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Spatially constrained rarefaction: incorporating the autocorrelated structure of biological communities into sample-based rarefaction

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Abstract: Rarefaction is a widely applied technique for comparing the species richness of samples that differ in area, volume or sampling effort. Despite widespread adoption of sample-based rarefaction curves, serious concerns persist. In this paper, we address the issue of the spatial arrangement of sampling units when computing sample-based rarefaction curves. If the spatial arrangement is neglected when building rarefaction curves, a direct comparison of species richness estimates obtained for areas that differ in their spatial extent is not possible, even if they were sampled with a similar intensity. We demonstrate a major effect of the spatial extent of the samples on species richness estimates through the use of data from a temperate forest. We show that the use of Spatially Constrained Rarefaction (SCR) results in species richness estimates that are directly comparable for areas that differ in spatial extent. As expected, standard rarefaction curves tend to overestimate species richness because they ignore the spatial autocorrelation of species composition among sampling units. This spatial autocorrelation is captured by the SCR, thus providing a useful technique for characterizing the spatial structure of biodiversity patterns. Further work is necessary to determine how species richness estimates and the shape of the SCR are affected by the method of spatial constraint and sampling unit density and distribution.

Abbreviations: SCR–Spatially Constrained Rarefaction, SAR–Species Area Relationship, CI–Confidence Interval

Introduction

Rarefaction represents a powerful method for calculating the expected number of species as a function of sampling effort. For this reason, it is widely used in community ecology and biodiversity research. The technique was introduced by Sanders (1968), based on the observation that species richness obtained from a sample of *n* individuals increases with *n*. As a consequence, a valid comparison of species richness estimated from different samples can be done only after "rarefaction" to the same number of individuals, *i.e.*, that with the lowest *n*. Sanders' (1968) rarefaction method provided the expected number of species for rarefied sample of 1 to *n* individuals. Hurlbert (1971) and Simberloff (1972) independently noted that the Sanders method was mathematically incorrect, and both arrived at the correct expression:

$$\overline{S\,O}_{in} = SO_n - \binom{n}{i}^{-1} \sum_{k \in G} \binom{n - n_k}{i}, \; i = 1,\ldots,n \qquad (1)$$

where $\overline{SO}_{in}$ is the expectation of SO_{in} when i individuals are resampled by means of simple random sampling without replacement from the collection of n individuals; G is the set of species observed in the collection of n individuals, SO_n is the total number of observed species, n_k is the number of individuals belonging to species k∈ G.

In most ecological surveys, it is impractical to obtain samples of a random collection of individuals. Frequently, sampling units are composed of clusters of individuals, such as those present within a given unit of space (e.g., the plants within a plot) or time (e.g., the insects captured in a light trap). Depending on the units used to express sampling effort, i.e., the number of individuals sampled or the number of sampling units, it is possible to calculate either *individual-* or *sample-based* rarefaction curves (Gotelli and Colwell 2001). The expected number of species in a collection of n sampling units can be calculated by a different version of formula (1) where n is the number of sampling units and n_k is the number of sampling units containing at least one individual of species k∈ G. According to Kobayashi (1974), the sample-based application of (1) was introduced by Shinozaki (1963), but the same formula was then "re-discovered" several times (Chiarucci et al. 2008b). Sample-based rarefaction curves

have been used to compare species richness across sites, for example, beetle species richness across two ecoregions of USA (Gering et al. 2003), snake species richness as a function of trap-days (Thompson et al. 2003), plant species richness of the biogeographic regions in Switzerland (Koellner et al. 2004), and plant species richness of different forests or nature reserves in Italy (Chiarucci and Bonini 2005, Chiarucci et al. 2008a). A formula for the variance of such curves was recently proposed (Colwell et al. 2004, Mao et al. 2005), although Fattorini (2007) showed that this formula is based on assumptions that are usually violated in ecological data.

Sample-based rarefaction curves are equivalent to some species-area curves when the sampling unit is an area. In particular, these curves correspond to a type III Species-Area Relationship (SAR) in the classification of Scheiner (2003). Such SARs are built from non-contiguous sampling units. The difference between a traditional SAR and a sample-based rarefaction curve is that in the latter the *x*-axis is the number of sampling units rather than the size of the area sampled, although one can be transformed into the other. By formula (1), all possible combinations of sampling units are considered for each *n* and, thus, traditional rarefaction curves correspond to the type IIIB curves of Scheiner's scheme: curves not using a spatially-explicit method for obtaining the combinations of sampling units.

Scheiner (2003) noted that the shape of a type III curve is to some extent a function of the spacing between the sampling units, often called the lag. Consequently, the problem of estimating species richness in a collection of *n* units depends on: (1) how many units are sampled, (2) the area of each unit (which together determine the total sampled area), and (3) the lag, which determines the extent of the samples, i.e., the area over which those units are spread (Condit et al. 1996, Palmer et al. 2002, Scheiner 2003, Chiarucci and Bonini 2005, Fattorini 2007, Hui 2008).

To our knowledge, the only previous examination of the effects of spatial autocorrelation on the properties of rarefaction curves was done by Collins and Simberloff (2009). They examined the robustness of individual-based rarefaction curves to violations of random and independent dispersion of individuals and species. This paper complements their efforts by examining spatial effects of sample-based rarefaction curves. In this paper, we (1) demonstrate the bias associated with the use of sample-based rarefaction curves (or type IIIB SARs) and (2) introduce a new technique to deal with this problem: the use of a spatially-constrained rarefaction curve.

The problem: spatial arrangement matters

In a given area, a sample-based rarefaction curve provides the expected (mean) number of species recorded by a set of *n* sampling units (Ugland et al. 2003, Fattorini 2007, Chiarucci et al. 2008b). Even if this method offers an elegant solution to the interpolation of the number of species collected as a function of sample size, it is affected by various spatial components as described above. When using sampling units of a given size, the shape of the rarefaction curve is determined by two factors: the number of units and the total extent. When comparing two areas sampled with different number of samples, the rarefaction to a similar number of sampling units should allow a direct comparison of species richness, especially if sampled areas have the same density of sampling units (Chiarucci and Bonini 2005). However, this approach considers only the effects of the first factor, the number of units, but ignores the second, the spatial extent of those units. The following example clarifies this issue.

Consider a comparison of species richness from two areas of different sizes: area A is 100 *ha*, while area B is 10 *ha* (Fig. 1). The two areas are sampled with the same intensity, e.g., one sampling unit per hectare, resulting in two samples of 100 and 10 units, respectively. To make the example clearer we can even consider that the mean number of species per sample unit is the same. The hypothetical sample-based

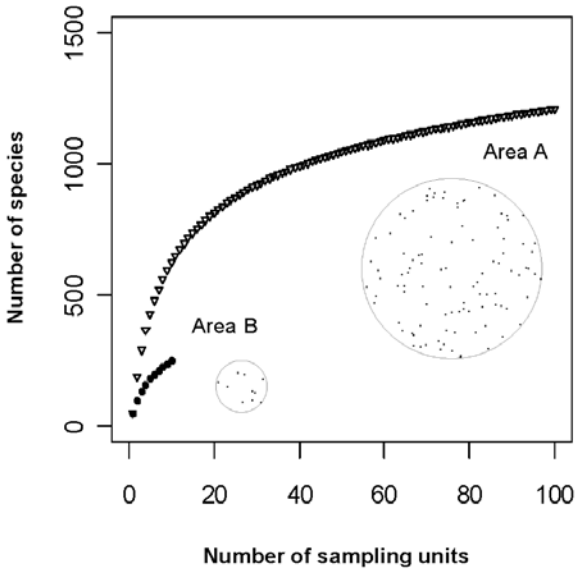

Figure 1. Hypothetical rarefaction curves showing the species richness of two differently sized areas sampled with a proportional number of sampling units. Area A is 100 ha and has been sampled by 100 units while area B is 10 ha and has been sampled by 10 units. The rarefaction curve of the larger area A (empty triangles) lies above the curve of the smaller area B (black dots) even for comparable sample sizes (number of sampling units corresponding to 1 to 10). The two circles represent the two sampled areas A (100 ha) and B (10 ha), while the points therein represent the sample units.

rarefaction curves for these two areas are shown in Fig. 1, with the curve for area A staying above the curve for area B, even at comparable sample sizes (from $n = 2$ to 10). The particular pattern will depend on the details of the data, but this general pattern will always hold if there is positive spatial autocorrelation (distance decay) in species distributions.

This rarefaction approach is commonly used for comparing species richness in regions of different sizes, under the expectation that rarifying to the same number of sampling units makes the estimates directly comparable. However, they are not directly comparable even for the similar number of sampling units ($n = 2$ to 10) because of the differing spatial extents. In particular, the curve for the larger area A was obtained by calculating the pooled species richness of all possible combinations ($n = 2, 3,... ,10$) of the 100 sampling units scattered over a larger extent than the 10 sampling units in area B. The larger area is likely to contain more species through two effects: (1) a larger area will contain more individuals, increasing the chances of encountering additional species drawn from the regional species pool in an explicitly spatial pattern (the "area *per se*" effect), and (2) a larger area will be more environmentally heterogeneous, thus containing species that differ in their ecological requirements, the "habitat diversity" effect (Connor and McCoy 1979). The greater total number of species in the area A sample creates the potential for combining sampling units with greater differences in species composition resulting in a rarefaction curve with a greater mean number of species for a given sample size.

Accordingly, because of the well known first law of geography ("Everything is related to everything else, but near things are more related than distant things", Tobler 1970), extent is one of the most important factors controlling differences in species composition. This law manifests itself in ecological processes as distance-decay patterns at both global and local scales, which result in a decrease of compositional similarity with increasing distance (Palmer 1995, 2005, Nekola and White 1999, Nekola and Brown 2007, Soininen et al. 2007). Accordingly, sample-based rarefaction curves will increase faster when sampling units are farther apart (Condit et al. 1996, Palmer et al. 2002, Hui 2008).

We demonstrate this effect with data from the Oosting Natural Area of the Duke Forest, North Carolina (Reed et al. 1993, Palmer et al. 2007). These data have been used to address several ecological questions related to spatial scale (e.g., Reed et al. 1993, Palmer and White 1994, Wagner 2003, Bacaro and Ricotta 2007, Schlup and Wagner 2008). The vegetation was sampled in a grid of 16 × 16 modules (256 contiguous modules) of 16 m × 16 m each. Six nested quadrats (with sides of 0.125 m, 0.25 m, 0.50 m, 1 m, 2 m, and 4 m) were located in the southwestern corner of each module and in each the presence of all vascular plant species was recorded (Reed et al. 1993). Three different grain sizes (the quadrats with sides of 0.125 m, 0.50 m and 4 m) were used in the current analyses. Sample-based rarefaction curves were constructed for each quarter of the whole area and the mean of the four estimates was calculated. We then compared this averaged sample-based rarefaction curve with one calculated for the same number of sampling units (64) but scattered over the whole area.

The rarefaction curves calculated for the smaller areas fell below the rarefaction curve calculated for the whole Oosting area for all three grain sizes (Fig. 2). The difference between the curve calculated as the mean of the four quarters and that calculated for the whole area increased with quadrat grain size. The estimates of species richness were, on average, 5.4%, 5.2% and 8.6% lower for curves built from quadrats of 0.125 m, 0.50 m and 4 m, respectively. This example demonstrates how a relatively small increase in extent can have a significant effect on species richness estimates. Thus, comparisons of species richness from areas with different extents are questionable, even when the number of sampling units is the same.

A solution: Spatially Constrained Rarefaction (SCR)

The problem described above can be solved by including spatial information when calculating the rarefaction curve. This information should be used at each step of the calculation, not at only a single step, as was done in the previous example. In that example the whole area was divided into 4 sub-areas and standard rarefaction curves were calculated within each quadrant, thereby retaining only some location information. Instead, we use a method in which the spatial proximity of sampling units is used as a constrained factor for building the entire curve. These curves are named Spatially Constrained Rarefaction (SCR) curves.

Consider the larger area A in Fig. 1, and curves built using combinations of up to 10 sampling units. For a SCR curve, those combinations would consist only of adjacent sampling units. The resulting curve allows for a direct comparison of the species richness of the areas A and B because it takes into account the effects of the spatial autocorrelation among sampling units. The sample-based rarefaction curves have not only a comparable number of sampling units but also a comparable spatial extent.

In creating a spatially-constrained curve, we combine adjacent sampling units. To do that, we must first decide what constitutes "adjacent." Various definitions can be applied (Dale 1998), among these are: *k*-Nearest Neighbor (*k*-NN, see e.g., Hastie et al. 2001 and references therein), *k*-Nearest Centroid Neighbor (*k*-NCN, e.g., Rutkowski et al. 2004), natural neighbors (Voronoi 1907), and γ-neighbors (Veltkamp 1992). *k*-NN consists of choosing the *n* neighbors closest to the original sampling point. *k*-NCN consists of choosing the next sampling unit that is closest to the centroid of the already selected units. Natural neighbors are defined through a Dirichlet tessellation (also referred to as a Voronoi tessellation, see Dugan 2005). With γ-neighbors an asymmetric notion of closeness is applied. In this paper, we use a method based on the *k*-Nearest Neighbor (*k*-NN). A discussion of the effects of different neighborhood rules is beyond the scope of this paper.

In using *k*-NN we adopted the following procedure: *i)* a random point was located within the area and its nearest sampling unit was used as the starting point; *ii)* the 2nd, 3rd, …., 256th sampling unit closest to that random point were determined; *iii)* a species accumulation curve was calculated using the resulting sequence of plots; *iv)* these steps were repeated 1000 times, generating 1000 spatially constrained accumulation curves from which a mean curve was calculated. This entire procedure was repeated for each of the three grain sizes. Those mean curves were compared with the non spatially-constrained curves calculated for the whole area from the previous comparison (Fig. 2, gray squares). We calculated bootstrapped 95% confidence intervals (CIs), avoiding the problems evidenced by Fattorini (2007) for the analytical formula (Colwell et al. 2004, Mao et al. 2005).

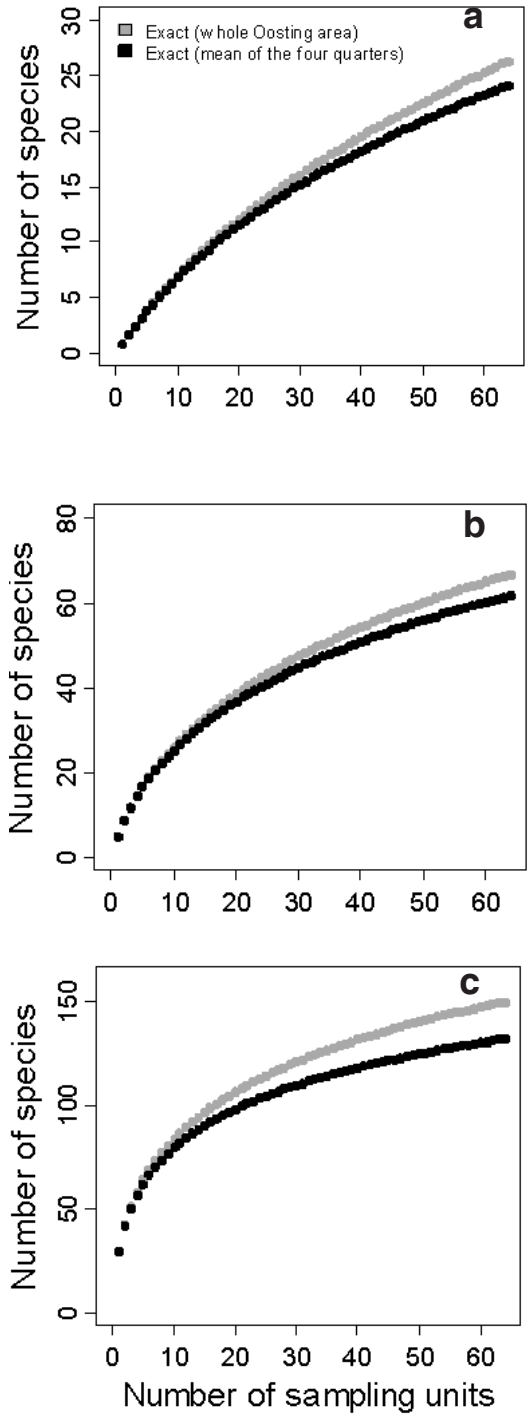

Figure 2. Comparisons between rarefaction curves calculated for the whole Oosting area (gray squares) and the mean of the four curves calculated for each of the four quarters of that area (black squares). Three plot sizes were used: a) 0.125 m × 0.125 m, b) 0.50 m × 0.50 m, c) 4 m × 4 m.

As expected, the sample-based SCR curves fell well below the curves for the whole area (Fig. 3) and the differences were larger than in the previous example. For the three grain sizes (0.125 m, 0.50 m, 4 m), the estimated species richness was on average lower by 4.4%, 10.8% and 12.1%, respectively. These differences were statistically significant based on the non-overlapping 95% CIs. Of course, the two estimates will converge at the combinations that include only one or all sampling units.

Conclusions

Our comparison of SCR curves with standard (non spatially-constrained) rarefaction curves confirms the importance of both spatial extent and grain. Others have observed that the effects of extent are often larger than those of grain (Condit et al. 1996, Palmer et al. 2002, Chiarucci and Bonini 2005, Hui 2008), although our analyses found that differences due to grain size for samples with similar extents (Fig. 3) were greater than those for samples of different extents (Fig. 2). Our results show that comparisons of species richness estimates from sample-based rarefaction curves obtained for sites that differ in extent can be misleading. All the components of spatial variation exert a role in controlling the rate of rise of the curves, but the distance separating the sampling units is certainly a primary one. The use of a spatially-constrained procedure in the construction of rarefaction curves accounts for the autocorrelated structure of biological communities, thereby providing more comparable species-richness estimates.

The use of rarefaction to account for difference in sampling effort is one example of the more general need to standardize species richness to a common grain when making comparisons across samples and studies (Scheiner et al. 2000). Comparisons of disparate areas are increasingly common in biogeography, community ecology and conservation biology for regional to global analyses of patterns of diversity and for quantifying site biodiversity (e.g., Mora et al. 2008). Although one of the most common means of standardizing richness today is to divide richness by area, this technique has been long and repeatedly discredited (Palmer et al. 2008). Because biodiversity measured as species richness is often used for conservation purposes, it is extremely important that biodiversity scores are not overestimated simply because of the distorting effects of spatial extent. Larger sites may be assessed as more diverse just because they nec-

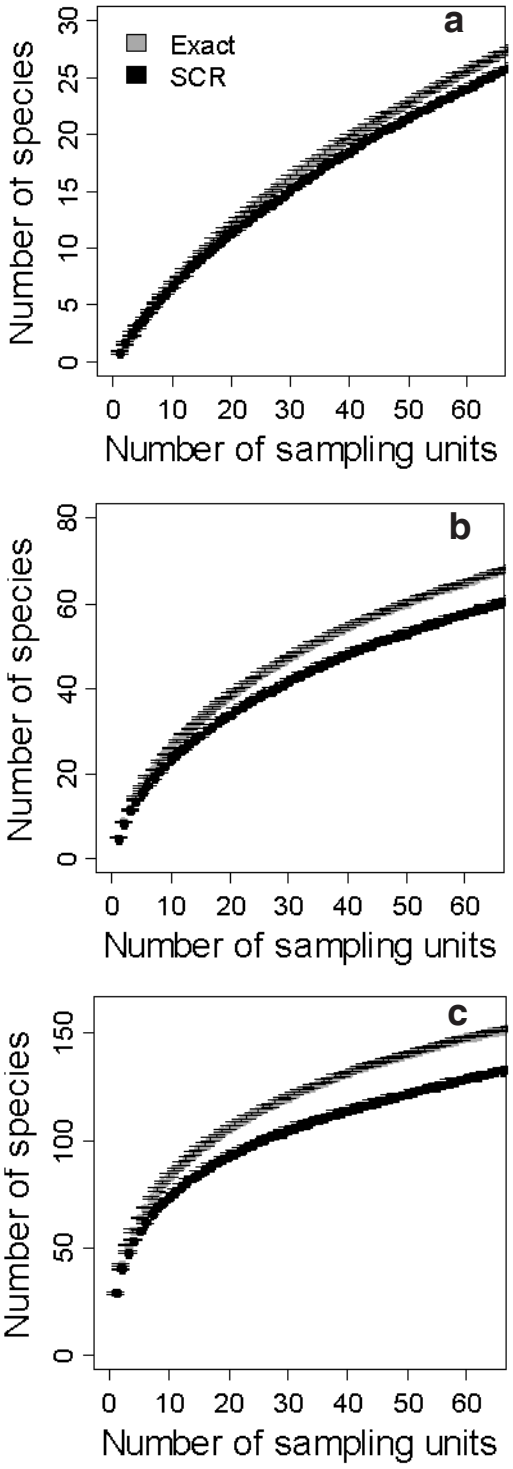

Figure 3. Comparisons between rarefaction curves calculated using a sample-based rarefaction method (gray squares) and a spatially-constrained method, the Spatially Constrained Rarefaction curve (SCR, black squares). Both were calculated for the whole Oosting area, but only the part up to 64 plots is shown). Three plot sizes were used: a) 0.125 m × 0.125 m, b) 0.50 m × 0.50 m, c) 4 m × 4 m. SCRs were calculated as the average of 1000 randomly-generated curves. The 95% CIs are based on 1000 bootstrapped samples.

essarily contain higher β diversity and the sampling units, consequently are more diversified in species composition. Spatially-constrained rarefaction may help to solve these problems.

Our exploration of these questions leaves several issues unaddressed. As mentioned previously, the effects of different neighborhood rules used to construct the curves need to be investigated. In this paper the areas all had the same density and spacing of the sampling units. Additional work is needed to look at the effects of both the mean and variance in spatial lag. Often, the spatial density of sampling units is lower for larger areas and therefore different methods are needed than those adopted here. Future refinements of the proposed approach might include constraining the samples based on the extent of the *n* sampling units, rather than on whether the units are adjacent.

Scheiner (2003) classified species-area curves into a general system composed of six types. In this classification type IIIB corresponds to traditional, non spatially-constrained sample-based rarefaction curves, while type IIIA curves match the spatially-constrained curves presented here. Scheiner (2003) wrote "Examples of nearly all types of curves can be found both in the early and contemporary literature, except for the Type IIIA curve, for which I was unable to find any examples". Now the theoretical classification imagined by Scheiner (2003) is completed by the Spatially Constrained Rarefaction curve.

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