Research

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Assessing the functional turnover of species assemblages with tailored dissimilarity matrices

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It is often suggested that community functional diversity is an appropriate predictive measure of ecosystem functioning, particularly if relevant species traits for the ecological property of interest are carefully selected. However, methods for selecting traits are often based on expert knowledge or on theoretical models of ecosystem functioning, but usually do not include explicitly developed quantitative procedures. Here we propose to construct a so-called 'tailored dissimilarity matrix' between species assemblages to emphasize their functional turnover in response to some user-defined ecological property.

First, a subset of community weighted mean trait values (CWM) is selected by stepwise regression on the ecological process of interest. The selected CWM values are then replaced by the residuals of the least-squares regressions of each single CWM on the ecological process of interest and pairwise Euclidean distances between the residual values at each sampling site are calculated. We illustrate the advantages of the tailored approach using two distinct plant and bee communities under contrasting fire regimes in temperate forests of southern Switzerland. Our results demonstrated that, unlike for the original CWM values, the tailored approach optimized the degree of functional differentiation among bee and plant species assemblages, i.e. the species functional turnover, with respect to different fire regimes.

Functional diversity is increasingly identified as an important concept in ecology for studying the effects of community structure on ecosystem functioning (Hooper et al. 2005, Grime 2006). In its broadest sense, functional diversity can be defined as the range and distribution of trait values in a community (Díaz and Cabido 2001, Tilman 2001).

Several studies have concluded that functional diversity tends to correlate more strongly than traditional species-diversity with ecosystem functions such as productivity (Tilman et al. 1997, Hooper and Dukes 2004, Petchey et al. 2004, Hooper et al. 2005), resilience to perturbations or invasion (Dukes 2001, Bellwood et al. 2004), and regulation in the flux of matter (Waldbusser et al. 2004).

To summarize the range and distribution of trait values in a given community, a variety of measures have been proposed which include a priori classifications of species into a reduced number of functional groups, the sum (Walker et al. 1999) or average (Botta-Dukat 2005, Ricotta 2005, Schmera et al. 2009) of functional distances between species pairs in multivariate functional trait space, and distances between species along hierarchical and non-hierarchical classifications (Petchey and Gaston 2002, Ricotta and Moretti 2008).

Recently, Mason et al. (2005) and Villéger et al. (2008) argued that functional diversity cannot be adequately summarized by a single index. Instead they proposed to quantify three separate components of diversity: functional richness, functional evenness, and functional divergence. This classification is similar to the distinction between species richness and evenness in species-diversity studies (Ricotta 2007). Likewise, Lepš et al. (2006) argue that the range and distribution of values within single traits is often the most ecologically relevant information in examining the mechanisms linking community structure to ecosystem functioning (Mason et al. 2003).

However, no matter how the community functional organization is summarized, functional differences among species must always be quantified on the basis of some species traits. This raises the important methodological question of how many and which traits to use, how to weight them, how to combine them (with different scales) and whether biological conclusions are sensitive to such choices (Lepš et al. 2006, Lavorel et al. 2008, Poos et al. 2009).

In this framework, a critical point is the selection of relevant functional traits (Pillar and Sosinski 2003, Weigelt et al. 2008, Pavoine et al. 2009). Knowledge may come from sources as different as observational or experimental studies, expert knowledge or theoretical models of community and ecosystem functioning (reviewed by Petchey and Gaston 2006). However, in spite of this large variety of approaches, these functional relationships often remain obscure. For instance, in examining the effects of diversity on ecosystem functioning, the basic assumption is that functionally similar assemblages have similar ecological properties, such that two species assemblages are said to be functionally similar if they resemble each other with respect to some user-defined ecological property. In principle, increasing the dimensionality of functional spaces by the progressive use of more diverse and mutually uncorrelated (or minimally correlated) traits leads to a more accurate estimate of similarity. Nonetheless, the use of increasingly higher dimensional spaces suffers from the fact that these enhanced spaces usually do not have any intrinsic biological relationship to the property that we are attempting to estimate. For this reason we need to develop functional spaces that are strongly associated with the ecological property of interest.

Largely unknown to ecologists, researchers involved in biostatistics and chemometrics have made significant advances in developing 'tailored' (sensu Gute et al. 2002) or 'supervised' (sensu Pollard and van der Laan 2008) multivariate spaces derived from collections of parameters that optimize their association with a priori-selected properties. The purpose of our paper is thus to describe a general approach for quantifying pairwise functional dissimilarity between species assemblages emphasizing the turnover of these in response to some user-defined ecological property. As an illustration of the method we focus on changes in functional trait composition of diverse bee and plant communities along a post-fire successional gradient expressed in time elapsed since the last fire in temperate chestnut forests of southern Switzerland.

Methods

Study area

The study took place in an area of uniform south-facing slopes (450–850 m a.s.l.) extending over 165-km^2 in the Locarno region, southern Switzerland (46°09′N, 08°44′E). The vegetation is dominated by stands of former coppice of European chestnut *Castanea sativa*. The climate is mild with wet summers and relatively dry winters. Further details on the study area are given in Moretti et al. (2002) and Moretti and Legg (2009). The study area is a fire prone region that is mainly characterized by fast-spreading surface fires of low-medium intensity that occur during the winter dry period, coinciding with vegetation dormancy (December to April). These fires maintain a mosaic of vegetation patches with different post-fire ages (Moretti et al. 2009), which are considered to be of conservation importance according to the European Habitat Directive of 1992. After fire, trees recover to a full canopy within 15–20 years (Delarze et al. 1992).

Table 1. Description of the study sites. The sites are assigned to one of four categories based on broad vegetation types along the successional gradient of time elapsed since the last fire.

Fire categories	Site code	Years since last fire	Site description
Freshly burned	1–2	0	bare soil, standing dead trees, luxuriant herb and scrub layer (DBH < 5 cm).
	3	1	
	4–5	2	
Intermediate	6–7	6	dense chestnut *Castanea sativa* coppice stand with high number of dead young shoots (DBH 5–10 cm).
	8	7	
	9–10	10	
	11	14	
	12	17	
Mature	13	22	mature coppice stand with dense canopy cover (DBH 15–20 cm).
	14–15	24	
Unburned	16–21	⩾35	old coppice stand out of turn with dense canopy cover (DBH 20–30 cm).

DBH = diameter at breast height.

Sampling design

We chose 21 sites with different times elapsed since the last fire (from 0 to > 35 years; Table 1). Fire-history data were obtained from the National and regional wildfire data base, and dendrochronological methods. We avoided pseudoreplication, by choosing, wherever possible, sites with similar fire regimes in different portions of the study area (Moretti et al. 2006). The 21 sites were tested for spatial independence of species assemblages using Mantel correlogram and permutation tests (see Moretti et al. 2006 for more details) so they were treated as independent in the present analyses.

Bees were sampled using window (interception) traps combined with yellow water-filled pans and placed 1.5 m above-ground; at each of the 21 sites, three window traps were installed (distance between sites ca 300 m). The traps were emptied weekly from March to September 1997. For further details, see Moretti et al. (2004). All adult bees were identified to species level. Each species was described in terms of 24 functional traits belonging to nine trait groups (Table 2). The selection of traits was based on characteristics that are recognized as important in bee autoecology (Westrich 1989, Michener 2000) and among those that relate to different ecosystem processes (Biesmeijer et al. 2006, Fontaine et al. 2006).

In each site vascular plants were sampled using a seven-point species cover–abundance scale (Braun-Blanquet 1964) within three 10 × 10 m quadrats. The quadrats were recorded in May–June and again in August in order to identify as many species as possible and to include species with different phenologies. Plant species were described in terms of 27 functional traits belonging to 13 trait groups (Table 3). The selected plant traits are widely-used traits relevant to most taxa, and are based on well-articulated methodologies and consistent measurement.

Functional trait composition

To assess the functional trait composition of plants and bees at each sampling site we combined the species by sites matrix of each species group with the corresponding species by traits matrix. This was done by calculating the community-weighted mean trait values (CWM) at each site as the average of trait values weighted by the relative abundances of each species (Garnier et al. 2004, Lepš et al. 2006, Moretti et al. 2009). This metric is often understood as defining the dominant traits in a community and is computed simply as:

$$\mathrm{CMW}_{jk} = \sum_{i=1}^{S} p_{ik} x_{ij} \tag{1}$$

Table 2. Description of the bee functional traits used in the study. Traits were described for each species according to published sources or researcher expertise (where published information for a particular species was not available).

Bee functional group/trait	Data type	States
1. Nesting specialization		
No nest building	binary	boolean 0/1 variables
Excavator in the ground	binary	
Excavator in woody substrate	binary	
Building nest with mud	binary	
Renter on the ground, particularly in snail shells	binary	
Renter of pre-existing nest and holes above the ground	binary	
2. Parasitic status		
Cleptoparasitic (i. e. solitary parasitic bee)	binary	boolean 0/1 variables
Social parasitic	binary	
Non-parasitic	binary	
3. Pollen transport		
Carried 'accidentally' on body	binary	boolean 0/1 variables
Carried internally in the crop	binary	
Carried on the legs	binary	
Carried on legs and body	binary	
Carried on the underside of abdomen	binary	
4. Habitat specialization	ordinal	1. generalist; 2. intermediate; 3. specialist
5. Flower access	ordinal	1. restricted to tubular flowers; 2. both tubular and open flower types; 3. open flowers
6. **Feeding specialization**	ordinal	1. no lectic status (= no feeding specialization)[a]; 2. polylectic[b]; 3. oligolectic[c]; 4. monolectic[d]
7. Social status	ordinal	1. solitary; 2. variable; 3. social
8. Flight phenology		
Flight season start	quantitative	month
Flight season end	quantitative	month
Mean flight duration	quantitative	no. of months
9. **Dispersion**	quantitative	inter-tegula distance (μm)

[a]having no pollen collecting requirements (i.e. a cleptoparasite); [b]pollen collecting on a number of species from different plant families; [c]pollen collecting restricted to plants within the same plant family; [d]pollen collecting at a single species. The functional traits selected by stepwise forward regression are shown in bold character (see the section: 'Construction of tailored dissimilarity matrices').

where CWM_{jk} is the community-weighted mean value of trait j at site k, p_{ik} is the relative abundance of species i (i = 1, 2, …, S) at site k, and x_{ij} is the value of trait j for species i. This operation generated new traits by sites matrices for each species group. For insect count data, a $\log_{10}$ transformation of the number of individuals of each species was used to reduce the effect of extreme values and the higher abundances of dominant species (de Bello et al. 2007); for plant abundance data the seven-point Braun-Blanquet ordinal scale was used. Here it is worth noting that as ordinal scales assign values to objects based on their ranking with respect to one another, it is immaterial which end of the scale is assigned the high values or the low values; the only important thing is that the relative positions of objects in the ranking sequence is respected.

All species singletons occurring only in one site were removed to exclude casual occurrences from the analysis. Binary and ordinal variables were handled as quantitative variables; all CWM values were computed with an Excel macro freely available at: <http://botanika.bf.jcu.cz/suspa/FunctDiv.php> (Lepš et al. 2006) and scaled between 0 and 1.

Construction of tailored dissimilarity matrices

Our goal was to apply the 'tailored' approach for constructing two matrices of pairwise dissimilarities among sampling sites that emphasize the functional response of bees and plant communities to post-fire succession. The procedure for constructing such tailored dissimilarity matrices is derived in three steps (Fig. 1). Firstly (step 1), we used simple forward stepwise regression to select a subset of N out of the original community weighted mean traits for each species group that 'best' explains the dependent variable of interest (i.e. time since last fire). In step 2, the matrices of 21 sites per N CWM values retained by stepwise regression are transformed to form new multivariate matrices of 'functional association profiles' (Pollard and van der Laan 2008) that explicitly relate the individual sites to the time since last fire. This transformation is achieved by substituting for each out of the N selected functional traits, the original CWM values with the corresponding residuals of the (univariate) least-squares regression of CWM versus the time since last fire. As residuals are widely used in statistics for assessing subject-specific contributions, for regressions with a decent fit, species assemblages with similar association profiles (i.e. similar residual values for the selected functional traits) are intuitively thought to resemble each other with respect to the ecological property of interest (Pollard and van der Laan 2008). For instance, for traits of little function-specific relevance, there should be no particular pattern in the residuals such that the observed differences among species assemblages are due to mere random oscillations. Conversely, for relevant traits with a strong connection

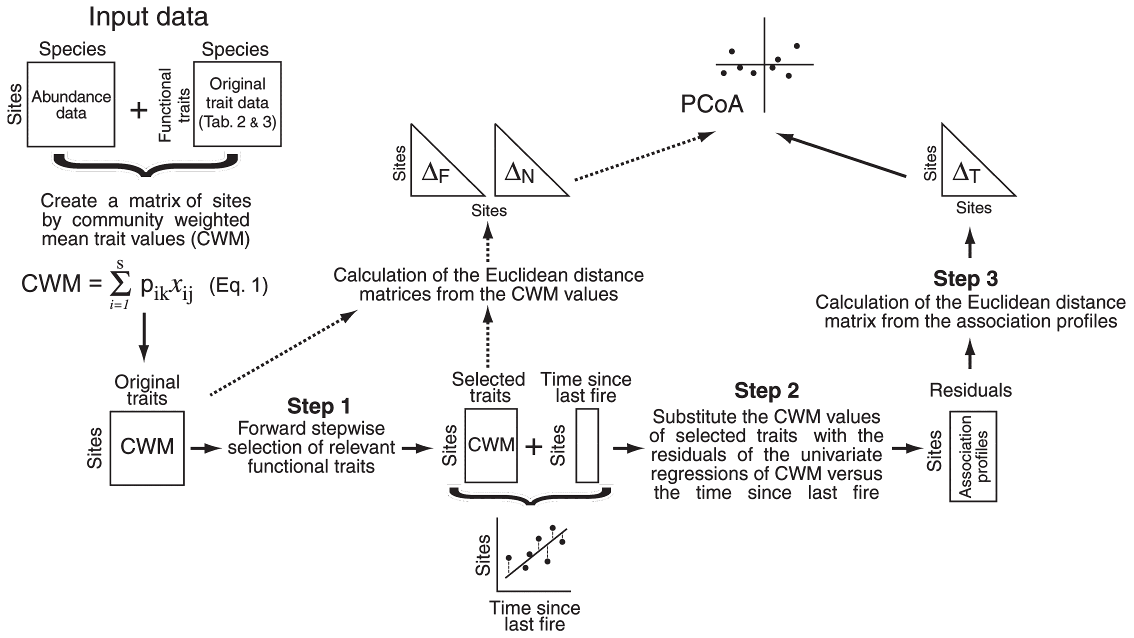

Figure 1. Diagram showing the step-by-step statistical method. Black arrows show the proposed method for constructing the tailored dissimilarity matrix Δ_T, dotted arrows show the alternative pathways used for comparison.

to the function of interest, significant positive autocorrelation in the residuals is expected, such that assemblages with similar residuals will demonstrate, on average, consistent functional behavior. Finally (step 3), pairwise Euclidean distances between the association profiles of each sampling site were calculated for both species groups. To test the performance of the tailored distance matrices Δ_T in maximizing the association between the functional attributes of plants and bees at each sampling site and the time since last fire, we compared Δ_T with two additional matrices obtained by computing pairwise Euclidean distances between species assemblages from the CWM values of: 1) the full set of all original functional traits in Table 2 and 3 (Δ_F), and 2) the subset of N functional traits selected with the stepwise regression procedure (Δ_N). The association of Δ_T with Δ_F and Δ_N was then compared by simple visual inspection of the two-dimensional ordination plots of a principal coordinate analysis (PCoA), which is the natural choice if ordination is done from a dissimilarity matrix (Anderson 2006). All ordinations were performed with the program package SYN-TAX 2000 (Podani 2001).

Results

Bee assemblages

In the study area we collected 145 bee species. About half of the dominant and subdominant species shifted in relative abundance along the post-fire successional gradient. *Andrena minutula* was the most abundant species in all successional stages. *Lasioglossum morio* was dominant during the early post-fire stages and its abundance decreased gradually as succession proceeded, while *A. mellifera*, a sub-dominant species immediately after fire, became dominant in the unburned sites. Overall, species richness declined with time elapsed since fire (Moretti et al. 2009).

From a functional viewpoint, in unburned sites, bees tended to be long-distance dispersers (with large inter-tegula distances), non-parasitic, feeding specialists, transporting pollen on the abdomen, and being active early in spring and for a long time during the vegetation season. Fire affected the functional organization of bee assemblages in several ways. Freshly burned sites were characterized by species that start and finish flying late in the season and with more than one generation per year. Bees at freshly burned sites were short-tongued, solitary, low-dispersal species, and displaying diverse modes of pollen transport, in particular internally in their crop. They also displayed several nesting specialization, with a high proportion of species excavating their nests in wood and nesting in existing cavities.

For bees, seven out of the original 24 functional variables in Table 2 were selected by stepwise regression; these variables included one ordinal trait (feeding specialization), three quantitative traits (start and end of the flight season, and inter-tegula distance), and three binary traits (renter on the ground, non-parasitic status and pollen transport on the abdomen). In the ordination plots of Δ_F and Δ_N (Fig. 2) the four fire categories are mixed with each other, but this is not the case with the residuals. For instance, the ordination plot of Δ_T shows a strong quasi-linear gradient that relates the functional organization of the bees assemblages to the time elapsed after fire. Accordingly, if pairwise functional distances are computed from the association profiles of the species assemblages, roughly 87% of the system variance is related to the first principal ordination axis. This gradient is not evident when all functional traits are used, nor when the distance matrix is calculated from the seven CWM values selected by stepwise regression.

Plant assemblages

We recorded 94 vascular plants. Several plant species were sampled separately in the tree, shrub and herb strata, amounting

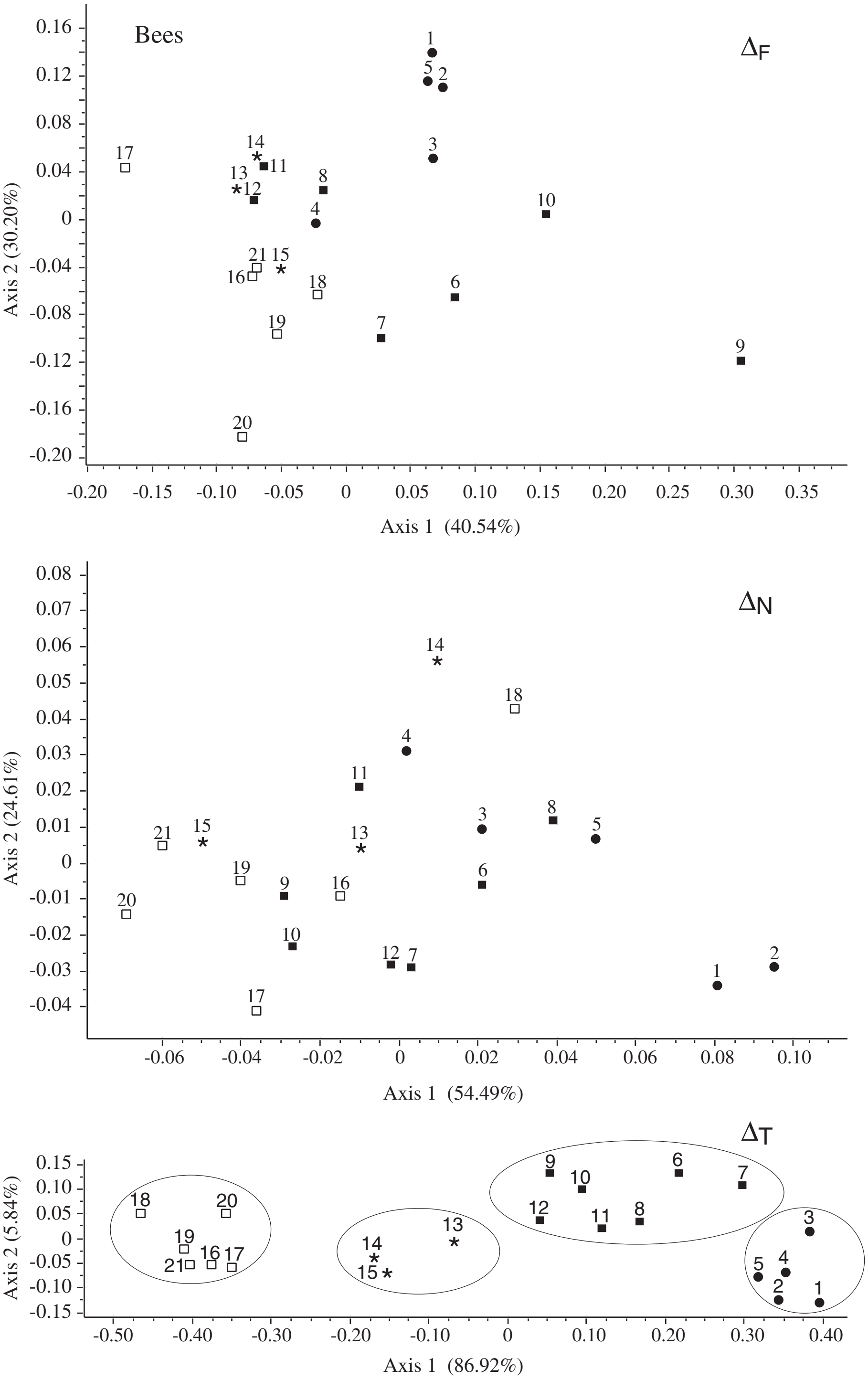

Figure 2. Two-dimensional ordination plots for bees of a principal coordinate analysis (PCoA) on the distance matrices Δ_F (obtained from all CWM traits), Δ_N (obtained from stepwise selection of the original CWM traits), and Δ_T (obtained from the linear regression residuals of the selected traits; see Methods and Fig. 1). For each matrix the numbers in brackets are the percentages of system's variance associated with the principal coordinate axes. The ellipses in the third ordination plot represent the four fire categories of Table 1. Black circles represent the sampling sites belonging to the first fire category (FC1), black squares belong to FC2, asterisks to FC3, and white squares to FC4.

to a total of 120 recorded plant types; 23 types were recorded on average per site. Unburned sites were mostly characterized by late successional stage forests with a closed and diverse tree canopy (e.g. *Castanea sativa* woodlands with *Prunus avium, Robinia pseudacacia, Tilia cordata* and *Sorbus aria*), as well as shade tolerant and evergreen species, like *Hedera helix, Prunus laurocerasus, Trachicarpus fortunei* or *Dryopteris borreri*. Conversely, more recently burned sites tended to have more open canopies with denser bush and grass cover. *Castanea sativa* together with *Molinea littoralis* and *Pteridium aquilinum* were the most abundant species at all successional stages, while *Teucrium scorodonia*, *Rubus* sp. and *Cytisus scoparius* increased in abundance during the early post-fire stages and decreased rapidly afterwards. *Betula pendula* and particularly *Quercus petraea* were typical subdominant species of late successional stages.

From a functional viewpoint, unburned sites were associated with shade-tolerant perennial forest species, with short flowering duration, pollinated by wind, and with large seeds dispersed by animals. Recent fires were associated to annual plant species, especially ruderal geophytes and therophytes with long flowering duration, pollinated by insects, and with very light seeds dispersed by wind. Plant species tolerant of high temperatures decreased with time since last fire, while shade-tolerant plants increased with time since fire.

For plants, 15 out of the original 27 functional traits of Table 3 were selected by stepwise regression, including seven ordinal traits (life form, sprout insulation, lateral spread, and Ellenberg's indicator values: humidity, reaction, nitrogen, and light), three quantitative traits (flowering duration and Grime's S and R strategy types), and five binary traits (pollinated by wind, zoochorous and anemochorous dispersal, and two habitat types: most commonly present in cultivated areas or in shrublands).

In the ordination plots of Δ_F and Δ_N (Fig. 3) the group of freshly burned sites separates from the others more sharply than in the ordination of Δ_T, while the remaining three fire categories are indistinguishable from each other. This is because, species in freshly burned sites are usually annual species with a more ruderal character and longer flowering duration than species of less recently burned sites. Nonetheless, like for bee assemblages, if functional distances between sites are computed

Table 3. Description of the plant functional traits used in the study. Traits were described for each species according to published sources or researcher expertise (where published information for a particular species was not available).

Plant functional group/trait	Data type	States
1. Habitat, i.e., species most commonly present in:		
rocky areas (R)	binary	boolean 0/1 variables
cultivated areas (A)	binary	
meadows (M)	binary	
shrublands (S)	binary	
forests (F)	binary	
2. Pollen vector*		
pollinated by wind	binary	boolean 0/1 variables
pollinated by animals	binary	
3. Agent of dispersal		
anemochorous	binary	boolean 0/1 variables
zoochorous	binary	
4. Ellenberg Indicator values:		
temperature (T)	ordinal	ordinal integers, ranging from a low score of 1 to a high score of 9
continentality (K)	ordinal	
nitrogen (N)	ordinal	
reaction (pH)	ordinal	
humidity (F)	ordinal	
light (L)	ordinal	
5. Maximum height	ordinal	1. herbs and sub-shrubs (<150 cm); 2. shrubs 150–300 cm; 3. trees (>100 cm)
6. Seed weight	ordinal	0. no seed produced; 1. seed too small to be measured; 2.<0.2 mg; 3. 0.2–0.5 mg; 4. 0.5–1.0 mg; 5. 1.0–2.0 mg; 6. 2.0–10.0 mg; 7. >10 mg
7. Leaf persistence	ordinal	1. aestival green; 2. partial evergreen; 3. evergreen
8. Life history	ordinal	1. annual; 2. usually biennial; 3. perennial
9. **Life form**	ordinal	1. phanerophyte and nano-phanerophyte; 2. ph-ch; 3. chamaephyte; 4. ch-h; 5. hemicryptophyte; 6. h-g; 7. geophyte; 8. therophyte
10. **Sprout insulation**	ordinal	1. vulnerable to fire damage; 2. moderately vulnerable; 3. moderately insulated; 4. well insulated
11. **Lateral spread**	ordinal	1. therophytes, lateral spread of exceedingly limited extent and duration; 2. perennials with compact unbranched rhizomes or forming small tussocks (Ø 10 cm); 3. perennials with rhizomatous systems or large tussocks (Ø 10–25 cm); 4. perennials attaining Ø 25–100 cm; 5. perennials attaining Ø > 100 cm
12. Grime's CSR strategy		
competitor (C)	quantitative	fuzzy coded values ranging from 0 to 100 such that C+S+R = 100
stress tolerant (S)	quantitative	
ruderal (R)	quantitative	
13. Flowering phenology:		
flowering start	quantitative	month
flowering duration	quantitative	no. of months

*For the purposes of this study ferns were included with wind-pollinated plants since the dispersal of spores that ensures genetic mixing is primarily through wind and no association with pollinating insects is expected. The functional traits selected by stepwise forward regression are shown in bold character (see the section: 'Construction of tailored dissimilarity matrices').

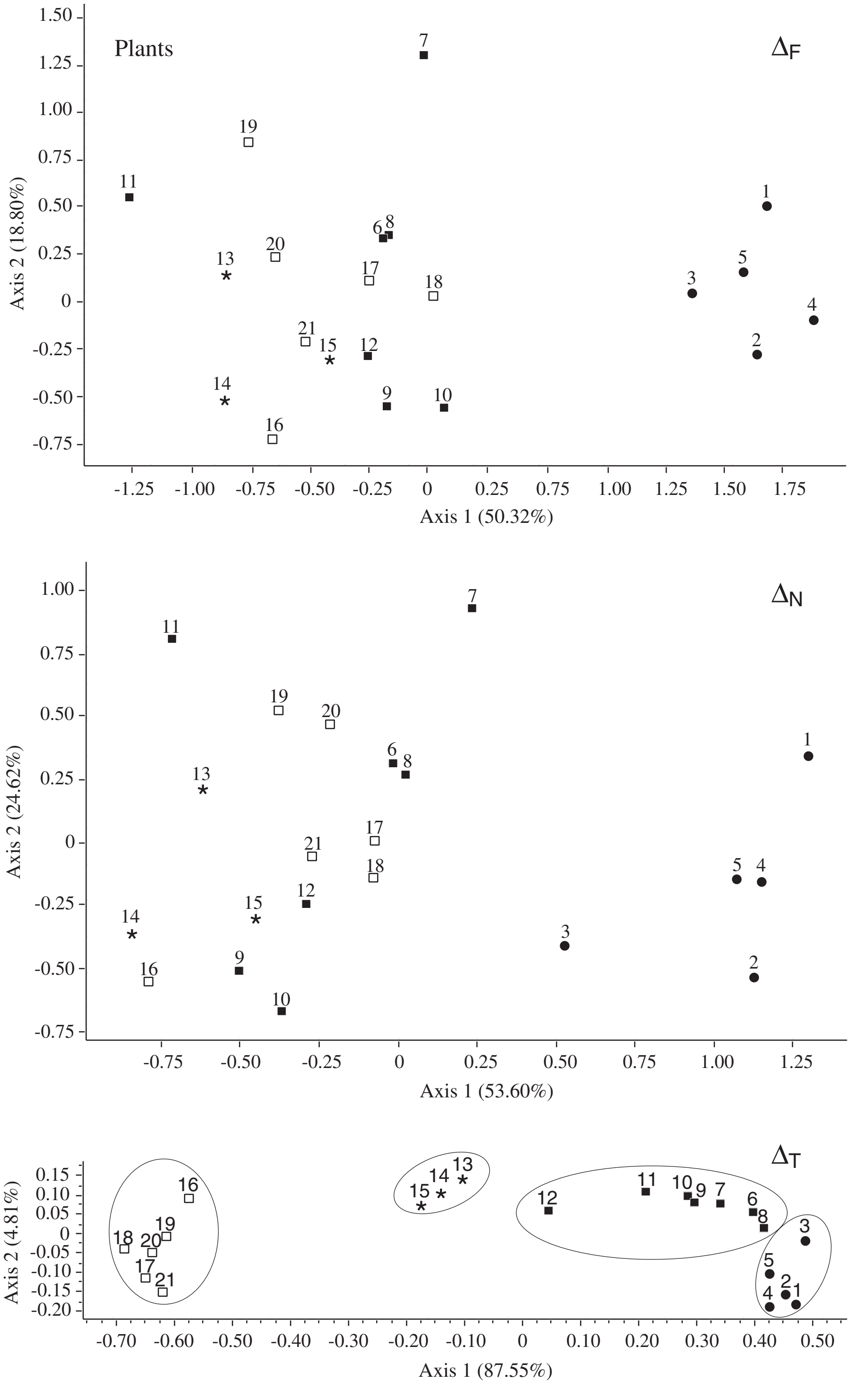

Figure 3. Two-dimensional ordination plots for plants of a principal coordinate analysis (PCoA) on the distance matrices Δ_F (obtained from all CWM traits), Δ_N (obtained from stepwise selection of the original CWM traits), and Δ_T (obtained from the linear regression residuals of the selected traits; see Methods, and Fig. 1). For each matrix the numbers in brackets are the percentages of system's variance associated with the principal coordinate axes. The ellipses in the third ordination plot represent the four fire categories of Table 1. Black circles represent the sampling sites belonging to the first fire category (FC1), black squares belong to FC2, asterisks to FC3, and white squares to FC4.

from the transformed data, most of the variance of Δ_T is associated to the first axis of the corresponding ordination plot (Fig. 3). This result emphasizes a clear ecological pattern that would not have been emerged without an appropriate data transformation with the freshly burned sites located at one extreme of the gradient and the unburned sites at the opposite end.

Discussion

There is still considerable debate about how the functional organization of biological communities should be measured (Petchey and Gaston 2006, Podani and Schmera 2006, Poos et al. 2009). Such debate is nourished by the fact that since traditional diversity measures condense the information of multivariate datasets of high dimensions with single scalars based on distinct objectives and motivations, information is inevitably lost and there is no perfect function capable of uniquely characterizing all aspects of functional diversity. Also, as emphasized by a number of authors (Lepš et al. 2006, Lavorel et al. 2008), in functional ecology studies, method can affect the sign and the strength of the connection of diversity with ecosystem functioning. Consequently, it is critical to define the appropriate functional traits and their relative weighting.

Recently, Weigelt et al. (2008) used a weighted version of Rao's quadratic diversity to find which type of functional traits in experimental grassland communities is most strongly correlated with spatial variability of aboveground biomass production. They found that the relationship between the spatial stability in biomass production and species diversity within experimental plant communities is mainly controlled by two traits: rooting depth and clonal growth form, which have a biomass-stabilizing effect. In contrast, the observed relationship was only weakly supported when other functional components of diversity were considered. More generally, well-targeted traits with direct relation to the ecological properties of interest are usually better predictors of community behavior than less relevant traits, such that the selection of the most appropriate traits needs to be specific to target function and ecological processes (Lepš et al. 2006, Petchey and Gaston 2006, Pavoine et al. 2009).

In this paper, rather than proposing an additional scalar measure of functional diversity, we followed the approach of Lepš et al. (2006) that the range and distribution of values within single traits is frequently the most appropriate information in analyzing the relationships between community structure and ecosystem functioning and suggested a method for constructing pairwise functional dissimilarity matrices between species assemblages in terms of their association with some user-defined ecological property. Beginning from an original set of CWM values per species assemblage, we first used stepwise regression to select the traits carrying the most significant information on the ecological property of interest (i.e. post-fire succession). Next, for the subset of N functional traits retained by the stepwise regression, we fitted a linear regression model for each CWM versus the time since last fire. Finally, we used the N-dimensional vectors of linear regression residuals to calculate a tailored distance matrix among sampling sites aimed at optimizing the degree of functional differentiation among bee and plant communities with respect to different fire regimes. After constructing the tailored dissimilarity matrix, standard ordination or clustering methods can be applied to identify subpopulations of related samples with similar behavior with respect to some user-defined ecological property (Pollard and van der Laan 2008). Based on these sample groups, it would then be possible to identify both indicator and keystone species that are related to particular ecological or functional properties of the ecosystem.

In the context of our study, we focused on changes in functional trait composition of diverse plant and bee communities in contrasting fire-driven systems in temperate chestnut forests of southern Switzerland. According to our results, fire reduces canopy cover and induces physical and chemical changes to the soil that may be important throughout the post-fire succession. It is not surprising that the time elapsed since the last fire selected plant traits related to the physical-chemical soil properties by promoting low-nitrogen and drought-tolerant plant species, as well as species adapted to a more continental climate that tolerate fluctuations in temperature. Also, for bees, post-fire conditions selected traits related to feeding resources (e.g. feeding specialization and seasonal flight start and duration), nesting conditions (e.g. nest renter on the ground), and dispersal strategies to best use overall available resources.

As shown with our data, tailored dissimilarity spaces seem to be a promising tool for examining the effects of CWM's response to stressors on ecosystem functioning by testing hypotheses on the effect that the observed shift in CWM of a particular trait or trait group might have on the ecosystem function. According to Mokany et al. (2008) shift in mean trait values (CWM) largely determine ecosystem processes. To this regard, the tailored approach and his performance in highlighting shifts in community trait assemblages caused by a particular stressor might be crucial for the early warning of possible changes in ecosystem function and related key species at the early stage of an environmental change.

While ordination based on pairwise distances between the full set of CWM values are only a sub-optimal tool for detecting the species functional turnover with respect to different fire regimes, tailored dissimilarities seem appropriate to emphasize these effects. The high amount of system's variance associated to the first PCoA axis obtained from the ordination of the matrix of transformed data Δ_T clearly indicates a strong structured response of both communities (plants and bees) with regard to the ecological process of interest and the importance of residual analysis for summarizing such response. For instance, while classical linear regression analysis usually assumes that the residuals are statistically independent of the predictor variables, here we hypothesize that for relevant traits that are strongly connected to the function of interest, there is a tendency for residuals of similar size and sign to be clustered together showing a positive association in the error of one observation with the error of the next. For our data, the Durbin–Watson statistic that is usually applied for evaluating the presence of a serial correlation of residuals from a regression analysis (i.e. whether or not residuals for adjacent observations are correlated, indicating that the observations in the data file are not independent) indicates that there is statistical evidence of positive residual correlation for all selected functional variables for plants and bees at the $p < 0.05$ level. Accordingly, if consistent group of assemblages with similar residuals exist, it can be hypothesized that a significant relationship between community organization and ecosystem functioning is present.

As concerns the strategy adopted for selecting the relevant functional variables, some researchers may argue that the classical forward stepwise regression method adopted in this paper is not necessarily the most adequate procedure. For instance, though forward regression has the great advantage of being applicable even when the initial data set contains more explanatory variables than sites, it is known to be overly liberal in the inclusion of highly correlated explanatory variables in the regression model, thus leading to an inflated type I error (Blanchet et al. 2008).

However, our ultimate aim is not to obtain the most parsimonious multiple regression model between functional traits and age since the last fire, but rather to identify a set of traits that is functionally related to the dependent variable. The residuals of the univariate linear regressions between the selected traits and the dependent variable are then used to construct a function-specific pairwise distance matrix among sampling sites that optimizes their relationship with the dependent variable itself. While this relationship may be of little evidence if only a small number of traits is used, the combination of many function-related traits will possibly reinforce the observed pattern even in presence of a high degree of collinearity. In this framework, we consider the selection of all relevant functional traits more important than model parsimony. Nonetheless, those who believe variable selection should rely on more parsimonious models should adopt different selection methods, like Akaike criteria (Burnham and Anderson 2002) or the modified forward selection procedure proposed by Blanchet et al. (2008).

Also, as concerns the metric used for computing the dissimilarity matrix among sampling sites, we used the Euclidean distance, which is one of the most commonly recommended distances to measure functional dissimilarity based on trait values (Mouchet et al. 2008). Though the Euclidean distance is known to be affected by scale differences among the selected variables giving at the same time excess weight to correlated variables, in our case all CWM values were scaled between 0 and 1, while, as discussed in the previous paragraphs, variable correlation is not necessarily seen as a major drawback. Nonetheless, as the choice of the distance measure used for constructing the tailored dissimilarity matrix may significantly affect the results obtained, a more complete approach would consist in testing all combinations of distances and clustering methods (including consensus trees), and then selecting the most reliable one (Mouchet et al. 2008).

Finally, though our principal aim is not to propose a new diversity measure, it is worth noting that, according to Whittaker (1972), any pairwise dissimilarity matrix among species assemblages is a meaningful expression of beta diversity (Legendre et al. 2005, Ricotta and Marignani 2007, Ricotta and Burrascano 2008, Schmera et al. 2009). It follows that tailored dissimilarity matrices may represent a significant step forward in the direction of constructing beta diversity measures that summarize the degree of functional differentiation among species assemblages, or functional turnover, with respect to a given ecological property of interest.

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