

An improved method for searching plant functional types by numerical analysis

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Abstract. The use of plant functional types (PFTs) to describe patterns and processes in plant communities has become essential to study and predict consequences of global change on vegetation and ecosystem processes. A PFT is a group of plants that, irrespective of phylogeny, are similar in a given set of traits and similar in their association to certain variables, which may be factors to which the plants are responding or effects of the plants in the ecosystem. To define PFTs relevant traits must be selected and an appropriate method must be used to classify plants into types. We critically review methods used for the analysis of PFT-based data and describe a new recursive algorithm to numerically search for traits and find optimal PFTs. The algorithm uses three data matrices: describing populations by traits, communities by these populations and community sites by environmental factors or effects. It defines PFTs polythetically by cluster analysis, revealing plant types whose performance in communities is maximally associated to the specified environmental variables. We test the method with data from natural grassland communities of southern Brazil, which were experimentally subjected to combinations of grazing levels and N-fertilizer. The new method is found to be better than similar analytical procedures previously described. Redundancy among traits is discussed and a procedure for comparing alternative solutions is presented based on the similarity in terms of PFT responses between different trait subsets. The concept of PFT response group is illustrated by example.

Keywords: Congruence; Grassland; Grazing; Plant form; Nitrogen; Optimization; Redundancy; Response group; Trait.

Introduction

Ecologists often describe plant communities by species composition and by data analysis reveal compositional patterns in time or space and connections with environmental variables. However, the validity of the conclusions is restricted by phytogeographical boundaries, for the potential species pool is not the same everywhere. Furthermore, variability within species, which may be important in some processes, cannot be taken into account in species based community descriptions. Functional classifications of plants have been used as an

alternative to overcome the limitations of species based descriptions and will be essential for studying and predicting the consequences of global climate change on vegetation and ecosystem processes.

The idea of defining plant types that are, in some way, related to function is not new in ecology (Warming 1895; Raunkiaer 1908, in Raunkiaer 1934, among others; review in Pillar & Orlóci 1993a). Several terms have been used that express the same idea (e.g. growth-forms, life forms, strategies, guilds) despite inconsistencies in terminology pointed out by Semenova & van der Maarel (2000). More recently the term *plant functional type* (PFT) has been suggested with a broader connotation (Steffen et al. 1992; Lavorel & Garnier 2002). We adopt the definition that a PFT is a group of plants that, irrespective of phylogeny, are similar in a given set of traits and similar in their association to certain variables. These variables may be factors to which the plants are responding, e.g. soil conditions, disturbance regime or effects of the plants in the ecosystem, e.g. biomass production, litter accumulation. The former involves the definition of functional response groups and the latter functional effects groups (Lavorel & Garnier 2002). However, we may often be unable to distinguish response from effect (e.g. grazing is affected by vegetation composition and at the same time selectively removes biomass).

The main problem in adopting a PFT-based approach is how to define the plant types. Relevant traits must be selected and an appropriate method used to classify plants into types. In the traditional species based approach the classification is given to ecologists by the plant taxonomists and these problems are of no direct concern. In the PFT-based approach, however, ecologists have to search for relevant traits to define the plant types. We believe this task can be helped by numerical analysis.

In this paper we review methods used for the analysis of PFT-based data and describe a new algorithm to analytically search for traits and to define optimal PFTs. In the new algorithm, plant types maximally associated to specified environmental factors or effects are defined polythetically by cluster analysis. In this way a number

of PFTs maximally associated to environmental variables and defined according to a number of traits can be achieved. We evaluate the method with data from natural grassland communities of southern Brazil, which had been experimentally subjected to combinations of grazing levels and N-fertilizer.

Trait-based data and analysis

Fig. 1 illustrates the kind of data involved when a PFT based approach is adopted, in which communities are described by the composition of plant populations and each population is described by a set of traits. We define a population as a group of plants belonging to the same species and acceptably homogeneous for the traits being considered. The data are organized in matrices for the analysis: matrix **B** describes populations by traits and matrix **W** describes the communities by the presence/absence or quantities of these populations. A third matrix (**E**) describes the community sites by variables (qualitative or quantitative) such as environmental and disturbance factors or ecosystem effects.

We envisage the search for PFTs as a recursive process, taking into account the three matrix descriptive approach. Step 1 is the *a priori* selection of a certain number of plant traits that are known or suspected to be ecologically relevant for the chosen factors or effects. Any qualitative or quantitative trait measured at the individual or population level, being easy or difficult to observe, can be used. Step 2 is to collect the data, involving the description of plant populations for these traits and communities for the composition of the defined populations and environmental variables. If the traits are constant or have acceptably low variability within species, it is more practical to describe the communities by species and then describe the species by the traits, which allows the use of existing databases. In this

case the PFTs will be groups of species. If within species variability is high, populations that are reasonably homogeneous for the traits have to be delimited within a species and locally described within a community. In that case populations of the same species may belong to different PFTs, thus taking into account genotypic or phenotypic plasticity. Step 3 is data analysis to search for the most relevant traits for the chosen objective and to define PFTs accordingly. The process can be restarted from the first step if the analysis does not indicate, for the given objective, satisfactorily relevant traits among those initially selected.

Different approaches have been adopted for the analysis of trait-based data. The analysis may involve only matrix **B** (in this case a species \times traits matrix) without reference to or not having the description of communities (e.g. Grime et al. 1997; Gitay et al. 1999). Patterns, such as species groups or trends of variation in ordination space, are interpreted as an indication of the existence of PFTs, but for this it must be assumed that the traits evaluated in the species are functional at the community level. The assumption may be true for traits that are direct manifestations of function such as the traits evaluated by Grime et al. (1997), but we should be wary that observations of plants growing in isolation and under controlled conditions may not correctly reflect behaviour in a given community. This approach, therefore, must be complemented by further validation to verify if the identified plant types are functional in the sense, for instance, that they consistently appear under given environmental conditions.

The analysis may use matrices **B** and **W**, as defined in Fig. 1, coupled in different ways. One alternative is the method described by Feoli & Scimone (1984), which uses the matrix product **BW**, resulting in matrix **V** of traits \times communities. Matrix **V** is then used in multivariate analysis to reveal trends in trait variation in the community set. Díaz et al. (1992) and Díaz & Cabido (1997), among others, used this method. One condition for the matrix multiplication is that the traits in **B** should be binary or in a commensurable scale if quantitative. The matrix multiplication approach is interesting to identify traits that are correlated at the community level and to identify environmental connections to these trends (matrix **E**). However, the main disadvantage of this method is that the conclusions, in terms of trait patterns, may not be directly translated into plant types, as plant types are not defined at all. The existence of groups of traits with correlated response at the community level does not necessarily indicate they will manifest consistently in the same plant types.

Plant types may be defined by pooling, in matrix **B**, identical populations for the traits and then pooling, in matrix **W**, the corresponding population quantities within

Populations	Traits		Communities		
	Leaf Size	Height	1	2	3
A	2	1	5	25	0
B	1	2	40	0	0
C	2	1	0	20	10
D	1	4	0	10	0
E	1	2	0	0	20
F	1	1	0	0	20

$$\mathbf{B} = \begin{bmatrix} 2 & 1 \\ 1 & 2 \\ 2 & 1 \\ 1 & 4 \\ 1 & 2 \\ 1 & 1 \end{bmatrix}$$

$$\mathbf{W} = \begin{bmatrix} 5 & 25 & 0 \\ 40 & 0 & 0 \\ 0 & 20 & 10 \\ 0 & 10 & 0 \\ 0 & 0 & 20 \\ 0 & 0 & 20 \end{bmatrix}$$

$$\mathbf{E} = \begin{bmatrix} 0 & 100 & 200 \\ 4 & 9 & 14 \end{bmatrix}$$

Fig. 1. Example with the three matrices involved in the analysis of PFT based data. Matrix **B** contains the description of populations by traits, matrix **W** the description of communities by the quantities of each population and matrix **E** the description of the community sites by variables.

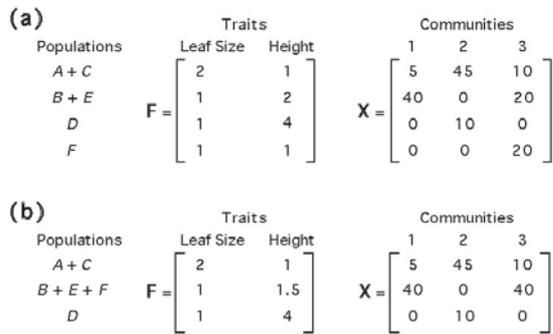


Fig. 2. Example illustrating the method for the analysis of PFT-based data, involving the pooling of populations for the traits in matrix **B** (see Fig. 1), generating matrix **F**. In (a) the pooling is based on monothetic classification and only identical populations are pooled, in (b) on polythetic classification by cluster analysis and similar populations are pooled, in this case defining three types. The quantities in matrix **W** (see Fig. 1) of populations A and C, and populations B and E, plus F in (b), were pooled accordingly, generating matrix **X**.

the communities (Orlóci & Orlóci 1985; Pillar & Orlóci 1993a). Plant types are in this way delineated by monothetic classification (Fig. 2a). The classification is monothetic given that by imagining the clustering process hierarchically and divisively, adding one trait at each clustering step, the splitting of populations at each step is based on the states of a single trait. In this case the splitting is done exhaustively into as many branches as the number of states in the corresponding trait. Traits of any kind may be used but if a trait is a continuous variable, or a discrete variable with a large number of states, for the purpose of having a monothetic classification it should be rescaled into a small number of discrete classes and treated as a nominal trait. After pooling, a matrix 'F' of PFTs by traits and another matrix 'X' of PFTs by communities are generated. As an alternative, fuzzy plant types (Pillar & Orlóci 1991) may be defined by pair-wise similarities between PFTs based on matrix **F**. The similarities range from 0 to 1 and are taken as degrees of belonging to fuzzy types (matrix **U**); the corresponding quantities in the communities are found by matrix multiplication ($T = UX$). Matrices **X** or **T** can be used in multivariate analysis to reveal trends in crisp or fuzzy PFT variation in the community set and to identify associations with environmental conditions (matrix **E**).

McIntyre & Lavorel (2001) identified PFTs by combining different methods to analyse data obtained by the three matrix descriptive approach. In general terms their steps were: (1) species response groups were graphically identified by inspection of canonical ordination results of matrix **W** with respect to environmental con-

ditions in **E**, (2) species groups were similarly identified in the ordination with matrix **B**, (3) traits most responsive to the environmental factors (matrix **E**) were identified by general linear model analysis, (4) information from steps 2 and 3 was combined to identify which species groups (syndromes) were more homogeneous regarding the most responsive traits and (5) information from steps 1 and 4 was combined to identify groups of species belonging to the same group from step 4 which were also found in the same response group in step 1. This procedure seems difficult to implement in an automatic algorithm for general use, since subjective judging is involved in steps 1 and 2.

Automatic optimization methods are available for searching by numerical analysis relevant traits and PFTs with data obtained by the three-matrix descriptive approach (Pillar & Orlóci 1993a, b; Pillar 1999). The analytical problem is to find a subset of traits and with them define plant types so that a maximum association is revealed with environmental factors or effects. PFTs so defined are likely more functional than PFTs defined by using non-optimal traits (Pillar 1999). By using a recursive algorithm (Fig. 3), at any given iteration a subset of traits is extracted from the initial set in matrix **B**. With these traits plant types are defined by monothetic classification and pooling performed as previously described (Fig. 2a). Crisp or fuzzy plant types may be defined. The objective function maximized is a measure of congruence, a matrix correlation $\rho(D;\Delta)$ between compositional dissimilarities (**D**), given by the PFTs, and environmental dissimilarities of the community sites (**Δ**). In monothetic classification the number of PFTs in which populations will be grouped is a function of the number of observed combinations of trait states. Therefore, too many PFTs tend to be defined when the number of populations, traits and trait states are large, which is not practical and has detrimental effects for the analysis by producing a large number of zeroes (indeterminacy) in matrix **X**, and consequently enhancing non-linearity in the community data.

New optimization algorithm

We describe an algorithm to search for traits and a number of PFTs maximally associated to environmental factors or effects. The algorithm is similar to Pillar's (1999) as in the previous description, but at any given recursive iteration a cluster analysis is involved to define PFTs by polythetic classification based on the matrix of populations by traits (Figs. 2b and 3). Cluster analysis is applied to each new matrix **C** of populations by a subset of traits extracted from matrix **B** according to the algorithms described below. The traits may be

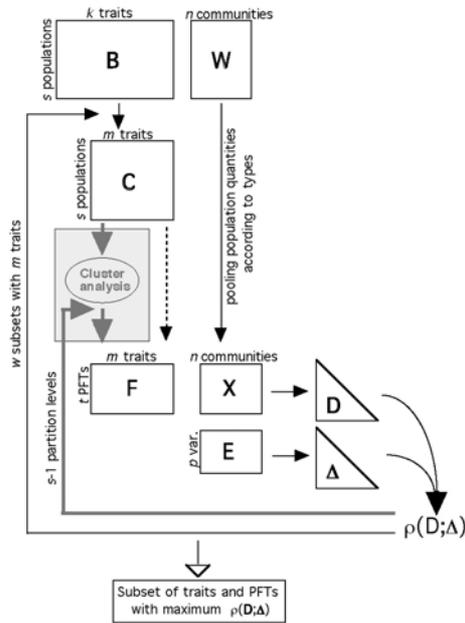


Fig. 3. Algorithm to find, by numerical analysis, an optimal trait subset in PFT based data of matrices **B**, **W** and **E** (see Text and Fig. 1). The definition of types may be monothetic (as in Pillar 1999) when no cluster analysis is involved and identical populations for the traits define the types (dashed line) or polythetic, as described in this paper, when types are defined by cluster analysis and different partition levels (number of groups) are evaluated (grey box). The number w of trait subsets is $w_1 = 2^k - 1$ if all subsets are evaluated or $w_2 = (k^2 + k) / 2$ if a stepwise procedure is adopted.

binary, qualitative, quantitative or a mixture of different types of traits. A proper resemblance function between populations must be chosen according to the type of traits; furthermore, any clustering procedure may be applied (e.g. Podani 2000 for a review on resemblance and clustering procedures). To reduce computations identical populations for the traits may be pooled before cluster analysis. The algorithm is implemented in software (SYNCSA) developed by the first author (see App. 1).

As in any cluster analysis the problem of choosing the number of PFTs (partition level) arises. This is solved in the algorithm by additionally searching, for each trait subset, a partition level that maximizes the objective function (Fig. 3). That is, for each partition level defining t PFTs, a new matrix **X** is generated by pooling, within communities, the performance values of populations belonging to the same PFTs. Dissimilarities are then computed from matrix **X** and evaluated for congruence, which is the matrix correlation coefficient $\rho(\mathbf{D};\mathbf{\Delta})$, where **D** is the dissimilarity matrix of communities based on the composition of PFTs (matrix **X**) defined by a given subset of traits at a given partition level (t groups), and **Δ** is the distance matrix of the same

community sites but based on the environmental factor(s) or effect(s) (matrix **E**).

The number of iterations is a function of the number of trait subsets evaluated (number of different **C** matrices generated) and the maximum number of PFTs. As described in Pillar (1999), two alternative algorithms differ greatly in respect of computation load. The full algorithm checks all possible subsets of traits with sizes varying from $m = 1$ to k , where k is the total number of traits in matrix **B** (Fig. 3). The number of subsets in this case is $w_1 = 2^k - 1$. A stepwise algorithm has much lower computation need, where the number of trait subsets is $w_2 = (k^2 + k) / 2$. The forward stepwise algorithm starts evaluating subsets with size $m = 1$, until among the k traits the one that maximizes the objective function is found. Then evaluation of subsets with $m = 2$ follows until finding the trait (among the remaining $k - 1$ traits) that, when added to the first, maximizes the function. The process continues up to $m = k$. Thus, for each trait subset j , where $j = 1$ to w_1 (or w_2), partitions with $t = 2$ to s PFTs, where s is the number of populations in the data set, are evaluated for congruence. When s is large it may not be convenient to evaluate congruence beyond a maximum number of PFTs. Also, when there is only one trait in the subset and it is qualitative, the number of PFTs cannot be less than the number of trait states. The final output of the procedure is a trait subset and number of PFTs that maximized congruence with the environmental variable(s).

As a consequence of correlation (redundancy) among traits, it may turn out that different trait subsets are very similar in terms of congruence $\rho(\mathbf{D};\mathbf{\Delta})$. Redundancy arises from traits that are associated or from traits nearly constant in the data set (Pillar 1999). The elimination of one of two associated traits or of a nearly constant trait will cause little change in the groups defined by cluster analysis and by consequence in the resulting matrix **X** of PFTs by communities. We can measure redundancy by the matrix correlation coefficient $\rho(\mathbf{D}_h;\mathbf{D}_i)$, where \mathbf{D}_h is the dissimilarity matrix of communities based on the composition of PFTs defined by a given subset h of traits, at a given partition level, and \mathbf{D}_i is the dissimilarity matrix of the same communities but based on the composition of PFTs defined by another subset i of traits. A high $\rho(\mathbf{D}_h;\mathbf{D}_i)$ will indicate that the h th subset of traits is defining a matrix of PFTs by communities very similar to the one given by the i th subset of traits. The results of different solutions may be compared to find if there is any alternative solution with high congruence with the environmental variable(s) and that could offer a more parsimonious subset of traits, with high redundancy with the optimal trait subset though not being the one with the highest congruence.

Case study

We tested the method with data from an experiment evaluating the effect of N-fertilizer and grazing levels on natural grassland located in Eldorado do Sul, Brazil (Sosinski 2000). A set of 14 rectangular experimental plots, sizes between 150 and 600 m², had been subjected for five years (Gersy Maraschin and collaborators) to combinations of N-fertilizer (0, 30, 100, 170 and 200 kg-N.ha⁻¹.yr⁻¹) and grazing levels (4, 6, 9, 12 and 14 kg of forage dry matter per 100 kg of cattle live weight). In each experimental plot five quadrats of 0.5 m × 0.5 m were examined, these were located systematically on one transect parallel to the largest dimension, across the middle portion of the plot. The species found were estimated for cover abundance and locally described for traits in each quadrat. For the analysis we used 13 traits (Table 1); as a result the data contain trait descriptions of 533 different populations belonging to 81 species. Within-species variability for most of the traits was high and therefore plants of the same species may have been described differently in different quadrats, while within-species variability in the same quadrat was taken care of by sampling at least three plants in case of more abundant species. For the analysis the data from quadrats within each plot were pooled.

The optimization algorithm was applied using N-addition and grazing level as environmental variables. Plant types were defined by UPGMA clustering based on Gower's similarity index using at each iteration the subset with *m* traits (for resemblance and clustering methods see e.g. Podani 2000), where *m* varied from one to 13 traits. Gower's formula is a mean of *m* partial similarities computed according to variable type, i.e. binary, qualitative or quantitative traits; quantitative traits are standardized by the range and the function was modified to count matching absences in binary traits. Communities were compared by chord

distances in matrix **D** and by Euclidean distances, after standardization of variables to unit variance, in **Δ**.

With the full algorithm an optimal trait subset was found with five traits defining 23 PFTs (Table 2a). The optimal traits were growth form, plant inclination, persistence, leaf shape and leaf area, which defined PFTs that when used in community descriptions produced a maximum congruence level of 0.666 taking into account both environmental factors. If a monothetic definition of PFTs is adopted with the same five traits, a total of 82 distinct PFTs would be found and the congruence would be much lower than the maximum observed with 23 PFTs polythetically defined (Fig. 4). Also, the optimal solutions using monothetic definition of PFTs or the stepwise algorithm resulted in lower congruence than the optimal solution with polythetic definition (Table 2). Regarding computation demand, the analysis with our data set, in a Macintosh G4 (400 MHz), took ca. 1.2 s per trait subset when defining polythetic PFTs. The most critical factor for total computation demand, after the number of traits, is the number of populations, which in this case was very large.

In addition to the optimal solution, the recursive algorithm has also pointed to alternative solutions in terms of trait subsets and partition levels, which have shown high congruence with grazing and N-levels though not the highest one (Table 2b). The correlations $\Delta(\mathbf{D}_h; \mathbf{D}_t)$ between these alternative solutions are in Table 3, including other non-optimal solutions using species or all traits. The congruence $\rho(\mathbf{D}; \mathbf{\Delta})$ of each solution to the environmental description of the community sites, the target for the PFT optimization algorithm, is also presented (Table 3). How far from the target, in relative terms, are the different ways to describe the plant communities is an indication of optimality. A low environmental congruence was found when using all traits defining five PFTs polythetically (maximum congruence with all traits, see Table 2a) or

Table 1. Traits used for description of plant species in natural grassland communities, Eldorado do Sul, Brazil (Sosinski 2000). All leaf traits refer to the leaf blade. Trait type codes: 1. Binary; 2. Qualitative; 3. Quantitative (ordered classes).

Label	Type	Trait and trait states
lf	2	Life form: 1 = phanerophyte; 2 = chamaephyte; 3 = hemicryptophyte; 4 = geophyte; 5 = therophyte
gf	2	Growth form: 1 = solitary; 2 = rosette; 3 = caespitose
pi	3	Plant inclination: 1 = prostrate, 2 = semi-erect, 3 = erect
he	3	Canopy height at estimated 'centre of gravity' of standing biomass: 1 = < 7.5 cm; 2 = 7.5 - 14; 3 = 14 - 22.5; 4 = 22.5 - 30; 5 = 30 - 40; 6 = > 40 cm
re	1	Reserve structures: 0 = absent; 1 = present
se	2	Seasonality of growth: 1 = winter growing; 2 = summer growing
pe	1	Persistence: 0 = not perennial; 1 = perennial;
ll	3	Leaf length: 1 = < 4.3 cm; 2 = 4.3 - 8.6; 3 = 8.6 - 13; 4 = 13 - 17.3; 5 = 17.3 - 21; 6 = > 21 cm
sh	3	Leaf shape: width/length rescaled into classes = 1 = < 0.38; 2 = 0.38 - 0.76; 3 = 0.76 - 1.13; 4 = 1.13 - 1.56; 5 = 1.56 - 2.25; 6 = > 2.25
la	3	Leaf area: leaf length × width rescaled into classes = 1 = < 11.2 cm ² ; 2 = 11.2 - 22.3; 3 = 22.3 - 36.48; 4 = 36.48 - 38.85; 5 = 38.8 - 67.2; 6 = > 67.2 cm ²
tx	3	Leaf texture: 1 = membranous; 2 = herbaceous; 3 = coriaceous; 4 = succulent; 5 = fibrous
ts	3	Leaf resistance to traction: 4 classes, estimated by pulling by hand until breaking
su	2	Leaf surface: 1 = prickly; 2 = spiny; 3 = other

Table 2. Results of the recursive optimization algorithm applied to 14 experimental grassland plots described by cover/abundances of plant populations, described by 13 traits (Table 1). The correlation $\rho(\mathbf{D};\mathbf{\Delta})$ between community variation, as given by plant types, and variation in nitrogen and grazing levels was maximized. Communities compared by chord distances in matrix \mathbf{D} and Euclidean distances, after standardization of variables, in $\mathbf{\Delta}$. Plant types defined by cluster analysis (UPGMA) based on Gower similarity index for the trait subset (function modified to count matching absences in binary traits). The same recursive algorithm found optimal number of groups for each trait subset size. Maximum congruence was found with five traits, 23 PFTs, as indicated in italics in (a). In (b) additional suboptimal solutions are given. Data from Sosinski 2000.

a.			
Trait subset label	Number of groups	Congruence $\rho(\mathbf{D};\mathbf{\Delta})$	Trait subset
1	4	0.469	sh
2	13	0.595	lf he
3	20	0.623	lf pi he
4	29	0.643	lf pi re ts
5	23	<i>0.666</i>	<i>gf pi pe sh la</i>
6	19	0.650	lf pi re pe la ts
7	23	0.648	lf pi re pe sh la tx
8	22	0.621	lf pi he re pe la tx ts
9	10	0.608	lf pi he re pe le sh la ts
10	12	0.568	lf pi he re pe le sh la tx ts
11	17	0.499	lf gf pi he re pe le sh la tx su
12	25	0.426	lf gf pi he re pe le sh la tx ts su
13	5	0.110	lf gf pi he re se pe le sh la tx ts su

b.			
Trait subset label	Number of groups	Congruence $\rho(\mathbf{D};\mathbf{\Delta})$	Trait subset
2	19	0.662	lf pi re la ts
3	19	0.650	lf pi re pe la ts
4	23	0.648	lf pi re pe sh la tx *
5	15	0.629	pi he sh la tx
6	13	0.624	lf pi he re la
7	9	0.621	pi he sh
8	14	0.619	pi sh la
OptMo	12	0.526	pi lf re **

* Identical to optimal trait subset given by polythetic PFTs, stepwise algorithm; ** Optimal trait subset found by monothetic PFTs, stepwise algorithm.

using the species, supporting the need for optimization. As a result of redundancy between traits, different solutions resulted in highly correlated community distance matrices.

Redundancy among traits is also evident in the PCoA (Principal Coordinates Analysis) ordination of the matrix of PFTs by five optimal traits (Fig. 5). The ordination method is described in, e.g., Podani (2000) and was performed by program MULTIV (Pillar 2001). Optimal and other traits pointed by suboptimal solutions (Table 2b) define common trends of variation in the data matrix. The first ordination axis reflects variation in growth-form (from caespitose to solitary), which is associated to other traits such as leaf texture, area, shape and resistance to traction. The second ordination axis is related to variation in life-form (from hemicryptophyte to therophyte), plant inclination (from prostrate to erect) and persistence (perennial or not perennial).

The matrix with 14 communities (experimental plots) described by 23 optimal PFTs was subjected to PCoA (Principal Coordinates Analysis) (Fig. 6). The analysis

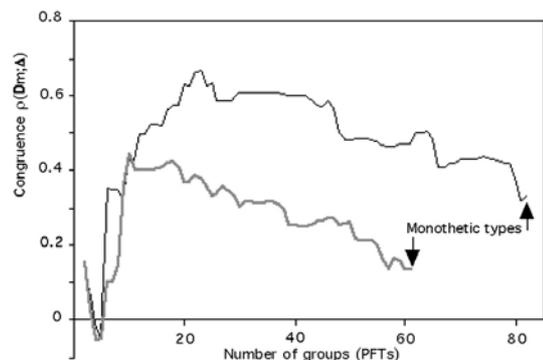


Fig. 4. Effect of the number of PFTs in the congruence $\rho(\mathbf{D};\mathbf{\Delta})$; data from 14 experimental plots on natural grassland, Eldorado Sul, Brazil (Sosinski 2000). The factors defining $\mathbf{\Delta}$ are grazing and nitrogen addition. The black line refers to the optimal trait subset (gf, pi, pe, sh, la), the grey line to a suboptimal trait subset (gf, pi, pe, tx, ts). The maximum number of groups in both cases refers to a monothetic definition of PFTs.

Table 3. Correlation coefficients between alternative ways of analytically describing natural grassland communities, Eldorado do Sul, Brazil. Each alternative was defined by distances between communities (a total of 91 pair-wise distances between 14 communities) based on different descriptors: In Env the descriptors are levels of grazing and nitrogen (the target for the PFT optimization algorithm). OptPo is the optimal solution of the optimization algorithm in terms of trait subsets and number of PFTs defined polythetically (maximum correlation with Env; see Table 2a); 2-8 are sub-optimal solutions of the same algorithm (see Table 2b); OptMo was the optimal solution using monothetic definition of PFTs (see Table 2b); AllPo used all traits defining five PFTs polythetically and Spp used species only. Data from Sosinski (2000).

	OptPo	2	3	4	5	6	7	8	OptMo	AllPo	Spp	Env
OptPo	1.00											
2	0.72	1.00										
3	0.69	0.94	1.00									
4	0.70	0.84	0.80	1.00								
5	0.80	0.67	0.66	0.70	1.00							
6	0.61	0.79	0.76	0.91	0.72	1.00						
7	0.71	0.63	0.62	0.69	0.81	0.67	1.00					
8	0.69	0.64	0.61	0.73	0.82	0.78	0.72	1.00				
OptMo	0.60	0.75	0.72	0.88	0.67	0.87	0.76	0.66	1.00			
AllPo	0.35	0.22	0.18	0.27	0.26	0.19	0.30	0.04	0.27	1.00		
Spp	0.24	0.14	0.05	0.21	0.22	0.13	0.10	0.13	0.13	0.55	1.00	
Env	0.67	0.66	0.65	0.65	0.63	0.62	0.62	0.62	0.53	0.11	-0.10	1.00

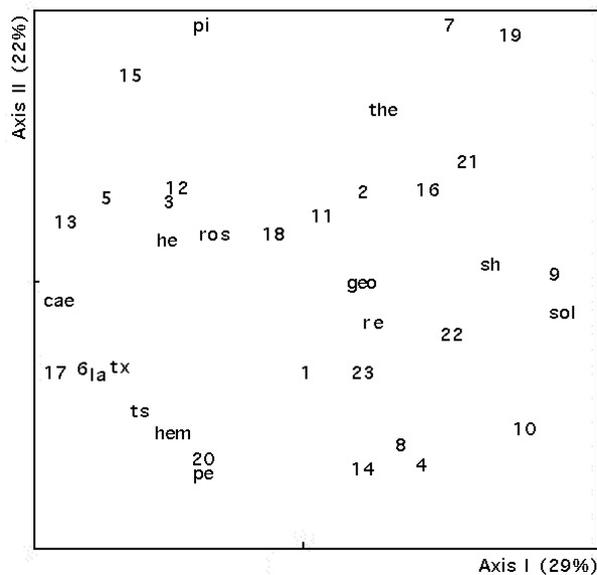


Fig. 5. Principal Coordinates Analysis of 23 PFTs defined by the optimal trait subset with five traits (gf pi pe sh la). The ordination method is based on Gower similarity index between PFTs for the five optimal traits (function modified to count matching absences in binary traits). Numbers identify the PFTs as in Table 4. The optimal and additional traits that were pointed by at least one of the sub-optimal solutions in Table 2b are also plotted on the basis of their correlation with the axes after rescaling. Qualitative traits (gf and lf) were expanded in as many binary traits as the number of states, i.e. growth-form was expanded in *sol*, *ros*, *cae* for states 1 to 3 and life form in *hem*, *geo*, *the*, for states 3 to 5. See Table 1 for trait labels and states.

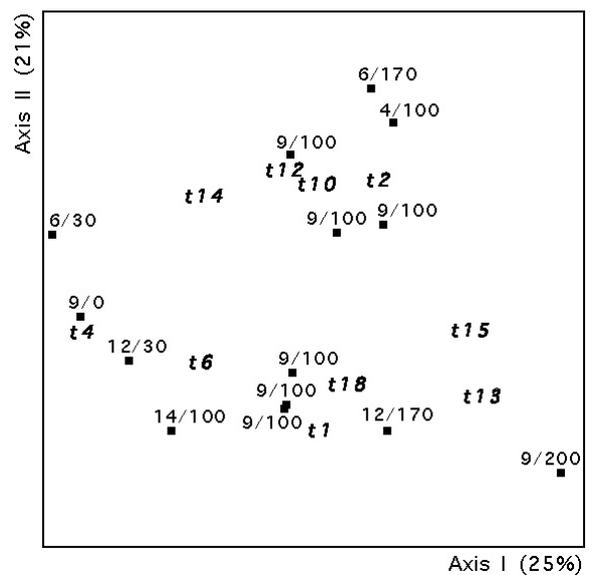


Fig. 6. Principal Coordinate Analysis of 14 experimental plots on natural grassland under different levels of grazing and nitrogen, Eldorado do Sul, Brazil (Sosinski 2000). Numbers indicate available forage (4 - 14 kg per 100 kg cattle live weight) and N-level (0 - 200 kg.ha⁻¹.yr⁻¹). Communities described by 23 PFTs (Table 4; Fig. 5) defined by an optimal trait subset with five traits (maximum $\rho(\mathbf{D};\mathbf{\Delta})$ for nitrogen and grazing levels). PFTs most correlated ($r > 0.45$) with at least one of the axes are indicated (*t1*, *t2*, ...).

Table 4. Trait description of 23 optimal PFTs defined by cluster analysis (UPGMA) of 456 populations, on the basis of five traits (in italics). For qualitative traits the most frequent state in the group is shown. For binary or quantitative traits the rounded average in each PFT is shown. See Table 1 for description of trait states. The traits in italics were found optimal (maximum $\rho(\mathbf{D};\mathbf{\Delta})$ for nitrogen level and grazing level); the additional traits were pointed by at least one of the very close sub-optimal solutions (see Table 2b). PFTs most correlated with at least one of the ordination axes in Fig. 6 are indicated in italics with their quantities in experimental treatments ordered by N addition level under low and high grazing pressure. These PFTs were also classified in response groups defined by the most similar PFTs in their performance in the experimental plots.

Response groups	Traits											Grazing and N levels						
	<i>gf</i>	<i>pi</i>	<i>pe</i>	<i>sh</i>	<i>la</i>	<i>lf</i>	<i>re</i>	<i>ts</i>	<i>tx</i>	<i>he</i>	9	12.5	14	12.5	9	5.5	4	5.5
	PFTs										0	30	100	170	200	30	100	170
1	<i>4</i>	1	1	1	3	3	3	1	2	2	5.6	4.8	4.4	1.4	0.4	5.2	0.6	0.8
1	<i>6</i>	3	3	1	1	3	3	0	2	2	3.6	3.2	3.6	0.6	2.4	2.6	2	1.2
2	<i>1</i>	1	3	1	1	3	4	1	2	2	2.8	5.4	5.4	5.4	3.8	2.2	3.2	2.4
2	<i>18</i>	1	2	1	1	4	4	1	2	2	0	0	2	1.6	0.6	0.2	1	0
4	<i>15</i>	3	2	0	1	3	5	0	1	2	0	0	0	0	1	0	0	0.4
4	<i>13</i>	3	2	1	1	3	3	0	3	2	1.4	0.6	0.6	2.6	5.6	0	0	0.8
3	<i>14</i>	1	1	1	1	3	3	0	2	2	2.6	1.6	0.8	2	0	2.8	2	2.8
3	<i>12</i>	2	2	1	2	3	3	0	2	2	1.6	1.8	1.2	1.2	0.6	1.2	1.8	3.2
3	<i>10</i>	1	1	1	6	2	3	0	2	2	1.2	0.2	0	0	0.2	0	1.4	0.6
3	<i>2</i>	1	2	1	2	2	4	1	2	2	3.8	4.2	3.6	2.8	3.4	2.8	3.6	8
	20	3	1	1	3	3	3	0	2	2	3							
	21	1	2	1	5	1	4	1	1	1	2							
	22	1	3	1	4	2	4	1	2	1	3							
	3	2	2	1	3	5	3	0	3	2	2							
	7	1	2	0	2	1	5	0	1	2	3							
	9	1	1	0	3	1	5	0	1	1	2							
	5	3	2	1	1	2	3	0	1	2	3							
	8	1	1	1	1	2	3	0	1	2	2							
	11	1	2	1	2	3	4	1	1	3	3							
	16	1	2	1	4	2	3	0	1	1	3							
	19	1	2	0	5	2	5	0	1	1	2							
	17	3	3	1	1	5	3	0	3	3	3							
	23	1	3	1	3	4	4	1	2	2	4							

was performed with software SYNCSEA (see App. 1). A gradient defined by N-addition was revealed on the horizontal ordination axis while another gradient related to grazing intensity was on the vertical axis. The PFTs that were the most strongly correlated with these gradients were indicated. We defined response groups as groups of PFTs the most positively correlated in their performance in the plots, not necessarily similar in terms of traits (Table 4). Response groups were identified by applying cluster analysis to the matrix containing performances of PFTs in the communities (UPGMA based on correlation between PFTs); only the PFTs most correlated with the ordination axes in Fig. 6 were classified. The left most PFT (*t4*) characterizes plots with the lowest N-addition and medium grazing intensity; it has solitary growth form, prostrated habit, and leaves with more rounded shape (width/length ratio close to one), as also inferred from the trait trends depicted in Fig. 5. On the other extreme, PFTs *t13* and *t15*, typical of plots with the highest N-addition and medium grazing intensity, have caespitose growth form, semi-erect habit, leaves with more linear shape (low

width/length ratio), the plants are also taller. The PFTs at the top of the diagram, characterizing plots under high grazing intensity, also reveal variation related to the level of N-addition. At the left of the diagram, with less N-addition, PFT *t14* has solitary, prostrate, shorter plants with linear leaves, while at the other extreme, communities with more N added are characterized by PFT *t2* formed by solitary, semi-erect, taller plants; in intermediate positions the communities are characterized by rosette, semi-erect, short plants (*t12*) or solitary, short plants with more rounded leaves (*t10*).

Discussion

Clearly, by adopting the three-matrix approach the analysis of trait-based community descriptions can reveal plant types with maximum association with environmental factors or effects. Therefore, the types so defined are likely to be more functional than in previous methods (e.g. Grime et al. 1997; Gitay et al. 1999) that did not take into account community and ecosystem level information. Furthermore, our method identifies plant types, which is not the case in previous methods using matrix multiplication as in Feoli & Scimone (1984), Díaz et al. (1992) and Díaz & Cabido (1997) which can identify correlated traits but not plant types directly.

The advantage of optimizing traits and PFTs by numerical analysis of trait-based data was clearly illustrated by the case study. Community patterns revealed by multivariate analysis of data in which the trait subset and the number of PFTs are optimized can have higher association with the environmental variables than patterns pointed out by non-optimal trait or species based data. It may be said that this approach is circular, for the environmental variables are the same used in the optimization. Yet, there is no more circularity than when using regression analysis in which factors are added or removed to improve the fit to the model. In our case traits are added or removed to maximize the correlation with the environmental variables.

The method we have proposed that uses a polythetic definition of PFTs has demonstrated ease of use and advantages over previous optimization algorithms. The effect of partition level became evident, indicating that a polythetic definition of PFTs is better when compared to the monothetic definition used by Pillar (1999). Furthermore, the optimal solution with polythetic definition resulted in higher environmental congruence than the optimal solution using monothetic definition of PFTs. Also, the full algorithm, by examining all possible trait subsets gave an optimal solution with higher congruence than the stepwise algorithm.

The data included traits measured in a continuous scale, which were rescaled in a small number of discrete classes for the purpose of allowing a monothetic classification and its comparison with a polythetic definition of PFTs. However, for a polythetic classification there is no need for such a simplification, which may lead to information loss. For the data used in the example, however, we did not find improvement in the congruence level (results not shown) when the full information of the quantitative traits were considered.

It could be argued that redundancy among traits may cause similar effects as in regression analysis when the estimation of regression coefficients is weakened by correlated explanatory variables. The effect of redundant

traits in the optimization algorithm we describe is solely that by adding a trait that is redundant will cause little change in the PFTs defined by cluster analysis and by consequence in the resulting community description. A high degree of redundancy may be observed in trait-based data sets, which will result in having several, almost equally good solutions in terms of traits to define PFTs. In this case the cost of measuring traits may be taken into account to balance the optimality of the solution regarding environmental congruence and the cost of measuring the traits. It could also be added that traits that can be measured accurately might be preferred over those that cannot. Also, some traits might be more easily interpreted in ecological terms than others. It is important to differentiate, however, redundancy at the population level, which is indicated by the degree of association between traits based on a matrix of populations by traits, and trait redundancy at the community level, which is the result of redundancy at the population level plus its manifestation in terms of different plant types and quantities in the matrix of populations by communities.

The distinction between PFTs and response groups is important. In this context a response group is defined as a group of PFTs that are similarly correlated to a given environmental gradient, irrespective of their differences in terms of traits. A community is often composed of different PFTs indicating the same environmental conditions. A corollary to this is that trait averages at the community level might not be correlated with a given environmental variable, even with a high congruence found between the same environmental variables and compositional differences given by PFTs defined by these traits.

The method we described could identify traits and PFTs optimal for the factors considered in the case study (nitrogen and grazing levels). Whether the same traits and PFTs would be consistently found by analysing other data sets from other regions with different species pools is still open to scrutiny. The method, however, is suitable for jointly analysing such data, without being restricted by species pool, which allows the evaluation of a very relevant question in ecology: If consistent patterns are found based on similar gradients but different species pools, we can conclude that there is indeed convergence in community evolution. A worked example on this problem, using a different data set, has been shown by Pillar (1999).

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App. 1.

A free distribution version (SYNCSA Minor), which can handle small data sets, is available at the journal's web page <http://www.opuluspress.se/pub/archives/index.htm> or at <http://ecoqua.ecologia.ufrgs.br>. The application can run under Windows or Macintosh systems.