Discriminating trait-convergence and trait-divergence assembly patterns in ecological community gradients

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Abstract

Question: Whereas similar ecological requirements lead to trait-convergence assembly patterns (TCAP) of species in communities, the interactions controlling how species associate produce trait-divergence assembly patterns (TDAP). Yet, the linking of the latter to community processes has so far only been suggested. We offer a method to elucidate TCAP and TDAP in ecological community gradients that will help fill this gap.

Method: We evaluated the correlation between trait-based described communities and ecological gradients, and using partial correlation, we separated the fractions reflecting TCAP and TDAP. The required input data matrices describe operational taxonomic units (OTUs) by traits, communities by the quantities or presence-absence of these OTUs, and community sites by ecological variables. We defined plant functional types (PFTs) or species as community components after fuzzy weighting by the traits. The measured correlations for TCAP and TDAP were tested by permutation. The null model for TDAP preserves the trait convergence, the structure intrinsic in the fuzzy types, and community total abundances and autocorrelation.

Results: We applied the method to trait-based data from plant communities in south Brazil, one set in natural grassland experimental plots under different nitrogen and grazing levels, and another in sapling communities colonizing *Araucaria* forest patches of increasing size in a forest-grassland mosaic. In these cases, depending on the traits considered, we found strong evidence of either TCAP or TDAP, or both, that was related to the environmental gradients.

Conclusions: The method developed is able to reveal TCAP and TDAP that are more likely to be functional for specified ecological gradients, allowing establishment of objective hypotheses on their links to community processes.

Introduction

Community assembly has puzzled ecologists because it apparently involves two paradoxical trends. Species in a community tend to be more similar in their ecological requirements, which may lead to trait convergence (underdispersion), but species coexistence may be restricted by their trait similarity, leading to trait divergence (overdispersion). Limiting similarity (MacArthur & Levins 1967) is a form of assembly rule (Diamond 1975), in which a pattern arising from the interactions controls how species associate, while trait convergence is a pattern that arises from environmental filters (Keddy 1992; Weiher & Keddy 1995; Weiher et al. 1998; Wilson 1999). If this is true, a community is not only a random gathering of species with traits enabling the species to overcome environmental filters but also enabling the species to coexist. There is therefore a need to elucidate trait patterns of convergence and divergence in community assembly. Further, how these patterns relate to ecological gradients may reveal assembly rules or constraints that can be used to predict community structure (Weiher & Keddy 1995) and ecosystem function (Diaz et al. 2007).

Since both convergence and divergence refer to patterns resulting from different processes of community assembly from a regional species pool, and to avoid uncertainty in the accepted usage of the term 'assembly rule' (Keddy 1992; Weiher & Keddy

1995; Keddy & Weiher 1999; Wilson 1999), we adopt here the terms *trait-convergence assembly pattern* (TCAP) and *trait-divergence assembly pattern* (TDAP). Both patterns can be found in the species composition of communities along ecological gradients. A TCAP is identified when sites nearby on the ecological gradient consistently contain species with similar traits and changes in these traits are related to the gradient. Generally speaking, a TDAP is identified when the turnover in trait-based community components is related to the gradient but the communities contain species with dissimilar traits. As explained later, to reveal TDAP, the effects of TCAP must be filtered out.

The idea of TCAP related to ecological gradients has antecedents in Raunkiaer (1934), in the development of methods of data analysis (Dolédec et al. 1996; Legendre et al. 1997), and in rules predicting community composition (e.g. Box 1981; van der Valk 1981). Moreover, the idea of TDAP has antecedents in Warming (1909): "species differing widely, not only in physiognomy but also in their whole economy, may be associated." While evidence of TDAP is used to justify community ecology (Wilson 1999, 2007; Grime 2006), actually finding TDAP is not easy, in comparison to finding TCAP.

There is some empirical support for limiting similarity in communities where plants with similar functional traits coexist less often than expected at random (Wilson 2007). For instance, limiting similarity was evidenced for pollinators in plant communities (Armbruster 1986), for plant height, shoot biomass, leaf area, and stem diameter in wetland communities (Weiher et al. 1998), for traits related to rooting patterns and leaf water control in a sand dune community (Stubbs & Wilson 2004), and for the proportion of leaf area exposed for removal by mowing in a lawn community (Mason & Wilson 2006). Further evidence for limiting similarity has been found indirectly based on guild proportionality (Wilson & Roxburgh 1994; Mason & Wilson 2006).

Nevertheless, the constraints linking TDAP to community processes have so far only been suggested, e.g., that species can more readily coexist if they reduce competition for pollinators (Armbruster 1986), have differing water-use patterns (Stubbs & Wilson 2004), different leaf angles and canopy structures (Wilson & Roxburgh 1994), or different light capture and response to defoliation (Mason & Wilson 2006). Fukami et al. (2005) observed over time, in a succession, a trend of increasing convergence in trait-based species groups and a steady divergence in species composition, but the latter was not demonstrated using traits. Weiher et al. (1998) found plant trait dispersion varied along a gradient of soil P in wetlands, which was interpreted as increasing competition for light, where available light at the soil surface would decrease with increasing soil fertility. Notwithstanding, an operational approach to discriminating TDAP from TCAP and relating the patterns to community processes is still lacking. An analysis of trait-based community data that takes into account ecological gradients could perhaps fill the gap mentioned by Wilson (2007) and disentangle processes leading to TDAP. Comprehensive trait-based data sets are now readily available (Knevel et al. 2003) and would allow searches for such patterns. In this regard, searching for TDAP linked to gradients would also align with recommendations offered by McGill et al. (2006) for creating more quantitative and predictive community ecology. One problem in this task is that responses of species to the physical environment may obscure the search for patterns (Wilson 1999), since TCAP and TDAP may show paradoxical trends.

In this paper, we offer a new method to discriminate between TCAP and TDAP in communities. While previous attempts did not explicitly consider ecological gradients in the analysis (e.g., Stubbs & Wilson 2004), or only looked for TCAP (Dolédec et al. 1996; Legendre et al. 1997), in our method we evaluated the correlation between trait-based described communities and ecological gradients, and using partial correlation, were able to separate components reflecting TCAP and TDAP. We used a null model to test the magnitude of the measured correlations between TCAP, TDAP, and ecological gradients. We then applied this method to cases illustrating its utility to search for TDAP and TCAP in exploratory analysis and in testing related hypotheses. One strength of the method is that it can be used for either a priori specified plant types, such as species, or for plant functional types (PFTs) found by cluster analysis and based on traits.

Methods

Required input data

For the analysis, we need (Fig. 1a) data containing a matrix **B** of species described by traits that are believed to be functional for the ecological processes of interest; another matrix **W** containing the abundances or presence-absence of these species
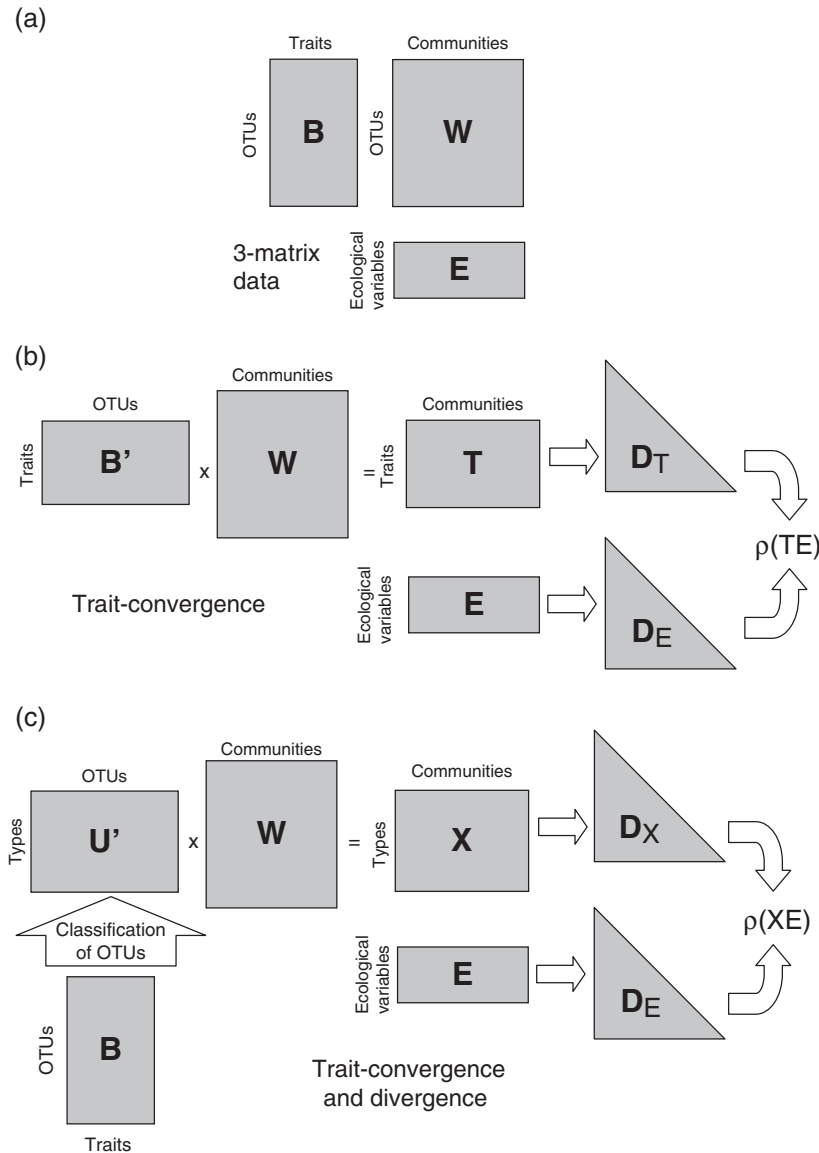
Fig. 1. Scaling up of trait-based data to the community level to reveal trait-convergence and trait-divergence assembly patterns related to ecological gradients. The three data matrices needed for the analysis are in (**a**), where **B** describes Operational Taxonomic Units (OTUs) by traits, **W** the communities by abundances or presence-absence of OTUs, and **E** the community sites by one or more ecological variables. The procedure in (**b**) finds trait-convergence assembly patterns (TCAP) related to **E**, via the computation of $\rho(\mathbf{TE})$, the matrix correlation between dissimilarity matrices $\mathbf{D_T}$ and $\mathbf{D_E}$ computed after **T** and **E**, where $\mathbf{T} = \mathbf{B'W}$. The procedure in (**c**) finds trait-divergence and trait-convergence assembly patterns related to **E**, via the computation of $\rho(\mathbf{XE})$, the matrix correlation between $\mathbf{D_X}$ and $\mathbf{D_E}$ computed after **X** and **E**, where $\mathbf{X} = \mathbf{U'W}$, and **U** contains degrees of belonging of OTUs to a priori defined types, such as species, or to types defined by the traits. See main text for additional explanations.

in communities; and a matrix **E** that describes the community sites according to one or more ecological variable of interest. Such a three-matrix approach has antecedents (Pillar & Orlóci 1993a, b; Dolédec et al. 1996; Legendre et al. 1997; Pillar 1999b). The variables in **E** may refer to factors to which the plant community responds or to effects of the plant community on ecosystem processes (Lavorel & Garnier 2002; Blanco et al. 2007). When the trait description in **B** is local, **B** and **W** may refer to individuals or local populations instead of species, in which case within-species variation may be taken into account (Pillar & Sosinski 2003; Müller et al. 2007). Data may also refer to genera or other taxo-

nomic units. Henceforth, for the sake of generality, we use the well-known term *operational taxonomic unit* (OTU) for individuals, local populations, species, or any other taxonomic units to which the trait description refers.

The data in **B** may contain a mixture of binary and quantitative (ordinal, interval, ratio scales) traits, but may not have qualitative (nominal) traits. Nominal traits can be expanded into binary traits for the analysis. Ordinal traits should be appropriately treated (Podani 2005); their transformation to ranks, taking ties into account (Kendall & Gibbons 1990), is a reasonable solution (Podani 1999).

Scaling-up of traits

A comparative trait-based analysis of communities will require scaling up of the trait-based data held in **B** to the community level, so far described by **W**. There are various ways to scale up traits and, as we will see, the choices have consequences for the perception of TCAP and TDAP.

In one alternative (Feoli & Scimone 1984; Díaz et al. 1992; Díaz & Cabido 1997), matrix multiplication defines $\mathbf{T} = \mathbf{B}'\mathbf{W}$ with the trait quantities in the communities (Fig. 1b). As we explain later, the scaling-up of traits to **T** enables perception of TCAP. **W** may be adjusted to unit column totals prior to multiplication, in which case a row in **T** will hold the averages of a trait in each community. Since the trait set may be a mixture of binary and quantitative data obtained using different measurement scales, correct standardization of the traits (rows) in **T** is needed. Other methods are based on analogous matrix multiplication, but involve the three matrices **B**, **W**, and **E**: the RLQ method (Dolédec et al. 1996), which requires the inclusion of weight matrices, and the fourth-corner method (Legendre et al. 1997), for which **W** must be a binary matrix.

In another alternative (Pillar & Orlóci 1993a, b; Pillar 1999b; Pillar & Sosinski 2003, with applications in Louault et al. 2005; Blanco et al. 2007; Müller et al. 2007), which can be traced back to Orlóci & Orlóci (1985), the OTUs are classified into types (Fig. 1c). The classification may be based on the traits in **B** or be specified a priori (see further explanation below). The classification of OTUs in a given number of *t* types defines an incidence matrix **C** of each OTU *i* for each type *g*; and from this a matrix **U** with crisp or fuzzy degrees of belonging of the OTUs to the types is derived (see further explanation below). By matrix multiplication, $\mathbf{X} = \mathbf{U}'\mathbf{W}$ will contain the composition of the com-

munities in terms of these types (each row in **X** will refer to a type). As we will see, the scaling-up of traits to **X** enables perception of TDAP.

Both **T** and **X** can be related to **E** indirectly by matrix correlation, by measuring how the patterns in **T** and **X** are associated to ecological gradients in **E**. To relate **T** to **E** (Fig. 1b), a proper distance matrix of communities ($\mathbf{D}_\mathrm{T}$) is computed using **T**, and another distance matrix of the community sites ($\mathbf{D}_\mathrm{E}$) is computed using **E**. Then the matrix correlation $\rho(\mathbf{TE}) = \rho(\mathbf{D}_\mathrm{T};\mathbf{D}_\mathrm{E})$ will measure the level of congruence between variations in **T** and **E**, analogous to the correlation used in a Mantel test. Similarly, the matrix correlation $\rho(\mathbf{XE}) = \rho(\mathbf{D}_\mathrm{X};\mathbf{D}_\mathrm{E})$ between **X** and **E** is defined (Fig. 1c).

PFTs or species

When the classification of OTUs into types is based on the traits in **B**, we may refer to such a type as a plant functional type (PFT). In this case, the rows in **X** will be PFTs. Cluster analysis of OTUs may be monothetic (Pillar & Orlóci 1993a, b; Pillar 1999b) or polythetic (Pillar & Sosinski 2003). Any clustering method may be used. In this way, cluster analysis and the resulting classification at a given partition level will define incidence matrix **C**.

However, incidence matrix **C** may be defined by any a priori classification of OTUs, not necessarily by cluster analysis of the trait data in **B**. Thus, our method is also applicable when the interest lies not on TDAP based on PFTs but on other units such as species, in which case matrix **C** refers to the classification of OTUs into species. In this case, the rows in **X** will be species, which is the focus of this paper. Further, as shown below, fuzzy weighting is a method to transfer trait information to the community level without the need to use the traits to define PFTs.

Crisp or fuzzy types

Crisp types are defined when each OTU can only belong to one type, i.e., the degrees of belonging for a given OTU are $u_{ig} = 1$ for one type and $u_{ig} = 0$ for all other types. In this case $\mathbf{U} = \mathbf{C}$.

In this paper we use fuzzy types only, which are defined by degrees of belonging u_{ig} in the interval [0, 1], i.e., each OTU may simultaneously belong to more than one type with certain degrees of belonging (Pillar & Orlóci 1991, see also Zadeh 1965 and Roberts 1986). Furthermore, for each OTU, the degrees of belonging to the *t* types must add to a unit. When **U** is fuzzy, **X** will thus contain the perfor-

mances of the types (PFTs or other types such as species) fuzzy weighted by the traits.

We derived fuzzy degrees of belonging of OTUs to the types by averaging resemblances, based on the traits in **B**, i.e.,

$$u_{ig} = \frac{1}{n_g} \sum_{j=1}^{n} s_{ij} c_{jg},$$

where u_{ig} is the degree of belonging of OTU i in group g, n_g is the number of OTUs in type g, s_{ij} is the resemblance between OTUs i and j, and $c_{jg} = 0$ or 1 is one element of **C** indicating whether OTU j belongs to type g. This is followed by adjustment of the degrees of belonging to a unit total for each OTU. When the resemblances between OTUs are similarities, e.g., using the Gower index, which gives a similarity in the range 0 to 1, the computation of degrees of belonging ends here. When the resemblances are dissimilarities, e.g., Euclidean distances, the one-complement of the degrees of belonging is taken and further adjusted to a unit total for each OTU. The use of the Gower index is advantageous for handling mixed measurement scales in **B** (Podani 1999).

To avoid artefacts arising from the possible presence of OTUs that are identical in terms of the traits in **B**, in a first step the computation of fuzzy u_{ig} should involve only the subset of non-identical OTUs. Then, in a second step, the original set is recomposed by attributing to the other OTUs the same computed u_{ig} of their identical OTUs.

Trait-convergence and trait-divergence assembly patterns

What are the implications of scaling trait-based data into **T** or **X**? We use examples with artificial data to illustrate this point in Fig. 2. In Fig. 2a, the community average trait value increases along the gradient **E**; in Fig. 2b, it is constant; and in Fig. 2c, it increases and then remains constant on the same gradient. When $\rho(\mathbf{TE})$ is large, communities that are more similar in traits are also more similar for the ecological factor(s) or effect(s) of interest. Thus $\rho(\mathbf{TE})$ measures convergence of traits (TCAP) on the ecological gradient. Indeed, $\rho(\mathbf{TE}) = 1$ in Fig. 2a and $\rho(\mathbf{TE}) = 0$ in Fig. 2b, and in Fig. 2c trait convergence is intermediate.

By scaling up traits into **X**, $\rho(\mathbf{XE})$ is high for the data in both artificial examples in Fig. 2a and b. Thus, a large $\rho(\mathbf{XE})$ may indicate that either or both TCAP and TDAP are related to **E**. To remove the trait-convergence component from $\rho(\mathbf{XE})$, we compute the partial matrix (Mantel) correlation

$$\rho(\mathbf{XE.T}) = \frac{\rho(\mathbf{XE}) - \rho(\mathbf{XT})\rho(\mathbf{TE})}{\sqrt{1 - \rho(\mathbf{XT})^2}\sqrt{1 - \rho(\mathbf{TE})^2}}$$

where $\rho(\mathbf{XT}) = \rho(\mathbf{D_X};\mathbf{D_T})$ is the matrix correlation between the abovementioned distance matrices $\mathbf{D_X}$ and $\mathbf{D_T}$. The function is not defined when $\rho(\mathbf{TE}) = 1$ or $\rho(\mathbf{XT}) = 1$, in which case $\rho(\mathbf{XE.T}) = 0$. The partial matrix correlation $\rho(\mathbf{XE.T})$ will measure the magnitude of the effect of TDAP in $\rho(\mathbf{XE})$. The example with artificial data in Fig. 2b shows maximum $\rho(\mathbf{XE.T})$ (which is minimum in Fig. 2a and intermediate in Fig. 2c).

Why can we always deduce that $\rho(\mathbf{XE.T})$ expresses TDAP? First, there will be no TCAP detected by $\rho(\mathbf{TE})$ when trait averages are constant or not related to the environmental gradient, i.e., $\rho(\mathbf{TE}) = 0$. Second, there will be neither TCAP nor TDAP in $\rho(\mathbf{XE})$ when community composition after fuzzy weighting by the traits is constant or not related to the environmental gradient, i.e., $\rho(\mathbf{XE}) = 0$. Thus, by definition, if $\rho(\mathbf{XE})$ is not null, it may express only TCAP (i.e., $\rho(\mathbf{XE.T}) = 0$), only TDAP (i.e., $\rho(\mathbf{TE}) = 0$), or both. Further, it should be noted that TCAP is defined when trait convergence is found consistently along the gradient (Fig. 2a), while for TDAP, trait divergence is observed only in parts of the gradient (Fig. 2b).

Equivalent results can be obtained by applying regression models. In one model, the $n(n-1)/2$ distances for n communities in $\mathbf{D_T}$ form the explanatory variable, and the corresponding distances in $\mathbf{D_X}$ the response variable. Another model uses the same explanatory variable $\mathbf{D_T}$, with $\mathbf{D_E}$ as the response variable (Legendre 2000). The residuals of these models ($\mathbf{D_{Xres}}$ and $\mathbf{D_{Eres}}$) define matrix correlation $\rho(\mathbf{XE.T}) = \rho(\mathbf{D_{Xres}};\mathbf{D_{Eres}})$, which is identical to $\rho(\mathbf{XE.T})$ computed by partial correlation.

Searching for optimal traits

The iterative method of Pillar & Sosinski (2003) can be used to search for an optimal trait subset taken from **B** in order to maximize the chosen objective function. The objective function in this case is $\rho(\mathbf{XE.T})$ for TDAP and $\rho(\mathbf{TE})$ for TCAP. To search for optimal traits to reveal TDAP of species (or other specified types) related to one or more ecological factors, the classification of OTUs is given a priori, and the computation algorithm will take from **B** all possible trait combinations, starting with one trait, and then for each trait subset will perform all the analytical steps needed to evaluate
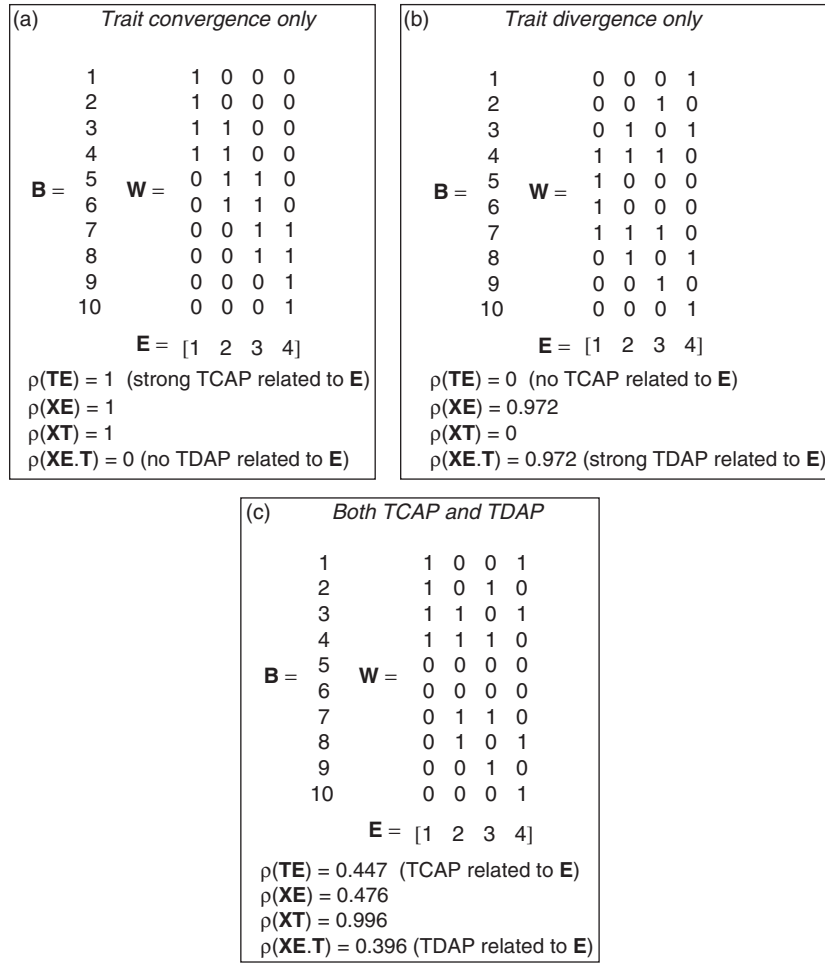
Fig. 2. Examples with artificial data showing maximum expression of (**a**) only trait-convergence assembly pattern (TCAP), (**b**) only trait-divergence assembly pattern (TDAP), or (**c**) both TCAP and TDAP. Matrices **B** and **E** are the same in (**a-c**), where **B** describes 10 species by one quantitative trait, with states ranging from 1 to 10. Matrix correlation $\rho(\mathbf{XE})$ was computed after fuzzy weighting of species in **X**. Fuzzy weighting was based on Gower similarities between species computed on their trait description in **B**. Matrix **E** indicates a gradient. Binary matrix **W** is arranged in such a way to maximize TCAP, TDAP, or to produce a combination of both according to the gradient in **E**. See main text and Appendix S1 for details.

(a) Trait convergence only

$$
\mathbf{W} =
\begin{array}{cccc}
1 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 \\
1 & 1 & 0 & 0 \\
1 & 1 & 0 & 0 \\
0 & 1 & 1 & 0 \\
0 & 1 & 1 & 0 \\
0 & 0 & 1 & 1 \\
0 & 0 & 1 & 1 \\
0 & 0 & 0 & 1 \\
0 & 0 & 0 & 1
\end{array}
$$

$\mathbf{E} = [1\ 2\ 3\ 4]$

$\rho(\mathbf{TE}) = 1$ (strong TCAP related to **E**)
$\rho(\mathbf{XE}) = 1$
$\rho(\mathbf{XT}) = 1$
$\rho(\mathbf{XE.T}) = 0$ (no TDAP related to **E**)

(b) Trait divergence only

$$
\mathbf{W} =
\begin{array}{cccc}
0 & 0 & 0 & 1 \\
0 & 0 & 1 & 0 \\
0 & 1 & 0 & 1 \\
1 & 1 & 1 & 0 \\
1 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 \\
1 & 1 & 1 & 0 \\
0 & 1 & 0 & 1 \\
0 & 0 & 1 & 0 \\
0 & 0 & 0 & 1
\end{array}
$$

$\mathbf{E} = [1\ 2\ 3\ 4]$

$\rho(\mathbf{TE}) = 0$ (no TCAP related to **E**)
$\rho(\mathbf{XE}) = 0.972$
$\rho(\mathbf{XT}) = 0$
$\rho(\mathbf{XE.T}) = 0.972$ (strong TDAP related to **E**)

(c) Both TCAP and TDAP

$$
\mathbf{W} =
\begin{array}{cccc}
1 & 0 & 0 & 1 \\
1 & 0 & 1 & 0 \\
1 & 1 & 0 & 1 \\
1 & 1 & 1 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 1 & 1 & 0 \\
0 & 1 & 0 & 1 \\
0 & 0 & 1 & 0 \\
0 & 0 & 0 & 1
\end{array}
$$

$\mathbf{E} = [1\ 2\ 3\ 4]$

$\rho(\mathbf{TE}) = 0.447$ (TCAP related to **E**)
$\rho(\mathbf{XE}) = 0.476$
$\rho(\mathbf{XT}) = 0.996$
$\rho(\mathbf{XE.T}) = 0.396$ (TDAP related to **E**)

$\rho(\mathbf{XE.T})$. For TCAP, the same algorithm will be used, but maximizing $\rho(\mathbf{TE})$. To search for TDAP of PFTs (we do not do this in the examples in this paper), the computation algorithm will in addition apply cluster analysis to the data defined by each trait subset before evaluating the objective function for a specified range of partition levels (see Pillar & Sosinski 2003). The output will indicate the trait subset and, if this is the case, partition levels, thus maximizing the objective function for each number of traits.

Null model

In order to check for statistical significance, the observed partial correlation $\rho(\mathbf{XE.T})$ for TDAP is tested by permutation against a null model. The null model should retain most of the real data structures except for the one that is to be tested (Tokeshi 1986; Stubbs & Wilson 2004). For this, the row vectors (OTUs) of **U** are randomly permuted among rows, keeping each row vector intact. By matrix multiplication, $\mathbf{X}_{\text{RND}} = \mathbf{U}'_{\text{RND}}\mathbf{W}$ defines one possible composition of the same types in each community under the null model. In this way, the null model preserves the intrinsic correlation structure between types in **U**. Also, since matrix **W** is unchanged, the total performance in each community is preserved, which also incorporates any temporal or spatial autocorrelation in the null model. Further, matrix **B**, and therefore **T**, as well as **E**, are kept unchanged over randomization, since any trait convergence expressed in the correlation $\rho(\mathbf{TE})$ between $\mathbf{D}_{\text{T}}$ and $\mathbf{D}_{\text{E}}$ must be incorporated into the null model.

At each random permutation, a new value of $\rho(\mathbf{X}_{RND}\mathbf{E.T})$ is computed and compared to the observed $\rho(\mathbf{XE.T})$. The probability P sought for the hypothesis test is the proportion of $\rho(\mathbf{X}_{RND}\mathbf{E.T})$ values that are not smaller than the observed $\rho(\mathbf{XE.T})$ in a large number of permutations (at least 1000 permutations in our analyses). We reject the null model when $P \leq 0.05$. A significant $\rho(\mathbf{XE.T})$ will indicate the existence of non-random TDAP related to the traits and ecological gradient(s) considered.

Type I error of this permutation test was assessed using simulated data sets taken from the real data we analyzed in Case Studies 1 and 2 (see next sections). For this, we produced a large number of possible combinations of traits (up to six traits) by using the iterative algorithm described in the previous section. After this, the rows of matrix $\mathbf{U}$ for each data set were randomly permuted among rows and the data used as input in a permutation test. In this way, for Case 1, a total of 2509 random data sets were generated, for which the proportion of null hypothesis rejection was 0.0502 when adopting $\alpha = 0.05$. For Case 2, a total of 21 777 random data sets were generated and the proportion of null hypothesis rejection was 0.0509 with the same α. Thus, we consider the permutation test unbiased within the range of data sets used in this paper.

Adopting the same principles, we also tested the statistical significance of the matrix correlation $\rho(\mathbf{TE})$ for TCAP against a null model. For this, the row vectors of trait matrix $\mathbf{B}$ were permuted among rows, keeping each row vector intact. The correlation between traits in $\mathbf{B}$ is kept constant and matrix $\mathbf{W}$ is unchanged. By matrix multiplication, $\mathbf{T}_{RND} = \mathbf{B}'_{RND}\mathbf{W}$ defines one possible configuration of trait averages in each community under the null model. Next, to find the probability P for $\rho(\mathbf{TE})$ under this null model, we adopted an analogous procedure to that already explained for testing $\rho(\mathbf{XE.T})$. A significant $\rho(\mathbf{TE})$ indicates non-random TCAP related to the traits and ecological gradient(s) considered.

Further analyses

After identifying TCAP and TDAP, it may be necessary to perform exploratory analysis in order to simplify data complexity and ease interpretation. Among other possibilities, we may apply well-known ordination techniques to matrices $\mathbf{B}$, $\mathbf{T}$, and $\mathbf{X}$ separately, and canonical ordination on $\mathbf{T}$ or $\mathbf{X}$ restricted by $\mathbf{E}$. Further, when TDAP of species are identified, the species may be grouped after into types using cluster analysis based on the same traits

in $\mathbf{B}$ responsible for the patterns at the community level.

We could apply non-metric ordination (NMDS) to the abovementioned matrix $\mathbf{D}_{Xres}$ to reveal a synthetic view of TDAP. Non-metric ordination (NMDS) is required since $\mathbf{D}_{Xres}$ is unlikely to hold Euclidean metric properties. However, correctly interpreting TDAP in NMDS with regard to the species or other types does not seem possible, since in the removal of $\mathbf{D}_T$ from $\mathbf{D}_X$ the link between $\mathbf{D}_X$ (now in $\mathbf{D}_{Xres}$) and the species composition (in $\mathbf{X}$) may be lost. Therefore, for interpreting the patterns, we are left with using ordination of matrix $\mathbf{X}$, understanding that it may reflect both TDAP and TCAP. Yet, defining $\mathbf{X}$ based on traits that maximize the expression of TDAP minimizes this problem.

Computer program

The method was implemented by V.P using the software SYNCSA, available at http://ecoqua.ecologia.ufrgs.br.

Case Studies

Case study 1: natural grassland, experimentally controlled factors

We tested the method using the data of Pillar & Sosinski (2003) from an experiment evaluating the effect of N fertilizer and grazing levels on natural grassland in Eldorado do Sul, Brazil (30°05′52″S, 51°41′14″W, 31 m a.s.l.). Fourteen experimental plots were subjected during 5 years to limited 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) using a central composite design. In the fifth year, each experimental plot was described by five systematically placed quadrats of 0.5 m×0.5 m. The species found were estimated for cover abundance and locally described for traits in each quadrat. We used seven quantitative (ordinal) traits (Table 1a), which were transformed to ranks for the analysis. Within-species variation was taken into account and therefore the data in matrix $\mathbf{B}$ included the trait description of 827 populations (OTUs) belonging to 81 species. The quadrats in each experimental plot were pooled for the analysis (for this, matrix $\mathbf{B}$ remained intact while columns in $\mathbf{W}$ were pooled and the extra ones in $\mathbf{E}$ were trimmed).

Table 1. Plant traits chosen for description of populations in the natural grassland experiment in south Brazil in (a), and the trait subsets maximizing, at the community level, the expression of trait-divergence and trait convergence assembly patterns related to nitrogen and grazing gradients in (b). All traits were taken as ordinal.

(a) Traits

Labels	Traits and trait states
pi	Plant inclination (1:prostrate, 2:semi-erect, 3:erect)
he	Canopy height at estimated "center 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)
ll	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	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	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	Leaf texture (1: membranous; 2: herbaceous; 3: coriaceous or fibrous)
ts	Leaf resistance to traction (4 classes, estimated by pulling by hand until broken)

(b) Trait-divergence (TDAP) and trait-convergence (TCAP) assembly patterns

Gradient	TDAP		TCAP	
	Nitrogen	Grazing	Nitrogen	Grazing
Optimal trait subset	Plant inclination and height, leaf area and shape	Leaf texture, resistance and length	Plant inclination and leaf shape	Leaf resistance and area
$\rho(\mathbf{TE})$	0.269	0.232	*0.521*	*0.420*
	$P = 0.115$	$P = 0.100$	$P = 0.002$	$P = 0.007$
$\rho(\mathbf{XE})$	0.500	0.392	0.585	0.481
$\rho(\mathbf{XT})$	0.901	0.882	0.967	0.965
$\rho(\mathbf{XE.T})$	*0.617*	*0.408*	0.374	0.318
	$P = 0.001$	$P = 0.010$	$P = 0.017$	$P = 0.035$

With this data set, we searched for traits revealing TDAP of fuzzy species related to the N fertilizer levels in one case, and to the grazing levels in another case. In both cases, we also searched for traits maximizing the expression of TCAP.

The results (Table 1b) show that the traits maximally revealing TDAP of fuzzy species associated to N levels, at a highly significant level of partial correlation ($\rho(\mathbf{XE.T}) = 0.617$, $P = 0.001$), were plant inclination and height, and leaf area and shape. The traits maximally revealing TDAP of species related to grazing levels, at a significant partial correlation level ($\rho(\mathbf{XE.T}) = 0.408$, $P = 0.010$), were leaf texture, resistance, and length. On both gradients, the level of TCAP expressed by these traits was moderate and marginally significant ($\rho(\mathbf{TE}) = 0.269$, $P = 0.115$ for N, and $\rho(\mathbf{TE}) = 0.232$, $P = 0.100$ for grazing).

Although TDAP of fuzzy species were identified, in order to simplify the presentation of results, after finding optimal traits, we classified the species into groups using the optimal traits and called such groups PFTs. For this, we applied cluster analysis (complete linkage method) on the Gower similarity matrix of species computed on the average matrix of traits by species, considering only the traits that were optimal for each ecological gradient. We tested group partition sharpness by bootstrap resampling and chose a number of groups that were sharp at a probability threshold of $P > 0.05$ (Pillar 1999a).

The communities were then compared (chord distances on matrix **X**) using the composition of species after fuzzy weighting by the optimal traits, and then analyzed by Principal Coordinates Analysis (Fig. 3a and b). Also, the variation of these and the other traits at the population level is depicted in the PCOA ordination in Fig. 3c and d, which used the trait averages for each species (from matrix **B**; and all traits, including the ones not selected as optimal for the gradients are projected on the ordination space). As seen in Fig. 3c and d, there is a high level of redundancy among traits, which is indicated by the large proportion of total variation in the trait data accounted for by the first two ordination axes. Further, more correlated traits are closer in the diagrams.

By integrating the information at community (Fig. 3a) and population (Fig. 3c) levels along the N gradient, and the groups (PFTs) already identified (see also Supporting Information, Appendix S2a), we find, in a broad view, that plants that were taller, more erect, and with smaller, linear leaves (PFT-2), and plants of medium height and medium inclination, with larger, linear leaves (PFT-1), co-occurred in communities under higher N levels, while PFT-1 and shorter, very prostrate plants, with medium-size, round leaves (PFT-3) co-occurred in communities under lower N levels.

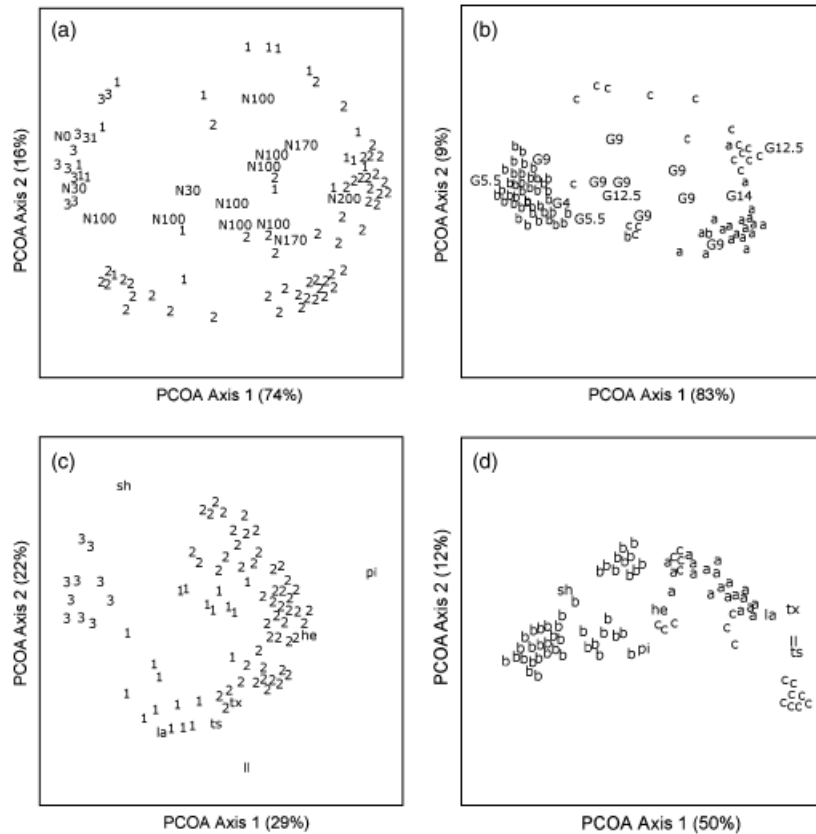Similarly (Fig. 3b and d, and Appendix S2b), along the grazing gradient, plants with shorter,

Fig. 3. Trait-divergence assembly patterns of species in natural grassland communities under experimental levels of nitrogen (N) and grazing in south Brazil. The diagrams in (**a**) and (**b**) were generated by PCOA of communities based on chord distances computed on the composition of species after fuzzy weighting by traits; the labels in (**a**) identify N levels and in (**b**) the grazing levels of the experimental plots; in both diagrams the species are plotted according to their rescaled correlations with the ordination axes and identified in (**a**) by the same group labels as in (**c**), and in (**b**) by the same group labels as in (**d**). In (**a**) fuzzy weighting was defined by plant inclination, height, and leaf area and shape, and in (**b**) by leaf texture, resistance and length, which were the optimal traits for the expression of trait-divergence assembly patterns related to the specified gradients (see Table 1). The PCOA diagram in (**c**) shows the species as described by the optimal traits mentioned in (**a**); the labels identify the traits (see Table 1a) and the species by the corresponding group (PFT) found by cluster analysis based on the optimal traits, using complete linkage method on Gower similarities of species; the optimal and the other traits were projected on the diagram based on their correlations with the axes. The diagram in (**d**) followed the same procedure, but using the same traits as in (**b**).

round leaves, with a softer texture and low resistance to traction (PFT-b) characterized the heavier grazing plots (lower forage on offer levels), while plants with longer, linear leaves, a harder leaf texture and high resistance to traction (PFT-c), and plants with longer, linear leaves with a medium texture and medium resistance to traction (PFT-a) co-occurred in lighter grazing level plots.

The traits maximizing the expression of TCAP along the N gradient were plant inclination and leaf shape, with a relatively high and significant matrix correlation ($\rho(\mathbf{TE}) = 0.521$, $P = 0.002$, Table 1b). The traits maximizing TCAP along the grazing gradient were leaf resistance and area, and the correlation was somewhat lower but significant

($\rho(\mathbf{TE}) = 0.420$, $P = 0.007$, Table 1b). Some of these traits coincide with those maximally revealing TDAP related to the gradients. The fact that the same trait can be both a component of TCAP and a component of TDAP is illustrated by the example in Fig. 2c, where both convergence and divergence are present for the same trait. The association between some of these traits and the ecological gradients is shown in Fig. 4: plants were more erect with increasing N levels (Fig. 4a), while they had stronger leaves with increasing forage on offer (decreasing grazing levels, Fig. 4b).

On both N and grazing gradients, TDAP expressed by the same traits maximizing TCAP was weaker but significant ($\rho(\mathbf{XE.T}) = 0.374$, $P = 0.017$
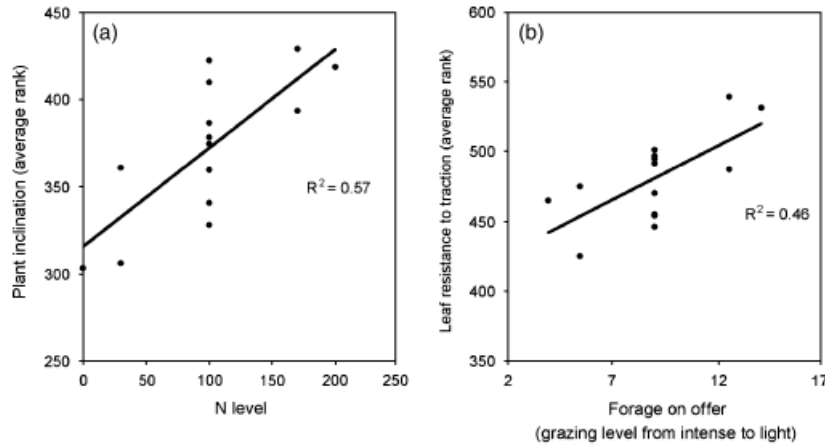
Fig. 4. Patterns of trait convergence found in natural grassland communities under experimental levels of nitrogen and grazing in south Brazil. The diagrams relate community-level averaged traits with nitrogen (**a**) and grazing (**b**) gradients; the traits were among those that, with other traits or individually, maximized the expression of trait convergence on these gradients (see Table 1b), i.e., plant inclination and leaf resistance to traction.

Table 2. Plant traits chosen for description of woody plant species colonizing *Araucaria* forest patches of different development stages in south Brazil in (a), and the trait subsets maximizing, at the community level, the expression of assembly rules and trait convergence related to the patch size gradient in (b). Seed size was taken as quantitative, seed number and diaspore size as ordinal (transformed to ranks) and the others as binary traits.

(a)	Traits and trait states
ss	Seed size (mean seed diameter in mm)
sn	Seed number (1: single seeded diaspore, 2: two to five seeds per diaspore, 3: more than five seeds per diaspore)
ds	Disapore size (1. small, 2: medium, 3: large)
be, dr, ar, ot	Diaspore type (be: berry, dr: drupe, ar: arillate seed, ot: other)
ye, or, re, wh, gr, vi, bl, br	Diaspore color (ye: yellow, or: orange, wh: white, gr: green, vi: violet, bl: black, br: brown)

(b) Trait-divergence (TDAP) and trait-convergence (TCAP) assembly patterns

Optimal traits	TDAP	TCAP
	Drupe, fruit color (yellow, violet, black)	Arillate seed, drupe, black fruit
$\rho(\mathbf{TE})$	0.154 ($P = 0.912$)	*0.551 ($P = 0.050$)*
$\rho(\mathbf{XE})$	0.265	0.342
$\rho(\mathbf{XT})$	0.973	0.373
$\rho(\mathbf{XE.T})$	*0.509 ($P = 0.077$)*	0.176 ($P = 0.650$)

for N; $\rho(\mathbf{XE.T}) = 0.318$, $P = 0.035$ for grazing, Table 1b).

The results therefore indicate that contrasting species in terms of traits co-occur in the same communities, and that the change in species composition, after removing the effect of TCAP, is highly correlated to the ecological gradient considered. We interpret this as strong evidence of TDAP related to N and grazing levels in these grassland communities. The results evidenced traits, shared or not with those expressing TDAP, that enhance the perception of TCAP, i.e., the similarity among plants occurring at the same gradient levels. Therefore, both TDAP and TCAP can be detected in these communities, depending on traits and ecological gradient.

Case 2: colonization of Araucaria forest patches

In this case, we use trait-based data of woody species colonizing *Araucaria* forest patches of different sizes in a forest-grassland mosaic in south Brazil (Duarte et al. 2007). The data describe 38 colonizer species by seed size, seed number, and disperser attraction traits related to diaspore size, type, and color (data published in the Appendix of Duarte et al. 2007). Ordinal traits were transformed to ranks. Nominal traits were expanded into binary data. Thus, 15 traits were considered: seed size, seed number; and the diaspore traits size, berry, drupe, other fruit type, with arillate seed, yellow, orange, red, white, green, violet, black, and brown (Table 2a). The abundance of saplings of these species was
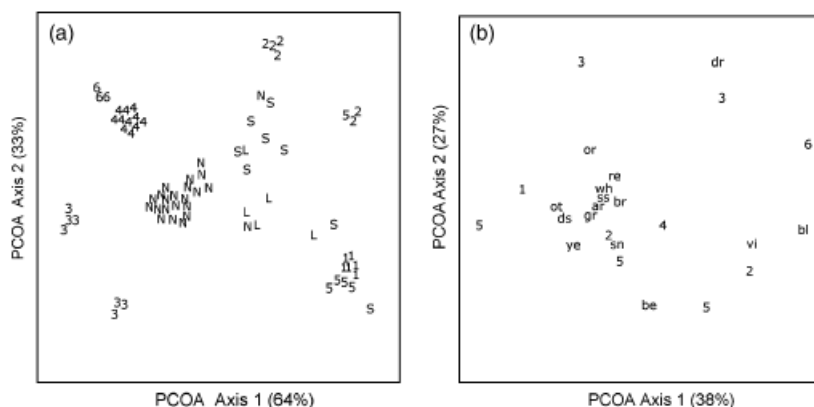
Fig. 5. Trait-divergence assembly patterns of colonizer plant species in *Araucaria* forest patches of different patch sizes in a Campos grassland matrix in south Brazil. The PCOA ordination diagram of communities in (**a**) was generated on chord distances computed on the composition of species after fuzzy weighting by the traits fruit type (drupe) and fruit color (yellow, violet, black), which maximized the expression of TDAP related to forest patch size (see Table 2b). The letter labels identify the patch size type (L: large patches, S: small patches, N: nurse plants). The species are plotted according to their rescaled correlations with the ordination axes and identified by the corresponding PFT shown in (**b**). The PCOA ordination of species in (**b**) was based on the Gower index between species based on the abovementioned traits; the species are identified by the corresponding PFT found by cluster analysis (Wards's method, on the same Gower similarities between species); since there are identical species for the traits, some coordinates overlap; all 15 traits describing the species are projected on the diagram (see labels in Table 2a).

evaluated in 36 forest patches (Duarte et al. 2006). Forest patch size, varying from 36 to 1900 m^2, from nurse plants to large patches, was taken as the ecological factor after log transformation. We used forest patch size as a proxy for forest development stage. We expect plant community patterns in this case are determined by a process mediated by ecological mechanisms related to forest patch size that affect the disperser fauna, such as diet preferences and habitat use (Duarte et al. 2007).

The results (Table 2b) indicate the traits maximally revealing fuzzy-weighted species-based TDAP related to forest patch size, with a marginally significant partial correlation level of $\rho(\mathbf{XE.T}) = 0.509$ ($P = 0.077$), were fruit type (drupe) and fruit color (yellow, violet, black). The level of TCAP expressed by these traits was low and not significant ($\rho(\mathbf{TE}) = 0.154$, $P = 0.912$).

We followed the same procedure as in the grassland example to explore, by ordination and classification, the population and community patterns revealed by these traits (Fig. 5a and b, Appendix S3).

The species in PFT-1 characterized small and large forest patches (Fig. 5a); some of them presented larger arillate seeds, others small- to medium-sized berries that were neither black nor violet (Fig. 5b, Appendix S3). Species in PFT-1 were absent from nurse plants and only found in small and large forest patches; while among the other species, some

were also present under nurse plants, in particular those in PFT-3, PFT-4, and PFT-6. In general, the species under nurse plants were a subset of the colonizer species pool found in small and large forest patches. The species in PFT-2 had small- to medium-sized violet and black (also red) berries. The species in PFT-3 had small to medium black (also orange or red) drupes. The species in PFT-4 had small to medium black berries. The species in PFT-5 had medium to large yellow (also red, green, and violet) berries or other fruit types. The species in PFT-6 had small drupes that were violet and black (also red).

The traits maximizing the expression of TCAP were diaspore type (drupe, arillate seed) and color (black) ($\rho(\mathbf{TE}) = 0.551$, $P = 0.050$, Table 2b). The TDAP expressed by the same traits maximizing TCAP was weak and non-significant ($\rho(\mathbf{XE.T}) = 0.176$, $P = 0.650$). The association between some of these traits and the ecological gradient is shown in Fig. 6. The proportion of species with drupe fruit type decreases with patch size (Fig. 6a), while mean seed size (which was not selected as optimal for TCAP) shows a weak increasing trend on the gradient.

The results for this case also indicate that some contrasting species (grouped in PFTs) in terms of traits co-occurred in the same forest patches, and that the change in species composition, after removing the effect of TCAP, was
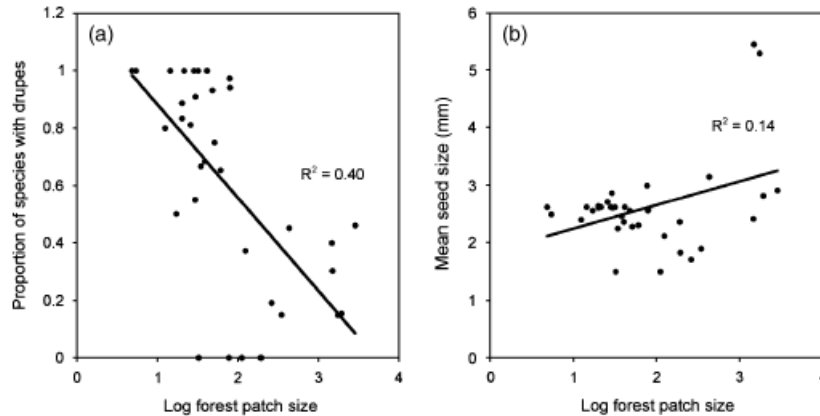
Fig. 6. Patterns of trait convergence found in communities of colonizer woody plant species in *Araucaria* forest patches of different patch sizes developing in a Campos grassland matrix. The diagrams relate community-level averaged traits (proportion of species with drupes and mean seed size) with log forest patch size. Drupe fruit type, but not mean seed size, was among the traits that maximized the expression of trait convergence on this gradient (see Table 2b).

correlated with forest patch size, although at a marginal significance, which can be interpreted as weaker evidence of TDAP than in the previous example.

Discussion

The results show that the method is able to discriminate TCAP and TDAP related to a specified set of ecological variables in community gradients. By scaling up trait-based data from the population to the community level, and testing by permutation against appropriate null models, the method can reveal TCAP and TDAP that are more likely functional for these gradients. This is especially important for TDAP, since finding divergence patterns is not as easy as for TCAP (Wilson 1999). Our method therefore fills an important gap in the literature, by allowing ecologists to search and test for TCAP and TDAP with field data, or with field data in combination with data drawn from trait databases (e.g., Knevel et al. 2003). The available methods either search for TCAP only (Dolédec et al. 1996; Legendre et al. 1997), or do not consider ecological gradients when looking for divergence. Most evidence of divergence patterns (Wilson & Roxburgh 1994; Stubbs & Wilson 2004; Mason & Wilson 2006) does not consider any explicit ecological gradient apart from within community variance in guild proportions, trait distances and other test statistics for limiting similarity, which for some traits were found to be more extreme than expected by chance, allowing only the suggestion of links between pattern and ecological gradients.

Further, the method used by Weiher et al. (1998) to relate trait dispersion to an environmental gradient may be limited when the same traits also show convergence.

There is consensus in the literature that both patterns of trait convergence and trait divergence exist in communities, but there is no consensus on the contexts in which trait convergence or divergence would be more relevant (Grime 2006; Wilson 2007). One hypothesis is that local disturbances enhance species coexistence and trait divergence, while productivity-related plant traits would be less variable on a local scale, and thus enhance the expression of trait convergence along productivity gradients (Thompson et al. 1996; Grime 2006). Environmental effects in our method are no longer a "nuisance, obscuring or mimicking the assembly rules" (Wilson 1999) but rather are the effects being searched for. By finding how TCAP and TDAP relate to ecological gradients, community ecologists may be able to state and test objective hypotheses on the links of patterns to community processes, and may be closer to finding assembly rules or constraints predicting community structure and ecosystem function.

Since, in our method, we find TCAP and TDAP that are linked to the specified ecological gradients, the lack of TCAP or TDAP related to the gradient considered in one context does not necessarily indicate there is no TCAP or TDAP related to other gradients, or to the same gradients but measured on a different spatial or temporal scale. Further, trait divergence may just as well arise by stochastic processes (Hubbell 2001; Ulrich 2004), in which case it would be evidenced by methods not taking into

account environmental gradients (e.g., Stubbs & Wilson 2004), but not by our method. That is, the sole fact that more similar organisms are found coexisting less often than expected at random may reveal divergence patterns that are unrelated to any known ecological factor. The TDAP we found by correlation to the ecological gradients may reflect real responses to these or other correlated ecological factors.

The described method is flexible and applicable under different data frameworks. We now summarize some of its strengths. It applies to traits measured using different scales (binary and quantitative). The OTUs may be taxonomic units, such as species, or may be individuals or local populations, in which case the study of community patterns related to within-species variation is allowed. Community data may contain presence-absence or quantities. The proposed iterative algorithm may find trait subsets maximizing the expression of either TCAP or TDAP related to specified ecological variables. Further, and above all, since the community components are fuzzy weighted by the traits, the method is applicable to identify TDAP of a priori types, such as species. Grouping species into functional types is not a prerequisite for distinguishing TDAP and, obviously, is not needed for TCAP. If the types were not fuzzy weighted by the traits, we could not define TDAP of species and identify the traits most responsible for the pattern. As in our study cases, TDAP of species can be identified and then the species further classified in PFTs based on the traits, but this is not part of the method for discriminating TCAP and TDAP. Finding TDAP of species is particularly advantageous because the patterns are not dependent on the partition level used to identify PFTs (Pillar & Sosinski 2003).

Phylogenetic relationships among the OTUs may also influence to some degree the assembly patterns in response to environmental gradients (Westoby et al. 1995; Duarte et al. 2007). Procedures for controlling phylogeny on species traits could be employed prior to analyses (e.g., Duarte et al. 2007), but whether this would be the most appropriate way to evaluate the influence of phylogeny on community assembly patterns remains an open question.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed computations for the examples using artificial data presented in Fig. 2. The data show (a) maximum expression of trait-convergence assembly pattern (TCAP), (b) trait-divergence assembly pattern (TDAP), or (c) both TCAP and TDAP.

Appendix S2a. Traits revealing TDAP maximally related to nitrogen levels and the corresponding PFTs (groups of species) identified by cluster analysis.

Appendix S2b. Traits revealing TDAP maximally related to grazing levels and the corresponding PFTs (groups of species) identified by cluster analysis.

Appendix S3. Plant traits in woody plant species colonizing *Araucaria* forest patches of different development stages.

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