A parsimonious combination of functional traits predicting plant response to disturbance and soil fertility

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Abstract

Questions: 1. How many traits associated with persistence and regeneration are necessary to predict the response of plants to soil fertility and disturbance? 2. Are correlated changes in trait expressions linked to the response of functional groups to fertility and disturbance?

Location: Lower Frankonia, Germany.

Methods: On 120 plots located in managed and abandoned grasslands, fields, and vineyards, we recorded species composition, disturbance intensity, soil water and nutrients, and ten candidate traits for 75 species. We used a novel method which is based on three steps: (1) logistic regression to separate responsive from non-responsive species; (2) iterative clustering of all possible combinations of the candidate traits including regression of each cluster in response to the environmental variables; (3) selection of the trait combination that performed best with respect to goodness of fit of all clusters from this combination. Bivariate trait relationships across functional groups were analysed with reduced major axis regression (RMA).

Results: The parsimonious trait combination consisted of life span, specific leaf area (SLA), canopy height, and seed number. The 'acquisitive' functional groups in terms of SLA and height were linked to higher fertility and earlier disturbance, while the 'retentive' groups related to lower fertility and later disturbance. Investment in reproduction, however, displayed a reverse relation. SLA and canopy height showed correlated shifts in two pairs of co-occurring functional groups.

Conclusions: A small number of traits is sufficient to predict the response of species. Plants need a higher increment in SLA to reach the same height, if start of disturbance is earlier. Linkages between traits shift from generative to vegetative with increasing fertility and earlier start of disturbance. Functional groups enable shifts in scaling relationships between traits to be analysed, in contrast to the analysis of single traits.

Keywords: Canopy height; Habitat model; Plant functional group; Plant life span; SLA; Seed mass; Seed number.

Nomenclature: Rothmaler (1994).

Abbreviation: LRM = logistic regression model; PFG = Plant functional group; RMA = Major axis regression; SLA = Specif Leaf Area.

Introduction

Former agricultural landscapes in Northwest Europe were characterised by rather uniform disturbance frequencies, as almost all landscape elements were used by farming people (Hobohm 2000). In the past century, sites of minor productivity were abandoned, while land use intensity has increased on others (e.g. Peppler-Lisbach 2003). In the past two decades, however, many abandoned areas became managed again (e.g. by mowing, grazing, burning), this time for conservation, with disturbance frequencies ranging from once a year to every third or fifth year, depending on the progress of secondary succession and species vulnerability to extinction. This study analyses trait-environment relations in a landscape that has undergone such land use changes.

In traditional landscapes with rather uniform disturbance regimes, life history features relating to plant persistence should mainly respond to landscape-specific variations in fertility. Increasing variation in land management results in a larger disturbance gradient and may thus promote increasing variation in plant traits related to growth and regeneration. Among other traits, shifts in expression of life form, plant height, clonal spread, seed mass, seed bank longevity and flowering time were found to respond to abandonment of grassland (Kahmen & Poschlod 2004), grazing intensity and productivity (Lavorel et al. 1999; Bullock et al. 2001; McIntyre & Lavorel 2001; Pakeman 2004; De Bello et al. 2005; Peco et al. 2005), and to management of fields, field margins and hedgerows (Kleyer 1999). Other studies provided little or no support for trait responses to grassland use (e.g. Lindborg & Eriksson 2005). Here, we ask whether there is a minimal combination of plant traits related to persistence and regeneration that allows us to predict species response to disturbance and soil fertility.

Life histories develop in relation to trade-offs between traits. Genetically and physiologically determined trade-offs such as the well-known seed number – seed mass trade-off or SLA – leaf life span trade-off (e.g. Westoby et al. 2002) can be identified by finding negative correlations between

these traits across large sets of species. Similarly, positive scaling relations were found between leaf traits (Wright et al. 2004) or leaf, stem and root biomass (Enquist & Niklas 2002). Across environments, biomass allocation to regeneration and persistence traits is supposed to change, enforced by functional responses to environments (Cornelissen 1999; Suding et al. 2003). Plant functional groups (PFGs; Lavorel & Garnier 2002), when occupying different niches along environmental gradients, may reflect these changes by displaying correlated changes in trait expressions linked to regeneration and persistence. We ask whether such changes can be related to the response of functional groups to fertility and disturbance.

To date there is no standard procedure to identify functional groups (Nygard & Ejrnæs 2004). In many studies, each trait is treated separately and trait values are lumped across all species of a plot to e.g. a mean or a frequency (Díaz & Cabido 1997; Kahmen & Poschlod 2004; Vesk et al. 2004). Effectively, trait responses to the environment are predicted for an 'average species' of the community. Such approaches are valuable to identify and to rank single plant functional traits with respect to environmental factors. However, co-occurring species often exhibit different life histories representing alternative generative and vegetative pathways to survival in a certain environment (Kleyer 1999; Semenova & van der Maarel 2000). In this case, averaging trait values across all species in a community is questionable.

An alternative is to first cluster species according to trait attributes and then analyse the response of the resulting plant groups with similar trait attributes to environmental factors (e.g. Kleyer 1999; Deckers et al. 2004), which is advantageous, because species identity is kept during the statistical process. Correlations between traits across species of different clusters may represent trade-offs or benefits. However, if clustering is performed prior to environmental ordination, it remains unknown whether all traits used for clustering are responsive traits. If non-responsive traits contribute to the clustering result, relations between functional groups and environments can be of low predictive power (Nygard & Ejrnæs 2004).

Our approach is to search the species-traits-environment space for a parsimonious set of functional traits that generates the best predictions of functional groups on environmental gradients. Optimisation procedures can yield such results. Pillar & Sosinski (2003) developed a method based on the fourth-corner method of Legendre et al. (1997), suitable for treatment designs. For the present study we focus on direct gradient analysis and predictive statistical modelling. Habitat models based on generalised linear modelling formalise habitat-environment-relationships, quantify habitat quality and allow statistical interpretation and evaluation with respect to model significance, calibration and validation (Kleyer et al. 1999/2000). Several regression procedures are available (Quinn & Keough 2002), such as logistic regression models (LRM), Poisson regression, and generalised additive models. Among them, logistic regression stands out as the technique most often used in case of binary response variables (Schröder & Reineking 2004) and because of parsimony (Austin 2002).

In this study, we used a novel approach to functional group analysis based on predictive habitat modelling with LRMs. We defined plant functional response groups (PFGs) as plants with similar trait attributes and similar response to environmental variables (Lavorel & Garnier 2002). This required species to be identified as significantly responding to any of the environmental variables considered. We selected ten candidate traits for their known or assumed responses to disturbance and soil fertility (see examples in e.g. Chapin et al. 1993; Kleyer 1999; McIntyre & Lavorel 2001; Grime 2001; Lavorel and Garnier 2002; Kahmen & Poschlod 2004; Pakeman 2004). Based on the responsive species set, we then searched for the most parsimonious set of traits combining into PFGs that exhibit (1) the best responses to the environmental variables and (2) represent as many of the responsive species as possible. This method enabled us to derive trait response hierarchies, to assess the relevance of persistence versus regeneration traits in response to disturbance and soil resources, and to show how scaling relationships between two traits (e.g. Enquist & Niklas 2002) vary with shifts in the disturbance regime.

Methods

Study area and sampling design

The study area covered ca. 25 km² of dry grasslands, fields, fallow vineyards and shrubland at the western edge of the Hassberge mountains in Lower Frankonia, southern Germany (50°03' N, 10°35' E). The geological substrate consists of clay stone, sandstone clays and clay marl stone (Rutte 1981). Mean annual precipitation amounts to 650-700 mm, the mean annual temperature is 7.5-8.5 °C. Beside farmland and pastures, viticulture along the southward facing slopes was an important source of income in the past. Steep slopes are still sporadically grown with grapes. Most of the sloped land has been abandoned or is being used as grassland and meadow with fruit trees, often sustained by state subsidy to promote conservation.

We used random stratified sampling to set up 120 plots with a size of 2 m × 2 m (Guisan & Zimmermann 2000). The sampling design was based on a land use map and a topographical map of the study area. From these maps, 600 sites were randomly selected with the help of a Geographical Information System. We then broadly categorised each site with respect to topography (slope and aspect), land use, and abandonment (chronosequences of aerial photos).

Topography was the main indicator of fertility (with sunny slopes indicating rather dry sites), while land use and time of abandonment indicated disturbance intensity (with vineyards and fields indicating strong disturbance, while grasslands indicated comparatively weaker disturbances). This data set was used for stratification (Table 1). The number of selected sites per stratum was not completely balanced, because site availability was limited in some strata. Only one plot was randomly placed within each site to avoid pseudoreplication. The environmental conditions at each plot were characterised by more detailed field measurements.

Environmental variables, species occurrences, traits

Environmental variables. To determine measures of soil fertility, soil samples were taken from each soil layer within 60 cm depth at each plot. Layer thickness and stone content were determined on site, while the following parameters were investigated in the laboratory: texture (following Anon. 1996), soil density (Schlichting et al. 1995), pH, calcium carbonate ($CaCO_3$) (according to Scheibler in Schlichting et al. 1995), plant available potassium (K) and phosphorus (P) (ammonia-lactate solution according to Egner & Riehm in Schachtschnabel et al. 1984), total carbon (C) and total nitrogen (N) content (GCM Carlo-Erba C/N-Analyser). Soil physical parameters, namely plant available water (PAW), water permeability in saturated soil (kf), soil aeration (AC), and effective cation exchange capacity (CEC_{eff}) were calculated from texture and soil density according to Anon. (1996). Additionally, slope angle and aspect were recorded, the latter coded as a binary variable (W to SE aspect = sunny slopes, NW to E aspect = shady slopes).

We characterised land use related disturbances by five variables for each plot (Table 2): frequency of disturbance events per year, two broad categories for biomass removal by a single disturbance event, and start of disturbance. Using stereo aerial photos, disturbances occurring above or below the soil surface in the year 1997 were determined to characterise a change in management within the past five years. Some mown grassland sites were occasionally grazed by shifting flocks of sheep, but the impact on the vegetation was low and therefore was not considered in the analysis.

Response variables. For all vascular species presence/ absence data were collected. Species selected for trait measurements had to be prevalent in at least 10% of the sampling plots. This threshold was also considered appropriate to allow logistic regression modelling (e.g. Steyerberg et al. 2001). Specific leaf area (SLA), canopy height, and seed mass were recorded in the field according to Knevel et al. (2005). Trait measurements in the field were timed in such a way that site management did not affect the results. The total seed number per individual / ramet was calculated as follows: Six inflorescences were collected from six different individuals / ramets at different sites and the total number of inflorescences per individual / ramet was counted. Then, seeds per inflorescence were counted and multiplied by the number of inflorescences. Other relevant trait attributes were collected from literature sources (Table 3).

Individuals sampled for trait measurements in the field were selected from the total range of species occurrences within the environmental space. The final trait value assigned to a species was the average over all sampled individuals. This approach could not account for any trait plasticity between sites. Otherwise, if we had assigned different trait values to a species based on collections from different populations (see Garnier et al. 2006), we would have needed to inflate the number of plots considerably to receive an appropriate number of observations for each 'ecotype' of a species and its respective trait average. This was logistically impossible.

Table 1. Number of sites per stratum.

	Dry sites		Mesic sites	
	Grasslands	Vineyards	Grasslands	Fields
1-3 disturbances per yr	22	6	22	6
Abandoned < 5 yr	6	12	6	6
Abandoned > 5 yr	11	11	6	6

Tabel 2. Disturbance parameters and Rank category.

Disturbance	Rank	Explanation
Frequency	0.01	Longer than every 10 years
	0.13	Every 6 - 10 years
	0.27	Every 2 - 5 years
	0.33	Every 3rd. year (roto-tilling)
	0.5	Every 2nd. year (roto-tilling)
	1	1× (roto-tilling or mowing 1× per year)
	2	2× (mowing 2× per year or extensive grazing)
	3	3× (mowing + grazing)
	4	4× (intensive grazing)
	5	5× (arable fields or vineyards)
Biomass loss	50	ca. 50% of biomass destroyed (above-ground disturbance) (mowing, grazing, or both)
	100	ca. 100% of biomass destroyed (below-ground disturbance) (arable, vineyards, roto-tilling)
Below-ground disturbance 1997	0	No below-ground disturbance 5 years before year of study
	1	Below-ground disturbance 5 years before year of study (arable, vineyards, roto-tilling)
Above-ground disturbance 1997	0	No above-ground disturbance 5 years before year of study
	1	Above-ground disturbance 5 years before year of study (mowing, grazing, both)
Start of disturbance	1 - 53	First disturbance event in year expressed as week number; week 53 stands for fallow

Indices

Indices were calculated for categorical traits for which information was compiled from literature; i.e. seed longevity, plant life span, presence of stolons or rhizomes, woodiness, and clonal extension (Table 3). This became necessary, because trait information available in the literature was not consistent for many species. For instance, three out of ten authors may denote a species as biennial, the other seven as perennial. The indices use the number of literature records for each category as a measure of membership to the category. They also describe the probability of a trait to develop towards the highest rank. The probability is based on the position of the other trait attributes relative to the highest rank (e.g. annual = 0, biennial = 0.5, perennial = 1.0), weighted by the number of records in the literature assigned to the categories (Eq. 1). For instance, plant life span is redefined as the ability to become perennial. This places the categories in an ordinal order with 'perennial' as the highest rank. The seed longevity index is a well-known example for this approach (Thompson et al. 1998).

$$I = \frac{\sum_{i=1}^{n} x_i * (\frac{i-1}{n-1})}{\sum_{i=1}^{n} x_i} \qquad (1)$$

I = Index
i = trait category rank
n = total number of trait categories of the trait
x_i = number of literature records for trait category

If results were contradictory, the species was excluded. An example is the plant life span of *Medicago lupulina*, a species denoted as either annual or as perennial in different literature sources. According to the index following Eq. 1, this species is located in the vicinity of 'biennial', which is not consistent with the literature records.

Statistical analysis

The statistical analysis is explained in detail in App. 1. It had three objectives requiring three steps:

Separating responsive from non-responsive species prior to the determination of functional groups. This step was necessary, because traits of a species cannot respond to the environmental factors used in our study, if the species itself does not respond to these factors. We used logistic regression with presence / absence values of the species as the dependent variable and the environmental variables listed in Table 4 as predictors.

Building functional groups from combinations of candidate traits (Fig. 1). The statistical procedure performed individual cluster analyses of all possible combinations of the ten candidate traits (Table 3). For each cluster of species with similar trait expressions, a regression then estimated the probability of co-occurrence of all species in this cluster in response to the environmental variables. An optimum occurred where most species of the group were present. A cluster was called a functional group if the regression model was sufficiently calibrated. An alternative approach would be to model all occurrences of species of a group separately (see Nygard & Ejrnæs 2004). However, this would lead to multiple occurrences per site if two or more species belonging to one cluster

Table 3. Traits, their units or attributes and references (field measurements according to Knevel et al. 2005).

| Trait	Units, attributes	References
SLA	mm².mg⁻¹	Field measurements
Canopy height	mm	Field measurements
Seed mass	mg per seed	Field measurements
Start seed shedding	month	Poschlod et al. (2003)
Seed number	number	Field measurements
Clonal extension (rank towards extended tillers)	0.0 - not clonal	
	0.5 - < 10mm	
	1.0 - >10mm	www.leda-traitbase.org
Plant life span (rank towards longer life-cycle)	0.0 - annual	
	0.5 - biennial	
	1.0 - perennial	www.leda-traitbase.org
Rank in presence of below ground rhizomes	0.0 - no stolons or rhizomes	
	0.5 - above-ground stolons	
	1.0 - below-ground rhizomes	www.leda-traitbase.org
Woodiness (rank to be woody)	0.0 - not woody	
	0.5 - woody at base	
	1.0 - woody	www.leda-traitbase.org
Seed longevity in soils	< 0.3 - transient	
	0.3-0.55 - short-term persistent	
	> 0.55 - long-term persistent	www.leda-traitbase.org.
		Classification according to R. Bekker, pers. comm.

Where `mm².mg⁻¹` means $mm^2.mg^{-1}$.
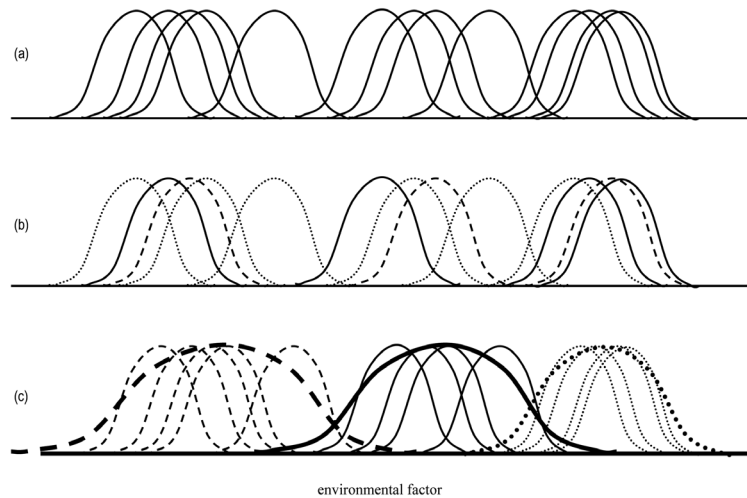
Fig. 1. Clustering and regression procedure for hypothetical species belonging to three clusters (dotted, dashed and continuous lines); (**a**) response curves of responsive species (results from step 1); iterative clustering and logistic regression (step 2) resulting in (**b**) models of low quality yielding no functional response group as species of a cluster do not co-occur, and (**c**) clusters yielding significant, well calibrated functional response group models as species of each cluster co-occur.

co-occurred and violated the assumption of statistical independence (Legendre et al. 1997).

Identifying a parsimonious trait combination that yields a maximum number of functional groups. As the final parsimonious functional trait combination we selected the combination consisting of the smallest number of traits, with the largest number of clusters with sufficiently calibrated models that altogether comprised the highest number of species. Eventually, these reflected the minimum number of traits necessary to predict a maximum number of species.

To show that variation in trait space is independent of phylogeny, we first extracted the phylogenetic relations between the responsive species from the database BIOLFLOR (Klotz et al. 2002), transformed them into a patristric distance matrix (Lososová et al. 2008) and compared the phylogenetic distance matrix with a distance matrix derived from the final responsive species × responsive traits matrix by a Mantel test.

Reduced Major Axis regression (RMA, also known as model II regression) was used to describe bivariate relationships between traits. Trait variables are biologically interdependent and have similar variation associated to them due to measurement error. In this case, ordinary least squares regression is considered inappropriate (Niklas 1994), because it keeps the x-values fixed, and finds the line which minimizes the squared errors in the y-values, whereas RMA tries to minimize both the x- and the y-errors. RMA regression was done with the software PAST (version 1.56b, Hammer et al. 2001)

Results

Resource supply

The sites formed a large resource gradient ranging over several orders of magnitude (Table 4). The nutrient-poorest soils contained no measurable available P, while the richest sites showed values of > 4400 kg.ha^{-1} (e.g. fallow arable fields, cultivated vineyards). N ranged from ca. 210 to 23 000 kg.ha^{-1}. Spearman correlation was 0.62 between P and K, and 0.57 between C and N.

Table 4. Resource and disturbance gradients (SD = standard deviation; P = plant-available phosphorus; CO_3 = calcium carbonate; C = carbon; C/N = Carbon-nitrogen-ratio; kf = Water permeability in saturated soil; AC = soil aeration; K = plant-available potassium; N = nitrogen; PAW = Available soil water; CEC_eff = Effective cation exchange capacity; Biomass loss = biomass loss by disturbance; Dist_ag5 = disturbance above soil surface 1997; Dist_bg5 = disturbance below soil surface 1997; Frequency = disturbance frequency; Start of disturbance = week of first disturbance impact)

Factor	Min.	Max.	Mean	SD
P [kg.ha^{-1}]	0	4424	503	613
CO_3 [kg.ha^{-1}]	0	$2.8*10^6$	$5.7*10^5$	$6.4*10^5$
C [kg.ha^{-1}]	0	$2*10^5$	$6,3*10^5$	$4.4*10^4$
C/N 0	52	8	6	
Kf [cm.d^{-1}]	1	41	10	9
Aeration [Vol%]	2	82	22	13
K [kg.ha^{-1}]	352	$13.7*10^3$	2360	1876
N [kg.ha^{-1}]	210	$2.3*10^4$	8150	4322
pH 4.4	7.5	6.8	0.7	
PAW [mm]	11	165	75	30
CEC_eff [cmol_c*kg^{-1}]	5	39	30	10
Slope [°]	0°	30°	12	8
Aspect	0 (shade)	1 (sun)	-	-
Dist_ag5	0 (no)	1 (yes)	-	-
Dist_bg5	0 (no)	1 (yes)	-	-
Frequency	0.01	5	-	-
Biomass loss [%]	50	100	-	
Start of disturbance	19	53	40	-

Because of these associations P and C were excluded from the analysis. Furthermore, CO_3 (correlation with pH = 0.67), C/N (correlation with pH = – 0.53), water permeability (correlation with cation exchange capacity = – 0.85) and soil aeration (correlation with soil water = 0.78) were excluded. The correlation between pH and soil water was – 0.34 indicating that base-poor sites supply more soil water than base-rich sites.

Disturbance intensity

Arable fields and vineyards represented the land use with the highest disturbance intensity, frequency and biomass loss, whereas fallow arable fields and fallow grasslands were the least disturbed plots with disturbance return intervals of 2-5 years, 6-10 years, and more than 10 years. Grazed and mown plots ranged from a disturbance frequency of four times per year by intensive grazing to mowing once per year. There were negative associations between start of disturbance and frequency (– 0.53) as well as above-ground disturbance history (– 0.72).

Responsive species

In step 1 of the statistical analysis 75 species were used. Following stepwise logistic regression, 51 responsive species with models of sufficient calibration remained. Three species could not be modelled at all, because no environmental variable was significant so that a valid model could be developed. Models of 21 species were not sufficiently calibrated. Six of them had low prevalences in the data set, i.e. *Crataegus monogyna*, *Dianthus carthusianorum*, *Hypericum perforatum*, *Ononis repens*, *Tragopogon pratensis* and *Vicia tetrasperma*. The remaining 15 species showed scattered response along the enviromental gradients.

Functional response groups

Out of the 51 responsive species, 48 were clustered, while three species had to be omitted due to missing seed number values. The most parsimonious trait combination covering a maximum of responsive species consisted of SLA, canopy height, plant life span and seed number. With this trait combination, six PFGs comprising 40 species met the goodness of fit thresholds (Table 5), all other trait combinations yielding less PFGs. Variation of plant life span, SLA, canopy height and seed number

Table 5. Plant functional response groups. Clusters marked * did not meet the goodness of fit criteria. (PFG = plant functional response group; AUC = area under ROC (Receiver Operating Characteristic) Curve; R^2_N = R^2-value according to Nagelkerke (1991). Numbers in brackets give prevalences.

PFG (cluster)	AUC	R^2_N	Species (prevalence)	No. of species
1	0.910	0.4843	*Rosa canina* agg. (22)	1
2*	0.765	0.2821	*Cornus sanguinea* (10), *Prunus spinosa* (38)	2
3	0.863	0.3745	*Cirsium arvense* (18), *Galium verum* (22)	2
4*	0.789	0.1794	*Bromus hordeaceus* (9), *Bromus sterilis* (11), *Cerastium brachypetalum* (30), *Galium aparine* (15), *Rhinanthus minor* (18), *Thlaspi perfoliatum* (24)	6
5	0.893	0.4681	*Anthoxanthum odoratum* (22), *Holcus lanatus* (21), *Poa trivialis* (14)	3
6	0.810	0.3057	*Convolvulus arvensis* (41), *Leontodon hispidus* (16), *Lolium perenne* (9), *Luzula campestris* (26), *Rumex acetosa* (31), *Saxifraga granulata* (13), *Taraxacum officinale* agg. (50), *Veronica chamaedrys* (27)	8
7	0.811	0.3391	*Achillea millefolium* (66), *Alopecurus pratensis* (26), *Avenula pubescens* (23), *Brachypodium pinnatum* (17), *Centaurea jacea* (29), *Dactylis glomerata* (66), *Euphorbia cyparissias* (23), *Lathyrus pratensis* (17), *Lotus corniculatus* (39), *Origanum vulgare* (10), *Trisetum flavescens* (44)	11
8	0.773	0.3124	*Bromus erectus* (26), *Centaurea scabiosa* (10), *Festuca ovina* agg. (49), *Knautia arvensis* (23), *Plantago lanceolata* (48), *Plantago media* (33), *Poa pratensis* agg. (82), *Potentilla neumanniana* (17), *Primula veris* (22), *Ranunculus acris* (18), *Ranunculus bulbosus* (28), *Salvia pratensis* (34), *Sanguisorba minor* (52), *Trifolium pratense* (38), *Trifolium repens* (19)	15
unclustered species			*Fragaria viridis* (46), *Inula conyza* (10), *Viola hirta* (28)	3

among the responsive species was unrelated to the phylogeny of these species (Mantel statistic $r = 0.03$, not significant; $p = 0.3$).

Besides plant life span, SLA was a distinctive feature for most PFGs. Canopy height and seed number showed higher coefficients of variation indicating that the species in the clusters are less similar with respect to these traits. None of the four traits displayed a relevant and significant correlation (i.e. $r_{Spearman} > 0.4$) with any other candidate trait except for life span with clonal extension ($+ 0.53$) and below-ground rhizomes ($+ 0.69$), canopy height with start seed shedding ($+ 0.49$) and woodiness ($+ 0.46$), and seed mass with seed number ($- 0.57$).

Soil water or pH were the only factors explaining the occurrence of the woody species of Clusters 1 and 2. Cluster 2 missed our R^2_N-goodness of fit threshold to become a PFG by only 0.018. Woody species showed very low SLA values, high seed number (with high coefficient of variation), and tall canopy height. The herbaceous species of cluster 3 were characterised by their tall growth and high seed number (Table 3). Cluster 4 with annual species was not considered for a PFG due to a badly calibrated habitat model.

PFG 8 comprised perennials with low SLA, low canopy height and intermediate seed number that occurred on sites with low K (and P, being correlated with K) and continuous biomass loss by mowing (Table 6, Fig. 2). PFG 8 co-occurred with PFG 7 on sites with low fertility, but extended to sites with more available soil water. PFG 7 had higher mean SLA and height than PFG 8. Compared to PFGs 7 and 8, species of PFG 6 had lower canopy height and seed number but higher SLA. They were found in early mown meadows with ample water supply. PFG 5 represented a perennial syndrome of intermediate growth, very high SLA and low seed number, responding to low pH and early mowing. As pH was negatively correlated with soil water, the niches of PFG 2 and 5 were similar (Fig. 2). For the co-occurring PFGs 8 and 7 as well as 6 and 5, scaling relationships existed between canopy height and SLA (Fig. 3). Co-occurring species of these PFGs needed to increase SLA to become larger. PFGs 8 and 7 on sites with low fertility and PFGs 6 and 5 on sites with higher water supply mainly differed in SLA, but not in canopy height. The scaling factor for the species of PFG 6 and 5 was lower, which indicates that a higher increment in SLA was needed to reach the same height under conditions of early mowing as compared to late mowing. Across all species belonging to PFGs 8, 7, 6, 5, reproductive investment as the product of seed mass and number scaled negatively with SLA (RMA slope $= - 0.2$; correlation $r = - 0.4$, P value $= 0.02$).

For most clusters, the probability of all species to co-occur exceeded 0.4, except for species-rich PFG 8 (Fig. 2). Thus, higher species numbers per cluster can be expected to lead to a lower probability of species co-occurrence, probably due to cumulative effects of dispersal limitation.
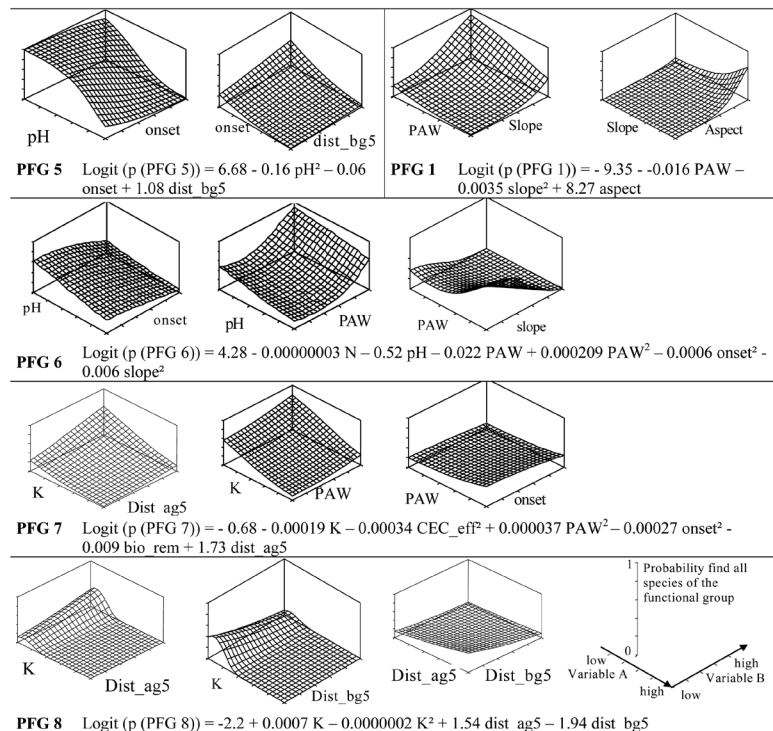

Fig. 2. Response surfaces and regression functions of functional groups. Abbreviations of environmental factors and their minimum and maximum values are given in Table 3.

PFG 5 Logit (p (PFG 5)) = 6.68 - 0.16 pH² – 0.06 onset + 1.08 dist_bg5

PFG 1 Logit (p (PFG 1)) = - 9.35 - -0.016 PAW – 0.0035 slope² + 8.27 aspect

PFG 6 Logit (p (PFG 6)) = 4.28 - 0.00000003 N – 0.52 pH – 0.022 PAW + 0.000209 PAW² – 0.0006 onset² - 0.006 slope²

PFG 7 Logit (p (PFG 7)) = - 0.68 - 0.00019 K – 0.00034 CEC_eff² + 0.000037 PAW² – 0.00027 onset² - 0.009 bio_rem + 1.73 dist_ag5

PFG 8 Logit (p (PFG 8)) = -2.2 + 0.0007 K – 0.0000002 K² + 1.54 dist_ag5 – 1.94 dist_bg5

Discussion

Responsive species

Habitat models based on stepwise logistic regression allow a rigorous identification of environmental predictors that determine the niche of species and PFGs. For this purpose, long gradients of environmental predictors are desirable, as they enable the realised niches of many species to be captured (Austin 1990). In the study area, phosphorus and nitrogen differed by 100- and 1000-fold, respectively. However, the gradient of available P is less than half of what has been found in an urban landscape (Kleyer 2002), indicating that very fertile conditions are absent. Great differences were also found in disturbance parameters, especially in frequency and start.

The 51 responsive species responded to very different environmental predictors. There was no single factor that stood out to determine the occurrence of all species. Another 21 species did not respond to any predictor with sufficient goodness of fit, obviously because most gradients were not long enough to include limits of the realised niche, although they spanned orders of magnitude. At the scale of a single landscape, ranges of environmental predictors are inevitably restricted and do not encompass the full distribution of abundant and unspecialised species. Such predictors do not contribute
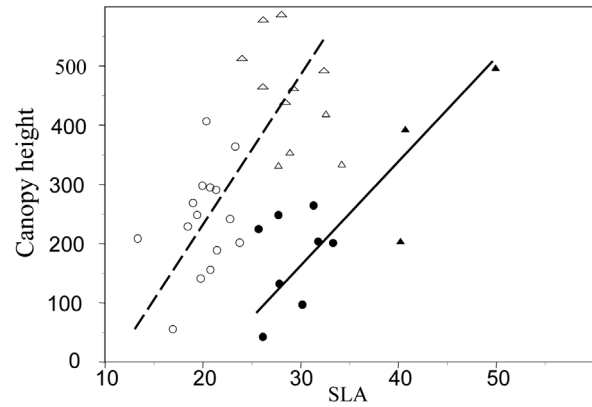

Fig. 3. Reduced major axis relationships between SLA and canopy height. Empty circles = PFT 8, empty triangles = PFT 7, filled circles = PFT6, filled triangles = PFT 5. Dashed line indicates RMA slopes for PFT 8 and 7: Canopy height = – 295 + 26*SLA (r^2 = 0.41); PFTs 6 and 5: Canopy height = – 315 + 16.7*SLA (r^2 = 0.63).

to the regression model. On the other hand, gradients can be too long for rare and specialised species. Niche breadth can then only be determined on smaller scales with higher sampling resolution and smaller environmental variation (Thuiller et al. 2004).

Table 6. Coefficients of variation (CV) and mean or category of the traits for each PFG. Bold indicates the minimal trait set. Grey marked PFGs did not meet the quality requirements. Note that PFG 1 consists of only one species. Min, Max: smallest, highest trait value in the species trait matrix. Seed number × mass is the product of seed number and seed mass. It was not used in the clustering process. Note that seed number is counted per shoot. Therefore, shrubs or trees have higher seed numbers than herbaceous plants.

PFG		1	2	3	4	5	6	7	8	Min	Max
No. species	N	1	2	2	6	3	8	11	15		
Life span	State	per	per	per	ann	per	per	per	per	ann	per
	CV	-	0.00	0.00	2.45	0.00	0.00	0.00	0.00		
SLA	Mean	13.0	18.2	20.6	28.5	40.3	28.60	28.1	19.9	11.7	49.5
[mm.mg⁻¹]	CV	-	0.04	0.35	0.18	0.13	0.10	0.11	0.13		
Canopy height	Mean	928	1294	619	262	393	207	463	241	10	1366
[mm]	CV	-	0.08	0.28	0.57	0.40	0.49	0.20	0.37		
Seed number	Median	3623	923	1290	163	169	119	316	271	16	4432
	CV	-	1.27	0.36	1.49	0.24	1.05	0.70	0.54		
Seed mass [mg]	mean	22.63	1.20	0.66	3.85	0.31	2.28	2.15	2.00	0.02	427.13
	CV	-	231.15	0.42	1.00	0.53	2.09	1.69	0.91		
Seed number × mass [mg]	mean	81985	51264	782	553	50	162	387	446	13.57	61524
	CV	-	0.28	0.06	1.11	0.55	1.03	1.09	0.96		
Woodiness index	mean	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	CV	-	0.00	0.00	0.00	0.00	0	0.00	0.00		
Index towards	mean	1	1.00	1.00	0.00	0.67	0.79	0.87	0.62	0.00	1.00
below-ground rhizomes	CV	-	0.00	0.00	0.00	0.22	0.26	0.19	0.27		
Clonal extension	mean	1	1.00	1.00	0.00	0.83	0.95	0.91	0.85	0.00	1.00
	CV	-	0.00	0.00	0.00	0.35	0.10	0.22	0.24		
Start seed shedding	median	9	9	8	6	6	7	7	6	5	10
(month)	CV	-	0.00	0.09	0.19	0.09	0.18	0.18	0.13		
Seed longevity index	mean	0.00	0.35	0.34	0.36	0.6	0.45	0.33	0.37	0.00	0.83
	CV	-	0.61	0.79	0.86	0.37	0.15	0.74	0.49		

Trait response hierarchies

We searched for a parsimonious trait combination yielding a maximum number of PFGs with sufficiently calibrated regression models. This combination consisted of only four out of the ten candidate traits: plant life span, seed number, SLA and canopy height. Using seed mass, starting month of seed shedding, clonal extension, stolons / rhizomes, woodiness, and seed bank longevity in the clustering process, either alone or in all possible combinations, led to models with less predictive value. This indicates a functional response hierarchy, i.e. the four traits are superior to the other traits in determining trait-environment relations. However, correlation of seed number with seed mass, plant life span with clonal extension and canopy height with woodiness indicate that the four traits respond as proxies for plant persistence and regeneration functions that are built on broader suites of traits.

Within responding trait combinations, the coefficient of variation (CV) is an indicator of consistency, i.e. low trait variation across all species of a PFG can be interpreted as high environmental pressure towards a uniform trait response. Apart from plant life span, SLA was the trait showing the lowest CV across all PFGs, followed by canopy height and seed number.

Westoby (1998) suggested a plant strategy scheme based on seed mass, SLA and canopy height. He deductively defined these traits as being sufficient to represent plant strategies across scales and regions. Our four traits resulted inductively from an optimisation procedure and, as a matter of fact, are quite similar to those proposed by Westoby. Seed number was more responsive than seed mass, but both traits were negatively correlated. However, another study using the same methods in a landscape characterised by light grazing and large differences in water availability yielded a parsimonious set of five traits of which the most important was the capacity to develop aerenchyma (Kühner & Kleyer 2004). This suggests that (1) a limited set of functional traits suffices to predict plant responses in a given landscape, but (2) there is no generally applicable trait set across all scales and regions.

Functional groups in response to fertility and disturbance

The R^2_N-values of the PFG models did not exceed 0.5, indicating sufficiently, but not excellently calibrated models. This is because our approach estimated the probability of co-occurrence of all species of a cluster in response to the environmental variables. The higher the number of species per cluster, the lower is the probability that all species of this cluster really co-occur

in a 2 m × 2 m plot, due to accumulating stochasticity in the small-scale distribution patterns of the species. Hence, the R^2_N-values were generally lower than in single-species models. However, if clusters exhibited R^2_N-values lower than 0.3, we considered them to be insufficiently calibrated, such as Cluster 4. Half of the species of Cluster 4 occurred at relatively low nutrient levels and intermediate disturbance frequencies: *Cerastium brachypetalum*, *Thlaspi perfoliatum*, *Rhinanthus minor*. On the otherhand *Bromus sterilis*, *B. hordeaceus* and *Galium aparine* occurred at more fertile conditions. Both groups differed also in their traits, the former with mean SLA = 23 mm².mg^{-1}, mean canopy height = 130 mm and mean seed number × weight = 195 mg and the latter with mean SLA = 32 mm².mg^{-1}, mean canopy height = 334 mm and mean seed number × weight = 912 mg. Each of the sub-groups could probably be a PFG on its own which was not detected by the statistical analysis.

In Cluster 3, *Galium verum* and *Cirsium arvense* were combined, because they are similar with respect to plant life span, SLA, height, and seed number. The two species co-occurred on field margins and abandoned vineyards, however, we consider this PFG not plausible, as the two species strongly differ in some traits not used in our study, namely deep root buds versus buds on shallow rhizomes as well as high versus low dispersability.

Recent land use change suggests that disturbance exhibits large and increasing variation in the study area as well as in other traditional agricultural landscapes (Kleyer 1999). Disturbance frequency was chosen to represent this variation, but did not come out as a relevant predictor. For instance, we expected the woody species of Cluster 1 and 2 to respond to disturbance frequency, i.e. to occur only on fallow sites. However, the only explaining factors were pH and soil water. This is probably explained by the fact that shrub encroachment is not a very deterministic process in the region, i.e., many long-term abandoned sites are still inhabited by herbaceous communities while others are densely covered by shrubs. Changes in disturbance frequency can affect vegetation and its trait composition with a considerable time lag, depending on the dynamics of secondary succession. Logistic regression models of presence / absence data may not be suitable to capture these dynamics, because (1) they assume static conditions (Guisan & Zimmermann 2000), and (2) presence / absence requires stronger changes in species composition than changes in abundance. However, the clusters themselves can be interpreted as belonging to different successional stages, with clusters 1, 2, and 3 representing late successional stages. Decreasing SLA values of PFGs from earlier to later successional stages are in line with results found elsewhere (Garnier et al. 2004; Lindborg & Eriksson 2005).

Many formerly abandoned sites are now managed for

conservation, while more fertile grasslands are mown or grazed for agricultural purposes. Management was reflected by other disturbance predictors, namely onset and continuity of disturbance. As both SLA and canopy height contribute to a plant's expansion and its capacity to acquire carbon, combinations of both traits should respond to management (Westoby et al. 2002; Diaz et al. 2004). Our results show that the two more 'acquisitive' groups 6 and 5 increase with higher fertility and earlier disturbance, whereas the more 'retentive / conservative' groups 8 and 7 occur at sites with lower fertility and later disturbance. Fig. 3 shows that the variation in trait combinations underlying this classification is only due to SLA, not to canopy height. Several studies found 'conservative' species with low SLA to occur on sites with low fertility or rainfalls and 'acquisitive' with high SLA on sites with high fertility or rainfall (Poorter & de Jong 1999; Fonseca 2000). However, conservative and acquisitive species can also co-occur at the same site, displaying similar niches with respect to fertility and disturbance. When start of disturbance is the same for all species of a community, larger plants in that community need to grow faster. Canopy height then depends on potential relative growth rate (potRGR), including costs of supportive structures. Relative growth rate can be expressed as net assimilation rate × leaf mass fraction × SLA, with SLA showing the largest effect on potRGR (Lambers & Poorter 1992; Wright & Westoby 1999). Thus, the scaling relationship between SLA and canopy height may simply represent the effect of SLA on potRGR. Consequently, when meadows are mown earlier, SLA and thus growth rate should increase faster to reach the same height as in meadows which are mown later. This is shown by the lower RMA slope (Fig. 3).

A correlated upward shift in SLA and canopy height in two co-occurring PFGs should result in competition for light, as recently demonstrated by Gaucherand et al. (2006). We suppose that co-occurrence despite competition can be attributed to the early start of disturbance in preventing dominance of PFG 5 over 2 (e.g. Schaffers 2002) and to inter-annual resource variation at dry sites alternately favouring PFG 1 and 3. Such variation was notably strong in clay soils at south-facing slopes in the study area (Vetterlein pers. comm.).

Investment in reproduction expressed as product of seed number and mass showed a reverse relation to SLA. Correspondingly, higher investment (groups 8, 7) was related to less fertile conditions, while lower investment was related to higher fertility and earlier disturbance (groups 6, 5). This indicates environment-induced changes in trait expression, shifting from generative to vegetative as fertility increases and growth period until first mowing decreases. On the other hand, high investments in reproductive traits of PFGs occurring at infertile

sites reflect increasing effort in tracking spatiotemporal variation of suitable habitat conditions. Our results support the view that investment in reproduction trades off with investment in growth (Harper 1977). Case studies reviewed by Obeso (2002) showed a correlation between reproductive effort and both vertical ('vegetative') and lateral ('clonal') growth that was significantly more negative than positive. Our results do not support the contrasting view that regenerative traits are decoupled from vegetative traits (Grime et al. 1988; Lavorel & Garnier 2002). However, the correlation between reproductive investment and SLA is quite low, indicating that the conclusions are not as straightforward as desirable.

Conclusions

We present a novel method for the functional analysis of plant-environment relations which meets several requirements. First, we can predict the realised niche of each species and functional group. Each group responded to different combinations of environmental factors suggesting that resource limitations of trait combinations are different. On the other hand, realised niches of different PFGs did also overlap which indicates that several strategies are viable at a single site. Secondly, responding functional trait combinations were separated from non-responding trait combinations. Together with the CV of trait values per functional group, this indicates a landscape-specific trait response hierarchy. Thirdly, functional groups offer the opportunity to analyse shifts in scaling relationships between traits along environmental gradients, in contrast to single trait analysis. This offers new perspectives in linking plant allocation theory with the dynamics of resources on the landscape scale.

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App. 1. Statistical analysis (see Fig. A1).

Step 1: Response of single species

To separate responsive from non-responsive species we applied a stepwise logistic regression for each single species. Species included into the procedure needed to be prevalent in at least 10% of the sampling plots.

After having checked for multicollinearity (and ensuing exclusion of variables in case of a correlation coefficient ≥ 0.5), the environmental factors listed in Table 3 were included as explanatory variables in the logistic regression analysis (including their squares). The regression models were evaluated using AUC- and R^2_N-values as goodness of fit measures (Nagelkerke 1991; Hosmer & Lemeshow, 2000). We used an AUC–threshold of 0.7 and a R^2_N-threshold of 0.3 which a model had to meet to be processed further. At the end of step 1 we received regression models and cross-validated predicted occurrences for single responsive species. All species with insufficiently calibrated models (i.e. below the above-mentioned thresholds) were declared non-responsive and omitted from further analysis.

Step 2: Response of plant functional groups

The responsive species were merged with the trait matrix and clustered into groups with similar trait values. We used Euclidean distance and Ward's clustering method as the latter is known to produce clusters of about the same size (SAS-Institute, Anon. 1989). From a series of screening tests, an eight cluster solution proved to be the best compromise concerning evenly distributed cluster size, although single species clusters may still occur. Trait values were standardised to mean 0 and standard deviation 1 before clustering. The procedure was iterated for each possible combination of candidate traits. We started by clustering the responsive species on the basis of only one trait, then doing all combinations of two traits, followed by three traits etc., each time receiving eight different clusters of species.
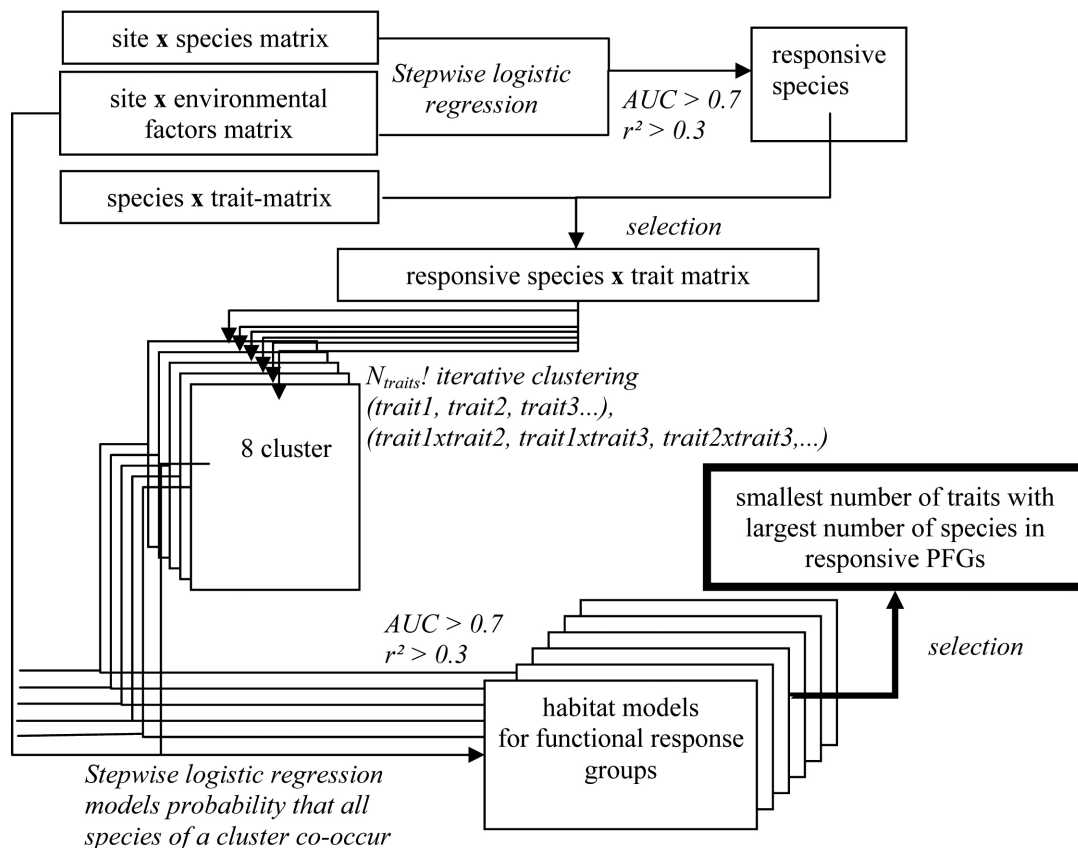
Fig. A1. Overview of the statistical procedure.

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After each clustering procedure, a new matrix was generated from the basic species x plots matrix. In this clusters x plots matrix, the number of species belonging to a cluster was counted at each plot and related to the total number of species belonging to this cluster. For instance, if two species from a total of eight species in a given cluster were found in a plot, the cell of the matrix would contain 2/8. Each cluster was then used as dependent variable in a stepwise logistic ordinal regression (events–trial option; SAS-Institute, 1989), with the number of species found in the plots divided by the total number of species of this cluster as observations and the environmental variables as predictors. The regression estimated the probability of co-occurrence of all species in this group in response to the environmental variables for a given cluster of species with similar biological traits. An optimum occurred where most species of the cluster were present. If the model was sufficiently calibrated (AUC > 0.7, $R^2_N > 0.3$) the cluster met the definition of a plant functional response group, i.e. a group of plants with similar trait values and similar response to environmental gradients. We did not use Bonferroni corrections of p-values, because (1) each clusters x plots matrix as input table for the regression consisted of new values, and (2) only the AUC- and R^2_N-values, not the p-values, were used to select the final trait combination.

Step 3: Selection of a parsimonious combination of functional traits

Many trait combinations yielded at least some clusters with sufficiently calibrated habitat models. As final, parsimonious functional trait combination we selected the combination consisting of the smallest number of traits, with the highest number of sufficiently calibrated PFG models that altogether comprise the highest number of species. The SAS macros (SAS-Institute, Anon. 1989) are available from the authors on request. Additional computations were done in SPSS and R.