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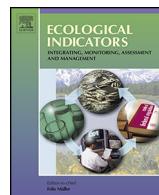
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Short Communication

Incorporating spatial autocorrelation in rarefaction methods: Implications for ecologists and conservation biologists



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ABSTRACT

Recently, methods for constructing Spatially Explicit Rarefaction (SER) curves have been introduced in the scientific literature to describe the relation between the recorded species richness and sampling effort and taking into account for the spatial autocorrelation in the data. Despite these methodological advances, the use of SERs has not become routine and ecologists continue to use rarefaction methods that are not spatially explicit. Using two study cases from Italian vegetation surveys, we demonstrate that classic rarefaction methods that do not account for spatial structure can produce inaccurate results. Furthermore, our goal in this paper is to demonstrate how SERs can overcome the problem of spatial autocorrelation in the analysis of plant or animal communities. Our analyses demonstrate that using a spatially-explicit method for constructing rarefaction curves can substantially alter estimates of relative species richness. For both analyzed data sets, we found that the rank ordering of standardized species richness estimates was reversed between the two methods. We strongly advise the use of Spatially Explicit Rarefaction methods when analyzing biodiversity: the inclusion of spatial autocorrelation into rarefaction analyses can substantially alter conclusions and change the way we might prioritize or manage nature reserves.

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1. Introduction

Biogeography and ecology are deeply permeated by the spatial nature of their data ([Legendre, 1993](#)). Several types of spatial analysis and statistics are routinely used to determine how spatial structure affects the movement of individuals, species distributions, the structure and composition of species assemblages, and to predict the consequences of spatial heterogeneity ([Fortin et al., 2012](#)). Geo-referenced data are increasingly available (e.g., [Martellos and Attorre, 2012](#)) and are being used to address pressing

planetary challenges from climate change and increased human-driven land use. Such uses require spatio-temporal analyses that take into account the spatial and temporal extent and grain of the data ([Fortin et al., 2012; Bacaro et al., 2012a,b](#)).

Traditionally, the analysis of species richness at relatively large extents has relied on the use of standardized sampling at smaller extents combined with the use of statistical estimators for extrapolating to larger extents ([D'Alessandro and Fattorini, 2002; Chiarucci et al., 2003, 2011](#)). However, robust methods for such extrapolation are not routinely used. The development of methods for such sampling and extrapolation offers new challenges and opportunities ([Palmer et al., 2002; Engemann et al., 2015](#)). Rarefaction curves (RCs) have been extensively used to compare species richness among very different types of habitat and biota (e.g., [Heilmann-Clausen and Christensen, 2004; Schneider and Culver, 2005; Sogin et al., 2006; Roesch et al., 2007; Koellner et al., 2004; Chiarucci](#)

Abbreviations: RC, rarefaction curve; SA, spatial autocorrelation; SER, Spatially Explicit Rarefaction; SCI, Site of Community Importance.

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et al., 2008b; Acosta et al., 2009; Bacaro et al., 2012a,b). Rarefaction allows comparisons of species richness among data sets by standardizing estimates to an equal-effort basis. Species richness estimates increase with the number of sampling units (e.g., plots, traps; Fairbanks and McGwire, 2004). Therefore, a suitable comparison of species richness estimated from data sets of different sample sizes should be done only after rarefying each to an equal sampling effort, such as area or number of sampling units (Gotelli and Colwell, 2001). 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.

Formally, given a collection of n sampling units, sample-based rarefaction provides the expected number of accumulated species as the number of sampling units increases from 1 to n . This is often obtained by repeatedly resampling the pool of n sampling units at random without replacement and plotting the average number of species recorded by 1, 2, ..., n sampling units (Gotelli and Colwell, 2001).

An analytical formulation for the calculation of the rarefaction curve was first developed by Shinozaki (1963), and later independently rediscovered by a number of authors during the 1970s (Kobayashi, 1974; Holte, 1975; Engen, 1976; Smith et al., 1979) and in the last decade (Ugland et al., 2003; Colwell et al., 2004). Chiarucci et al. (2008a) described the history of the multiple discoveries of sample-based rarefaction as a classical example of geographical and linguistic bias in scientific literature. If G denotes the set of species observed in the collection of n sampling units, S_n denotes the total number of observed species, and n_k denotes the number of sampling units containing at least one individual of species $k \in G$, then, the expected number of species S_i is:

$$S_i = S_n - \binom{n}{i}^{-1} \sum_{k \in G} \binom{n - n_k}{i}, \quad i = 1, \dots, n \quad (1)$$

This equation describes the expectation of S_i when i samples are randomly resampled without replacement (Chiarucci et al., 2008a). This estimator is unbiased if the spatial distribution of individuals is random (Kobayashi, 1982; Gotelli and Colwell, 2001; Collins and Simberloff, 2009) and it can be used for comparisons among data sets if sample sizes are sufficient and the data sets were sampled in a similar way (Abele and Walters, 1979). The latter two requirements are easy to control and/or adjust for either in the initial sampling design or in choosing which data sets to compare. However, individuals are almost never randomly distributed in space, either due to heterogeneity of environmental factors or non-random dispersal of individuals. Thus, it is necessary to develop rarefaction methods that account for such non-random distributions.

Recently, Chiarucci et al. (2009) defined a new type of rarefaction curve, termed Spatially Constrained Rarefaction (SCR) that accounts for the spatially-autocorrelated structure of biological communities. In this paper we refer to this method by the somewhat more accurate name of Spatially Explicit Rarefaction (SER). This method addressed the problem of spatial autocorrelation by building the rarefaction curve based on the adjacency of the sampling units (see Chiarucci et al., 2009 for a full description of the rationale and method). More recently, Bacaro et al. (2012a) developed “pointpattern” and “SCR” routines in the R environment for calculating a SER, making this technique readily available. To our knowledge, however, the use of SERs has not become routine (a recent ecological application can be found in Janišová et al., 2014). Conversely, a plethora of recent studies (e.g., Hardersen and Corezzola, 2014; Siegloch et al., 2014; Braze et al., 2014; Jung et al., 2014; Giesecke et al., 2014; Xu et al., 2014a,b) and statistical software (see, for example, Oksanen et al., 2015; Cardoso et al., 2015) continue to use Nonspatially Explicit Rarefaction methods. In this

paper, we aim at demonstrating how SERs can overcome the problem of spatial autocorrelation in the analysis of plant or animal communities.

2. Case studies

To illustrate how the two methods (RCs and SERs) differ in practice and why Spatially Explicit Rarefactions should be preferred, we re-analyzed two published vegetation datasets (Ciccarelli, 2014; Chiarucci et al., 2008a). The examples differ both in sampling strategies and vegetation type, and demonstrate the generality of our conclusions.

2.1. Example 1: coastal dune plant communities

The first example was a vegetation survey carried out on coastal dune plant communities. Dune ecosystems are diverse in terms of both environmental heterogeneity and species composition (Van Der Maarel, 2003; Martínez and Psuty, 2004). Furthermore, the dynamic nature of sandy coastal habitats, together with the strong zonation patterns exhibited by the vegetation make dune communities the focus of several national and international conservation efforts and policies. We analyzed a set of plots collected in the coastal sand dunes of two Protected Areas (PA) along the Tuscan littoral of Italy (Fig. 1): Migliarino-San Rossore-Massaciuccoli Regional Park (MSRM) and Maremma Regional Park (MP). The coastal dune ecosystems of both parks are part of the Natura 2000 network. Plant species data were collected using a systematic sampling design. In each protected area, the entire coastal system (20 km and 10 km in length for MSRM and MP parks, respectively) was divided into sections of 1 km. Within each section (13 for MRSR and 7 for MP) a transect was randomly located orthogonal to the seashore. The lengths of the transects varied depending on dune morphology and width. Along each transect, species presences were recorded in contiguous 1 m × 1 m plots. Sampling occurred between May 2010 and August 2011; for further details,

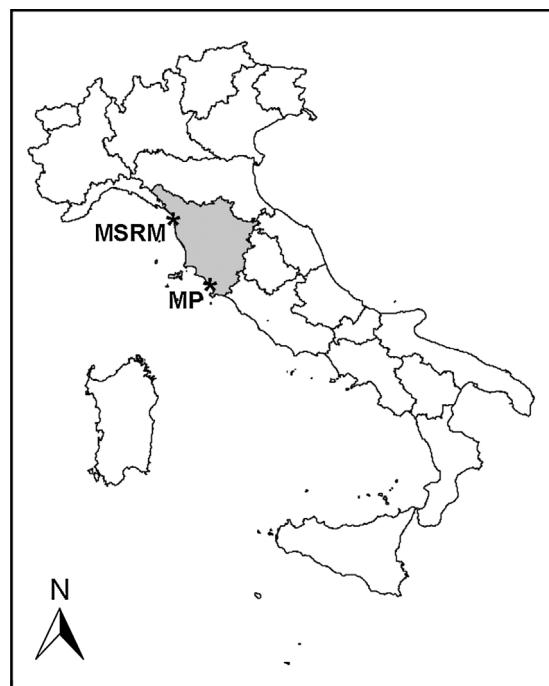


Fig. 1. The locations of the Migliarino-San Rossore-Massaciuccoli Regional Park (MSRM) and the Maremma Regional Park (MP) in the northern and southern parts of Tuscany, Italy, respectively.

Table 1

The total number of sampled plots and diversity values (alpha and gamma) for the Nature 2000 areas compared in this study (for both the worked examples). The common sampling effort is the area of the least sampled data set within a comparison.

Nature reserve/SCI	Number of plots	Total species richness (gamma)	Mean plot species richness (alpha)	Richness at the common sampling effort – SER	Richness at the common sampling effort – RC
Migliarino San Rossore Massaciuccoli Regional Park (MSRM)	675	53	4.15	34.62	44.94
Maremma Park (MP)	305	39	3.52	39.00	39.00
Montagnola Senese (MNS)	137	570	32.85	187.76	195.54
Crete dell'Orcia e del Formone (FOR)	86	472	33.37	167.44	201.35
Castelvecchio (CAS)	11	191	42.27	191	191

see [Ciccarelli \(2014\)](#). For each park, classic rarefaction curves (RCs) and Spatially Explicit Rarefaction curves (SERs) were calculated. For RCs we used the “specaccum” function within the “vegan” R package ([Oksanen et al., 2015](#)). For SERs we used the R routines “pointpattern” and “SCR” ([Bacaro et al., 2012a](#)). From a practical point of view, SERs are constructed by accumulating species of nearest plots for the given n number of plots sampled. This is done by firstly ordering plots according to their minimum distance and then performing an accumulation curve for each ordered sequence. The rarefaction curve (SER) was then calculated as the mean of the n accumulation curves.

As expected, the larger area sampled in the MSLR compared to the MP area resulted in a higher observed species richness (53 vs. 39 species, respectively; [Table 1](#)). [Fig. 2](#) compares the RCs and SERs for the two parks. As expected, the SERs increased less steeply than the RCs resulting in lower estimates of species richness at a given extent. Notably, at any given extent, the relative ranking of the two parks was reversed for the two methods and, overall the RC method always estimated higher species richness than the SER method ([Table 1](#)). Typically in rarefaction analyses, species richness estimates are standardized at the sample size of the smaller data sets, which was 305 plots for these data. At that extent, the RC method estimated a species richness of 44.9 for MSLR compared to the total of 39 species observed for MP. In contrast, the SER method estimated only 34.6 species for the MSLR. Thus by accounting for spatial structure, we can conclude that the MP is more diversified than the MSLR. This example shows how the inclusion of spatial autocorrelation into rarefaction analyses can alter conclusions and

eventually even change the way we might prioritize or manage nature reserves.

2.2. Example 2: Sites of Community Importance

The second example was a survey of plant species occurrence within the Sites of Community Importance (SCIs) of the Province of Siena, Italy. The complete survey is described in [Chiarucci et al. \(2012\)](#) and a subset of these data was previously analyzed in [Chiarucci et al. \(2008b\)](#). The dataset consists of 604 vegetation plots collected across the entire network of 17 SCIs ([Fig. 3](#)). A grid of $1\text{ km} \times 1\text{ km}$ cells were laid across the network and a random point selected within each; plant presences were recorded for a $10\text{ m} \times 10\text{ m}$ plot centered at each point. For this paper, we analyzed data from three SCIs ([Table 1](#)): Montagnola Senese (MNS), Crete dell'Orcia e del Formone (FOR), and Castelvecchio (CAS). The three SCIs differ for main land-cover types: thermophilous oak forests, mesophilous oak forests and *Castanea sativa* dominated forests (MNS), agricultural areas, dry grasslands, pastures, badland vegetation, shrublands and riverbed vegetation (FOR), and thermophilous deciduous forest and evergreen forests (CAS).

SERs and RCs were calculated as in the first example. Similar to the other example, the rank orderings of the curves produced by the two methods were reversed ([Fig. 4](#)). For the estimate of species richness at the common sampling effort (11 plots), using RCs the species richness ranking was FOR (201.3 species), MNS (195.5 species) and CAS (191 species); SERs produced exactly the opposite ordering, CAS (191 species), MNS (187.8 species) and FOR (167.4 species).

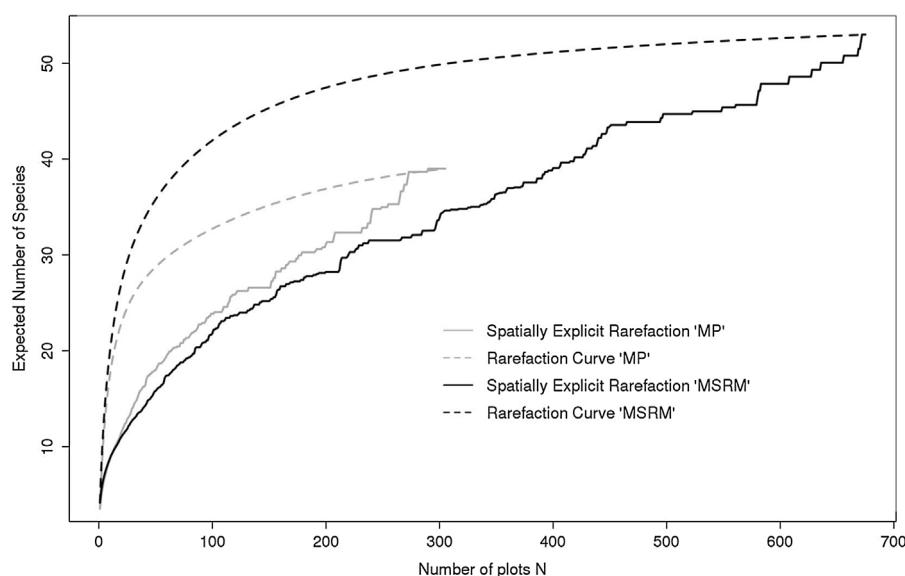


Fig. 2. Classic and Spatially Explicit Rarefaction curves for the two coastal dune parks. For the SERs, the Maremma Park (MP) shows on average more species than those collected in an equal-sampled area in the Migliarino San Rossore Massaciuccoli Park (MSRM), the reverse of the pattern of the RCs.

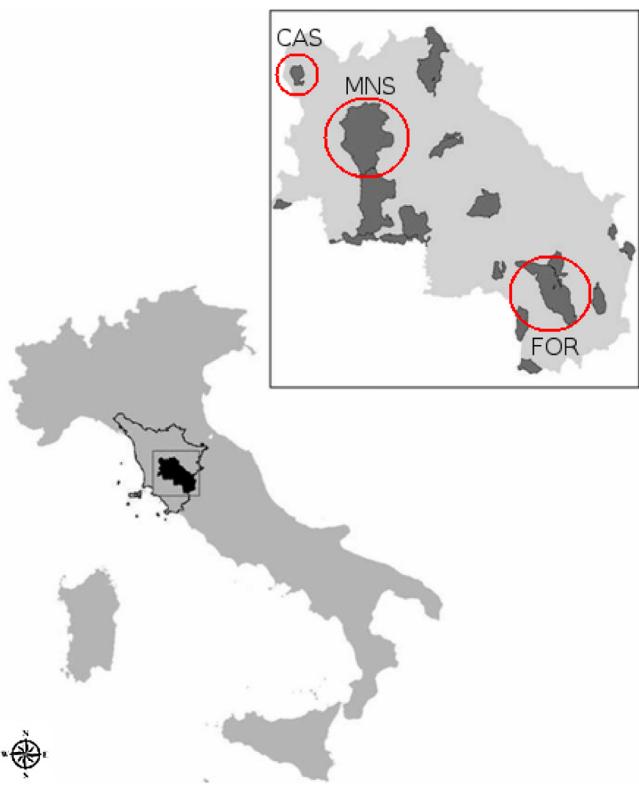


Fig. 3. The locations of the Natura 2000 Network in Siena Province and the three SCIs included in example 2 (MNS, FOR and CAS).

Again, rarefaction methods were shown to be susceptible to spatial autocorrelation.

3. Discussion

Our analyses demonstrate that using a spatially-explicit method for constructing rarefaction curves can substantially alter estimates of relative species richness. It is just as important to consider spatial autocorrelation as it is to note data extent and grain for such comparisons. The analysis of how the spatial configuration of sampling units influences species richness estimates has become an important issue (Kühn, 2007) because species richness is one of the simplest and most popular diversity measures, with intuitive mathematical and statistical properties (Chao and Jost, 2012; Chiarucci et al., 2011). Our results do not indicate that all previous analyses that used or compared RCs are flawed. However, as stated by Kühn (2007), “if spatial autocorrelation is ignored we simply do not know if we can trust the results at all.” Therefore, the presence of residual spatial autocorrelation should always be tested for in spatial ecology and appropriate methods should be used if there is evidence of a significant spatial autocorrelation (Cressie, 1993; Fortin and Dale, 2009; Bacaro et al., 2011; Fortin et al., 2012). Spatially-explicit methods should routinely be used in rarefaction analyses and be included in the development of new methods. Recently, both functional (Ricotta et al., 2012) and phylogenetic rarefactions (Chao et al., 2015) have been proposed, but neither of those two new methods considered the spatial structure of the data. If the effects of spatial autocorrelation were included, we predict similar results as seen here.

Just accounting for spatial autocorrelation of samples may not address all of the effects of spatial patterning, which are needed to compare different datasets. The shape of a sample-based rarefaction curve is controlled by several factors, including the extent, grain and number of sampling units (Wiens, 1989; Palmer and

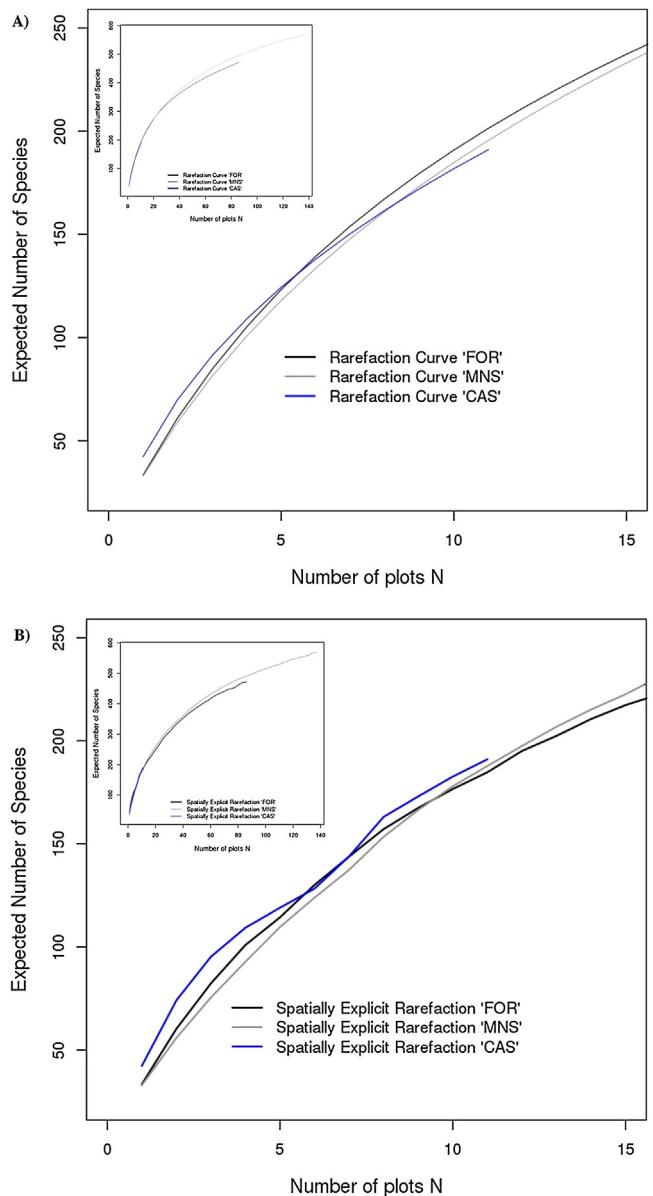


Fig. 4. Rarefaction curves for the three SCIs (A). SER curves for the three SCIs (B). The rank ordering of the latter curves is the reverse of the former curves.

White, 1994; Nekola and White, 1999; Dungan et al., 2002). The other key factor is summarized by the first law of geography (“Everything is related to everything else, but near things are more related than distant things”, Tobler, 1970). This law is apparent as distance-decay patterns at both global and local scales that result in a decrease of compositional similarity with increasing distance (Palmer, 2005; Nekola and White, 1999; Nekola and Brown, 2007; Soininen et al., 2007; Bacaro et al., 2012b). From this pattern, we expect sample-based rarefaction curves to increase faster when sampling units are farther apart (Condit et al., 1996; Palmer et al., 2002; Chiarucci et al., 2008a; Hui, 2008) because greater habitat heterogeneity is likely to lead to greater total species richness (Diamond, 1988; Palmer et al., 2002). Because of this effect, differences in species richness among data sets could be at least partly due to difference in the extent of the sampling units. (Palmer, 2007; McGlinn and Palmer, 2011). Similarly, we predict that deviations between RCs and SERs to increase as a direct function of the spatial autocorrelation among sampling units. Methods that account for such effects still need to be developed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.04.026>. These data includes Google maps of the most important areas described in this article.

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