

Functional analysis
and
modelling of vegetation

Plant functional types in
a mesocosmos experiment and a mechanistic model

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This work is motivated by the exigency of predictive tools for vegetation development that enables the correct decisions to be taken now.

Chapter 1

Introduction

Substantial changes in climate, demography, and economic situations are expected to occur, even in the near future. If political organisations are expected to act now, they need to know what the effect of their decisions on the environment will be. Organisations like the Intergovernmental Panel on Climate Change (IPCC) develop scenarios which allow the politicians to place their political strategy in one of the scenarios and see the likely result of it on global change (IPCC 2001). Scientists investigating the effects of politics on the environment combine the results of e.g. climate, economic development, and demographic models, because the global climate is a very complex system influenced by many variables (IPCC 2000).

Global change (climatic and economic) will also result in changes in land use activities and hence is likely to cause changes in the vegetation in large areas of the planet. Since the vegetation is an important factor influencing the climate, its state is not only important in itself as a resource for human interests, but predictions of vegetation development are also important parts of climate change models (IPCC 2000).

After assessing climate change on a global scale, a regionalisation is required, because most political decisions are made on the regional scale. Here vegetation modelling can be used as a tool to inform politicians, whether the land use activities common in their area will be feasible in the future or whether the land use has to be adapted to the changing conditions. Modelling always requires a simplification of the system, because implementing too many processes in a model may decrease the systematic error of a system but also increases the statistical error. A minimal total error is reached at a certain intermediate point of complexity (Wissel 1989). One way to simplify vegetation is to group species which perform similarly in the system and subsequently model only the group but not the single species (functional grouping).

Plant functional types

Functional classification of plants in a broader sense has a long history in botanical science (review by Gitay & Noble 1997). This in turn has led to a variety of ideas and concepts using functional classifications. A summary of the definitions highlighting their differences is given by Gitay & Noble (1997). I will use the definition by Lavorel et al. (1997) of plant functional types being 'non-phylogenetic groupings of species which perform similarly in a ecosystem based on a set of common biological attributes'. The challenge in functional grouping can be described as finding the optimal grouping. Many authors have offered procedures for functional groupings (reviews in Gitay & Noble 1997 and Nygaard & Ejrnaes 2004). The first distinction can be made between groupings based on expert knowledge (e.g. Noble & Slatyer 1980) and methods applying statistical techniques to field data or experimental results (Woodward & Cramer 1996). One way of statistical grouping is to use biological attributes to establish the groups, leading to 'emerging groups', which can be correlated to environmental factors afterwards to establish functionality (e.g. Lavorel *et al.* 1997; Kleyer 1999a). This approach is criticised by Nygaard & Ejrnaes (2004) for potentially leading to groups of less predictive power. Another way of grouping is to use the biological attributes and the field observation of vegetation and abiotic parameters simultaneously. Among these techniques are ordination techniques (Doledec et al. 1996), generalised linear modelling (GLM) (McIntyre & Lavorel 2001) or multivariate analysis in combination with matrix multiplication (Diaz & Cabido 1997).

The idea of behind functional analysis of vegetation is to explain or predict plant communities with respect to the biological attributes of the species. In a greenhouse experiment I manipulated the environmental parameter and recorded the establishing plant assemblage. A review of the available statistical methods for functional vegetation analysis has led to the conclusion that all of them are of limited applicability to my experimental data. Some of the methods analyse each biological attribute separately and combine the results later on to form PFTs (e.g. Jauffret & Lavorel 2003). This approach is questionable as will be explained in Chapter five. Methods involving GLMs require continuous gradients or large data sets and methods involving ordinary statistics like ANOVA modelling (Nygaard & Ejrnaes 2004) ignore some important dependencies within the data as I will explain below.

Null models

The grouping of the PFTs is based on species performance in relation to environmental factors and traits, which have to be assessed by a statistical method. Ordinary statistics, e.g. Chi square statistics or ANOVA modelling, require independence of observations (Legendre & Legendre 1998). Although monocultures of species may occur, the vegetation of most sites is composed of several species which in turn influence each other directly or indirectly, hence the use of ordinary statistics to analyse the performance of species in mixtures is questionable on theoretical grounds. This does not imply that previous analyses using these techniques resulted in incorrect groups or response types, because, as Nygaard & Ejrnaes (2004) point out, 'this dependency is an inherent feature of the observation and modelling of the realised niche of species, e.g. the response of species to gradients given other co-occurring species' is determined. Hence the presence of other species at the same site is seen as an 'integral part of the treatment'.

Null models are able to cope with a variety of dependencies within the data structure. They offer a valuable tool for vegetation analysis not only on theoretical grounds (not requiring independent data points), but also because they can incorporate additional information e.g. site characteristics into the analysis, likewise it is done with using co-variables in multivariate techniques. Null models are pattern generating models, based on randomisation of ecological data. They are designed with respect to some ecological or evolutionary processes of interest by fixing some elements of the data, while others are allowed to vary (Gotelli & Graves 1996). Designing a null model requires decisions about *which* elements of the data are allowed to vary in *what* way. Hence it challenges the researcher to implement the ecological hypothesis in a valid procedure. This challenge may be seen as an interesting task, because the required formalisation of the hypothesis into a symbolic form can help formulating the hypothesis explicitly. It can also be rewarding to see how much the artificial null communities resemble the ecological data. Despite the applicability of null modelling, they are used relatively rarely in vegetation science and I know of no example of a functional vegetation analysis using this technique. There are several reasons that contribute to this, for instance the lack of knowledge as well as the unavailability of sophisticated tools. Statistical analysis of ecological data requires a substantial computational effort. Hence, most scientists, use statistical software packages. Although some of these packages

also offer randomisation tests, they are relatively limited in the way in which the researcher can modify the randomisation procedure. Hence, the implementation of the null model has to be done by the researcher which requires computational skills as well as a considerable time amount for programming and testing the application. However, several tools for null model analysis, developed by scientists, are already available (for a list of available programs refer to Manly 1996). I have developed a procedure for functional analysis of vegetation data using null models and implemented it into a program for which a manual is given in the appendix. It is offered to other researchers in the hope of promoting functional analysis by providing a single tool which optimises plant functional types and delivers their response to environmental factors in a single step. A detailed description of the null models used in the developed tool is given in the Chapters three and five as well as in the manual.

Another reason for the few published analyses using null models may be that there is still a considerable debate in the literature on the validity of results gained with certain null models (for a review on this subject refer to Gotelli & Graves 1996). Not only the philosophical basis of the null models is questioned, but randomisation procedures implementing the null models are subject to some scepticism as well, which in turn advances their development. One example is the 'sequential swap' algorithm (Manly 1995). It is an algorithm for a null model maintaining species diversity and species rarity and it is used to detect structures in presence / absence matrices which for example can be related to competition. Sanderson et. al (1998) developed a randomisation procedure ('the knight turn') for the same null model and concluded that the "results from previous studies are flawed", because his results did not resemble the results of the 'sequential swap' algorithm. Gotelli (2001) not only demonstrated that the randomisation procedure suggested by Sanderson et. al (1998) is biased, which has led to the contradictory results, but also showed that the sequential swap has a potential bias. Though the debate about the 'sequential swap' may be seen as resolved by the publication of a frequency correction of the 'sequential swap' (Zaman & Simberloff 2002), the question of whether the potential bias of the sequential swap leads to misinterpretation of ecological data remains to be answered. Chapter two answers this question with a meta-analysis of 291 published presence absence matrices.

The developed procedure for functional analysis of vegetation data determines the responses of PFTs to environmental factors. These responses can be used for predictive modelling of PFT distributions.

Mechanistic models

A first distinction can be made between statistical and mechanistic models. Statistical models are limited to the gradient range present in the data. Predictions of vegetation at sites with new site conditions, e.g. combinations of environmental factors that are not covered by the analysed data set, are very uncertain. Mechanistic models are not limited in the gradient range as long as the processes incorporated in the model remain valid. While statistical models may be very close to the data due to curve fitting, as compared to mechanistic models, they are not as general, as they do not provide theoretical insight. For the task of vegetation modelling with plant functional types it is straightforward to use mechanistic models incorporating plant traits explicitly. One of these models is LEGOMODEL, an individual based ecological field model (Kleyer 1999b). The modelling assumptions of LEGOMODEL are described in Chapter four and to a larger extent in Lehsten (1994). LEGOMODEL simulates the succession of herbaceous plant functional types in gradients of fertility and disturbance. It simulates plant individuals as entities occupying space to extract resources. It does not require any experimental data on the response of the functional types but generates a prediction of the occurrence of PFTs solely based on the traits of the PFTs and the environmental conditions. For a further development and an assessment of the validity of the model, it is necessary to know the main sensitivities of LEGOMODEL. A sensitivity analysis of the survival rate to variations of single traits as well as to combinations of traits (syndromes) is performed in Box 1.

Functional trait hierarchies

If plant traits determine the performance of a plant type (species), which is the basic assumption behind the concept of PFTs as well as of LEGOMODEL, it is important to assess the functionality of the traits for several reasons. One reason is, that measuring species traits is time consuming and for some traits measuring is also very expensive, hence a concentration on relevant traits allows more species to be incorporated. The concentration on a few traits may also allow a meta-analysis of field experiments to be carried out (Westoby 1998) and will result in a reduction of complexity to be incorporated

in the vegetation model which in turn lowers the statistical error of the simulation results. In Chapter five it is demonstrated that the response of a syndrome to the environmental factor cannot be predicted by simply combining the responses from the traits considered separately. Hence, it is shown that traits differ in their functionality. A method to derive functional hierarchies is proposed in Chapter four. Although it is used with a simulated data set, the approach can also be used when analysing field data.

Westoby (1998) proposes a plant strategy scheme incorporating only the traits specific leaf area (SLA), canopy height, and seed mass (LHS-scheme). These traits are relatively easy to measure and a substantial amount of data on these traits is already available in the literature (Westoby 1998). However, the strategy scheme is only applicable if the traits capture enough plant variability to functionally represent the floristic diversity. Since the scheme has been developed for meta-analysis of experiments conducted within different biota, the appropriateness of the approach can only be tested using field data. Several field studies have already demonstrated the functionality of traits within the LHS-scheme, analysing traits separately (see Chapter four). Using a mechanistic model (LEGOMODEL) the functional hierarchy of the traits of the LHS-scheme is determined and predictions are made of the occurrence of functional types in gradients of fertility and disturbance in Chapter four. The simulation results are compared with published studies, which also allows conclusions on the validity of LEGOMODEL to be drawn.

Mesocosmos experiments

Modelling is one way to investigate vegetation development, experiments are another possibility to gain insight in the problem. Experimental approaches are commonly used to assess the response of vegetation to changes in environmental conditions, e.g. the effects of increased temperature, levels of CO₂, precipitation and N deposition are experimentally investigated by Zavaleta et al. (2003). Instead of applying a treatment to an existing ecosystem, Körner (1994) suggests to artificially simplify a system in its complexity to make it more manageable than the in situ system, without losing the characteristic parts of its diversity. Such an approach will not yield a full understanding of the system, with the possibility to explain and exactly predict every possible behaviour. It will, however, allow the investigation of trends of potential changes following environmental manipulations by observing a selected number of key parameters only. It can also fill the gap between the potted growth chamber

experiment, where every parameter is artificially modified and controlled and the real world that bears a high complexity, making it impossible to distil the principles of functioning and interaction. A mesocosmos experiment is conducted at a scale of 2*2m, with a small species set, aimed at representing the relevant parts of the functional variation. It is described and analysed in Chapter five, also testing the applicability of the developed statistical procedure at real data.

Thesis outline

This thesis investigates the succession of plant functional types using two approaches. A mesocosmos experiment is conducted in which a set of species with a wide range of trait states forms after a succession of three years. The specific conditions of the experiment required a new statistical procedure to be developed. This procedure optimises plant functional type grouping and derives the response of the PFTs to the treatment. It is presented using an artificial data set with a known structure for reasons of explanations and to demonstrate its validity. The developed statistical procedure incorporates the use of null models. Null models and the results of studies which apply them are still controversially discussed in the literature. A meta-analysis assessing the relevance of a potential bias of a specific null model is conducted using a large set of published presence / absence matrices. The mesocosmos experiment is analysed, plant functional types are formed and their response is determined.

The second approach incorporates the use of an individual based ecological field model LEGOMODEL. The succession of plant functional types is simulated in a gradient of fertility and disturbance using the Leaf-Height-Seed strategy scheme by Mark Westoby (1998). The simulation predicts the distribution of plant functional types within the analysed gradients and hypothesises a functional hierarchy of traits.

A synthesis of the presented results and methods is derived and a perspective investigates the relevance of the work for recent research activities.

The development of the statistical method, the analysis of the field data, and the simulation were carried out by myself and I had the responsibility for the manuscripts. Chapters two to four were written in collaboration with co-authors, as indicated in the chapter headings.

Part I:

Identification of PFTs:

null models and statistics

Chapter 2

Null models for occurrence pattern: Assessing the bias of the sequential swap

Abstract

The analysis of co-occurrence matrices is a common practice to evaluate community structure. The observed data are compared with a “null model”, a randomised co-occurrence matrix derived from the observation by using a statistic, e.g. the C-score, sensitive to the pattern investigated. The statistical properties and computational applicability of the randomisation methods have been debated by several authors. The most frequently used algorithm, ‘sequential swap’, has been criticised for not sampling with equal frequencies thereby calling into question the results of earlier analysis. Theoretical considerations show that the C-score distribution is biased towards higher values. Hence an increased Type II error makes this analysis more conservative. We assess the bias of the C-score of the ‘sequential swap’ using 291 published presence/absence matrices of ecological field data. In 116 of these matrices, the p-value differed by more than 5% between the ‘sequential swap’ algorithm with and without frequency correction. A significant deviation of the C-score in three of the matrices was not correctly identified due to this effect and one matrix was not correctly identified as strong statistically significant by the sequential swap. Previous studies using the sequential swap can be expected to be slightly conservative if the generated statistic is positively related to the C-score, however the bias is only effecting the significance if the biased p-value is very similar to the significance level or if the matrices are relatively small. In the case of small matrices, the biased C-score may strongly influence the ecological interpretation. We also assess the number of necessary swaps to assure the significance of matrix, and suggest a simple error estimation for the p-value. For any matrix in the data set 10^4 swaps were sufficient.

Introduction

Analysing co-occurrence data has become a common practice in ecology to study the community structure within single observations (Gotelli *et al.* 1987) as well as to verify general ecological theories by using meta-analysis of

co-occurrence matrices (Gotelli & McCabe 2002). All these analyses require a randomisation of the observed data, i.e. (0, 1)- matrices, to which the observed pattern is compared. Although a number of different null models is used to test different ecological hypotheses (e.g. Gotelli (2000) compares nine different null models), most authors use the null model proposed by Connor and Simberloff (1979) of retaining row and column sums simultaneously to incorporate site effects such as island size as well as rarity of species to account for species dependent characteristics such as niche breadth. The basic assumption for each analysis is that if the observed co-occurrence matrix differs by much with respect to a certain pattern from the total set of unique matrices then there is a structure which can be ecologically interpreted. Since it is only possible to calculate this total set for relatively small matrices (as we will show below), a randomisation algorithm is applied to sample a subset of matrices, which will then be compared to the observed matrix. The investigated pattern is often summarised within a single score which is extreme for structured matrices. If this score is not significantly different between observed and randomised matrix, no pattern can be detected. To evaluate the co-occurrence between species, the number of perfect checkerboard pairs or the C-Score (Stone & Roberts 1990) is used by several authors (e.g. Wilson 1987; Feeley 2003).

A valid randomisation algorithm has to sample all matrices with fixed row and column sums at equal frequencies. The choice of the randomisation algorithm has been shown to influence the result of the study. In a re-analysis of a presence / absence matrix from the Vanuatu avian fauna, Sandersson (1998) concluded that the "results from previous studies are flawed" due to an inappropriate null model (randomisation algorithm) while Gotelli (2001) showed by using probability calculations that the null model used by Sandersson (1998), the 'Knight's Tour' is biased towards not sampling all matrices with equal frequencies, which in term has led to contradictory results. However, the 'sequential swap' algorithm is also prone to sample matrices with unequal frequencies depending on the observed matrix (Gotelli 2001). This controversy about null models has lead to publications reporting results using several randomisation algorithms (e.g. Feeley 2003). While Miklos & Podani (2004) developed a new unbiased randomisation method, we suggest using the original 'sequential swap' and performing a frequency correction afterwards as described by Zaman & Simberloff (2002). Another issue when applying a randomisation procedure is the minimum number of randomisation needed for an

analysis. Since the matrices sampled by the 'sequential swap' are not independent of each other, this question is not straight forward. We suggest a simple error estimation procedure which allows us to evaluate the quality of the generated p-value, e.g. it shows whether we sampled enough matrices. We assess the bias of the sequential swap and the necessary number of swaps using a large collection of published matrices.

Material and Methods

Data

The applicability of null models and especially of the 'sequential swap' has been discussed using the data set of the Vanuatu avifauna (Diamond & Marshall 1979; Wilson 1987; Stone & Roberts 1990). We use this data set and calculate the p-value of the C-score. Additionally, to illustrate the relevance of our approach we use 291 published matrices, collected by Patterson and Atmar (1986) and calculate the p-values of the C-scores as well as their differences obtained with and without a frequency correction of the 'sequential swap'.

Scores

We use the checkerboard score (C-score) to illustrate our analysis (Roberts & Stone 1990). It measures the mean number of pairs of species and islands with one species occurring on one island only and the second occurring on the second island only. The number of checkerboards involving species i and j can be calculated as follows:

$$C_{ij} = (r_i - S_{ij})(r_j - S_{ij}). \quad (1)$$

Where r_i is the sum of the i^{th} row and S_{ij} is the number of islands that the two species share. There are $P = m(m-1)/2$ species pairs for m species, hence the C-score is:

$$C = \sum_{i < j} C_{ij} / P. \quad (2)$$

Randomisation Algorithms

The 'sequential swap' (Manly 1995) randomly selects a pair of rows and a pair of columns. If one species occurs only at the first site and the other species occurs only at the other site, these species are interchanged, i.e. after the

swap the first species is assigned to the second site and the other species is assigned to the first site. Thus, both row and column sums are kept constant. If swapping was not possible, a new pair of rows and columns is selected. For each generated matrix the statistic (e.g. C-score) is calculated and compared with the statistic calculated for the observed matrix.

To ensure that all statistical requirements are met, the full set of matrices with fixed row and column sums could be generated and used for the analysis. Generating the full set by sampling is only feasible for relatively small datasets and requires that we know the total number of unique matrices in advance in order to stop calculating when the set is complete. A formula for the precise number of matrices with given row and column totals was given by Wang and Zhang (1998) and simplified by Perez-Salvador *et al.* (2002). If k is the number of rows or columns whichever is lower, then the reduced formula requires the evaluation of certain terms inside $(k-2)(k-1)/2$ nested sums. For small k the calculation is possible, e.g. the 4×180 -matrix of the used data collection has the enormous number of 4.7×10^{68} matrices with the same row and column totals. However, gradually increasing k shows an exponential growth of computation time, so that a calculation of the precise number seems impossible if $k > 12$.

The frequency distribution of the matrices

If the total number of possible matrices is known, an unbiased selection (with replacement) of n elements from this set should give on average the following number of different matrices:

$$N(n) = N_{\max} \left(1 - \left(1 - \frac{1}{N_{\max}} \right)^n \right). \quad (3)$$

Where N_{\max} is the maximum number of unique matrices with fixed row and column sums and $N(n)$ is the expected value of unique matrices. An algorithm prone to oversampling would generate a lower number than $N(n)$. To see this, consider the random variable X_i , which is 1 if the i -th matrix is chosen at least once during the n selections and 0 otherwise. Because of independence this last event occurs with probability $(1 - 1/N_{\max})^n$, so the expectation of X_i is $1 - (1 - 1/N_{\max})^n$. Note, that the expectation of $X_1 + \dots + X_{N_{\max}}$ is the wanted quantity, so the formula follows from the additivity of the expected value.

The frequency correction of the swap algorithm

The generation of random matrices by the 'sequential swap' can be seen as a Markov process in which each unique matrix is one state. There are as many ways (possibilities to swap) to reach different states as there are checkboards within a given matrix. Since the selection of the positions to swap is random, the probabilities to go from one state to any other are equal and their sum is one (Zaman & Simberloff 2002). As an example consider the matrix published by Maly and Doolittle (1977). There are five unique matrices with the same row and column sums (M_0 - M_4) representing five states of the Markov process (Appendix A.1). The probabilities of going from one state to another are drawn in figure A.1.1. Table A.1.1 lists the transition probabilities, the C-score and the stable state probabilities. If a large number of swaps is performed, matrix M_0 will be sampled in 25% of the cases, while each other matrix will be sampled only in 18.75% of all cases. If this matrix would be analysed using the sequential swap, the resulting expected C-score would be 0.2167 instead of the correct value of 0.2133. The sampling proportion is similar to the proportion of the C-scores. A correction of the frequency at which a state is reached can therefore be performed by weighting each state with the C-score. Calculating the expected C-score would result in the formula:

$$\overline{C_{corr}} = \frac{n}{\sum_{i=1}^n \frac{1}{C_i}} \quad (4)$$

or in general considering any statistic:

$$\overline{S_{corr}} = \frac{\overline{C_{corr}} \sum_{i=1}^n \frac{S_i}{C_i}}{n}. \quad (5)$$

Where n denotes the number of swaps, C_i is the C-score of the i^{th} matrix, and S may be any statistic like the V-ratio or the number of perfect checkboards (Gotelli 2000). For further explanation see Zaman and Simberloff (2002).

To obtain the probability of reaching a certain score, the frequency of each matrix has to be weighted by the ratio of $\overline{C_{corr}} / C_i$ (see example in A.1). In a histogram of the C-scores generated by the original algorithm, all bars

representing C-scores higher than the expected value $\overline{C_{corr}}$ would therefore become smaller and all bars of C-scores smaller than the expected value would become higher.

Minimum number of required swaps

Several authors suggest to start sampling from a matrix near to the stable state distribution, either by invoking a 'burn in period' for the swap algorithm e.g. the first randomised matrices are discarded (Manly & Sanderson 2002; Zaman & Simberloff 2002), or by generating the start matrix with a fill algorithm (Miklos & Podani 2004). When performing an analysis, not only the number of total sampled matrices, but also the number of discarded matrices have to be chosen. Miklos and Podani (2004) suggest to make as many swaps as there are ones in the matrix.

It is known that $\lim_{n \rightarrow \infty} p(n) \rightarrow p$ (Zaman & Simberloff 2002). We suggest to calculate not only the p-value, but also its standard deviation (SD). The randomisation should stop when (i) the p-value plus SD is below the required significance level, or (ii) SD is below 0.01.

Results

The Vanuatu data set

The C-score of the Vanuatu data set (Diamond & Marshall 1979) is 9.5299. Performing 10^6 swaps gives a mean value $\overline{C} = 9.1299$ and a corrected mean value $\overline{C_{corr}} = 9.1290$. The p-value generated by the sequential swap is $9.4 \cdot 10^{-5}$ and the frequency corrected p-value is $8.969 \cdot 10^{-5}$. Both are highly significant. The standard deviation for the p-value after 10^6 swaps is 0.0014, after $2 \cdot 10^4$ swaps the sum of the p-value and the standard deviation is below 0.01, hence $2 \cdot 10^4$ swaps are sufficient to show that the Vanuatu data set has a strong statistical deviation from the null hypothesis of a random distribution with regard to the C-score.

The Patterson and Atmar data set

Using 291 matrices collected by Patterson and Atmar (1986), we calculated the p-value of the C-score for each matrix using the sequential swap with and without correction (Fig. 2.1). Compared with the original algorithm, the frequency corrected 'sequential swap' identifies three more matrices as statist-

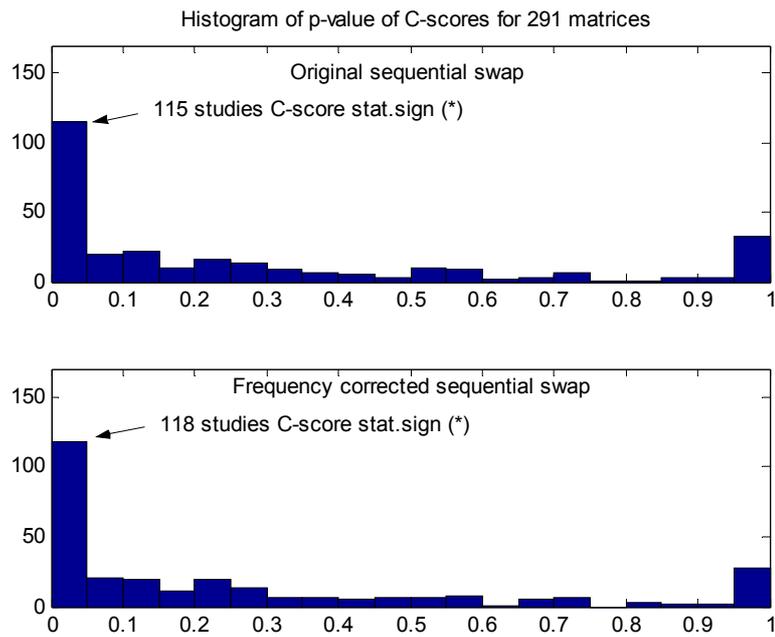


Figure 2.1 C-scores histograms of differences between the p-values of the C-score between the original sequential swap and the frequency corrected sequential swap, using 10000 swaps and 291 published datasets.

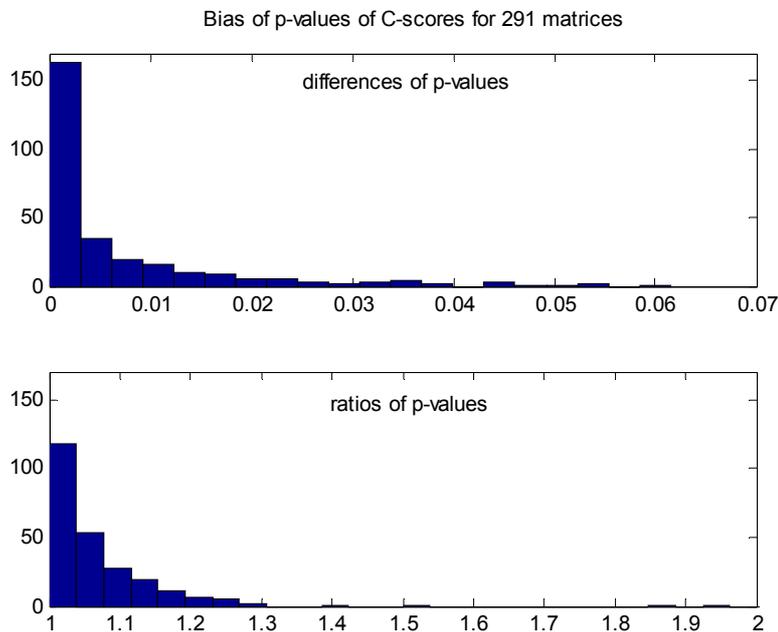


Figure 2.2 Histograms of the total and relative deviations of the p-values for the C-score generated by the sequential swap and the frequency corrected sequential swap, using 10000 swaps and 291 published datasets.

cally significant ($p < 0.05$) and one extra matrix at the $p < 0.01$ level. These matrices have uncorrected p-Values of 0.486, 0.0466, 0.0365 and 0.0085 and the corrected p-Values are 0.0527, 0.0552, 0.0674 and 0.0102 respectively. The total and relative differences of the p-values derived by the two algorithms are displayed in figure 2.2. Though the total p-values are relatively similar (maximum total difference is 0.062), they differ quite substantially relative to each other. In 116 out of 291 matrices the differences are over 5% and in 62 matrices they are more than 10%.

For all matrices with a significant deviating C-score, the standard deviation of the p-value is below 0.1 after 10000 swaps.

Discussion

The search for structure in presence/absence matrices has a long history in ecology, as in many cases this is the only available data set. Since Connor and Simberloff (1979) published their assembly rules, there has been an ongoing debate on the methods to detect structure and how to interpret them (for a review see Gotelli and Graves (1996)). One of the still open questions is the choice of the correct algorithm to generate random matrices with fixed row and column totals (Gotelli 2001). Although the sequential swap has been shown to oversample certain matrices depending on the observed data set, Gotelli (2001) suggests using the sequential swap since the possible bias is out-weighted by the computational demand of the 'random Knight Tour', which is believed to be unbiased. Zaman and Simberloff (2002) investigated the statistical properties of the 'sequential swap' and suggest weighting the calculated statistic by the number of neighbouring matrices (which is related to the C-score). Miklos & Podani (2004) suggested a 'trial swap' in which the statistic is weighted with the number of attempts to find an appropriate pair of rows and columns to perform a swap. Hence the statistic is calculated not only after each successful swap but also for each swap attempt. When using the trial swap, one has to bear in mind that the number of performed trial swaps are not equal to the number of performed swaps, as every swap contains effectively several trial swaps. Both methods deliver similar results. Our results show that there are published data sets in which the original sequential swap indicates no significant difference in the C-score while frequency corrected swap finds a significant difference. However, the differences in the p-values are very low, as

the maximum difference between corrected significant and uncorrected insignificant p-values is below 0.03. The bias depends on the relative differences in the C-score (or number of checkerboards), which are relatively low for big matrices like the Vanuatu data set, with a C-score ranging from 9.0 to 9.5 (7%) and higher (25%) for small matrices like the one in the appendix 1. However, in only 4 out of 291 matrices the bias had an influence on the significance. Hence in most cases the influence of other factors (e.g. overlooking a species at a certain site, correct species identity or species status determination) can be expected to influence the result more than the bias in the 'sequential swap' algorithm. By assessing the standard deviation of the p-value the question of necessary swaps is solved. The p-value itself can be justified against a potential bias towards the observation since this bias greatly influences its standard deviation. Using a 'burn in period' or a fill algorithm to generate the starting matrix is also valid and will eventually reduce the number of necessary swaps.

In most studies a histogram of the C-score is plotted or the individual C-scores are stored for the significance analysis. In this case the correction can be performed afterwards without increasing the sampling effort. The correction can also be performed using only the histogram of the C-score of a study without a recalculation.

Sanderson *et al.* (1998) criticises the sequential swap for incorporating the structure of the original matrix. Following this argument one might expect that the sample is biased towards the observation. In cases where the distance of unique matrices (e.g. the minimum number of swaps required to transform any one matrix into the other) is lower than the number of performed swaps, this effect might occur. In all cases the number necessary swaps to get a standard deviation of the p-value below 0.01 was well below the performed 10000 swaps, hence we have no indication that this effect might occur.

Though we showed that the bias of the sequential swap on the C-score may be low, as long as the matrix is relatively large, we suggest using the frequency correction by Zaman and Simberloff (2002). The potential bias of other scores is unknown, nevertheless, we suggest using the frequency corrected 'sequential swap' for any score. Stopping the randomisation algorithm after a certain standard deviation of the p-value is reached (e.g. testing every 1000 swaps) can shorten the procedure and assures the quality of the p-value.

We hope that we have contributed to clarifying the statistical properties of the 'sequential swap' and we encourage researchers to use it.

Chapter 3

Fourth Corner Generation of Plant Functional Types

in collaboration with Peter Harmand and Michael Kleyer

Abstract

Plant functional types (PFTs) or groups are now widely established to understand plant –environment relations. Different statistical methods are used in the literature to form PFTs. 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 parameters. Another way is to search for associations of occurrence data, environmental parameters 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 types by developing new randomisation procedures for presence/absence data of plant communities. Previous PFT groupings used either predefined groups or emergent groups of the global species pool and assessed their functionality. However, since not all PFTs might form emergent groups or may be known by experts, we used a permutation procedure to optimise functional grouping. We tested the method using a 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. Functional trait combinations could be clearly distinguished from non-functional combinations. The results are compared with the method suggested by Pillar (1999) for the identification of plant functional types.

Introduction

The prediction of vegetation response to climate or land use change has demonstrated a need for a functional classification of plants based on plant

traits (Lavorel & Garnier 2002). Trait analysis may contribute to a general understanding of plant allocation strategy and plant – environment relations (Wright *et al.* 2002) and help to scale up from population viability analysis to risk assessment of communities (Henle *et al.* 2004). This has been done using knowledge-based a priori grouping (Condit *et al.* 1996) or multivariate methods such as clustering (Skarpe 1996).

The number of functional types or groups identified in a study varies according to the number of recorded traits, the species set and the classification method involved (Bugmann 1996; Nygaard & Ejrnaes 2004), which probably limits generalisations across studies. With respect to methods, the problem is to link three tables with different statistical units into a fourth one, which can then be subjected to further analysis. The three tables are a site \times environmental factors matrix, a species \times site matrix, and a species \times traits matrix. Such an analysis should comply with the definition of plant functional types (PFTs) as groups of species that respond similarly to environmental settings and share common functional trait attributes (Lavorel *et al.* 1997; Semanova & van der Maarel 2000). Both requisites together discriminate this type of analysis from single trait analysis (e.g. Kahmen & Poschlod 2004; Vesik *et al.* 2004). One general objective of PFT analysis is to identify trade-offs between traits with a significant relation to environmental factors (i.e. the functional traits Suding *et al.* 2003). Trade-offs operate at the species level. Hence, if trade-offs between functional traits are to be found, species identity has to be kept during the statistical process of identifying PFTs. In many studies published so far, this is not the case (Fernandez *et al.* 1993; Jauffret & Lavorel 2003). The simple combination of the species \times site matrix with the species \times traits matrix pools all species at a given site towards a single value per trait (e.g., the mean of a metric trait variable, or frequencies of nominal trait classes). Since information on cross-trait relations 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 syndromes, i.e. groups of species based on combinations of traits, have been published but none of them has been accepted as a standard procedure so far (Nygaard & Ejrnaes 2004). Among these approaches we find complex multivariate ordination techniques (Doledec *et al.* 1996; Lavorel *et al.* 1999) generalised linear modelling in combination with ordinations (McIntyre & Lavorel 2001), or logistic regression models of func

tional groups (Kleyer 1999a, 2002). The statistical analysis also depends on the study design, i.e. whether predictors are continuous gradients or categorical treatments (factors). Here, we will concentrate on treatment designs and trait values in discrete classes. Legendre *et al.* (1997) developed the so called '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 with the use of null models. Null models generate patterns based on randomisation of ecological data. To account for ecological processes, some elements of the data are held constant while others are allowed to vary stochastically to generate occurrence patterns that would be expected in the absence of a particular ecological mechanism (Gotelli & Graves 1996). Hence, to detect plant functional types based on ecological attributes, a null model has to be indifferent to plant traits and treatments.

The fourth corner method (Legendre *et al.* 1997) uses a null model technique to classify species into groups of similar response to environmental conditions and similar trait attributes. Null models reflect different ecological hypotheses by using appropriate permutation procedures. Four different null models are proposed by Legendre *et al.* (1997) in their investigation of a fish assemblage. One null model permutes the rows of the observed matrix to test the association between types and habitats. The resulting matrix of p-values can be used to answer the question: 'What range of sites is occupied by a given fish type ("realised niche breadth")?', which is different from the question: 'Which types are occurring at a certain site ("community assembly")?'. To answer this question, a different null model is necessary.

Another approach aimed to identify optimal plant functional types is the procedure proposed by Pillar (1999). It permutes the traits and searches the optimal trait combination by a similarity analysis. However, if PFTs are conceived as syndromes, the aim is not only to identify the functional traits but also the trait states forming syndromes.

When categorisation of trait data is necessary, choosing appropriate category ranges is an important issue. Inappropriate category ranges might lead to insignificant functional groups and to not detecting the whole functional pattern in the data set. To optimise PFTs, the minimal number of classes and

their ranges, necessary to represent the functional variation of a trait, needs to be identified. While Legendre *et al.* (1997) only consider the relationship between single traits and environmental parameters, we extended the fourth corner method to determine functionality of trait syndromes (Lavorel *et al.* 1997) in relation to combinations of environmental parameters.

We propose a procedure to identify plant functional types based on presence / absence data of species, their biological trait data and data on the environmental conditions of the sampled sites. A permutation procedure generates a large set of all reasonable plant groups by combining subsets of trait classes. Each group is tested for functionality against the environmental variables by the fourth corner method and an optimal plant functional type categorisation is chosen. The procedure allows to integrate plant functional trait and plant functional type analysis. We will also apply the algorithm of Pillar (1999) to compare and evaluate results.

Methods

Test Data generation

To demonstrate the procedure, we generated a test data set which incorporates the structure that the algorithm is aimed to detect, as suggested by Semanova & van der Maarel (2000). We use disturbance as the only environmental factor, with four levels and 20 replications for each level. Virtual plant communities are constructed on the basis of four traits. The traits are plant height (4 classes), seed number (3 classes), spacer length (3 classes: no, short and long spacer) and colour of flowers (4 classes). Combining the traits height, seed number and spacer length results in a total of 36 plant types. The four classes of colour are randomly assigned to the plants species. For each species \times site combination, a proportion of occurrence is calculated by incorporating a linear relationship of the single trait plant height to disturbance and a more complex relationship of a syndrome of seed number and spacer length.

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 (Kleyer 1999a; Aarssen & Jordan 2001 see Figure 3.1).

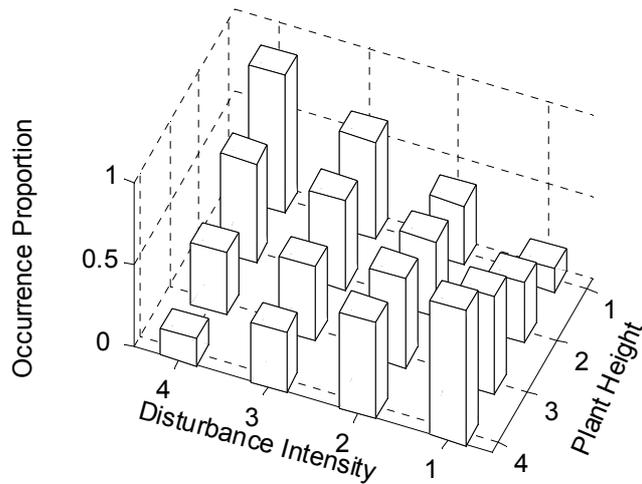


Figure 3.1 The relationship between height and occurrence proportion for four disturbance intensities in the test data set. Under rarely disturbed site conditions (disturbance intensity = 1), tall plants (plant height = 4) are superior, while small plants (plant height = 1) have the highest occurrence proportion at highly disturbed sites.

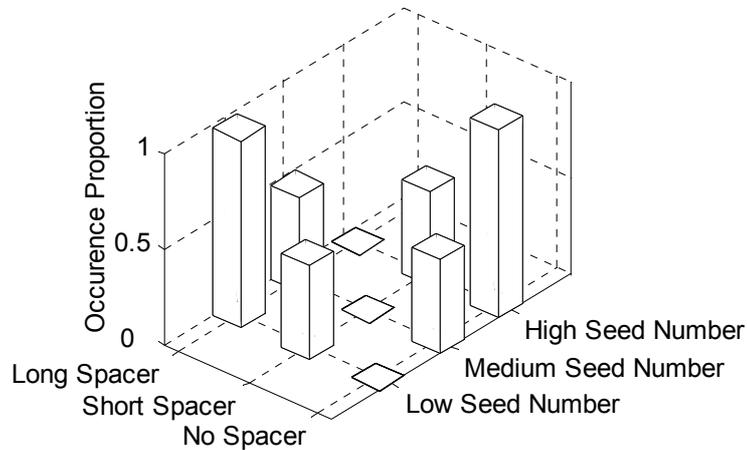


Figure 3.2 The relationship of spacer length, and seed number to occurrence proportion for highly disturbed conditions in the test data set. The combination of high seed number / no spacers or low seed number / long spacer is advantageous under highly disturbed conditions. In case of intermediate and low disturbance, the trait attributes are evenly distributed and not shown here.

We assume that syndromes of seed number and spacer length are advantageous only at the highest disturbance level while being not functional at lower disturbance levels. At intensely disturbed sites (e.g. fields), species may either maximise their seed production for dispersal, or invest in rapidly regenerating elongated rhizomes, having only limited resources left for seed production (see Figure. 3.2). The generation of the test data set is explained in detail the appendix A.2.2.

Plant type definition

The definition of plant types incorporates the choice of traits as well as ranges of the ordinal trait attributes forming a type. In order to obtain the most powerful set of PFTs, we systematically generate all reasonable trait class combinations. For practical reasons the minimum class range and the maximum number of classes will be fixed. Species with a certain combination of trait classes belong to a 'plant type' (PT). These plant types are subjected to the fourth corner method to determine whether they are considered as functional or not.

If 6 different heights are measured in the trait data set and the minimum class range is set to 2, a total of 4 classifications are possible ([1-2;3-4;5-6], [1-3;4-6], [1-2;3-6], [1-4;5-6] see also example in appendix). Each combination or syndrome is tested. The total of required tests will be the product of the number of classifications for all single traits.

The fourth corner method

To extend the fourth corner method by Legendre *et al.* (1997) from single trait to PFT analysis, we used different null models and replaced the trait matrix by a plant type matrix that represents all possible trait combinations. The presence / absence of a set of k species on m sites is recorded in matrix A ($k \times m$). Another matrix B ($k \times n$) assigns each species (row) to a plant type (column). The four matrices for B derived from the example above are listed in the appendix. The environmental factors are classified, and matrix C lists the treatments (rows) applied to each site (columns).

The matrix product $D=CA'B$ lists the frequency at which each species type occurs at a given environmental factor (Fig. 3). Matrix D can also be derived by constructing an inflated data table as shown in the appendix (Tab. A.1). These count data are not suitable for Chi-square testing, because the observations are not independent of each other (several species may occur per site). A ran

domisation (null model) test is used instead of a classical test. Matrix A is permuted and for each permutation (A_{per}) a new matrix D_{per} is computed ($D_{per}=CA_{per}'B$). For each cell in D, the frequency of containing a higher or equal value than the associated cells in the set of D_{per} is calculated. If an entry in D is only rarely smaller than or equal to the corresponding entries in D_{per} , the trait combination is thought to occur more often than expected by the null model, and is positively related to the environmental factor. Given a large set of permutations, this frequency is an estimator of the one- tailed probability (p-value) of $D(\text{cell})\geq D_{per}(\text{cell})$. If the p-value of a certain trait class combination is below 0.05, the grouping is considered to be functional with respect to the associated environmental factor. Values higher than 0.5 indicate a negative association i.e. the plant type occurs less often than expected by the null model. In this case we listed the probability of generating a lower or equal value in D and indicated this with a (-) sign at the p-value.

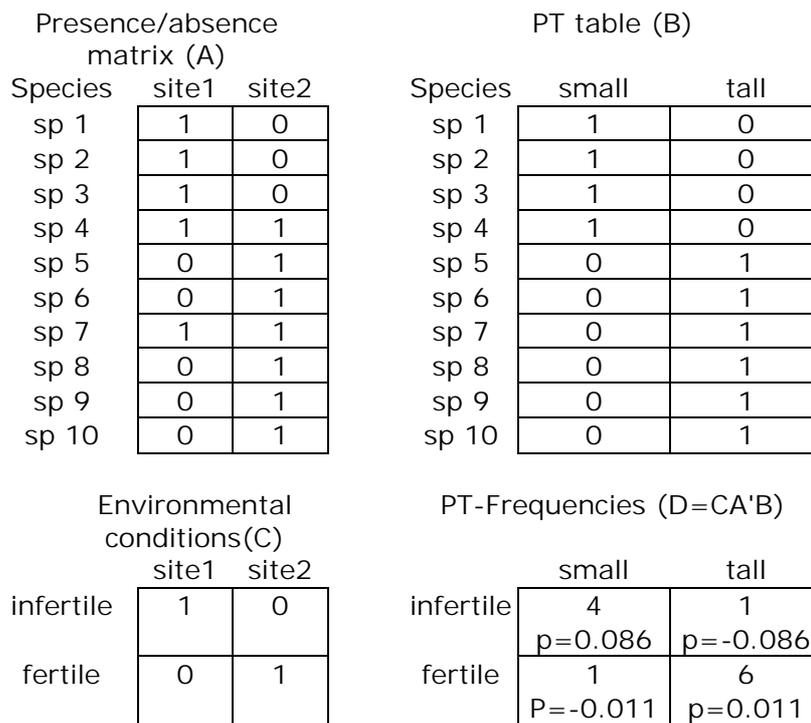


Figure 3.3 The fourth corner method incorporates three matrices of observed values (A,B,C). All observations have to be classified, a 1 marks the membership of each site or species to the associated environmental or trait class. The fourth statistic is calculated as $D=C\times A'\times B$. It lists the frequency at which each species type occurs at each environmental state. The p-values shown in matrix D indicate the probabilities at which the cell value generated by the null model is equal to or more extreme than the cell values caused by the observation.

Legendre *et al.* (1997) correct their p-values to accommodate for the increased probability of committing a Type I error in the case of multiple simultaneous tests. We decided not to correct the p-values, because (i) each plant type will be compared individually against the occurrence of the same type in the null model and (ii) no indirect comparisons are made between different plant types or treatments.

For any combination of trait classes, a matrix of p-values is generated. An optimal set is chosen as a compromise of a minimal number of plant types and a maximal strength of relationship of plant types to the environmental factors (of number of significant p-values). If a PT shows a significant relationship to an environmental factor ($p\text{-value} < 0.05$), then subdividing it may increase the number of significant p-values of the classification. However, if the p-values have the same sign, the smaller set is preferred as long as it has the same explanatory value. In this case the larger set will be discarded. The same applies to the subdivision of several PTs into more PTs. From the remaining set of PT categorisations, the one with the highest number of p-values (n_{ps}) below a threshold (e.g. < 0.05) is chosen (see appendix for an example). In case that several classifications are similar according to these criteria, the categorisation with the lowest total sum of significant p-values is preferred. This procedure is useful, if the whole set of species has to be categorised and no special attention is paid to certain species or types.

Null models

To test for plant type functionality, we use the 'lottery' model (Sale 1978; Legendre *et al.* 1997). It assigns randomly chosen species to each site until all sites have the same species number as found at the observed sites.

All species have the same chance of being chosen. If the plant types consist of different numbers of species within the total species pool, this can be taken into account by multiplying all cells in D with the average number of species per plant type divided by the number of species covered by the plant type that corresponds to the cell. The uncorrected null model assumes the occurrence probabilities of species per plant type to be similar, e.g. if a plant type comprises more species than another plant type, it is also expected to have a higher occurrence frequency by the null model. The corrected version assumes the absolute number of species per plant type to be similar, e.g. all plant types are expected to have similar occurrence frequencies. The correction is per

formed prior to comparison of D_{per} to D .

We derive the realised niche of a PFT by using the sequential swap algorithm (Manly 1995). It selects a pair of sites and a pair of species at random. If one species occurs only at the first site and the other species occurs only at the second site, these species are interchanged, i.e. after the swap the first species is assigned to the second site and the other species is assigned to the first site. Thus, both row and column sums are kept constant. Since the sequential swap algorithm has been shown to be biased, we use a corrected version as suggested by Zaman & Simberloff (2002). Sampling all matrices with the correct frequency is not the only necessity for a valid permutation algorithm, it should also give independent and "sufficiently different" matrices. One way to achieve this, is to discard $n-1$ of the generated random matrices in every step, i.e. the first random matrix A_1 used is actually the n -th among the generated matrices, the second matrix A_2 is the $2n$ -th and so on. This procedure is the most conservative among the different ways to use the swap algorithm (Stone & Roberts 1990). Often the number n of swaps is fixed arbitrarily. We used the 'noise test' (Gotelli 2000) to find the appropriate swapping rate n for the test data set. Applying the fourth corner method after 100 swaps on a test data matrix with maximum association results in p -values above 0.1. Hence we decided that 100 swaps are sufficient in order to generate an independent permutation.

Identification of optimal plant functional types by similarity analysis

Another method for PFT identification was proposed by Pillar (1999). The traits of the PFTs are permuted, and the trait set maximising 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 PFTs is thought to be optimal. We applied the method to 100 test data sets, with the trait colour randomly assigned, in order to estimate the correlation coefficient and its standard deviation.

Results

Although the algorithm is designed to analyse syndromes, we start by using single traits. Each set of PTs produced a matrix of p -values of the relationship of the plant type to the treatment. A total of 1000 null matrices was generated.

Communities from PFTs Relationship from of a single trait

The p-values for a grouping considering only plant height are listed in table 3.1. Tall plants occur more frequently than small plants at rarely disturbed sites and vice versa. However, when using all four classes of plant height, the intermediate height classes 2 and 3 are not significantly related to intermediate disturbance levels resulting in 12 p-values below 0.05. If three height classes are used instead of four classes, occurrence of the medium high plant type is unrelated to the treatments. We consider the categorisation into two height classes to be optimal, because it has as many significant p-values as the second categorisation, but comprises a smaller set of PTs, and the number of significant p-values per PT is higher than in the first categorisation which is a subdivision of the last one.

Table 3.1 PFTs categorised for vegetation composition, based on plant height. Separating four, three or two height classes results in a total of 12 (4 PTs) or eight (2-3 PTs) statistically significant p-values ($p < 0.05$). Although the classification in four PTs results in the highest number of p-values below 0.05, the categorisation into two classes is preferred, because the small and the very small PT of the first PT set are subdivisions of the small PT from the last PT categorisation and the number of p-values per PT does not increase. The values indicate the association (sign) and the statistical significance (p-values).

Nr. of PTs	Trait class Height (h)	P-values of response to disturbance regime			
		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

Unrelated traits: colour

None of the 100 test data sets with the trait colour assigned at random yielded significant p-values for the colour – disturbance relationship at a sig

nificance level of 0.05. Hence, the Type I error is below 0.05.

PFTs from trait combinations (syndromes)

Plant types formed on the basis of the traits seed number or spacer length show a significant relationship at highly disturbed sites, with the extreme trait classes being more frequent than expected from the null model. This corresponds to the relationship displayed in figure 2. Combining both traits leads to nine PTs (3 classes \times 3 classes). Plant types combining high seed number and low spacer length or low seed number and high spacer length are competitive advantageous, while equal classes for seed number and spacer length are disadvantageous at highly disturbed sites. All other trait combinations are not functional. The p-values for categorisation based on the traits spacer length and seed number (separately and combined) are listed in table 3.2.- 3.3.

Combining traits increases Type II error, because the total difference between the now smaller groups decreases, yielding less significant p-values. This effect results in insignificant p-values for all PTs at medium disturbed conditions, and for medium sized PTs under rarely disturbed conditions, if a set of 36 PFTs is formed considering the three traits height, spacer length and seed number. The p-values for such a categorisation are given in the appendix A.2.3.

Table 3.2 PFTs are generated by the ‘lottery’ model, generating 1000 randomised matrices for vegetation composition: The association is based on spacer length. The values indicate the association (sign), and the statistical significance (p-values). This classification is only functional under intensely disturbed conditions.

Trait class	P-values of response to disturbance regime			
	1	2	3	4
Spacer (p)				
short (1)	n.s.	n.s.	n.s.	0.0460
medium (2)	n.s.	n.s.	n.s.	-0.0010
long (3)	n.s.	n.s.	n.s.	0.0310
Seed number (s)				
low (1)	n.s.	n.s.	n.s.	0.0060
medium (2)	n.s.	n.s.	n.s.	-0.0010
high (3)	n.s.	n.s.	n.s.	0.0410

Table 3.3 PFTs are generated by the 'lottery' model for vegetation composition. Three classes for spacer length (p: no spacer = 1; short spacer = 2; long spacer = 3) and three seed number classes (s; low seed number = 1; medium seed number = 2; high seed number = 3) are permuted leading to nine PT's . The values indicate the association (sign), and the statistical significance (p-values). This classification is also only functional under intensely disturbed conditions.

Trait class		P-values of relationship to disturbance regime			
Spacer (p)	Seed (s)	1	2	3	4
1	1	n.s.	n.s.	n.s.	-0.0010
1	2	n.s.	n.s.	n.s.	n.s.
1	3	n.s.	n.s.	n.s.	0.0010
2	1	n.s.	n.s.	n.s.	n.s.
2	2	n.s.	n.s.	n.s.	-0.0010
2	3	n.s.	n.s.	n.s.	n.s.
3	1	n.s.	n.s.	n.s.	0.0010
3	2	n.s.	n.s.	n.s.	n.s.
3	3	n.s.	n.s.	n.s.	-0.0010

The niche of a PFT

We applied the null model with fixed row and column sums to analyse the niche of a PT. Table 3.4 lists the associations and p-values for each type - treatment combination for the trait plant height. The differences to the results of the 'lottery' model (Table 3.1) are marginal because of the symmetry in the height – disturbance relationship. For more complex relationships the results differ.

Table 3.4 The realised niche of the PFT is determined using the sequential swap. 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 height – disturbance relationship

Trait class	P-values of response to disturbance regime			
	1	2	3	4
Height (h)				
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 p-values for the realised niche of plant types composed of the traits seed number, and spacer length are listed in table 3.5. The plant type without spacers and low seed number is absent under highly disturbed conditions (Figure 3.2). Hence its occurrence is positively related to the other treatments where it occurs. Plant types with only one trait being of medium size occur under highly disturbed conditions with the same frequency as in the other treatments. The method detects no significant difference in the number of occurring species of these types ($p > 0.05$).

Table 3.5 The realised niche of the PFT is formed based on the traits spacer length and seed number. 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 permuted to nine PT's. The values indicate the association (sign), and the statistical significance (p-values).

Trait classes		P-values of relationship to disturbance regime			
Spacer (p)	Seed (s)	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

Correlation of dissimilarities

The trait combination plant height, spacer length and seed number gained the highest Pearson correlation coefficient ρ using the procedure by Pillar (1999) which conforms to the structure incorporated in our test data. It is followed by the combinations plant height and spacer length and the combination height, spacer length and colour. The ranking of the ρ -values and the associated plant traits is listed in table 3.6. Since the trait colour was assigned at random, we listed means and standard deviations derived from 100 different test data sets for each trait combination. The ordering in the lower ranks is highly random, while the first ranks are correctly determined with a high probability. The single trait colour has the lowest correlation coefficient.

Table 3.6 The optimal trait set is derived with the algorithm by Pillar (1999) for the test data set. The Pearson correlation coefficient ρ is calculated for the dissimilarity matrices of the sites by species (squared cord distance) and sites by the environmental parameters (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 can not 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.

Pearson ρ	Std.	Trait combination
0.910	0.000	Height, Spacer Length, Seed Number
0.809	0.000	Height, Spacer Length
0.619	0.011	Height, Spacer Length, Colour
0.604	0.000	Height, Seed Number
0.598	0.000	Spacer Length, Seed Number
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

Discussion

All trait – disturbance relationships incorporated in the test data set could be detected using the extended fourth corner method and PFTs were discriminated. Non-functional traits (colour) were not included in the generated PFTs.

Syndrome versus single trait analysis

After a literature review of life history traits associated with disturbance and abiotic factors, Marby *et al.* (2000) concluded, that the importance of analysing multiple character (e.g. syndromes) instead of single traits was supported by the wide range of traits thought to be functional by different authors. Not only the traits thought to be functional differed, but also the relationship between traits and environmental factors.

Jauffret and Lavorel (2003) use a generalised 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 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 functionality. Whether such complex relationships are relevant for 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 PTs with either high seed number or long spacers, are positively related to highly disturbed treatments, the combination of both trait states is disadvantageous (Figure 3.2, Table 3.5). Forming PFTs only from single trait analysis would not produce a valid PT factor relationship in this case.

Another issue in forming PFTs by single trait analysis is to assure that the trait states co-occur in the species, likewise it is done by Jauffret and Lavorel (2003). All PTs identified by the proposed method comprise species since our null model only randomises the observed data. The necessity of analysing syndromes instead of combining single trait analysis was also found by Marby *et al.* (2000) who analysed 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.

Null models

To identify co-occurring PFTs in a given treatment we used the 'lottery' 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 types perform better than others. Using the model without correction assigns -on average- the same number of species to each plant type. It therefore evaluates whether the observed plant types occur proportional to the number of species they cover. However, if total species number per plant type is of concern, normalising 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 PTs which were observed more frequently than others.

The frequency of occurrences indicates which PT will dominate within a treatment.

If not PFT composition per treatment (community analysis) but occurrence of a PFT across treatments (niche analysis) is concerned, a different null model is required. The environmental control model (Whittaker 1956) 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 of different environmental conditions, the method is biased to overestimate the frequencies of species that tend to occur at species rich sites in the observation 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 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 classified into discrete classes and each site has to be assigned to a combination of factor classes (treatments). The ability to correctly discriminate PFTs (Type I error) is strongly influenced by the number of sites and the number of traits used to compose the PFTs. Increasing the amount of sites may allow to incorporate more traits into PFT generation.

Comparison with other approaches

Our method advances the fourth corner method developed by Legendre *et al.* (1997). The original method focuses on a test of the global relationships between single traits and environmental factors, less on testing each possible combination of traits. A second branch in the three-table joint analysis is based on correspondence analysis and include the RLO technique (Doledec *et al.* 1996; Ribera *et al.* 2001) or consecutive multivariate techniques (McIntyre & Lavorel 2001). A third branch resides in the framework of Generalised Linear Modelling and logistic regression techniques (Kleyer 1999a; Jauffret & Lavorel 2003). Among these techniques, the approach probably most similar to ours is of Nygaard & Ejrnæs (2004) who start with an a priori classification of functional groups with classification trees. Subsequently, they also use an inflated

matrix ('list file') based on Legendre *et al.* (1997) and proceed with Analysis of Variance using cross-validation to assess generality of their models. Similar to Legendre *et al.* (1997), they only test a global relation of functional types with treatments which restricts understanding the contribution of individual trait combinations to plant – environment relations. The latter can be achieved by optimisation methods as presented in our approach or by Pillar (1999; 2003). Moreover, we consider null models as a straightforward method to cope with lack of independence between observations in an inflated matrix.

The results of the optimisation procedure by Pillar (1999) are valid for the test data set and contingent with the results of our extended fourth corner method. However, it detects the functional traits, not the direction of the association to the environmental parameters, or their significance. His algorithm will deliver a trait ranking, even if none is functional, while our method tests the significance of association for each PT to each environmental factor. Pillar (2003) enhanced his method by using a cluster analysis to find the optimal trait classes of the PTs. However, he still uses the correlation of dissimilarities to discriminate the optimal trait set, hence the results concerning our data set would be similar.

Perspective

If several traits influence the occurrence of a species, they can be expected to differ in their importance. If the data set comprises species differing sufficiently in their trait attributes, the trait hierarchy can be inferred as described in the results section.

The presented null models are based on presence / absence data, because this is the most common data format. Using abundance data can improve such an analysis (Gotelli *et al.* 1987). This extension can be done by designing a new null model which suits this kind of data.

The results of the presented method can readily be used to build scenarios of future vegetation development. Applying the 'lottery' model and projecting the derived PFT- 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 types. The uncorrected p-values of

the 'lottery' model compare the probability of occurrence of each species of the PFT compared to a total occurrence probability in the whole data set. Projecting these values on a map of site conditions displays the relative habitat suitability. Likewise it is done with multiple regressions (GLM) for single species (Guisan & Zimmermann 2000). Hence, these projections may be used for predictive habitat distribution modelling of PFTs.

Part II:

Modelling of PFTs

a mechanistic model

Chapter 4

Trait hierarchies and sequence effects in simulated community assembly using the leaf-height-seed plant ecology strategy scheme

in collaboration with Michael Kleyer

Abstract

Several sets of traits are suggested to establish plant functional types. While extensive analyses of experimental data are made to select traits that predict the response of plants to environmental factors, few studies use a simulation approach to predict suites of functional traits. This paper focuses on the trait set suggested by Mark Westoby (1998): specific leaf area (SLA), plant height and seed mass. We simulated the assemblage of plant types on a gradient of fertility and disturbance and assessed the functionality of the suggested traits. We also characterised how invasibility depends on disturbance and fertility. We present the results of a spatially explicit simulation using LEGOMODEL, an individual based, ecological field model. The competitive superior trait states as well as the functional hierarchy change between different treatments. Plant height always determines competitive success, while seed mass is more relevant for survival than SLA at fertile sites and vice versa at infertile sites. High fertility as well as low disturbance leads to low diversity of functional types. The invasibility of a plant community depends on the combination of fertility and disturbance. Communities characterised by strong competitors show a strong resistibility even in the absence of the best fitted plant type.

Introduction

On the community and landscape scale, plant functional response to environmental change is often studied by analysing the composition of plant traits across communities. This is done under the premise that suites of morphological and physiological traits represent adaptive responses to environmental conditions (Stebbins 1974; McIntyre *et al.* 1999). Traits are correlates to basic life history processes such as photosynthesis or demographic survival rates that are hard to quantify for larger species pools (Garnier 1997). Trait-based func

tional responses to environmental factors were demonstrated in observational, experimental, and long-term permanent plot studies (Fernandez *et al.* 1993; Kleyer 1999a; McIntyre *et al.* 1999; Fonseca *et al.* 2000; Craine *et al.* 2001; Jauffret & Lavorel 2003), and also across contrasting landscapes (Kleyer 2002).

Although functions such as persistence, expansion, generative reproduction, vegetative regeneration and dispersal all are necessary for the long-term survival of plant populations, it is unlikely that all of these functions share similar relevance across all possible environments. We expect that e.g. habitat qualities stable in space and time will require a more consistent response in persistence traits than in dispersal or regenerative traits (Grime *et al.* 1988; Shipley *et al.* 1989; Diaz & Cabido 1997). On the other hand, habitats with frequent and severe disturbance impacts may require a more consistent response in dispersal and regenerative traits than in persistence traits. In any given environment, a certain hierarchy in principal response functions such as persistence, regeneration and dispersability can be expected. On large environmental gradients, we expect a turnover of such functional hierarchies. The extent of this turn-over, the interplay and the trade-offs between response functions on environmental gradients appear to be largely unknown. Up to now, most authors have concentrated on the specific plant traits that contribute to just one or two of these principal functions. For instance, traits such as canopy height, leaf size, mass and lifespan, branching, woodiness, sclerophylly, stem and leaf dry matter content all contribute to the vertical expansion of plants and their capacity to acquire carbon. Several studies have addressed the relative importance of such traits for a single function such as carbon gain across several environments (e.g. Wright & Westoby 2003). In this context, a distinction is necessary between genetic or 'primary' trade-offs among traits and 'secondary' environment – enforced trade-offs (Westoby *et al.* 2002; Suding *et al.* 2003). Primary trade-offs (e.g. leaf life span - specific leaf area, seed size - seed number) result in strong correlation (Westoby *et al.* 2002) and their evolution may also be analysed in terms of hierarchies (Worley *et al.* 2003). Secondary trade-offs (e.g. high above-ground disturbance frequency favours low height and high vegetative regeneration) are in the focus of trait hierarchies as presented here, and need to be discussed in their interaction with primary trade-offs.

To determine hierarchies, trait composition of community or landscape species pools has to be analysed in relation to the environmental factors or gradients that structure them. For large species numbers, 'soft' traits such as seed number, plant height etc. can be more easily identified from measurements (Cornelissen *et al.* 2003) or databases (Knevel *et al.* 2003) than 'hard' traits with demonstrated links to plant function (e.g. demographic survival rates, carbon gain, Diaz *et al.* 1999). Consistency of trait states among species ordered along environmental gradients can then be seen as an indicator for trait hierarchies (Kleyer 2002).

The term hierarchy has been frequently used in the context of competition, where it denotes competitive superiority of species measured against e.g. a phytometer (Keddy *et al.* 2002) or as growth of a target species in pairwise mixture relative to growth of target in monoculture (Wilson & Keddy 1986; Miller & Werner 1987; Shipley 1993). Several studies also analyse the variation of life history traits in competitive hierarchies (Walck *et al.* 1999; Howard & Goldberg 2001; Keddy *et al.* 2002). Competitive hierarchies rank the performance of species in assuming that ranks are the outcome of a single process, i.e. competition among species. Trait hierarchies rank consistency of trait states across species pools, based on species performance. They show which traits are most functional for occurrence / survival. No *a priori* reference is made to processes such as competition, colonisation, or stress tolerance, although trait states can be interpreted as biological correlates to plant functions as persistence, regeneration or dispersability. A concept related to trait hierarchy turnover is that of rank reversals of a single trait driving rank reversals of the relative fitness of species. This was elaborated in the framework of coexistence theory (Chesson 1985; Kitajima & Bolker 2003). An example for a key trait in this context is Relative Growth Rate (RGR) in relation to light gradients (Sack & Grubb 2001).

Trait hierarchies order the relevance of plant traits for survival, an approach that is preceded by plant strategy concepts. Among the many conceptual strategy schemes that have been proposed (e. g. Van Valen 1971; Gadgil & Solbrig 1972; Whittaker & Goodman 1979) the C-S-R triangle of Grime (1974; 1979) has received special attention in plant ecology. A challenge to all these strategy schemes still is to clearly characterise the sets of biological attributes that make up the elements of a certain strategy and enumerate the species that can be assigned to the strategy (Hodgson *et al.* 1999). These shortcom

ings have motivated Westoby (1998) to propose a simple strategy scheme composed of three quantifiable traits. The traits are specific leaf area (SLA), plant height, and seed mass. The position of a species within the three-dimensional space of the axes SLA, height and seed mass may be regarded as a representation of ability to persist in its habitat or to colonise distant habitats. Specific leaf area is correlated with relative growth rate (Garnier 1997; Wright & Westoby 1999) and thus related to competitive ability, together with plant height (Gaudet 1988; Tilman 1988). Seed weight is associated with dispersal, establishment, and seed bank longevity (Bekker *et al.* 1998; Thompson 1998; Kidson & Westoby 2000).

The charm of the LHS scheme is simplicity. Its applicability, however, depends on whether the three traits capture enough plant variability to functionally represent the floristic diversity along major environmental gradients such as fertility, disturbance, and fragmentation. This can only be tested if predictions are available regarding the success of plant types composed of combinations of the three traits in different environments.

In this paper we use a simulation approach to predict LHS combinations for different disturbance regimes on soils with low and high fertility. We are interested in combinations of the three traits SLA, plant height and seed size that perform best in the simulated environments and in a hierarchy of these traits across different environments. We ask whether all three traits are equally functional for survival in all environments (no hierarchy), whether there is a superior trait across all environments (constant hierarchy), or, whether different traits are functional for certain environments (environment-driven hierarchy)?

We also use the LHS scheme to simulate the invasion of a superior plant type. Invasive species are able to alter the resident community structure or even drive other species to extinction (Mooney & Drake 1986). To understand biological invasions, it is necessary to investigate the effect of external and internal factors which influence the susceptibility of natural ecological communities to invasiveness. Several factors have been shown to affect the invasibility of communities. These are vegetation composition (Van der Putten *et al.* 2000), disturbance regime (Burke 1996), the amounts of unused resources present (Davis *et al.* 2000) as well as species richness (Elton 1958). While studies based on observed patterns in the field found either positive or neutral relationships between diversity and invasibility (Lonsdale 1999; Van der Putten

et al. 2000), theoretical considerations (Elton 1958) supported by experimental evidence argue for a negative relationship between species diversity of resident communities and invasiveness (Knops *et al.* 1999; Naeem *et al.* 2000; but see Wardle 2001). Inconsistent results were found concerning the contribution of traits to invasiveness of (exotic) species or community invasibility. In a large-scale observational study, the local and regional abundance of ca. 400 exotic species on Mediterranean islands did correlate less to plant traits than to biogeographical origin (Lloret *et al.* 2004). In experiments, invasiveness correlated to plant traits and invasibility to resource availability (Milbau *et al.* 2003) or standing biomass (Troumbis *et al.* 2002). Trait composition of successful invaders may change during a successional series (Thompson *et al.* 2001).

In the context of this study, the extent to which sequence effects alter trait hierarchies shows the impact of sequence effect vs. environmental factors on community assembly.

The LHS scheme may provide a suitable reduction of traits to construct simple resident communities of plant types whose LHS composition can be compared to that of the invader.

Methods

The model

We used LEGOMODEL (Kleyer 1999b), an individual based, ecological field model (Wu *et al.* 1985; Czaran 1998). It simulates populations of plant types that occupy space to extract resources for growth and regeneration. Plant types originate from simple building rules, able to express different trait attributes according to the specific initialisation of the plant type. The resulting architecture of each plant is predefined by the building rules but also influenced by its local environment including interaction with other plants. The simulation starts with randomly dispersed seeds, germinating in the next time step. A growing plant consists of different modules: stem, leaves, roots, and stolons or seeds for regeneration (Figure 4.1). The plant extracts the resources needed for further growth and regeneration according to the area of light exposed leaves and the soil volume penetrated by its roots. A proportion of the assimilate a ramet of a clonal individual has gained is pooled among the system of connected ramets and redistributed to all ramets (clonal integration).

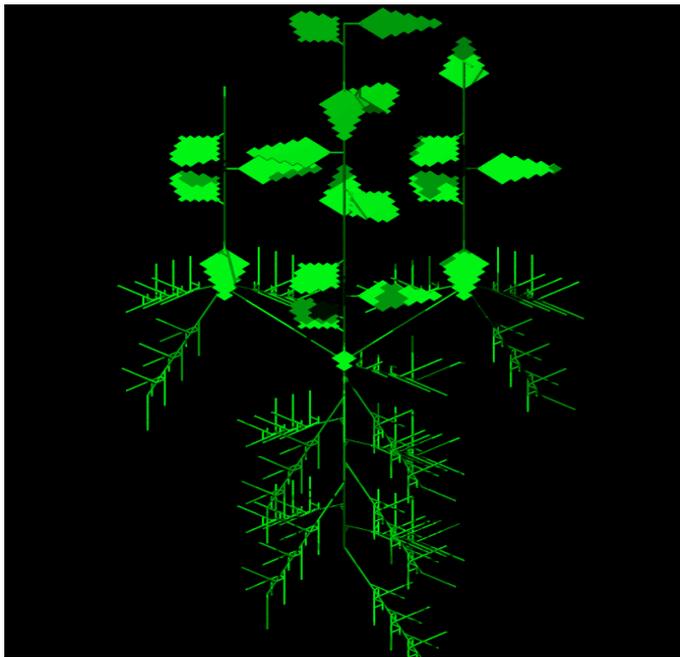


Figure 4.1 Typical growth of a tall plant in LEGOMODEL. The gained resources are distributed between the mother plant and the two ramets (right and left). The plants consist of the modules stem, leaves, spacer, roots or seeds.

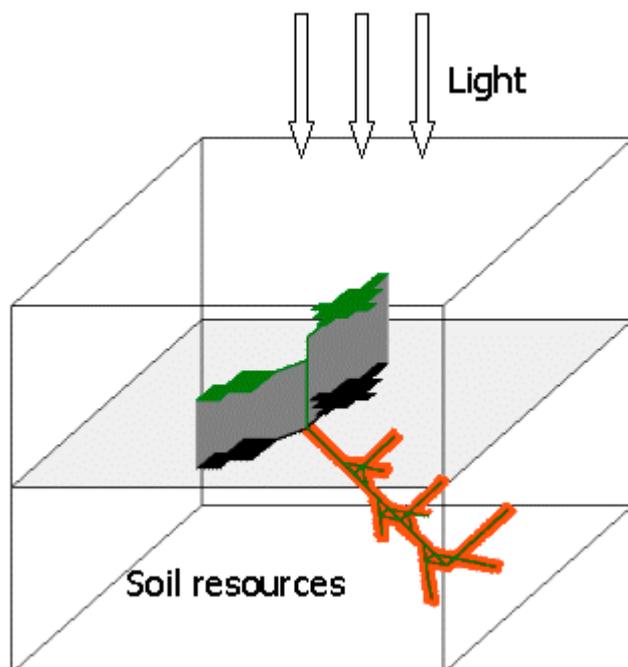


Figure 4.2 Ecological fields incorporated in LEGOMODEL. Below each leaf a directed light depletion zone and around each root cell a soil resource depletion zone is formed. Resource depletion zones are growth barriers for other plants.

Leaves and roots of the virtual plant generate resource depletion zones (Figure. 4.2). Resource depletion zones are growth barriers for other plants.

Shaded leaves produce no assimilate but still respire, hence consume assimilate in every time step. Plant growth is externally inhibited by adjacent resource depletion zones, or internally by lack of assimilate which is consumed by respiration. The resources available to an individual plant depend on the distance from adjacent depletion zones. The energy gain of every time step is calculated as follows (see Tilman 1988):

$$E_{gain} = \min(\text{light}_{gain}, \text{soilresource}_{gain}) - \sum^{plant} (\text{module} \bullet \text{respiration}_{module}) \quad (6)$$

Shaded seeds are dormant until light reaches the surface, either due to disturbance or senescence of the shading plant. Seed dormancy is limited to one year and maximum plant age is set to six years. Except plant height, specific leaf area and seed size and correlated attributes (see below), all other trait parameters in LEGOMODEL were kept constant.

To simulate the LHS traits, we incorporated the following trade-offs:

- Plant types with low SLA require more assimilate to build up leaf tissue than plants with high SLA (construction costs SLA high / low = 1 / 1.6), which in turn leads to a lower growth-rate (Garnier 1997; Wright & Westoby 1999). These plants are subsequently able to conserve assimilate more effectively by making a better use of the same amount of extracted soil resources.
- Seed mass is correlated with the amount of assimilate needed for seed production. The same amount of energy may produce fewer, but bigger seeds or more, but smaller seeds (Kidson & Westoby 2000). Big seeds provide more assimilate to the seedling than small ones.
- Plant height is correlated with leaf area and root length to provide a constant root/shoot ratio.

The model is designed to simulate the course of succession of the plant type assemblage according to disturbance and soil resource supply. Disturbance is incorporated by cutting of all plant parts higher than 10 cm. Soil fertility influences the efficiency of the root modules in extracting resources. All resource depletion zones around a root or below a leaf cell are removed once the plant part is removed, due to disturbance or senescence.

Simulation Scenarios

We simulated six treatments, i.e. monthly cutting, yearly cutting, and cutting once every nine years on soils of low and high fertility. The traits of the LHS scheme were simulated with two states, i.e. low vs. high specific leaf area, low vs. high plant height and low vs. high seed weight. Hence, $2^3 = 8$ plant types took part in the study (Table 4.1). We started by initialising 20 seeds of each plant type randomly dispersed over an empty site of a size equally to 4 m². The assembly trajectories of the developing communities are recorded over a time period of 100 years with 400 replications.

Table 4.1 Trait state attributes of the plant types incorporated in LEGOMODEL. The relative differences between trait state high and low are 1.6 for SLA, 3 for height and 2 for seed mass.

Plan type	SLA	Height	Seed Mass
1	low	high	high
2	low	high	low
3	low	low	high
4	low	low	low
5	high	high	high
6	high	high	low
7	high	low	high
8	high	low	low

A survivorship analysis for censored data assessed the success of the various plant types. We ranked the performance of all plant types for each treatment by comparing their survival times across all repetitions. Cox F-Test for singly censored data (Lee 1980) was used to test for differences between survivorship of two plant types, for an example calculation see Appendix A.4.2. If a plant type displayed a significantly higher survivorship than another plant type, it received a higher rank. If differences between two plant types were not significant, both plant types got the same rank. A detailed description together with an example is given in the Appendix A.4.1. From the results, we took the type with the highest survival rate to further study sequence effects. In these runs, this type was initialised after 20 years of simulation time, when the remaining plant types already assembled to communities. The runs then carried on for another 100 years.

Trait hierarchy

The hierarchy of traits is based on the consistency of trait states (high vs. low) across the ranking of the surviving plant types. For instance, if two plant types are on the first rank and both are of small height and high SLA while seed mass differs in its state, then plant height and SLA are more functional than seed weight. If the second rank is occupied by a plant type having also small height but low SLA, the resulting hierarchy will be: plant height > SLA > seed weight. As the eight plant types represent a complete permutation of the three LHS traits, we could build the hierarchy by analysing the variance of the trait states across the ranks for each treatment separately. For each trait, we counted the number of ranks (from the first rank on downwards) for which the corresponding state remained constant. The higher the number, the higher is the position of the trait in the functional hierarchy.

Sequence effects

To analyse the resistance of the plant assemblages to invasions, the differences in the survival rates between synchronous and asynchronous (delay of the dominant type) initialisation of the plant types were compared across treatments. The differences are given as a percentage of decrease in survival over 100 years under delayed initialisation compared to synchronous initialisation. A one-tailed test of differences of percentages (Sachs 1992) was performed.

Results

At high fertility and low or medium disturbance intensity, the assembly is deterministic and of low diversity. Two plant types exclude all other types after 80 years (Figure 4.3). The type with highest rank has high SLA, height and seed mass, while the second has high height and seed mass, but low SLA. If fertility is low, the type with low height, SLA and seed mass is always at the first rank, regardless of the disturbance level. In these treatments, the community assembly is more stochastic (i.e. none of the plant types attains 100 % survivorship) and of higher diversity. If highly disturbed, plant types at the first rank (plant type 4 & 7) are small, with high SLA and a high seed weight under fertile conditions and low SLA and low seed mass under infertile conditions. The ranking for medium disturbed and rarely disturbed sites are similar at fertile as well as at infertile sites, although the differences between the types are some

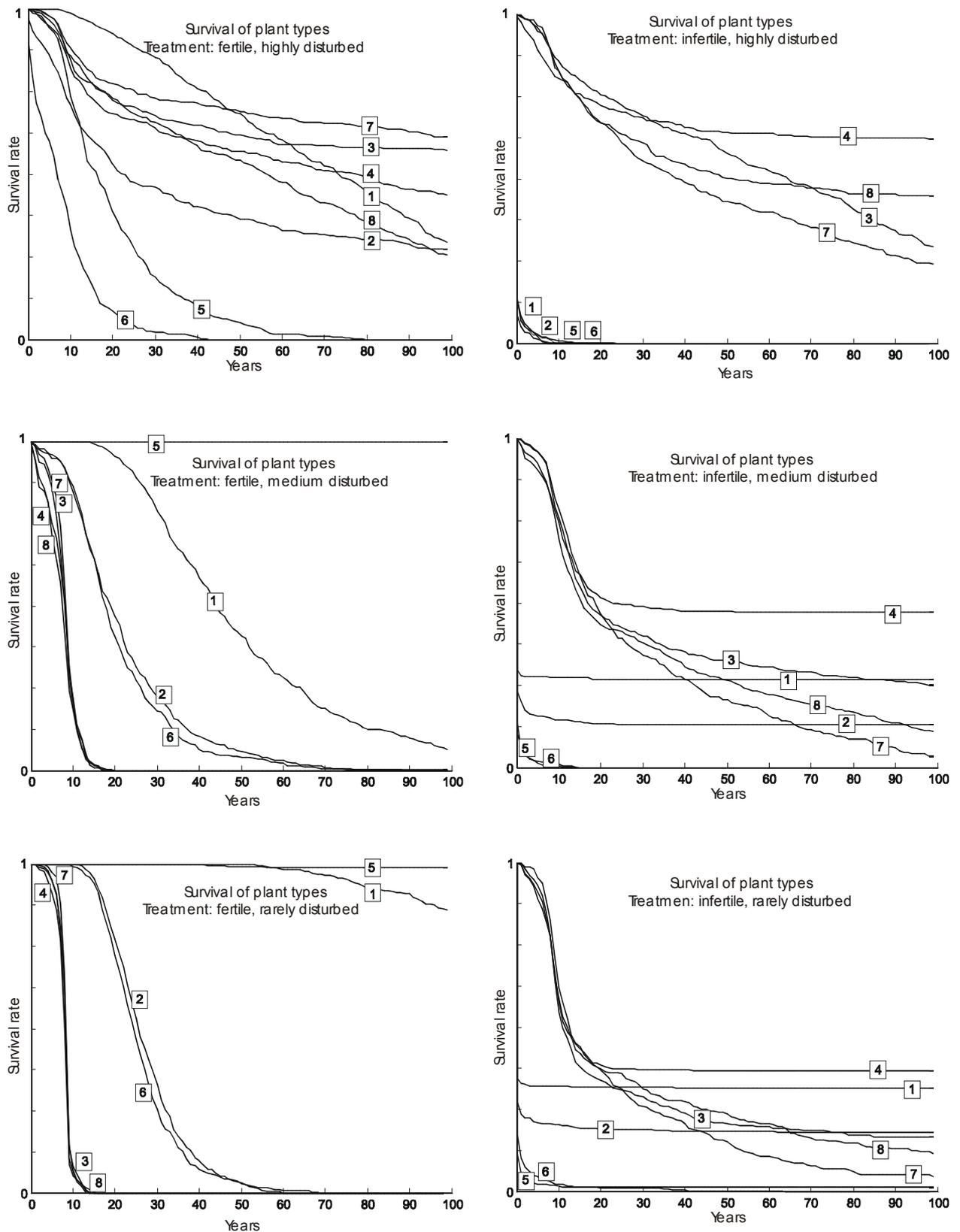


Figure 4.3 Survival curves of eight plant types simulated over 100 years in six treatments. The traits of the plant types are listed in table 4.1.

times not significant, However, the survival curves show strong differences of individual survival between the different treatments. At fertile sites, the functional diversity (number of surviving plant types) is positively affected by disturbance.

Trait hierarchy

The functional trait hierarchy (Table 4.3) shows the importance of traits and indicates the superior attribute (in parentheses). The functional trait hierarchy is not concordant across all treatments. Plant height is the superior trait across all treatments. Under fertile site conditions it is followed by seed mass and then SLA, while SLA is more important than seed mass under infertile site conditions.

Table 4.2 Ranking of plant types (synchronous initialisation, $p < 0,05, n = 400$). The ranking was generated using Cox-F Test for singly censored data (Lee 1980), see appendix for a detailed description and an example.

Rank	High fertility			Low fertility		
	Highly disturbed	Medium disturbed	Rarely disturbed	Highly disturbed	Medium disturbed	Rarely disturbed
1	7	5	5	4	4	4
2	3	1	1	3	3	3 8
3	4	2	2	8	8	
4	1	6	6	7	7	1 7
5	8	7	7	1 2 6	1	
6	2	3	3		2	2
7	5	8	8		5 6	6
8	6	4	4	5		5

Table 4.3 Hierarchy of functional traits and superior trait state attributes. The functionality of traits is derived from table 4.2. A trait is more functional than another if the change of its state occurs later in the competitive ranking of plant types (see table 4.1 for the traits). H: high trait state; L: low trait state

Disturbance	High soil fertility	Low soil fertility
Highly	height (L) > seed mass (H) > SLA(H)	height (L) > SLA(L) > seed mass(L)
Medium	height (H) > seed mass (H) > SLA(H)	height (L) > SLA(L) > seed mass(L)
Rarely	height (H) > seed mass (H) > SLA(H)	height (L) > SLA(L) = seed mass(L)

The optimal trait states are indicated in parentheses in table 4.3. All simulated regimes produce a ranking in which the benefit of a trait state is independent of all other trait states (only one attribute changes from one rank to another). A tall plant is competitively superior only at yearly and monthly cut

ting regimes on fertile soil. On all other regimes small plants are superior. High SLA and seed mass are advantageous at high fertility levels, while low SLA and low seed weight are superior at low soil fertility. This difference is not significant at rarely disturbed sites with low soil fertility.

Invasion resistance

We simulated sequence effects by a delayed initialisation of the plant type that was most successful in the previous simulations. For each treatment, the community is assembled from the less successful plant types during the first 20 years, then the delayed plant type enters the community and the assembly carries on for another 100 years. The decrease in survival of this plant type from synchronous to asynchronous initialisation is given in table 4.4. Except for the intermediately disturbed treatment on infertile soil, delayed entering leads to a decrease in survival. At high fertility, decreasing disturbance intensity increases the resistance against the invader, i.e. survival of the formerly successful plant type is suppressed more in the less disturbed community. At infertile sites, invasion resistance of the most frequently disturbed sites is higher than on rarely disturbed sites, followed by medium disturbed sites with even slightly better survival chances after delayed initialisation.

Table 4.4 Invasiveness of the most successful plant type

Decrease in survival after 100 years due to a delay of 20 years in initialisation. A one-sided z test of differences between percentages (Sachs 1992) proved all differences to be significant ($p=0.05$, $n=400$). ** = $p<0.01$.

Treatment	High soil fertility		Low soil fertility		Effect of fertility
	Type	Percentage	Type	Percentage	
Highly disturbed	7	41%	4	76%	- (**)
Medium disturbed	5	60%	4	-9%	+ (**)
Rarely disturbed	5	86%	4	45%	+ (**)

At equal disturbance intensity, an increase in fertility leads to a decrease of invader success except for the most frequently disturbed sites (Table 4.4).

Discussion

We tested the suitability of the LHS scheme for a virtual plant assemblage across several treatments and assessed the effects of a delayed arrival of plant types in an established assemblage.

Our model is individual based and simulates community assembly on a single patch. LEGOMODEL includes:

- soil resources and disturbance intensity as major environmental constraints,
- trade-offs in allocation to plant height, leaf mass and size, and seed weight that translate in building rules for plant types,
- spatially explicit competition limited to neighbouring plants, based on local resource depletion zones (ecological fields).

It therefore meets the requirements for predictive ecological theory as formulated by Silander and Pacala (1990) and Tilman (1990). Recent modelling approaches emphasise the value of spatially explicit competition mechanisms based on ecological fields or 'fields of neighbourhood' (Berger & Hildenbrandt 2000) which depart from the mean field assumption (Law et al. 2000).

Other modelling approaches also use suites of morphological and regenerative traits to simulate the assembly of communities. A classical model is the Vital Attributes model from Noble & Slatyer (1980) with several derivatives (Moore & Noble 1990; Lavorel 2001).

Mustard *et al.* (2003) used a simulation approach in which the parameter combinations of plant types were able to evolve over several generations.

Similar to our results, fertile sites with low disturbance were characterised by tall plants with medium SLA. Likewise, a second type with medium height and a high SLA occurred mainly at high disturbance levels. LEGOMODEL exhibits major differences to the model of Mustard *et al.* (2003) only in case of SLA under infertile conditions. Here, we predict low SLA which is in line with empirical studies (Poorter & De Jong 1999; Fonseca *et al.* 2000). Seed weight is not modelled by Mustard *et al.* (2003).

Height

Across all treatments, plant height is the superior trait. At high fertility, seed mass is more consistent than SLA, while SLA is more consistent than seed

mass at low fertility. Different disturbance treatments do not alter the ranking of the traits themselves, they only alter the trait states, i.e. the states of height and seed mass shift from 'high' to 'low' in frequently disturbed treatments.

Plant height reflects investment in supportive structures necessary for space utilisation. In our model, leaves assimilate and respire while stems only respire. Each increment in vertical growth requires a positive balance of assimilation and respiration in the previous time step and implies construction costs. After reaching height at maturity, assimilation and respiration continue and investment in construction is finished. Growth also requires sufficient soil resources. Thus, plant types are favoured that allocate less to support structure at infertile treatments. If the return interval between disturbance impacts and removal of biomass is short, small plant height is superior even on fertile sites, because investments in construction until height at maturity are shorter and assimilation can pay off into seed production earlier. Our modelling results concerning height in relation to disturbance and fertility are in line with earlier models (Tilman 1988). Fernandez *et al.* (1993) showed in a study of Mediterranean grasslands that the relative abundance of species with different attributes varies with the level of stress (water and nutrient availability) and disturbance (grazing and ploughing) concluding that "the main trend in variation is related to plant size". Walck *et al.* (1999) found the competitive hierarchy also closely related to plant size in an experiment.

Seed mass

Our model includes the seed mass – seed number trade-off as seed number is assimilate gained divided by seed mass. If the seed mass is small, more seeds are produced. In the absence of any hazard, smaller seeds should be advantageous for population increase. However, in an environment with abundant light and resource depletion zones, a larger seed mass conveys more reserves to the establishing seedling. If the first leaf of a seedling is growing into a light depletion zone, larger seed reserves make the formation of a second leaf possible, probably outside of a depletion zone, even if the balance of assimilation and respiration of the first leaf is negative. Growing empirical evidence supports the seed mass -- seed number trade-off in plants (Turnbull *et al.* 1999; Jakobsson & Eriksson 2000) and the functional importance of larger seed mass when the seedling encounters hazards such as deep shade or inter-specific competition from other seedlings (Westoby *et al.* 2002). Effects of seed size on competitive ability in sand dunes are also found by Rees (1995).

Leishman (2001) experimentally showed under fertile undisturbed conditions, that there is a “competitive hierarchy among species based on seed size where larger seeded species beat smaller seeded species”.

SLA

Specific leaf area or its inverse, Leaf Mass Area, has been regarded as a useful indicator of leaf strategy (Westoby *et al.* 2002), because it reflects physical strength of the leaf and is correlated with relative growth (Westoby 1998), which in turn is correlated with productivity or fertility (Poorter 1989). Strong negative correlations of SLA were also found to leaf lifespan (review in Westoby *et al.* 2002) and photosynthetic capacity of leaves (Reich *et al.* 1999). Construction costs tend to be similar among leaves with high and low SLA (Poorter & De Jong 1999). Longer life-span of leaves with lower SLA permits conservation of acquired resources (Eckstein *et al.* 1999; Aerts & Chapin 2000; Westoby *et al.* 2002). This may be especially true for habitats not characterised by frequent disturbance impacts (e.g. mowing, Ryser & Urbas 2000).

Corresponding to our results, several studies found species with low SLA more likely to occur on sites with low fertility or rainfalls and those with high SLA on sites with high fertility or rainfall (Poorter & De Jong 1999; Fonseca *et al.* 2000). In LEGOMODEL, SLA was implemented based on the simplifying assumption that leaves with low SLA require more assimilate for growth, while resource conservation at maturity would be higher with low SLA.

As an effect of the different assimilate requirements, the relative growth rate is proportional to SLA as found by Westoby (1998).

Trait hierarchy

Although high SLA is a relevant trait for rapid growth and effective space utilisation, our model predicts that high seed mass is more important than high SLA under fertile conditions. This hierarchy is reversed under infertile conditions. Is there any empirical evidence for this prediction? We know of only one observational study that directly applied the LHS scheme (Lavergne *et al.* 2003). However, the authors did not use disturbance and fertility as explanatory environmental factors. A study of Landsberg *et al.* (1999) showed a strong association of canopy height to grazing response, while the association of SLA and seed size was variable. A recent meta-analysis of species response to grazing in Australian dry shrublands and woodlands did not find any significant relation with traits including height, SLA, and seed size (Vesk *et al.* 2004).

Other studies may include also more than the three traits of the LHS scheme, but often one of the three traits is missing. This makes it difficult to compare the functional hierarchy found in our model to the results of such studies. Diaz *et al.* (2001) found that height was the best single predictor for grazing response, while SLA had only a small predictive value. Seed mass was not included. On a disturbance / fertility gradient plane, Kleyer (1999a; 2002) found that height was the most consistent trait, while regenerative traits such as seed size contribute to alternative pathways of occurrence / survival at a single combination of disturbance intensity and fertility. In these studies, SLA was not included.

Our simulated trait hierarchies remain invariant to disturbance regimes within each fertility treatment but change across fertility treatments. Keddy *et al.* (2000; 2002) argued that competitive hierarchies are relatively independent of the environment, i.e. rank reversals are not to be expected if the environment shifts from high to low fertility. This has relevance for trait hierarchies, because similar to competitive hierarchies between species, it is the plant performance (or plant type performance in our simulations) that is measured. In their competition experiments, Keddy *et al.* (2000; 2002) recorded the percent reduction in biomass of a 'phytometer' species grown together with a test species under two fertility regimes. According to the data, this phytometer must have been a very weak competitor because almost all test species reduced its biomass in both the high and low fertility treatments. They found that the relative competitive performances of the test species are similar at high and low fertility. However, if the phytometer species is the weakest competitor in the whole species set, reduced nutrient fertility will confer no competitive advantage to this species. On the other hand, if a phytometer with a more moderate competitive ability had been grown together with test species exhibiting a range of high to low competitive abilities, then rank reversals between high and low fertility treatments would have been more probable.

Diversity

Our simulations show that diversity interacts with both fertility and disturbance. It decreases with increasing fertility and decreasing disturbance. However, it also decreases at high disturbance and low fertility. This result is consistent with a combination of the humped-back model (Grime 1974) and the Intermediate Disturbance Hypothesis (Huston 1979). In these concepts, dominant species competitively exclude other species if dominance is not bro

ken by either stress at low fertility levels or by disturbance. On the other hand, many species are unable to regenerate at high levels of either stress or disturbance. At intermediate disturbance or stress levels, plant species diversity is supposed to be maximised (Grime 1973; Connell 1978; Huston 1979). There is growing empirical evidence for both concepts with respect to species diversity (Goldberg & Miller 1990; Grace 1999; Gough *et al.* 2000; Shea *et al.* 2004) and diversity of functional groups (Kleyer 1999a, 2002).

Sequence effects

Sequence effects represent a test for the stability of a trait hierarchy. Stable trait hierarchies should show resilience to delayed entering in the assembly process, in particular if the invader is the formerly superior plant type. This means the invader should regain its former position in the rank order of survivorship. Our results show that invader success increases with disturbance under fertile conditions. It peaks at intermediate disturbance if fertility is low. Note that height remains the first order trait and only the third order trait (SLA or seed mass) is reversed in the hierarchy, if sequence effects appear (data not shown). This suggests that the underlying model is that of a change from founder control and inhibition at the high fertility / low disturbance corner to increasing redistribution of competitive interactions at the intermediate disturbance / low fertility corner (Connell & Slatyer 1977). Disturbance and stress play an important role in breaking established founder control. Release from competitive interactions provides higher chances of establishment for the invader and thus higher invasibility of the resident community.

In our model, deterministic assemblies with low diversity exhibit higher sequence effects than more stochastic assemblies. Likewise, the trait hierarchy is more stable if the assembly is more stochastic and diverse. While experimental studies (Robinson & Edgemon 1988) as well as theory (Elton 1958) suggest a negative association between biological diversity and invasibility, due to increased competition in species rich communities, most observational field studies find no support for such a negative association (e.g. Naeem *et al.* 2000 and references therein). Moore *et al.* (2001) emphasise that species-poor communities can be more saturated than species-rich communities. This depends on the size of the community species pool (Partel *et al.* 1996; Grace 1999) which is small when either abundant resources enable dominance or high disturbance excludes species with low regeneration (Shea *et al.* 2004). Co-variation of extrinsic factors such as fertility and disturbance controlling

invader success has been stressed by Naeem *et al.* (2000) as “the most likely explanation” for the conflicting results between experimental and observational studies. According to Moore *et al.* (2001), a negative relationship between richness and invasibility is likely in systems where recruitment is limited. This is not the case in our single patch simulations in which all plant types have equal chances for recruitment.

Our simulation experiment supports the observational results by Robinson *et al.* (1995) and Wiser *et al.* (1998) that invasibility is positively related to functional diversity, as long as the resident functional diversity results from extrinsic factors. The simulation result that invasibility is positively affected by disturbance under fertile conditions was also experimentally found by Crawley *et al.* (1999).

Limitations of the LHS strategy scheme

Life history features as life cycle, aerenchyma, clonal growth, position of regenerative buds, and seed appendices in relation to dispersal agents were not included in the LHS scheme (Westoby 1998). There is evidence that more than the LHS traits are relevant for plant strategies (Poschlod *et al.* 2000). For instance, the position of regenerative buds can be essential for discriminating perennial plant types surviving under below-ground disturbance regimes (e.g. tilling) versus above-ground regimes (e.g. mowing, Kleyer 1999a; Sparrow & Bellingham 2001; Klimesova & Klimes 2003). To account for this shortcoming of the LHS scheme, we only modelled above-ground disturbance. On the other hand, our simulations show that no LHS trait is negligible within our template of disturbance / fertility regimes.

LEGOMODEL has produced hypotheses on the hierarchy of plant traits during assembly of plant communities that correspond to empirical results. We provide predictions of LHS trait combinations for certain fertility / disturbance regimes. The wider applicability of the LHS scheme has to be demonstrated by further field work.

Box 1

Viability of plant trait combinations: The sensitivity of LEGOMODEL an individual based ecological field model

Abstract

A sensitivity analysis of LEGOMODEL is performed. A factorial design is carried out for the plant traits incorporated in the Leaf-Height-Seed scheme for different fertility and disturbance regimes. The resulting survival probabilities are displayed. Differences in the disturbance regime have only a limited effect on the survival probabilities, while different fertility levels strongly influence the survival by excluding larger plant types which survive even high disturbance levels in monoculture. The sensitivity of other plant traits is assessed by logical analysis of the modelling procedure.

Introduction

The individual based, ecological field model LEGOMODEL has been used to derive predictions on the occurrence of plant functional types (PFTs) in the previous chapter. The survival of the PFTs was only assessed from simulation runs performed with mixtures of species. A PFT may become extinct in such a simulation because of competitive exclusion by other PFTs or because of abiotic factors. The site conditions may be either only be outside the realised niche or also be outside the fundamental niche. The further development of LEGOMODEL requires the knowledge of the sensitivities to allow comparisons with other models e.g. LAMOS (Lavorel 2001) or field results. Deterministic models like the 'vital attribute model' (Noble & Slatyer 1980) incorporated in LAMOS allow the sensitivity to be assessed by analysing the incorporated rules. The sensitivity of stochastic models can only be assessed by analysing a number of simulation runs. While LEGOMODEL has a stochastic component, it also incorporates many deterministic processes. I therefore analysed a set of simulation runs and also discussed the sensitivity of additional parameters with respect to the modelling procedure.

Methods

Several methods for the design of a sensitivity analysis are suggested in the literature (e.g. Saltelli et al. 2000). Since the simulation result was a single variable (survival) and the main focus of the analysis was on the three traits of the LHS-scheme (SLA, plant height, seed weight, see Chapter four), I decided to take a full factorial design by simulating all reasonable combinations of the three trait states. A pre-analysis using a One At a Time approach (Saltelli et al. 2000) was performed to derive the range of the trait attributes to be incorporated in the parameter set. Each parameter range was subsequently divided by ten and the attribute sets of the three traits were combined. Thousand PFTs (10^3) were formed, and the survival of each PFT in monoculture was analysed (full factorial design *sensu* Saltelli et al. 2000). LEGOMODEL parameterises a plant type with 14 parameters. It is not reasonable to fix all model parameters except the one analysed because of trade-offs between traits as explained in Chapter four. The trade-offs incorporated in the sensitivity analysis are the same that were used in the previous chapter. The survival rate strongly depends on the simulation time (see chapter four). Survival is assessed over the time span of approximately five generations (25 years; maximum life span: 5 years). Hundred simulations were carried out for each PFT and environmental parameter combination. Two different levels of fertility (fertile / infertile) and three levels of disturbance (no disturbance / yearly mowing / monthly mowing) were simulated leading to a total of 60,000 simulation runs over 100 years. The modelling approach of LEGOMODEL is described in the previous chapter and in more detail in (Lehsten 1994). The simulated plant was perennial with long spacers. The mother plant supported its vegetative siblings up to five years. One third of the available assimilate was annually invested in seed production which started in the first year. The seed bank remained viable for one year. All other parameter were correlated to the varied traits.

Results

The pre-analysis revealed that the range of interest for the trait plant height is between 10 and 100 cells in the simulated cube (1 cell equals 1 cm). The seed weight is set to values between one and 50 energy units, and the specific leaf area ranges between 22 and 35 in the analysis. The survival probabilities are displayed for the six environmental parameter sets in figure B.1.

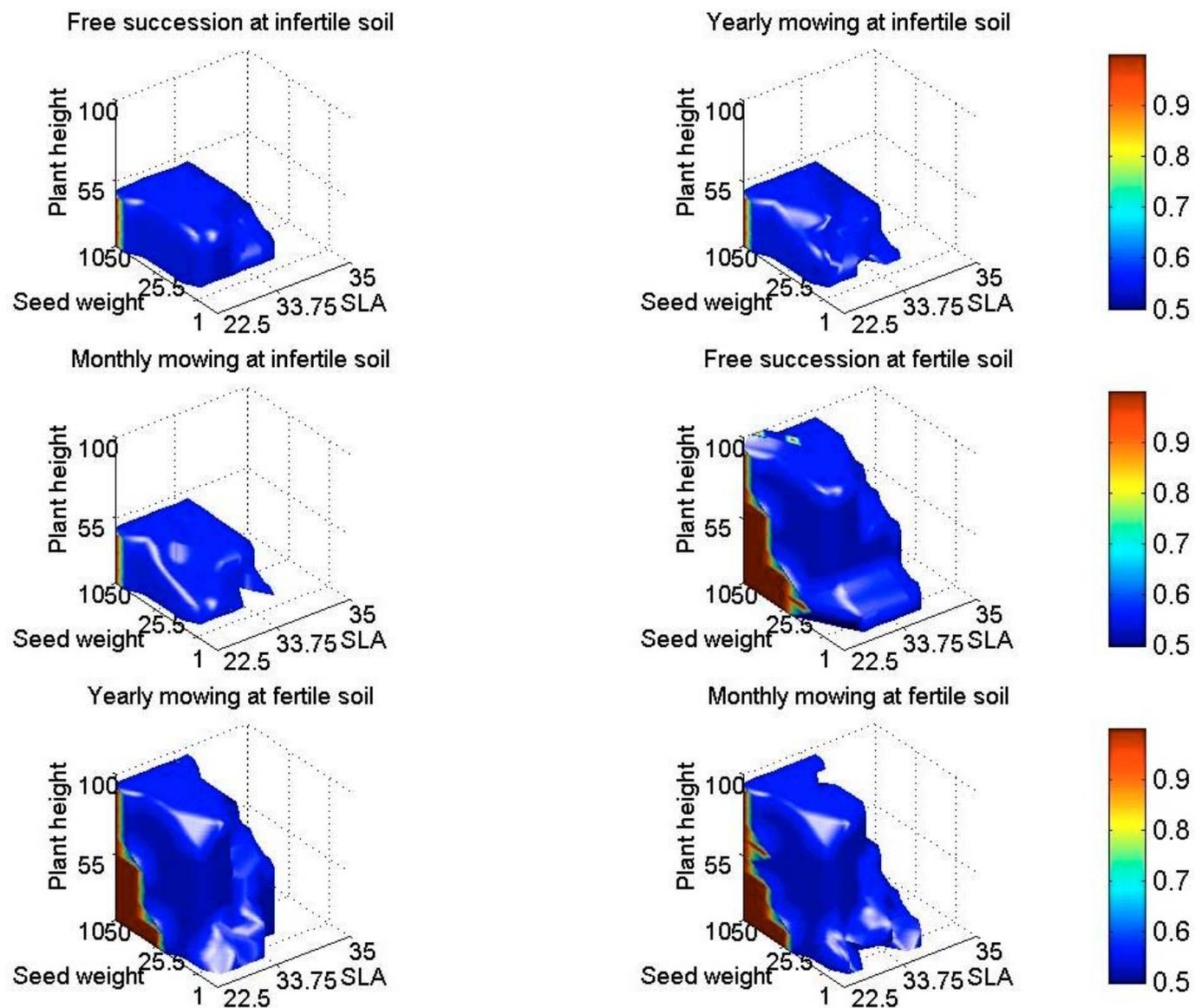


Figure B.1 Survival probabilities of plant functional types at different fertility and disturbance levels in LEGOMODEL. Each PFT was simulated for 25 years according to five generations. The trait seed mass has no upper limit. The survival probabilities depend on the fertility level, and are indifferent to the applied disturbance regimes.

The simulated results show, that all three traits influence the viability of the plant type. However, while SLA and plant height have a maximum value, there is no limit indicated for seed weight.

Discussion

Since the simulated plants are perennials, they do not rely on generative reproduction once established. This is the reason why there seems to be no maximum value for the parameter seed weight. If the seed weight is too high, the plant stops producing seeds.

Comparing the figures also shows that fertility has an influence on the survival, but the disturbance regime has not. All simulated plants have the ability to re-grow if parts of the biomass are removed. Mowing takes place at a height of 10 cells (approx. 10 cm) which allows even potentially tall plants to establish viable populations. Survival is unaffected by disturbance as long as the sword height is at least above a single leaf.

Sensitivity to other traits

As only perennial plants are concerned, seed parameters like seed longevity and year of seed production do not influence survival. Annuals may need a long seed longevity if more than one intensive disturbance event (below ground) occurs at a year. Time of vegetative support of daughter plants is not a sensitive parameter either.

The internodal distance in connection with the plant height determines the number of leaves of the individual plant. Within the simulated plant types it is set to one eighth, allowing the plant to produce eight leaves that do not shade each other. If the ratio is too low, too many leaves are produced and the plant dies, because it has to maintain too much shaded, hence non-assimilating but still respiring tissue (data not shown). Tall plants with too few leaves are also not viable (internodal distance too high).

The rhizome length and maximum depth are correlated to the canopy height, internodal distance and leaf size to keep the root shoot ratio constant. The assimilate gained in every time step is calculated by a minimum function incorporating the captured soil resources and the amount of light-exposed leaves. If only one resource-capturing part is enlarged (either above or below ground), this can be positive for the plant as long as the associated resource is in short supply e.g. root depth on infertile soil. If, on the other hand, the root

depth is increased too much, then assimilation does not increase, because the area of light exposed leaves is limiting the assimilation. Since the additional root tissue respire the survival rate may be lowered (data not shown).

Conclusion

Only the sensitivity to the trait plant height depends on the environmental conditions, if only the traits SLA, potential plant height, and seed weight, are considered. This is in strong contrast to the simulation of species mixtures in the previous chapter which shows that there is a strong effect of the disturbance and fertility level on the competitive hierarchy. It can therefore be concluded that the realised niche in LEGOMODEL is much more affected by the environmental conditions than the absolute niche.

Part III

Application of PFTs a mesocosmos experiment

Chapter 5

Generation of plant functional types by combination of
single trait analysis is not permitted -
Results of a greenhouse experiment
on the assembly of plant communities in gradients of
fertility and disturbance.

Abstract

Question: If several traits influence species composition, is it necessary to form syndromes of trait values during the data analysis or is it sufficient to analyse each trait separately and to form plant functional types (PFTs) by combining the results of single trait analyses? Can the assembly of plant communities in gradients of fertility and disturbance be explained with respect to plant functional types?

Location: Greenhouse in northern Germany.

Methods: A mesocosmos experiment was carried out with fertility and disturbance treatments on experimental grassland. A fourth corner method modified for PFT generation was applied to analyse single traits and syndromes. Each trait is analysed separately and the response of the formed PFT is classified as either positive, negative or non-significant. The responses for syndromes predicted by single trait analysis are compared with the calculated response of the syndrome.

Results: A correct response was predicted for only 35 out of 56 syndromes by combining single trait analysis. An optimisation analysis of syndromes discards the traits biomass and SLA and an optimal set of four PFTs is formed.

Conclusions: The supposition, that the response of PFTs can be assessed by combining the results of single trait analysis is based on the assumption that all traits are equally functional. It was shown that for the analysed data the predicted response of PFTs differed substantially from response derived by analysing syndromes. Hence, when PFTs are formed from single trait analysis, the functional hierarchy of the traits has to be assessed first.

Introduction

There is a general agreement, that the response of plants to environmental factors can be linked to plant traits. Many publications classify species into groups of similar trait attributes and similar factor response (see references below). Especially the need of predictive tools in the prospect of land use and climate change has stimulated the use of plant functional types (PFTs) in connection with vegetation models. With respect to community structure functionality is also seen as strategy (Grime 1974; Grime 1979; Westoby 1998; Westoby *et al.* 2002).

Though functional interpretation of vegetation data has been common in recent publications, the techniques are only recently introduced into this field and no standard technique or evaluation criteria for functionality have been established (Nygaard & Ejrnaes 2004). The approaches to classifying species range from expert knowledge (Noble & Slatyer 1980) to multivariate techniques based on the trait attributes of the species, e.g. 'emergent groups' (Kleyer 1999a; Jauffret & Lavorel 2003). These classifications may subsequently be correlated to environmental gradients to establish functionality (Kleyer 2003). While the first approach is not reproducible, the second is criticised for potentially leading to functional groups of low predictive power, because the response of the species to the environment is ignored (Nygaard & Ejrnaes 2004). To optimise functionality of the classification, and hence predictive power, the classification should use species trait data, species site data and the environmental parameter of the sites simultaneously. Legendre *et al.* (1997) developed a method which simultaneously incorporates the species \times site matrix, the species \times trait matrix and a site \times factor matrix listing the environmental parameter at the sites. They called the method 'the fourth corner method' and coined the term 'fourth corner problem' for functional interpretation of such a data set. Several authors developed solutions to the fourth corner problem. Within these approaches there are multivariate ordination techniques, (Doledec *et al.* 1996; Lavorel *et al.* 1999) generalised linear modelling in combination with ordination (Jauffret & Lavorel 2003), logistic regression (Kleyer 1999a) or ANOVA modelling (Nygaard & Ejrnaes 2004) of functional groups. Some of the methods analyse the trait response of each trait separately and derive the response of syndromes (groups of species based on combinations of traits) by combining single trait responses e.g. Jauffret & Lavorel (2003). While several studies pointed out the importance of analysing several

traits instead of single traits e.g. Marby et al. (2000), the question of whether these traits needs to be analysed as syndromes instead of performing independent single trait analyses and combining the results remains. To answer this question, the 'fourth corner method' has been extended for functional vegetation analysis. A null model for frequency data is incorporated and the species \times trait matrix is replaced by a species \times syndrome matrix. Thereby the method is changed from single trait analysis to syndrome analysis. An assessment of the differences of the PFT responses predicted by combining single trait analysis versus real response using syndrome analysis is made. We also suggest a method for the optimisation of PFT classification based on response strength and PFT size.

Plant functional types are used as a tool in models of future vegetation development. Another way to gain insight into vegetation development is the use of experiments. Greenhouse experiments have the advantage over field experiments, that all environmental factors can be controlled and hence the level of environmental noise is reduced. It also allows to avoid re-colonisation effects by species from adjacent sites or outside the experimental area. Often, they work normally on a pot scale, which limits the interpretability multi species experiments are hardly possible (Gibson et al. 1999) because at this scale. A greenhouse experiment was performed on the mesocosmos scale. This allows to simplify the studied system (a grassland community) to a manageable degree which still covers large parts of the functional diversity. Instead of applying treatments to an already formed community, we started by sowing plants with a wide range of traits attributes on bare ground and followed the succession under different disturbance and fertility treatments.

Single trait as well as syndrome responses to differences in fertility and disturbance are analysed and an optimal set of plant functional types is formed explaining the three years of succession.

Methods

The Greenhouse Experiment

The experiment was carried out in two greenhouses in the Botanical Garden of Oldenburg (Germany). The fertility gradient was generated by removing the topsoil of one greenhouse and transferring it to the other. Additionally, NPK fertiliser was biannually applied equivalent to 13 kg N/ha. The soil was heat

sterilised and in January 2000 sowing took place. The plants were allowed to establish till June 2000. The greenhouses were separated into 4 m² plots (app. 2×2m), separated by plastic plates from 10 cm above till 30 cm below ground and by a textile net from the ground up to a height of 1.8m. Five disturbance treatments were applied, monthly mowing (8 times a year), mowing twice a year, mowing every second year and free succession. The treatments were arranged in a latin square design. 32 species were chosen to represent a variety of trait attributes. The chosen species and their traits are listed in the appendix A.4.1. At least two phylogenetically distant species were chosen for each predefined plant type. Species selection was done by expert knowledge.

Each plot had a permanent counting frame (1m², separated into 10×10 subplots) installed in the centre to minimise edge effects. Presence / absence was recorded for each subplot after 3 years. We recorded plant rooting and plant covering e.g. plant parts growing into an adjacent subplot.

Trait measurement

Although the species were chosen to represent predefined plant types, we measured the traits canopy height, SLA, and biomass according to the protocol of Cornelissen *et al.* (2003). The trait life cycle / spacer length was taken from the literature (Klimes & Klimesova 1999). The optimal way to analyse the functionality of traits in relation to treatments is to measure each trait as expressed under each treatment. However, since we were not able to grow each species in monoculture under each treatment, we measured each trait as expressed under 'optimal' conditions, e.g. under fertile undisturbed conditions.

Statistical analysis

The objective to plant functional type formation is to find the smallest PFT set with the highest explanatory value. We formed all reasonable plant type (PT) sets and tested the categorisation for functionality using the extended fourth corner method. A plant type (PT) with a significant response to a treatment is a functional plant type (PFT).

Plant type definition

Each trait was separately categorised by forming all possible trait classifications given some constraints to limit calculation effort. Three conditions prevented the set from becoming extraordinarily large: minimum class width, maximum class number and precision e.g. minimum difference of the class

ranges between different classifications. The minimum difference between categorisations is set to the minimum class width in our analysis. After each trait was categorised separately, the final PT set is formed as the combination of all trait categorisations. All trait classifications include the case of a categorisation into one class, if this trait classification is later found to be optimal, then the trait is not functional. The trait plant height was categorised into two classes with a minimum class width of 5 cm, which lead to a total of 18 different classifications. Biomass and SLA were also classified into two classes with a minimum class width of 5g or $2\text{m}^2\cdot\text{kg}^{-1}$ leading to six respective 15 different classifications. Life cycle is divided into annual (ann) and perennial (per) and the perennial species have either short or long spacers. There are four different ways to categorise groups according to life cycle / spacer length ([ann or per] [ann / per] [ann or short spacer / long spacer] [ann / short spacer / long spacer]).

For the syndrome analysis, a total of 6,840 classifications ($19\cdot 6\cdot 15\cdot 4$) was tested using the extended fourth corner method. If it indicated a significant deviance from the null model for a certain PT, e.g. a p-value below 0.05, the categorisation was considered to be functional.

The extended fourth corner method

Legendre et al. (1997) relate single traits to environmental factors. To test combinations of trait classes (i.e. plant types) for functionality, the species \times trait matrix was replaced by a species \times plant type matrix.

The fourth corner method combines a presence / absence matrix of k species recorded on m sites A ($k\times m$), a trait matrix B assigning each species to a type ($k\times n$) and a third matrix C listing the classified factors of each site ($l\times m$) to a fourth matrix D ($l\times n$). If all matrices contain only 0's and 1', the matrix product $D = CA'B$ lists the frequency of species types occurring at a certain factor. Since the observations are not independent of each other (several species occur at one site), a randomisation (null model) test is used instead of a classical test e.g. Chi square. For further explanations of the original fourth corner method refer to Legendre et al. (1997).

If the columns of matrix B represent plant types (i.e. trait state combinations) instead of single trait states as in the analysis of Legendre et al. (1997), matrix D lists the frequency of occurrences of plant types with respect to the factors. We also replace matrix A with the number of occupied subplots (fre

quencies; 1-100) of each species and site instead of species presence / absence. Hence, the matrix product D lists the number of occupied subplots for each PT – environmental factor combination.

Matrix A is permuted and for each permutation (A_{per}) a new matrix D_{per} is computed ($D_{\text{per}}=CA_{\text{per}}'B$). For each cell in D , the frequency of containing a higher or equal value than the associated cells in the set of D_{per} is counted. If a value in D is only rarely larger than or equal to the corresponding value in D_{per} , the trait combination is thought to occur less often as expected by the null model, and is therefore negatively related to the treatment. Given a large set of permutations, this frequency is an estimator of the one tailed probability (p-value) of $D(\text{cell}) \geq D_{\text{per}}(\text{cell})$. The grouping is considered functional with respect to a certain environmental factor, if the p-value of a certain trait class combination is below 0.05. Values higher than 0.5 indicate a negative association, i.e. the plant type occurs less often than expected by the null model.

Null models

Null models generate patterns based on randomisation of ecological data. To account for ecological processes, some elements of the data are held constant while others are allowed to vary stochastically to generate occurrence patterns that would be expected in the absence of a particular ecological mechanism (Gotelli & Graves 1996). Hence, to detect plant functional types based on ecological attributes, a null model has to be indifferent to plant traits. The optimal null model reflects all ecological processes except the one to be tested by the model (Gotelli & Graves 1996). To account for a species-specific niche breadth and a treatment-specific species diversity, the species diversity per site as well as the rarity of the species are incorporated into the null model. Several algorithms are proposed for this task if presence / absence data are concerned e.g. the 'sequential swap' (Manly 1995) or the 'random knight tour' (Gotelli 2001). To enhance the statistical power frequency data was used, and a new algorithm was developed. The randomised units are the hundred subplots of the sampled 1*1m area in the centre of each plot. These subplots cannot be treated as independent sampling units, since they are smaller than some plant individuals and plants are also known to have a clumped distribution in space (Maestre & Cortina 2002). A species-specific size correction was incorporated in the model. The average size (ratio of subplot where a species roots to subplot that it covers) was calculated for each species and treatment. If a species had no occurrence under a given treatment, this size ratio was set

to one which is the minimum possible value. Instead of a species number per plot, the total number of species recordings within all subplots was calculated for each plot. The randomisation procedure starts with an empty plot, randomly selects a species and places as many recordings as calculated before as the average size until the total number of records for that plot is reached. The probability of choosing a species is proportional to its occurrence in the observed data divided by its average size. The last chosen species may not have the full number of recordings placed in the plot. A single randomisation is finished when all plots are filled.

Legendre et al. (1997) decided to correct their individual p-values to accommodate for the increased probability of committing a Type I error in the case of multiple simultaneous tests. We decided not to correct the p-values, because (i) each plant type will be compared individually against the occurrence of the same type in the null model and (ii) no indirect comparisons are made between different plant types or treatments.

For any combination of trait classes, a matrix of p-values is generated. The choice of an optimal classification depends on the focus of the investigator. The proposed criteria may be adjusted to the task of the study. Our procedure chooses an optimal set as a compromise of a minimal number of plant types and a maximal strength of relationship of plant types to the environmental factors (of number of significant p-values) in two steps. In the first step all sets are compared with each other. If a PT of one set is covered by several PTs of the other set and the number of significant p-values for the PT of the first set is greater than or equal to the average number of significant p-values of the subdivided PTs in the subdivided set, then the subdivided set is discarded. In the second step the largest categorisation with the highest average number of significant p-values per PT is chosen from the remaining set. The same applies to the subdivision of several PTs into more PTs. In case that several classifications are similar according to these criteria, the categorisation with the smallest number of PFTs is preferred. If this does not lead to a single categorisation, the one with the lowest sum of significant p-values is chosen or the one with the trait classes width being most similar.

Results

Single traits analysis

The trait measurements and the frequency matrices are listed in the Appendix A.4.1 and A.4.2. Although the proposed procedure was developed to form an optimal PFT set each trait will be separately analysed first. Table 5.1 lists the optimal classifications for each trait and its relationship to the treatments. Except for the combination of biannual mowing and biomass and of spacer length and soil fertility, a classification is found that results in significant PT treatment relationships.

Biomass and plant height seem to be related to each other which leads to relatively similar results with the exception that the trait - treatment relationship of the trait biomass is less significant. We therefore discarded the trait biomass for the comparison of single trait versus syndrome analysis for reasons of simplicity. The trait plant height shows a relatively linear response to fertility. Hence, many categorisations are significant and the trait class limit of 100 cm is chosen, because it makes the classes ranges similar (plant height ranges from 3.5cm to 205cm).

Combining the optimal trait classifications of the remaining three traits results in twelve syndromes. The predicted response of the syndromes are formed by combining the single trait response. The prediction is the response that most of the traits have assigned to the treatment. In case that all possible responses are combined (positive, negative and inconsistent), an inconsistent response is predicted. For instance, the predicted response of the PFT with short spacers, small height and low SLA to the treatment biannual mowing would be to combine one positive response (for life cycle/ spacer length) and two negative responses (for plant height and SLA) which would result in a predicted negative response of the syndrome to biannual mowing. The response of the twelve PFTs are also analysed as syndromes using the same technique as for the single trait analysis (see Table 5.2). The PFT with short spacers, small height and low SLA has a positive response to the treatment biannual mowing which is contradictory to the response predicted before. Table 5.3 lists the predictions for all syndromes and the calculated response for the syndromes present in the data set. The calculated responses of 35 out of 56 syndrome - treatment relationships are contradictory to the predictions.

Table 5.1 The optimal classification and the relationship of plant traits versus treatments using fourth corner statistic. Significance and sign of trait state treatment relationship are indicated as follows: ++ : $p < 0.01$; +: $p < 0.05$; a negative sign (- or --) indicates an inverse relationship, p -values > 0.05 are given in full.

Treatment	Trait								
	Spacer length / Life cycle			Height		SLA		Biomass	
Opt. Classification	ann.	short	long	0-100cm	> 100cm	0-21m ² *kg ⁻¹	>21 m ² *kg ⁻¹	0-5.2g	>5.2g
Fertile	--	++	-0.1	--	++	--	++	--	++
Infertile	--	--	++	++	--	++	--	++	--
Opt. Classification	ann.	short	long	0-100cm	0-100cm	0-21	>21	0-5.2g	>5.2g
Undisturbed	--	++	--	--	++	--	++	--	++
Biannual Mowing	--	++	--	--	++	--	++	-0.06	-0.07
Mowing twice a y.	--	--	++	++	--	++	--	++	--
Mowing 8 times a y.	--	--	++	++	--	++	--	++	--
Biannual rototilling	++	--	++	--	++	--	++	--	++

Table 5.2 Calculated response of the syndromes to the treatments. The PFTs one, three, four and eight are not represented in the data set. For each plant type the responses of the single traits are listed in the left column. Plant height is categorised into plants smaller or taller than 100cm and SLA is divided into below (low) or above (high) $21\text{m}^2\cdot\text{kg}^{-1}$. Significance and sign of trait state treatment relationship are indicated as follows: ++ : $p<0.01$; +: $p<0.05$; otherwise the p-values and its response (+/-) is given, ($p>0.05$).

Treatment/ Trait	Relationship of syndrome to treatment											
PFT	1	2	3	4	5	6	7	8	9	10	11	12
Spacer I. / Life cycle	ann.	ann.	ann.	ann.	short	short	short	short	long	long	long	long
Height	small	small	tall	tall	small	small	tall	tall	small	small	tall	tall
SLA	low	high	low	high	low	high	low	high	low	high	low	high
Fertile		--			--	++	0.2		-0.2	--	++	++
Infertile		--			++	--	++		++	++	--	--
Undisturbed		--			--	++	--		--	--	++	++
Biannual mowing		--			++	+	0.3		--	0.5	++	++
Mowing twice a y.		--			++	--	++		++	++	--	--
Mowing 8 times a y.		--			++	--	++		++	++	--	0.2
Biannual rototilling		++			--	0.4	--		0.3	--	++	--

Table 5.3 Predicted and calculated response of PFT to treatment

The prediction is made by combining the responses of the single life cycle/traits spacer, plant height and SLA listed in Table 5.1. A '+' sign depicts a positive, a '-' sign a negative and a 'n' stands for a not significant response. For each plant type the responses of the single traits are listed in the left column. The first sign is the response of the trait life cycle / spacer length, the second sign is the response of the trait plant height, the third sign is the response of SLA. The overall prediction is the most frequent sign. e.g. a +++ would result in a predicted positive relationship of the PFT to the treatment. The combination of a '+', a '-' and a 'n' is predicted as a 'n'. Except for the four plant types that did not occur in the data set, the response to the treatment found by directly analysing the syndromes is listed in the right column. The correct predictions e.g. cases in which the real response is equal to the majority of the single trait responses, and the incorrect predictions are also listed. In 35 out of 56 cases the majority of the single trait responses was similar to the real PFT response. The prediction of syndrome response by simply combining single traits responses is therefore not valid.

Treatment/ Trait		Predicted and real relationship of PFT to treatment																											
PFT	Spacer l. / Life c.	1		2		3		4		5		6		7		8		9		10		11		12					
		ann.	ann.	ann.	ann.	short	short	short	short	short	short	long	long	long	long	long	long	long	long	long	long	long	long	long	long	long			
Height	SLA	small	small	tall	tall	small	small	tall	tall	small	small	tall	tall	small	small	tall	tall	small	small	tall	tall	small	small	tall	tall	small	small	tall	tall
		low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high
		pre	cal	pre	cal	pre	cal	pre	cal	pre	cal	pre	cal	pre	cal	pre	cal	pre	cal	pre	cal	pre	cal	pre	cal	pre	cal	pre	cal
Fertile		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Infertile		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Undisturbed		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Biannual Mowing		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Mowing twice a y.		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Mowing 8 times a y.		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Biannual rototilling		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Correct predictions				7						6		6		1				5		4		1				5			
Incorrect predictions				0						1		1		6				2		3		6				2			

Syndrome analysis

The twelve syndromes (of which eight occur in the data set) of table 5.2 are derived by optimising single trait classes. If not single traits but syndromes are analysed the procedure discards the traits SLA and biomass and results in the PFT set listed in table 5.4. The trait classes are different from the single trait optimisation, the trait height is optimally classified in plants smaller (taller) than 180 cm, while the single trait analysis leads to a distinction between plants being taller or smaller than 100 cm. All syndrome treatment responses are statistically significant. A list assigning each species to a PFT is given in the Appendix A.4.1

Table 5.4 Relationship of optimal PFT set to treatment. The trait plant height is categorised into small plants of height 0-180 cm and tall plants with more than 180 cm canopy height. The other trait incorporated is life cycle / spacer length which is either annual (ann.) or for perennial species indicates a short spacer (short) or a long spacer (long). The only two tall species (*Urtica dioica* and *Phalaris arundinacea*) both have long spacers, hence only four out of the possible six plant types are in the formed set.

PFT	1	2	3	6
Spacer length / Life cycle	ann.	short	long	long
Height	small	small	small	tall
Fertile	--	++	--	++
Infertile	--	--	++	--
Undisturbed	--	++	--	++
Biannual mowing	--	++	--	++
Mowing twice a y.	--	--	++	--
Mowing 8 times a y.	--	--	++	--
Biannual rototilling	++	--	--	++

Discussion

Combining single traits vs. syndrome analysis

Comparing the results of both methods shows that the first method is questionable. It relies on the assumption that all traits act independently of

each other and that all traits share equal relevance. Several studies have shown that there is a hierarchy of traits determining the success of a species. Diaz et al. (2001) found that plant height was the best single predictor for grazing response, while SLA had only a small predictive value. On a disturbance / fertility gradient plane, Kleyer (1999; 2002) found that plant height was the most functional e.g. consistent trait, while regenerative traits such as seed size contribute to alternative pathways of occurrence / survival at a single combination of disturbance intensity and fertility. The question of whether such a hierarchy of traits determining the performance of a species is independent of the environmental factors is not answered yet, though theoretical considerations argue against such an independence (in prep). If no such universal trait hierarchy can be inferred, it is necessary to analyse the response of syndromes directly. Another issue in favour of syndrome analysis is that the response of the species forming a PFT does not have to be similar, but the average response has to be significant to form a valid PFT. Hence, if new groups are formed as a subset of a previously formed group, this new group can have a different response if it is formed by species which had a response differing from that of the group as a whole. This effect can even lead to differences in the predicted and the real responses if all single traits predict a similar response.

Evaluation of the extended fourth corner method

Nygaard & Ejrnaes (2004) suggest to judge a method for functional modelling according to four criteria: simplicity, flexibility to use different data types, statistical interpretability and usability of the results for the prediction of new data.

Whether the extended fourth corner method is regarded as simple, depends strongly on the statistical preferences of the researcher. However, the method generates an optimised PFT set and its trait environment relationship in one step. Though only two null models for two data types are mentioned in this paper, the Windows program available for download offers three more null models testing different ecological hypotheses and is suitable for presence / absence data, abundance data or frequency data. The optimal set is derived automatically, after specifying the null model and the classification constraints. The statistical interpretability is given by the p-value assigned to each PFT - treatment response which can also be used for the predictive modelling of PFT distribution given an appropriate set of known environmental factors. While the effort for the researcher is relatively low (using the offered tool), the calcula

tion effort is considerable high and increases exponentially with the number of traits involved. The program can calculate up to 20,000 categorisations at once, e.g. the optimal PFT may be generated out of a categorisation using four traits with eleven different categorisations per trait ($11^4=14641$) on recent personal computers. However, this limits only the ability to generate optimised PFTs. If the PFT set is known in advance, e.g. as a result of a different statistical technique, or if it is formed to test a specific ecological hypothesis, no limits are set in terms of the number of incorporated traits to calculate the response of a given PFT set.

Comparison with other studies

Several other methods are proposed for functional analysis of vegetation data. Only methods generating syndromes and their environmental response are considered in the following. The five step procedure by Jauffret & Lavorel (2003) combines the results of single trait analysis with an analysis of the actual response of species to perennial plant cover. It first identifies the actual response of species to the factors using a multivariate technique. Subsequently 'emerging groups' are formed based on traits and the attribute response of each trait is identified using a generalised linear model (GLM). The syndromes and response types are formed by combining the single trait responses for the species, and comparing the results with the actual species response to grazing in a way, that decreaser (increaser) response types were composed by species showing a declining (increasing) response to perennial cover and having a majority of decreaser (increaser) attributes. Hence, the validity of the response of the functional types formed by analysing the traits independently was assured by comparing the response predicted by the combined single trait analysis with the actual response of the species. The five step method uses GLMs to assess the trait response of single traits. If a trait is only functional in combination with a certain attribute of a different trait or over a certain part of the analysed gradient, the GLM may fail to detect the functionality. In this case the method will still produce valid results but may have a lower predictive power as an analysis forming syndromes prior to assessing the response.

Nygaard & Ejrnaes (2004) approached the fourth corner problem by merging the three lists (species×sites; species×traits and environment×sites) into a list file in which each single observation of a species was listed in a row with columns representing species abundance, environmental variables and trait attributes. This list file was then further processed to model the success of

different species as a function of environmental conditions and functional identity. The functional types were not formed on the basis of their experimental data, but based on a larger data set of established vegetation which may have led to the relatively poor performance of the ANOVA model on the experimental data based on PFTs. The applied re-sampling method gave a statistical proof for the validity of the models. However, it generates a single value assessing the performance of the model. It does not differentiate between different parts of the gradient or different PFTs. The proposed 'extended fourth corner method' calculates a p-value for each treatment – PFT response. Hence, even if the response is only significant for a single PFT and over a limited part of the gradient, the method will detect this PFT response. Nygaard & Ejrnaes (2004) point out that an extension of the 'fourth corner method' by Legendre et al. (1997) including species abundance has not yet been developed. This problem is not considered as solved by the proposed null model for frequency data including size correction and the additional null model in the offered tool for abundance data. They also mention that the fact that either matrix B (species \times site) or matrix C (sample \times environmental condition) has to be represented by binary data which "puts a severe limit to the applicability of the method in functional plant ecology" (Nygaard & Ejrnaes 2004). However, a reduction of trait states into a binary variable of PFT membership is exactly what is needed for PFT modelling. By replacing the species \times trait matrix B by a species \times PFT matrix, the fourth corner method becomes applicable without limitations to the task of PFT analysis. These PFTs may either be predefined by expert knowledge or clustering or optimised using the results of the fourth corner method. In any case, the 'fourth corner analysis' will deliver valid responses for the PFT classification within matrix B in a relatively simple way. By changing the null model, the method can be adapted to different data types as well. Nygaard & Ejrnaes (2004) realise that the biotic interaction violates the statistical independence between the observations which is required to carry out their analysis technique. They argue, that this dependency is an inherent feature of niche modelling and may be regarded as an integral part of the environment, e.g. they model the response of species to gradients given other co-occurring species. We consider the use of null models as a much more acceptable way to deal with dependencies between observations.

Ecological relevance of PFT grouping

The data set contained a relatively small number of species. The functional responses could therefore be expected to be caused by a small number of traits. The optimisation is performed on the basis of the very strict criterion which demands each PFT to have a significant response to each treatment. It results in a set of four PFTs formed on the basis of the traits life cycle/spacer length and plant height. If this criterion is relaxed, larger sets of PFTs will be generated. The results concerning height in relation to disturbance and fertility are in line with theoretical models (e.g. Tilman 1988). Fernandez *et al.* (1993) showed in a study of Mediterranean grasslands that the relative abundance of species with different trait attributes varies with the level of stress (water and nutrient availability) and disturbance (grazing and ploughing) concluding that “the main trend in variation is related to plant size” which is in line with our result that the two tall species respond positively to fertility and low disturbance frequency. Walck *et al.* (1999) found the competitive hierarchy to be also closely related to plant size in an experiment.

The annual plant type shows a negative response to fertile as well as to infertile soils. All plots (both treatments) are occupied mainly by perennial species. All treatments except the rototiled treatment are representatives of middle European grassland management practices, and the fact that vegetative regeneration is more dominant in grasslands was also found by Eriksson & Jakobsson (1998) and Kahmen & Poschlod (2004). The small plant type with short spacers responds positively to fertility, while the small plant type with long spacers responds negatively. This response is supported by theoretical considerations of the foraging theory that predicts a shortening of spacers at resource-rich microsites as it reduces the proportion of misplaced spacers (Cain *et al.* 1996). While the annual plant type responds negatively to both fertility treatments, it has a positive response to rototiling. Here the dominance of perennials was broken and annuals were able to re-establish, because annuals tend to have a higher seedling growth rate as perennials (Garnier 1992). A positive response of annuals to deeply disturbed sites was also established by Kleyer (1999a). The response of the tall plant type to the disturbance treatment is consistent with the findings that plant height is negatively correlated to disturbance frequency (Fernandez *et al.* 1993; Kleyer 1999a). The result that the small PFT with long spacers responds positively to the undisturbed and bi-annual mown treatment, while the long PFT responds positively to these treat

ments, is contradictory to earlier findings of Kleyer (1999a) that large lateral expansion is a general feature of PFTs that concentrate at low disturbance intensity. Theory predicts that long spacers would be advantageous in patchy environments where they enable the plant to reach available microsites, because there they out-weigh the disadvantage of the higher production costs for the plant. From visual inspections, the plots that were mown less than annually appeared less patchy than the other mown plots, because the dead material of the preceding year (mainly *Phalaris arundinacea*) covered large parts of the area leaving only little space for re-growth, while regeneration sites were created by the treatment in the plots mown at least annually. It may therefore be a scale effect that within the plot size of 2×2m the availability of free microsites was too low for long spacers to be advantageous at sites disturbed less intensively.

Perspective

Mark Westoby proposed a simple classification scheme to enable a meta-analysis of experimental or field results based on the traits plant height, SLA and seed mass. The assumption behind these scheme is that these three traits are sufficient to explain vegetation composition. This reductive approach is necessary if vegetation has to be analysed over a wide range of environmental factors e.g. biota. However, within a smaller area or ecological space the functional traits can be expected to differ between different investigations.

A tool is developed which can generate PFTs and also calculate the response of the PFT to the factors in a single step. Hence, the resulting PFTs can be directly transferred to a predictive model (mechanistic or statistical) and the calculated response can be used to assess the quality of such a vegetation model. It can also be used to test ecological hypotheses of trait - (syndrome -) factor response by testing only the hypothetical categorisation. The method was used to generate PFTs from a greenhouse experiment of grasslands. The next step is to test the validity of the mesocosmos predictions on field data. Though the p-values generated by the presented model are no total occurrence probabilities, the offered tool incorporates a null model deriving such values which can be used as a habitat suitability index as done with multiple regressions (GLM) for single species (Guisan & Zimmermann 2000). Projecting these values to a map of site conditions can generate a maps of predicted distribu

tions of PFTs. By offering a tool for the proposed method, we hope to encourage researchers to apply the extended fourth corner method and to use the opportunities given by a functional analysis of vegetation data.

Chapter 6

Synthesis and Perspective

The application of models to predict the development of vegetation requires techniques for functional grouping and analysis of the present vegetation. Such techniques have to fulfil several criteria to be applicable in a wider range. It should be relatively simple to allow the application to be carried out without extensive statistical knowledge. It should be flexible to use different kinds of data, it should be statistically interpretable, making the results reproducible without expert knowledge, and its results should be usable for the prediction of new data (Nygaard & Ejrnaes 2004).

The proposed extended fourth corner statistic fulfils all of these criteria. The implementation in a computer program also allows its wide application by anyone interested. The statistical properties (Type I and Type II error) were tested by analysing a simulated data set with a known structure and the applicability was proven on an experimental data set. The offered procedure can be separated into two parts, one calculating the response of a group of species to an environmental factor and a second part optimising the plant functional type classification. At present, the optimisation criteria are fixed to select the smallest PFT set with a significant response to each factor state. Though this is plausible for my problem, other optimisation criteria may be more suitable for other purposes. A researcher may be especially interested in significant responses at certain factor combinations for the extent of allowing the classification to be indifferent to other factor combinations. In this case he can scan the saved summary file for the most suitable combination. However, the application could be made better usable by allowing the user to define the optimisation criteria explicitly. The second part of the procedure could also be adapted to more data types or relationships to be tested by incorporating more null models. While it may be impractical to allow the user to design a new null model within the application, a new functionality may be added allowing data randomised by the user to be loaded. These data may either be simulated data or even be recorded field data. Hence, the null community may be formed in the field (experiment), allowing the researcher to increase the level of realism.

The simulations using LEGOMODEL generated plausible plant functional type assemblages, as the comparison with field results of other researchers revealed. LEGOMODEL was used to simulate the assemblage of plant functional types, based on the plant strategy scheme proposed by Westoby (1998). This strategy scheme uses only the traits specific leaf area (SLA), canopy height, and seed mass. These traits are easy to measure and are thought to capture enough variation to functionally represent floristic variability at a global scale.

At a much larger scale, the presented greenhouse experiment showed that the traits SLA and seed mass were negligible while plant height remained functional. Seed mass is functionally connected to the processes of dispersal and (re-)establishment (Begon *et al.* 1996). Dispersal was explicitly limited to a short range by separating the experimental plots with textile nets. Establishment for perennial species, which were dominating the plots, was a singular event in the beginning of the experiment. The ability to grow in shaded areas, which is associated to larger seeds, did not influence the performance of the species either, because the soil was bare and sterilised before sowing. Afterwards, vegetative spread was more important than generative reproduction, as common in middle European grasslands (Eriksson & Jakobsson 1998; Kahmen & Poschlod 2004). The specific leaf area was functionally important if considered separately. However, the categorisation based on life cycle, spacer length, and plant height delivered a stronger PFT-treatment response. The mesocosmos experiment investigated a system with artificially decreased diversity which also was at a larger scale than common grasslands. The results can therefore be expected to differ to some extent from field results. Especially the responses of PFTs with different spacer lengths may be attributed to these differences in scale. The results of LEGOMODEL concerning plant height were similar to the field results, spacer length was not varied in the simulations. Seed mass may become important, if the experiment is carried on for a longer time, while the result of LEGOMODEL, that high SLA is competitively advantageous at fertile soil and low SLA at infertile soil, was also shown experimentally. While the disturbance regime did not influence the competitive ability of plant types differing only in SLA in LEGOMODEL, significant effects were shown in the experiment. There may be several reasons attributed to this. Although the scale of LEGOMODEL is much finer than the scale of many other vegetation models (e.g. LAMOS, Lavorel 2001), it still works on a much coarser scale than the processes acting in the experiment. The processes incorporated in the plant

growth model are approximations which have to be relatively crude in order to still be able to parameterise them and to keep the statistical error of the model low. However, a more realistic implementation of the processes influenced by SLA may lead to a better performance of LEGOMODEL.

Despite the shortcomings of LEGOMODEL, it is already in a state where it is applicable not only to model general PFT factor responses but also to apply the results to predict vegetation development at actual field sites. To do so, the present abiotic parameters of fertility and disturbance have to be mapped. If the simulation of the present state leads to similar PFT assemblages as there are now, the model can be expected also to yield reasonable results for future development. The scenarios of future abiotic conditions can subsequently be simulated, starting from an already assembled community representing the present state. The resulting probabilities of occurrence can be transferred into maps of predicted occurrences of plant functional types for each scenario. The extended fourth corner method can be used to test, whether the predictions of the present state correspond to the recorded vegetation.

This thesis covers a range from functional vegetation analysis to predictive vegetation modelling. The focus of this work lies on the methodology, because despite its necessity, the concept is relatively new, rarely applied and hence tools and experience of its applicability are low. Hopefully, more projects will explicitly use functional vegetation analysis and predictive vegetation modelling also for tasks at local scales, like optimising management strategies for cultural landscapes, nature protection or within renaturation projects.

Summary

The focus of this thesis lies on the functional analysis and modelling of vegetation. A functional, instead of a species-oriented, approach is necessary to reduce the complexity to a level that can be handled by models of vegetation. Vegetation models are able to predict the development of the vegetation under changing environmental conditions, for instance due to climate change.

The thesis is divided into three parts.

A statistical method for the optimisation of plant functional types (PFTs) is developed in the first part. The 'fourth corner method' by Legendre et al. was adapted to the task of functional grouping of plants. It was transformed from a single trait based method to a technique analysing the response of syndromes, e.g. suites of trait attributes, to environmental factors. The method uses several null models, which allow species to be categorised according to different purposes. A simulated data set with a known structure is used to explain the method and to assess the Type I and Type II errors.

The application of null models is controversially discussed in the literature. The results of the methods are partly questioned because of the unknown influence of systematic errors of the procedures. In a meta-analysis I investigated the effect of the potential bias of the 'sequential swap' algorithm. I analysed 291 published presence / absence matrices. The analysis revealed that especially for small matrices an increased Type II error occurs. However, the algorithm delivers correct significance levels for the 'C-score', for a large proportion (287 out of 291 matrices). The 'C-score' is an index for the co-occurrence of species.

The mechanistic model LEGOMODEL is used in the second part of the work to simulate the assemblage of vegetation in gradients of fertility and disturbance. The modelling approach is explained and a sensitivity analysis of key parameters of the model is performed. The relationship of the survival of a plant type in monoculture to the plant traits canopy height, specific leaf area is analysed using a full factorial design. The resulting survival probabilities are displayed for different fertility and disturbance levels. The survival in monoculture is independent of the applied disturbance regimes. The relationship between survival and SLA or seed mass is independent of the fertility

Summary

level, while the sensitivity to the trait canopy height strongly depends on the fertility level. LEGOMODEL was also used to generate predictions of the vegetation assemblage under different levels of fertility and disturbance using the Leaf-Height-Seed (LHS) scheme proposed by Mark Westoby. The LHS scheme characterises the strategy of a species, using only the traits SLA, canopy height, and seed mass. A comparison of the simulated results with field studies reveals many similarities. The simulated results are also used to construct a functional hierarchy of traits. Plant height is always the most functional trait, followed by SLA at fertile sites and seed mass at infertile sites. The disturbance regime has profound effects on the competitive hierarchy of the plant types, but not on the functional trait hierarchy.

In the third part of the thesis, a mesocosmos experiment is analysed, which was carried out to investigate the assemblage of plant communities at different fertility and disturbance levels. I applied the developed statistical technique and tested the applicability for a functional analysis of field data. A new null model was developed, which can handle frequency data instead of presence / absence data. The 32 species which took part in the experiment were categorised by the optimisation algorithm into four functional types with a significant response to each treatment. One type included perennial species taller than 180 cm, the second type was formed by annuals and the other two types were perennial species smaller than 180 cm differing in their spacer lengths. The data of the experiment was also used to test the validity of the approach of deriving the response of syndromes (combinations of trait states) by a simple combination of the responses of the single trait responses. The predictions of the responses derived by this technique were shown to be incorrect for a large percentage of the syndromes.

A synthesis of the work is drawn, showing the connections between the parts and a perspective shows how research could proceed and which application fields for the different methods are promising. The developed statistical method has been implemented in a computer program which is attached to the work.

Zusammenfassung

Diese Arbeit befasst sich mit der Analyse und Modellierung von Vegetation unter funktionalen Gesichtspunkten. Eine funktionale Betrachtungsweise ist notwendig um, zum Beispiel im Hinblick auf globale Erwärmung oder demographisch bedingte Veränderungen, die Entwicklung der Vegetation vorherzusagen. Die Arbeit gliedert sich in drei methodische Bereiche.

Im ersten Teil wird ein statistisches Verfahren zur Optimierung von funktionalen Pflanzentypen (PFT) entwickelt. Dazu wird die ‚Fourth Corner Method‘ von Pierre Legendre et al. modifiziert. Diese Methode zur Analyse der Relationen zwischen biologischen Eigenschaften und Umweltfaktoren wird zu einem Verfahren zur Ermittlung der Beziehungen zwischen dem Auftreten von Gruppen von Arten und Umweltfaktoren erweitert. Es werden verschiedene Nullmodelle entwickelt, die eine Gruppierung unter unterschiedlichen Gesichtspunkten ermöglichen. So können die funktionellen Typen entweder hinsichtlich ihres Auftretens in der Pflanzengesellschaft oder bezüglich der Veränderungen in ihrem Vorkommen zwischen verschiedenen Standorten charakterisiert werden. Das Verfahren wird an einem simulierten Datensatz mit einer bekannten Struktur erläutert, so dass eine Abschätzung der Fehler erster und zweiter Art möglich ist. Die Anwendung von Nullmodellen wird teilweise kontrovers in der Literatur diskutiert. Ein besonderes Augenmerk ist dabei auf die systematischen Fehler, die bei Methoden, die auf Randomisierung basieren zu erwarten sind, gerichtet. Im Rahmen einer Metaanalyse wird untersucht, wie sich der potentielle systematische Fehler des ‚sequential swap‘ Algorithmus auswirkt. Eine Analyse von 291 publizierten Präsenz / Absenz Matrizen ergibt, dass der systematische Fehler bei kleinen Matrizen zu einem deutlich erhöhten Fehler zweiter Art führen kann. In diesen Fällen kann das Verfahren als zu konservativ betrachtet werden. Bei der überwiegenden Mehrzahl (287 von 291) der analysierten Matrizen hatte dieser potentielle Fehler jedoch keinen Einfluss darauf, ob die Matrix als unzufällig in Bezug auf den ‚C-score‘, einer Kennzahl für das gemeinsame Vorkommen von Arten (co-occurrence), eingestuft wurde. Der zweite Teil der Arbeit befasst sich mit der Modellierung von Vegetations-sukzessionen mit mechanistischen Modellen. Dabei wird das Modell LEGOMODEL benutzt. Die Modellierungsansätze werden beschrieben und es wird eine Sensitivitätsanalyse durchgeführt. Die Abhängigkeit der Überlebens-wahrscheinlichkeit von Pflanzenmerkmalen wie Wuchshöhe, spezifischem Blatt-

gewicht und Samengewicht wird bei unterschiedlichen Nährstoffangeboten und Störungsintensitäten untersucht und graphisch dargestellt. Das Überleben der Pflanzentypen ist in Monokultur unabhängig vom Störungsregime. Die Nährstoffverfügbarkeit im Zusammenspiel mit der Wuchshöhe ist sehr sensitiv, während sich hinsichtlich spezifischer Blattfläche und Samengewicht nur minimale Unterschiede in den Überlebenswahrscheinlichkeiten bei unterschiedlichen Nährstoffangeboten erkennen lassen. LEGOMODEL wird auf ein in der Literatur vorgeschlagenes globales Pflanzenklassifikationsschema angewendet, welches nur die Merkmale spezifisches Blattgewicht, Wuchshöhe und Samengewicht berücksichtigt. Es wird die Sukzession einer Pflanzengesellschaft bei unterschiedlichen Nährstoff- und Störungsverhältnissen simuliert. Die Simulationsergebnisse werden mit Ergebnissen aus Feldstudien verglichen und es wurde eine Übereinstimmung in weiten Bereichen gefunden. Außerdem werden die simulierten Daten benutzt, um eine funktionale Hierarchie der Merkmale zu formulieren. Wuchshöhe ist unter allen Umweltbedingungen das wichtigste Merkmal. Samengewicht ist auf fruchtbaren und spezifisches Blattgewicht auf unfruchtbaren Standorten das zweitwichtigste Merkmal. Das Störungsregime hat zwar Einfluss auf die Wettbewerbsfähigkeiten der einzelnen Pflanzentypen aber keinen Einfluss auf die funktionale Hierarchie. Der dritte Teil analysiert einen im Rahmen der Arbeit durchgeführten Mesokosmosversuch. Für die im ersten Teil vorgestellte statistische Methode wird ein neues Nullmodell entwickelt, welches in der Lage ist, mit Frequenzdaten zu arbeiten. Außerdem wird die Fragestellung untersucht, ob es zulässig ist, das Verhalten eines funktionalen Pflanzentypen, der sich aus einer Kombination verschiedener Merkmale ergibt, als Summe der Beziehungen der einzelnen Merkmale zu den erklärenden Variablen zu betrachten. Es stellt sich heraus, dass durch Kombination von Einzelmerkmaluntersuchungen erzeugte Vorhersagen nur ungenügend mit dem wirklichen Verhalten der funktionalen Typen in Bezug auf die Umweltfaktoren übereinstimmen. Für den Versuch, in welchem 32 Arten auf vorher sterilisiertem Boden gesät wurden und über drei Jahre das Störungsregime und die Nährstoffverhältnisse manipuliert wurden, wird eine Klassifizierung in vier Pflanzentypen als optimal ermittelt. Die Gruppierung in Arten mit einer Wuchshöhe von über 180cm (diese Gruppe beinhaltet nur zwei mehrjährige Arten mit langen Ausläufern), einjährige Arten, Arten kleiner als 180 cm mit langen Ausläufern und solche mit kurzen Ausläufern ergibt bei jedem Treatment ein statistisch signifikantes Modell. In einer Synthese werden die Beziehungen zwischen den einzelnen Teilen der Arbeit hergestellt und es werden weitere An-

wendungsmöglichkeiten der vorgestellten Methoden in einem perspektivischen Ausblick erläutert. Die entwickelte Analysetechnik ist in einem Programm implementiert welches zusammen mit einer Programmbeschreibung an die Arbeit angegliedert ist.

References

- Aarsen, L.W. & Jordan, C. Y. (2001) Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. *Ecoscience* 8: 471-477.
- Aerts, R. & Chapin, F. S. (2000) *The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns*. In: Advances in Ecological Research, Vol 30. 1-67
- Begon, M., Harper, J. L. & Townsend, C. R. (1996) *Ecology*. Blackwell Science Ltd., Oxford.
- Bekker, R. M., Schaminée, J. H. J., Bakker, J. P. & Thompson, K. (1998) Seed bank characteristics of Dutch plant communities. *Acta Bot. Neerl* 47: 15-26.
- Berger, U. & Hildenbrandt, H. (2000) A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. *Ecol. model.* 132: 287-302.
- Bugmann, H. (1996) Functional types of trees in temperate and boreal forests: Classification and testing. *J. Veg. Sci.* 7: 359-370.
- Burke, M. J. W., Grime J. P. (1996) An experimental study of plant community invasibility. *Ecology* 77: 776-790.
- Cain, M. L., Dudle, D. A. & Evans, J. P. (1996) Spatial models of foraging in clonal plant species. *American Journal of Botany* 83: 76-85.
- Chesson, P. L. (1985) Coexistence of Competitors in Spatially and Temporally Varying Environments - a Look at the Combined Effects of Different Sorts of Variability. *Theoretical Population Biology* 28: 263-287.
- Condit, R., Hubbell, S. P. & Foster, R. B. (1996) Assessing the response of plant functional types to climatic change in tropical forests. *J. Veg. Sci.* 7: 405-416.
- Connell, J. H. (1978) Diversity in Tropical Rain Forests and Coral Reefs - High Diversity of Trees and Corals Is Maintained Only in a Non-Equilibrium State. *Science* 199: 1302-1310.
- Connell, J. H. & Slatyer, R. O. (1977) Mechanism of succession in natural communities and their role in community stability and organisation. *Am. Nat.* 111: 1119-1144.
- Connor, E. F. & Simberloff, D. (1979) The assembly of species communities : chance or competition? *Ecology* 60: 1132-1140.
- Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51: 335-380.
- Craine, J. M., Froehle, J., Tilman, D. G., Wedin, D. A. & Chapin, I. F. S. (2001) The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos* 93: 274-285.
- Czaran, T. (1998) *Spatiotemporal Models of Population and Community Dynamics*. Chapman & Hall, London.
- Davis, M. A., Grime, J. P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88: 528-534.
- Diamond, J. M. & Marshall, A. G. (1979) Origin of the Hebridean Avifauna. *Emu* 76: 187-200.
- Diaz, S. & Cabido, M. (1997) Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8: 463-474.
- Diaz, S., Cabido, M. & Casanoves, F. (1999) *Functional implications of trait-environment linkages in plant communities*. In: The search for assembly rules in ecological communities (eds. E. Weiher and P. A. e. Keddy). 338-362. Cambridge University Press, Cambridge.
- Diaz, S., Noy-Meir, I. & Cabido, M. (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? *J. Appl. Ecol.* 38: 497-508.
- Doledec, S., Chessel, D., terBraak, C. J. F. & Champely, S. (1996) Matching species traits to environmental variables: A new three-table ordination method. *Environ. ecol. stat.* 3: 143-166.
- Eckstein, R. L., Karlsson, P. S. & Weih, M. (1999) Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytologist* 143: 177-189.
- Elton, C. S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Eriksson, O. & Jakobsson, A. (1998) Abundance, distribution and life histories of grassland plants: a comparative study of 81 species. *Journal of Ecology* 86: 922-933.

- Feeley, K. (2003) Analysis of avian communities in Lake Guri, Venezuela, using multiple assembly rule models. *Oecologia* 137: 104-113.
- Fernandez, A. R., Laffraga, J. M. & Ortega, F. (1993) Strategies in mediterranean grassland annuals in relation to stress and disturbance. *J. Veg. Sci.* 4: 313-322.
- Fonseca, C. R., Overton, J. M., Collins, B. & Westoby, M. (2000) Shifts in trait-combinations along rainfall and phosphorus gradients. *J. Ecol.* 88: 964-977.
- Gadgil, M. & Solbrig, O. T. (1972) The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. *American Naturalist* 106: 14-31.
- Garnier, E. (1992) Growth Analysis of Congeneric Annual and Perennial Grass Species. *Journal of Ecology* 80: 665-675.
- Garnier, E. C., P., Guillermin, J.-L. & Sonié, L. (1997) Specific leaf area and leaf nitrogen concentration in annual and perennial grass species growing in Mediterranean old-fields. *Oecologia* 111: 490-498.
- Gaudet, C. L. K., P. A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* 334: 242-243.
- Gibson DJ, Connolly J, Hartnett DC, Weidenhamer JD (1999) Designs for greenhouse studies of interactions between plants. *J. Ecol.* 87:1-16
- Gitay, H. & Noble, I. R. (1997) *What are functional types and how should we seek them?* In: Plant functional types (eds. T. M. Smith, H. H. Shugart and F. I. Woodward). Cambridge University Press, Cambridge.
- Goldberg, D. E. & Miller, T. E. (1990) Effects of different resource additions on species diversity in an annual plant community. *Ecology* 71: 213-225.
- Gotelli, N. J. (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606-2621.
- Gotelli, N. J. (2001) Swap and fill algorithms in null model analysis: rethinking the knight's tour. *Oecologia* 129: 281-291.
- Gotelli, N. J. & Graves, G. R. (1996) Null models in ecology. Smithsonian Institution Press, Washington.
- Gotelli, N. J., Lewis, F. G. & Young, C. M. (1987) Body-size differences in a colonizing amphipod - mollusk assemblage. *Oecologia* 72: 104-108.
- Gotelli, N. J. & McCabe, D. J. (2002) Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology* 83: 2091-2096.
- Gough, L., Osenberg, C. W., Gross, K. L. & Collins, S. L. (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos* 89: 428-439.
- Grace, J. B. (1999) The role of community biomass and species pools in the regulation of plant diversity. *Oikos* 92: 193-207.
- Grime, J. P. (1973) Competitive Exclusion in Herbaceous Vegetation. *Nature* 242: 344-347.
- Grime, J. P. (1974) Vegetation classification by reference to strategies. *Nature* 250: 26-31.
- Grime, J. P. (1979) Plant Strategies and Vegetation Processes. Wiley, Chichester.
- Grime, J. P., Hodgson, J. G. & Hunt, R. (1988) Comparative plant ecology. Unwin Hyman, London.
- Guisan, A. & Zimmermann, N. E. (2000) Predictive habitat distribution models in ecology. *Ecol. model.* 135: 147-186.
- Henle, K., Davis, K. F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* 13: 207-251.
- Hodgson, J. G., Wilson, P. J., Hunt, R., Grime, J. P. & Thompson, K. (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* 85: 282-294.
- Howard, T. G. & Goldberg, D. E. (2001) Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology* 82: 979-990.
- Huston, M. (1979) A general theory of species diversity. *Am. Nat.* 81-101.
- IPCC (2000) *Scenario Driving Forces*. In: Special Report on Emissions Scenarios (eds. N. Nakicenovic and R. Swart). Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge.
- IPCC (2001) *Climate change 2001: Synthesis Report*. Cambridge University Press for the Intergovernmental Panel on Climate Change, Cambridge.
- Jakobsson, A. & Eriksson, O. (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88: 494-502.
- Jauffret, S. & Lavorel, S. (2003) Are plant functional types relevant to describe degradation in arid, southern Tunisian steppes? *J. Veg. Sci.* 14: 399-408.

- Kahmen, S. & Poschod, P. (2004) Plant functional trait responses to grassland succession over 25 years. *J. Veg. Sci.* 15: 21-32.
- Keddy, P., Gaudet, C. & Fraser, L. H. (2000) Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. *J. Ecol.* 88: 413-423.
- Keddy, P., Nielsen, K., Weiher, E. & Lawson, R. (2002) Relative competitive performance of 63 species of terrestrial herbaceous plants. *J. Veg. Sci.* 13: 5-16.
- Kidson, R. & Westoby, M. (2000) Seed mass and seedling dimensions in relation to seedling establishment. *Oecologia* 125: 11-17.
- Kitajima, K. & Bolker, B. M. (2003) Testing performance rank reversals among coexisting species: crossover point irradiance analysis by Sack & Grubb (2001) and alternatives. *Funct. Ecol.* 17: 276-281.
- Kleyer, M. (1999a) Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. *J. Veg. Sci.* 10: 697-708.
- Kleyer, M. (1999b) Individuenbasierte Modellierung von Sukzessionen pflanzlicher Wuchstypen bei unterschiedlichen Störungsintensitäten und Ressourcenangeboten. *Verhandlungen der Gesellschaft für Ökologie* 28: 185-189.
- Kleyer, M. (2002) Validation of plant functional types across two contrasting landscapes. *J. Veg. Sci.* 13: 167-178.
- Klimes, L. & Klimesova, J. (1999) CLO-PLA2 - a database of clonal plants in central Europe. *Plant Ecology* 141: 9-19.
- Klimesova, J. & Klimes, L. (2003) Resprouting of herbs in disturbed habitats: is it adequately described by Bellingham-Sparrow's model? *Oikos* 103: 225-229.
- Knevel, I. C., Bekker, R. M., Bakker, J. P. & Kleyer, M. (2003) Life-history traits of the northwest European flora: The LEDA database. *J. Veg. Sci.* 14: 611-614.
- Knops, J. M. H., Tilman, D., Haddad, N. M., Naeem, S., Mitchell, C. E., Haarstad, J. & Siemann, E. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2: 286-293(8).
- Körner, C. (1994) *Scaling from Species to Vegetation: The Usefulness of Functional Groups*. In: Biodiversity and Ecosystem Function (eds. E. D. Schulze and H. A. Mooney). Springer Verlag, Berlin.
- Landsberg, J., Lavorel, S. & Stol, J. (1999) Grazing response groups among understorey plants in arid rangelands. *J. Veg. Sci.* 10: 683-696.
- Lavergne, S., Garnier, E. & Debussche, M. (2003) Do rock endemic and widespread plant species differ under the Leaf-Height-Seed plant ecology strategy scheme? *Ecology Letters* 6: 398-404.
- Lavorel, S. (2001) LAMOS : A LANDscape MOdelling Shell for studying the role of landscape scale processes in global change effects. *GCTE News* 17: 5-6.
- Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16: 545-556.
- Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T. D. A. (1997) Plant functional classification from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol.* 12: 474-478.
- Lavorel, S., Rochette, C. & Lebreton, J. D. (1999) Functional groups for response to disturbance in Mediterranean old fields. *Oikos* 84: 480-498.
- Law, R., Dieckmann, U. & Metz, J. A. J. (2000) *The Geometry of ecological interactions*. Cambridge University Press, Cambridge.
- Lee, E. T. (1980) *Statistical Methods for survival data analysis*. Wadsworth Inc., Belmont.
- Legendre, P., Galzin, R. & Vivien, M. (1997) Relating behavior to habitat: Solutions to the fourth-corner problem. *Ecology* 78: 547-562.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. Elsevier, Amsterdam.
- Lehsten, V. (1994) *Simulation of Plant Successions with Plant Functional Types*; Diploma Thesis, Rostock.
- Leishman, M. R. (2001) Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93: 294-302.
- Lloret, F., Medail, F., Brundu, G. & Hulme, P. E. (2004) Local and regional abundance of exotic plant species on Mediterranean islands: are species traits important. *Global Ecology and Biogeography* 13: 37-45.

- Lonsdale, W. M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522.
- Maestre, F. T. & Cortina, J. (2002) Spatial patterns of surface soil properties and vegetation in a Mediterranean semi-arid steppe. *Plant and Soil* 241: 279-291.
- Maly, E. J. & Doolittle, W. L. (1977) Effects of island area and habitat on Bahamian land and fresh-water snail distribution. *Am. Mid. Nat* 97: 59-67.
- Manly, B. (1996) Randomization, Bootstrap and Monte Carlo Methods in Biology. Second Edition edn. Chapman and Hall, London.
- Manly, B. & Sanderson, J. G. (2002) A note on null models: Justifying the methodology. *Ecology* 83: 580-582.
- Manly, B. F. J. (1995) A note on the analysis of species co-occurrences. *Ecology* 76: 1109-1115.
- Marby, C., Ackerly, D. & Fritz, G. (2000) Landscape and species-level distribution of morphological and life history traits in a temperate woodland flora. *J. Veg. Sci.* 11: 213-224.
- McIntyre, S. & Lavorel, S. (2001) Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *J. Ecol.* 89: 209-226.
- McIntyre, S., Lavorel, S., Landsberg, J. & Forbes, T. D. A. (1999) Disturbance response in vegetation--towards a global perspective on functional traits. *J. Veg. Sci.* 10: 621-630.
- Miklos, I. & Podani, J. (2004) Randomization of presence-absence matrices: Comments and new algorithms. *Ecology* 85: 86-92.
- Milbau, A., Nijs, I., Van Peer, L., Reheul, D. & De Cauwer, B. (2003) Disentangling invasiveness and invasibility during invasion in synthesized grassland communities. *New Phytologist* 159: 657-667.
- Miller, T. E. & Werner, P. A. (1987) Competitive effects and responses between plant species in a first-year old-field community. *Ecology* 68: 1201-1210.
- Mooney, H. A. & Drake, J. A. (1986) Ecology of biological invasions of North America and Hawaii. Springer Verlag, New York.
- Moore, A. D. & Noble, I. R. (1990) An Individualistic Model of Vegetation Stand Dynamics. *Journal of Environmental Management* 31: 61-81.
- Moore, J. L., Mouquet, N., Lawton, J. H. & Loreau, M. (2001) Coexistence, saturation and invasion resistance in simulated plant assemblages. *Oikos* 94: 303-314.
- Mustard, M. J., Standing, D. B., Aitkenhead, M. J., Robinson, D. & McDonald, A. J. S. (2003) The emergence of primary strategies in evolving virtual-plant populations. *Evol. Ecol. Res.* 5: 1067-1081.
- Naeem, S., Knops, J. M. H., Tilman, D., Howe, K. M., Kennedy, T. & Gale, S. (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91: 97-108(12).
- Noble, I. R. & Slatyer, R. O. (1980) The Use of Vital Attributes to Predict Successional Changes in Plant-Communities Subject to Recurrent Disturbances. *Vegetatio* 43: 5-21.
- Nygaard, B. & Ejrnaes, R. (2004) A new approach to functional interpretation of vegetation data. *J. Veg. Sci.* 15: 49-56.
- Partel, M., Zobel, M., Zobel, K. & van der Maarel, E. (1996) The species pool and its relation to species richness: Evidence from Estonian plant communities. *Oikos* 75: 111-117.
- Patterson, B. D. & Atmar, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagoes. *Biol. J. Linnean Soc.* 28: 65-82.
- Perez-Salvador, B. R., de-los-Cobos-Silva, S., Gutierrez-Andrade, M. A. & Torres-Chazaro, A. (2002) A reduced formula for the precise number of (0,1)-matrices in A(R,S). *Discret. Math.* 256: 361-372.
- Pillar V (1999) On the identification of optimal plant functional types. *J. Veg. Sci.* 10:631-640
- Pillar VD (2003) An improved method for searching plant functional types by numerical analysis. *J. Veg. Sci.* 14:323-332
- Poorter, H. (1989) *Interspecific variation in the relative growth rate: On ecological causes and physiological consequences*. In: Causes and consequences of variation in growth rate (eds. H. Lambers, M. L. Cambridge, H. Konings and T. L. Pons). SPB Academic Publishing, The Hague.
- Poorter, H. & De Jong, R. (1999) A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* 143: 163-176.

- Poschlod, P., Kleyer, M. & Tackenberg, O. (2000) Databases on life history traits as a tool for risk assessment in plant species. *Zeitschrift für Ökologie und Naturschutz* 9: 3-18.
- Rees, M. (1995) Community structure in sand dune annuals: is seed weight a key quantity? *Oikos* 78: 116-126.
- Roberts, A. & Stone, L. (1990) Island-Sharing by Archipelago Species. *Oecologia* 83: 560-567.
- Robinson, J. V. & Edgemon, M. A. (1988) An Experimental Evaluation of the Effect of Invasion History on Community Structure. *Ecology* 69: 1410-1417.
- Ryser, P. & Urbas, P. (2000) Ecological significance of leaf life span among Central European grass species. *Oikos* 91: 41-50.
- Sachs, L. (1992) *Angewandte Statistik*. Springer Verlag, Berlin.
- Sack, L. & Grubb, P. J. (2001) Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? *Funct. Ecol.* 15: 145-154.
- Saltelli, A., Chan, K. & Scott, E., Marian (2000) *Sensitivity analysis*. Wiley & Sons Ltd, Chichester.
- Sanderson, J. G., Moulton, M. P. & Selfridge, R. G. (1998) Null matrices and the analysis of species co-occurrences. *Oecologia* 116: 275-283.
- Semenova, G. V. & van der Maarel, E. (2000) Plant functional types - a strategic perspective. *J. Veg. Sci.* 11: 917-922.
- Shea, K., Roxburgh, S. H. & Rauschert, E. S. J. (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* 7: 491-508.
- Shipley, B. (1993) A Null Model for Competitive Hierarchies in Competition Matrices. *Ecology* 74: 1693-1699.
- Shipley, B., Keddy, P. A., Moore, D. R. J. & Lemky, K. (1989) Regeneration and Establishment Strategies of Emergent Macrophytes. *J. Ecol.* 77: 1093-1110.
- Silander, J. A. & Pacala, S. W. (1990) *The application of plant population dynamic models to understanding plant competition*. In: *Perspectives on plant competition* (eds. J. B. Grace and D. Tilman). 67-92, Academic Press, San Diego.
- Skarpe, C. (1996) Plant functional types and climate in a southern African savanna. *J. Veg. Sci.* 7: 397-404.
- Sparrow, A. D. & Bellingham, P. J. (2001) More to resprouting than fire. *Oikos* 94: 195-197.
- Stebbins, G. L. (1974) *Flowering plants: Evolution above the species level*. Bleknapp Press, Harvard, MA.
- Stone, L. & Roberts, A. (1990) The checkerboard score and species distributions. *Oecologia* 85: 74-79.
- Suding, K. N., Goldberg, D. E. & Hartman, K. M. (2003) Relationships among species traits: Separating levels of response and identifying linkages to abundance. *Ecology* 84: 1-16.
- Thompson, K., Bakker, J.P., Bekker, R.M. & Hodgson, J.G. (1998) Ecological correlates of seed persistence in soil in the north-west European flora. *J. Ecol.* 86: 163-169.
- Thompson, K., Hodgson, J. G., Grime, J. P. & Burke, M. J. W. (2001) Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. *J. Ecol.* 89: 1054-1060.
- Tilman, D. (1988) *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton.
- Tilman, D. (1990) Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58: 3-15.
- Troumbis, A. Y., Galanidis, A. & Kokkoris, G. D. (2002) Components of short-term invasibility in experimental Mediterranean grasslands. *Oikos* 98: 239-250.
- Turnbull, L. A., Rees, M. & Crawley, M. J. (1999) Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.* 87: 899-912.
- Van der Putten, W. H., Mortimer, S. R., Hedlund, K., Van Dijk, C., Brown, V. K., Lepä, J., C. Rodriguez-Barrueco, J. Roy, T. A. Diaz Len, D. Gormsen, G. W. Korthals, Lavorel, S., I. Santa Regina & Smilauer, P. (2000) Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. *Oecologia* 124: 91-99.
- Van Valen, L. (1971) Group selection and the evolution of dispersal. *Evolution* 25: 591-598.
- Vesk, P. A., Leishman, M. R. & Westoby, M. (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *J. Appl. Ecol.* 22-31.
- Walck, J. L., Baskin, J. M. & Baskin, C. C. (1999) Relative competitive abilities and growth characteristics of a narrowly endemic and a geographically widespread *Solidago* species (Asteraceae). *American Journal of Botany* 86: 820-828.

- Wang, B. Y. & Zhang, F. Z. (1998) On the precise number of (0,1)-matrices in $U(R,S)$. *Discret. Math.* 187: 211-220.
- Wardle, D. A. (2001) Experimental demonstration that plant diversity reduces invasibility - evidence of a biological mechanism or a consequence of sampling effect? *Oikos* 95: 161-170.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199: 213-227.
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. & Wright, I. J. (2002) Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125-159.
- Whittaker, R. H. & Goodman, D. (1979) Classifying species according to their demographic strategy 1. Population fluctuations and environmental heterogeneity. *Am. Nat.* 113: 185-200.
- Wilson, J. B. (1987) Methods For Detecting Nonrandomness In Species Cooccurrences - A Contribution. *Oecologia* 73: 579-582.
- Wilson, S. D. & Keddy, P. A. (1986) Species Competitive Ability and Position Along a Natural Stress Disturbance Gradient. *Ecology* 67: 1236-1242.
- Wissel, C. (1989) Theoretische Ökologie: Eine Einführung. Springer Verlag, Berlin.
- Woodward, F. I. & Cramer, W. (1996) Plant functional types and climatic changes: Introduction. *Journal of Vegetation Science* 7: 306-308.
- Worley, A. C., Houle, D. & Barrett, S. C. H. (2003) Consequences of hierarchical allocation for the evolution of life-history traits. *Am. Nat.* 161: 153-167.
- Wright, I. J. & Westoby, M. (1999) Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *J. Ecol.* 87: 85-97.
- Wright, I. J. & Westoby, M. (2003) Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Funct. Ecol.* 17: 10-19.
- Wright, I. J., Westoby, M. & Reich, P. B. (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *J. Ecol.* 90: 534-543.
- Wu, H., Sharpe, P. J., Walker, J. & Pendridge, L. K. (1985) Ecological field theory: a spatial analysis of resource interference among plants. *Ecol. model.* 29: 215-243.
- Zaman, A. & Simberloff, D. (2002) Random binary matrices in biogeographical ecology - Instituting a good neighbor policy. *Environ. ecol. stat.* 9: 405-421.
- Zavaleta, E. S., Shaw, M. R., Chiariello, N. R., Thomas, B. D., Cleland, E. E., Field, C. B. & Mooney, H. A. (2003) Grassland responses to three years of elevated temperature, CO₂, precipitation, and N deposition. *Ecological Monographs* 73: 585-604.

Appendix

A.1 Example calculation of the expected frequencies and C-scores by the 'sequential swap' and the frequency corrected 'sequential swap'.

The matrix (M_0) published by Maly and Doolittle (1977) has only 5 unique randomisations (M_0 - M_4) with fixed row and column totals. Figure 1.1 shows the five matrices and the transition probabilities.

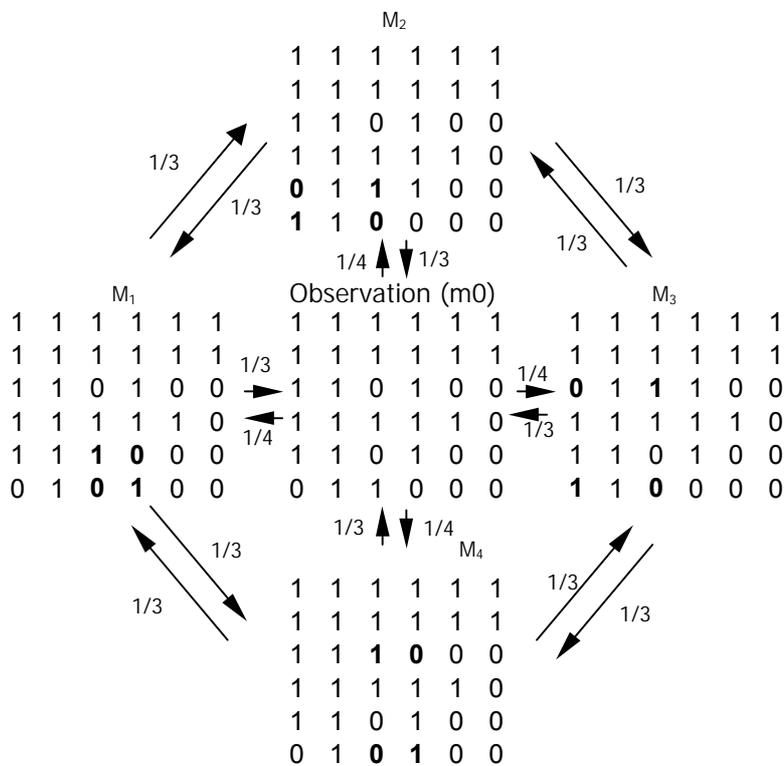


Figure B.1 Unique matrices and transition probabilities of the Maly and Doolittle (1977) data set

Table B.1 lists the transition probabilities, the C-score and the stable state probabilities of each matrix using the sequential swap. Note that the stable state probabilities are proportional to the C-score.

Matrix nr	0	1	2	3	4	C-score	Stable state prop.
0	0	1/4	1/4	1/4	1/4	0.2666	0.25
1	1/3	0	1/3	0	1/3	0.2000	0.1875
2	1/3	1/3	0	1/3	0	0.2000	0.1875
3	1/3	0	1/3	0	1/3	0.2000	0.1875
4	1/3	1/3	0	1/3	0	0.2000	0.1875
Mean						0.2133	

The C-score derived by the sequential swap is:

$4 * 0.20 * 0.1875 + 1 * 0.2666 * 0.25 = 0.2167$, while the correct C-score using equal frequencies for each state is: $4 * 0.20 * 0.20 + 1 * 0.2666 * 0.20 = 0.2133$.

Frequency correction :

$$\overline{C_{corr}} = \frac{n}{\sum_{i=1}^n \frac{1}{C_i}}$$

Consider a simulation with 10000 swaps, the expected frequencies of the C-scores generated by the sequential swap would be 2500 times 0.2666 and 7500 times 0.2. The mean C-score generated by the sequential swap is 0.2167. The correction would be calculated as:

$$\overline{C_{corr}} = \frac{1000}{2500 * \frac{1}{0.2666} + 7500 * \frac{1}{0.2}}$$

$$\overline{C_{corr}} = 0.2133$$

The probability of reaching a C-score as extreme as the observation by using the sequential swap is 0.25 while the correct probability is 0.20 (Tab 1.1).

The frequency correction would give a corrected p-value as follows:

$$\overline{p_{corr}} = \frac{\sum_{i=1}^n \frac{C_{corr}}{C_i}}{n} \quad \text{for } C_i \geq C_{obs}$$

$$\overline{p_{corr}} = \frac{0.2133 * 2500}{0.2666 * 10000}$$

$$\overline{p_{corr}} = 0.2$$

The frequency corrected sequential swap derives a p-value of 0.200 which is equal to the theoretical expectation while the uncorrected version gives a p-value of 0.213.

A.2 The fourth corner analysis

A.2.1 Example generation of PFTs using the fourth corner method

Sp.	Height (h)
sp 1	1
sp 2	1
sp 3	2
sp 4	2
sp 5	3
sp 6	4
sp 7	5
sp 8	6
sp 9	6
sp 10	6

	site1	site2
infertile(inf.)	1	0
fertile(fert.)	0	1

Sp.	site1	site2
sp 1	1	0
sp 2	1	0
sp 3	1	0
sp 4	1	1
sp 5	0	1
sp 6	0	1
sp 7	1	1
sp 8	0	1
sp 9	0	1
sp 10	0	1

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

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

h	PFT (B)	
	s	t
1	1	0
1	1	0
2	1	0
2	1	0
3	1	0
4	0	1
5	0	1
6	0	1
6	0	1
6	0	1

h	PFT (B)	
	s	t
1	1	0
1	1	0
2	1	0
2	1	0
3	1	0
4	1	0
5	0	1
6	0	1
6	0	1
6	0	1

h	PFT (B)		
	s	m	t
1	1	0	0
1	1	0	0
2	1	0	0
2	1	0	0
3	0	1	0
4	0	1	0
5	0	0	1
6	0	0	1
6	0	0	1
6	0	0	1

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

D=CA'B

	s	t
Inf.	4	1
Fert.	1	6

	h	t
inf.	4	1
fert.	2	5

	s	t
inf.	4	1
fert.	3	4

	s	m	t
inf.	4	0	1
fert.	1	2	4

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

	s	t
inf.	0.02	-0,02
fert.	-0.001	0,001

	s	t
inf.	0.1	-0.1
fert.	-0.1	0,1

	s	t
inf.	0.02	-0.02
fert.	0.16	0.16

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

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

Grouping criteria n_{ps} = total number of p-values below 0.05

1.PT set	2.PT set	3.PT set	4.PT set
$n_{ps}=4$	$n_{ps}=0$	$n_{ps}=2$	discarded

The optimal PFT classification is into two height classes of 1-2 and 3-6.

A.2.2 Construction of the test data set

Matrix A –observation data

Four treatments with 20 replicates each result in 80 sites and therefore 80 columns in matrix A. The species diversity is set to 20, for simplicity reasons each species may occur only once, hence 1600 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 –trait data

The heights are distributed according to the following table:

Height	Nr. of species at disturbance level			
	1	2	3	4
1	8	6	4	2
2	6	5	5	4
3	4	5	5	6
4	2	4	6	8

Each site with a disturbance level one has eight species with height four, six species with height three, four species have the height two and two species are of height one.

The traits seed number and spacer length are equally distributed at disturbance level 1-3.

The Heights are distributed according to the following table:

Trait		Disturbance level		
Spacer	Seed nr.	1-3	4	
		all sites	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 two 3's are randomly set.

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.

A.2.3 Response of virtual plant types

Tab. A. 3 PFTs are generated by the 'lottery' model for vegetation composition using the three traits. 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 (Tab. 1), taking all three traits into account leads to insignificant p-values. The total frequencies of the PFT's are lowered, hence p-values are decreased.

Trait class			P-values of response to 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
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

A.3 Functional hierarchies

A.3.1 Construction of the functional trait matrix

Consider the ranking of plant types at high soil fertility and medium disturbed soil conditions in table 4.2. If we also list the traits of the species in the first 5 ranks we get the following table:

Table A.3.1 Ranking and traits of the plant types at medium disturbance and high soil fertility of table 4.2.

Rank	Plant type	SLA	Height	Seed Mass
1	5	high	high	high
2	1	low	high	high
3	2	low	high	low
4	6	high	high	low
5	7	high	low	high
Rank position of trait attribute change		1	4	2

The trait plant height changes between the fourth and fifth position of the plant type ranking, while seed mass changes between the second and the third and SLA after the first position. Hence, the functional trait hierarchy is:

plant height > seed mass > SLA. Since there are significant differences between all considered ranks, no trait is non-functional. Our trait hierarchy focuses on the survival, and not on the extinction, hence we consider the first ranks of the hierarchy.

A.3.2 Cox F test for singly censored data

The Cox F-Test has the following procedure

1: rank the observed times of extinction of in the combined sample: t_i

2: r is the rank number in increasing order of magnitude

calculate $t(rn) = 1/n + 1/(n-1) + \dots + 1/(n-r+1)$ $r = 1, \dots, n$

calculate means of $t(rn)$ for equal ranks

3: divide the sum of the $t(rn)$ scores by the number of extinction occurring for each sample t_A and t_B

4: t_A/t_B is assumed to have an F distribution with $2 \cdot n_A, 2 \cdot n_B$ (n_A : number of extinctions of plant type A) degrees of freedom. Critical regions for testing

$H_0: S_1 = S_2$ against $H_1: (S_1 > S_2), H_2 (S_1 < S_2)$ are respectively

$t_1/t_2 > F(2n_1, 2n_2, \alpha)$, $t_1/t_2 < F(2n_1, 2n_2, \alpha)$

An example simulation may run two different treatments over 100 years with 5 replicates each.

Two plant types take part in the simulation. Their extinction times in years are:

A: 10 21 33 45 50

B: 33 52 100+ 100+ 100+

a plus sign denotes that plant type survived the simulation time.

The calculation can be done conveniently in a table:

Table A.3.2 Example calculation of Cox F-Test for singly censored data.

Rank	t_i	$t(rn)$	$t(rn)$ of sample A	$t(rn)$ of sample B
1	10	$\frac{1}{10} = 0,1$	0.1	
2	21	$\frac{1}{10} + \frac{1}{9} = 0,2111$	0.211	
2	33	$\frac{1}{10} + \frac{1}{9} + \frac{1}{8} = 0,3361$	0.407	
4	33	$0.3361 + 1/7 = 0.4790$	} = 0.4075	0.407
5	45	$0.4790 + 1/6 = 0.6456$		0.646
6	50	$0.6456 + 1/5 = 0.8456$	0.846	
7	52	$0.8456 + 1/4 = 1.0956$		1.0956
8	100+	$1.0956 + 1/3 = 1.429$		1.429
9	100+	1.429		1.429
10	100+	1.429		1.429
sum			2.21	5.79

$$t_A = 2.21/5 = 0.4420$$

$$t_B = 5.79/2 = 2.90$$

$$t_A/t_B = 0.44/2.90 = 1.527$$

$$F(10, 2, 0.95) = 0.287$$

$$1.527 < 0.287$$

Since $t_A/t_B < F(10, 2, 0.95)$ plant type B has a significant better survival than plant type A ($\alpha = 0.05$).

A.4 Data of the mesocosmos experiment

A.4.1 Plant traits and PFT classification

Species of the mesocosmos experiment with allocated traits and functional classification by the extended fourth corner method (chapter 6). The responses of the functional types are indicated in table 5.4.

Life cycle / spacer length (1: annual, 2: perennial with short spacers, 3: perennial with long spacers); functional types (1: annuals, 2: small perennials with short spacers, 3: small perennials with long spacers, 4: tall perennials).

Species name	Height cm	SLA m ² ·kg ⁻¹	Biomass g	Life cycle/ spacer length	Functional type
<i>Alopecurus pratensis</i>	71	21.8	1	2	2
<i>Apera spica-venti</i>	71	23.3	0.27	1	1
<i>Arenaria serpyllifolia</i>	7	11.1	0.13	1	1
<i>Arrhenatherum elatius</i>	96	32.1	0.39	2	2
<i>Bellis perennis</i>	4	25.9	0.64	2	2
<i>Bromus erectus</i>	37	20.5	0.13	2	2
<i>Centaurea jacea</i>	30	22.6	0.83	2	2
<i>Chenopodium album</i>	81	21.2	61.57	1	1
<i>Coronilla varia</i>	65	23.9	3	3	3
<i>Cynosurus cristatus</i>	37	22.3	0.57	2	2
<i>Festuca ovina</i>	37	12.6	0.068	2	2
<i>Festuca rubra</i>	53	16.8	0.092	2	2
<i>Galeopsis tetrahit</i>	102	41.9	29.92	1	1
<i>Galium verum</i>	62	9.6	2.09	3	3
<i>Glechoma hederacea</i>	4	20.8	0.058	3	3
<i>Lathyrus pratensis</i>	32	29.1	3.45	3	3
<i>Luzula campestris</i>	23	26.9	0.13	3	3
<i>Origanum vulgare</i>	74	17.9	2.53	3	3
<i>Papaver rhoeas</i>	96	29.6	17.93	1	1
<i>Phalaris arundinacea</i>	205	21.0	9.04	3	4
<i>Poa annua</i>	13	38.1	0.023	2	2
<i>Poa pratensis</i>	38	16.2	0.17	3	3
<i>Ranunculus acris</i>	111	17.1	6.96	2	2
<i>Rumex acetosa</i>	55	23.0	14.58	2	2
<i>Saxifraga tridactylites</i>	4	2.5	0.12	1	1
<i>Silene vulgaris</i>	48	32.4	1.23	2	2
<i>Solidago canadensis</i>	170	20.7	37.94	3	3
<i>Stellaria media</i>	25	89.7	0.36	1	1
<i>Tanacetum vulgare</i>	105	19.9	11.34	3	3
<i>Thymus serpyllum</i>	10	25.8	0.67	3	3
<i>Trifolium repens</i>	14	20.5	0.73	3	3
<i>Urtica dioica</i>	190	33.6	14.64	3	4

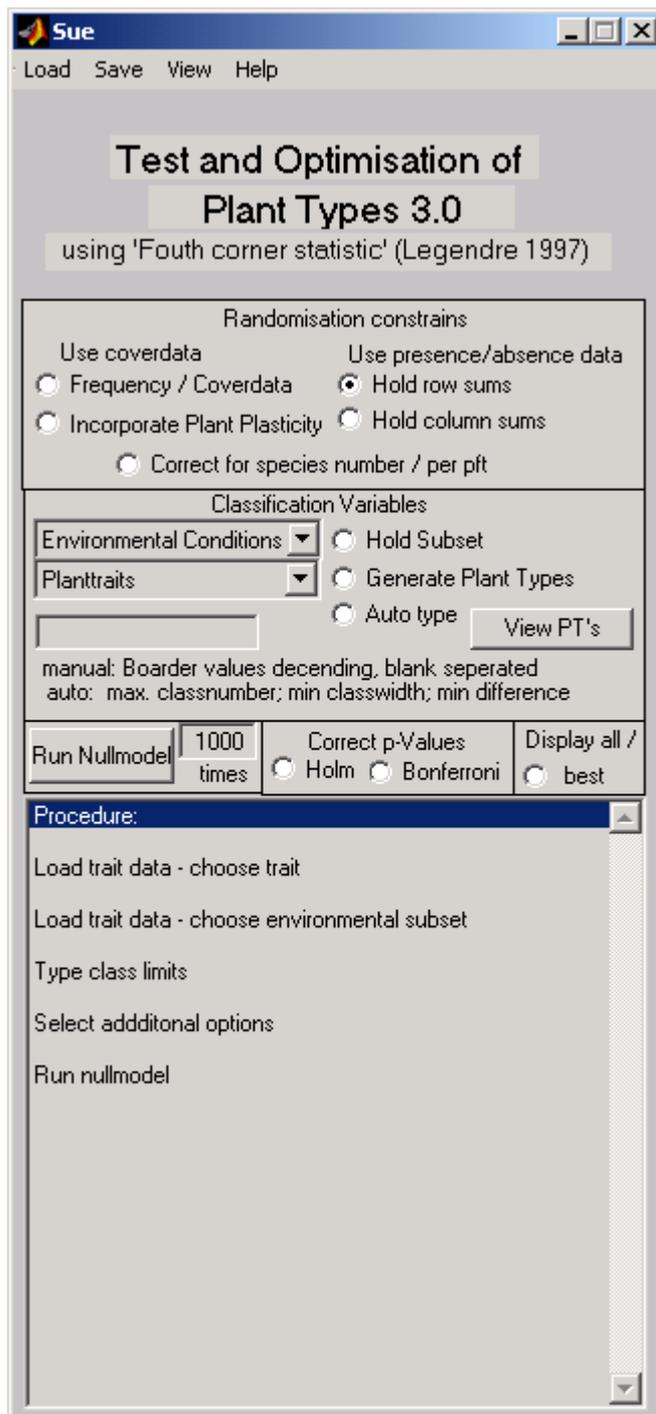
A.4.2 Frequency matrix The vegetation of the plots in the mesocosmos experiment and the treatment of the plots is listed below. Frequency is recorded as percentage of subplots in which the species occurs. The plots were placed in two greenhouses. One was fertilised with 13 kg/ha N (fertile treatment) while the top soil of the second greenhouse was removed (infertile treatment). The disturbance treatments were arranged in a latin-square design.

Plot	Frequency: percentage of subplots with occurrence																												Treatment								
	<i>Alopecurus pratensis</i>	<i>Apera spica-venti</i>	<i>Arenaria serpyllifolia</i>	<i>Arrhenatherum elatius</i>	<i>Bellis perennis</i>	<i>Bromus erectus</i>	<i>Centaurea jacea</i>	<i>Chenopodium album</i>	<i>Coronilla varia</i>	<i>Cynosurus cristatus</i>	<i>Festuca ovina</i>	<i>Festuca rubra</i>	<i>Galeopsis tetrahit</i>	<i>Galium verum</i>	<i>Glechoma hederacea</i>	<i>Lathyrus pratensis</i>	<i>Luzula campestris</i>	<i>Origanum vulgare</i>	<i>Papaver rhoeas</i>	<i>Phalaris arundinacea</i>	<i>Poa annua</i>	<i>Poa pratensis</i>	<i>Ranunculus acris</i>	<i>Rumex acetosa</i>	<i>Saxifraga tridactylites</i>	<i>Silene vulgaris</i>	<i>Solidago canadensis</i>	<i>Stellaria media</i>	<i>Tanacetum vulgare</i>	<i>Thymus serpyllum</i>	<i>Trifolium repens</i>	<i>Urtica dioica</i>	Fertility	Disturbance			
FS1	0	0	0	69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	0	0	0	9	0	0	0	0	0	0	0	0	25	fertile	no disturbance		
FD1	4	0	0	16	0	0	1	0	0	0	0	0	0	0	0	0	2	0	18	88	0	0	1	59	0	10	0	0	0	0	0	0	3	fertile	rototiling		
FE1	0	0	0	83	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	13	0	0	0	17	0	0	0	0	0	0	0	0	0	fertile	mowing every 2 y.		
FM1	0	0	0	80	0	0	0	0	0	3	1	4	0	1	16	1	2	1	0	9	0	0	16	25	0	0	0	1	0	0	0	0	0	fertile	mowing twice a y.		
FL1	9	0	0	47	0	2	7	0	0	34	0	29	0	2	16	9	13	4	0	5	0	4	25	25	0	0	1	6	0	1	0	0	5	fertile	mowing 8 times a y.		
FS2	3	0	0	68	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	17	0	0	2	25	0	0	0	0	0	0	0	0	2	fertile	no disturbance		
FD2	0	0	0	94	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	39	0	0	0	21	0	0	0	0	0	0	0	0	0	0	fertile	rototiling	
FE2	1	0	0	66	0	0	0	0	0	0	0	0	0	0	3	6	0	0	0	22	0	0	0	8	0	0	0	0	0	0	0	0	0	38	fertile	mowing every 2 y.	
FM2	1	0	0	75	0	0	0	0	0	4	3	1	0	1	12	1	3	0	0	2	0	6	13	28	0	0	0	0	0	0	0	0	0	1	fertile	mowing twice a y.	
FL2	2	0	0	70	0	0	1	0	0	8	0	21	0	5	26	5	11	1	0	0	0	6	21	39	0	0	1	1	0	0	0	0	0	4	fertile	mowing 8 times a y.	
FS3	0	0	0	72	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	23	0	0	6	18	0	0	0	0	0	0	0	0	0	0	0	fertile	no disturbance
FE3	0	0	0	75	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	12	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	fertile	mowing every 2 y.
FL3	0	0	0	38	0	2	0	0	0	3	13	14	0	11	80	9	3	7	0	1	0	32	25	44	0	1	1	0	0	0	0	0	0	12	fertile	mowing 8 times a y.	
FM3	1	0	0	79	0	0	0	0	0	1	0	0	0	0	18	2	0	0	0	0	0	3	28	31	0	0	0	0	0	0	0	0	0	1	fertile	mowing twice a y.	
FE4	3	0	0	40	0	0	0	0	0	5	0	0	0	0	0	6	0	0	0	48	0	0	2	17	0	0	0	0	0	0	0	0	0	0	6	fertile	mowing every 2 y.
FD3	0	0	0	28	0	0	0	1	0	0	0	0	0	0	0	9	0	1	0	67	0	1	2	58	0	0	0	0	0	0	0	0	2	0	fertile	rototiling	
FS4	0	0	0	63	0	0	0	0	0	5	0	0	0	0	0	5	0	0	0	56	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	fertile	no disturbance
FL4	3	0	0	52	0	3	6	0	0	16	0	44	0	4	22	15	15	3	0	1	0	10	25	32	0	2	2	0	0	0	0	0	0	2	fertile	mowing 8 times a y.	
FM4	0	0	0	90	0	0	0	0	0	1	0	1	0	0	2	12	3	0	0	6	0	3	15	32	0	0	0	0	0	0	0	0	0	0	2	fertile	mowing twice a y.
FE5	4	0	0	70	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	25	0	0	0	18	0	0	0	0	0	0	0	0	0	0	1	fertile	mowing every 2 y.
FD4	0	0	0	93	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	20	0	1	0	22	0	0	0	0	0	0	0	0	0	0	0	fertile	rototiling
FS5	0	0	0	42	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	67	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	fertile	no disturbance
FD5	0	0	0	72	0	0	0	0	0	1	0	0	0	0	4	4	0	0	0	58	2	6	1	26	0	0	0	0	0	0	0	0	0	0	0	fertile	rototiling
IS1	0	0	0	43	0	3	0	0	0	11	33	0	0	0	8	5	45	0	0	3	0	0	9	30	0	2	1	0	0	0	0	1	2	infertile	no disturbance		
ID1	3	0	0	21	0	0	1	0	0	0	4	6	0	0	1	59	16	0	20	12	1	2	10	20	0	11	1	0	2	0	61	0	infertile	rototiling			
IE1	0	0	0	39	0	0	0	0	0	10	50	0	0	0	21	14	30	0	0	0	0	0	15	18	0	10	0	0	0	0	0	0	0	0	infertile	mowing every 2 y.	
IM1	1	0	0	66	2	0	1	0	0	21	49	0	0	2	33	61	36	0	0	0	0	2	35	9	0	0	1	0	0	0	34	0	infertile	mowing twice a y.			
IL1	0	0	0	13	12	3	7	0	0	57	69	2	0	2	50	36	36	14	0	0	0	5	43	24	0	0	5	0	0	0	0	0	0	0	infertile	mowing 8 times a y.	
IS2	0	0	0	69	0	0	0	0	0	5	39	0	0	0	4	3	2	0	0	0	0	0	9	15	0	0	0	0	0	0	0	0	0	0	0	infertile	no disturbance
ID2	2	0	0	27	0	0	0	0	0	0	2	8	0	0	20	17	14	0	35	0	0	8	27	24	0	6	1	0	0	0	28	0	infertile	rototiling			
IE2	0	0	0	58	0	0	0	0	0	0	18	0	0	0	2	6	11	0	0	4	0	0	38	24	0	0	0	2	0	0	0	0	0	0	infertile	mowing every 2 y.	
IM2	0	0	0	45	0	4	0	0	0	23	37	7	0	2	4	21	30	0	0	0	0	0	13	19	0	0	0	0	0	0	0	64	0	infertile	mowing twice a y.		
IL2	1	0	0	5	1	7	0	0	0	57	52	0	0	6	1	30	76	1	0	0	0	0	23	32	0	1	0	1	0	0	61	0	infertile	mowing 8 times a y.			
IS3	0	0	0	70	0	0	0	0	0	12	1	2	0	0	1	7	9	0	0	0	0	0	8	18	0	0	0	0	0	0	0	0	0	0	0	infertile	no disturbance
IE3	0	0	0	65	0	0	0	0	0	12	5	14	0	1	2	18	23	0	0	0	0	0	13	18	0	0	0	0	0	0	0	0	0	0	0	infertile	mowing every 2 y.
ID3	0	0	0	86	0	0	2	0	0	0	0	4	0	0	0	19	4	1	5	0	0	9	3	15	0	0	0	0	0	0	1	0	0	0	infertile	rototiling	
IL3	1	0	0	15	14	12	0	0	0	24	68	1	0	14	64	68	61	8	0	0	0	5	40	23	0	11	14	7	2	15	6	0	infertile	mowing 8 times a y.			
IM3	0	0	0	50	6	20	0	0	0	19	41	1	0	7	9	64	69	8	0	0	0	5	20	28	0	15	7	0	0	7	8	0	infertile	mowing twice a y.			
IE4	0	0	0	38	1	0	0	0	0	33	45	0	0	5	6	26	37	2	0	0	0	0	18	13	0	5	7	0	1	0	0	1	infertile	mowing every 2 y.			
ID4	0	0	0	78	0	0	0	0	0	0	1	0	0	0	0	33	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	infertile	rototiling		
IS4	0	0	0	81	0	0	0	0	1	2	6	0	0	2	13	4	4	0	0	0	0	2	10	17	0	0	0	0	0	0	1	0	0	infertile	no disturbance		
IL4	0	0	0	5	15	11	7	0	0	52	67	0	0	15	20	25	45	8	0	0	0	0	36	29	0	16	11	4	0	11	7	0	infertile	mowing 8 times a y.			
IM4	1	0	0	71	0	1	0	0	0	17	35	0	0	0	9	32	28	0	0	0	0	0	13	21	0	2	6	0	1	0	31	0	infertile	mowing twice a y.			
IE5	0	0	0	65	2	1	0	0	0	0	44	0	0	4	1	11	18	1	0	2	0	0	11	15	0	11	1	1	0	0	0	0	0	infertile	mowing every 2 y.		
IS5	0	0	0	90	1	0	0	0	0	0	2	2	0	0	0	22	10	2	40	0	0	0	5	37	0	0	1	0	4	0	13	0	infertile	no disturbance			

A.5 Software developed within the work

A.5.1 Sue: a tool for the optimisation of plant functional types.

I adapted the fourth corner method by Legendre et al. (1997) to the task of plant functional grouping. The method is implemented in a Matlab ® script. A stand alone version is hosted by the landscape ecology group at the University of Oldenburg.



General approach

This program calculates the so called fourth corner statistic. A species \times site matrix, a species \times trait matrix and an matrix of the environmental conditions at the sites are combined and the occurrence of groups of species in the filed data is compared with that of a null model. The result characterises the response of the species group to an environmental factor. Different data types can be used by choosing different null models. The procedure is also able to optimise functional grouping.

Steps of the analysis

1. Load the data
2. Chose the null model
3. Categorise the species or initialise the automatic categorisation
4. Chose environmental factor or factor combination
5. Set number of simulations
6. Set correction procedure

7. Set Display type

(best classification / all classification ; including species)

8. Push the <Run Nullmodel> button

9. Interpret the result

Manual

1. Load the data

Four files have to be loaded for the analysis. All files have to be tab limited text files. Empty fields are not allowed in the lists. The absence of a species has to be marked with a zero. An additional file containing the plant size is required for one null model.

1.1 |Load | Observational data | ; a species \times sites list with frequencies or presence / absence data; no headlines and no species names. All values have to be positive numeric integer values.

1.2 |Load | Trait data | ; a species \times trait list listing the measured trait values or categorical variables (e.g. for life cycle) use the dot <.> instead of the comma <,> as decimal marker. A head line (column header) gives the trait names.

1.3 |Load |Environmental data|; a site \times factor state list. With a column header naming the factors. While the traits are categorised by the procedure, the environmental factors need to be categorised before. The list must only contain integer values greater than zero. For instance, if the factor pH has to be categorised in values below six, values between six and eight and values above eight, then the column with the column header 'pH' consists only of the values 1 (pH<6), 2 (6<pH<8) and 3 (pH>8).

1.4 | Load | Species names | ; a list of the names of the species without column header.

1.5 | Load | Plant size | ; a list of the plant size in number of occupied sub plots by a single plant per site without column header. This file is only required by the null model incorporating plant plasticity. The minimum size is one. Zero values are not allowed.

2. Chose the null model

Five null models are implemented using different data types and searching for different pattern. For more details of model 2.1.1 and 2.1.2 refer to *Numerical*

Ecology by Legendre et al. 1998, or to chapter three. Null model 2.1.3 is explained in detail in chapter two and null model 2.1.5 in chapter five.

2.1 Presence absence data

If frequency data has been loaded, it is transformed to presence absence data by these models.

- 2.1.1 |Hold row sums| If only the <Hold row sums> radio button is checked, the environmental control model is applied which randomises the entries in the observed matrix in each row, hence the number of sites at which each species occurs remains constant. This model indirectly assumes that the species diversity is similar at each site. If the radio button <Correct for species number / per PFT> is checked, a correction is applied taking a site specific species diversity into account (see chapter three for details).
- 2.1.2 |Hold column sums| If only the <Hold column sums> radio button is checked, the lottery model is applied which randomises the entries in the observed matrix in each column, hence the species diversity per site remains constant. This model indirectly assumes that the number of sites at which the species occurs is similar for each species. If the radio button <Correct for species number / per PFT> is checked, a correction is applied taking a species specific rarity into account (see chapter three for details).
- 2.1.3 |Hold row sums| and |Hold column sums| If both radio buttons are checked, the sequential swap procedure is applied maintaining species diversity per site and species rarity. (see chapter three for details).

2.2 Quantitative occurrence data

- 2.2.1 |Frequency / Cover data | This null model is a version of the sequential swap using abundance data instead of presence absence data. The single records are swapped in a way that the number of records per site and per species remains constant. For instance the following matrix

11	3		10	4
5	6	may be swapped to	6	5

without changing row or column sums.

- 2.2.2 |Incorporate Plant Plasticity| This null model incorporates a treatment specific plant size. The full procedure or this null model is described in chapter 5.

3. Categorise the species or initialise the automatic categorisation

Either the response of a single categorisation or of many categorisations can be calculated. If a trait is selected in the pull down menu, a list showing all trait values per species is displayed.

3.1 Single categorisation: Select the trait to be categorised, in the plant trait pull down menu and type the group limits in the text field below. For instance if the trait 'plant height' is selected and the entry in the text field is :
| 0 10 15 200 |, than three PTs are formed, the first including all species from height ≥ 0 and height ≤ 10 ; the second plant type will be of height > 10 and height ≤ 15 and the last plant type will be of height > 15 and height ≤ 200 . If a syndrome has to be defined, check the | Generate Plant Types| button and proceed by classifying the next trait. If a new trait is chosen (for syndromes), text field will be cleared.

3.2 Automatic categorisation: Select the trait to be categorised in the plant trait pull down menu. Type the three parameter of the automatic classification in the text field below. The first number is the maximum number of trait classes to be formed, the second number is the minimum trait class width, and the last number is the minimum difference between the classifications. Check the auto type button after the first parameter categorisation is filled in the text field.

For instance if the parameter | 3 4 3 | are set, than all categorisations with either 1, 2 or 3 trait classes are formed. Each class has a minimum width of 4. All formed classifications are compared with each other and categorisations, which in which all trait classes are too similar (difference between associated limits below 3) are discarded. All remaining categorisations will be displayed. The automatic classification of several traits can be combined if the |Generate Plant types| radio button is checked.

4. Chose environmental factor or factor combination

The factors to be included in the analysis can be chosen in the pull down menu. After choosing a factor, the number of sites, number of different treatments and the number of replicates of each treatment is displayed. Combination of factors can be selected by checking the <Hold Subset> button.

5. Set number of simulations The number of simulated null communities is set to 1000 by default. The value can be changed by typing a number next to the <Run Nullmodel> button. The smallest possible p-value is one divided by the number of simulations.

6. Set correction procedure The p-values may either be corrected using the Holm procedure or the Bonferroni method. By checking one of the checkboxes above the list field. For both methods refer to *Numerical Ecology* by Legendre et al. 1998.

7. Set Display type

You can either chose to display all categorisations (required if only a single categorisation is tested), or you may check the display all / best button, to list the best categorisation only. If |View| |Display PFT-species name| is ticked, than the species names for each PFT are displayed.

8. Push the <Run> button

The analysis may take a while (seconds to days) depending on the number of simulations and the number of different categorisations to be tested. If several categorisations are tested, than each time a categorisation has been finished, its number is displayed either in the MS-DOS window or the Matlab command window.

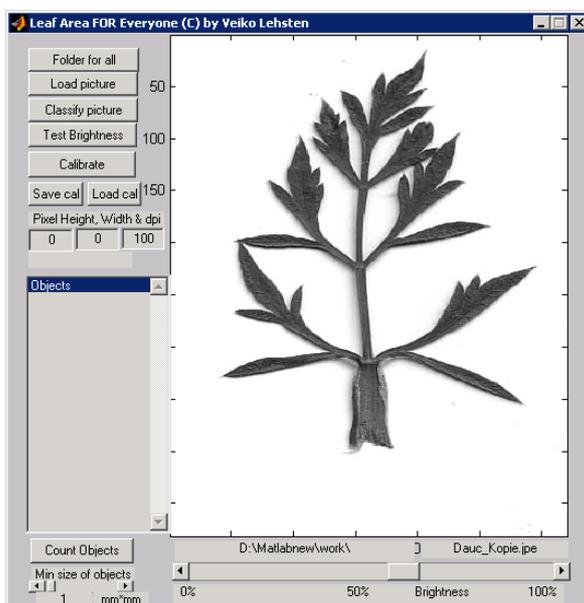
9. Interpret the result

After finishing the calculation, the program will display the trait state intervals (Group Intervals) of the grouping, the observed frequencies for each group at sites of each factor combination, the selected factor, the number of sites, the number of treatments, the umber of replicates per treatment, and a factor (factor combination) \times PT matrix of the response of the PT to each factor (combination of factors), e.g. the p-values. If syndromes are formed, the PFTs occurring in the data set are listed and the factor \times PT matrix is reduced to the PTs which have at least a single occurrence in the data set.

A.5.2 Lafore: LeafAreaFOREveryone

The analysis incorporated the measurement of leaf area. Although, there are commercial leaf scanner, the available device where ineffective in its usage. The scanning was very time consumptive and the accuracy of the resulting leaf areas could not be estimated. Common scanning devices are relatively cheap (compared to leaf scanning devices) and since Cornelissen et al. (2003) suggest to hydrate the leaves before scanning, the analysis can be done easily in a laboratory allowing the use of a common scanner.

I programmed a tool which calculates the leaf area using a scanned image of the leaf.



Leaf image loaded in the tool

Manual:

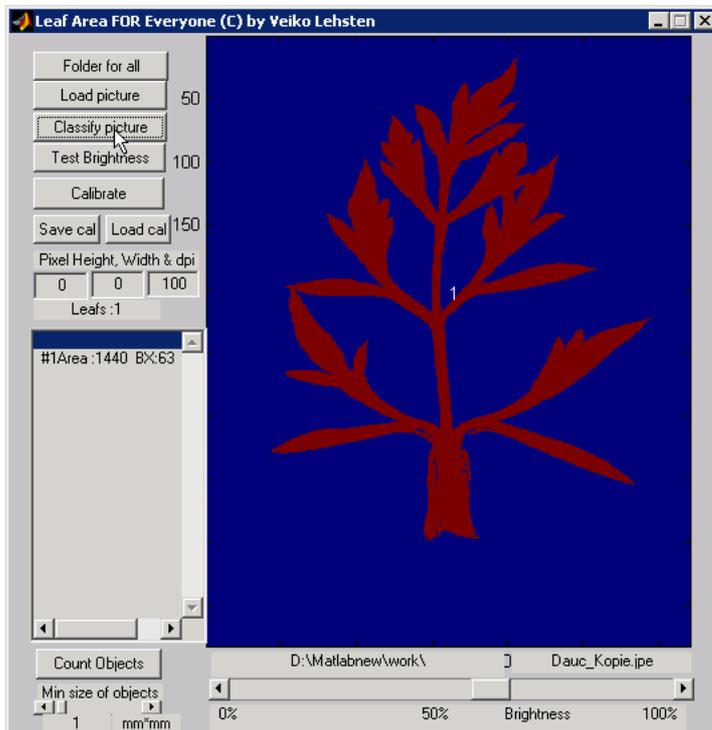
General approach:

Lafore counts the pixel that are darker than a reference value that can be set using the lower right scrollbar. The number of pixels is multiplied with the size of one pixel resulting in the leaf area. Pixel height and width (or scan resolution) have to be known in advance.

General steps:

1. Scan Leaves/Seeds with any scanning tool
2. Load images in Lafore and calibrate Lafore or type scanning resolution
3. Test brightness (if necessary)

4. Classify image (single picture/whole folder)



Leaf image classified by Lafore, the leaf area is displayed in the left field, the recognised leaf area is marked in red, the leaves are consecutively numbered and the number is displayed.

5. Type/Load the data into your data sheet (e.g. Excel)

1.

Before using Lafore, the leaves or seeds have to be already scanned, Lafore is no scanning tool. The image types <.tif>, <.bmp> and <.jpg> are recognised, The standard file type is <.tif>.

Make sure you follow the requirements of appropriate processing of the leaves (e.g. watering) or seeds (e.g. cleaning). Make sure that the scanning resolution is high enough for the classification of small leaves. The leaves/seeds have to be easy recognisable on the image.

Scan resolution

Lafore is no scanning tool. The scanning itself has to be performed prior classification

The scan resolution should be set to a value, that allows to recognise all important features of the leaf, if viewed with an ordinary graphics program. The program counts pixels, hence less pixel result in a less accuracy. However, big files

may cause problems on some computers and take longer to scan. If the pixel size is 0.254 (100 dpi) a leaf of 5 mm* 1mm has $5 \text{ mm}^2 / 0.254 \text{ mm}^2 = 77.5$ pixel. Whether this is enough depends on the required accuracy.

Below is a list of the scan resolutions that I use:

Leaf size	dpi
>1cm ²	100
0.5 cm ²	300
<5 mm ²	600

If small leaves are scanned, do not scan the whole area, but select a smaller size to limit the file size.

2.

Before using Lafore, the pixel size or the scanner resolution has to be set. You can either simply type in the pixel height and width of the scanned picture, if known, or if you don't know the exact scanning resolution let Lafore calculate the pixel size in the following way:

Scan any object from which you know the exact width and height (e.g. a coin). Press <Calibrate> (the fields pixel height and width have to be set to 0 before). Choose the image containing the scanned object in the following dialog box. Type in the object height and width in the appropriate fields.

Press <Do calibration> again. The picture should now change its color and the actual pixel size and height is displayed. The program is now calibrated.

Repeat this any time the resolution of the pictures changes.

The values for the actual pixel size can be saved by pressing <Save cal> and specifying a file name. If you are using the same scanner on the same resolution again you can load the value by pressing <Load cal>.

3.

To classify an image you have to load it first by pressing <Load picture> and then press <Classify picture>. The colours of the picture change according to the recognised leaves.

If you can't distinguish the leaves clearly you can change the brightness with the scrollbar on the right bottom and classify them again.

If there is dust on the image, set the minimum size of objects to be recognised with the scrollbar on the left bottom.

The classification is done by comparing the brightness of the leaf with the background. If you have very bright leaves, you might use a dark sheet as back-

ground and invert the image in any photo processing program before classification.

NOTE: The minimum size of objects is set to 1 mm*mm by default, you may have to lower this for small leaves or seeds.

The values for the leaves are displayed: (counted from up-left to down-right)

Area: area of the leaf

BX: width of the rectangular box that could be drawn about the leaf

BY: height of the rectangular box that could be drawn about the leaf

If you want to use BX and BY as leaf length and width, make sure the leaves are placed properly.

You can classify all pictures in a folder by pressing <Folder for all>, double click on one of the images in the folder and choose a place and name for the output file containing the data. Be careful with these option and control the values afterwards. I found out, that sometimes the lid of the scanner was not closed properly or the brightness has to be readjusted for some leaves, due to other reasons.

The data from this new file can either be opened by any word-processing program (e.g. Notepad) or loaded directly into a data sheet. The values are separated by semicolons and the first two lines are the column header.

The first field contains the folder of the image, the second contains the name of the classified picture. The following fields are the Area, BX- and BY-values of all leaves in the image.

All values are in the same unit as the pixel height and width.

For seed counting you can disperse the seeds on the scanner (use a transparency below and above), load the image and press <Count Objects>.

Make sure you set the minimum size of objects to the appropriate value.

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Curriculum vitae

Name: Veiko Lehsten

Date of birth: 11.07.1974

Nationality: German

Educational history I

1981- 1988 Public school in Krakow am See

1988 -1993 Special school for mathematics, techniques and science, 'Albert Einstein Gymnasium Rostock'

Compulsory service

1993 -1994 Bird warden at the biological station 'Vogelinsel Langenwerder' of the University of Rostock

Educational history II

1994 -1997 Student of Landscape management and environmental protection at the University of Rostock

1997 -1998 Visiting student at the University of East Anglia Norwich, GB; at the School of Environmental Sciences Main subjects: Ecological Interactions, Conservation Biology, Aquatical Ecology and Evolution

1998 - 1999 Degree 'Diplomingenieur für Landeskultur und Umweltschutz' of the University of Rostock

1999 - 2004 Dissertation at the Institute of Biology and Environmental Science at the University of Oldenburg

Employment

2003 – 2004 Scientist for ecological modelling within the EU VISTA Project

Erklärung

gemäß § 10 Abs. 2 der Promotionsordnung der Fakultät für Mathematik
und
Naturwissenschaften der Carl-von-Ossietzky-Universität Oldenburg.

Hiermit erkläre ich ehrenwörtlich, die vorliegende Arbeit in allen Teilen selbständig und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben. Diese Dissertation hat weder in gleicher noch in ähnlicher Form in einem anderen Prüfungsverfahren vorgelegen. Des weiteren erkläre ich, dass ich früher weder akademische Grade erworben habe, noch zu erwerben versucht habe.

Oldenburg, den 28.10.2004

Veiko Lehsten