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Original Articles

Rarefaction of beta diversity

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ABSTRACT

Beta diversity has long been used to summarize the amount of variation in species composition among a set of *N* sampling units. However, while classical beta diversity provides an estimate of multiple-site dissimilarity among all sampling units, it is not informative on the changes of multiple-site dissimilarity as a function of sampling effort. For gamma diversity, this pattern is usually represented as a species accumulation curve, which is the graph of the number of observed species when the number of plots varies from 1 to *N*. Here, we will show that species accumulation curves may also be used to summarize directional and non-directional beta diversity as a function of sampling effort. The behavior of the proposed measures of beta diversity is illustrated with one worked example on plant species in Mediterranean coastal vegetation. We believe this approach to the measurement of beta diversity provides a relevant contribution to summarize multiple-site dissimilarity as the result of a species turnover process, rather than as a static indicator. For directional species accumulation curves, the method, for which we provide a custom R function, further allows summarizing the spatial autocorrelation in species composition among plots along an a-priori defined spatial, temporal or environmental gradient.

1. Introduction

Whittaker (1960, 1972) introduced the concept of beta diversity (the amount of variation in species composition among a set of sampling units) for linking mean local-scale diversity (or alpha diversity) to the diversity of the broader regional species pool (gamma diversity). Since then beta diversity has become a primary tool for connecting the spatial structure of species assemblages to ecological processes and there is a huge literature on its measurement and summarization (for a review, see e.g. Tuomisto, 2010a,b; Anderson et al., 2011). According to Whittaker's proposal, given a community composition matrix of *S* species in *N* plots (or sampling units), beta-diversity can be calculated as the ratio of the diversity of the pooled set of plots and mean species diversity within each plot, such that $\beta = \gamma/\alpha$. This metric of beta diversity summarizes multiple-site dissimilarity within the community composition matrix. However, it does not provide any information on the changes of multiple-site dissimilarity when the number of plots varies from 1 to *N*. For gamma diversity, this variation is traditionally represented as a species accumulation curve, a graph of the number of observed species as a function of sampling effort or the area sampled (Gotelli and Colwell, 2001). In this view, the species accumulation curve represents gamma diversity as the outcome of the sampling process rather than as a fixed summary statistic. A distinction is usually made between directional and non-directional accumulation curves: directional curves summarize how species accumulate along an a-priori defined spatial, temporal or environmental gradient. By contrast, non-directional curves measure turnover in community structure without reference to any specific gradient.

In this paper, we show that species accumulation curves may also be used for summarizing directional and non-directional beta diversity.

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While beta diversity measures have been developed for a long time, there is a knowledge gap on how multiple-site dissimilarity changes in relation to sampling effort. The present manuscript fills this gap and shows how species accumulation curves can be used to summarize beta diversity as a function of sampling effort. This can be very useful to researchers attempting to identify the necessary sampling effort to correctly characterize beta-diversity. We also show that comparing the directional beta diversity of a given set of plots with its non-directional counterpart provides a measure of the spatial autocorrelation of species composition among plots induced by the non-random species sorting along the ecological gradient.

The paper is organized as follows: first, we present an overview on directional and non-directional species accumulation curves and their associated beta diversity measures. Next, to show the behavior of the proposed measures, a worked example is used with data on plant species cover in 68 plots of Mediterranean coastal vegetation.

2. Methods

2.1. Non-directional species accumulation curves and beta diversity

Sample-based accumulation curves are constructed for a set of N equal-sized plots by plotting the number of detected species S when the number of sampled plots increases from 1 to N (Scheiner, 2003; Scheiner et al., 2011). For non-directional curves, it is assumed that the position of the plots in physical or environmental space is irrelevant. Therefore, accumulation curves are generally constructed via permutation procedures by randomly resampling the N plots and then plotting the average number of species found in 1, 2, …, N plots (Gotelli and Colwell, 2001; Colwell et al., 2004). For standard resampling without spatial constraints, a mathematical expression for sample-based accumulation curves was first derived by Shinozaki (1963) and then independently re-discovered by several authors in the 1970s and then again in the 2000 (for a review, see Chiarucci et al., 2008). For species incidence (presence and absence) data, the average number of species detected by sampling all possible combinations of M equal-sized plots randomly and without replacement from a larger set of N plots, is given by:

$$S_M = \sum_{i=1}^{S}\left[1 - \frac{\binom{N-N_i}{M}}{\binom{N}{M}}\right] = S - \sum_{i=1}^{S}\left[\frac{\binom{N-N_i}{M}}{\binom{N}{M}}\right] \tag{1}$$

where S_M is an estimator of the number of species in the M plots, S the total number of species in the entire set of N plots ($N \geq M$), and N_i the number of plots that contain species i. The binomial ratio $\rho_{iM} = \binom{N-N_i}{M}/\binom{N}{M}$ is the probability that species i is not present in a randomly selected sample of M plots. Therefore, $\rho_{iM} = 0$ for $M > N - N_i$.

Species accumulation curves have been used for comparing species richness in assemblages of various sizes after rarefaction to a common level of sampling effort or sample completeness (Gotelli and Colwell, 2001; Colwell et al., 2004; Chao and Jost, 2012), and for extrapolating species richness to a larger area sampled (Colwell et al., 2012; Chao et al., 2014, 2015). Eq. (1) is also used for constructing individual-based accumulation curves relating the estimated number of species to the number of sampled individuals. In this case, M and N represent the sampled number of individuals and the overall population size, respectively (Hurlbert, 1971; Simberloff, 1972).

The estimated number of species S_M represents the gamma diversity in the M plots: $\gamma_M = S_M$. By contrast, alpha diversity does not change with M being always equal to S_1. This is easily shown considering that in Eq. (1) each plot appears an equal number of times for the calculation of S_M, irrespective of the value of M, such that $\alpha_M = S_1$ (see Ricotta et al., 2012, Appendix S3). From S_M and S_1 we can calculate an index of beta diversity for all values of M as (Chao et al., 2014):

$$\beta_M = \frac{S_M}{S_1} = \frac{\gamma_M}{\alpha_M} \tag{2}$$

According to Jost (2007), β_M can be interpreted as an 'effective number' of communities or plots. That is, the theoretical number of fully-distinct plots (no shared species) with mean species richness equal to α_M needed to produce the given value of beta diversity (see also Wilson and Shmida, 1984).

Like the original species accumulation curve, the curve of beta diversity built from the β_M values is a concave and increasing function of M (proof in Appendix 1). Therefore, the graph of β_M vs. M shows how the effective number of plots accumulates with sampling effort. Note however that β_M summarizes multiple-site dissimilarity among plots in the range $[1, M]$. This range is intuitively related to the very meaning of β_M as the effective number of maximally distinct plots. For a community composition matrix of S species × N plots, if all plots are compositionally identical, then $\beta_M = 1$ irrespective of the value of M. In that case, since $\alpha_M = \gamma_M$, one single 'effective' plot is enough to produce the observed value of β_M. By contrast, if the plots do not have any species in common, $\beta_M = M$, meaning that M maximally distinct plots with mean species richness α_M are needed to obtain the observed value of β_M. Therefore, since the range of β_M depends on M, the effective numbers of plots cannot be used for comparing beta diversity for different values of M. To remove this dependence, beta must first be rescaled onto the unit interval (Chao et al., 2012; Ricotta and Pavoine, 2015). The simplest way to rescale a given quantity X between zero and one is to use the linear transformation $(X - X_{\min})/(X_{\max} - X_{\min})$. This transformation gives a normalized measure of non-directional beta diversity (Harrison et al., 1992; Jost, 2007):

$$\beta_\eta = \frac{\beta_M - 1}{M - 1} \tag{3}$$

which can be interpreted as the average proportion of non-overlapping species in the M plots. When $M = 2$, it reduces to the classic Sørensen dissimilarity coefficient. The normalized measure β_η summarizes beta diversity in a fixed range of values ($0 \leq \beta_\eta \leq 1$) that is independent of M. That is, the minimum and maximum values that β_η can take are fixed constants that do not depend on the number of accumulated plots M. This lack of systematic constraints between β_η and M ensures that β_η can be used for comparing multiple-site dissimilarity at different values of M. For additional normalized dissimilarity measures of beta diversity, see Chao and Chiu (2016).

Normalization removes the (undesired) dependence of the range of β_η on M. However, it does not eliminate the dependence of beta on sampling effort, which is the main assumption of this paper. Therefore, for a given set of plots N, the variation in species composition β_η decreases as a function of the number of plots sampled (proof in Appendix 1). Due to this decreasing pattern, calling the graph of β_η vs. M an 'accumulation curve' is not the most appropriate choice. Therefore, like in Wilson and Shmida (1984), we use for these curves the more neutral term of 'community turnover' curves.

2.2. Directional species accumulation curves and beta diversity

The examination of turnover in species composition along a gradient requires explicit consideration of the order of plots in physical or environmental space (Vellend, 2001). To this end, given N plots ordered along a predefined gradient of interest, starting from one end of the gradient we can construct a directional species accumulation curve by sequentially adding the plots one after the other along that gradient and plotting the cumulative number of species found in 1, 2, …, N plots.

Because each directional accumulation curve is case-specific and depends on the distribution of plots along a user-defined gradient, it cannot be derived theoretically and a mathematical expression for this curve does not exist. Therefore, the values of alpha and gamma diversity along the gradient need to be calculated separately for each curve based on the specific order of plots. Beta diversity for all values of *M* can then be calculated as above:

$$\overrightarrow{\beta}_M = \frac{\overrightarrow{\gamma}_M}{\overrightarrow{\alpha}_M} \tag{4}$$

and

$$\overrightarrow{\beta}_\eta = \frac{\overrightarrow{\beta}_M - 1}{M - 1} \tag{5}$$

where the arrows on alpha, beta and gamma denote the directional nature of the turnover process. Unlike a non-directional accumulation curve, in the directional case the value of $\overrightarrow{\alpha}_M$ (i.e. the mean number of species in the *M* plots) is not constant. Rather, like $\overrightarrow{\gamma}_M$, it depends on the order of the plots along the gradient. Accordingly, the order in which individual plots are added affects the shape of the resulting accumulation curve, such that directional beta $\overrightarrow{\beta}_\eta$ is not necessarily a monotonically decreasing function of *M*.

To complete the picture, ‘constrained’ species accumulation curves which account for the arrangement of plots in physical or environmental space were introduced by Scheiner (2003, his Type IIIA curves) and first explored by Chiarucci et al. (2009). Order-free accumulation curves tend to overestimate the rate of increase in species richness because they ignore the autocorrelation of species composition among the sampling units. In contrast, constrained accumulation curves describe the increase in species richness as a function of both the sampling effort and the autocorrelation in species composition among plots.

In building a constrained accumulation curve, adjacent sampling units are combined step by step using the spatial or environmental proximity among plots as a constraining factor. Given a set of *N* plots, for each plot a directional species accumulation curve is constructed by sequentially adding the first, second, …, *k*-th nearest neighbor. This procedure is repeated for all *N* plots, generating *N* directional accumulation curves from which a mean constrained curve is calculated (Chiarucci et al., 2009; Bacaro et al., 2016). The resulting curve is thus an intermediate solution between a non-directional accumulation curve in which all possible combinations of 1, 2, …, *M* plots are used for building the curve and a pure directional curve in which the *N* plots are ordered along a single spatial or environmental gradient.

Denoting by $\overrightarrow{\gamma}_{jM}$ and $\overrightarrow{\alpha}_{jM}$ the gamma and alpha diversity of the *j*-th directional community turnover curve ($j = 1, 2, \ldots, N$), the constrained beta diversity $\bar{\beta}_M$ for a sequence of *M* plots can be calculated in analogy to Eq. (2) as the ratio of mean gamma to mean alpha:

$$\bar{\beta}_M = \frac{\bar{\gamma}_M}{\bar{\alpha}_M} = \frac{\sum_{j=1}^{N} \overrightarrow{\gamma}_{jM}/N}{\sum_{j=1}^{N} \overrightarrow{\alpha}_{jM}/N} \tag{6}$$

such that

$$\bar{\beta}_\eta = \frac{\bar{\beta}_M - 1}{M - 1} \tag{7}$$

The reasons for calculating beta as $\bar{\beta}_M = \bar{\gamma}_M/\bar{\alpha}_M$ instead of $\bar{\beta}_M = 1/N\sum_{j=1}^{N} \overrightarrow{\gamma}_{jM}/\overrightarrow{\alpha}_{jM}$ were discussed by Chao et al. (2014) in the context of the rarefaction of Hill numbers, and the reader is addressed to this paper for additional details.

The plot of $\bar{\beta}_\eta$ vs. *M* describes how ‘constrained’ beta diversity varies with increasing sampling effort. For each value of *M*, the difference between $\bar{\beta}_\eta$ (or $\overrightarrow{\beta}_\eta$) and the non-directional beta reflects the amount of autocorrelation in community composition among plots. This is because directional beta summarizes turnover in community structure along an a-priori ecological gradient and is thus directly influenced by the similarity in community composition among plots. By contrast, non-directional turnover is calculated with permutation procedures which ignore any autocorrelation in community structure. Therefore, a measure of autocorrelation for directional beta diversity can be calculated as the normalized difference between directional and non-directional beta:

$$\bar{\beta}_\phi = \frac{\beta_\eta - \bar{\beta}_\eta}{\beta_\eta + \bar{\beta}_\eta} \tag{8}$$

with $-1 \le \bar{\beta}_\phi \le 1$. Since the compositional dissimilarity among plots will often increase more slowly when sampling units are close to each other, usually $\beta_\eta > \bar{\beta}_\eta$ and $\bar{\beta}_\phi > 0$. Compositional autocorrelation occurs due to two processes: localized dispersal mechanisms and autocorrelation in environmental conditions. We therefore expect greater habitat homogeneity to lead to lower compositional heterogeneity among adjacent plots. If adjacent plots are compositionally very similar to each other, the difference $\beta_\eta - \bar{\beta}_\eta$ will be high, such that the normalized difference $\bar{\beta}_\phi$ will be high too. By contrast, if autocorrelation in community composition among adjacent plots is low, $\bar{\beta}_\eta$ will approach its random expectation β_η and $\bar{\beta}_\phi$ will be close to zero.

3. Worked example

We used vegetation plots sampled on recent (Holocene) coastal dunes occupying a narrow strip (< 150 m) of about 16 km length along the seashore on the Tyrrhenian coast of central Italy (Fig. 1). The vegetation of the dune profile follows a compressed zonation of habitats along a clearly defined sea-inland environmental gradient that drives considerable turnover in species composition and functioning over short distances: from the pioneer communities of the upper beach to the woody communities (Mediterranean macchia and evergreen forests) of the inland fixed dunes (Acosta et al., 2003).

Vegetation sampling was undertaken in spring (April-May) of 2006. Randomly generated GPS coordinates were used to define the sampling location of 2 × 2 m vegetation plots in the study area. In each plot, the cover of all vascular plant species was recorded using a 10% interval rank scale. A total of 68 plots were sampled and 61 species recorded (Appendix 2). For the 68 plots of coastal dune vegetation used in this study we produced:

i) A non-directional community turnover curve of β_η vs. *M* constructed according to Eq. (1–3).
ii) A spatially-constrained turnover curve of $\bar{\beta}_\eta$ vs. *M* (hereafter distance-based turnover curve), in which all plots are ordered according to their distance from the seashore. Carboni et al. (2011) showed that for coastal vegetation, distance from the seashore is related to a directional stress gradient of wind and soil parameters, ranging from the exposed conditions of the upper beach to the more sheltered conditions of the back dune. Therefore, plant communities located closer to the sea are generally subject to higher environmental stress and disturbance.
iii) A functionally-constrained turnover curve (hereafter trait-based turnover curve), in which all plots are ordered along an ecological gradient according to the functional characters of the most common species. For building this functional turnover curve, we defined an a-priori directional gradient in functional trait space. To do so, we used a set of plant functional traits measured for a subset of 42 dominant species. This subset of species was chosen by selecting the most common and abundant species within each habitat along the sea-inland gradient, that collectively account for ~80% of the standing live biomass (see Carboni et al., 2013 for details). This threshold has been shown to ensure a satisfactory description of overall community properties (Pakeman and Quested, 2007).

Three quantitative life-history traits were chosen based on their relevance to the functional ecology of plants in coastal dune environments (Carboni et al., 2016): plant height (cm), leaf dry mass content (LDMC; mg·g^{-1}) and seed mass (mg). These traits provide a good representation of the species global spectrum of form and function (Díaz

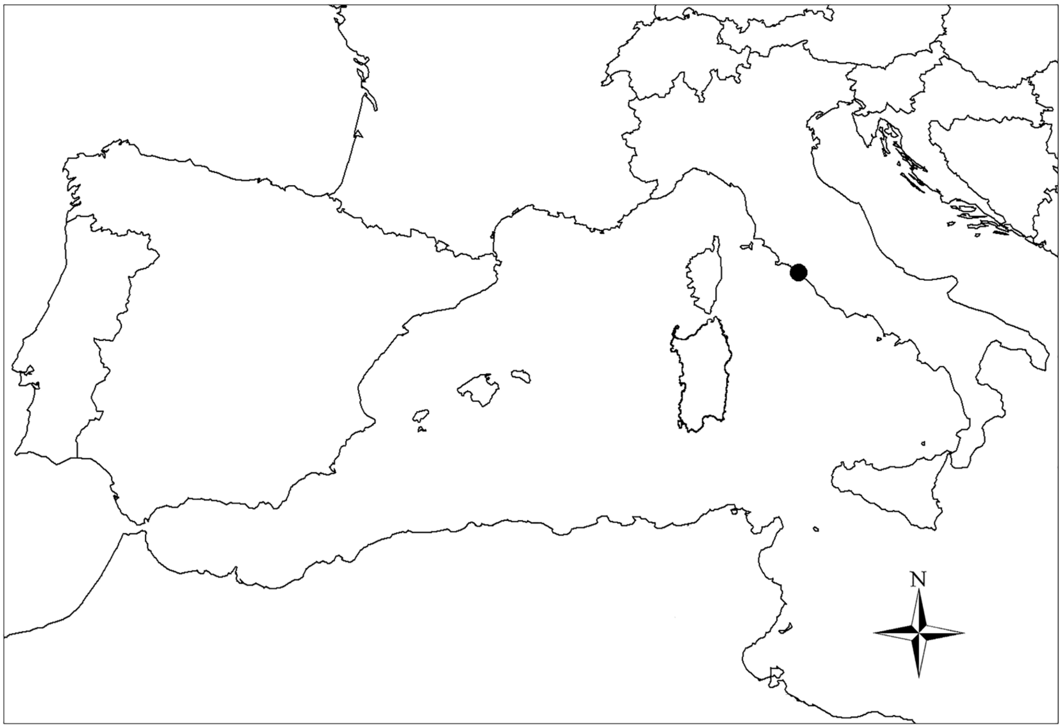

Fig. 1. Location of the study area.

et al., 2016) and are also correlated with the directional stress gradient of wind and soil parameters which shape the zonation of the coastal dune vegetation (Carboni et al., 2011, 2013). Because of environmental sorting of species according to habitat preferences along the sea-inland stress gradient, we expect that specific species combinations with particular suites of traits (e.g. short annual species with succulent leaves on the upper beach) should gradually be replaced along the gradient by other dominant species with different traits (e.g. tall perennial species on the main dune ridge). Carboni et al. (2013) showed that there was a significant relationship between sea-inland stress and community functional composition.

First, we calculated the Bray-Curtis pairwise dissimilarity among species based on the selected functional traits. Before calculations, traits were square root-transformed when necessary and scaled to unit length. We next calculated the pairwise functional dissimilarity among plots according to Pavoine and Ricotta (2014, Eq. (3)). The resulting plot-to-plot functional distance matrix was then used for constructing the constrained turnover curve of $\bar{\beta}_\eta$ vs. M. All curves were constructed using a custom R function available as an electronic appendix to this paper (Appendix 3).

4. Results

The directional and non-directional species accumulation curves of γ_M and $\bar{\gamma}_M$ vs. M, together with the corresponding community turnover curves of β_η and $\bar{\beta}_\eta$ vs. M. are shown in Figs. 2 and 3, respectively. Fig. 4 shows the amount of autocorrelation of directional beta diversity $\bar{\beta}_\phi$ as a function of sampling effort. As expected, the shape of the curves differs depending on which methods are used to construct the curves, thus providing a useful tool to characterize biodiversity patterns and to explore the relevance of selected functional traits or environmental variables in shaping community structure. Due to the very high autocorrelation of plots in functional space, the trait-based accumulation curve increases less steeply than the corresponding non-directional curve. That is, functionally similar plots are on average compositionally more similar to each other than expected by chance alone. As shown in Fig. 3, the lower rate of species accumulation of the trait-based curve

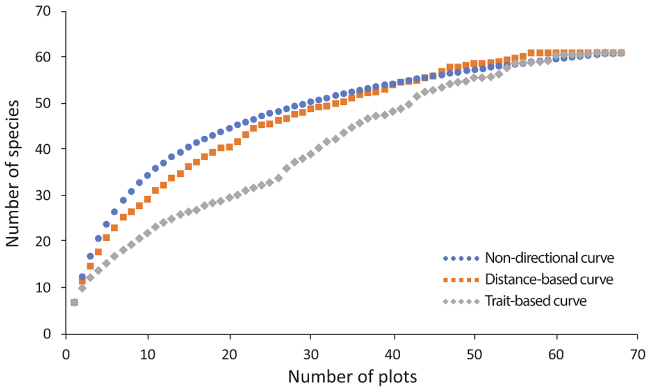

Fig. 2. Directional and non-directional species accumulation curves $\bar{\gamma}_M$ and γ_M vs. M. for the coastal dune communities of central Italy.

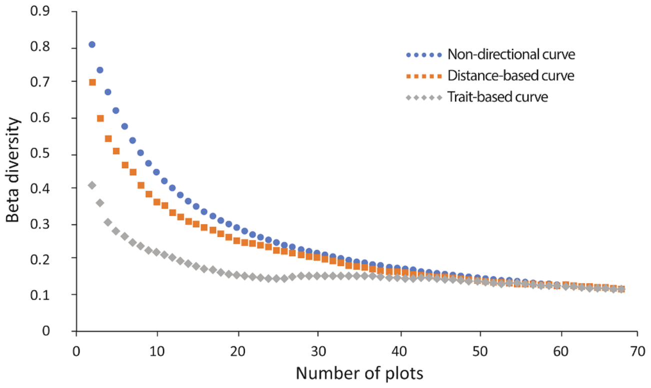

Fig. 3. Directional and non-directional community turnover curves $\bar{\beta}_\eta$ and β_η vs. M for the coastal dune communities of central Italy.

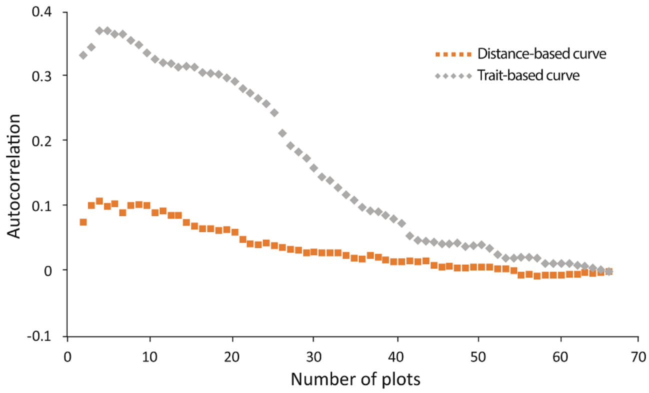

Fig. 4. Plot of the amount of autocorrelation of directional beta diversity $\bar{\beta}_{\phi}$ as a function of sampling effort M for the coastal dune communities of central Italy.

compared to the random non-directional curve results in a lower rate of turnover in community structure and thus in lower beta diversity.

On the other hand, the plot of the distance-based accumulation curve is very similar to that of the non-directional curve. That is, at least for our case study, distance from the seashore is a less effective indicator of the species sorting than trait-based differences. This is probably due to the effects of natural and anthropogenic disturbance, which tend to modify the natural zonation of vegetation along the dune profile giving rise to a complex mosaic of fragmented and intermingled communities. As shown in Fig. 4, for the distance-based curve, the autocorrelation of directional beta diversity is much lower than that of the trait-based curve and becomes negligible for $M > 45$, meaning that after this threshold the compositional turnover of the constrained distance-based curve does not substantially differ from random expectation. This example clearly shows how different degrees of autocorrelation in geographical or functional space can affect the estimates of gamma and beta diversity of community turnover curves.

5. Discussion

In this paper, we showed that community turnover curves provide a tool for summarizing various types of directional and non-directional beta diversity as a function of sampling effort. Azovsky (2011) separated two conceptually different curves: species-area and species-sampling effort relationships. The present manuscript deals mostly with species-sampling effort relationship, although directional analysis of real gradients with ordered plots goes a step further than simple species-sampling effort relationships *sensu* Azovsky (2011). The same approach can be extended for constructing incidence- or abundance-based community turnover curves either mathematically or with resampling methods for any taxonomic, functional or phylogenetic diversity metric (Walker et al., 2008; Ricotta et al., 2012; Chao et al., 2014, 2015). The resulting measures of beta diversity can then be compared among habitats sampled with different effort after rarefaction to the sample size of the smallest datasets. For examples, see e.g. Bacaro et al. (2016). In addition, if directional or non-directional beta diversity is calculated for a nested series of plots of different size, the resulting turnover curves can be used to analyze how beta diversity scales with local sample area, thus extending our results to species-area relationships (see Palmer and White, 1994; Mokany et al., 2013).

Finally, turnover curves can also be used for calculating the amount of autocorrelation in community composition for directional beta diversity compared to its non-directional counterpart. Species are almost never randomly distributed, either due to heterogeneity of environmental factors or to non-random dispersal mechanisms. Therefore, autocorrelation is a crucial aspect of directional turnover curves and appropriate methods should be used in diversity studies if there is evidence of significant clustering of species in physical or environmental space (Legendre, 1993; Fortin and Dale, 2009; Bacaro et al., 2016).

Previous methods to assess multivariate spatial community structure include distance-decay plots (Nekola and White, 1999; Qian and Ricklefs, 2007), multivariate variograms (Wagner, 2003) and Mantel correlograms (Borcard and Legendre, 2012). Our proposal adds a new tool to the ecologist toolbox as it allows to summarize autocorrelation in species composition along spatial, temporal or environmental gradients from community turnover curves.

Directional species accumulation curves have been typically used to summarize the decrease in species accumulation due to spatial autocorrelation along an environmental gradient compared to non-directional curves (e.g. Chiarucci et al., 2009; Bacaro et al., 2016). The same 'directional' approach can also be used to maximize the rate of species accumulation with a given effort so as to improve the efficiency of species inventories (Palmer et al., 2002; Rocchini et al., 2005). Because the sampling order of plots determines the slope of the accumulation curve, an optimal strategy to maximize species accumulation consists of using external data to choose the order of plots so that the resulting accumulation curve is the steepest possible (Rocchini et al., 2005). That curve is a special kind of directional turnover curve, which accumulates species at a faster rate compared to the corresponding random non-directional curves. As a consequence of this increased accumulation rate, the normalized difference between the non-directional and directional beta diversity measures takes negative values showing a general tendency towards a negative correlation in the compositional similarity of subsequent plots. This illustrates how our proposed metric of autocorrelation based on turnover curves can also be used as a synthetic criterion for defining optimization strategies in vegetation sampling, for example to show at what distance species composition is no longer autocorrelated. Thus, one can use this critical distance between sampling units to avoid spending time and resources on redundant information.

The idea of calculating an index of beta diversity from species accumulation curves has already been proposed in the past. Ricotta et al. (2002) suggested calculating beta diversity as the slope of the linearized species accumulation curve in semilogarithmic space according to Gleason (1922); Crist and Veech (2006) proposed an additive model of diversity decomposition for which beta diversity is obtained as the difference in species richness between the last and first points of the species accumulation curve: $\beta = \gamma - \alpha = S_N - S_1$. The main difference between these previous works and ours is that we do not treat beta diversity as a fixed quantity: the graph of beta vs. M shows how community turnover varies when M increases from 1 to N. Therefore, using accumulation curves, multiple-site dissimilarity or beta diversity is represented as the result of a species turnover process, rather than as a static indicator. For $M = N$, β_M reduces to the traditional Whittaker's (static) beta diversity for a set of N sampling units $\beta = \gamma_N/\alpha_N$.

We also showed that using the classical multiplicative formula $\beta_M = \gamma_M/\alpha_M$, a measure of beta is obtained which is easily interpretable in terms of 'effective number of plots'. However, due to the constraint $1 \leq \beta_M \leq M$ we cannot directly use this measure for comparing beta diversity for different numbers of plots. To remove the dependence on M, we can use the normalized measure $\beta_\eta = (\beta_M - 1)/(M - 1)$. This scaled version of beta diversity can be used for comparing community turnover for different values of M.

In principle, because of the fundamental constraint $M \times \alpha_M \geq \gamma_M \geq \alpha_M$ (Chao et al., 2012), a similar scaling can also be used for defining a normalized measure of gamma diversity $\gamma_\eta = (\gamma_M - \alpha_M)/(M \times \alpha_M - \alpha_M)$. However, since $\gamma_M = \alpha_M \times \beta_M$, a little algebra shows that $\gamma_\eta = \beta_\eta = (\beta_M - 1)/(M - 1)$, meaning that there is no fundamental difference between normalized beta diversity and normalized gamma diversity. For a given number of plots, the rescaled version of gamma diversity is *per se* a measure of community turnover, such that normalized beta diversity can be also expressed in terms of the relationship between gamma diversity and its extreme values: if

$\gamma_M = \alpha_M$ then $\beta_\eta = 0$; At the other extreme, if $\gamma_M = M \times \alpha_M$ then $\beta_\eta = 1$. Therefore, the scaled versions of beta diversity and gamma diversity lead to the same normalized measure of species turnover.

To conclude, by its very nature, community ecology usually deals with high-dimensional multivariate data and calls for summarizing methods and indices. However, by condensing the structure of a multidimensional community composition matrix into a single indicator, information is inevitably lost, such that a variety of indices is needed to answer a variety of ecological questions (Pavoine, 2016). Therefore, accurate knowledge of the basic properties of diversity measures becomes a necessary condition for comparing different habitats in ecologically meaningful ways. Given this, relying on metrics standardized for sampling effort can provide better means for identifying the most relevant biotic and abiotic drivers of community composition in different habitats and taking appropriate management decisions.

Author contribution statement

CR formulated the ideas. CR and SP developed the methodology. GB, DR and SP wrote the R code. AA and MC collected the data. All authors analyzed the data. CR, AC and SP led the writing of the manuscript; other authors provided editorial advice.

Compliance with ethical standards

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

Acosta, A.T.R., Stanisci, A., Ercole, S., Blasi, C., 2003. Sandy coastal landscape of the Lazio region (central Italy). Phytocoenologia 33, 715–726.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β-diversity: a roadmap for the practicing ecologist. Ecol. Lett. 14, 19–28.

Azovsky, A.I., 2011. Species-area and species-sampling effort relationships: disentangling the effects. Ecography 34, 18–30.

Bacaro, G., Altobelli, A., Cameletti, M., Ciccarelli, D., Martellos, S., Palmer, M.W., Ricotta, C., Rocchini, D., Scheiner, S.M., Tordoni, E., Chiarucci, A., 2016. Incorporating spatial autocorrelation in rarefaction methods: Implications for ecologists and conservation biologists. Ecol. Indic. 69, 233–238.

Borcard, D., Legendre, P., 2012. Is the Mantel correlogram powerful enough to be useful in ecological analysis? a simulation study. Ecology 93, 1473–1481.

Carboni, M., Acosta, A.T.R., Ricotta, C., 2013. Are differences in functional diversity among plant communities on Mediterranean coastal dunes driven by their phylogenetic history? J. Veg. Sci. 24, 932–941.

Carboni, M., Santoro, R., Acosta, A.T.R., 2011. Dealing with scarce data to understand how environmental gradients and propagule pressure shape fine-scale alien distribution patterns on coastal dunes. J. Veg. Sci. 22, 751–765.

Carboni, M., Zeleny, D., Acosta, A.T.R., 2016. Measuring ecological specialization along a natural stress gradient using a set of complementary niche breadth indices. J. Veg. Sci. 27, 892–903.

Chao, A., Chiu, C.-H., 2016. Bridging the variance and diversity decomposition approaches to beta diversity via similarity and differentiationmeasures. Methods Ecol. Evol. 7, 919–928.

Chao, A., Chiu, C.-H., Hsieh, T.C., 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93, 2037–2051.

Chao, A., Chiu, C.-H., Hsieh, T.C., Davis, T., Nipperess, D.A., Faith, D.P., 2015. Rarefaction and extrapolation of phylogenetic diversity. Methods Ecol. Evol. 6, 380–388.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67.

Chao, A., Jost, L., 2012. Coverage–based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93, 2533–2547.

Chiarucci, A., Bacaro, G., Rocchini, D., Fattorini, L., 2008. Discovering and rediscovering the sample–based rarefaction formula in the ecological literature. Community Ecol. 9, 121–123.

Chiarucci, A., Bacaro, G., Rocchini, D., Ricotta, C., Palmer, M., Scheiner, S., 2009. Spatially constrained rarefaction: incorporating the autocorrelated structure ofbiological communities into sample–based rarefaction. Community Ecol. 10, 209–214.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual–based and sample–based rarefaction, extrapolation and comparison of assemblages. J. Plant. Ecol. 5, 3–21.

Colwell, R.K., Mao, C.X., Chang, J., 2004. Interpolating, extrapolating, and comparing incidence–based species accumulation curves. Ecology 85, 2717–2727.

Crist, T.O., Veech, J.A., 2006. Additive partitioning of rarefaction curves and species–area relationships: unifying α–,β– and γ–diversity with sample size and habitat area. Ecol. Lett. 9, 923–932.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171.

Fortin, M.J., Dale, M.R.T., 2009. Spatial autocorrelation in ecological studies: a legacy of solutions and myths. Geogr. Anal. 41, 392–397.

Gleason, H.A., 1922. On the relation between species and area. Ecology 3, 158–162.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391.

Harrison, S., Ross, S.J., Lawton, J.H., 1992. Beta diversity on geographic gradients in Britain. J. Animal Ecol. 61, 151–158.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52, 577–586.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427–2439.

Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74, 1659–1673.

Mokany, K., Jones, M.M., Harwood, T.D., 2013. Scaling pairwise β-diversity and α-diversity with area. J. Biogeogr. 40, 2299–2309.

Nekola, J.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. J. Biogeogr. 26, 867–878.

Pakeman, R.J., Quested, H.M., 2007. Sampling plant functional traits: what proportion of the species need to be measured? Appl. Veg. Sci. 10, 91–96.

Palmer, M.W., Earls, P., Hoagland, B.W., White, P.S., Wohlgemuth, T., 2002. Quantitative tools for perfecting species lists. Environmetrics 13, 121–137.

Palmer, M.W., White, P.S., 1994. Scale dependence and the species-area relationship. Am. Nat. 144, 717–740.

Pavoine, S., Ricotta, C., 2014. Functional and phylogenetic similarity among communities. Methods Ecol. Evol. 5, 666–675.

Pavoine, S., 2016. A guide through a family of phylogenetic dissimilarity measures among sites. Oikos 125, 1719–1732.

Qian, H., Ricklefs, R.E., 2007. A latitudinal gradient in large–scale beta diversity for vascular plants in North America. Ecol. Lett. 10, 737–744.

Ricotta, C., Pavoine, S., 2015. A multiple–site dissimilarity measure for species presence/absence data and its relationship with nestedness and turnover. Ecol. Indic. 54, 203–206.

Ricotta, C., Pavoine, S., Bacaro, G., Acosta, A.T.R., 2012. Functional rarefaction for species abundance data. Methods Ecol. Evol. 3, 519–525.

Ricotta, C., Carranza, M.L., Avena, G.C., 2002. Computing β–diversity from species-area curves. Basic Appl. Ecol. 3, 15–18.

Rocchini, D., Andreini Butini, S., Chiarucci, A., 2005. Maximizing plant species inventory efficiency by means of remotely sensed spectral distances. Global Ecol. Biogeogr. 14, 431–437.

Scheiner, S.M., 2003. Six types of species–area curves. Global Ecol. Biogeogr. 12, 441–447.

Scheiner, S.M., Chiarucci, A., Fox, G.A., Helmus, M.R., McGlinn, D.J., Willig, M.R., 2011. The underpinnings of the relationship of species richness with space and time. Ecol. Monogr. 81, 195–213.

Shinozaki, K., 1963. Note on the species area curve. Proceedings of the 10th Annual Meeting of Ecological Society of Japan, 5 (in Japanese).

Simberloff, D., 1972. Properties of the rarefaction diversity measurement. Am. Nat. 106, 414–418.

Tuomisto, H., 2010a. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33, 2–22.

Tuomisto, H., 2010b. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography 33, 23–45.

Vellend, M., 2001. Do commonly used indices of β-diversity measure species turnover? J. Veg. Sci. 12, 545–552.

Wagner, H.H., 2003. Spatial covariance in plant communities: integrating ordination, variogram modeling, and variance testing. Ecology 84, 1045–1057.

Walker, S.C., Poos, M.S., Jackson, D.A., 2008. Functional rarefaction: estimating functional diversity from field data. Oikos 117, 286–296.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251.

Wilson, M.W., Shmida, A., 1984. Measuring beta diversity with presence-absence data. J. Ecol. 72, 1055–1064.

Appendix S1. Proofs

1. S_M is an increasing function of *M*.

The probability ρ_{iM} of not finding species *i* by sampling *M* equal-sized plots randomly and without replacement from a larger set of *N* plots $(N \geq M)$, is given by:

$$\rho_{iM} = \frac{\binom{N-N_i}{M}}{\binom{N}{M}}$$

where N_i is the number of plots that contain species *i*.

If $N_i > N - M$, $\rho_{iM} = 0$

Otherwise,

$$\text{if } N_i = 1,\ \rho_{iM} = \frac{N-M}{N}$$
$$\text{if } N_i = 2,\ \rho_{iM} = \frac{(N-2)!}{N!}\frac{(N-M)!}{(N-2-M)!} = \frac{(N-M)}{N}\frac{(N-M-1)}{(N-1)}$$
$$\text{if } N_i > 2,\ \rho_{iM} = \frac{(N-N_i)!}{N!}\frac{(N-M)!}{(N-N_i-M)!} = \frac{(N-M)}{N}\frac{(N-M-1)}{(N-1)}\cdots\frac{(N-M-N_i+1)}{(N-N_i+1)}$$

The estimated number of species in any *M* plots is $S_M = \sum_i (1-\rho_{iM}) = S - \sum_i \rho_{iM}$ (Eq. 1 in the main text), where *S* is the total number of species in the *N* plots. The equations above demonstrate that S_M is an increasing function of *M* as for any *i* and N_i, ρ_{iM} is a decreasing function of *M*.

The α diversity, defined as the average number of species in one plot is $S_1 = \sum_i N_i / N$. Indeed,

$$S_1 = S - \sum_i \frac{(N-N_i)!}{N!}\frac{(N-1)!}{(N-N_i-1)!} = S - \sum_i \frac{(N-N_i)}{N} = S - S + \sum_i \frac{N_i}{N} = \frac{\sum_i N_i}{N}$$

2. S_M and β_M are both concave.

The second derivative of S_M is always negative as shown below.
For all *i*,

$$\rho_{iM} = \prod_{k=0}^{N_i-1} \frac{N-M-k}{N-k}$$

[Note that the above general equation for ρ_{iM} is always valid as, when $N_i > N - M$, it equals zero]

$$\frac{\partial \rho_{iM}}{\partial M} = \sum_{k=0}^{N_i-1} -\frac{1}{N-k}\left(\prod_{u=0,u\neq k}^{N_i-1}\frac{N-M-u}{N-u}\right)$$

$$\frac{\partial^2 \rho_{iM}}{\partial M^2} = \sum_{k=0}^{N_i-1} -\frac{1}{N-k}\left(\sum_{u=0,u\neq k}^{N_i-1} -\frac{1}{N-u}\prod_{v=0,v\neq k,v\neq u}^{N_i-1}\frac{N-M-v}{N-v}\right)$$

$$\frac{d^2 S_M}{dM^2} = -\sum_{i}\sum_{k=0}^{N_i-1}\frac{1}{N-k}\left(\sum_{u=0,u\neq k}^{N_i-1}\frac{1}{N-u}\prod_{v=0,v\neq k,v\neq u}^{N_i-1}\frac{N-M-v}{N-v}\right) < 0$$

The concavity of S_M implies that

$$\frac{S_M - S_{M-1}}{M-(M-1)} \geq \frac{S_{M+1}-S_M}{(M+1)-M}$$

and thus $S_M - S_{M-1} \geq S_{M+1} - S_M$ for all $M > 1, M < N\text{-}1$.

The expressions for S_{M-1}, S_M and S_{M+1} are:

$$S_{M-1} = S - \sum_i \left(\prod_{k=0}^{N_i-1}\frac{N-M+1-k}{N-k}\right)$$

$$S_M = S - \sum_i \left(\prod_{k=0}^{N_i-1}\frac{N-M-k}{N-k}\right)$$

$$S_{M+1} = S - \sum_i \left(\prod_{k=0}^{N_i-1}\frac{N-M-1-k}{N-k}\right)$$

As a consequence,

$$S_{M-1} - S_M = \sum_{i \text{ such that } N_i=1}\frac{1}{N} + \sum_{i \text{ such that } N_i>1}\frac{N_i}{N}\left(\prod_{k=1}^{N_i-1}\frac{N-M-k}{N-k}\right)$$

and

$$S_M - S_{M-1} = \sum_{i \text{ such that } N_i=1}\frac{1}{N} + \sum_{i \text{ such that } N_i>1}\frac{N_i}{N}\left(\prod_{k=1}^{N_i-1}\frac{N-M+1-k}{N-k}\right)$$

For all sums over *i* such that $N_i > 1$, all factors in brackets in the numerators of $S_M - S_{M-1}$ are greater than those of $S_{M+1} - S_M$ by 1 unity. Other numerators and the denominators are equal in $S_M - S_{M-1}$ and in $S_{M+1} - S_M$. This indeed confirms that $S_M - S_{M-1} \geq S_{M+1} - S_M$.

The measure of β diversity given in Eq. 2 of the main text is:

$$\beta_M = \frac{S_M}{S_1}$$

S_1 is a constant that does not depend on *M*. Therefore, β_M increases with *M* giving rise to a concave curve. Also, the interpretation of β_M as an 'effective number of plots' (*sensu* Jost 2007; see main text), is valid only if the increase of β_M from *M* to $M+1$ is not higher than one. That is, $\beta_{M+1} - \beta_M \leq 1$. We highlighted above that $S_1 = \sum_i N_i / N$. The above expression for $S_{M+1} - S_M$ can be summarized as follows:

$$S_{M+1} - S_M = \sum_i \frac{N_i}{N} f\left(N_i, M\right)$$

with $0 \leq f\left(N_i, M\right) \leq 1$ for all N_i and *M* ($f(N_i, M) = 0$ if $N_i > N-M$). This yields that for all *M* ($1 \leq M < N-1$), $S_{M+1} - S_M \leq S_1$, thus demonstrating that $\beta_{M+1} - \beta_M \leq 1$. The case $\beta_{M+1} - \beta_M = 1$ is obtained when $N_i = 1$ for all *i* species (i.e. when all plots contain different species).

3. β_η is a decreasing function of *M*.

The equation for β_η is:

$$\beta_\eta = \frac{\beta_M - 1}{M - 1}$$

The fact that the function S_M is concave implies that the mean of the first *M* differences between two successive values of S_M is lower than the mean of the first $M-1$ differences:

$$\frac{\left(S_{M+1} - S_M\right) + \left(S_M - S_{M-1}\right) + \ldots + \left(S_3 - S_2\right) + \left(S_2 - S_1\right)}{M} \leq$$
$$\frac{\left(S_M - S_{M-1}\right) + \left(S_{M-1} - S_{M-2}\right) + \ldots + \left(S_3 - S_2\right) + \left(S_2 - S_1\right)}{M - 1}$$

This inequality is equivalent to

$$\frac{S_{M+1} - S_1}{M} \leq \frac{S_M - S_1}{M - 1}$$

and thus to

$$\frac{\beta_{M+1} - 1}{M + 1 - 1} \leq \frac{\beta_M - 1}{M - 1}$$

meaning that normalized beta diversity β_η is a decreasing function of sampling effort *M*.

References

Jost, L. (2007) Partitioning diversity into independent alpha and beta components. Ecology, 88, 2427–2439.

Appendix S2. Composition matrix and functional trait values of the dominant species for the coastal dune communities of central Italy

Plot number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
Distance from the sea (m)	5.80	13.08	13.08	13.68	16.54	16.55	16.85	17.53	20.16	20.75	20.96	21.99	25.09	25.49	28.21	28.47	29.11	31.11	31.17	31.84	32.04	33.78	34.76	34.88	36.35	37.45	37.71	40.68	41.51	43.96	45.32	45.49	46.66	47.22	47.25	48.05	49.56	50.19	51.71	52.99
Ammophila arenaria subsp. australis	0	0	0	0	0	9	0	5	0	0	0	0	0	7	0	5	0	0	0	7	2	0	0	0	0	9	0	0	0	0	0	0	0	0	0	7	0	0	0	0
Anthemis maritima	1	0	0	0	0	2	0	2	0	0	0	0	0	3	5	3	5	0	2	3	2	0	0	3	1	3	0	3	1	0	3	5	2	2	0	0	0	2	0	1
Asparagus acutifolius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Atriplex halimus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bromus diandrus subsp. maximus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Cakile maritima	0	3	2	1	3	1	2	1	2	1	1	2	0	1	0	0	2	0	0	0	0	0	0	0	1	0	1	0	1	0	3	0	0	0	0	0	0	0	0	0
Calystegia soldanella	3	0	0	0	1	0	0	0	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Catapodium rigidum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Centaurea sphaerocephala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	2	0	0
Centaurium erythraea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Cerastium semidecandrum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chamaesyce peplis	2	1	0	2	2	0	1	0	0	0	1	1	0	2	0	0	2	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0
Cistus creticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clematis flammula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crucianella maritima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	7	0	0	3	0	0	0	7	0	0	0	1	7	0	0	0	0	5	0	0
Cutandia maritima	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	3	0	0	0	0	2	0	0	2	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	1
Cyperus capitatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	3	0	0	3	1	0	0	2	0	0	0	0	0	1	0	0	0	1	0	0
Daphne gnidium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dasypyrum villosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Daucus carota	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinophora spinosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Elymus farctus subsp. Farctus	5	0	0	2	1	0	0	0	1	0	3	0	0	2	2	0	3	0	2	1	2	0	0	0	3	2	2	3	5	0	2	5	0	2	5	3	0	1	0	3
Eryngium maritimum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphorbia paralias	0	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hedera helix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Helichrysum stoechas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Hordeum murinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juniperus oxycedrus subsp. macrocarpa	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	9	0
Lagurus ovatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0
Lolium temulentum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera implexa	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	0
Malcomia ramosissima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Medicago littoralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	7	2	0	0	7	2	2	0	0	0	0	0	0	0	1	2	0	0	0	0	2	0	0
Medicago marina	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	2	3	1	0	3	3	1	1	0	1	2	0	2	0	0	3	0	0	0	1	0	3
Osyris alba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Otanthus maritimus subsp. maritimus	0	0	0	5	0	1	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Pancratium maritimum	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0	3	0	0	0	0	0	0	0	0	3	0	0	5	3	0	2	0	0	1	2	0	0	3	0	2
Phillyrea angustifolia	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	7	0	0	0
Phleum arenarium subsp. caesium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinus pinea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pistacia lentiscus	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum maritimum	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prasium majus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0
Pseudorlaya pumila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Quercus ilex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnus alaternus	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Rubia peregrina	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
Ruscus aculeatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salsola kali	1	2	3	2	3	0	2	2	2	2	2	2	0	1	0	1	2	0	0	1	0	0	0	0	2	0	2	0	1	0	0	0	0	1	0	3	0	0	0	0
Salvia verbenaca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Silene canescens	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	3	3	0	3	7	5	3	0	0	0	0	0	0	3	5	1	2	0	0	0	3	0	3
Sixalix atropurpurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smilax aspera	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5	0
Sonchus bulbosus	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
Sporobolus virginicus	0	0	0	0	0	0	0	2	0	0	0	0	0	2	2	1	0	1	2	0	0	0	2	2	0	0	2	0	0	0	1	0	0	0	0	0	0	1	0	2
Teucrium flavum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium cherleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triticum ovatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Urospermum dalechampii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vulpia fasciculata	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	2	0	0	3	0	1	0	2	0	0	0	0	0	0	2	0	0	0	0	1	0	2
Xanthium orientale subsp. italicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	Plant height (cm)	Square root transformed seed mass (g)	LDMC (mg/g)
53.00	53.91	54.74	55.35	55.77	55.92	56.33	56.44	57.14	58.43	60.23	60.81	60.82	61.38	61.56	67.41	72.55	74.14	78.01	78.05	82.48	90.65	91.37	93.25	94.37	97.37	99.31	133.99			
0	5	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100.10	1.62	384.30
0	1	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	17.80	0.74	93.39
0	0	0	0	0	0	1	1	0	1	0	0	2	0	2	1	0	0	0	0	0	2	2	3	0	0	2	2	61.60	3.07	441.46
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37.90	3.34	407.97
0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	23.00	2.68	71.02
0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5.80	8.63	119.51
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20.40	3.01	154.97
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.30	1.65	288.53
0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	3	0	0	0	5	2	0	0	0	66.50	0.93	383.97
0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	2	0	0	0	0	0	87.90	2.03	310.82
0	0	3	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17.20	1.49	344.83
0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14.00	1.17	380.57
0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37.80	0.44	219.85
0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	59.40	2.88	372.16
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	2	0	0	2	---	---	---
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27.10	5.14	166.71
0	0	0	0	2	0	0	0	0	0	1	5	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	41.00	3.78	343.06
0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29.40	3.18	188.21
0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22.90	2.61	265.61
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	---	---	---
0	0	0	2	0	0	0	0	0	0	2	0	0	3	1	0	0	0	0	0	3	0	1	0	0	0	1	0	45.60	0.10	370.69
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	0	5	0	2	0	2	0	0	3	0	2	0	0	9	5	3	9	9	2	2	0	0	7	5	181.00	10.83	465.52
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29.30	0.02	0.02
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	---	---	---
2	0	0	2	0	0	1	2	0	2	0	0	1	0	0	0	0	2	0	2	0	1	0	2	2	2	2	5	80.30	2.71	350.18
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.30	1.46	308.18
0	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13.60	0.77	458.13
0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	---	---	---
0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22.10	0.97	236.36
0	0	3	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	37.50	4.32	155.35
5	0	0	0	0	2	2	0	0	0	0	0	2	0	5	7	0	0	5	2	0	0	0	0	3	7	0	3	173.30	2.42	396.37
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	0	5	3	5	0	3	0	0	7	0	0	0	0	0	0	1	0	0	3	0	2	0	0	0	134.50	2.77	452.91
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	16.24	1.56	203.94
2	0	0	0	0	0	2	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	2	0	1	0	0	2	74.00	2.97	215.95
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.65	3.85	233.22
0	0	0	3	0	0	3	2	0	0	0	0	0	0	2	2	0	1	0	0	0	0	0	0	0	1	1	0	298.70	43.48	566.81
0	0	0	2	0	2	2	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	2	1	0	142.60	3.05	225.65
0	0	0	1	0	0	0	2	0	1	0	0	2	1	0	2	0	1	1	0	0	1	0	0	1	0	1	0	126.80	2.16	401.50
1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	---	---	---
0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	5.60	1.42	108.36
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15.80	0.58	190.68
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	25.70	1.54	225.74
5	0	1	2	0	3	3	2	3	3	0	0	2	3	2	3	0	0	5	2	1	3	3	2	3	2	2	2	135.80	3.62	326.55
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.15	0.55	158.67
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15.80	0.32	395.18
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	62.20	14.69	253.37
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	---	---
0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12.50	1.22	992.55
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	---	---	---

Appendix S3. R function ‘directionalSAC’

Disclaimer: users of this code are cautioned that, while due care has been taken and it is believed accurate, it has not been rigorously tested and its use and results are solely the responsibilities of the user.

Description: the function ‘directionalSAC’ calculates directional and non-directional accumulation and turnover curves as a function of sampling effort.

Dependencies: ‘vegan’ library.

Usage: `directionalSAC(community, gradient)`

Arguments:

community: a community data frame with *N* plots as rows, *S* species as columns. Both presence/absence and species abundances are allowed as entries. Plot names should be provided as row names on the data frame.

gradient: a vector of numeric values, a matrix, a data frame or an object of class ‘dist’.

If *gradient* is a vector, then plots are ordered along a single spatial or environmental gradient. The length of the vector must be the number of rows in object *community*. Values in the vector must be in the same order as plots in object *community*. If names are given to each value of the vector, then the row names in *community* must be equal as those in *gradient*. For example, values in the vector may be the latitude of each plot or an environmental variable such as the temperature.

If *gradient* is a matrix or a data frame, then each column of the matrix must be a gradient along which plots are ordered. Only numeric values are allowed. For example, values in the matrix may be environmental data such as the temperature, the precipitation, the elevation. The result given by the function is an average over all gradients specified by the matrix. The number of rows in the matrix must be the same as the number of rows in object *community*. If the matrix has row names, then they should be the same as in object *community*. There must be as many columns in gradient as there are gradients of interest (for example, as many columns as there are environmental variables).

If *gradient* is of class ‘dist’, then the result given by the function is an average over all possible directional accumulation curves. In that case, *gradient* contains any pairwise dissimilarity/distance measure among plots. If names are given in *gradient*, they should be the same as row names in *community*. As specified in the main text, adjacent plots are combined step by step using the specified distance among plots as a constraining factor. In the simplest case, given a set of *N* plots, for each plot, the first, second, ..., *k*-th nearest neighbor are determined and a directional species accumulation curve is constructed using the resulting sequence of plots. This procedure is repeated for all plots, generating *N* directional accumulation curves from which a mean spatially explicit curve is calculated. The resulting curve is thus an intermediate solution between a non-directional accumulation curve and a pure directional curve in which all plots are ordered along a single spatial or environmental gradient.

Outputs

An object of class ‘data.frame’ is returned containing the following statistics:

N_SCR: Directional species accumulation curve.

N_Exact: Non directional species accumulation curve (classic accumulation curve).

Alpha_dir: directional mean number of species $\bar{\alpha}_M$ in the *M* plots (for details on the calculation, see the main text).

Beta_M_dir: Directional beta diversity $\bar{\beta}_M$ as a function of sampling effort *M* (for details on the calculation, see the main text).

Beta_N_dir: Normalized directional beta diversity $\bar{\beta}_\eta$.

Beta_M: Non-directional beta diversity β_M as a function of sampling effort *M*.

Beta_N: Normalized non-directional beta diversity β_η as a function of sampling effort *M*.

Beta_Autocor: A normalized measure of autocorrelation $\bar{\beta}_\phi$ for directional beta diversity calculated as the normalized difference between directional and non-directional beta.

Function Syntax

```
directionalSAC <- function(community, gradient) {
  require(vegan)
  if (!inherits(community, "data.frame")){
    if(!inherits(community, "matrix"))
      stop("Object community must be of class data.frame or matrix")
  }
  if (!inherits(gradient, "dist")){
    if(!is.vector(gradient)){
     if(!is.matrix(gradient)){
      if(!is.data.frame(gradient))
      stop("Object gradient must be of class vector, matrix, data.frame or
dist")
  }}}
  if (any(community < 0))
    stop("Negative value in community")
  if (any(rowSums(community) < 1e-16))
    stop("Empty plots in community")
  if(is.null(rownames(community))) stop("Object community must have row names")
  if(is.vector(gradient)){
    if(length(gradient)!=nrow(community)) stop("Incorrect definition of object
gradient")
    if(!is.null(names(gradient))){
    if(any(!rownames(community)%in%names(gradient))) stop("Names in gradient
must be the same as row names in community")
    gradient <- gradient[rownames(community)]
    }
    Rgradient <- rownames(community)[order(gradient)]
    agg <- community[Rgradient, ]
```

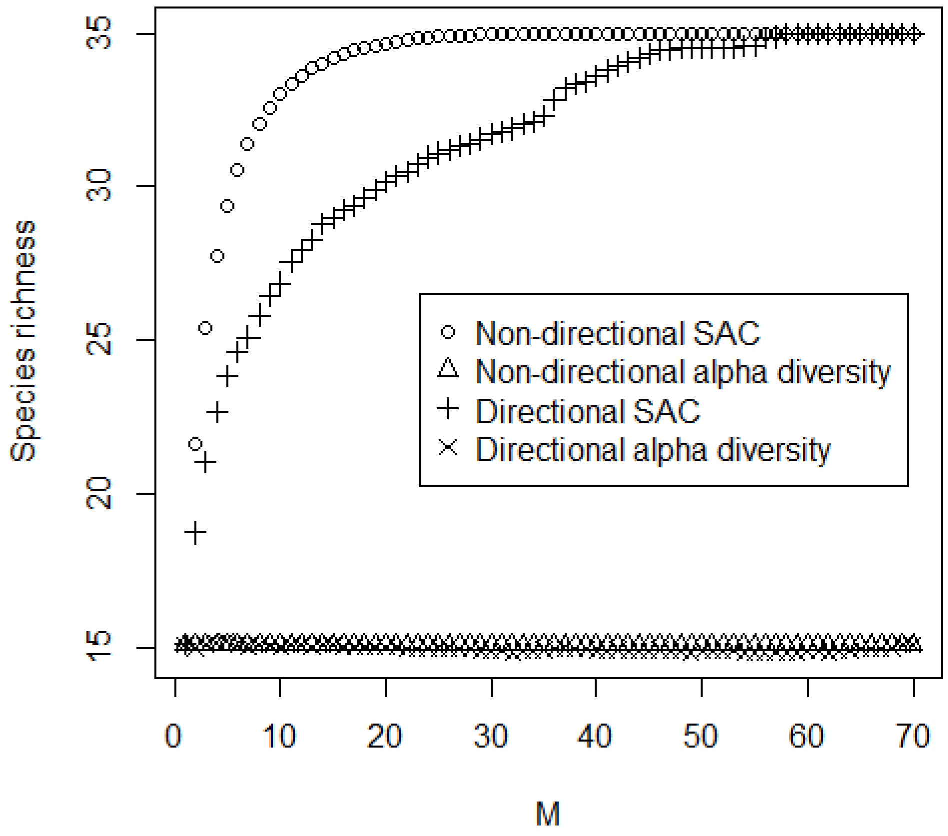
```
    richness <- specnumber(agg)
    average_alfa <- cumsum(richness)/(1:length(richness))
    average <- specaccum(agg, method="collector")$richness
  }
  else {
    if(!is.matrix(gradient)) gradient <- as.matrix(gradient)
    if(ncol(gradient)==1) stop("A gradient with a single quantitative variable
must be coded as a vector rather than as a matrix")
    if(nrow(gradient)!=nrow(community)) stop("Incorrect definition of object
gradient")
    if(!is.null(rownames(gradient))){
      if(any(!rownames(community)%in%rownames(gradient))) stop("Row names in
gradient must be the same as row names in community")
      gradient <- gradient[rownames(community), ]
    }
    res <- array(NA, c(ncol(gradient), nrow(gradient)))
    for(i in 1:ncol(gradient)){
      nami <- rownames(community)
      res[i, ] <- nami[order(gradient[, i])]
    }
    spatial_order <- t(res)
    f <- nrow(spatial_order)
    n <- ncol(spatial_order)
    result <- array(dim = c(f, n))
    alfa_average <- array(dim = c(f, n))
    for(i in 1:n) {
      agg <- community[spatial_order[, i], ]
      richness <- specnumber(agg)
      alfa_s <- cumsum(richness)/(1:length(richness))
      c <- specaccum(agg, method="collector")
      result[, i] <- c$richness
      alfa_average[, i] <- alfa_s
    }
    average <- rowMeans(result)
    average_alfa <- rowMeans(alfa_average)
  }
  beta_s <- average/average_alfa
  beta_S <- (beta_s-1)/((1:length(beta_s))-1)
  exact <- specaccum(community, method = "exact")
  beta_exact <- exact$richness/exact$richness[1]
  beta_N <- (beta_exact-1)/((1:length(beta_exact))-1)
  beta_norm_autocor <- (beta_N- beta_S)/(beta_N+ beta_S)
  SCR <- data.frame(as.matrix(average), as.matrix(exact$richness),
as.matrix(average_alfa), as.matrix(beta_s), as.matrix(beta_S),
as.matrix(beta_exact), as.matrix(beta_N), as.matrix(beta_norm_autocor))
  names(SCR) <- c("N_SCR", "N_Exact", "Alpha_dir", "Beta_M_dir",
"Beta_N_dir","Beta_M", "Beta_N", "Beta_Autocor")
  return(SCR)
}
```

Example with ‘mite’ data - requires the ‘vegan’ library

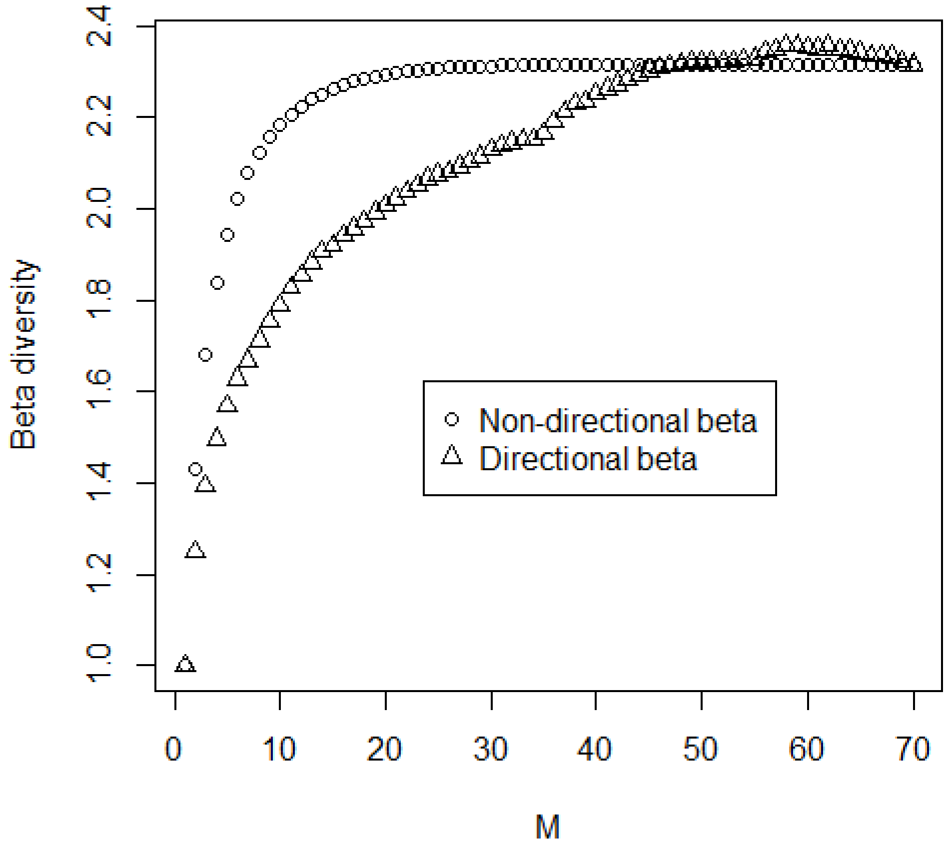
```
library(vegan)
data(mite)
data(mite.xy)
comm_matrix <- mite
```

Spatially-explicit curves

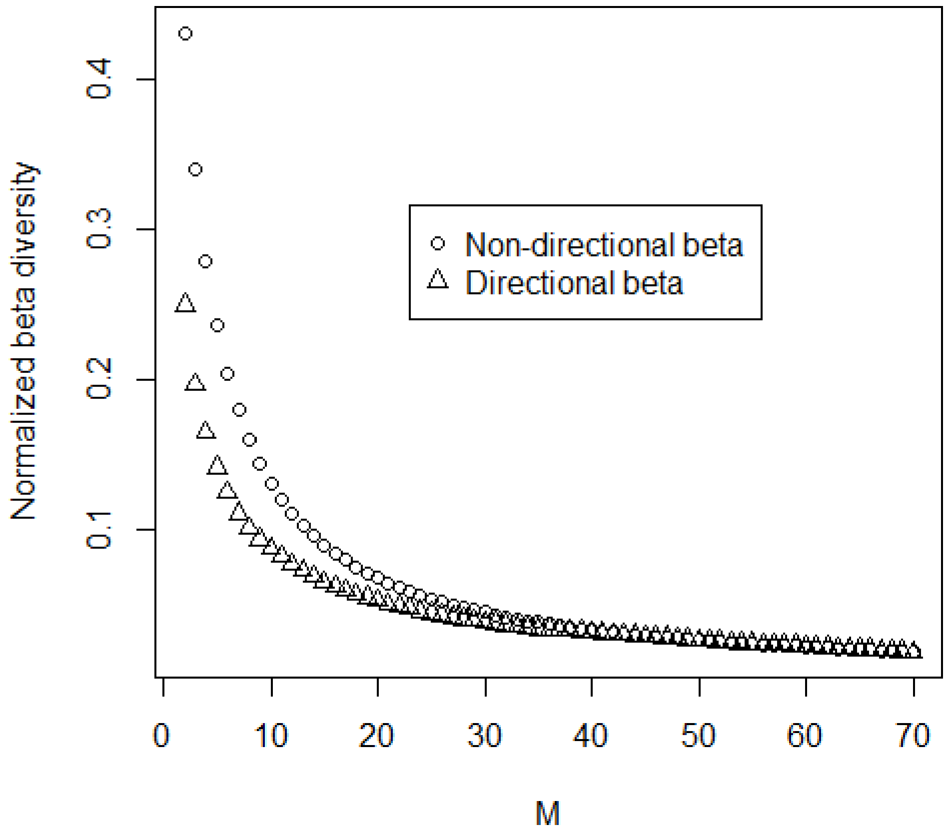
```
spatialdist <- dist(mite.xy) # to calculate the geographic distance between plots (Euclidean distance between the coordinates of the plots)

betas <- directionalSAC(comm_matrix, spatialdist) # to calculate directional and non directional beta diversity

plot(1:70, betas$N_Exact, xlab="M", ylab="Species richness", ylim=range(c(betas$N_Exact, betas$N_SCR, betas$Alpha, mean(apply(comm_matrix, 1, function(x) length(x[x>0]))))))
points(1:70,rep( mean(apply(comm_matrix, 1, function(x) length(x[x>0]))), 70), pch=2)
points(1:70, betas$N_SCR, pch=3)
points(1:70, betas$Alpha_dir, pch=4)
legend(locator(1), legend=c("Non-directional SAC", "Non-directional alpha diversity", "Directional SAC", "Directional alpha diversity"), pch=1:4) # click on the figure, on an empty area of the figure, to place the legend.
```



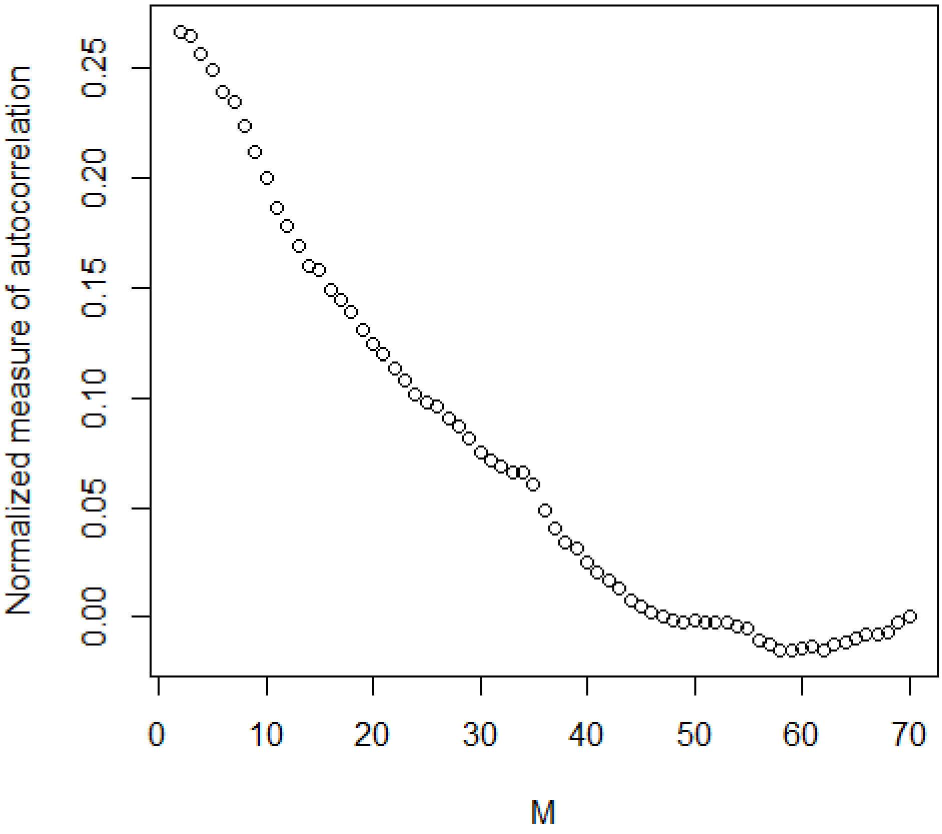
```
plot(1:70,      betas$Beta_M,      xlab="M",      ylab="Beta      diversity",
ylim=range(c(betas$Beta_M_dir, betas$Beta_M)))
points(1:70, betas$Beta_M_dir, pch=2)
legend(locator(1),   legend=c("Non-directional   beta",   "Directional   beta"),
pch=1:2) # click on the figure, on an empty area of the figure, to place the
legend.
```



```
plot(2:70,  betas$Beta_N[2:70],  xlab="M",  ylab="Normalized  beta  diversity",
ylim=range(c(betas$Beta_N_dir[2:70], betas$Beta_N[2:70])))
points(2:70, betas$Beta_N_dir[2:70], pch=2)
legend(locator(1),   legend=c("Non-directional   beta",   "Directional   beta"),
pch=1:2) # click on the figure, on an empty area of the figure, to place the
legend.
```



```
plot(2:70, betas$Beta_Autocor[2:70], xlab="M", ylab="Normalized measure of
autocorrelation")
```



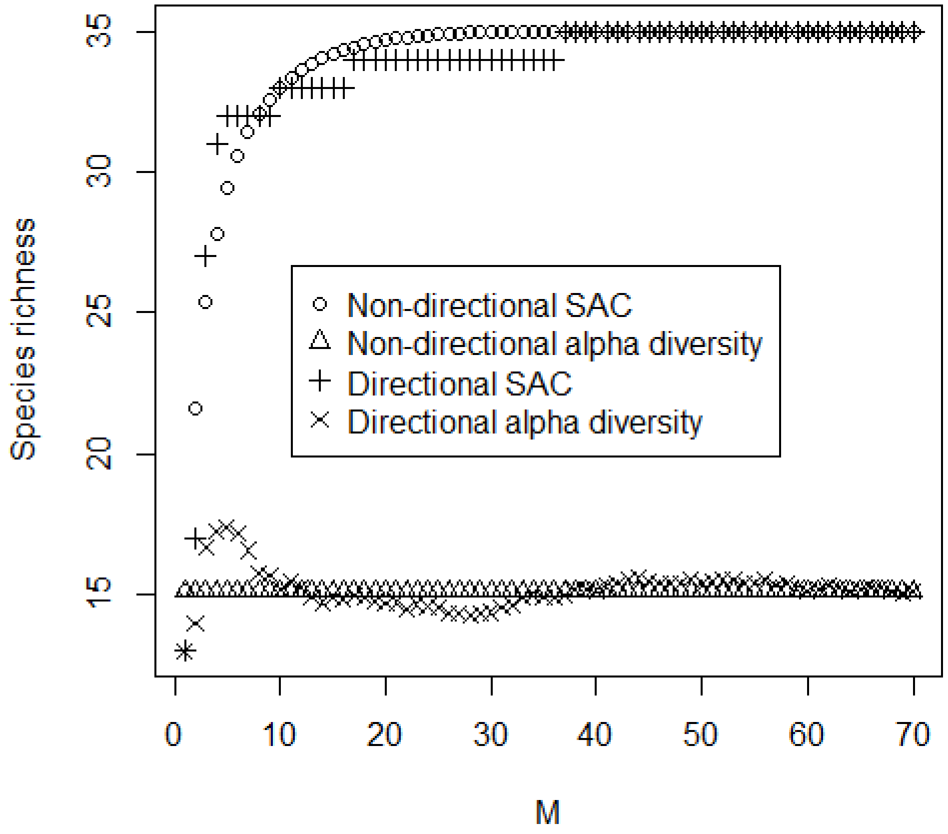
```
Environmental gradient
```

```
data(mite.env)
```

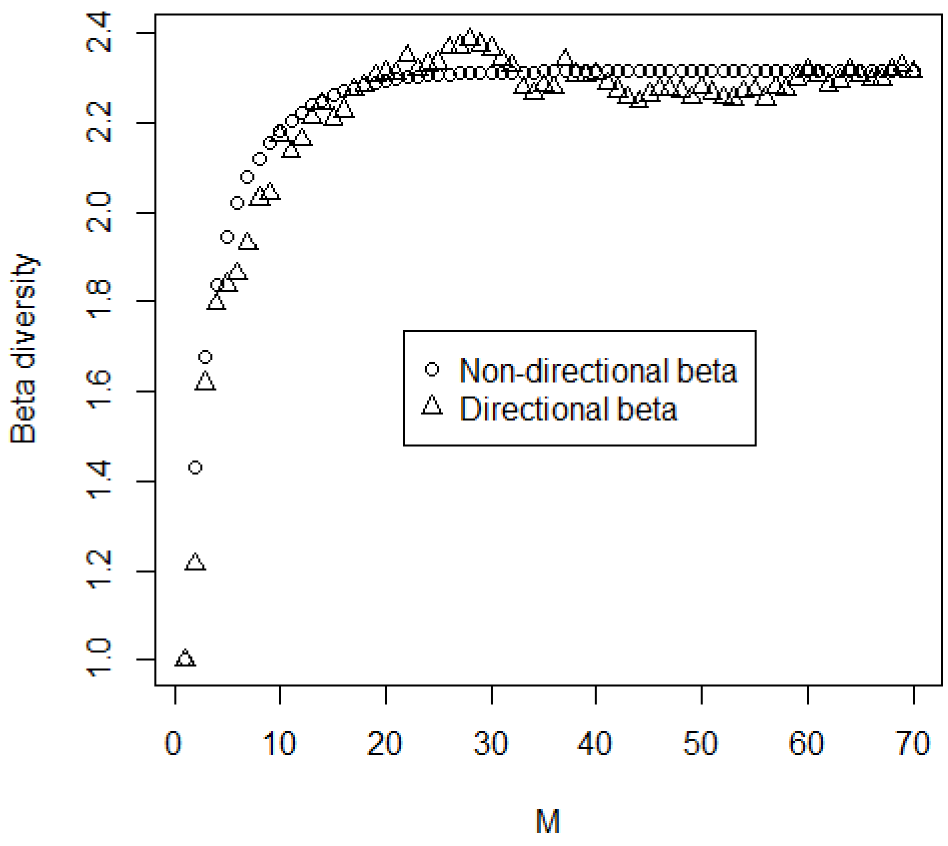
```
betae <- directionalSAC(comm_matrix, mite.env$SubsDens) # to calculate directional and non directional beta diversity
```

Here the environmental gradient was defined according to the substrate density (g/L).

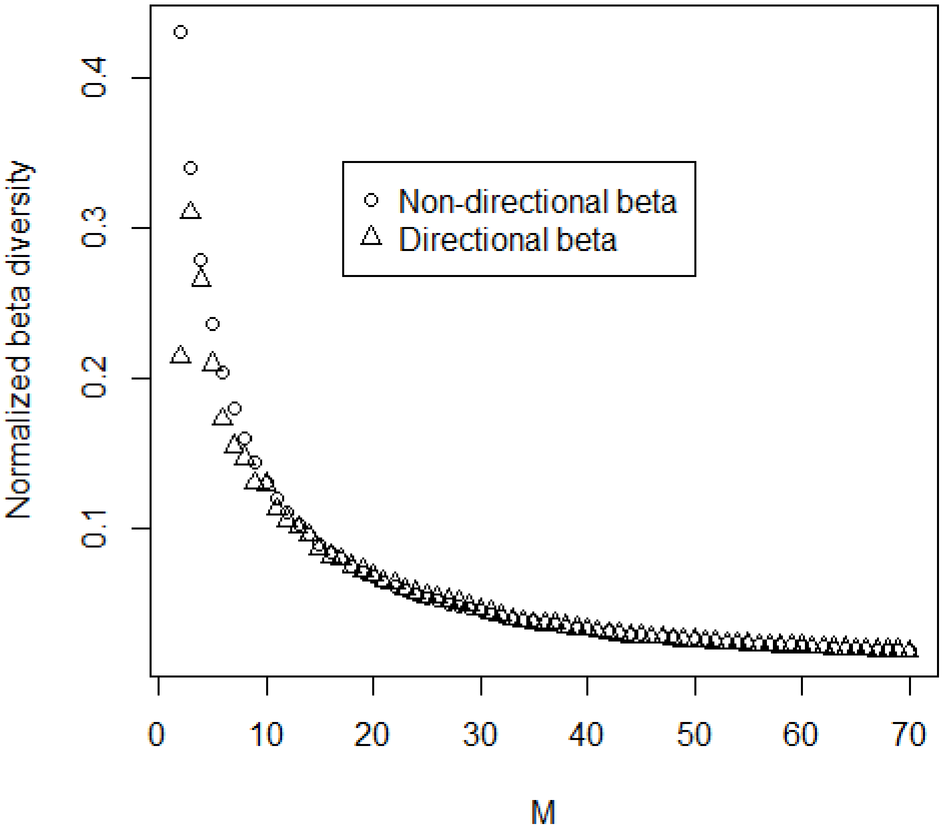
```
plot(1:70, betae$N_Exact, xlab="M", ylab="Species richness", ylim=range(c(betae$N_Exact, betae$N_SCR, betae$Alpha, mean(apply(comm_matrix, 1, function(x) length(x[x>0]))))))
points(1:70,rep( mean(apply(comm_matrix, 1, function(x) length(x[x>0]))), 70), pch=2)
points(1:70, betae$N_SCR, pch=3)
points(1:70, betae$Alpha_dir, pch=4)
legend(locator(1), legend=c("Non-directional SAC", "Non-directional alpha diversity", "Directional SAC", "Directional alpha diversity"), pch=1:4) # click on the figure, on an empty area of the figure, to place the legend.
```



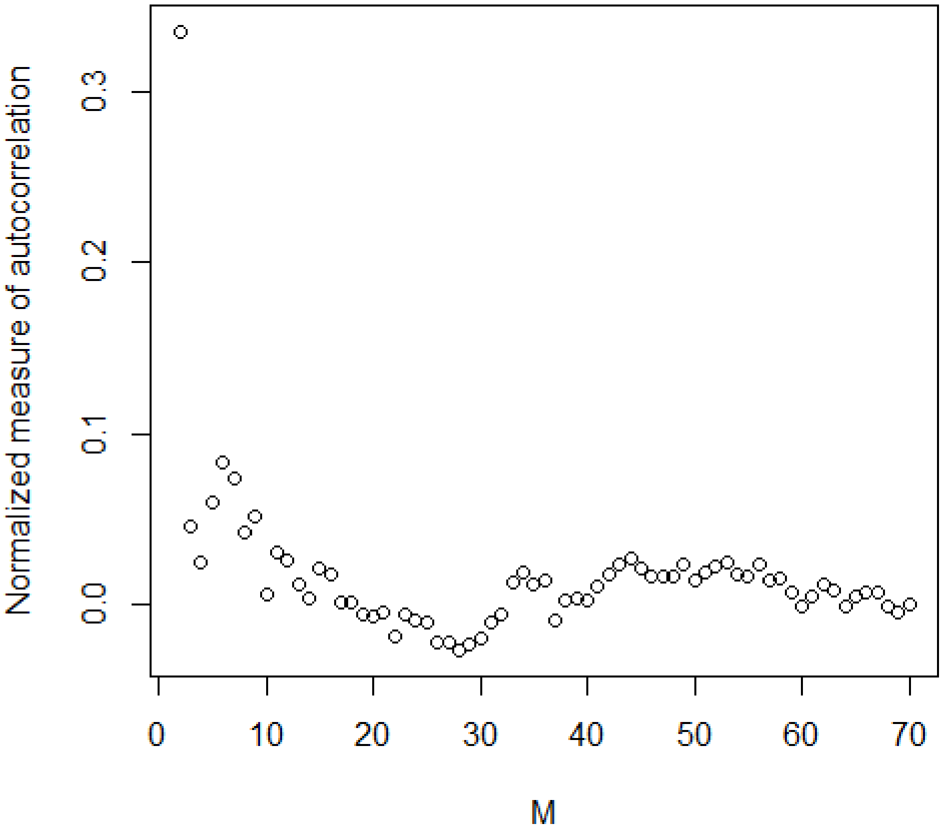
```
plot(1:70, betae$Beta_M, xlab="M", ylab="Beta diversity",
ylim=range(c(betae$Beta_M_dir, betae$Beta_M)))
points(1:70, betae$Beta_M_dir, pch=2)
legend(locator(1), legend=c("Non-directional beta", "Directional beta"),
pch=1:2) # click on the figure, on an empty area of the figure, to place the
legend.
```



```
plot(2:70, betae$Beta_N[2:70], xlab="M", ylab="Normalized beta diversity", ylim=range(c(betae$Beta_N_dir[2:70], betae$Beta_N[2:70])))
points(2:70, betae$Beta_N_dir[2:70], pch=2)
legend(locator(1), legend=c("Non-directional beta", "Directional beta"), pch=1:2) # click on the figure, on an empty area of the figure, to place the legend.
```



```
plot(2:70,  betae$Beta_Autocor[2:70],  xlab="M",  ylab="Normalized  measure  of
autocorrelation")
```

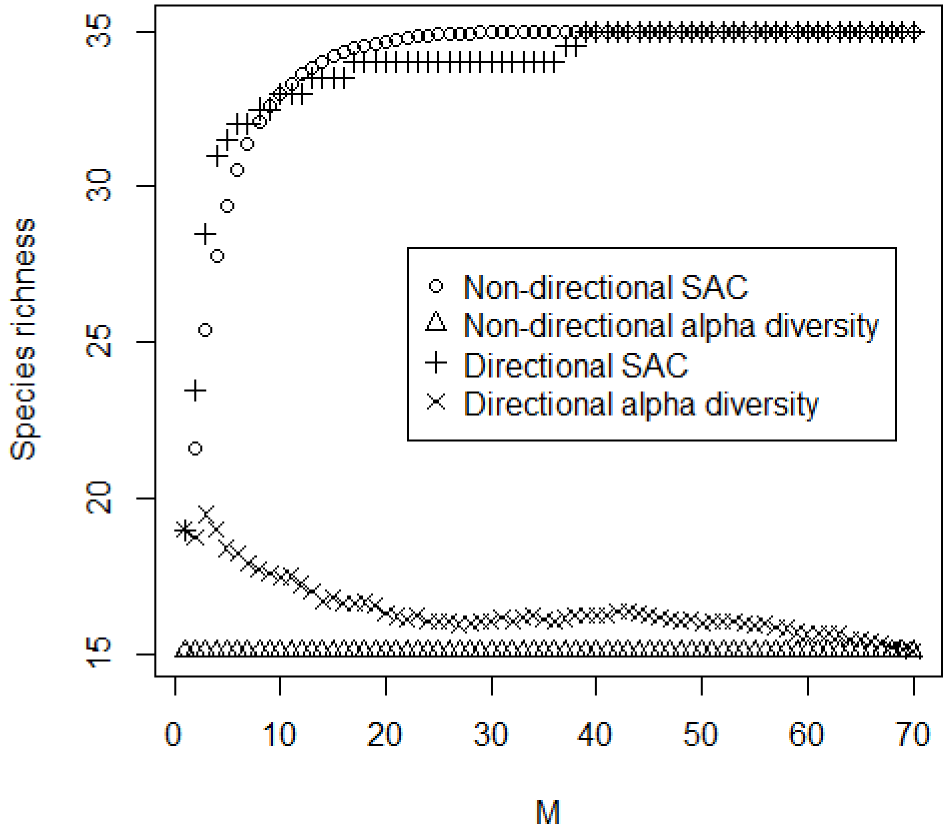


Now two environmental gradients are defined: one per quantitative environmental variable
The results are averaged over the gradients.

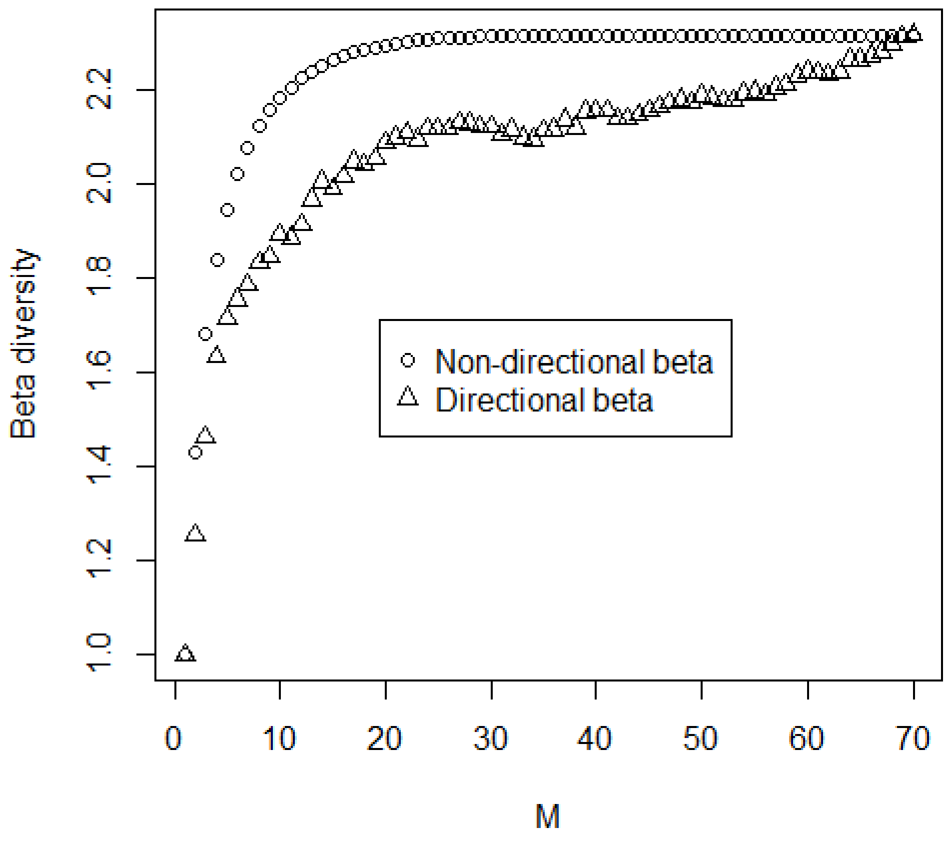
```
betaE <- directionalSAC(comm_matrix, as.matrix(mite.env[, 1:2])) # to calculate
directional and non directional beta diversity
```

Here the environmental gradient was defined according to the substrate density (g/L) and the water content of the substrate (g/L).

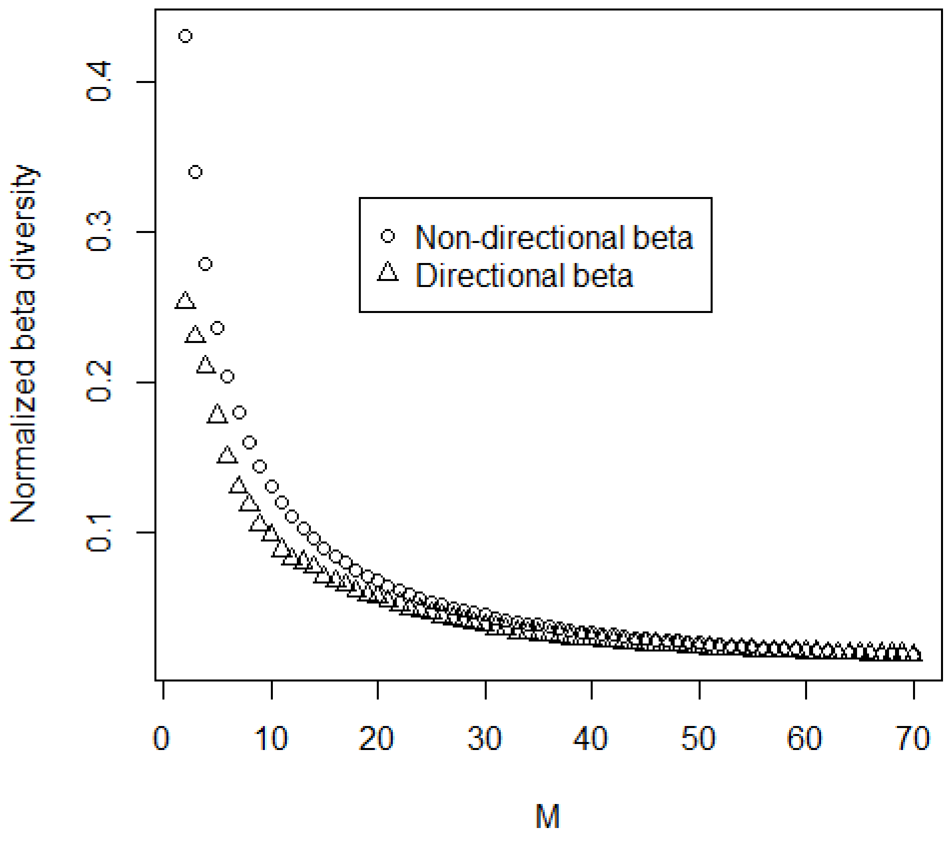
```
plot(1:70, betaE$N_Exact, xlab="M", ylab="Species richness",
ylim=range(c(betaE$N_Exact, betaE$N_SCR, betaE$Alpha, mean(apply(comm_matrix, 1,
function(x) length(x[x>0]))))))
points(1:70,rep( mean(apply(comm_matrix, 1, function(x) length(x[x>0]))), 70),
pch=2)
points(1:70, betaE$N_SCR, pch=3)
points(1:70, betaE$Alpha_dir, pch=4)
legend(locator(1), legend=c("Non-directional SAC", "Non-directional alpha
diversity", "Directional SAC", "Directional alpha diversity"), pch=1:4) # click
on the figure, on an empty area of the figure, to place the legend.
```



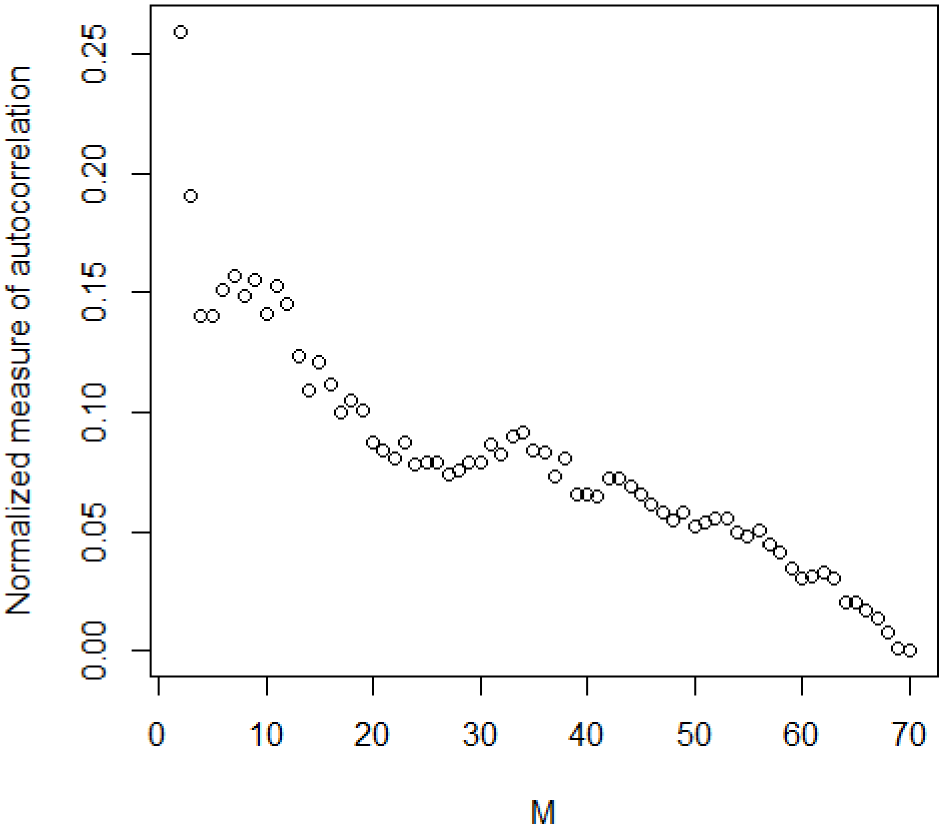
```
plot(1:70,       betaE$Beta_M,       xlab="M",       ylab="Beta       diversity",
ylim=range(c(betaE$Beta_M_dir, betaE$Beta_M)))
points(1:70, betaE$Beta_M_dir, pch=2)
legend(locator(1),   legend=c("Non-directional   beta",   "Directional   beta"),
pch=1:2) # click on the figure, on an empty area of the figure, to place the
legend.
```



```
plot(2:70,  betaE$Beta_N[2:70],  xlab="M",  ylab="Normalized  beta  diversity",
ylim=range(c(betaE$Beta_N_dir[2:70], betaE$Beta_N[2:70])))
points(2:70, betaE$Beta_N_dir[2:70], pch=2)
legend(locator(1),   legend=c("Non-directional   beta",   "Directional   beta"),
pch=1:2) # click on the figure, on an empty area of the figure, to place the
legend.
```



```
plot(2:70,  betaE$Beta_Autocor[2:70],  xlab="M",  ylab="Normalized  measure  of
autocorrelation")
```


Normalized measure of autocorrelation
0.00
0.05
0.10
0.15
0.20
0.25
0
10
20
30
40
50
60
70
M