean(abundances) = exp(4) and s.d. (abundances) = 10. Each of the three SADs had either 100 species in the original community (*black lines*) or 200 species in the original community (*grey lines*)

not as simple as just checking if the standard deviation of logged empirical abundances is reasonably similar between the samples to be compared, because the empirical standard deviation will change with total abundance even if the underlying dispersion is similar. This is illustrated in Fig. 4 where 2,000 species with a SAD equal to the "natural community" above (lognormal distribution with mean (log abundance) = 4 and s.d. (log abundance) = 2) is simulated with a varying number of individuals. Figure 4 also suggests a solution to this and that is to rarefy the samples to the same number of specimens and compare the dispersion of the samples with equal total numbers of individuals. If the dispersion of the two SADs is reasonably similar the rarefaction curves can be compared. A broader dispersion will result in an underestimation of species richness and a more narrow dispersion (abundances more equal) will result in a relative overestimation of species richness until an asymptotic level is reached (cf. Fig. 3).

Conclusions

The use of museum collections in quantifying broad-scale geographical patterns will probably be more important and common as such data becomes readily available. In this paper we have demonstrated the importance of treating such data carefully. If this is not done some artifictions may arise and we will end up trying to explain numbers and patterns that have no ecological meaning (Palmer et al. 2008).

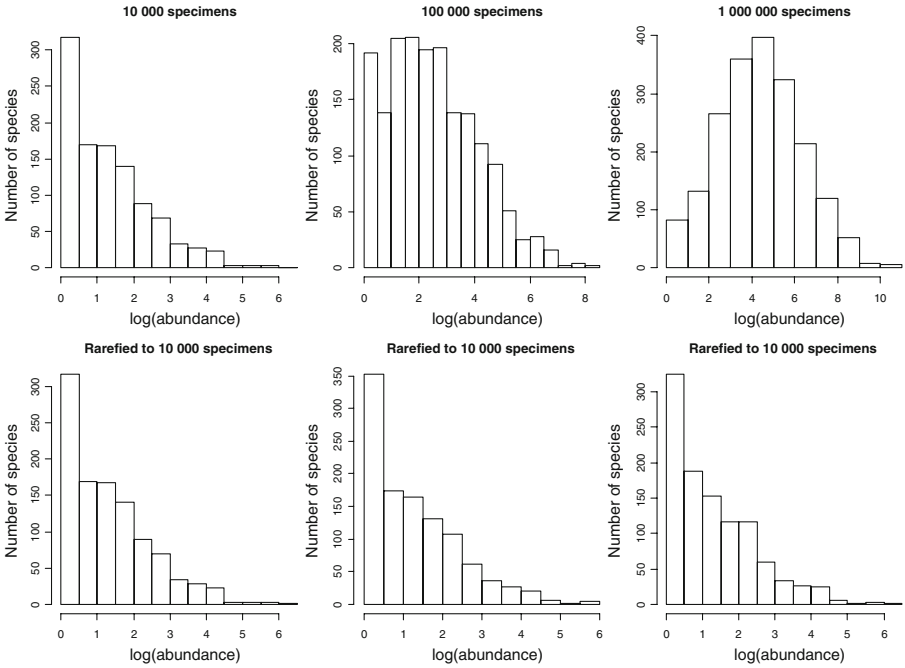

Fig. 4 Frequency distribution of species abundances showing the effect of sampling a different number of individuals. One community was simulated where the abundance of 2,000 species was simulated with a random draw from lognormal distribution mean (log abundances) = 4, s.d. (log abundances) = 2). Three different "sampling regimes" were simulated by randomly sampling individuals from these 2,000 species with replacement with a probability equal to the simulated abundance. In the first column 10,000 specimens were sampled, in the second column 100,000 specimens were sampled, and in the third column 1,000,000 specimens were sampled. In the upper row the raw observed frequency distribution of species abundances is given, whereas the lower row shows the frequency distribution of 10,000 specimens rarefied from the original sample. Although the original samples differ with sampling size the rarefied sample gives very similar SAD. The rarefaction curve also gives the same result independent of which one of the three upper frequency distributions are used (in this case it is the curve of the "natural community" in Fig. 3). Standard deviation for the frequency distribution is 1.21 for all distributions in the lower row. For the upper row the standard deviation are from left to right: 1.21, 1.66, and 1.94

Interpolation may introduce a humped pattern if sampling is incomplete, and one should pay special attention to samples close to the observational extremes when using this method. When using rarefaction we may end up with a mixture of evenness and richness in our estimates, with no or little clue as to how the samples really differ in richness. Before applying rarefaction to estimate species richness one should pay close attention to the frequency distribution of species abundances in the samples. In this respect it would be very useful if curators of museum collections were aware of the problems associated with quantifications of diversity. From a macroecological perspective it would be ideal if curators could identify to what degree the specimens are collected for a very specific purpose or if it was a more-or-less random collection of the flora in an area. However, the main conclusion of this paper should be that although interpolation and rarefaction may be able to correct for differences in sampling efforts to some extent, nothing can beat doing the sampling

properly and completely in the first place! Unfortunately this is, in many cases, an almost impossible task.

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