1 Introduction

The aim of this project was exploring the rules of assembling local plant communities from regional species pool applying trait-based approach. The two main processes during community assembly are environmental filtering and competition among co-existing species. The former leads to trait convergence: individuals of co-existing species have to survive and reproduce under the same modifying environmental conditions that select the same trait values. On the other hand, co-existing species have to differ in the way of their population regulation (limiting similarity) that leads to trait divergence. Trait convergence/divergence can be defined as significantly lower/higher diversity of trait values than expected by random sampling from the species pool.

On the theoretical ground we expect both environmental filtering and limiting similarity always influence the trait composition. Whereas, in the meta-analysis of 1966 tests from 21 papers by Götzenberg et al. (2012), only 18% of the tests detected significant departure from the randomness. One possible explanation of this contradiction is that statistical power of the applied tests is too low (the other one is the deficiency in selection of traits). Indeed, lot of different test statistics and randomization algorithms are used in the literature, but neither of them had been checked before our project. Therefore the planned project had two main parts: (1) developing new methods and testing existing ones applied in trait-based studies of assembly rules, and (2) case studies using these methods. This report mirror this structure. During the work new methodological problems arised (How to measure effect size, if the null distribution is highly skewed?), we reflected to recently published theories related to measuring functional diversity (i.e. possible generalizations of Hill's doubling property), and applied the developed simulation framework to test a recently proposed algorithm that estimates the relative role of dispersal, environmental filtering and competition in community assembly. Results of these additional studies (not promised in the original work plan) are also discussed in the next chapter of this report. Results of the case studies are summarized in the third chapter. Work in the two sites - Várhegy Forest Reserve, and Orgovány - have been done as planned. Furthermore, we have joined to an international research group that studied changes in trait-environment relationship during forest succession.

From the project results five papers have already published (Campetella et al. 2011, Botta-Dukát and Czúcz 2016, Götzenberger et al. 2016, Lhotsky et al. 2016b, 2016a). The following two submitted manuscripts are under review:

- Botta-Dukát Z. The generalized replication principle and the partitioning of functional diversity into independent alpha and beta components. *Ecography* (2nd revised version has been submitted)
- Botta-Dukát Z. Note on calculating standardized effect size (SES). *PeerJ*

The following manuscripts are under preparation and will be submitted within few months:

- Botta-Dukát Z. Critical evaluation of STEPCAM algorithm: assumptions and performance. Will be submitted to *Ecology*.
- Lhotsky B, Csecserits A, Kovács B, Botta-Dukát Z. Effect of environmental conditions to assembly of forest floor vegetation. Will be submitted to *PlosOne*.

Following the manual for final reports, I give only short summary of the published results and more details of the unpublished ones.

2 Theoretical and methodological studies

2.1 Individual-based simulation framework

The first step for testing the statistical methods of assembly rule studies is creating meta-communities with known assembly rules, where both Type I error rate and power of the test can be estimated. Previous attempts to check the ability of functional diversity indices to distinguish between trait convergence and trait divergence were based on algorithms that select species from the species pool following trait-based rules (Mouchet et al. 2010, de Bello et al. 2012, Aiba et al. 2013, Mason et al. 2013). The disadvantage of this approach is that it does not try to simulate the real processes, but only aims at reproducing the expected pattern (trait convergence or divergence). There is only one study so far (Münkemüller et al. (2012) which applied a spatially explicit, individual-based modeling strategy to simulate the real underlying community processes: i.e. individuals are born, survive, compete for resources, reproduce and die. However, even this study applied a cellular-automaton simulation model with only one individual in each cell, which means that one of the key processes (limiting similarity) could not be tested.

Our simulation procedure can be subdivided into five steps (Figure 1Figure):

1. **Initialization:** A total species pool is created. The number of communities comprising the meta-community and the number of individuals that co-exist in each community is defined. An environmental condition is defined for each community. For each species in the pool, three trait values are simulated; the first trait defines a species preference along the environmental gradient and thus defines the survival of a species in a given environmental condition, the second trait is used to calculate the pairwise strengths of competition between species, while the third one is neutral. From here on we will refer to these traits as 'environmental filtering trait', 'competition trait' and 'neutral trait', respectively. All traits are following beta distribution whose parameters can results to uniform or unimodal distribution, to bound values between 0 and 1. As an initial colonization of the local communities, the species in the total species pool populate the communities according to how well their environmental filtering trait matches the environmental condition in a community. As such, the survival probability of a species is modeled as a Gaussian survival curve, assuming a unimodal response to the environment (e.g. ter Braak 1986). This approach has also been used in other recent community assembly models (Jabot 2010, Münkemüller et al. 2015). In the following steps 2 to 5 the initial meta-community is repeatedly subjected to a series of processes simulating mortality, offspring reproduction, and establishment.
2. **Death of individuals**: In each community one random individual dies. Hence, the per capita death rate is independent of density
3. **Seed production:** Each community produces seeds where the number of seeds per species is determined by species abundances and the competitive effects among species (as defined by the competition trait). The competition between species is modeled as in the classical model of resource use of MacArthur & Levins (1967), i.e. a Gaussian curve represents the resource use of a species. The competition strength of two species is then determined by how much their resource response curves (i.e. their resource niches) overlap. Here, assuming an equal niche width for all species, the overlap of two species is represented by the exponential function of distance in the competition trait values.
4. **Dispersal:** Each seed has a probability to remain in its community of origin and a probability to disperse to any of the other communities, i.e. seeds of all species are

equally limited in their dispersal so that only a proportion of seeds can move freely throughout the meta-community within one generation. To keep dispersal simple, and since the meta-community is not spatially explicit, dispersal does not rely on more complex dispersal kernels, e.g. involving different dispersal probabilities for different species.

5. **Establishment:** The dead individual is replaced by one new individual from the seeds produced and dispersed (steps 3 and 4). The probability that an individual of a certain species is the one to replace the dead individual is defined by the number of seeds of that species and the survival probability for the given community.

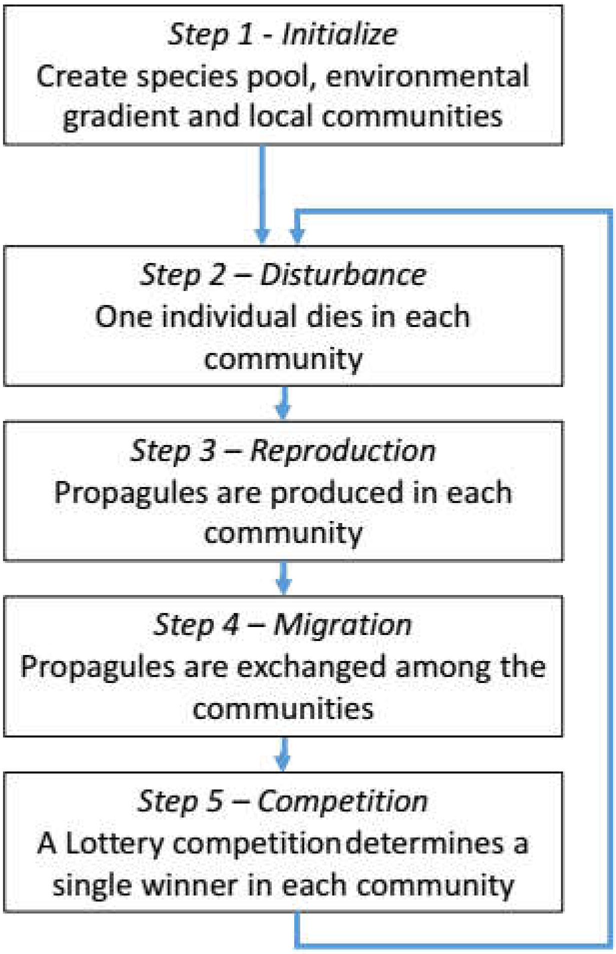


Figure 1. Flow-chart of the individual based simulation

Steps two to five are applied to each community for 300 times, and this is iterated 100 times, so that each individual in a community is replaced by a new one 100 times, i.e. there is a 100-fold complete turnover in individual identity.

Using different parameter setting allows (1) exploring the robustness of results against changing simulation parameters, and (2) by setting extreme parameter values completely switching off some effects (e.g. unlimited dispersal, no habitat filtering, no environmental heterogeneity, no interspecific competition).

2.2 Testing ability of functional diversity indices and randomization tests to detect trait convergence/divergence

The properties in randomization tests were analyzed in two studies: the first one (Botta-Dukát and Czúcz 2016) focused on the comparison between test statistics, while the second study (Götzenberger et al. 2016) the randomization strategies were evaluated.

In the first study, we selected five indices for testing based on the comprehensive review of Pavoine & Bonsall (2011) so as to represent all three components of functional diversity: richness, divergence and evenness (Mason et al. 2005, Villéger et al. 2008). We focused on indices calculated from distance matrices, as these are also applicable in phylogenetic studies, and offer a relatively straightforward way for incorporating intraspecific trait variation (de Bello et al. 2013, Carmona et al. 2016). Nevertheless, as there is no widely accepted distance-based measure of functional richness, and because it is known to be a good indicator of habitat filtering (e.g. Cornwell et al. 2006), we also examined the convex hull volume – which is thus the single metric in this study that is calculated directly from trait values. Information on the selected indices is summarized in Table 1.

Table 1. Overview of the tested functional diversity indices

Name	Description	Measured component[1]	Abundances used?	References
FRic	Convex hull volume (or range in the one-dimensional case)	functional richness	No	(Cornwell *et al.* 2006; Villéger *et al.* 2008)
RaoQ	Rao's quadratic entropy (=Mean distance among species weighted by species abundance)	functional richness and functional divergence	Yes	(Botta-Dukát 2005)
FEve	Evenness in the branch lengths of a minimum spanning tree	functional evenness	Yes	(Villéger *et al.* 2008)
Vd	Variance of distances	functional evenness	No	(Clarke & Warwick 2001)
Vnnd	Variance in the nearest-neighbor distances	functional evenness	No	(Weiher *et al.* 1998)

[1] sensu Laliberte & Legendre (2010)

Habitat filtering is expected to restrict the range of trait values and thus decrease the functional richness (Weiher et al. 1998, Cornwell et al. 2006). For this reason, habitat filtering is often considered to be indicated by lower than expected FRic values (e.g. Cornwell et al. 2006, Bernard-Verdier et al. 2012, Raevel et al. 2012). Our results pointed out that this relationship strongly depends on the environmental heterogeneity of the datasets studied (Willis et al. 2010, de Bello et al. 2012): the power of the tests becomes low if the gradient sampled is short relative to the tolerance width of the species. With low environmental heterogeneity, trait values get filtered almost the same way in all plots. Thus there is no considerable difference to be expected in their plot level minimum and maximum values, and consequently in the actual and expected values of FRic.

As Rao's quadratic entropy is expected to combine functional richness and functional divergence (Mouchet et al. 2010), its use for detecting a decrease in functional richness due to habitat filtering is justified. According to Raevel et al. (2012), environmental filtering may influence not only the range of trait values, but also the position of dominant species in the trait space (functional divergence sensu Villéger et al. 2008). Rao's quadratic entropy is influenced by both effects, which may be advantageous when the aim is the detection of environmental filtering. And yet, even though RaoQ may also be influenced by limiting similarity, we found it highly appropriate for detecting habitat filtering, too. One possible explanation for the superior performance of RaoQ is that it is less sensitive to extreme trait values than FRic (Cornwell and Ackerly 2009).

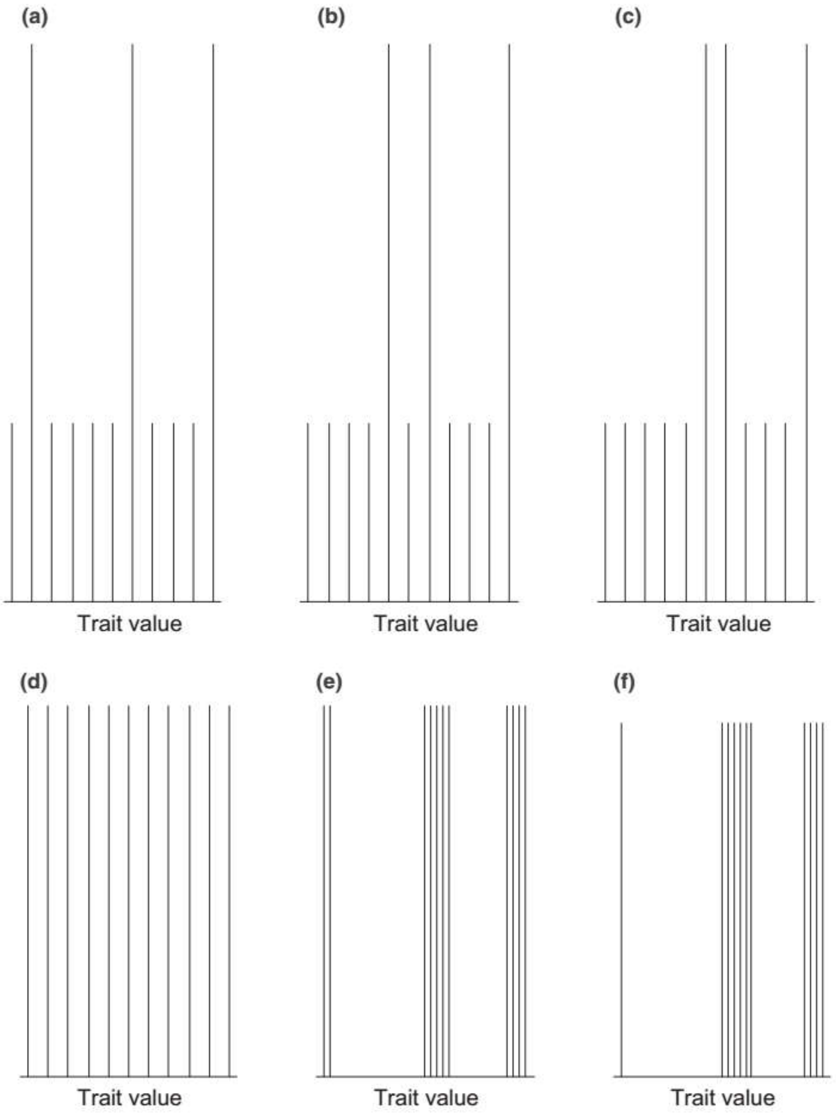


Figure 2. Hypothetical communities for illustrating that both FEve (a-c) and variance of nearest neighbor distance (Vnnd) (d-f) failed to correctly measure the functional evenness because they consider only the (nearest) neighbor species. Each vertical line represents a trait value of the species, while height shows the abundance. FEve is the same for community a) and b), while lower in c). Vnnd is zero in both communities d) and e), but high in community f). These examples illustrate the unfavorable property of these indices that considerably different communities may results in the same value of the index, while in other cases small community changes may cause major changes in the index values. Furthermore, pattern in communities a) and d) may be caused by limiting similarity, while the other patterns contradict this theory, but the values of the indices do not show this difference.

None of the indices that we tested proved unequivocally appropriate for detecting limiting similarity. Even the best performing, Rao's quadratic entropy (RaoQ) and variance of distances (Vd) indices, had relatively low statistical power using any randomizations with reasonable type I error rates. The theoretical minimum value of Vd is attained if the species are placed equidistantly in the trait space, thus relatively low values can emerge due to interspecific competition which is supposed to homogenize the size of gaps among species in the trait space. As we have already discussed, RaoQ combines aspects of functional richness (i.e. the range of trait values) and functional divergence (i.e. the position of dominant species relative to the center of trait range). It seems highly improbable that limiting similarity would influence RaoQ values through altering functional richness (Cornwell and Ackerly 2009, Bernard-Verdier et al. 2012). Under what conditions can limiting similarity lead to high functional divergence? Functional divergence is high if abundant species are situated near the border of the occupied trait space. Limiting similarity predicts that dominant species are situated as far as possible from one another in the trait space. When considering only one trait, functional divergence is maximal if dominant species are situated at the two opposite ends of the trait gradient. This is in agreement with the pattern expected due to limiting similarity for two dominant species but contradicts the expected equidistant spacing of dominants if there are more than two dominant species. Contrary to what its name suggests, FEve ("functional evenness index") was unsuitable for detecting limiting similarity. One possible explanation is that FEve considers only neighbors in trait space (true neighbors in the unidimensional space of our tests, which is generalized as a minimum spanning tree in the multidimensional case), while limiting similarity predicts that dominant species highly differ in traits (Figure 2).

The variance (or standard deviation) of nearest neighbor distances (Vnnd) is another metric frequently used to detect limiting similarity in studies with real data, but which did not work well for this purpose in our simulations. This index is often successfully used to detect even spacing of species along a trait axis, which is interpreted as a result of limiting similarity (e.g. Cornwell and Ackerly 2009, Katabuchi et al. 2012). Nevertheless, Vnnd is similar to FEve in that only neighboring trait values are considered. Accordingly, many fundamentally different patterns may result in the same Vnnd value (Figure 2), which might explain the poor performance of this popular and seemingly well-suited metric. Based on our negative test results, we suggest that neither Vnnd nor FEve should be used to detect limiting similarity or trait divergence.

Table 2. Overview of randomizations assessed in this study and their constraints on the sample and species margins of the community data, the trait correlation, and the connection between abundance and trait values of the species. Filled circles depict the existence of constraints, empty circles their absence.

		Samples		**Species**			**Traits**	
C1	species' abundances within samples across occurring species	●	●	●	○	●	●	●
C2	species' abundances within samples across all species	●	●	○	○	○	●	●
C3	sample abundances within each species across samples where the species occur	●	○	●	●	●	○	●
C4	sample abundances within each species across all samples	○	○	●	●	○	○	●
C5	species' presences with their abundance	●	○	●	●	○	○	●
T1	trait values across species (all traits together)	●	●	●	●	○	○	●
T2	trait values across species (traits independently)	●	●	●	●	○	○	○
T3	trait values across species (all traits together) within two abundance classes	●	●	●[1]	●[1]	○	●[1]	●
T4	trait values across species (traits independently) within two abundance classes	●	●	●[1]	●[1]	○	●[1]	○
Range	species' abundance and position but only across species within the community trait range	●	●	○	○	○	○	●

[1] For T3 and T4 the species are divided into two groups according to their total abundances over the plots. Trait values are then randomized within each of the two groups.

In the second study we compared ten randomization procedures that differ in their constrains (Table 2). We have studied all possible combinations (hereafter called scenarios) of the following five binary parameter settings: homogeneous vs. heterogeneous environment, habitat filtering switched on/off, limiting similarity switched on/off, distribution of traits is uniform or bell-shaped, 'environmental filtering' and 'competition trait' is independent or positively correlated. Our major results are summarized in Table 3. In general, this detailed study of randomization algorithms confirmed the results of the previous one: detecting habitat filtering is much more easy, while detection probability of limiting similarity is more sensitive to the conditions.

Table 3. Overview of main results of power and Type I error rate assessment under different simulation scenarios. For each of the theoretical mechanisms the randomizations with good power are noted and in which cases randomizations did not work well. Aspects of trait correlation and distribution are mentioned in the entries. Abbreviations: p/a – presence-absence. For abbreviations of randomizations see Table 2.

Scenario			Environmental filtering	Limiting similarity
Filtering	**Gradient**	**Competition**		
Yes	yes	yes	**Well detected by most methods. Better when abundance was considered**. C4, C5, T3 and T4 worked best. Correlated traits gave slightly less power.	**Detected best with C2, T1 and T2 and range.** Correlated traits considerably decreased the power. For correlated traits and p/a data, convergence of the competition trait can be detected.
Yes	no	yes	**In general low detection with abundance data by most randomizations,** but T1, T2 and C2 detect filtering, especially with p/a data.	**Much better detection with abundance data,** except with C3, C4 and C5**.**
No	no	yes	**In general low detection by most randomizations,** but T1, T2 and C2 detect some filtering. Divergence is detected for correlated traits.	**Better detection with abundance data**. Slightly less powerful with correlated traits in general. Good detection for p/a data only with correlated traits for all randomizations except C4 and C5.
No	no	no	**Fairly any problem with Type I Error rates**	**Fairly any problem with Type I Error rates**

2.3 New algorithm to measure standardized effect size

Randomization tests are widely used in ecology when the theoretical distribution of the test statistic under the null-hypothesis is unknown (Gotelli and Graves 1996). The aim of these tests may be twofold: decide if there is a significant departure from the null-model and measuring the amount of the departure. The amount of departure may be input of subsequent "meta"-analysis, e.g. when strength of trait convergence/divergence was studied along an environmental gradient, we can be interested in how these strength is changing along the gradient (e.g. Bernard-Verdier et al. 2012, Mason et al. 2012, Carboni et al. 2014). For measuring the departure from the null-expectation, often the standardized effect size (SES) were calculated referring to the paper of Gotelli & MacCabe(2002). SES measures the deviation from the random expectation in standard deviation units allowing the comparison of values between studies:

$$SES = \frac{I_{obs} - I_{rand}}{\sigma}$$

where I_{obs} = the observed value of the index, I_{rand} is the mean of the index in the random communities, σ = standard deviation of the index in the random communities (Gotelli and McCabe 2002). The index could be a co-occurrence based statistic (Gotelli and McCabe 2002), nestedness(Ulrich and Gotelli 2007), functional diversity (Mason et al. 2012) or any other measure that appropriate for the studied question.

Unfortunately, it is not widely known that SES is based on the assumption of an (approximately) normal distribution of the index if the null-hypothesis is true, or in other word its (approximately) normal distribution in random communities (Ulrich and Gotelli 2010). Therefore the validity of this assumption is rarely checked (but see Ulrich and Gotelli 2007, 2010).

For symmetric distributions – including normal or Gaussian distribution – the expected value and the median is the same, thus both can be estimated by the sample mean. If the observed index equals to the median of the null distribution, the corresponding p-value is 0.5, while if it equals to the expected value SES=0, therefore if the null distribution is symmetric SES=0 implies that p=0.5 and *vice versa* (Figure 3.a). This relationship does not hold for skewed distribution: mean is higher or lower than median in the right or left skewed distribution respectively. Therefore the sign of SES values has handful interpretation only for symmetric distribution (Figure 3.b).

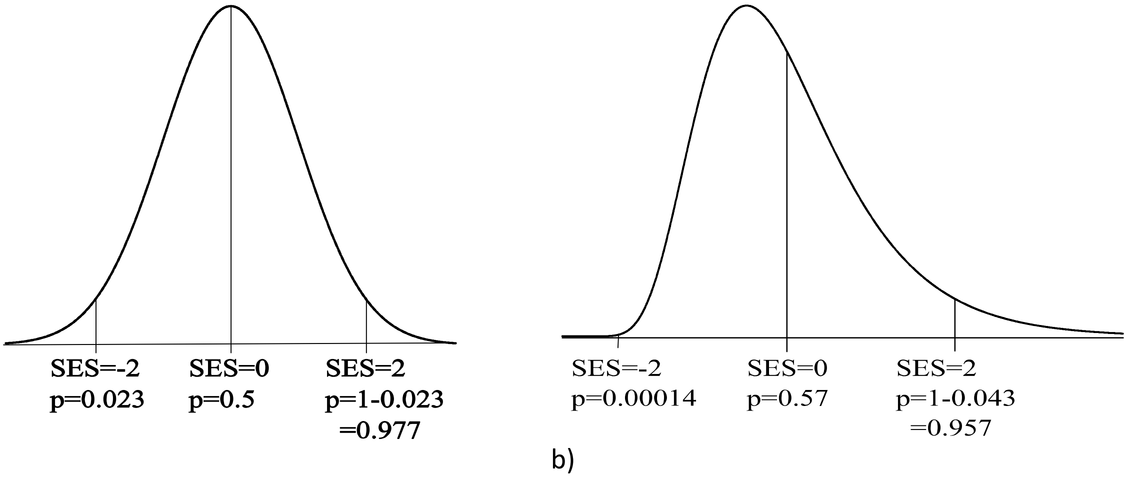


Figure 3. Position of three standardized effect size values (-2, 0, 2) and the related p-values in two-sided test for (a) a symmetric (normal) and right skewed (lognormal) distribution.

If positive and negative SES values have opposite biological meaning (e.g. trait convergence and divergence), it is a desirable property that their absolute values measure the departure from random expectation and the absolute values are comparable even if the signs differ. This property holds for symmetric continuous null distributions only (Figure 3).

Symmetry of distribution can be visually checked using histograms of values in random communities, but for small number of random communities it cannot lead to reliable decision (Figure 4). Therefore I suggest estimating skewness from data (possible estimators are reviewed by Joanes and Gill 1998). Since symmetry has to be checked for each studied community separately, estimating skewness is the only feasible option if the number of communities (number of calculated SES values) are high. Information of the calculated skewness values can be summarized can be summarized by boxplot (see Figure 5 for an example).

Two possible ways to avoid the above mentioned drawbacks of SES are applying transformed test statistic and using probit-transformed p-values for measuring effect size. Any monotonous transformation of test statistic than considerably decrease the skewness may be applied. Unfortunately, there is no generally applicable transformation that always can decrease the skewness to an acceptable level. If the distribution is right skewed, often log-transformation is applied to decrease the skewness. Figure 5Figure shows examples where log-transformation is effective and where it is not, depending on the selected test statistic.

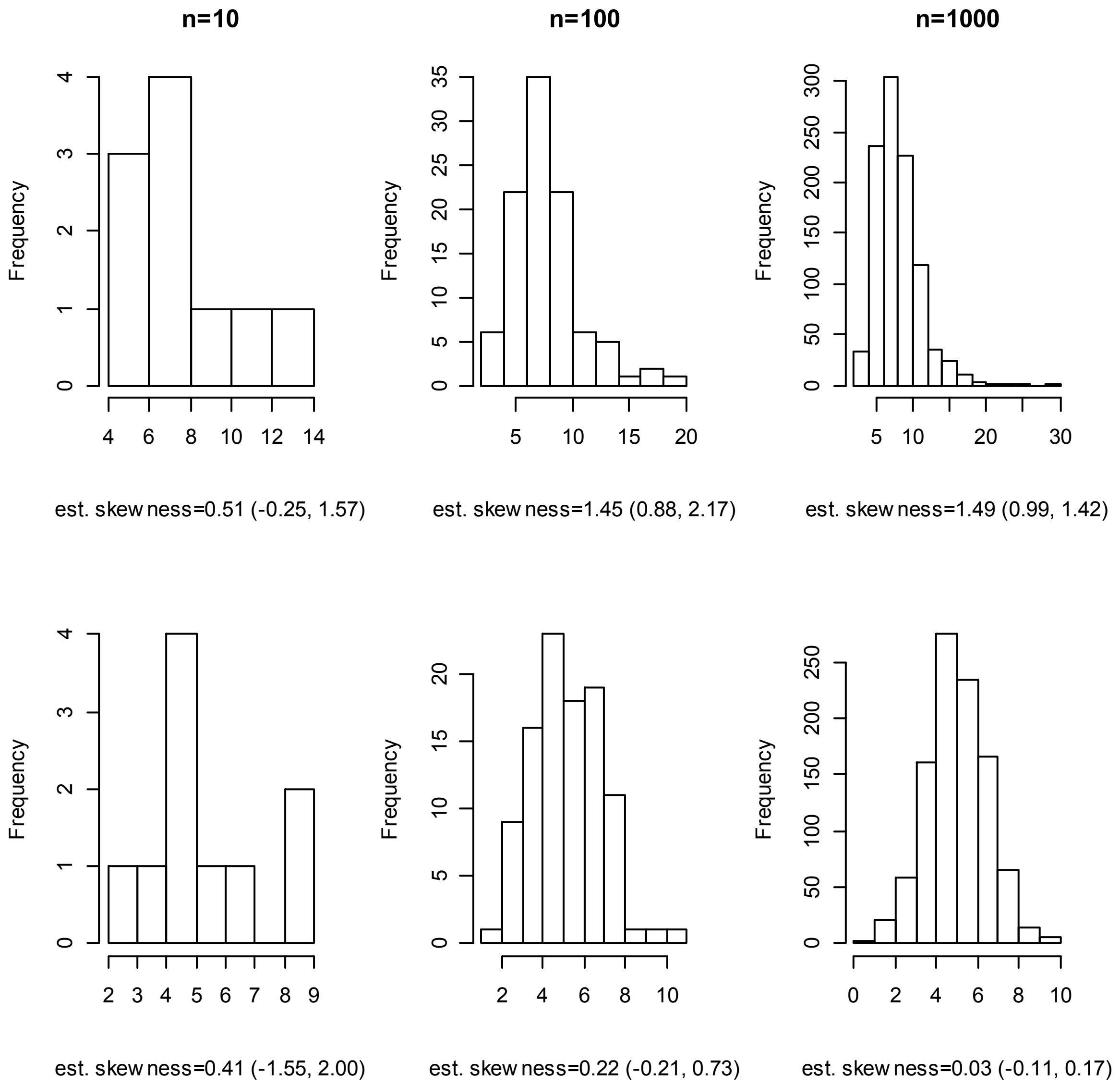
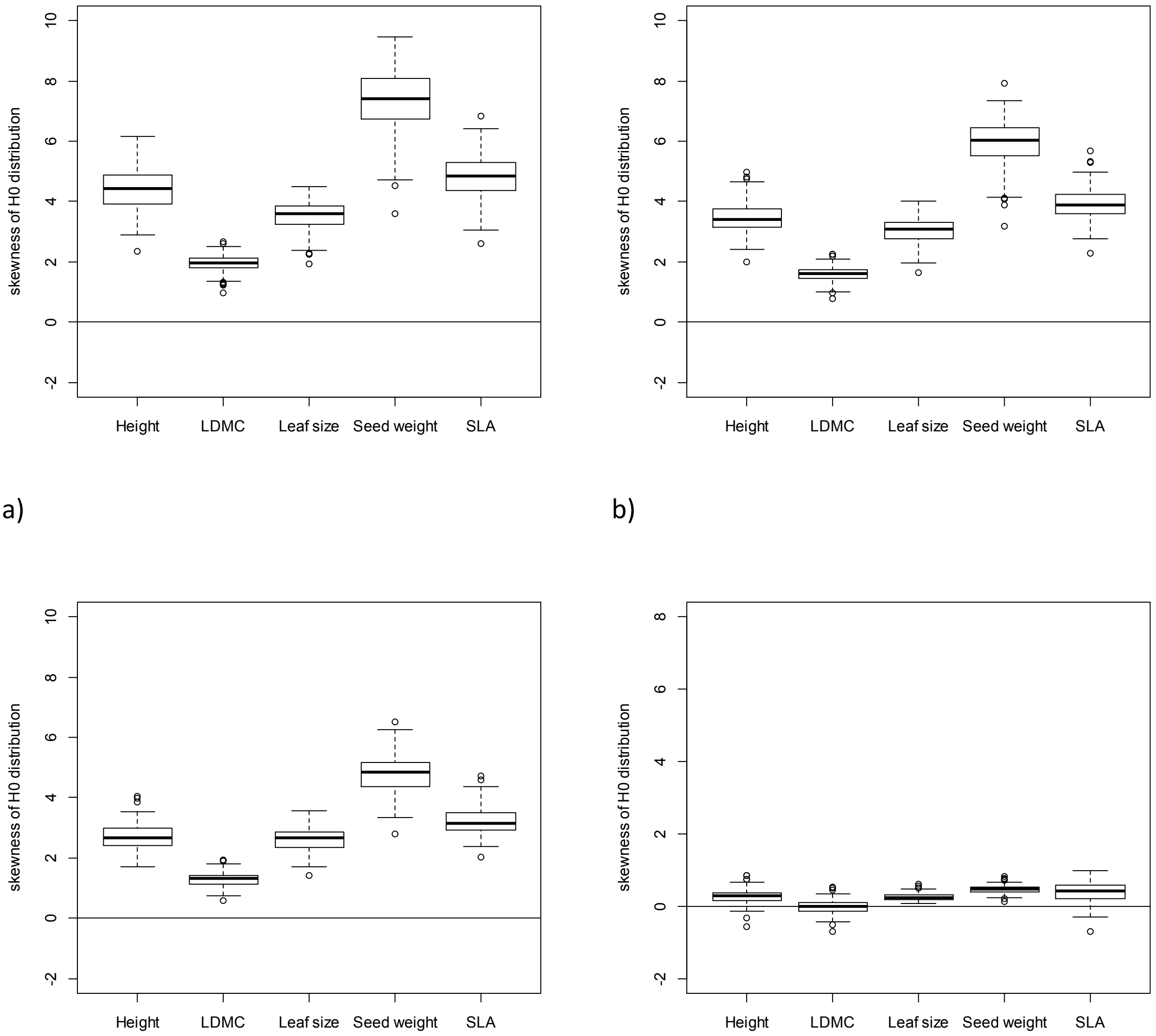


Figure 4. Histograms and estimated skewness with 95% confidence intervals in brackets for lognormally (upper row) and normally (bottom row) with different sample sizes (n). Parameters of both distribution was set up to be expected value = 8 and standard deviation =3. Skewness were estimated by *Skew* function of DescTools package (Signorell and mult. al. 2015) in R environment (R Core Team 2013)

Assuming normal distribution, SES can be used to estimate p-values (this approach is used eg. by Sanders et al. 2003, Schamp and Aarssen 2009, de Bello 2012): $p = 2 * \Phi(-|SES|)$, if the test is two-sided, $p = \Phi(-SES)$ if the alternative hypothesis (H1) is that $I_{obs}<I_{rand}$, and finally $p = \Phi(SES)$ if H1 is $I_{obs}>I_{rand}$, where Φ is the distribution function of standard normal distribution. Probit-transformation uses these relationships in an opposite manner, defining effect size as: $-\Phi^{-1}(p) = \Phi^{-1}(1-p)$. Without multiplying by minus one, the large negative values would mean the strong effect. Hereafter this value will be referred as *probit*(1-p).



a)

b)

c)

d)

Figure 5. Skewness of distribution of functional diversity in random communities using four different test statistics: a) generalized functional diversity with q=2 (^{2}D); b) log-transformed ^{2}D; c) Rao's quadratic entropy (Q); d) log-transformed Q. Random communities were generated for 103 plots resulting in 103 skewness values. See more details in Lhotsky et al. (2016b).

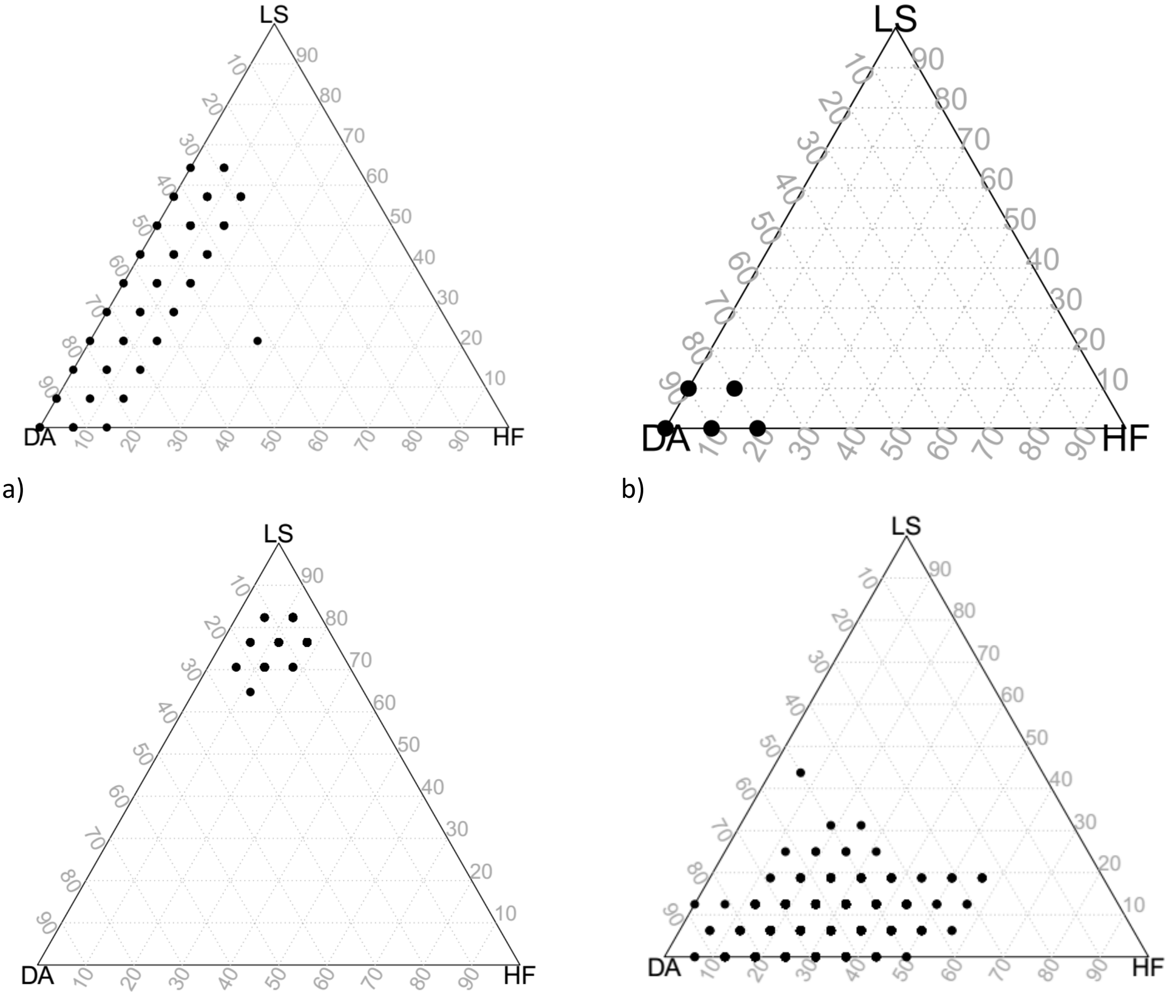
If normality criterion is satisfied, SES gives accurate estimation of effect size even if only few random communities are generated. Further and more important advantage of SES is that it is unbounded thus it can differentiate between large effect sizes, while using traditional approach the lowest p-value, and consequently the highest *probit*(1-p) depends on the number of generated random communities. In randomization tests p-values are generally estimated as:

$$\hat{p} = \frac{b+1}{n+1}$$

where n = number of random communities, b = number of random communities where the test statistic is more extreme than the observed value (e.g. Manly 1997). The possible minimum of $\hat{p}$ is 1/(*n*+1). Thus it is possible that two estimated *probit*(1-p) are the same because both equal to the possible maximum. Knijnenburg et al. (2009) provided a solution for this problem by fitting generalized Pareto-distribution of the most extreme random values and then estimating p-value form this fitted distribution.

2.4 Critique of STEPCAM algorithm

Van der Plas et al. (2014) has recently proposed an algorithm based on Markov Chain Monte Carlo approach that can overcome these limitations, and promised a method for estimating the relative role habitat filtering, limiting similarity and dispersal in assembling local communities from the regional species pool. The STEPCAM algorithm requires presence-absence community data and trait values of occurring species. It approaches the regional species pool by the set of species occurring in the dataset. The applied stochastic algorithm prunes this species pool to the size of local communities by sequential removing of species. In each step, removed species is selected based on rules related to either one of the three processes: dispersal, environmental filtering or competitive exclusion (limiting similarity). The relative role of the three processes is proportional to number of species removed by rules related to them.



a) b)

c) d)

Figure 6. Analysis of simulated communities by STEPCAM algorithm. Since the relative role of three analysed drivers (DA = dispersal limitation, HF = habitat filtering, LS = limiting similarity) sum up to 100%, they can be plotted in a ternary plot. The four subplots represent four simulated meta-communities each consisting 50 sub-communities. Two different parameter sets are used in the simulations, each based on the parameter values listed in Table 1 of Botta-Dukát and Czúcz (2016) with changes described below. In the first parameter set (a & b) the dispersal of propagules becomes unlimited by setting parameter *m*=1. In the second parameter set (c & d) dispersal remained unlimited and interspecific competition switched off by setting σ_B=0.

The algorithm uses two unrealistic hidden assumptions. It uses the same set of traits both in environmental filtering and limiting similarity rules, assuming that each trait plays role in both processes. However it is known from empirical studies (e.g. Lhotsky et al. 2016b) that this assumption is seriously violated, there is no enough a priori knowledge on the role of trait to suggest better assumption. The dispersal related removal of species is inversely related to its relative frequency in the dataset. The implicit assumption behind this rule is that at landscape scale species frequency is determined by their dispersal ability (i.e. species rare only if their dispersal is limited). It may be a reliable assumption in an environmentally homogeneous landscape (but in this case the role of environmental fitlering cannot be estimated, cf. Botta-Dukát and Czúcz 2016), but clearly invalid for environmentally heterogeneous landscape, where specialists of rare habitats are rare even if they are not dispersal limited at all.

The individual based simulation model developed in this project allows us to check if these unsatisfied assumptions distort the results. Analysis of simulated communities (Figure 6) proved that STEPCAM algorithm overestimate the importance of dispersal limitation: this effect was indicated as the major driver in three of four analyzed meta-communities with unlimited dispersal. On the other hand, the algorithm underestimates the importance of habitat filtering: it is indicated as unimportant factor even in meta-communities where dispersal was unlimited and inter-specific competition was switched off.

2.5 Comparing two generalizations of the replication principle

The replication principle was first proposed by Hill (1973) as an advantageous property of his family of diversity indices. Later Jost (2007) discovered that diversity measures satisfying this principle allow partitioning of gamma diversity into independent alpha and beta components by simple multiplicative partitioning. Despite the emerging agreement on measuring taxonomic beta-diversity by multiplicative partitioning of Hill diversity, there is no consensus on how to measure functional beta diversity. Two different generalizations of Hill numbers for measuring functional diversity were proposed by Leinster & Cobbold (2011, hereafter LC) and Chiu & Chao (2014, hereafter CC). Both generalizations attempted to satisfy the generalized replication principle, but they formulate it in different ways.

LC's argumentation starts from the relationship between Hill diversity and generalized mean. The formula for *r*-th order generalized mean of vector **x**, with weights in vector **w** is:

$$ {}^{r}M = \sum_{i=1}^{S} (w_i x_i^r)^{\frac{1}{r}} \qquad \text{(eq. 1.)} $$

Generalized mean is a generalization of arithmetic mean, which is a special case for *r*=1. According to the definition by Patil & Taillie (1979, 1982): diversity is the average rarity within a community weighted by relative abundances. Both Hill diversity and LC-diversity satisfy this definition if "average" replaced by "generalized mean of" (see Proof in Appendix 1). For Hill diversity the rarity is measured by the reciprocal of relative abundances (Patil and Taillie 1982). LC pointed out that relative abundance is a measure of "ordinariness" in the special case when similarity among species is zero, therefore they proposed mean similarity to species (including the focal species itself) as the general measure of "ordinariness", and its reciprocal for measuring rarity.

LC generalized the replication principle similarly to Ricotta & Szeidl (2009): if a sample is divided into *m* subsamples, no species appear in more than one subsample, species in different subsamples are totally dissimilar, and subsamples are equally sized and equally diverse, then diversity of the sample is *mD*, where *D* is the diversity of a subsample. It follows the logic of the original replication principle, but inserts an additional condition (i.e. "species in different subsamples are totally dissimilar"). Note that this condition would be superfluous for taxonomic diversity, where all species are regarded totally different.

CC first gave a simple derivation of Hill diversity: they suggest that *q*-th power sum of the relative abundances in the studied real sample and an idealized reference sample consisting of *D* equally abundant species is equal, if *D* is the *q*-th order diversity of the studied sample:

$$\sum_{i=1}^{s} p_i^q = D\left(\frac{1}{D}\right)^q \Rightarrow D = {}^qD = \left(\sum_{i=1}^{s} p_i^q\right)^{1/(1-q)} \qquad \text{(eq. 2.)}$$

Then they applied this derivation to p_ip_j products with weighting by the distance between i and j for deriving formulas for functional diversity:

$$\sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij}\left(p_ip_j\right)^q = D^2Q\left(\frac{1}{D}\frac{1}{D}\right)^q \Rightarrow D = {}^qD(Q) = \left(\sum_{i=1}^{s}\sum_{j=1}^{s}\frac{d_{ij}}{Q}\left(p_ip_j\right)^q\right)^{1/2(1-q)} \qquad \text{(eq. 3.)}$$

Note that for taxonomic diversity the idealized reference sample consists of equally abundant species, while for functional diversity furthermore each element of the distance-matrix, including its diagonal elements (i.e. distance the species from itself) is Q.

The diversity index by CC obeys the original form of replication principle; i.e. no additional condition on dissimilarity among species from different subsamples has to be inserted.

Both the functional diversity indices suggested by LC and CC reduce to Hill numbers of taxonomic diversity but under different conditions. The index by LC equals to Hill diversity if the similarity between any species pair is zero, while similarity of each species to itself is one. (But note that if similarity between species is interpreted as expected similarity between two randomly selected individuals and within-species variation is considered, similarity of a species to itself may be lower than one.) This condition fits well to the intuition that in traditional taxonomic diversity each species pair is treated as maximally different. CC's functional diversity reduces to Hill's taxonomic diversity if each value of the distance matrix (including values in the main diagonal) is the same. The latter case can occur only if between-species distance is interpreted as expected difference between two individuals randomly selected from the compared species (otherwise there are zeros in the main diagonal of the distance matrix) and the expected difference between two randomly selected individuals is the same irrespectively of their taxonomic affiliation. In such situation intra- and interspecific variation of trait values is the same, therefore by my intuition functional diversity should be independent from taxonomic diversity, not equal to it.

Because of the difference in the interpretation of replication principle, the two functional diversity families differ in conditions necessary for maximizing beta-diversity. Functional beta diversity of CC is always maximal if the taxonomic beta-diversity is maximal (i.e. there are no shared species), irrespectively of the functional dissimilarities among species. It means that if there are no shared species, the original formulas become totally insensitive to the changes in trait values. However, they later developed modified versions of multiple dissimilarities (published as a comment to the original paper) that attain their maximum value if assemblages are completely distinct and any species-pair from different assemblages are maximally distinct. LC functional beta-diversity is maximal if each species occurs only in one subsample (i.e. there are no shared species and thus taxonomic beta diversity is maximal) and similarity between any two species occurring in different subsamples is zero.

Differences in the replication principle also leads to different units of functional diversity, LC functional diversity value of a community can be interpreted as number of equally abundant, functionally totally distinct species that would generate the same diversity. Thus it unit is number of species. The measure ${}^qD(Q)$ of CC (eq. 3) “can be interpreted as ‘the effective number of equally abundant and (functionally) equally distinct species’ with a constant distance Q for all species pairs” (Chiu and Chao 2014), including distance of a species from itself. They also developed an other diversity measure (${}^qFD$ or total functional diversity) that measures the functional diversity in units of distance. It “quantifies the effective total distance between species of the assemblage. If ${}^qFD(Q) = u$, then the effective total distance between species of the actual assemblage with quadratic entropy Q is the same as that of an idealized assemblage having $(u/Q)^{1/2}$ equally abundant and equally distinct species with a constant distance Q for all species pairs.”

The functionally identical species principle was proposed by Solow et al. (1993): diversity should not be increased by the addition of a species if its minimum distance to the other occurring species is zero. More precise definition can be given by using the term “functionally identical species” (Weitzman 1992). Two species A_1 and A_2 are functionally identical if the distance between them is zero ($d(A_1,A_2)=0$) and they equally differ from any third species ($d(A_1,B)=d(A_2,B)$). Merging functionally identical species into one species (e.g. A1 and A2 into A), or, in opposite, dividing a species aggregate into functionally identical but taxonomically distinct species should not change the functional diversity (Weitzman 1992). Taxonomically distinct but functionally identical species can be called twin species, therefore following Weitzman (1992) satisfying this principle could be referred to as ‘twin property’.

The usefulness of this principle is debated. CC have added a comment to their paper where they argued that relevance of this principle depends on the goal of the study. They distinguished two major types of goals: relating functional diversity to ecosystem functioning (e.g. Tilman et al. 1997) and quantifying “the community resilience or adaptive capacity in the face of environmental changes” (Walker et al. 1999). It does not influence the ecosystem functions that many functionally identical species play a role in the ecosystem; therefore twin property makes sense in the first approach. On the other hand, functionally redundant (twin) species may help to buffer the effect of species loss (Díaz and Cabido 2001); therefore the twin property is not necessary in the second approach. The third possible goal is exploring the rules of community assembly (Götzenberger et al. 2012). While the other two approaches are related to diversity of effect traits (Lavorel and Garnier 2002), in the community assembly studies the diversity of response traits are considered. Species with same response traits would behave as neutral species, whose abundance and distribution are driven only by stochasticity (Hubbell 2001). The aim of community assembly studies is detecting the departure from this random expectation (either convergence due to environmental filtering or divergence due to limiting similarity), thus twin property makes sense in this approach too.

LC functional diversity obeys the functionally identical species principle, while CC functional diversity does not. If it makes a problem, this issue can be solved within framework of CC (as they suggested in a comment to their paper) by replacing term “species” with “operational functional unit” (OFU) as proposed by Ricotta (2005) and Schmera et al. (2009); two individuals belong to the same OFU, if they did not differ in their considered traits.

Properties of the two families of functional diversity are summarized inTable 4. It can be seen that both generalization has its own virtues. The importance of these virtues strongly depends on the aim of the study. For example, obeying identical species principle is a necessary condition of a functional diversity measure used for relating functional diversity to ecosystem functioning or exploring rules of community assembly. Therefore, I recommend using LC measure for these purposes. After merging functionally identical species into operational functional units CC measure also can be used in diversity-ecosystem function studies, but this solution cannot be used in community assembly studies. On the other hand, twin property is not necessary when our aim is quantifying the community resilience. In such cases CC measure probably outperforms LC functional diversity.

Table 4. Comparing some properties of the two functional diversity families developed from different generalization of replication principle. Desirable properties are highlighted by bold typeface.

Property	**LC functional diversity**	**CC functional diversity**
Obeys replication principle	in its modified version (see details in the main text)	in its original form
Reduces to original Hill diversity, if…	**… d_{ij}=1 for every $i \neq j$**	… if d_{ij}=constant, for every *i* and *j*, including *i*=*j*
If there are no shared species, functional beta-diversity…	**… depends on the trait similarities among subsamples**	… always maximal, but multiple dissimilarity measures sensitive to trait similarities are proposed
Obeys “twin property”:	**Yes**	only if species merged into operational functional units before the analysis
Beta-diversity ranges from 1 to number of subsamples	only for specific similarity/dissimilarity matrices	**always**
Sensitive to the values of scale parameter	depends on the way to transform distances into similarities	**always**

3 Case studies

3.1 Changing assembly rules along productivity gradient (Orgovány site)

The strength and the relative importance of environmental filtering and limiting similarity may change along productivity or stress gradients. While this hypothesis is widely accepted and proved by several case studies in various ecosystems (e.g. Mason et al. 2011, 2012, Pakeman 2011), there is stil controversy over the direction and causes of the changes (Carboni et al. 2014). The stress-dominance hypothesis predicts that it is environmental filtering and the resulting trait convergence that plays the major role in harsher environments, while limiting similarity and the resulting trait divergence will be more important in more favorable habitats (Weiher and Keddy 1995, Swenson and Enquist 2007, Coyle et al. 2014). In line with the stress-dominance hypothesis, Mason et al. (2011) found that niche overlap decreased with increasing productivity, indicating that limiting similarity has a stronger effect in more productive habitats. On the other hand, the opposite trend, transition from trait divergence to trait convergence with increasing productivity was found in other studies (e.g. Pakeman 2011, Mason et al. 2012, Carboni et al. 2014). This is in agreement with Grime’s prediction (2006, see also Mayfield and Levine 2010) that higher productivity should lead to trait convergence since increasing competition excludes species with traits associated with poorer competitive ability. Navas & Violle (2009) argued that trait convergence is expected at both ends of the productivity gradient, and trait divergence at medium productivity. Overall, there is still ongoing controversy on how the strength of trait divergence and convergence varies along productivity gradients.

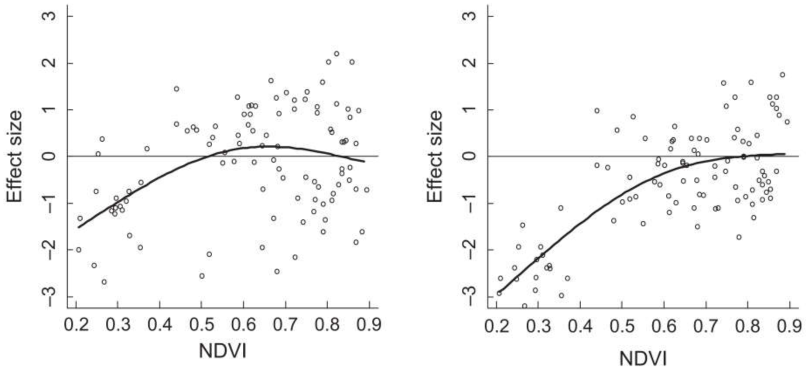
Trends may depend on which traits are involved in the study (Bernard-Verdier et al. 2012, Spasojevic and Suding 2012) and which part of the stress gradient is sampled (Bernard-Verdier et al. 2012). Therefore, trait convergence/divergence patterns should be analyzed along as long gradients as possible to test the predictions of the two competing theories, environmental filtering and limiting similarity. At the same time, the effects of other confounding factors, especially dispersal limitation should be reduced as much as possible. Sampling plots therefore have to be situated within a relatively small area, which limits the length of productivity gradients. As a consequence, previous studies were often conducted within a single habitat type [e.g. in dolomite (Bernard-Verdier et al. 2012), or wet grasslands (Carboni et al. 2014)]. The Kiskunság in Central Hungary is an ideal setting to overcome these limitations: due to its climate, diverse geomorphology and special soil characteristics, soil moisture availability is strikingly diverse, allowing us to study an extremely long productivity gradient within a relatively small area (Kovács-Láng et al. 2008). This gradient ranges from semi-desert like open sand grasslands through closed dry, mesic and wet grasslands to wetlands and reed beds.

The aim of this study was to answer the following questions:

1. Is there convergence, and for which traits?
2. Is there divergence, and for which traits?
3. Does their strength change with increasing productivity?
4. How do the optimal (mean) trait values and the values filtered out by environmental filtering vary along a productivity (stress) gradient?

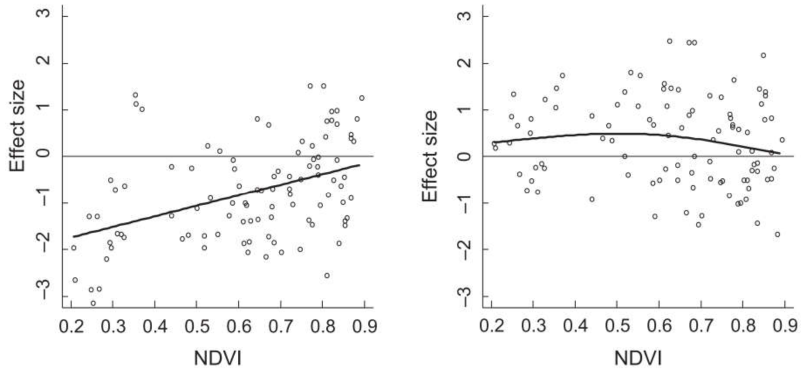
Fisher’s omnibus test found strong evidence for trait convergence when all traits were pooled. If traits were analysed independently, there was strong evidence for convergence, that is for the existence of environmental filtering in the case of canopy height, leaf size, SLA and ‘life span’. We found evidence of trait divergence and therefore of the existence of limiting similarity only in the case of LDMC and seed weight. The average effect of trait convergence was stronger under harsher conditions and became weaker with growing productivity in the case of canopy height, leaf size and SLA (Figure 7). There was an opposite trend for ‘life span’ and no significant changes in the case of ‘shoot form’ or if all traits were pooled. Trait divergence became weaker with growing productivity for seed weight, but there was a strong convergence for some plots with high NDVI. The strength of trait divergence for LDMC did not change significantly along the productivity gradient (Figure 7).

We found changes in the optimal (mean) and filtered out trait values along the productivity gradient. The community weighted mean of canopy height responded to the productivity gradient as expected: it increased with increasing productivity (Figure 8). Both the upper and lower boundaries increased, although the former’s increase was steeper. We can thus say that tall plants are filtered out in habitats with low productivity, while short ones in habitats with high productivity. Similar trends were observed for the CWM of leaf size, SLA and ‘life span’ (Figure 8). The upper boundary of leaf size increased steeply, while the lower boundary grew more moderately. The upper and lower boundaries for SLA run parallel with CWM; filtering is therefore mainly caused by the shift of the preferred value.



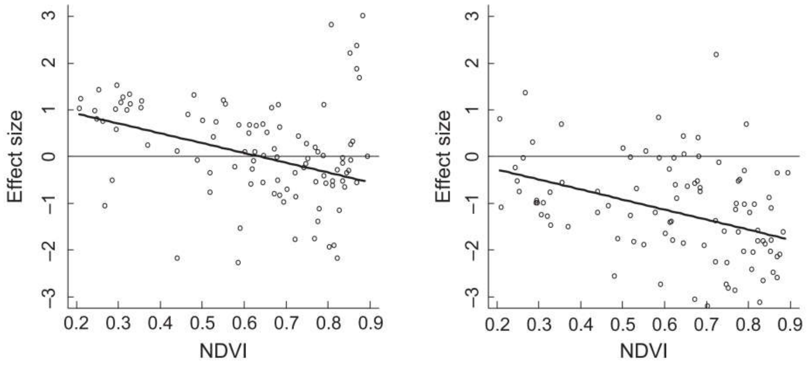
(a) height ($P<0.0001$)

(b) leaf size ($P<0.0001$)



(c) SLA ($P<0.0001$)

(d) LDMC ($P = 0.52$)

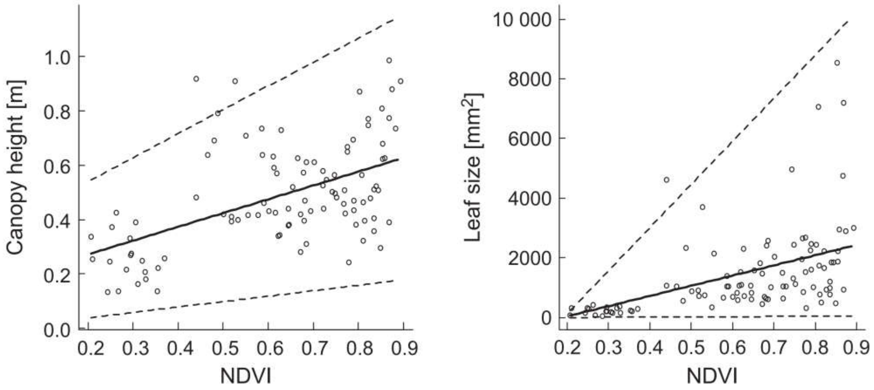


(e) seed weight ($P<0.0001$)

(f) life span (Axis1) ($P<0.0001$)

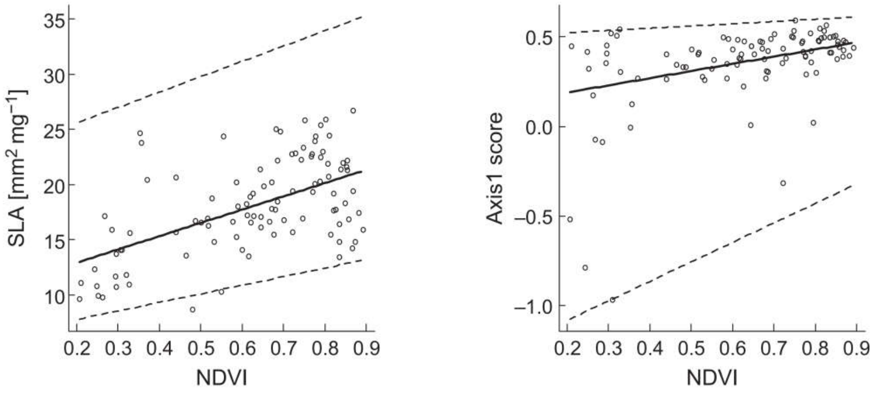
Figure 7. Effect sizes (probit-transformed p-values; see chapter 2.3) in plot-level tests of trait convergence/divergence along the NDVI (a proxy of productivity) gradient. Positive values indicate divergence, negative ones convergence. Absolute values higher than 1.95 mean that the plot-level test is significant at the 5% level. Lines are trends fitted by GAM; departure of the fitted trend from the horizontal line was tested, and the resulting P-values can be seen below the figures in brackets.

Our findings support the hypothesis that both environmental filtering and limiting similarity play a role in forming plant assemblages along our extremely long productivity gradient. When all traits were pooled, strong convergence was found, but the analysis of individual traits showed that even traits associated with similar functions (SLA and LDMC) can show a different pattern. For vegetative traits related to resource use, convergence was predominant, indicating the presence of environmental filtering. On the other hand, traits related to regeneration showed divergence, indicating limiting similarity. The strength of the assembly forming processes changed along the gradient: the filtering effect of the habitat was stronger under harsher environments, which supports the stress dominance hypothesis (Coyle et al. 2014). As productivity increased, environmental constraints on the traits related to resource use became weaker and the coexistence of various water and nutrient use strategies became possible. Due to this larger diversity in traits related to resource acquisition, the importance of differing in reproductive strategy become less important in maintaining stable coexistence.



(a) height

(b) leaf size



(c) SLA

(d) life span (Axis1)

Figure 8. Community-weighted trait values in the sampled plots (points), their trend (solid line) and the trend of lower and upper boundaries (dashed lines) along the NDVI (a proxy of productivity) gradient.

3.2 Assembly of forest herb layer (Várhegy site)

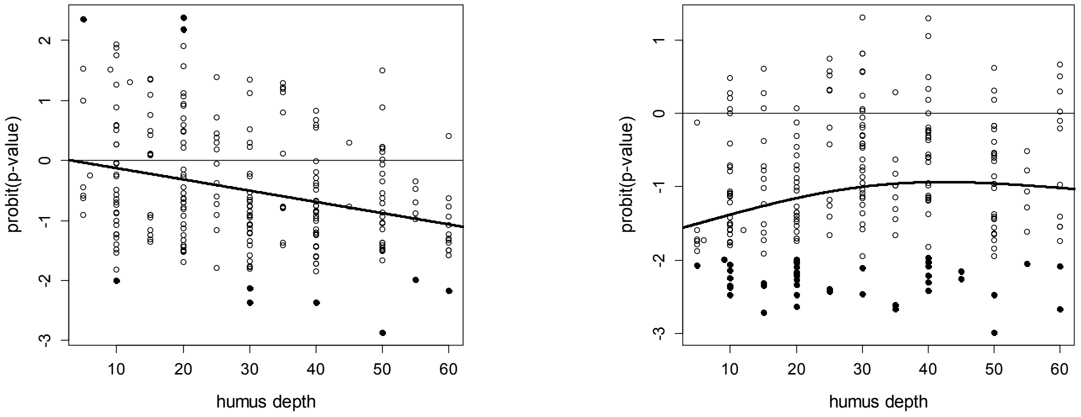
The Vár-hegy Forest Reserve is situated in the oak woodland zone of the Pannonian Ecoregion, in the Bükk Mountains (northern part of Hungary), belonging to the most southern part of the North-West Carpathians. It belongs to the Forest Reserve Network of Hungary, which was established in the 1990s to preserve unmanaged forest stands on free development as natural reference and to ensure legal basis and field facilities for long term ecological research (Horváth and Borhidi 2002). The size of its core area is 94 ha, the buffer zone is 245 ha, the altitude range from 300 to 600 m a.s.l.

The Vár-hegy Forest Reserve has diverse forest vegetation composed mainly by turkey oak – sessile oak forests, (Quercetum petraeae-cerris), oak – hornbeam forests (Carici pilosae – Carpinetum), downy oak forests (Corno – Quercetum pubescentis) and beech forests (Melitti – Fagetum). These strictly protected 120-130 years old stands has not been managed for 20-40 years. The core area was surveyed according to the “ERDŐ+h+á+l+ó” methodology in 2005-2008. The herb layer data of this survey were used in the case study.

This case study was devoted to the replication of the other one in Orgovány, thus we plan to study same questions by same methods. The only planned difference between the two case studies is in the considered environmental gradients. Productivity of the herb layer may limited by both nutrient and light availability, therefore we measured two proxy variables related to them: depth of humus layer and canopy cover.

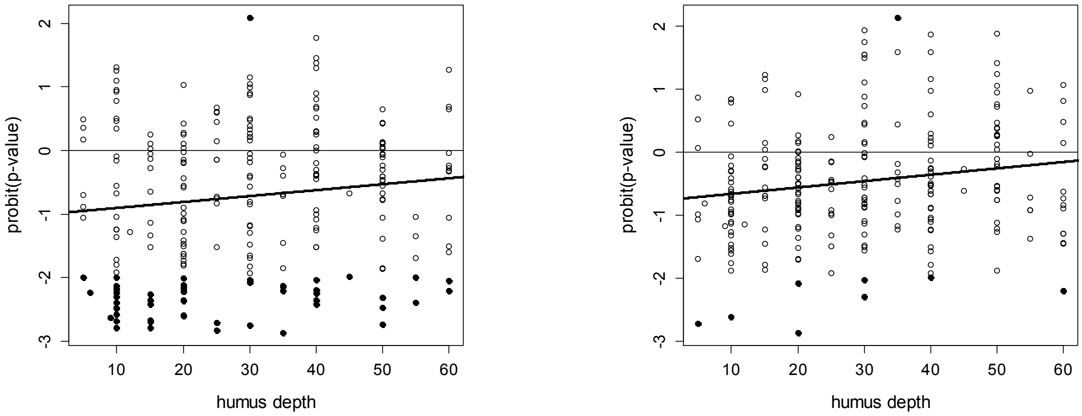
Table 5. Results of the Fisher's omnibus test. It combines the plot-level p-values of randomization test into an overall test statistic that approximately follows Chi-square distribution.

	Trait convergence		Trait divergence	
	Chi-square statistic	p-value	Chi-square statistic	p-value
Height	337.0369	1	**1092.089**	**<0.0001**
Leaf size	460.1924	1	**994.1651**	**<0.0001**
SLA	217.353	1	**1476.237**	**<0.0001**
LDMC	**2189.807**	**<0.0001**	125.1915	1
seed weight	388.9019	1	**1233.556**	**<0.0001**
PC1 (life span)	435.9075	1	**964.0892**	**<0.0001**
PC2 (shoot form)	533.1279	0.9999	**1445.117**	**<0.0001**



a) Lef size ($p=7.424*10^{-6}$)

SLA (p=0.00471)



seed weight (p=0.047905**)**

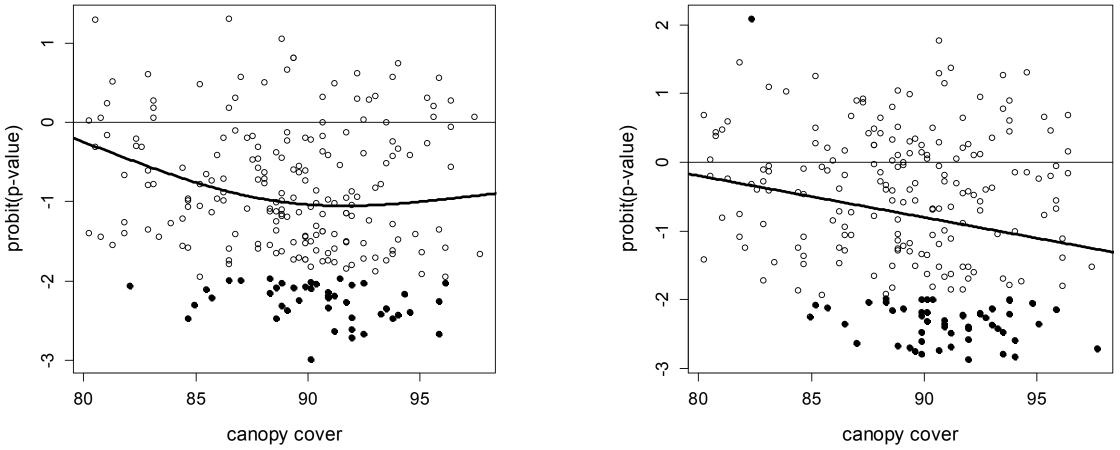
PC1 (life span) (p=0.00947)

Figure 9. Effect sizes (probit-transformed p-values; see chapter 2.3) in plot-level tests of trait divergence along the depth of humus layer gradient. Positive values indicate convergence, negative ones divergence. Absolute values higher than 1.95 mean that the plot-level test is significant at the 5% level. Lines are trends fitted by GAM; departure of the fitted trend from the horizontal line was tested, and the resulting P-values can be seen below the figures in brackets.

Contrary to the Orgovány Site, functional diversity for most traits was higher than random expectation (trait divergence), except LDMC that shows trait convergence (Table 5). Thus we can say that the dominant force of community assembly is the limiting similarity, however we tried to sample as long environmental gradients as possible to make possible detecting habitat filtering.

There is no general trend in the effect size of limiting similarity: for three of the six traits (SLA, seed weight, life span) the effect is decreasing with depth of humus layer, for height and shoot form there was no trend, while leaf size shows the opposite trend (Figure 9). Effect size in divergence of SLA and seed weight is higher if the canopy is closer, but canopy closure does not affect the divergence of other traits. Convergence in LDMC values is higher in deeper soils, but independent from canopy closure.

Results of this case study shows that trait-based assembly rules are contingent: the same trait could show convergent and divergent pattern under different environmental conditions and/or different species pool. Its worthy for further research if rules established Orgovány and Várhegy can be applied in other sites in the Kiskunság sand region and Hungarian oak forests, respectively.



a) SLA (p=0.00154) b) seed weight (p=0.001299)

Figure 10. Effect sizes (probit-transformed p-values; see chapter 2.3) in plot-level tests of trait divergence along the canopy cover gradient.

3.3 Changes of trait-environmental correlation during forest succession

This case study has been done in an international collaboration. The PI of this project joined the research group in the phase of data analysis only, but he has done the statistical analyses and contributed to the interpretation of the results.

The study area is located in the southern part of the Marche Region (Central Apennines, Italy) in the Monti Sibillini National Park. The area represents a silvipastoral system where coppice management with short time rotation (25–30 years) is traditionally applied to a large extent (more than 70%), also including beech (*Fagus sylvatica*) forests. Over the last decades the traditional coppice management of these systems are being gradually abandoned in 21% of present beech woodlands. 60 forest stands were chosen using a stratified sampling design based on an historical survey to represent the various stages of forest succession and landscape heterogeneity (Bartha et al. 2008). The following stratification criteria were used: age since last coppicing, bedrock (limestone and sandstone) and elevation classes (1000–1200 m and 1200–1400 m). We selected 14 easy-to-measure plant traits assumed to reflect key processes of forest dynamics. Seven traits were related to plant persistence, reflecting sharing or saving energy, and the presence of meristems (*Long-term spacer longevity, Storage, Long-term connection, Thickening, Extensive perennial root, Large bud bank*), three traits were related to spatial dispersal (*Seed mass, Short-distance seed dispersal, Seed releasing height*), and four traits were linked to plant growth and included *SLA, Fast lateral spread, Long spacers, Frequent multiplication*.

The data were analyzed by Model-Based Recursive Partitioning (MOB; Zeileis et al. 2008). MOB fits a model tree using the following steps:

1. Fit of a linear model (using community level trait data as the dependent variable, and one of the environmental variables as the independent variable) for all observations.
2. Assessing of the stability of the model parameters with respect to the partitioning variable (here stand age) and search for the locally optimal split. If the Bonferroni-corrected p-value of the optimal split is smaller than the significance level ($\alpha = 0.05$), data are divided into two parts, otherwise stop.
3. Re-fit of the model in both parts, and repeat from Step 2.

We used all five explanatory environmental variables (succession stand age, elevation, inclination, heat index (HI) and bedrock) that are presumed to affect trait–environment relationships at the landscape scale. Continuous environmental variables were centred prior to analysis. Hence the intercept parameter of the model can be interpreted as expected community weighted trait value for a given mean value of the respective environmental variable. This transformation does not influence the slope of the regression line.

About half of the plant traits showed significant correlations with the explanatory abiotic environmental variables. Most of these trait–environment relationships changed significantly between the age groups revealed by MOB: the trait-environment relationship proved to be stronger and steeper in older stands (Figure 11). This confirms the tested assumption that the correlations between traits and environmental factors would increase with succession age due to the decreasing role of chance factors. Our results lend support to this hypothesis. Only one trait (Large bud bank) showed correlation with one abiotic factor in sites younger than 14 years, while eight traits showed correlations with three environmental factors in older stages. According to the classic theory of vegetation succession (see Glenn-Lewin 1980) the predictive power of abiotic factors increases over time with a decreasing role of chance factors. Even in a very simple situation with constant environmental filtering, the correlation between vegetation and environment should increase along the assembly process due to the cumulative effect of pattern selection. We argue that species turnover probably plays an important role in determining the directional shift in trait values across sites and along gradients (Bartha et al. 2008, Cornwell and Ackerly 2009). In fact, in a plant-diversity focused chronosequence study in the same area, Bartha et al. (2008) found considerable species turnover along the chronosequence of post-coppice forest regeneration showing a clear trend—forest specialists increased whereas non-forest species decreased.

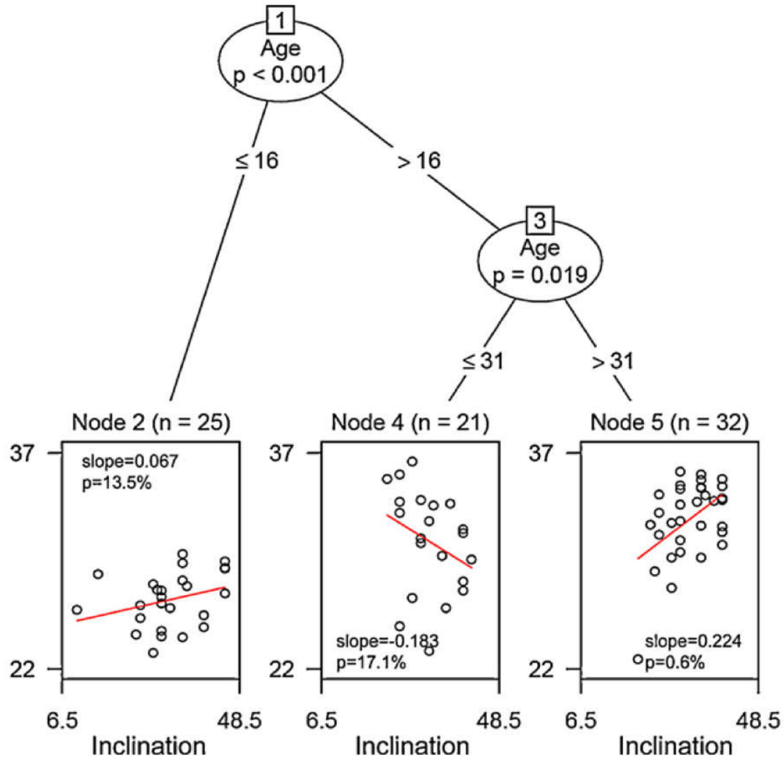


Figure 11. Illustration of the results of Model-Based Recursive Partitioning showing the relationship between inclination and SLA, using age as a splitting variable

4 Literature

Aiba, M., M. Katabuchi, H. Takafumi, S. S. Matsuzaki, T. Sasaki, and T. Hiura. 2013. Robustness of trait distribution metrics for community assembly studies under the uncertainties of assembly processes. Ecology 94:2873–2885.

Bartha, S., A. Merolli, G. Campetella, and R. Canullo. 2008. Changes of vascular plant diversity along a chronosequence of beech coppice stands, Central Apennines, Italy. Plant Biosystems 142:572–583.

de Bello, F. 2012. The quest for trait convergence and divergence in community assembly: are null-models the magic wand? Global Ecology and Biogeography 21:312–317.

de Bello, F., C. P. Carmona, N. W. H. Mason, M.-T. Sebastia, and J. Leps. 2013. Which trait dissimilarity for functional diversity: trait means or trait overlap? Journal of Vegetation Science 24:807–819.

de Bello, F., J. N. Price, T. Münkemüller, J. Liira, M. Zobel, W. Thuiller, P. Gerhold, L. Götzenberger, S. Lavergne, J. Lepš, K. Zobel, and M. Pärtel. 2012. Functional species pool framework to test for biotic effects on community assembly. Ecology 93:2263–2273.

Bernard-Verdier, M., M.-L. Navas, M. Vellend, C. Violle, A. Fayolle, and E. Garnier. 2012. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. Journal of Ecology 100:1422–1433.

Botta-Dukát, Z., and B. Czúcz. 2016. Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. Methods in Ecology and Evolution 7:114–126.

ter Braak, C. J. F. 1986. Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis. Ecology 67:1167–1179.

Campetella, G., Z. Botta-Dukát, C. Wellstein, R. Canullo, S. Gatto, S. Cheli, L. Mucina, and S. Bartha. 2011. Patterns of plant trait-environment relationships along a forest succession chronosequence. Agriculture, Ecosystems & Environment 145:38–48.

Carboni, M., F. de Bello, Š. Janeček, J. Doležal, J. Horník, J. Lepš, T. Reitalu, and J. Klimešová. 2014. Changes in trait divergence and convergence along a productivity gradient in wet meadows. Agriculture, Ecosystems & Environment 182:96–105.

Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2016. Traits Without Borders: Integrating Functional Diversity Across Scales. Trends in Ecology & Evolution 31:382–394.

Chiu, C.-H., and A. Chao. 2014. Distance-Based Functional Diversity Measures and Their Decomposition: A Framework Based on Hill Numbers. PLoS ONE 9:e100014.

Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs 79:109–126.

Cornwell, W. K., D. W. Schwilk, and D. D. Ackerly. 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87:1465–1471.

Coyle, J. R., F. W. Halliday, B. E. Lopez, K. A. Palmquist, P. A. Wilfahrt, and A. H. Hurlbert. 2014. Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. Ecography 37:814–826.

Díaz, S., and M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16:646–655.

Glenn-Lewin, D. C. 1980. The individualistic nature of plant community development. Vegetatio 43:141–146.

Gotelli, N. J., and G. R. Graves. 1996. Null Models in Ecology. Smithsonian Institution Press, Washington, D.C.

Gotelli, N. J., and D. J. McCabe. 2002. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. Ecology 83:2091–2096.

Götzenberger, L., F. de Bello, K. A. Bråthen, J. Davison, A. Dubuis, A. Guisan, J. Lepš, R. Lindborg, M. Moora, M. Pärtel, L. Pellissier, J. Pottier, P. Vittoz, K. Zobel, and M. Zobel. 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. Biological Reviews 87:111–127.

Götzenberger, L., Z. Botta-Dukát, J. Lepš, M. Pärtel, M. Zobel, and F. de Bello. 2016. Which randomizations detect convergence and divergence in trait-based community assembly? A test of commonly used null models. Journal of Vegetation Science 27:1275–1287.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. Journal of Vegetation Science 17:255–260.

Hill, M. O. 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54:427–432.

Horváth, F., and A. Borhidi, editors. 2002. A hazai erdőrezervátum-kutatás célja, stratégiája és módszerei. TermészetBÚVÁR Alapítvány Kiadó, Budapest.

Hubbell, S. P. 2001. A Unified Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Jabot, F. 2010. A stochastic dispersal limited trait based model of community dynamics. Journal of Theoretical Biology 262:650–661.

Joanes, D. N., and C. A. Gill. 1998. Comparing measures of sample skewness and kurtosis. Journal of the Royal Statistical Society: Series D (The Statistician) 47:183–189.

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

Katabuchi, M., H. Kurokawa, S. J. Davies, S. Tan, and T. Nakashizuka. 2012. Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. Journal of Ecology 100:643–651.

Knijnenburg, T. A., L. F. A. Wessels, M. J. T. Reinders, and I. Shmulevich. 2009. Fewer permutations, more accurate P-values. Bioinformatics 25:i161–i168.

Kovács-Láng, E., E. Molnár, G. Kröel-Dulay, and S. Barabás, editors. 2008. The KISKUN LTER: Long-term ecological research in the Kiskunság, Hungary. Institute of Ecology and Botany, Hungarian Academy of Sciences.

Laliberté, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545–556.

Leinster, T., and C. A. Cobbold. 2011. Measuring diversity: the importance of species similarity. Ecology 93:477–489.

Lhotsky, B., A. Csecserits, B. Kovács, and Z. Botta-Dukát. 2016a. New plant trait records of the Hungarian flora. Acta Botanica Hungarica 58:397–400.

Lhotsky, B., B. Kovács, G. Ónodi, A. Csecserits, T. Rédei, A. Lengyel, M. Kertész, and Z. Botta-Dukát. 2016b. Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. Journal of Ecology 104:507–517.

MacArthur, R., and R. Levins. 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. The American Naturalist 101:377–385.

Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Second Edition. Chapman & Hall, London.

Mason, N. W. H., F. de Bello, J. Doležal, and J. Lepš. 2011. Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. Journal of Ecology 99:788–796.

Mason, N. W. H., F. de Bello, D. Mouillot, S. Pavoine, and S. Dray. 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. Journal of Vegetation Science 24:794–806.

Mason, N. W. H., D. Mouillot, W. G. Lee, and J. B. Wilson. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118.

Mason, N. W. H., S. J. Richardson, D. A. Peltzer, F. de Bello, D. A. Wardle, and R. B. Allen. 2012. Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. Journal of Ecology 100:678–689.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093.

Mouchet, M. A., S. Villéger, N. W. H. Mason, and D. Mouillot. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology 24:867–876.

Münkemüller, T., F. de Bello, C. N. Meynard, D. Gravel, S. Lavergne, D. Mouillot, N. Mouquet, and W. Thuiller. 2012. From diversity indices to community assembly processes: a test with simulated data. Ecography 35:468–480.

Münkemüller, T., L. Gallien, and J. Travis. 2015. VirtualCom: a simulation model for eco-evolutionary community assembly and invasion. Methods in Ecology and Evolution 6:735–743.

Navas, M., and C. Violle. 2009. Plant traits related to competition: how do they shape the functional diversity of communities? Community Ecology 10:131–137.

Pakeman, R. J. 2011. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. Journal of Ecology 99:1143–1151.

Patil, G. P., and C. Taillie. 1979. An overview of diversity. Pages 3–27 *in* J. F. Grassle, G. P. Patil, W. Smith, and C. Taillie, editors. Ecological Diversity in Theory and Practice. International Cooperative Publishing House, Fairland, MD.

Patil, G. P., and C. Taillie. 1982. Diversity as a Concept and its Measurement. Journal of the American Statistical Association 77:548–561.

Pavoine, S., and M. B. Bonsall. 2011. Measuring biodiversity to explain community assembly: a unified approach. Biological Reviews 86:792–812.

van der Plas, F., T. Janzen, A. Ordonez, W. Fokkema, J. Reinders, R. S. Etienne, and H. Olff. 2014. A new modeling approach estimates the relative importance of different community assembly processes. Ecology 96:1502–1515.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raevel, V., C. Violle, and F. Munoz. 2012. Mechanisms of ecological succession: insights from plant functional strategies. Oikos 121:1761–1770.

Ricotta, C. 2005. A note on functional diversity measures. Basic and Applied Ecology 6:479–486.

Ricotta, C., and L. Szeidl. 2009. Diversity partitioning of Rao's quadratic entropy. Theoretical Population Biology 76:299–302.

Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. Proceedings of the National Academy of Sciences 100:2474–2477.

Schamp, B. S., and L. W. Aarssen. 2009. The assembly of forest communities according to maximum species height along resource and disturbance gradients. Oikos 118:564–572.

Schmera, D., T. Erős, and J. Podani. 2009. A measure for assessing functional diversity in ecological communities. Aquatic Ecology 43:157–167.

Signorell, A., and mult. al. 2015. DescTools: Tools for descriptive statistics.

Solow, A., S. Polasky, and J. Broadus. 1993. On the Measurement of Biological Diversity. Journal of Environmental Economics and Management 24:60–68.

Spasojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. Journal of Ecology 100:652–661.

Swenson, N. G., and B. J. Enquist. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. American Journal of Botany 94:451–459.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. Science 277:1300–1302.

Ulrich, W., and N. J. Gotelli. 2007. Null model analysis of species nestedness patterns. Ecology 88:1824–1831.

Ulrich, W., and N. J. Gotelli. 2010. Null model analysis of species associations using abundance data. Ecology 91:3384–3397.

Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301.

Walker, B., A. Kinzig, and J. Langridge. 1999. Plant Attribute Diversity, Resilience, and Ecosystem Function: The Nature and Significance of Dominant and Minor Species. Ecosystems 2:95–113.

Weiher, E., G. D. P. Clarke, and P. A. Keddy. 1998. Community Assembly Rules, Morphological Dispersion, and the Coexistence of Plant Species. Oikos 81:309–322.

Weiher, E., and P. A. Keddy. 1995. Assembly Rules, Null Models, and Trait Dispersion: New Questions from Old Patterns. Oikos 74:159–164.

Weitzman, M. L. 1992. On Diversity. The Quarterly Journal of Economics 107:363–405.

Willis, C. G., M. Halina, C. Lehman, P. B. Reich, A. Keen, S. McCarthy, and J. Cavender-Bares. 2010. Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. Ecography 33:565–577.

Zeileis, A., T. Hothorn, and K. Hornik. 2008. Model-based recursive partitioning. Journal of Computational and Graphical Statistics 17:492–514.