*Ecology*, 90(1), 2009, pp. 81–89

# Including intraspecific variability in functional diversity

M. V. CIANCIARUSO,[1,3] M. A. BATALHA,[1] K. J. GASTON,[2] AND O. L. PETCHEY[2]

[1]*Department of Botany, Federal University of São Carlos, P.O. Box 676, 13565-905, São Carlos, SP, Brazil*
[2]*Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN United Kingdom*

*Abstract.* Linking species and ecosystems often relies on approaches that consider how the traits exhibited by species affect ecosystem processes. One method is to estimate functional diversity (FD) based on the dispersion of species in functional trait space. Individuals within a species also differ, however, and an unresolved challenge is how to include such intraspecific variability in a measure of functional diversity. Our solution is to extend an existing measure to variation among individuals within species. Here, simulations demonstrate how the new measure behaves relative to one that does not include individual variation. Individual-level FD was less well associated with species richness than species-level FD in a single trait dimension, because species differed in their intraspecific variation. However, in multiple trait dimensions, there was a strong association between individual- and species-level FD and richness, because many traits result in a tight relationship between functional diversity and species richness. The correlation between the two FD measures weakened as the amount of intraspecific variability increased. Analyzing natural plant communities we found no relationship between species richness and functional diversity. In these analyses, we did not have to specify the source of intraspecific variation. In fact, the variation was only among individuals. The measure can, however, include differences in the amount of intraspecific variation at different sites, as we demonstrate. Including intraspecific variation should allow a more complete understanding of the processes that link individuals and ecosystems and provide better predictions about the consequences of extinctions for ecosystem processes.

*Key words: complementarity; functional classification; phenotypic diversity; plasticity; species richness; traits.*

## INTRODUCTION

Intraspecific variability (i.e., phenotypic and genetic differences among individuals within a species) has long been recognized as important in understanding ecology and evolutionary biology (Schlichting 1986, Wells and Pigliucci 2000, Bolnick et al. 2003, Sultan 2004). Intraspecific variability occurs for many aspects of development, physiology, and life history, and may be related to environmental constraints (Spicer and Gaston 1999, Callaway et al. 2003, Gaston 2003). It is also clear that functional traits (sensu Violle et al. 2007) play an important role in communities and the functioning of ecosystems (Chapin et al. 2001). For example, they can determine species competitive ability and coexistence (Begon and Wall 1987, Callaway et al. 2003), invasion ability (Sexton et al. 2001, Richards et al. 2006), and community functioning, such as nutrient dynamics (Madritch and Hunter 2003), resistance to disturbance (Reusch et al. 2005, Gamfeldt and Kallstrom 2007), and plant productivity (Norberg et al. 2001). It is an individual that gains carbon and nutrients from the environment, transfers plant tissues to higher trophic levels, and decomposes plant litter (Chapin et al. 2001). It is also at the individual level that competition for resources, niche width expansion (Bolnick 2001), and ultimately natural selection occurs (Vellend and Geber 2005). Therefore, some ecologists argue that the central focus in community ecology should be on individuals (e.g., DeAngelis and Gross 1992, Pachepsky et al. 2001, 2007), and many individual-based models have been proposed (e.g., Huston et al. 1988, Loreau 1998). In this sense, progress could be made by replacing species with individuals as the fundamental ecological accounting unit (Pachepsky et al. 2001, 2007).

Somewhat independently, functional traits rather than species per se are increasingly being used to understand ecological processes and, hopefully, turn ecology into a more predictive science (Díaz and Cabido 2001, McGill et al. 2006, Petchey and Gaston 2006). Even if the conceptual relevance of including the variability within species in the functional diversity has already been identified by some authors (Mason et al. 2005, Ackerly and Cornwell 2007, Pachepsky et al. 2007), up to now, none of the methods proposed for estimating functional diversity (see Petchey and Gaston 2006) gives a clear approach to incorporating information about individuals. That is, indices of functional diversity working with multiple traits do not include intraspecific variability, but rather use average trait values for species. Consequently, the functional properties of individuals and the

Manuscript received 9 November 2007; revised 20 May 2008; accepted 29 May 2008. Corresponding Editor: M. Holyoak.

[3] E-mail: cianciaruso@gmail.com

resulting state of the community cannot be linked, fueling the debate on the relationship between biological diversity and community function (Pachepsky et al. 2001).

Here, we present a straightforward extension to the measurement of functional diversity that accounts for intraspecific variation. We illustrate it using the functional diversity index, termed FD, proposed by Petchey and Gaston (2002, 2006). Since this measure contains information only about the uniqueness of species, and not about their relative abundances, one might choose to term it a measure of functional richness (Moulliot et al. 2005, but see Hurlbert 1971). Although measures of functional diversity are available that include species abundances (e.g., Rao 1982), whether these are more generally useful or applicable is far from resolved (see Ricotta [2005] and Petchey and Gaston [2006] for a review of the shortcomings of such measures).

We demonstrate with simulations how the new measure behaves relative to one that does not include individual variation. We also use data from plant communities where the attributes of individuals were measured. An attribute is the particular value taken by the trait at any place and time; within a species the trait may show different attributes along environmental gradients or through time (Violle et al. 2007). Field data allow us to consider sources of intraspecific variability that may be included in functional measures: first, variability among the individuals within a location, and second, variability among individuals that occurs between locations, perhaps due to environmental differences.

## Methods

### *Calculating FD*

Calculating FD involves four steps (Petchey and Gaston 2002, 2006): (1) assembling a trait matrix (species in rows and functional traits in columns), (2) converting the trait matrix into a distance matrix, (3) producing a dendrogram by clustering the distance matrix, and (4) calculating the total branch length of the dendrogram necessary to connect all species in the community. We used Euclidean distance and the unweighted pair group method with arithmetic averages (UPGMA) to produce, respectively, the distance matrix and the dendrogram (Podani and Schmera 2006, Petchey and Gaston 2007).

### *An individual-level FD measure*

To include intraspecific variation in FD, we suggest a simple change in the first step mentioned above. Instead of constructing a trait matrix with species in the rows, one can include individuals in the rows. This modification transforms a species-level approach into an individual-level one. Obviously, trait values for the individuals are required. This individual level measure of functional diversity (iFD) is defined as the total branch length of the functional dendrogram that can be constructed from information about individual's functional traits. It is an extension of the species-level FD measure (Petchey and Gaston 2002, 2006), and allows simultaneous inclusion of trait variation among and within species in a functional diversity measure.

### *Simulations*

To understand the relationship between species-level FD (spFD) and individual-level FD (iFD), we carried out simulations including one, three, and five traits as follows: (1) We assembled an individual-level trait matrix by assigning an attribute value to 10 individuals within each of 26 species (named with the letters A–Z for computational tractability). Attribute values were drawn at random from a normal distribution with standard deviation of $\mu \times \mathrm{E(CV)}$. The species trait value, $\mu$, was itself a random normal deviate with mean 0 and standard deviation 1. Manipulating the expected coefficient of intraspecific variation E(CV) allowed us to investigate the importance of the amount of intraspecific variability. Expected intraspecific trait variation ranged from 0 (no intraspecific variation, all individuals within a species are identical, $\mathrm{E(CV)} = 0\%$) to 5 (coefficient of variation around species mean value $= 500\%$). (2) We assembled a species-level trait matrix by aggregating the individual-level trait matrix. Here, trait matrices had species as rows and individual trait-averages as columns (the standard approach to estimate FD). (3) We assembled communities containing $S$ species drawn at random from the pool of 26 species, with $S = \{2, 4, 6 \ldots 26\}$, and 10 replicate assemblages at each richness level. (4) FD of each assemblage was estimated from both the individual-level trait matrix (to give iFD) and from the species-level trait matrix (to give spFD). We examined values of iFD and spFD with values of E(CV) from 0.0 to 5.0 in steps of 0.1 [0.0, 0.1, 0.2 ... 5.0] and carried out 400 independent simulations at each level of E(CV).

With these data we determined, first, how spFD and iFD were related to species richness, and second, how spFD and iFD were related to each other under different intraspecific variability levels. In the second case, we used a single species richness level to avoid the possible effect of multiple richness levels acting as a confounding factor. The results of analyses with several richness levels ($S = 5$, 15, and 25*)* were qualitatively very similar, so we present only the results for an intermediate richness level ($S = 15$ species). We also assessed the strength of spFD and iFD relationships by measuring the coefficient of determination, $r^2$, across a gradient of intraspecific variability.

### *Field data*

We compared individual and species-based FD across six Neotropical savannas (cerrado), using unpublished data sets (M. Cianciaruso and M. Batalha, *unpublished data*). These data sets comprised individual-level functional information on woody species from two different cerrado forms: four savanna woodlands (campo cerrado) and two woodlands (cerrado sensu stricto). Three savanna woodland sites (sites 1–3) are in close proximity and located in Emas National Park, central Brazil, under a tropical and humid climate, with wet summer and dry winter, classified as Aw following Köppen (1931). These savannas have been subjected to different fire regimes in the last 12 years (site 1, annual fires; site 2, biennial fires; and site 3, fire exclusion). The fourth site is a woodland within an experimental station in southeastern Brazil, protected from fire for at least 12 years. The fifth site is a savanna woodland, heavily disturbed by human activity in the past (fire, cattle ranch, and high dominance of herbaceous exotic species), located near the sixth and last site, a more preserved woodland, in the Federal University of São Carlos cerrado reserve, southeastern Brazil. Sites four to six are under a macrothermic temperate climate with rainy summer and not severely dry winter, that is, Cwa according to Köppen's (1931) classification. All six sites are on Oxisols. Such variability, especially the different disturbances to which each site is submitted, leads us to expect an effect on functional attribute values when a species occurs in several sites. Given the site's descriptions pointed above, we assumed they were independent one from the other. As our aim here was purely illustrative, we used only three functional traits (plant height, bark thickness, and basal area), measured for 10 individuals of each species at each site following a protocol for plant functional trait measurement (Cornelissen et al. 2003). We sampled 10 individuals because this is between the minimum and the preferred sample size to obtain an impression of a trait's variability (Cornelissen et al. 2003).

We attributed the functional trait values to each species in two different ways: first, we gathered all individuals from all species occurring in the six sites and drew randomly 10 of them to assemble an individual-level attribute matrix. That is, the location at which an individual was observed was ignored. Second, we assembled an attribute matrix in which individuals belonged to species and sites, since individuals from the same species but from different sites may exhibit differences in attribute values (Callaway et al. 2003, Gaston 2003, Sultan 2004). For each approach, we estimated the relationship between both FD indices and between them and species richness. We also computed the similarities in specific composition among areas using the Sørensen index (Magurran 2004). All analyses were conducted in R (R Development Core Team 2006).

## RESULTS

### *Simulations*

Both spFD and iFD were positively related to species richness (Fig. 1). Using a single trait, at intermediate levels of intraspecific variability (coefficient of variation equal to 50%), the association of spFD with species richness was higher than that of iFD (Fig. 1). Increasing the amount of intraspecific variability to 300% led to the appearance of a bifurcation in the relationship between iFD and species richness (Fig. 1c, one trait). However, when we included more traits, both iFD and spFD were tightly related with species richness, even at high intraspecific variability (Fig. 1b, c, three and five traits).

When individuals within a species had no variability in functional traits, iFD was equal to spFD, independently of how many traits were included (Fig. 2a). As intraspecific variability increased, the association between iFD and spFD became weaker (Fig. 2b, c), and when intraspecific variability was very high, there was a trend toward four distinct clusters of points in the relationship between the two FD measures when we included one trait dimension (Fig. 2c, one trait).

We found a negative relationship between the $r^2$ of the relationship between spFD and iFD and the level of intraspecific variability when we included one, three, and five traits (Fig. 3). That is, as intraspecific variability increased, iFD tended to be less closely associated with spFD.

### *Field data*

Species richness ranged from 19 to 28 among the six sites, and species similarity (Sørensen index) between pairs of sites varied from 0.13 to 0.82 (Table 1). Species turnover was low among sites that were close together (for example, among Emas National Park sites, sites 1 to 3) but high among distant sites (such as between Itirapina, site six, and Emas National Park sites). The mean amount of intraspecific variability ranged between 40% and 80% among functional traits.

There was no significant relationship between species richness and either spFD or iFD in both approaches (Fig. 4a, b, d, e). However, we found two contrasting patterns in the relationships between spFD and iFD. When "among-sites" intraspecific variability was not taken into account spFD and iFD were weakly related (Fig. 4c). It is important to notice that in this case spFD is the usual approach to measuring FD, since we used average trait attributes for each species. On the other hand, when we included among-site variability, spFD and iFD exhibited a strong positive relationship (Fig. 4f).

## DISCUSSION

### *Simulated effects of species richness and composition on iFD and spFD*

We found a positive association between species richness and both species-level FD and individual level FD. This largely results from the property of FD (species and individual level) whereby increases in species richness can only increase FD (or rarely cause no change) while decreases in species richness can only decrease FD (or rarely cause no change). This makes some form of positive association largely inevitable. However, the shape and scatter of the positive association is determined both by the number of traits, and whether FD is calculated at the species or individual level.

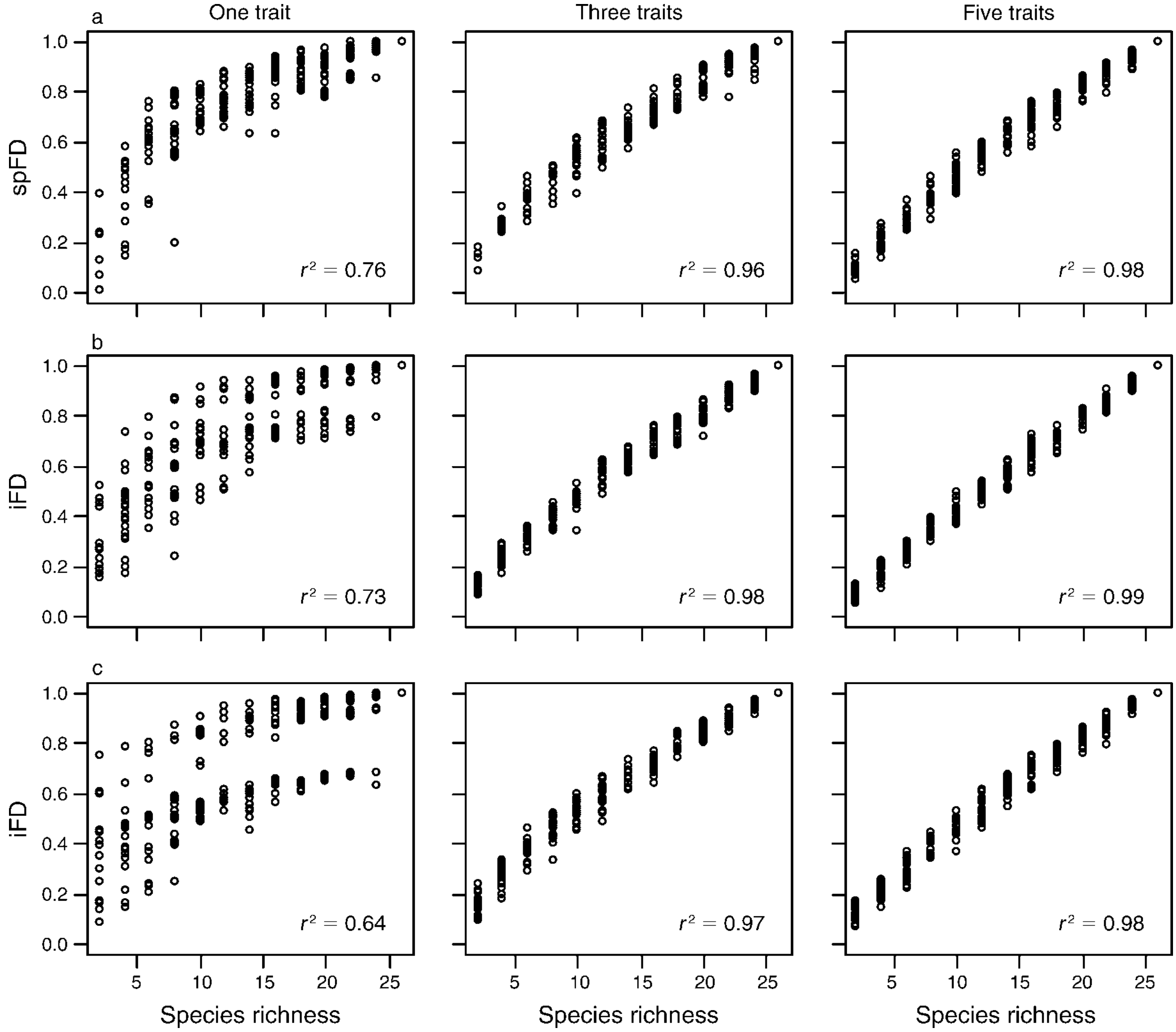

FIG. 1. Relationships between species richness and (a, top row) species-based functional diversity (spFD); (b, middle row) individual-based functional diversity (iFD) with one, three, and five trait dimensions when intraspecific variability level was intermediate (coefficient of variation equal to 50%); and (c, bottom row) individual-based FD when intraspecific variability level was very high (coefficient of variation equal to 300%).

The use of just a few traits causes a more saturating and scattered relationship regardless of the FD measure. The scatter represents the degree of importance of species identity (i.e., species composition), with higher scatter implying stronger effects of species identity and weaker effects of species richness. A single trait axis will always cause strong effects of community composition because some species are close to one another on that axis, whereas others are distantly separated (Petchey and Gaston 2002). In our simulations, for example, a two-species community could comprise by chance two identical species (spFD = 0), two very similar species (low spFD), or two very different ones (high spFD). The saturated shape with low numbers of traits results from the decreasing probability that a unique species will enter the community as species richness increases. At high levels of intraspecific variability, there was a bifurcation in the relationship between iFD and species richness at higher species richness (Fig. 1c).

We confirmed that this bifurcation was due to different species composition, with some communities containing more redundant species (and thus lower FD values) and others more complementary species (and thus high FD values). Confirmation was by examining the influence of these species' presence or absence on values of FD. The bifurcation is also explained by the presence or absence of a species with particularly high levels of intraspecific variability. Communities containing more complementary species and also more species with high intraspecific variability will have higher iFD than spFD, independently of the species richness level. In general, bifurcations and discontinuous distributions of functional diversity are expected when trait values are relatively clumped and a single trait is functionally

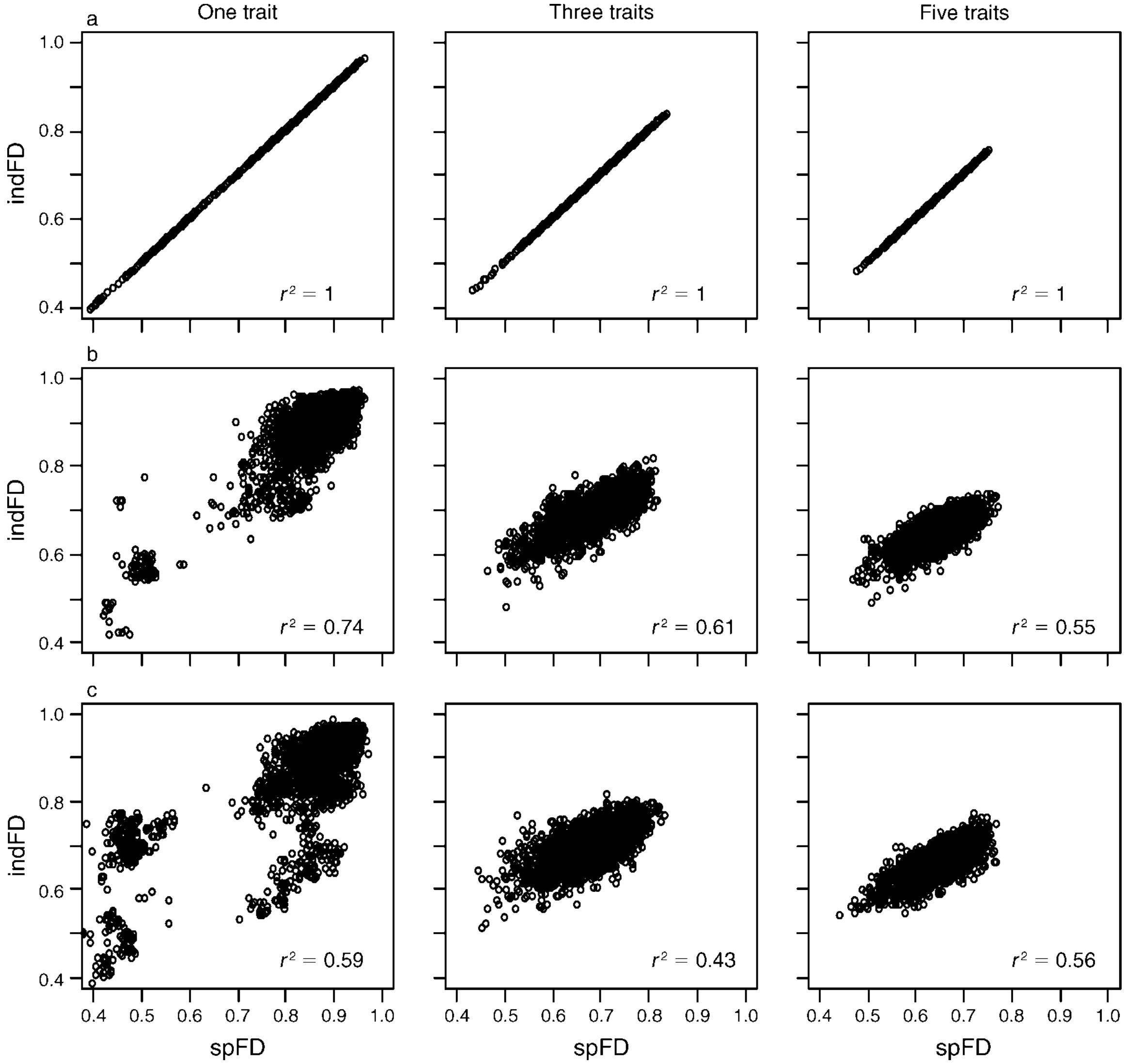

FIG. 2. Relationships between species- and individual-based FD (spFD and iFD) with one, three, and five trait dimensions, with (a, top row) no intraspecific variability, (b, middle row) intermediate intraspecific variability (coefficient of variation equal to 50%), and (c, bottom row) very high intraspecific variability (coefficient of variation equal to 300%). Note that when intraspecific variability increases (from a to c), the relationship between spFD and iFD becomes weaker.

important (see Fig. 4 in Petchey and Gaston 2002). The multiple trait dimensions present in some natural trait data sets create, however, a relatively continuous distribution of functional diversity values and, consequently, no bifurcations (see Fig. 5 in Petchey and Gaston 2002).

With higher number of traits (three and five), there is less scatter and more linearity in the relationship for both species and individual level FD. The lower scatter occurs because species are more equally different when there are several uncorrelated trait dimensions (Petchey and Gaston 2002). Species identity is less important when using higher number of traits than when using a single one: our finding here was that this holds true even when the measure of functional diversity includes intraspecific variation. The shape of the relationship also becomes more linear, for the same reason. The probability of adding a functionally novel species is relatively independent of species richness, because all species are novel in their own way.

While the relationship between iFD and species richness is more scattered than that of spFD and species richness with only one trait (Fig. 1a vs. 1b first column), the two relationships become very similar in shape and scatter with three or five traits (Fig. 1a vs. 1b, second and third column). This occurs because separation in three or five dimensions results in less overlap in trait space among individuals from different species. Hence the species identity of individuals dominates the relationship, and it becomes very similar to the

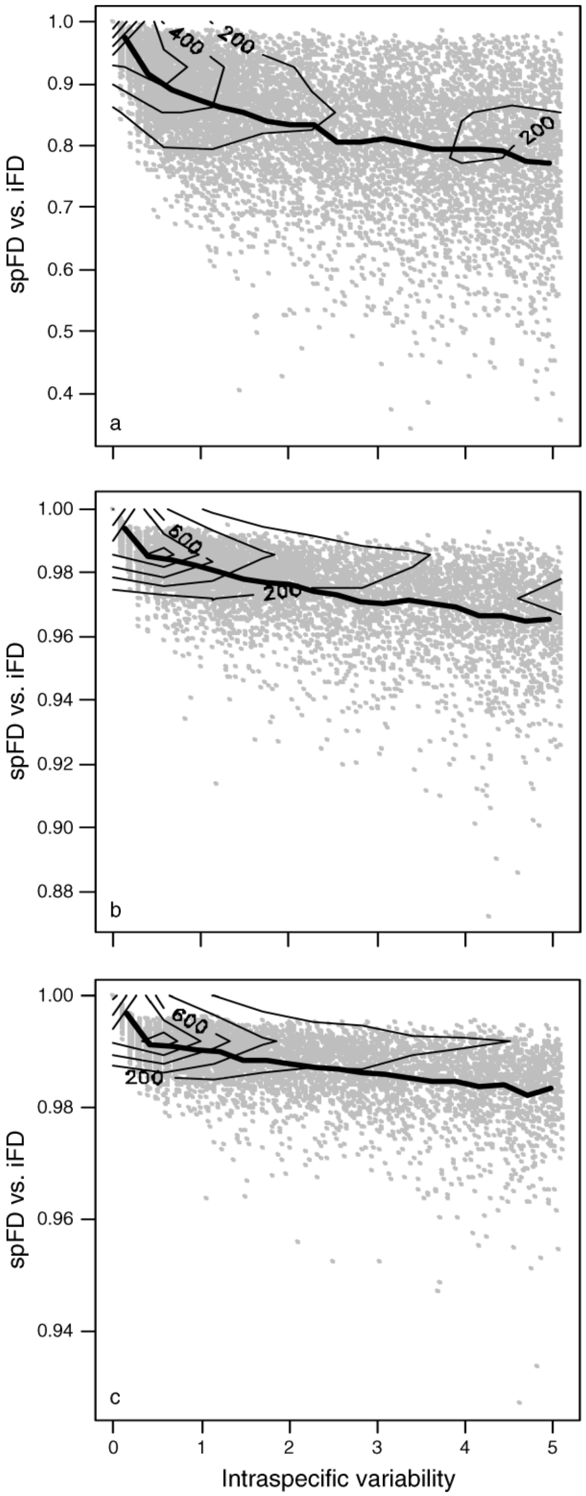

FIG. 3. Relationship between species- and individual-based FD relationships across a gradient of intraspecific variability, with (a) one trait dimension ($r^2 = 0.32$), (b) three traits dimension ($r^2 = 0.42$), and (c) five traits dimension ($r^2 = 0.41$). Thin black lines are density contours, which delimit regions of equal data point densities (indicated by the number in each contour line), and provide a better visualization of the points distribution in the figures. The thick black line shows $r^2$ averages.

species-level FD pattern. This illustrates the importance of the number of traits in measuring functional diversity (Petchey and Gaston 2006).

### *Simulated relationships between iFD and spFD*

To show the effects of including intraspecific variability in functional measures, we asked whether and to what degree this approach would be associated with a species-level measure. We also asked whether the relationship between the two indices is affected by different degrees of intraspecific variability. The rationale for this is that if iFD appears to be closely related to spFD, even at high levels of intraspecific variability, our measure would have little information different to spFD.

As a general pattern we found that as we increased intraspecific variability iFD and spFD became less closely associated. Since FD is a function of differences among objects in trait space (Petchey and Gaston 2002), adding an individual that lies at the same point as one that is already a member of a community causes no increase in functional diversity. Hence, when all individuals in a given species are identical (E(CV) = 0), iFD and spFD will be identical (Fig. 2a). As we increased intraspecific variability, individuals from different species should be either redundant or complementary and relationships between both indices should become weaker (Fig. 2b, c). Therefore, despite the number of traits included, iFD effectively captures differences in the amount of intraspecific variability that are not taken into account in the traditional species-level approach. When including one trait, as in the relationship between iFD and species richness, we found an effect of different levels of intraspecific variability and assemblage composition producing four different relationships (clumped points in Fig. 2c, one trait). Again, due to differences in specific compositions, some simulated communities were composed of species that were more complementary and thus had higher iFD and spFD. Other communities contained less complementary species, resulting in lower iFD and spFD values. At the same time, some communities presenting high spFD values, presented lower iFD values. This shows that at high levels of intraspecific variability individuals within a highly complementary species (thus high spFD) became redundant with other species (thus low iFD). When we simulated very high levels of intraspecific variability (i.e., coefficient of variation $> 300\%$), the association between iFD and spFD relationships and intraspecific variability became much more scattered (Fig. 3). At such high levels of variability, we might expect that species functional traits (i.e., the average from individual functional attributes) become meaningless, since individual attributes should vary enormously and species-trait identity would be lost. Nevertheless, there was a tendency for weaker associations between spFD and iFD as intraspecific variability increases (Fig. 3), corroborating the pattern we observed in Fig. 2.

TABLE 1. Woody species similarities (Sørensen index) among six sites used in the field data example.

| Site | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| 1 | **19** | | | | | |
| 2 | 0.72 | **28** | | | | |
| 3 | 0.68 | 0.82 | **28** | | | |
| 4 | 0.10 | 0.17 | 0.25 | **19** | | |
| 5 | 0.25 | 0.41 | 0.37 | 0.14 | **21** | |
| 6 | 0.13 | 0.26 | 0.17 | 0.18 | 0.38 | **26** |

*Notes:* Sites 1–3 (18°18′50″ S, 52°54′00″ W; 18°19′01″ S, 52°54′10″ W; and 18°17′28″ S, 52°53′41″ W; respectively) were nearby savanna woodlands located in Emas National Park, central Brazil. Site 4 (22°12′56″ S and 47°51′39″ W) was a woodland within an experimental station in Itirapina, southeastern Brazil. Sites 5 and 6 (21°58′08″ S, 47°51′47″ W and 21°58′45″ S, 47°52′09″ W, respectively) were a savanna woodland and a woodland in São Carlos, southeastern Brazil. Boldface numbers in the main diagonal line are species richness in each site.

### *Field data: effects of species richness and composition on iFD and spFD*

When using field data, we did not find significant relationships between either one of the FD indices (iFD and spFD) and species richness. One may argue that our results are perhaps explained by the low number of communities, the low range of species richness, and low species turnover between communities (Table 1). However, it is important to note that: first, the data we used are seldom available and, probably, nonexistent for most natural communities, since information on functional traits is normally provided only at the species-level. Second, low species turnover is inevitable in this case, since, for example, three of the communities (sites one to three) are near to one another. Moreover, here our principal aim was to demonstrate that iDF may be applied to field data. Using field data was useful to show that even communities with more species could have lower values of FD (either spFD or iFD; Fig. 4a, b, c, d, sites 2 and 3), so FD is not per se dependent on species richness (Petchey and Gaston 2002).

### *Field data: relationships between iFD and spFD*

When intraspecific differences among sites were not incorporated, the association between spFD and iFD was much lower (Fig. 4c) than when intraspecific variation among sites was made explicit (Fig. 4f). In the first approach, species composition had a strong

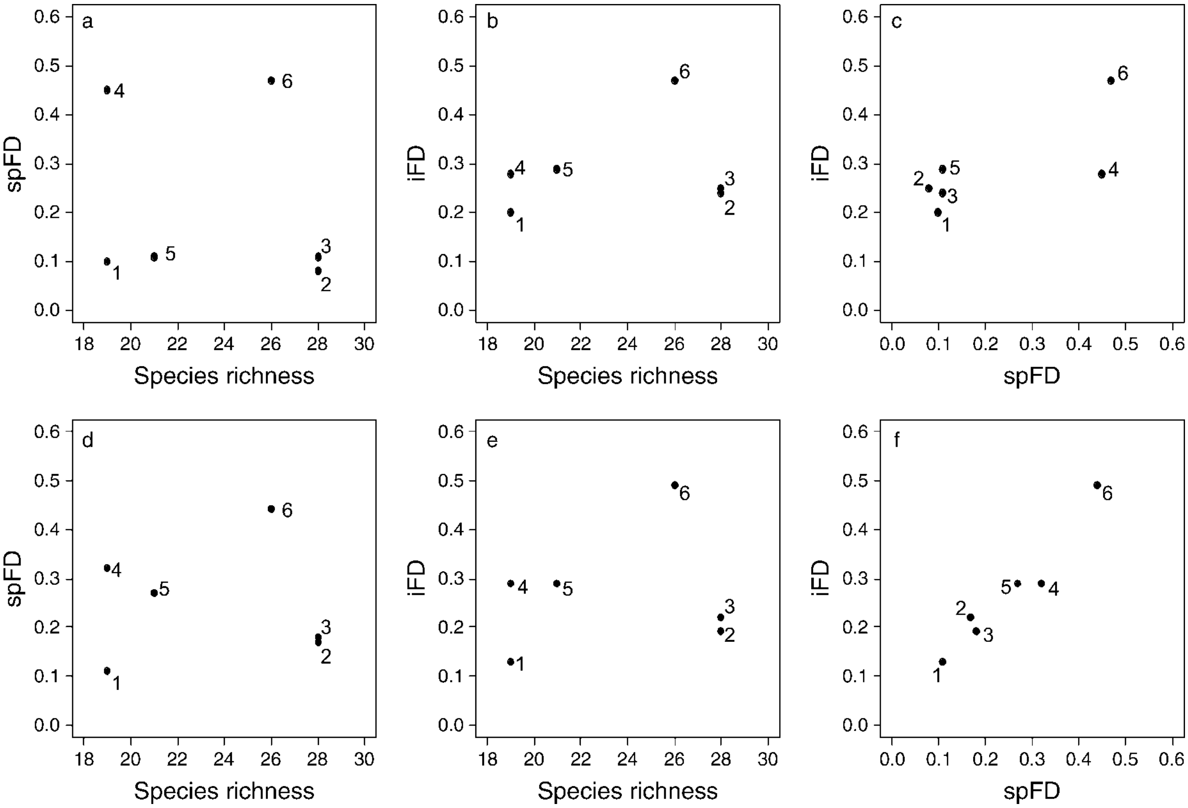

FIG. 4. Relationship between functional diversity (FD) and species richness in six Neotropical savanna woody communities when no "among-populations" intraspecific variability was allowed in (a) species-based FD vs. species richness ($r^2$ = 0.03) and (b) individual-based FD vs. species richness ($r^2$ = 0.06); (c) relationship between both FD measures ($r^2$ = 0.42). The same relationship when "among- and within-populations" intraspecific variability was allowed in (d) species-based FD vs. species richness ($r^2$ = 0.00) and (e) individual-based FD vs. species richness ($r^2$ = 0.03); (f) relationship between both FD measures ($r^2$ = 0.93). Numbers indicate the studied sites.

effect on spFD, aggregating communities that shared many species in common (sites 1, 2, 3, 5; Table 1) under similar spFD values (Fig. 4c). Here, as we gathered all individuals from all species occurring in the six sites and drew randomly 10 of them to calculate iFD, the amount of intraspecific variability should be similar within species co-occurring in different sites. In this sense, differences that may occur for both measures are somehow dependent on differences in species composition. However, whereas in this approach iFD includes intraspecific variability (especially for exclusive species in each site), spFD does not include any kind of intraspecific variability. In the second approach, we found a strong association between spFD and iFD, highlighting the different patterns FD should present depending on the functional information source. The positive relationship between spFD and iFD may be explained due to higher "among-sites" differences than "within-sites" ones. If functional traits of co-occurring species vary much more among than within sites, "among-sites" iFD values will be closer to "among-sites" spFD, since we can expect a great degree of redundancy among the individuals within a species in each site. Comparing the two approaches, we demonstrated that, for local scale studies, the traditional species-level approach is less informative, since species turnover should be low (Soininen et al. 2007) and occasional functional differences would be due solely to differences in species composition. As "among-sites" iFD is not directly associated with specific composition—individuals from a species from different sites may be redundant or complementary—it is a more suitable measure for these studies. Besides, when species intraspecific variation is higher among than within sites, "among-sites" spFD should be as suitable as "among-sites" iFD in including site-labeled intraspecific variation.

Up to now, all proposed functional diversity measures have assumed that individuals in a given community are equally important, even if they make disproportionate contributions to community function. For example, McGill et al. (2006) suggested that to be useful to community ecology, functional traits should vary more among than within species. This means that intraspecific variability has been assumed a priori to be irrelevant to functional diversity and, consequently, to community processes. On the other hand, there are several works reporting how variation among individuals of the same species is important for community functioning (e.g., Norberg et al. 2001, Madritch and Hunter 2003). For example, intraspecific variability permits niche breadth extension and is an integral part of survival mechanisms, resource capture, defense, and reproduction in plants and animals (Grime and Mackey 2002, Bolnick et al. 2003). Therefore, neglecting intraspecific variability in functional diversity measures should carry a disadvantage similar to that encountered in using functional group richness, since it excludes any functional differences that occur among organisms within groups (Petchey and Gaston 2006), in this case, species. Moreover, this runs the same risk as occurred when assuming that all species are equal, which proved to be unsatisfactory to answer the majority of ecological questions (Díaz and Cabido 2001). In short, ecologists presently have a tendency to assume that individuals within species are equal even knowing they are not. Thus, not surprisingly, there is not a consensus among them concerning the relationship of diversity and functioning (Pachepsky et al. 2001, Cardinale et al. 2006).

We have demonstrated how to include intraspecific variation in an existing index of functional diversity (Petchey and Gaston 2002, 2006), allowing us to relax two basic assumptions of most ecological models: that all individuals are identical and that they are all affected by each other and their environment in the same manner (Pachepsky et al. 2001, Bolnick et al. 2003). Other measures of functional diversity can include intraspecific variation in the same way, by changing the units of observation from species to individuals. This includes measures that incorporate information about the abundances of each species, but this remains an open question. It is important to notice that sampling intensity may affect iFD values. The simplest answer to how many individuals should be included is to sample enough individuals from all species to characterize the distribution of intraspecific variability, having an equal sample size for all species whenever possible. For plants, for example, a good starting point would be following the recommendations on sample size given in the handbook for measurement of plant functional traits worldwide (Cornelissen et al. 2003). Yet, another valid approach would be to extend to iFD the FD rarefaction suggested recently by Walker et al. (2008).

Even if there are still decisions to be made as to which and how many traits to include, whether they should be weighted, and how many individuals should be included, there are some interesting properties in an individual-level approach to functional diversity: (1) it includes individual variation in functional traits, which is important to several community processes, and (2) it allows the use of more accurate data in respect to functional traits and with an experimental design specific to test the hypothesis being studied. We can effectively include intraspecific variability using two approaches: "among-sites" spFD, when we have functional trait information from species occurring in different sites, and "among-sites" iDF, when we include both the differences in individual traits among and within-sites into FD. Further studies should reveal which sort of intraspecific variability is more useful to investigate how functional diversity is related to community functioning, especially at local scales.

## ACKNOWLEDGMENTS

M. V. Cianciaruso and M. A. Batalha are grateful to Fapesp and Capes, for financial support. O. L. Petchey is a Royal Society University Research Fellow, K .J. Gaston holds a Royal Society-Wolfson Research Merit Award, and M. A. Batalha receives a productivity grant from CNPq.

## Literature Cited

Ackerly, D. D., and W. K. Cornwell. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. Ecology Letters 10:135–145.

Begon, M., and R. Wall. 1987. Individual variation and competitor coexistence: a model. Functional Ecology 1: 237–241.

Bolnick, D. I. 2001. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. Nature 410: 463–466.

Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161:1–28.

Callaway, R. M., S. C. Pennings, and C. L. Richards. 2003. Phenotypic plasticity and interactions among plants. Ecology 84:1115–1128.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Chapin, F. S., O. E. Sala, E. Huber-Sannwald, and R. Leemans. 2001. The future of biodiversity in a changing world. Pages 1–4 *in* F. S. Chapin, III, O. E. Sala, and E. Huber-Sannwald, editors. Global biodiversity in a changing environment. Springer, Berlin, Germany.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335–380.

DeAngelis, D. L., and L. J. Gross. 1992. Individual-based models and approaches in ecology. Chapman and Hall, New York, New York, USA.

Díaz, S., and M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16:646–655.

Gamfeldt, L., and B. Kallstrom. 2007. Increasing intraspecific diversity increases predictability in population survival in the face of perturbations. Oikos 116:700–705.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, UK.

Grime, J. P., and J. M. L. Mackey. 2002. The role of plasticity in resource capture by plants. Evolutionary Ecology 16:299–307.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577–586.

Huston, M., D. L. DeAngelis, and W. M. Post. 1988. New computer models unify ecological theory. BioScience 38:682–691.

Köppen, W. 1931. Grundrisse der Klimakunde. Walter de Gruyter Company, Berlin, Germany.

Loreau, M. 1998. Biodiversity and ecosystem functioning: a mechanistic model. Proceedings of the National Academy of Science (USA) 95:5632–5636.

Madritch, M. D., and M. D. Hunter. 2003. Intraspecific litter diversity and nitrogen deposition affect nutrient dynamics and soil respiration. Oecologia 136:124–128.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Publishing, Oxford, UK.

Mason, N. W. H., D. Mouillot, W. G. Lee, and J. B. Wilson. 2005. Functional richness, functional eveness and functional divergence: the primary components of functional diversity Oikos 111:112–118.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21:178–185.

Moulliot, D. M., W. H. N. Mason, O. Dumay, and J. B. Wilson. 2005. Functional regularity: a neglected aspect of functional diversity. Oecologia 142:353–359.

Norberg, J., D. P. Swaney, J. Dushoff, J. Lin, R. Casagrandi, and S. A. Levin. 2001. Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. Proceedings of the National Academy of Science (USA) 98:11376–11381.

Pachepsky, E., J. L. Bown, A. Eberst, U. Bausenwein, P. Millard, G. R. Squire, G. Squire, and J. W. Crawford. 2007. Consequences of intraspecific variation for the structure and function of ecological communities. Part 2: Linking diversity and function. Ecological Modelling 207:277–285.

Pachepsky, E., J. W. Crawford, J. L. Bown, and G. Squire. 2001. Towards a general theory of biodiversity. Nature 40: 923–926.

Petchey, O. L., and K. J. Gaston. 2002. Functional diversity (FD), species richness, and community composition. Ecology Letters 5:402–411.

Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecology Letters 9:741–758.

Petchey, O. L., and K. J. Gaston. 2007. Dendrograms and measuring functional diversity. Oikos 116:1422–1426.

Podani, J., and D. Schmera. 2006. On dendrogram-based measures of functional diversity. Oikos 115:179–185.

R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨http://www.r-project.org⟩

Rao, C. R. 1982. Diversity and dissimilarity coefficients: a unified approach. Theoretical Population Biology 21:24–43.

Reusch, T. B. H., A. Ehlers, A. Hammerli, and B. Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proceedings of the National Academy of Science (USA) 102:2826–2831.

Richards, C. L., O. Bossdorf, N. Z. Muth, J. Gurevitch, and M. Pigliucci. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9: 981–993.

Ricotta, C. 2005. A note on functional diversity measures. Basic Applied Ecology 6:479–486.

Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. Annual Review of Ecology and Systematics 17: 667–693.

Sexton, J. P., J. K. McKay, and A. Sala. 2001. Plasticity and the genetic diversity may allow saltcedar to invade cold climates in North America. Ecological Applications 12:1652–1660.

Soininen, J., R. McDonald, and H. Hillebrand. 2007. The distance decay of similarity in ecological communities. Ecography 30:3–12.

Spicer, J. I., and K. J. Gaston. 1999. Physiological diversity and its ecological implications. Blackwell Science, Oxford, UK.

Sultan, S. E. 2004. Promising directions in plant phenotypic plasticity. Perspectives in Plant Ecology, Evolution and Systematics 6:227–233.

Vellend, M., and M. A. Geber. 2005. Connections between species diversity and genetic diversity. Ecology Lettters 8: 767–781.

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Walker, S. C., M. S. Poos, and D. A. Jackson. 2008. Functional rarefaction: estimating functional diversity from field data. Oikos 117:286–296.

Wells, C. L., and M. Pigliucci. 2000. Adaptive phenotypic plasticity: the case of heterophylly in aquatic plants. Perspectives in Plant Ecology, Evolution and Systematics 3: 1–18.