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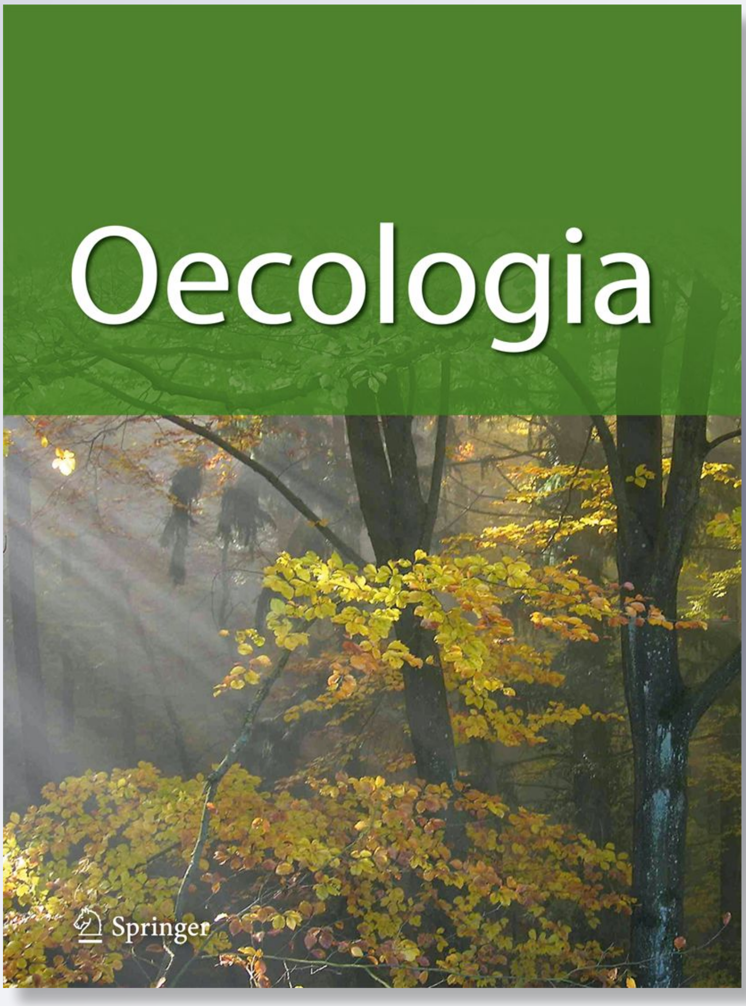
Oecologia

ISSN 0029-8549
Volume 167
Number 1

Oecologia (2011) 167:181-188
DOI 10.1007/s00442-011-1965-5



Oecologia (2011) 167:181–188
DOI 10.1007/s00442-011-1965-5

COMMUNITY ECOLOGY - ORIGINAL PAPER

CWM and Rao's quadratic diversity: a unified framework for functional ecology

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Received: 21 October 2010 / Accepted: 3 March 2011 / Published online: 22 March 2011

Abstract Assessing the effects of environmental constraints on community structure often relies on methods that consider changes in species functional traits in response to environmental processes. Various indices have been proposed to measure relevant aspects of community trait composition from different viewpoints and perspectives. Among these, the 'community-weighted mean trait value' (CWM) and the Rao coefficient have been widely used in ecological research for summarizing different facets of functional composition and diversity. Analyzing changes in functional diversity of bee communities along a post-fire successional gradient in southern Switzerland we show that these two measures may be used to describe two complementary aspects of community structure, such as the mean and the dispersion of functional traits within a given species assemblage. While CWM can be adequately used to summarize shifts in mean trait values within communities due to environmental selection for certain functional traits, the Rao coefficient can be effectively applied to analyze patterns of trait convergence or divergence compared to a random expectation.

Communicated by Roland Brandl.

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Keywords Ecological gradient · Environmental filters · Functional convergence/divergence · Niche space · Trait dispersion · Trait mean

Introduction

The concept of functional diversity has received considerable attention in community ecology because it captures information on species functional traits that is absent in measures of species diversity. We assume that species make a difference in the functioning of the ecosystem because of their differences in traits. Therefore, as species differ from one another in functionally important ways (Petchey and Gaston 2002), measures of community functional composition and diversity tend to correlate more strongly than those of traditional species-diversity with ecosystem functions, such as productivity (Petchey et al. 2004; Hooper et al. 2005), resilience to perturbations (Moretti and Legg 2009; Ricotta and Moretti 2010), or regulation of biogeochemical fluxes (Waldbusser et al. 2004).

The observed effects of species traits on ecosystem functioning raises the important question of how to measure functional composition and diversity (Lepš et al. 2006; Lavorel et al. 2008; Poos et al. 2009). To summarize the range and distribution of trait values in a given community, a variety of measures have been proposed (see Petchey and Gaston 2006 for a review). These indices include a priori classifications of species into functional groups, the sum (Walker et al. 1999) or average (Izsák and Papp 2000; Botta-Dukat 2005; Ricotta 2005; Schmera et al. 2009) of functional distances between species pairs in multivariate functional trait space, or dendrogram-based measures (see Petchey and Gaston 2002).

However, despite the number and variety of indices, no consensus has arisen on the sensitive question of how to measure the functional composition and diversity of a given community (Petchey and Gaston 2006; Villéger et al. 2008). Mason et al. (2005) and Villéger et al. (2008) argued that functional diversity cannot be adequately summarized by a single index and developed a classification of functional diversity indices with three types: functional richness, functional evenness, and functional divergence. According to Villéger et al. (2008), functional richness measures the amount of multidimensional trait space filled by the species in the community, functional evenness measures the evenness in the distribution of abundance in trait space, while functional divergence calculates the degree to which abundance distribution in multivariate trait space maximizes divergence in functional characters within the community.

Other researchers (e.g., Garnier et al. 2004; Lepš et al. 2006; Lavorel et al. 2008; Ricotta and Moretti 2010) claim that the range and distribution of values within single traits frequently provide the most appropriate information to analyze the relationships between community structure and ecosystem functioning. Garnier et al. (2004) proposed summarizing the functional composition of single traits with so-called 'community-weighted mean trait values' (CWMs), while Pavoine and Dolédec (2005) and Lepš et al. (2006) considered the Rao coefficient to be a good candidate for an efficient index of functional diversity.

Although both CWM and the Rao coefficient have been widely adopted in ecological research for summarizing different aspects of community trait composition (e.g., Lavorel et al. 2008; Mokany et al. 2008; Schumacher and Roscher 2009; Vandewalle et al. 2010), we believe it is important to incorporate these two measures into a unifying framework, emphasizing that they may be used to describe two complementary facets of the relationship between community structure and ecosystem functioning as the 'mean' and the 'dispersion' of functional traits within a given community. The remainder of the paper is organized as follows. First, we show the benefits of using CWM and the Rao coefficient for single-trait analysis. In the "Discussion" section, we generalize the proposed approach to the multivariate case.

Measuring single-trait diversity

Community ecologists are usually interested in determining how functional diversity relates to ecological processes. Answering this question may shed light on the influence of biotic and abiotic constraints on community structure and, ultimately, on the links between patterns of community trait assemblages and ecosystem functioning.

For the analyses, ecologists generally use three matrices (Villéger et al. 2008; Pillar et al. 2009; Pillar and Duarte 2010): a first matrix containing data on the abundance of S species at N sites, a second matrix in which the S species are described by τ functional traits that are believed to be relevant for the ecological processes of interest (Ricotta and Moretti 2010), and a third matrix describing the N sampled sites according to one or more environmental variables that are believed to affect the functional aspects of community structure.

Traits are defined here as species characters that are quantifiable. There are obviously a large number of potentially relevant traits for a given ecosystem process that are measured on a mixture of scales (binary, nominal, ordinal, and quantitative). Accordingly, prior to analysis, ordinal traits are usually transformed to ranks, while nominal traits are typically expanded into binary traits (see Podani 2005). For more complex approaches to dealing with nominal traits see, for example, Reynolds (1984), Chevenet et al. (1994), and Agresti (2007). Also, the values of the τ traits may refer to individuals or local populations instead of species; in this case within-species variation may be taken into account (Pillar and Sosinski 2003; Lepš et al. 2006; Lavorel et al. 2008).

To summarize, the distribution of values within the single traits of a given species assemblage, Garnier et al. (2004) proposed calculating the average of trait values weighted by the relative abundances of each species. This measure, usually known as the community-weighted mean trait value, is computed simply as:

$$\mathrm{CWM} = \sum_{i=1}^{S} p_i x_i \tag{1}$$

where CWM is the community-weighted mean value of a given functional trait, p_i is the relative abundance of species i ($i = 1, 2, \ldots, S$), and x_i is the trait value for species i.

From an ecological viewpoint, this metric is often understood as defining the dominant traits in a community and is directly related to the mass ratio hypothesis of Grime (1998) which considers the traits of the most abundant species to largely determine ecosystem processes (see Vile et al. 2006; Mokany et al. 2008).

Pavoine and Dolédec (2005) and Lepš et al. (2006) proposed measuring the functional diversity of single traits with the Rao (1982) quadratic diversity. This index is defined as the expected dissimilarity between two individuals of a given species assemblage selected at random with replacement:

$$Q = \sum_{i,j}^{S} d_{ij} p_i p_j \tag{2}$$

where d_{ij} is the dissimilarity (i.e., not necessarily a metric distance) between species i and j. It is easily shown that for $d_{ij} = 1$ for all $i \neq j$, and $d_{ii} = 0$ for all i, Q reduces to the well-known Gini–Simpson index. Some relevant mathematical properties of the Rao coefficient have been studied by a number of authors (Shimatani 2001; Pavoine et al. 2005; Ricotta and Szeidl 2006, 2009; Pavoine et al. 2009), and the reader is addressed to their papers for details.

From Eqs. 1 and 2 it immediately emerges that CWM and Q provide complementary information on community functional components: CWM quantifies the weighted mean of a given functional trait within a given species assemblage, while the Rao coefficient is a measure of trait dispersion or divergence sensu Villéger et al. (2008). It follows that while CWM adequately summarizes shifts in single-trait values within a given community, the Rao coefficient is best used for analyzing changes in trait dispersion. A general pattern of lower observed than expected trait dispersion supports the idea that environmental filters are central to the assembly of the community, whereas a higher trait dispersion compared to that expected by chance suggests the presence of mechanisms of limiting similarity that prevent coexisting species from being too similar (Grime 2006; Thompson et al. 2010). To clarify these differences, we focus here on changes in functional trait composition of distinct bee communities under contrasting fire regimes in temperate forests of southern Switzerland.

Methods

The study area is located along uniform south-facing slopes (450–850 m a.s.l.) extending over 11 × 15 km in the Locarno region (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, which favors a winter fire regime characterized by fast-spreading surface fires of low–medium intensity. Further details of the study area are given in Moretti et al. (2002) and Moretti and Legg (2009). In the study region, fire plays an important role in maintaining a mosaic of vegetation patches with different successional stages, with full recovery of the tree canopy occurring after 15–20 years (Moretti et al. 2009).

In the study area, 21 sites were selected according to the time elapsed since the last fire, varying from <1 (freshly burnt) to >35 years (Table 1). Fire-history data were obtained from national and regional wildfire data bases and using dendrochronological methods. We avoided pseudoreplication by selecting sites with similar fire regimes in different locations of the study area (Moretti et al. 2006). The 21 sites were tested for spatial independence of species assemblages using the Mantel correlogram and permutation tests (see Moretti et al. 2006 for more details), and were therefore treated as independent in the present analyses.

Table 1 Description of the study sites in southern Switzerland

Fire categories	Years since last fire	Site description
Freshly burned	0	Bare soil, standing dead trees, luxuriant herb and scrub layer (DBH <5 cm)
	1	
	2	
Intermediate	6	Dense chestnut (*Castanea sativa*) coppice stand with high number of dead young shoots (DBH 5–10 cm)
	7	
	10	
	14	
	17	
Mature	22	Mature coppice stand with dense canopy cover (DBH 15–20 cm)
	24	
Unburned	≥35	Old coppice stand out of turn with dense canopy cover (DBH 20–30 cm)

The sites are assigned to one of the four fire categories listed in the table on the basis of broad vegetation types along the successional gradient of time elapsed since the last fire

DBH diameter at breast height

Bees were sampled using window (interception) traps combined with yellow water-filled pans and placed 1.5 m above-ground; three window traps were installed at each of the 21 sites (distance between traps approx. 30 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 ten functional traits (Table 2) that were recognized as important in both bee autoecology (e.g., Westrich 1989; Michener 2000) and response to fire (Biesmeijer et al. 2006; Fontaine et al. 2006).

The CWM and the Rao quadratic diversity (Q) of each trait were calculated according to Eqs. 1 and 2, respectively. Both coefficients were computed with an Excel macro freely available at http://botanika.bf.jcu.cz/suspa/FunctDiv.php (see Lepš et al. 2006) setting the pairwise interspecies dissimilarity of the Rao coefficient to the Euclidean distance $d_{ij} = (y_i - y_j)$, which is the simplest possible distance between the values of a single variable y for two observations i and j. Species relative abundances were based on the number of individuals per species. All singleton species (i.e., those species occurring in one site only) were removed to exclude casual occurrences from the analysis. We next fitted a linear regression model for each CWM and Q value versus the time since last fire (TSLF). Statistical significance for all regression estimates (two-tailed test) is based on 9999 randomizations.

Table 2 Description of the bee functional traits used in this study

Bee functional trait	Data type	States	CWM (*R*)	Rao diversity (*R*)
Habitat specialization	Ordinal	(1) Generalist; (2) intermediate; (3) specialist	−0.083	−0.104
Flower access	Ordinal	(1) Restricted to tubular flowers; (2) both tubular and open flower types; (3) open flowers	−0.053	−0.040
Feeding specialization	Ordinal	(1) No lectic status[a]; (2) polylectic[b]; (3) oligolectic[c]; (4) monolectic[d]	−0.076	0.156
Social status	Ordinal	(1) Solitary; (2) variable; (3) social	0.514*	0.469*
Tongue length	Binary	Short tongue; long tongue	0.535*	0.654*
Voltinism	Quantitative	Number of generations per year	−0.314	−0.471*
Flight season start	Quantitative	Month	−0.693*	−0.176
Flight season end	Quantitative	Month	0.082	0.148
Mean flight duration	Quantitative	No. of months	0.383	0.168
Inter-tegula distance	Quantitative	Micrometers	0.603*	0.402

The last two columns show the correlation coefficient *R* of the linear regression models that best summarize the single-trait community-weighted mean trait values (CWMs) and the Rao diversity values versus the time since last fire

* $p < 0.05$

[a] No feeding specialization having no pollen collecting requirements (i.e., 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

Results

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 gradually decreased in abundance as succession proceeded, while *Apis mellifera*, a subdominant species immediately after fire, became dominant during the post-fire succession (see Moretti et al. 2009).

The results of the linear regressions of CWM and *Q* versus TSLF are shown in Table 2. From a functional viewpoint, the regressions of the single-trait CWM values versus TSLF show that there is a significant shift along the post-fire successional gradient in four of the ten traits analyzed. For example, freshly burned sites are characterized by species that start flying later in the season. Bees at freshly burned sites also tend to be short-tongued, solitary, and low-dispersal species (with shorter inter-tegula distances).

Accordingly, looking at the CWM values, tongue length, sociality, and inter-tegula distance are positively correlated to TSLF ($p < 0.05$; two-tailed test). To the contrary, the start of the flying season is negatively correlated to TSLF ($p < 0.05$), with late-season flying species being more abundant in the early post-fire successional stages.

At the same time, the values of the Rao quadratic diversity show that tongue length and sociality significantly diverge with increased time since the last fire (i.e., the expected pairwise species distances significantly increase with TSLF at $p < 0.05$), while voltinism significantly converges along the same gradient ($p < 0.05$). Here, it is worth mentioning that using two tests per functional trait, we chose to present *p* values without adjustments for multiple comparisons, such as Bonferroni or Holm corrections. While this approach reduces the risk of a Type II error (failing to reject a false null hypothesis), it increases the risk of an inflated Type I error in our conclusions (incorrectly rejecting a true null hypothesis). Also, the observed relationships may not always be linear; in which case, transformations (including transformations into ranks) or other approaches may be applied to increase their strength. However, as the aim of our paper is to present a unifying framework for CWM and the Rao index from a methodological viewpoint, these simplifications will not affect our conclusions.

Discussion

The functional structure of a community has emerged as an important aspect of biodiversity that influences ecosystem functioning and vice versa. For example, it is generally understood that species make a difference in the functioning of the ecosystem because of their differences in functional traits. Thus, the distribution of traits better describe the community functional composition and diversity than any other index that is based solely on species richness or on species abundance distributions (Norberg 2004). From among the large number of possible candidates, which traits actually matter for ecosystem functioning is a question that depends on the specific process of interest. Therefore, some authors argue that there is a need to examine single traits separately in order to unravel relevant traits from less relevant ones and to quantify, in a meaningful manner, the ability of various functional traits to summarize the relationships between community structure and ecosystem functioning (Garnier et al. 2004; Lepš et al. 2006; Lavorel et al. 2008).

Mason et al. (2005) and Villéger et al. (2008) developed a typology of functional diversity indices based on three different measures, namely, functional richness, functional evenness, and functional divergence, while Clarke and Warwick (2001) suggested measuring taxonomic diversity with two indices, namely, average taxonomic distance between species pairs and variance in taxonomic distances. The combination of these two measures was seen to provide a statistically robust summary of independent features of taxonomic diversity patterns within species assemblages.

In this paper, we propose a standard tool of indices that can be adequately used for summarizing different facets of community trait composition. Determination of how the observed functional patterns relate to environmental conditions may be useful to clarify the relationships between community structure and ecosystem function (Grime 2006; Díaz et al. 2007; Ackerly and Cornwell 2007; Pillar et al. 2009). For example, despite a long history of the study of why species coexist and assemble into communities, uncertainty persists regarding the importance of trait convergence and divergence in community assembly. In this paper, we showed that the Rao coefficient can be effectively applied for analyzing patterns of trait convergence or divergence (i.e., a decrease or increase in trait dissimilarity compared to a random expectation), while CWMs can be adequately used to quantify shifts in mean trait values due to environmental selection for certain functional traits. In this framework, some authors argue that a response of trait mean to environment also indicates convergence (e.g., Pillar et al. 2009; Pillar and Duarte 2010). This broader concept of functional convergence renders the simultaneous use of CWM and the Rao index even more interesting, as in this case convergence can be assessed by a combination of CWM and Q, while divergence can be only indicated by an increase in trait dissimilarity (see Pillar and Duarte 2010).

Likewise, while Lavorel et al. (2008) consider CWM to be a measure of 'functional diversity', most authors do not, based on the observation that the term 'diversity' is related to the concept of variety, variability, etc., whereas CWM is rather a measure of central tendency, like the mean or the median. For this reason, CWM was not included in two recent reviews of functional diversity indices (Mouchet et al. 2010; Schleuter et al. 2010). However, regardless of whether we consider CWM to be a measure of functional diversity or simply a measure of community trait composition, the proposed tool of measures allows the calculation of different aspects of community structure in a very flexible manner.

In our example, while functional shifts in mean trait values are mainly associated to (sub)dominant species with particular traits that are replaced by other (sub)dominant species with different traits, the increase/decrease in functional trait dispersal seems to be related to changes in the number of available niches along the ecological gradients. Therefore, along gradients, environmental filters with convergent or divergent effects may operate with different intensities on recruitment from the regional species pool to impose their effects on the similarity of the trait values exhibited by co-existing species (Weiher and Keddy 1999; Grime 2006).

According to our results, the post-fire successional gradient induces significant convergence/divergence in relevant traits. Freshly and recent burnt sites seem to create environmental filters that mainly affect floral forms and bloom phenology (and thus nectar availability). After a fire, bee communities appear in fact to be dominated by solitary species with a low dispersal ability and short tongues (thus with limited access to tube-corolla flowers) and which start flying late in the season, thus possibly favoring warm-loving species. Such bee communities host both temporal specialists (monovoltines) and generalists (bivoltines), having one and two generations per season, respectively.

With post-fire succession, part of the forest recovers, providing a mosaic of open and closed stands that enhance more functional diverse bee communities comprising both solitary and social species with short and long tongues and different dispersal abilities. At the same time, late post-fire successional stages shift the community composition towards social bees with high dispersal abilities and long tongues, thus able to access resources over long distances that also include tube-corolla flowers. Bee communities at late post-fire successional stages become temporally more specialized, favoring monovoltine species (one generation per season) that start flying early in spring and have a long activity season, thus accessing resources over a longer period of time.

Here, it is worth mentioning that CWM and the Rao coefficient are not completely independent of each other. In fact, for all bounded variables, dispersion necessarily goes to zero as the mean approaches the upper or lower bounds of the variable range. This effect is particularly evident in the case of binary traits, such as tongue length (Table 2). For binary traits, the trait mean expresses the relative proportion of a given trait in a community such that the value of the Rao index is minimized for CWM = 0 or 1, while for CWM = 0.5, the Rao index will indicate a maximally dispersed trait distribution in the community. In this case, CWM and the Rao index express basically the same information and, in many cases, the two measures will be highly correlated. For example, for the case of tongue length, the correlation coefficient between CWM and the Rao index is $R = 0.894$.

From a more technical viewpoint, while the Rao coefficient offers a large (and desirable) flexibility in the selection of the dissimilarity measure d_{ij}, an important property of Q is that, for a given trait τ, if the dissimilarity measure is set to half the square Euclidean distance $d_{ij} = \frac{1}{2}(y_i - y_j)^2$, quadratic diversity is nothing else than the variance of τ (Rao 1982). This observation may possibly lead to a more frequent application of well-known statistical tools (i.e., variance decomposition, etc.) for single-trait analysis, for example for decomposing the functional diversity of an assemblage into a within-species component (i.e., the extent of functional diversity due to intraspecific trait variability) and a between-species component (Lepš et al. 2006; Rao 2010).

As shown by Champely and Chessel (2002), this variance also equals the weighted average of the square Euclidean distances between the trait values of each species in the assemblage and the corresponding CWM value:

$$Q_{\mathrm{Var}} = \sum_{i}^{S} p_i (x_i - \mathrm{CWM})^2 \tag{3}$$

In addition to single-trait analysis, for some ecological questions it might be interesting to combine multiple traits together. Accordingly, in many studies, the relationship between community structure and ecosystem functioning has been explored in the functional volume spanned by multiple traits (e.g., Petchey et al. 2007; Ricotta and Moretti 2010; Thompson et al. 2010).

In the multivariate case, the Rao coefficient is very flexible in combining individual dissimilarity matrices obtained from single traits into a compound multivariate dissimilarity matrix (Lepš et al. 2006). If d_{ij} is calculated using the Gower distance (Pavoine et al. 2009), the value of the Rao index obtained from the combination of a given set of traits is equal to the average of Q calculated for single traits. Here, Champely and Chessel (2002) noted that for any coefficient of the form $\frac{1}{2} d_{ij}^2$ where d_{ij} is a dissimilarity coefficient that is embeddable in Euclidean space (for details, see Gower and Legendre 1986), it is possible to derive a multivariate version of Eq. 3

$$Q_{\mathrm{Euc}} = \sum_{i}^{S} p_i \|z_i - \bar{z}\|^2 \tag{4}$$

where z_i and z_j are two points corresponding to species i and j embedded in a Euclidean space, such that $d_{ij} = \|z_i - z_j\|$ and $\bar{z}$ is the centroid of the species distribution in the multidimensional trait space (i.e., a multivariate analogue of CWM). In this view, the work of Champely and Chessel (2002) opens the way for generalizing the calculation of CWMs to multiple traits, while Laliberté and Legendre (2010) recently suggested that, at least for unweighted presence–absence data, the distance of the single species from the centroid of the species distribution in multivariate functional space $\bar{z}$ can be used for a formal statistical test of differences in functional diversity between different communities. For details, see Anderson (2001, 2006) and Laliberté and Legendre (2010).

In summary, since different diversity measures have been defined based on distinct objectives and motivations, a clear understanding of the basic properties of CWM and the Rao coefficient may be beneficial for quantifying relevant aspects of community organization in the most appropriate manner (Ricotta 2005). The most important methodological decisions are how many and which traits to use, how to code them, and the method to be used to calculate dissimilarity. Nonetheless, the same decisions have to be made even if other indices of functional diversity are used (see, for example, Lepš et al. 2006; Lavorel et al. 2008). Therefore, we see this flexibility more as an advantage than a disadvantage as it allows ecologists to compute relevant aspects of functional diversity from different viewpoints and perspectives.

Acknowledgments We thank Andreas Mueller (Swiss Federal Institute of Technology, Zurich) and Stuart P.M. Roberts (University of Reading) for providing bee traits. Insightful comments and suggestions of two anonymous referees on a previous draft of this paper are also warmly acknowledged.

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