

Fourth-corner generation of plant functional response groups

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Abstract Plant functional response groups (PFGs) are now widely established as a tool to investigate plant—environment relationships. Different statistical methods to form PFGs are used in the literature. One way is to derive emergent groups by classifying species based on correlation of biological attributes and subjecting these groups to tests of response to environmental variables. Another way is to search for associations of occurrence data, environmental variables and trait data simultaneously. The fourth-corner method is one way to assess the relationships between single traits and habitat factors. We extended this statistical method to a generally applicable procedure for the generation of plant functional response groups by developing new randomization procedures for presence/absence data of plant communities. Previous PFG groupings used either predefined groups or emergent groups i.e. classifications based on correlations of biological attributes (Lavorel et al *Trends Ecol Evol* 12:474–478, 1997), of the global species pool and assessed their functional response. However, since not all PFGs might form emergent groups or may be known by experts, we used a permutation procedure to optimise functional grouping. We tested the method using an artificial test data set of virtual plants occurring in different disturbance treatments. Direct trait-treatment relationships as well as more complex associations are incorporated in the test data. Trait combinations responding to environmental variables could be clearly distinguished from non-responding combinations. The results are compared

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with the method suggested by Pillar (J Veg Sci 10:631–640) for the identification of plant functional groups. After exploring the statistical properties using an artificial data set, the method is applied to experimental data of a greenhouse experiment on the assemblage of plant communities. Four plant functional response groups are formed with regard to differences in soil fertility on the basis of the traits canopy height and spacer length.

Keywords Canopy height · Plant · Fourth-corner method · Functional groups · Functional response groups · Null models · Plant traits · Seed weight · Spacer length

1 Introduction

The ability to predict vegetation response to climate or land use change requires a functional classification of plants based on plant traits (Lavorel and Garnier 2002). Trait analysis may contribute to a general understanding of plant allocation strategies, plant—environment relationships (Wright et al. 2002) as well as upscaling strategies for population viability analysis to risk assessment of communities (Henle et al. 2004). This has previously been done using knowledge-based *a priori* grouping (Condit et al. 1996) or multivariate methods such as clustering (Skarpe 1996).

The number of functional groups identified in any particular study varies according to the number of recorded traits, the species set, and the classification method (Bugmann 1996; Nygaard and Ejrnaes 2004) which limits generalisations across studies. The critical methodological problem is to link three tables with different units into a fourth one that replaces species by functional groups and can therefore be subjected to further analysis. The three tables are an environmental factors \times site matrix, a species \times site matrix, and a species \times traits matrix. Such an analysis should comply with the definition of plant functional groups (PFGs) as groups of species that respond similarly to environmental settings and share common functional attributes (Lavorel et al. 1997; Semenova and van der Maarel 2000). The simultaneous fulfillment of these conditions differentiates this type of analysis from a conventional single trait analysis (e.g. Kahmen and Poschlod 2004; Vesik et al. 2004). One general objective of PFG analysis is to identify trade-offs between different traits having significant relationships with environmental factors (called functional traits in the present paper, following Suding et al. 2003). Trade-offs operate at the species level; if trade-offs between functional response traits are to be found, species identity has to be maintained during the statistical process of identifying PFGs. In many studies published so far, this is not the case (e.g. Fernandez et al. 1993; Jauffret and Lavorel 2003), as the simple multiplication of the site \times species matrix ($m \times k$) with the species \times traits matrix ($k \times n$), which produces a site \times traits matrix ($m \times n$), pools all species at a given site into a single value per trait (e.g. weighted means of a metric variable, or frequencies of nominal classes). Since information on cross-trait relationships at the species level is lost before entering the environmental ordination, negative correlation between traits cannot be interpreted as trade-offs.

Several approaches to develop plant functional groups have been published, but none of them has been accepted as a standard procedure so far (Nygaard and Ejrnaes

2004). Among them are complex multivariate ordination techniques (Doledec et al. 1996; Lavorel et al. 1999), generalised linear modeling in combination with ordination (McIntyre and Lavorel 2001), or logistic regression models of functional response groups (Kleyer 1999, 2002). Another approach aimed to identify optimal plant functional groups is the procedure proposed by Pillar (1999). It permutes the traits and searches for the optimal trait combination by a similarity analysis. In terms of yielding PFGs, the aim is not only to identify the functional traits *per se* but also the combination of attributes or trait classes that form a functional group of species. The statistical analysis also depends on the study design, i.e. whether environmental predictors are continuous gradients or categorical treatments (factors). Here, we will concentrate on treatment designs which are coded like factors. Legendre et al. (1997) developed the ‘fourth-corner method’ to relate single traits to environmental factors using the product of the three matrices. The resulting traits \times environmental factors matrix lists the number of species with a certain trait attribute recorded at sites with similar environmental factors as long as all matrices contain only zeros and ones. The test of the null hypothesis that treatments have no effect on the trait distribution is performed by using null models which generate randomized patterns of ecological data. Some elements of the data are held constant, while others are allowed to vary stochastically to account for underlying ecological processes (Gotelli and Graves 1996). The ‘fourth-corner method’ (Legendre et al. 1997) uses a null model technique to analyze the relationship between biological traits and environmental conditions (habitat characteristics), thereby calculating the correlation of predefined species groups with similar trait attributes to environmental variables.

One of the resulting matrices of P -values can be used to answer the question: ‘What range of sites is occupied by a given species group (realised niche breadth)?’, which is different from the question: ‘Which groups are occurring at a certain site (community assembly)?’. To answer this question, a different null model is necessary. Legendre et al. (1997) do not consider groups, but only the relationship between single traits and environmental variables.

In the present paper, we use the fourth-corner method to investigate the relationships between trait class combinations i.e. groups (Lavorel et al. 1997) and environmental variables.

We propose a procedure to create and compare various groupings of species according to their biological attributes into functional response groups. The method is applied to an artificial data set and its results are compared to the results of an analysis of the same data using a procedure to identify optimal plant functional types by Pillar (1999) to demonstrate its statistical merits. Finally, we also analyze a greenhouse experiment on the assembly of plant communities at different levels of fertility and disturbance.

2 Methods

2.1 Test data generation

We generated an artificial test data set (see Appendix 3) and applied the proposed method, as suggested by Semenova and van der Maarel (2000). We used disturbance

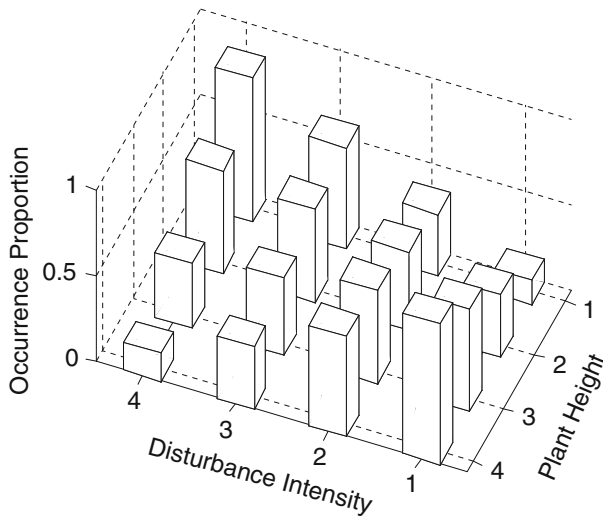


Fig. 1 The relationship between height and occurrence proportion for four disturbance intensities in the test data set. Under rarely disturbed site conditions (disturbance intensity = 1), tall plants (plant height = 4) are superior, while small plants (plant height = 1) have the highest occurrence proportion at highly disturbed sites

as the only environmental variable, with four levels and 20 replications for each level. Virtual plant communities were constructed on the basis of four traits, which are plant height (4 classes), seed number (3 classes), spacer length (distance of mother plant from clonal offspring, 3 classes: no, short and long spacer) and colour of flowers (4 classes). Combining the traits height, seed number, and spacer length resulted in a total of 36 plant groups. The four classes of colour were randomly assigned to the plant groups in order to represent a non-responsive trait. For each species \times site combination, a proportion of the occurrences was assigned by (i) incorporating a linear relationship of plant height with disturbance and (ii) a more complex relationship of a syndrome of seed number and spacer length. Here we follow the definition of the term syndrome coined by [McIntyre et al. \(1999\)](#) as a combination of trait attributes. When considering only above-ground disturbance such as mowing, small plants were found to prevail at intensively disturbed sites (e.g. lawns), while tall plants become dominant at less disturbed sites (see Fig. 1).

We assumed that certain combinations of seed number and spacer length are functional only at the highest disturbance level. They are not responsive at lower disturbance levels. At intensely disturbed sites (e.g. fields), species may either maximize their seed production for dispersal, or invest in rapidly regenerating elongated rhizomes, having only limited resources left for seed production (see Fig. 2). These two traits are evenly crossed with the trait plant height. A detailed description of the construction of the test data set is given in Appendix 3.

2.2 Plant group definition

Aggregating plants to plant groups requires traits as well as ranges of the ordinal trait attributes forming a group to be chosen. Due to limitations of computing power,

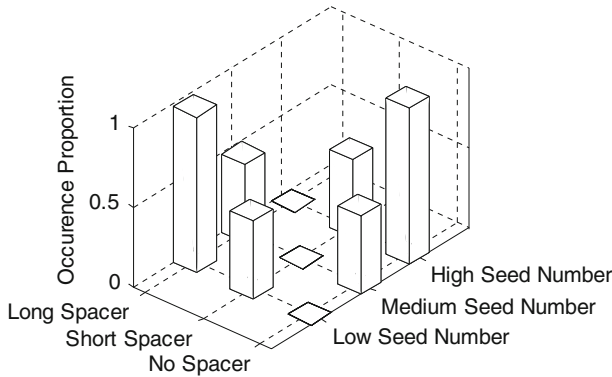


Fig. 2 The relationship of spacer length, and seed number to occurrence proportion for highly disturbed conditions in the test data set. The combination of high seed number/no spacers or low seed number/long spacer is advantageous under highly disturbed conditions. In case of intermediate and low disturbance, the trait attributes are evenly distributed and not shown here

it is often not feasible to generate all possible trait class combinations while testing their response. However, all trait values are measured with a limited precision, and many of them vary according to growth conditions. We took this into account by systematically generating a subset by fixing the minimum class range and the maximum number of classes. Species sharing a combination of trait classes belong to a ‘plant group’ (PG). A new table was constructed for these plant groups. It replaced the original traits-by-species table and was subjected to the ‘fourth-corner method’ in order to determine whether the classification is responsive. If this is the case, a plant group (PG) was called a plant functional group (PFG). Consider the following example:

If 6 different heights were measured in the trait data set and the minimum class range is set to 2, a total of 4 classifications are possible ([1–6]; see also example in Appendix 1). Each combination of syndromes was tested and the total number of required tests will be the product of the number of classifications for all single traits.

2.3 The fourth-corner method

To extend the ‘fourth-corner method’ by Legendre et al. (1997) from single trait to PFG analysis, we replaced the species \times trait matrix by a plant group matrix that represents all reasonable trait combinations, each combination representing a logically possible species.

The presence/absence of a set of k species on m sites was recorded in matrix \mathbf{A} ($k \times m$) (Fig. 3). Another matrix \mathbf{B} ($k \times n$) assigned each species (row) to a plant group (column), based on a common combination of trait classes. Different class ranges for each trait yielded different matrices \mathbf{B}_i , as exemplified in Appendix 1. To find the optimal classification for each trait, each matrix \mathbf{B}_i was subjected to the fourth-corner analysis. Matrix \mathbf{C} ($p \times m$) contained in its rows the treatments applied to each site (columns).

Fig. 3 The fourth-corner method incorporates three matrices of observed values (**A**, **B**, **C**). All observations have to be classified, a 1 marking the membership of each site or species to the associated environmental or trait class. The fourth matrix is calculated as $\mathbf{D} = \mathbf{C} \times \mathbf{A}' \times \mathbf{B}$. It lists the frequency at which each species group occurs under the associated environmental conditions. The *P*-values shown in matrix **D** indicate the probabilities at which the cell value generated by the null model is more extreme than or equal to the cell value of the observation

Presence/absence matrix (A)			PG table (B)		
species	site1	site2	species	small	tall
sp 1	1	0	sp 1	1	0
sp 2	1	0	sp 2	1	0
sp 3	1	0	sp 3	1	0
sp 4	1	1	sp 4	1	0
sp 5	0	1	sp 5	0	1
sp 6	0	1	sp 6	0	1
sp 7	1	1	sp 7	0	1
sp 8	0	1	sp 8	0	1
sp 9	0	1	sp 9	0	1
sp 10	0	1	sp 10	0	1

Environmental conditions(C)			PG-Frequencies ($\mathbf{D}=\mathbf{CA}'\mathbf{B}$)		
	site1	site2		small	tall
infertile	1	0	infertile	4 p=0.086	1 p=-0.086
fertile	0	1	fertile	1 p=-0.011	6 p=0.011

The matrix product $\mathbf{D} = \mathbf{CA}'\mathbf{B}$ (\mathbf{A}' is the transposed matrix of **A**) listed the frequencies at which each plant group occurs at a given treatment (Fig. 3). Matrix **D** could also have been derived by constructing an inflated data table as described by Legendre et al. (1997). These count data were not suitable for Chi-square testing, because the observations were not independent of each other (several species may occur at one site) thus requiring randomization (null model) test. Matrix **A** was permuted and for each permutation \mathbf{A}_{per} a new matrix \mathbf{D}_{per} was computed ($\mathbf{D}_{\text{per}} = \mathbf{CA}'_{\text{per}}\mathbf{B}$). For each cell in **D**, the frequency of cases containing a value greater than or equal to the associated cells in the set of \mathbf{D}_{per} was calculated. For this we followed the common practice of including the observed value of the statistic to the distribution generated by the $10^3 - 1$ permutations (Hope 1968, see also Manly 1997) unless stated otherwise. If an entry in \mathbf{D}_{per} is only rarely greater than or equal to the corresponding entries in **D**, the trait combination is thought to occur more often than expected by the null model, and is positively related to the treatment. Given a large set of permutations, this frequency is an estimator of the one-tailed probability (*P*-value) of $\mathbf{D}(\text{cell}) \geq \mathbf{D}_{\text{per}}(\text{cell})$. If the *P*-value is below 0.05, the group is considered to respond to the associated treatment. Values higher than 0.5 indicate a negative association, i.e. the plant group occurs less often than expected by the null model. In this case a (–) sign indicates the probability of generating a value less than or equal to the value in **D**.

Legendre et al. (1997) corrected their *P*-values to accommodate the increased probability of committing a Type I error in the case of multiple simultaneous tests. We did not correct the matrix of *P*-values in the optimization process, because the

P-values are only used to rank the classification. However, when we drew ecological conclusions from the final partition into PFG's, we did correct the *P*-values as Legendre et al. (1997) did.

2.4 Optimization criteria

Criteria to find PFGs with optimal trait class ranges can be chosen according to different objectives. One might aim at a small set of PFGs with strong relationships between each PFG and all treatments—at the expense of not identifying PFGs which only have significant relationships to some treatments (case 1). On the other hand, a larger set of PFGs can result in more significant PFG—treatment relationships in total, but fewer per PFG (case 2).

If the analysis is carried out to find relevant PFGs to be incorporated in a mechanistic model (e.g. Lehsten and Kleyer 2007), a small number of plant functional groups is required with a strong response to the treatment (case 1). In this situation the first optimization method would be chosen. If, on the other hand, a more precise view on the effect of an environmental variable on a certain system is investigated (e.g. the effect of different levels of land use intensities on the occurrence of plant functional groups, Castro et al. submitted), the second optimization criterion would be appropriate (case 2).

The optimal set of PFGs is chosen in a two-step procedure. In the first step, a selection is carried out by discarding sets which are subdivisions of other sets without an increase in the explanatory value. The second step chooses the optimal set from the reduced collection of PFG sets.

Next we specify the first step: if a small set of PFGs with a high average number of significant *P*-values per PFG is preferred (case 1), all classifications are discarded, in which subdivided PFGs yield a smaller or equal average number of significant *P*-values per PFG. If a larger set is preferred (case 2), only the classifications in which the subdivided PFG has significant *P*-values with the same type of response (negative or positive, see below) as the undivided PFG are discarded. For instance, if the subdivision results in two PFGs, one having a positive and one having a negative relationship to the treatment, while the undivided PFG has a negative relationship, then the subdivided set will not be discarded.

The step of discarding sets is necessary to assure that the procedure is not skewed towards large sets. From all sets with equal explanatory value, only the smallest set is retained.

In the second step, the categorization with the highest number of significant *P*-values is chosen from the remaining set. This categorization is optimal with respect to the selected criterion (see Appendix 1 for an example). If several sets are similar according to this criterion the set with the smallest number of PFGs is preferred. If this does not result in a unique selection the one with the most even distribution of limits is chosen. If that is still not sufficient to make a decision, the one with the lowest total sum of significant *P*-values is preferred.

This procedure is useful, if the whole set of species has to be categorized and no special attention is paid to certain species or groups. If, on the other hand, the

response of a certain set of predefined plant groups is of interest, one can write the plant groups directly into matrix **B** and apply the fourth-corner analysis without any optimization.

2.5 Null models

To test for plant group responsiveness, we used the ‘lottery’ model (Sale 1978; Legendre et al. 1997). This null model permutes species occurrences at random within each site. The null hypothesis is that the number of niches per site is fixed and that all species have an equal chance of establishment and persistence. The alternative hypothesis is that some species perform better at some sites and will out-compete other species. This model is aimed to detect competitive advantages of one species over the other species. If the analysis is not performed at the species level, but at the PFT level, it can detect competitive advantages (or disadvantages) of PFTs over other PFTs. If the plant groups consist of different numbers of species within the total species pool, this can be taken into account by multiplying all cells in **D** by the average number of species per plant group divided by the number of species covered by the plant group that corresponds to the cell. The uncorrected null model assumes the occurrence probabilities of species per plant group to be similar, e.g., if a plant group is comprised of more species than another plant group, it is also expected to have a higher occurrence frequency according to the null model. The corrected version assumes the absolute number of species per plant group to be similar, e.g. all plant groups are expected to have similar occurrence frequencies. The correction is performed prior to comparison of \mathbf{D}_{per} to **D**.

To derive the realized niche of a PFG we used a null model with fixed row and column sums. Legendre et al. (1997) used the ‘Environmental control model’ which fixes only the row sums for a similar task. The hypothesis stated by this null model is that all sites are equally suitable for all species, their occurrence probability thus being similar at each site. The alternative hypothesis is that some species are better suited at some sites with optimal conditions. This model also relies on the assumption that all sites have similar species diversity. However, species diversity has been shown in various studies to depend on the site conditions such as area of the site, disturbance regime, or climate. Therefore, we included this constraint in the null model. We used the sequential swap algorithm (Manly 1997) and applied a bias correction (Zanman and Simberloff 2002). The ‘noise test’ (Gotelli 2000) was applied to find the appropriate thinning rate in both data sets (100 swaps).

2.6 Identification of optimal plant functional response groups by similarity analysis

Another method for PFG identification was proposed by Pillar (1999). The traits of the PFGs were systematically permuted and the optimal trait set was chosen by maximizing the correlation coefficient (Pearson ρ) between the ecological distances of the sites based on the environmental factors and the distances of the same sites based on the observed PFGs. We applied the method to 100 test data sets, to each of which

the trait attribute for the trait colour was assigned at random in order to estimate the correlation coefficient and its standard deviation.

2.7 The Greenhouse experiment on the assembly of plant communities

The experiment was carried out in two greenhouses in the botanical garden of Oldenburg. In order to produce differences in soil fertility, the topsoil from one greenhouse was removed and transferred to the other. The fertile soil received an additional application of NPK fertiliser equivalent to 13 kg N/ha. Furthermore, five disturbance treatments were applied; monthly moving (eight times a year), moving twice a year, moving every second year, rotating every second year and free succession (no treatment). The combined fertility/disturbance treatments were applied to four to five replicates each. The plots were arranged in a latin-square design and each plot was separated from the other plots by netting above ground and by plastic plates below ground (down to a depth of 30 cm). Sowing of 32 plant species took place after heat sterilisation of the soil in January 2000 and species frequencies were recorded in 2002. The list of species and their traits is given in the Appendix 4 (Table A4.1). Their occurrences can be found in [Lehsten \(2005\)](#). Traits were measured according to [Cornelissen et al. \(2003\)](#) and quoted as mean values of 20 specimens. Since trait sampling was destructive, we did not sample the species in the plot, but growing under optimal conditions. Hence, the trait attributes represent potential values for optimal conditions as suggested by [Cornelissen et al. \(2003\)](#). The trait values for spacer length were taken from a database ([Klimes and Klimesova 1999](#)).

Plant functional response groups were formed based on the traits canopy height and spacer length. Forming all possible classifications of canopy height alone leads to a maximum of $1.07 * 10^9$ classifications. Bearing in mind that there are only two treatments, the data were binned into two classes of canopy height with a minimum class width of 5 cm and a minimum difference of classification of 5 cm. These parameters allow 19 classifications of canopy height to be defined.

3 Results

Although the algorithm was designed to analyse PFGs, we started by using single traits for both data sets. Each set of PGs produced a matrix of *P*-values of the relationship of the plant group to the treatment.

3.1 Test data—plant height only

The *P*-values for a grouping based only on plant height are listed in Table 1 for a subset of the possible classifications (see also Table A2.1 in the Appendix). Tall plants occurred more frequently than small plants at rarely disturbed sites and vice versa. However, when using all four classes of plant height, intermediate height classes 2 and 3 were not significantly related to intermediate disturbance levels. If three

Table 1 PFGs categorized for vegetation composition, based on plant height

No. of PGs	<i>P</i> -values of the relationships				
	Trait class	Disturbance regime			
	Height (h)	1	2	3	4
4	Very small (1)	−0.001	−0.009	0.009	0.001
	Small (2)	−0.012	n.s.	n.s.	0.011
	High (3)	0.012	n.s.	n.s.	−0.018
	Very high (4)	0.001	0.012	−0.013	−0.001
3	Small (1)	−0.001	−0.005	0.015	0.001
	Medium (2–3)	n.s.	n.s.	n.s.	n.s.
	High (4)	0.001	0.011	−0.010	−0.001
2	Small (1–2)	−0.001	−0.026	0.025	0.001
	High (3–4)	0.001	0.026	−0.025	−0.001

This table lists a subset of the possible trait class combinations. A full list is given in Table A1.2.1. Separating four, three or two height classes results in a total of twelve (4 PGs) or eight (2–3 PGs) statistically significant *P*-values ($P < 0.05$). Although the classification into four PGs results in the highest number of *P*-values below 0.05, the categorization into two classes is preferred, because the small and the very small PG of the first PG set are subdivisions of the small PG from the last PG categorization and the number of significant *P*-values per PG does not increase. The values indicate the association (sign) and the statistical significance (*P*-values)

height classes are used instead of four, the intermediate plant group was not responsive to the treatments. We considered the categorization into two height classes to be optimal, because the small and the very small PG of the first PG set are subdivisions of the small PG from the last PG categorization and the number of significant *P*-values per PG does not increase. The third classification was preferred to the second because of its smaller number of PGs. Three classifications in two height classes were possible [1–4], all resulting in the same number of significant *P*-values. The first classification was preferred, because the class limits are most evenly distributed.

3.2 Test data—colour

Using 1,000 test data sets in which the trait colour was assigned at random, we found 4.85% significant *P*-values for the colour—disturbance relationship at a significance level of 0.05, i.e. false positive results. Hence, the randomisation test controlled the Type I error as required.

3.3 Test data—plant groups

Combining the traits seed number and spacer length led to nine PGs (3 classes \times 3 classes), of which three syndromes (no spacer and low seed number; short spacer and medium seed number; long spacer and high seed number) were disadvantageous ($P \leq 0.001$), two combinations were advantageous ($P \leq 0.001$) to the other trait com-

binations and the remaining syndromes showed no response (n.s.). The values correctly reflect the relationships incorporated in the artificial data set.

Combining traits yielded fewer significant P -values, which may result from the reduced total differences between the now smaller groups as well as from the reduced number of observations in each test, which in turn increased Type II error. Forming a set of 36 PFGs considering the three traits of height, spacer length and seed number, resulted in statistically insignificant relationships for all PGs under medium disturbed conditions, and for medium sized PGs under rarely disturbed conditions, see Table A2.2 in the Appendix 2. This table shows that the calculated P -values correspond to the expectation for all PGs.

3.4 The niche of a PFG

We applied the null model with fixed row and column sums (sequential swap algorithm, Manly 1997) to analyze the niche of a PG. The hypothesis behind this null model is that all sites are equally suitable for all species, the alternative hypothesis being that some species perform better at certain sites because of suitable growth conditions. These sites form their ‘realized niche’. Table A2.3 (Appendix 2) lists the associations and P -values for each group—treatment combination for the trait plant height for the classification in four PGs. The differences from the results of the ‘lottery’ model (Table 1) are marginal because of the symmetry in the height-disturbance relationship, but the results differ for more complex trait-environment relationships. The P -values for the realized niche of plant groups composed of the traits seed number and spacer length are listed in Table 2. The plant group without spacers and low seed number was absent under highly disturbed conditions (Fig. 2) and responds positively to the other treatments. Plant groups with only one trait being in the medium class occurred under highly disturbed conditions with the same frequency as in the other treatments. Accordingly, the method detected no significant difference in the number of occurring species of these groups ($P > 0.05$).

3.5 Correlation of dissimilarities

Using the procedure by Pillar (1999), the trait combination plant height, spacer length and seed number gave the highest Pearson correlation coefficient ρ (0.910), followed by the combinations plant height and spacer length (0.809) and the combination height, spacer length and colour (0.619). This conforms to the structure incorporated in our test data. The ranking of ρ -values and associated plant traits is listed in Table A2.4 in the Appendix 2. Since the trait colour was assigned at random, we list means and standard deviations derived from 1000 different test data sets for each trait combination. The lower ranks are highly random, while the first ranks are correctly determined with a high probability. The single trait ‘colour’ has the lowest correlation coefficient. These results confirm that the traits plant height, spacer length and seed number were correlated with the occurrence of species within our artificial test data set.

Table 2 The realized niche of the PFG of the artificial data set based on the traits spacer length and seed number

Trait classes		Disturbance regime			
Spacer	Seed	1	2	3	4
1	1	0.001	0.001	0.003	−0.001
1	2	n.s.	n.s.	n.s.	n.s.
1	3	−0.001	−0.001	−0.001	0.001
2	1	n.s.	n.s.	n.s.	n.s.
2	2	0.001	0.001	0.002	−0.001
2	3	n.s.	n.s.	n.s.	n.s.
3	1	−0.001	−0.001	−0.004	0.001
3	2	n.s.	n.s.	n.s.	n.s.
3	3	0.001	0.001	0.003	−0.001

Three classes for spacer length (p; 1=no spacer, 2=medium spacer length, 3=long spacer) and three seed number classes (s; 1=low seed number, 2=medium seed number, 3=high seed number) are combined to nine PGs. The values indicate the association (sign), and the statistical significance (P -values)

3.6 The greenhouse experiment

The greenhouse experiment was designed to investigate the assembly of plant communities in terms of the probabilities and total number of occurrences of plant groups (realized niche breadth) at the different sites, but not in terms of community structure. Therefore, we only applied the ‘lottery’ model for the classification of species.

The optimization procedure maximized the total number of significant trait—treatment relationships hence aiming for a larger set of PFTs (see 2.4 Optimization criteria). The functional classification as well as the species traits are given in Table A4.1 in the Appendix 4.

3.7 Single trait analysis of the greenhouse experiment

Figure 4 displays the expected and observed values of plant occurrences based solely on the trait canopy height using the ‘lottery’ null model without correction for plant group size. Under fertile soil conditions, the observed values of plant group occurrence below a certain canopy height were always below the expectation (though sometimes not significantly). Class limits that determine plant groups could therefore be chosen freely. Under infertile soil conditions, the expected value was above the observed value up to a height of 37 cm and below the observed value for all other canopy heights.

The first criterion for optimization was to reach the highest number of P -values smaller than 0.05. Eleven out of 19 classifications result in the same number of P -values smaller than 0.05. Hence, all of them were equally valid and the classification into a small (smaller than 78 cm) and a tall plant group (taller than 78 cm) was chosen, because it results in the most similar class width.

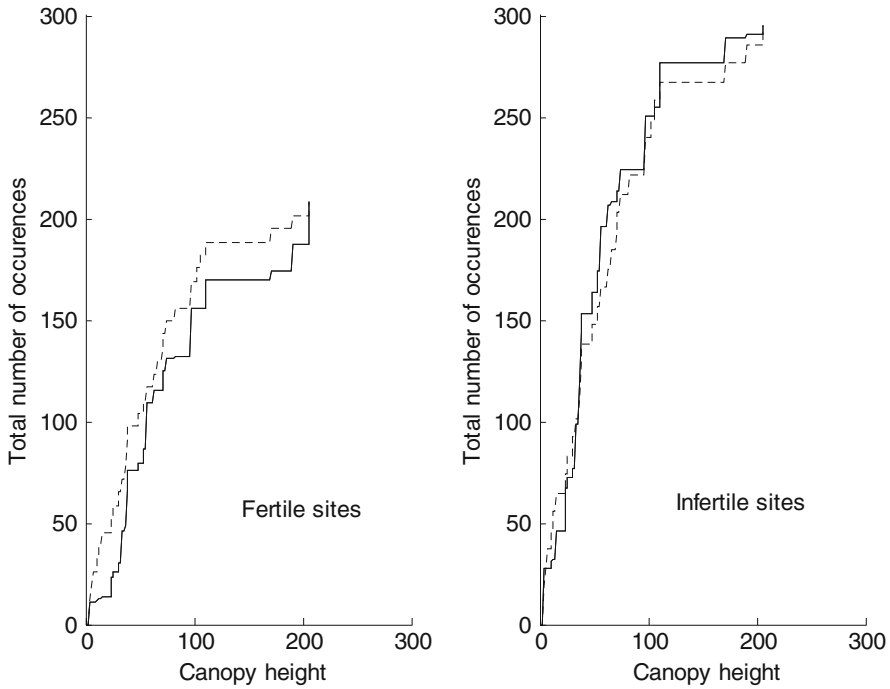


Fig. 4 Expected (dashed line) and observed (solid line) number of occurrences of species smaller than a certain canopy height. The expected values are based on the assumption that all sites have a fixed species diversity, but species are randomly distributed ('lottery model'). Note that the total number of occurrences is greater at infertile sites than at fertile sites

Table 3 *P*-values for single trait classifications based on canopy height and spacer length using the model of fixed number of species per site ('lottery model')

	Small	Tall	Annual or short spacer	Long spacer
<i>Uncorrected for species per PFG</i>				
Infertile site	0.024	-0.024	-0.001	0.001
Fertile site	-0.001	0.001	-0.03	0.03
<i>Corrected for species per PFG</i>				
Infertile site	0.001	-0.001	0.004	-0.042
Fertile site	0.001	-0.001	0.114	-0.191

Small PFGs comprise species with a canopy height below 78 cm. Uncorrected values indicate *P*-values for increased or decreased (-) probability of occurrence. Corrected values list *P*-values for increased or decreased (-) total occurrence

Though the relationship between fertility and canopy height was positive as might be expected, applying the fourth-corner method with a correction for plant group size results in a different relationship. Table 3 shows that small species were more frequent and tall species are less frequent under both fertile and infertile conditions. Here, the total number of occurrences was evaluated, while the chance of occurrences for a species within a PG was considered in the former analysis.

Table 4 *P*-values for trait syndrome classifications based on canopy height and spacer length using the model of fixed number of species per site ('lottery model')

	PFG small, annual or short spacer	PFG small, long spacer	PFG tall, annual or short spacer	PFG tall, long spacer
<i>Uncorrected for species per PFG</i>				
Infertile site	−0.001	0.001	0.001	−0.001
Fertile site	−0.001	0.48	0.001	0.002
<i>Corrected for species per PFG</i>				
Infertile site	0.001	0.001	−0.001	−0.001
Fertile site	0.001	0.039	−0.004	−0.037

Small PFGs comprise species with a canopy height below 104 cm. Uncorrected values indicate *P*-values for increased or decreased (−) probability of occurrence. Corrected values list *P*-values for increased or decreased (−) total occurrence

Table 3 also displays the *P*-values for plant groups formed solely on spacer length. Though species with long spacers has a higher probability of occurrence, the total number of occurring species with long spacers was lower than the number of the other species (though the relationship is not significant under infertile conditions). This effect occurred, because the number of species which were either annual or had short spacers is higher than the number of species with long spacers (see Table A4.1 in the Appendix 4).

3.8 Plant group analysis of the greenhouse data

Combining the traits canopy height and spacer length led to a total of 38 PG classifications. The optimal classification (according to the above-mentioned criterion) had four PFGs (see Table 4). The changing point between small species and tall species was at a height of 104 cm. Seven out of eight PFG factor relationships were significant.

The *P*-values indicate an increased probability of occurrence for small species with long spacers or tall species with short or no spacers at infertile sites, while all other species (PFGs) had a lower chance of occurrence. At fertile sites, tall species had a higher chance of occurrence and small species with short or no spacers had a lower chance of occurrence (upper part of Table 4, uncorrected *P*-values).

Similar to the single trait—treatment relationship, the plant group—treatment relationship also differed substantially between the probabilities of occurrence and the total number of occurrences of species within a plant group because of different numbers of species per plant group. Regardless of the fertility treatment, total occurrences of small plants were higher than total occurrences of tall plants. Here, spacer length has only a marginal influence on the *P*-values (lower part of Table 4).

4 Discussion

All trait—disturbance relationships incorporated in the artificial test data set could be detected using the extended fourth-corner method.

4.1 Comparison with other approaches

The original method developed by Legendre et al. (1997) focuses on establishing relationships between single traits and environmental factors and not on testing all possible combinations of traits. A second branch in the three-table joint analysis is based on correspondence analysis and includes the RLQ technique (Doledec et al. 1996; Ribera et al. 2001) or consecutive multivariate techniques (McIntyre and Lavorel 2001). A third branch resides in the framework of Generalized Linear Modeling and logistic regression techniques (Kleyer 1999; Jauffret and Lavorel 2003). Among these techniques, the one by Nygaard and Ejrnæs (2004) is most similar to ours. Similar to Legendre et al. (1997), they test a global relationship of functional response groups to treatments, which restricts the understanding of the contribution by individual traits or trait combinations to plant—environment relationships. The latter can be achieved by optimization methods as presented in our approach or by Pillar (1999, 2003). Moreover, we consider null models as a straightforward method in order to cope with the lack of independence between observations.

The results of the optimization procedure by Pillar (1999) are correct for the artificial test data set. However, it detects only the functional response traits, but neither the direction of the association to the environmental variables nor their significance. His algorithm will result in a trait ranking, even if none is functional-responding, while our method tests the significance of the association of each PG to each environmental factor. Pillar (2003) enhanced his method by using a cluster analysis to find the optimal trait classes of the PGs. However, he still uses the correlation of dissimilarities to discriminate the optimal trait set. Hence, the results concerning our data set would be similar.

To identify co-occurring PFGs in a given treatment we used the ‘lottery’ null model (Sale 1978). It hypothesizes a founder-controlled community with no differences in competitive ability between species. The alternative hypothesis to this model is that species belonging to certain plant groups perform better than others. Using the model without correction assigns, on average, the same number of species to each plant group. It therefore evaluates, whether the observed plant groups occur proportional to the number of species they cover. However, if total number of species per plant group is of concern, normalizing group sizes assumes not the occurrence probabilities of single species but the expected number of species per group to be equal. The alternative hypothesis is that there are some PGs which were observed more frequently than others. The frequency of occurrences indicates which PG will dominate within a treatment.

If the occurrence of a PFG across treatments (niche analysis) is of interest (not PFG composition per treatment for community analysis), a different null model is required. The environmental control model (Whittaker and Goodman 1979), as used by Legendre et al. (1997), assumes species occurrence to be independent of environmental factors. The alternative hypothesis is that a given species is confined to appropriate environmental conditions. While the number of observations of each species (rarity) is seen as a constraint, no interactions between species (e.g. competition, mutualism) are assumed. If the species diversity differs between sites with different environmental conditions, the method is biased because it overestimates the frequencies of species

that tend to occur at species-rich sites and *vice versa*. Hence, we decided to use a null model with fixed row and column sums to fix species rarity and diversity per site.

The artificial test data set incorporates only one environmental gradient. However, various gradients may influence the species composition simultaneously. To incorporate several environmental factors, each factor needs to be categorized into discrete classes and each site has to be assigned to a combination of factor classes (treatments). The ability to correctly discriminate PFGs (Type I error) is strongly influenced by the number of sites and the number of traits used to compose the PFGs. Increasing the number of sites may allow one to use more traits for PFG generation.

4.2 Syndrome versus single trait analysis

Marby et al. (2000) concluded that the importance of analyzing multiple traits (e.g. syndromes), rather than single traits, is supported by a wide range of traits which different authors consider to be functional-responding. Not only the traits thought to be functional-responding differed, but also the relationships between traits and environmental factors.

Jauffret and Lavorel (2003) used a generalized linear model to identify the attribute response to a factor. Attributes showing a significant response in frequency in one direction of a factor were labelled as ‘decreaser’ or ‘increaser’ according to the direction of the response, or as ‘inconsistent’, if no significant changes along the gradient could be detected. This procedure would label the traits seed number and spacer length as ‘inconsistent’ in our artificial test data set, because the frequency of each state of these traits is similar over the whole disturbance gradient. However, the combination of the traits has a high functional response. Whether such complex relationships are relevant to field data or only occur in our artificial test data set, has to be shown by further field work.

A trait effect may even be reversed depending on another trait attribute. While the occurrence of PGs with either high seed number or long spacers is positively related to highly disturbed treatments, the combination of both trait states is disadvantageous (Fig. 2). Determining PFGs from single trait analysis would not produce a valid PG factor relationship in this case.

Another issue in the determination of PFGs by single trait analysis is to ensure that the trait classes co-occur in the species (Jauffret and Lavorel 2003). All PGs identified by the proposed method comprise species, since our null model only randomizes the observed data. The necessity of analyzing functional groups instead of combining single trait analysis is also stressed by Marby et al. (2000) who analyzed species level distribution of traits in a temperate woodland flora and associated the environmental conditions with different groups of traits which tend not to co-occur within species.

4.3 The Greenhouse experiment

The classification of species from the greenhouse experiment on the assembly of plant functional response groups was performed using the traits canopy height and spacer length. Both traits are responsive on a single trait basis. Our results concerning plant

height are consistent with the expectation that tall plants have a higher probability of occurrence at fertile sites. Since ploughing with a subsequent regeneration from seeds or subsurface buds was only applied to one fifth of the plots, we also expected long spacers to be advantageous regardless of the fertility level. The simultaneous analysis of the two traits resulted in a set of four plant functional response groups for which a significant relationship between the probability of occurrence of a species within the PFG and the treatment was found for seven out of eight PFG—treatment combinations. Here, the separation between tall and small plants was made at a height of 104 cm—instead of 78 cm for the single trait analysis—hence, a combination of the optimal trait classes for single traits would not lead to the optimal grouping at a multi-trait level. Tall plants have an increased chance of occurrence at fertile sites regardless of their spacer length, similar to the single trait analysis. Small plants with short or no spacers have a decreased chance of occurrence at both fertility levels. This trait combination would be attributed to intensely and frequently disturbed conditions, which only occurred in a small proportion of the experiment. The increased probability of occurrence of tall species with short or no spacers at infertile sites is a result of the relative high abundance of a single species, *Ranunculus acris*, which limits the relevance of this PG for both treatments.

5 Perspectives

We have presented null models based on presence/absence data. Using abundance data can improve such an analysis (Gotelli et al. 1987) and this extension can be done by designing a new null model which suits this kind of data. The results obtained using our method can be used to build scenarios of vegetation development under changing environmental conditions. Applying the ‘lottery’ model and projecting the derived PFG-environmental conditions relationships on a hypothetical map of site conditions (incorporating climate or land use change) results in a map of communities of plant functional response groups. Such maps are, for instance, available to future land use for different climate change scenarios (e.g. Reginster and Rounsevell 2006).

Our method requires all environmental factors to be arranged in classes or treatments, while GLMs predict species occurrences over continuous gradients. This may be a disadvantage if sampling points are evenly spaced and classification of the gradient, i.e. dividing the variable representing the gradient into classes is problematic. However, it has the advantage of requiring fewer data to detect a significant relationship by reducing the continuous gradient into several classes. The proposed method is also able to deal with heteroscedastic data and will give a valid result for the proportion of the gradient (or the treatments) for which the vegetation responds to the environmental variable. A program applying the procedure, including an additional null model for frequency data as well as the test data set, can be obtained from the authors.

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Appendix 1 Example generation of PFGs using the fourth-corner method

Species traits		Treatment (matrix C)		Presence / Absence (matrix A)		
Sp.	Height (h)		site1 site2	Sp.	site1	site2
sp 1	1	infertile(inf.)	1	0	1	0
sp 2	1		0	1	1	0
sp 3	2	fertile(fert.)			1	0
sp 4	2				1	1
sp 5	3				0	1
sp 6	4				0	1
sp 7	5				1	1
sp 8	6				0	1
sp 9	6				0	1
sp 10	6				0	1

Possible classifications according to plant height (h) into small (s) medium (m) and tall (t) sized species. constraints: minimum class number:2 minimum class size:2

1.PG set				2.PG set				3.PG set				4.PG set				
PG (B)		PG (B)		PG (B)		PG (B)		PG (B)		PG (B)		PG (B)		PG (B)		
Sp.	h	s	t	h	s	t	h	s	t	h	s	t	h	s	m	t
sp 1	1	1	0	1	1	0	1	1	0	1	1	0	1	1	0	0
sp 2	1	1	0	1	1	0	1	1	0	1	1	0	1	1	0	0
sp 3	2	1	0	2	1	0	2	1	0	2	1	0	2	1	0	0
sp 4	2	1	0	2	1	0	2	1	0	2	1	0	2	1	0	0
sp 5	3	0	1	3	1	0	3	1	0	3	1	0	3	0	1	0
sp 6	4	0	1	4	0	1	4	1	0	4	1	0	4	0	1	0
sp 7	5	0	1	5	0	1	5	0	1	5	0	1	5	0	0	1
sp 8	6	0	1	6	0	1	6	0	1	6	0	1	6	0	0	1
sp 9	6	0	1	6	0	1	6	0	1	6	0	1	6	0	0	1
sp 10	6	0	1	6	0	1	6	0	1	6	0	1	6	0	0	1

Matrix B contains a 1 if the species is assigned to the PG stated in the column.

D=CA'B

inf.	s	t	h	t	s	t	s	m	t
fert.	4	1	4	1	4	1	4	0	1
	1	6	2	5	3	4	1	2	4

The p-values generated by the fourth-corner method using the 'lottery' model (Legendre *et. al* 1997).

inf.	s	t	s	t	s	t	s	m	t
fert.	0.02	-0.02	0.1	-0.1	0.02	-0.02	0.001	-0.2	-0.2
	-0.001	0.001	-0.1	0.1	0.16	0.16	-0.02	0.4	0.001

The tall plant group from the first set comprises the medium and tall plant group of the fourth set. The average number of significant P-values for the subdivided plant groups (m and t; 1/2 = 0.5) is lower than the number of significant P-values for the tall PG in the first categorisation (2/1 = 2). The fourth set will therefore be discarded.

Grouping criterion n_{ps} = total number of P-values below 0.05

1.PG set	2.PG set	3.PG set	4.PG set
$n_{ps} = 4$	$n_{ps} = 0$	$n_{ps} = 2$	Discarded

The optimal PFG classification is into two height classes of 1–2 and 3–6

Appendix 2 Results of the fourth corner analysis of the artificial test data set

Table A2.1 Full set of PFGs categorized for vegetation composition, based on plant height. The values indicate the association (sign) and the statistical significance (*P*-values)

No. of Comb.	<i>P</i> -values of the relationships				
	Trait class	Disturbance regime			
	Height (h)	1	2	3	4
1	Very small (1)	-0.001	-0.009	0.009	0.001
	Small (2)	-0.012	n.s.	n.s.	0.011
	High (3)	0.012	n.s.	n.s.	-0.018
2	Very high (4)	0.001	0.012	-0.013	-0.001
	Small (1)	-0.001	-0.005	0.015	0.001
	Medium (2-3)	n.s.	n.s.	n.s.	n.s.
3	High (4)	0.001	0.011	-0.010	-0.001
	Small (1-2)	-0.001	-0.027	0.024	0.001
	Medium (3)	0.012	n.s.	n.s.	-0.018
4	High (4)	0.001	0.012	-0.013	-0.001
	Small (1)	-0.001	-0.009	0.009	0.001
	Medium (2)	-0.012	n.s.	n.s.	0.011
5	High (3-4)	0.001	0.026	-0.024	-0.001
	Small (1-3)	-0.001	-0.009	0.012	0.001
	High (4)	0.001	0.009	-0.012	-0.001
6	Small (1-2)	-0.001	-0.026	0.025	0.001
	High (3-4)	0.001	0.026	-0.025	-0.001
7	Small (1)	-0.001	-0.010	0.012	0.001
	High (2-4)	0.001	0.010	-0.012	-0.001

Table A2.2 PFGs are generated by the ‘lottery’ model for vegetation composition using the three traits

<i>P</i> -values of the relationships						
Trait class			Disturbance regime			
Height	Spacer	Seed	1	2	3	4
1	1	1	-0.007	n.s. (-0.2)	n.s. (0.3)	-0.0002
1	1	2	-0.005	n.s. (-0.2)	n.s. (0.3)	0.002
1	1	3	-0.001	n.s. (-0.1)	n.s. (0.2)	0.0001
1	2	1	-0.0006	n.s. (-0.1)	n.s. (0.2)	0.0005
1	2	2	-0.006	n.s. (-0.2)	n.s. (0.3)	-0.0002
1	2	3	-0.005	n.s. (-0.2)	n.s. (0.3)	0.003
1	3	1	-0.0001	n.s. (-0.2)	n.s. (0.1)	0.0001
1	3	2	-0.002	n.s. (-0.2)	n.s. (0.3)	0.0032
1	3	3	-0.005	n.s. (-0.2)	n.s. (0.3)	-0.0002
2	1	1	n.s. (-0.2)	n.s. (-0.5)	n.s. (0.4)	-0.0001
2	1	2	n.s. (-0.3)	n.s. (-0.5)	n.s. (0.4)	n.s. (0.09)
2	1	3	n.s. (-0.2)	n.s. (-0.5)	n.s. (0.3)	0.0001
2	2	1	n.s. (-0.2)	n.s. (-0.5)	n.s. (0.4)	n.s. (0.07)
2	2	2	n.s. (-0.2)	n.s. (-0.5)	n.s. (0.4)	-0.0001
2	2	3	n.s. (-0.2)	n.s. (-0.5)	n.s. (0.4)	n.s. (0.1)
2	3	1	n.s. (-0.2)	n.s. (-0.5)	n.s. (0.4)	0.0001
2	3	2	n.s. (-0.2)	n.s. (-0.5)	n.s. (0.4)	n.s. (0.1)
2	3	3	n.s. (-0.2)	n.s. (-0.5)	n.s. (0.4)	-0.001
3	1	1	n.s. (0.2)	n.s. (0.3)	n.s. (-0.5)	-0.001

Table A2.2 continued

P-values of the relationships						
Trait class			Disturbance regime			
Height	Spacer	Seed	1	2	3	4
3	1	2	n.s. (0.2)	n.s. (0.4)	n.s. (-0.5)	n.s. (-0.3)
3	1	3	n.s. (0.2)	n.s. (0.4)	n.s. (-0.5)	0.02
3	2	1	n.s. (0.1)	n.s. (0.3)	n.s. (-0.5)	n.s. (-0.2)
3	2	2	n.s. (0.2)	n.s. (0.4)	n.s. (-0.5)	-0.0001
3	2	3	n.s. (0.2)	n.s. (0.4)	n.s. (-0.5)	n.s. (-0.3)
3	3	1	n.s. (0.2)	n.s. (0.4)	n.s. (-0.5)	0.02
3	3	2	n.s. (0.2)	n.s. (0.4)	n.s. (-0.5)	n.s. (-0.3)
3	3	3	n.s. (0.2)	n.s. (0.4)	n.s. (-0.5)	-0.0003
4	1	1	0.02	n.s. (0.3)	n.s. (-0.2)	-0.0002
4	1	2	0.02	n.s. (0.3)	n.s. (-0.2)	-0.01
4	1	3	0.02	n.s. (0.3)	n.s. (-0.2)	n.s. (-0.2)
4	2	1	0.006	n.s. (0.2)	n.s. (-0.1)	-0.0003
4	2	2	0.02	n.s. (0.3)	n.s. (-0.2)	-0.0001
4	2	3	0.003	n.s. (0.3)	n.s. (-0.1)	-0.001
4	3	1	0.02	n.s. (0.3)	n.s. (-0.2)	n.s. (-0.2)
4	3	2	0.02	n.s. (0.3)	n.s. (-0.2)	-0.02
4	3	3	0.02	n.s. (0.3)	n.s. (-0.2)	-0.005

Under medium disturbance regimes (2–3), no significant association was detected. Although very tall and very low species show significant differences from the null model community, if this trait is considered alone (Table 1), taking all three traits into account leads to insignificant *P*-values. The total frequencies of the PFG’s are reduced, hence *P*-values are decreased

Table A2.3 The realized niche of the PFG is determined using the sequential swap

No. of PGs	P-values of the relationships				
	Trait class	Disturbance regime			
	Height (h)	1	2	3	4
4	Very small (1)	-0.001	-0.006	0.005	0.001
	Small (2)	-0.013	n.s.	n.s.	0.017
	High (3)	0.011	n.s.	n.s.	-0.019
	Very high (4)	0.001	0.010	-0.003	-0.001

The association is based on plant height, separating four height classes. The values indicate the association (sign), and the statistical significance (*P*-values). These associations are similar to the associations derived by the ‘lottery’ model because of the symmetry in the height—disturbance relationship

Table A2.4 The optimal trait set is derived with the algorithm by Pillar (1999) for the test data set

Pearson ρ	Std.	Trait combination
0.910	0	Height, spacer length, seed number
0.809	0	Height, spacer length
0.619	0.011	Height, spacer length, colour
0.604	0	Height, seed number
0.598	0	Spacer length, seed number

Table A2.4 continued

Pearson ρ	Std.	Trait combination
0.578	0.006	Height, spacer length, seed number, colour
0.332	0.013	Height, seed number, colour
0.276	0.022	Spacer length, seed number, colour
0.271	0.015	Height, colour
0.062	0.027	Spacer length, colour
0.060	0.026	Seed number, colour
0.002	0.030	Colour

The Pearson correlation coefficient ρ is calculated for the dissimilarity matrices of the sites by species (squared cord distance) and sites by the environmental variables (Euclidian distance). The traits plant height, spacer length and seed number influence the species occurrence in the test data set. This combination has the highest correlation coefficient. Trait sets not including colour are fully deterministic. Hence, the standard deviation is zero. The correlation coefficient for single traits except colour cannot be calculated, since, for example, each different plant height class occurs at least once in each site, leading to a dissimilarity matrix of sites with only zeros. Using different trait class classifications did not increase the Pearson correlation coefficients within our data set

Appendix 3 Construction of the test data set

Matrix A—observation

Four treatments with 20 replicates each result in 80 sites and hence 80 columns in matrix **A**. The species diversity is set to 20. Each species may occur only once, for simplicity reasons; hence, 1,600 species and rows are in Matrix **A**. The first 20 rows have a 1 in the first column, the second 20 rows in the second line and so on.

Matrix B—traits

The heights are distributed according to Table A3.1.

Table A3.1 Distribution of the trait canopy height of virtual plants in the artificial data set

Height/treatment	No. of species			
	Disturbance level 1	Disturbance level 2	Disturbance level 3	Disturbance level 4
1	8	6	4	2
2	6	5	5	4
3	4	5	5	6
4	2	4	6	8

At the highest disturbance level, the traits seed number and spacer length are distributed according to Table A3.2.

Matrix C—treatment

The first 20 columns (sites) have a 1 in the first row, i.e. they belong to the first treatment recorded. The second 20 columns have a 1 in the second row and so on.

Table A3.2 Distribution of the traits spacer length and seed number of the virtual plants

Treatment/trait		Disturbance level 1–3	Disturbance level 4	
Spacer	Seed no.		10 sites	10 sites
1	1	2	0	0
2	1	2	2	1
3	1	2	7	6
1	2	2	1	2
2	2	2	0	0
3	2	2	2	2
1	3	3	6	7
2	3	2	1	1
3	3	3	0	0

The traits seed number and spacer length are equally distributed at disturbance levels 1–3. To maintain constant species diversity, two sites received three instead of two species of similar trait state. Twenty sites have the disturbance level four, of which ten have a similar trait distribution

Appendix 4 Results of the greenhouse experiment

Table A4.1 Species of the greenhouse experiment with allocated traits and optimized functional classification by the extended fourth-corner method

Species name	Height cm	Life cycle/ spacer length	Functional group
<i>Alopecurus pratensis</i>	71	2	1
<i>Apera spica-venti</i>	71	1	1
<i>Arenaria serpyllifolia</i>	7	1	1
<i>Arrhenatherum elatius</i>	96	2	1
<i>Bellis perennis</i>	4	2	1
<i>Bromus erectus</i>	37	2	1
<i>Centaurea jacea</i>	30	2	1
<i>Chenopodium album</i>	81	1	1
<i>Coronilla varia</i>	65	3	2
<i>Cynosurus cristatus</i>	37	2	1
<i>Festuca ovina</i>	37	2	1
<i>Festuca rubra</i>	53	2	1
<i>Galeopsis tetrahit</i>	102	1	1
<i>Galium verum</i>	62	3	2
<i>Glechoma hederacea</i>	4	3	2
<i>Lathyrus pratensis</i>	32	3	2
<i>Luzula campestris</i>	23	3	2
<i>Origanum vulgare</i>	74	3	2
<i>Papaver rhoeas</i>	96	1	1
<i>Phalaris arundinacea</i>	205	3	4
<i>Poa annua</i>	13	2	1
<i>Poa pratensis</i>	38	3	2
<i>Ranunculus acris</i>	111	2	3
<i>Rumex acetosa</i>	55	2	1
<i>Saxifraga tridactylites</i>	4	1	1
<i>Silene vulgaris</i>	48	2	1
<i>Solidago canadensis</i>	170	3	4

Table A4.1 continued

Species name	Height cm	Life cycle/ spacer length	Functional group
<i>Stellaria media</i>	25	1	1
<i>Tanacetum vulgare</i>	105	3	4
<i>Thymus serpyllum</i>	10	3	2
<i>Trifolium repens</i>	14	3	2
<i>Urtica dioica</i>	190	3	4

The responses of the functional groups are indicated in Table 4. Life cycle/spacer length (1: annual, 2: perennial with short spacers, 3: perennial with long spacers); Functional groups (1: small annuals or perennials with short spacers, 2: small perennials with long spacers, 3: tall annuals or perennials with short spacers, 4: tall perennials with long spacers)

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Peter Harmand grew up as a pure mathematician (functional analysis) in Berlin, where he also received his PhD in 1983. Following longer stays in Paris and Texas A&M, he became a senior lecturer at the University of Oldenburg. Here, he developed a strong interest in mathematical modeling and its ecological application, both from an analytical as well as a stochastic perspective.

Michael Kleyer is professor for Landscape Ecology at the University of Oldenburg, Germany. His long-term research field centers on the understanding of functional relationships between vegetation and land use change. His recent work has focused on predictive models of plant functional group responses to regional environmental gradients, based on field data and simulations. GIS-based scenarios allow to link abiotic landscape information with plant and animal response models. He received his PhD in landscape ecology from the University of Hohenheim, Germany, in 1990 and has extensive experience in collaborative research programmes concerning trait—environment relationships.