**Universidade Federal de São Carlos**

Centro de Ciências Biológicas e da Saúde

Programa de Ecologia e Recursos Naturais

**A inclusão da abundância na diversidade funcional aumenta o seu poder**

**de previsão?: teste em uma comunidade de cerrado**

**Raquel Carolina Miatto**

**São Carlos – SP**

**2011**

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**Raquel Carolina Miatto**

Dissertação de Mestrado apresentada à Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de Mestre em Ecologia e Recursos Naturais

**São Carlos – SP**

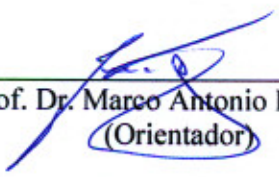**2011**

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**Aprovada** em 04 de março de 2011

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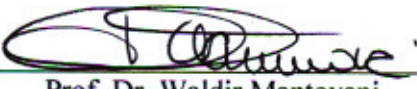
Presidente
_____
Prof. Dr. Marco Antonio P. L. Batalha
(Orientador)

1º Examinador _____
Profa. Dra. Maria Inês Salgueiro Lima
PPGERN/UFSCar

2º Examinador _____
Prof. Dr. Waldir Mantovani
USP/São Paulo-SP

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**Sumário**

**Resumo**

Assumindo que medidas de diversidade tradicionais são estimativas grosseiras do funcionamento de comunidades e que medidas que incorporam informações dos traços funcionais são melhores do que as tradicionais, medidas de diversidade funcional são bastante utilizadas atualmente. Contudo, raramente é testado se, de fato, a inclusão dos traços funcionais em estimativas de biodiversidade aumenta nosso poder preditivo. Além disso, medidas de diversidade funcional baseadas em dendrogramas geralmente não consideram a abundância. Em uma área de cerrado no sudeste brasileiro, testamos se a inclusão dos traços funcionais leva a um aumento no poder preditivo ao relacionar a diversidade funcional ao funcionamento da comunidade quando comparada a medidas de diversidade tradicionais. Demonstramos que é possível incluir a abundância em medidas de diversidade funcional baseadas em dendrogramas e testamos se a inclusão da abundância eleva o poder preditivo da diversidade funcional em comparação à comumente calculada. Nenhuma medida de diversidade relacionou-se ao funcionamento da comunidade, inclusive a diversidade funcional. Porém, mostramos que é possível incluir a abundância em medidas de diversidade funcional baseadas em dendrogramas, apesar da maioria dos índices estar correlacionada.

**Palavras-chave:** decomposição de serapilheira, dendrograma, funcionamento de comunidades, savana, traços funcionais

**A inclusão da abundância na diversidade funcional aumenta o seu poder de previsão?: teste em uma comunidade de cerrado** [1]

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3 LRH: Miatto, Cianciaruso, Carvalho, and Batalha

4 RRH: Including Abundance in Functional Diversity

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11 **Does the Inclusion of Abundance in Functional Diversity Increase its Predictive**

12 **Power?: Test in a Brazilian Savanna**

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14 **Raquel C. Miatto[1, 3], Marcus V. Cianciaruso[2], Gustavo H. de Carvalho[1], Marco A.**

15 **Batalha[1]**

16

17 [1]Departament of Botany, Federal University of São Carlos, PO Box 676, São Carlos 13565-
18 905, SP, Brazil;
19 [2]Department of Ecology, Federal University of Goiás, PO Box 131, Goiânia
20 74001-970, GO, Brazil.
21

23 [3] Corresponding author; e-mail: rmiatto@yahoo.com.br

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**ABSTRACT**

Assuming that traditional measures of diversity are rough predictors of functioning and that measures that incoporate information about functional traits are better predictors than the traditional ones, functional diversity measures are intensely used nowadays. However, whether the inclusion of functional traits in biodiversity estimation indeed increases our predictive power is rarely tested. Moreover, dendrogram-based functional diversity measures usually do not take abundance into account. By sampling a southern cerrado site in Brazil, we tested whether, when compared to traditional diversity measures, the inclusion of functional traits leads to an increased predictive power in relating functional diversity to community functioning. We demonstrated that it is possible to include abundance in dendrogram-based functional diversity, and tested whether, when compared to functional diversity as usually calculated, the inclusion of abundance leads to an increased predictive power. No diversity measure was related to community functioning, including functional diversity. Nevertheless, we showed that it is possible to include abundance in dendrogram-based functional diversity measures, even if most indices were correlated with each other.

**RESUMO**

Assumindo que medidas de diversidade tradicionais são estimativas grosseiras do funcionamento de comunidades e que medidas que incorporam informações dos traços funcionais são melhores do que as tradicionais, medidas de diversidade funcional são bastante utilizadas atualmente. Contudo, raramente é testado se, de fato, a inclusão dos traços funcionais em estimativas de biodiversidade aumenta nosso poder preditivo. Além

1    disso, medidas de diversidade funcional baseadas em dendrogramas geralmente não

2    consideram a abundância. Em uma área de cerrado no sudeste brasileiro, testamos se a

3    inclusão dos traços funcionais leva a um aumento no poder preditivo ao relacionar a

4    diversidade funcional ao funcionamento da comunidade quando comparada a medidas de

5    diversidade tradicionais. Demonstramos que é possível incluir a abundância em medidas de

6    diversidade funcional baseadas em dendrogramas e testamos se a inclusão da abundância

7    eleva o poder preditivo da diversidade funcional em comparação à comumente calculada.

8    Nenhuma medida de diversidade relacionou-se ao funcionamento da comunidade, inclusive

9    a diversidade funcional. Porém, mostramos que é possível incluir a abundância em medidas

10   de diversidade funcional baseadas em dendrogramas, apesar da maioria dos índices estar

11   correlacionada.

12

13   *Key words:* community functioning; dendrogram; functional traits; litter decomposition;

14   savanna.

15

1   THE STRUCTURE AND FUNCTIONING OF BIOLOGICAL COMMUNITIES MAY BE DETERMINED BY

2   biological diversity, since species interact through competition and facilitation and they can

3   be complementary or redundant on resource use (Bertness & Callaway 1994, Hooper &

4   Vitousek 1997). Many studies about the relationship between diversity and community

5   functioning used originally species richness as a measure of diversity (Díaz & Cabido

6   2001). However, traditional diversity indices have been considered crude estimations of

7   community structure and functioning due to the loss of information, since they reduce the

8   vast group of factors that governs a community, such as genotypic composition and

9   functional types to a simple list of species (Rousseau *et al.* 1999, Díaz & Cabido 2001).

10   Moreover, community functioning seems to be more related to functional trait identity and

11   number than to species richness itself (Tilman *et al.* 1997, Díaz & Cabido 2001). Assuming

12   that traditional measures of diversity are rough predictors of functioning and that measures

13   that incoporate information about functional traits are better predictors than the traditional

14   ones (Díaz & Cabido 2001, Petchey 2004), functional diversity measures are intensely used

15   nowadays (Petchey & Gaston 2006).

16    Despite these assumptions, whether the inclusion of functional traits in biodiversity

17   estimation indeed increases our predictive power is rarely tested. Although trait-based

18   measures of diversity are considered a tool for explaining the role of organisms in

19   communities and the ecological impacts of their loss (Petchey & Gaston 2006), their

20   superior predictive power in comparison with richness or other traditional measures of

21   diversity has been demonstrated in few studies, such as Tilman *et al.* (1997), for

22   productivity; Joshi *et al.* (2000), for plant resistance against parasites; and Scherer-

23   Lorenzen (2008), for decomposition rates. Since all these studies were carried out in

24   experimental grasslands, the assumed relationship between functional diversity and

1　functioning needs to be tested in complex, natural communities, including tropical ones

2　(Hillebrand & Matthiessen 2009).

3　　The functional diversity index called "FD" (Petchey & Gaston 2002, 2006) measures the

4　extension of complementarity among species trait values and estimates species similarity as

5　a function of their functional traits (Petchey & Gaston 2002, 2006). The greater the

6　differences between the trait values, the higher the FD and, thus, the higher the

7　complementarity in resources use (Petchey & Gaston 2002, 2006). What is expected in this

8　case is that communities with higher functional diversity will operate in a more efficient

9　way (Tilman *et al.* 1997). FD is robust and seems to predict better community functioning,

10　when compared to species richness, traditional diversity indices, and functional group

11　richness (Petchey *et al.* 2004). Nevertheless, one of the limitations of FD is that species

12　abundances are ignored and, as a consequence, community evenness is not considered, that

13　is, rare and abundant species are considered to have the same effect upon community

14　functioning. In this sense, FD may be considered more as a functional richness measure

15　than as a functional diversity one. Aware of this limitation, Petchey and Gaston (2006)

16　asked whether it was possible "to incorporate evenness into measures based on

17　dendrogram".

18　　Abundance distribution is considered the most fundamental measure in ecology, because

19　it describes how the individuals in a community are partitioned among rare and common

20　species, reflecting how species pack in time (Pachepsky *et al.* 2001). Usually only

21　functional diversity measures based on pairwise distances include abundance (for example,

22　Rao 1982, Mason *et al.* 2003, 2005). These measures, however, present some undesirable

23　properties: (1) they violate the monotonicity principle, meaning that their values can

24　decrease with the inclusion or increase with the exclusion of a given species, what is

1 counterintuitive (Ricotta 2005, Petchey & Gaston 2006), and (2) they incorrectly assume

2 pairwise distances to be independent, leading to an inflated estimate of functional diversity

3 (Petchey & Gaston 2006). Since the performance of a species depends on both its traits and

4 its abundance (Reiss *et al.* 2009), a dendrogram-based measure of functional diversity that

5 incoporates species abundances would combine the best properties of both approaches

6 (Petchey & Gaston 2006).

7     In phylogenetic approaches, several indices have been developed, some of which take

8 into account species abundances (see Allen *et al.* 2009 for references). One of them is the

9 so-called "phylogenetic entropy" (PE; Allen *et al.* 2009). PE generalises the Shannon index

10 to incorporate species relatedness, using the branch lengths of a rooted phylogenetic tree.

11 PE is aimed to help conservation management decisions, by favouring communities in

12 which highly distinct species are more abundant, and presents "weak species monotonicity"

13 (Weikard *et al.* 2006), which ensures protection to rare species. One of the promising

14 features of this index is the possibility to use functional, instead of phylogenetic,

15 relatedness and so to include abundance in functional diversity.

16     Even if it is possible to include abundance in dendrogram-based functional diversity

17 measures, this inclusion will only be justified if our predictive power in relating functional

18 diversity to community functioning increases. Studying a southern cerrado site at fine-

19 scale, we measured functional traits of woody species and used litter decomposition rate as

20 a surrogate for community functioning, since decomposition is important in nutrient

21 cycling and may be more related to functional diversity than to traditional diversity

22 measures (Scherer-Lorenzen 2008). We presented extensions of both FD and PE to obtain

23 measures of functional diversity that take abundance into account and, in one case,

24 intraspecific variation as well. In sum, we aimed (1) to test whether, when compared to

1   traditional diversity measures, the inclusion of functional traits leads to an increased

2   predictive power in relating functional diversity to community functioning; (2) to

3   demonstrate that it is possible to include abundance in dendrogram-based functional

4   diversity, and (3) to test whether, when compared to FD as usually calculated, the inclusion

5   of abundance leads to an increased predictive power.

6

7   **METHODS**

8

9   We carried out this study in a woodland savanna site, with 86 ha, at Federal University of

10  São Carlos, southeastern Brazil (21º58' S, 47º51' W and 22º 00' S, 47º52' W). The site is

11  under Cwa climate (Köppen 1931), with wet summer and dry winter. Mean annual rainfall

12  and temperature lie around 1500 mm and 21ºC, respectively. We established a 50 m x 50 m

13  grid, with 100 contiguous plots, each one with 25 m$^2$, where we sampled all woody

14  individuals with stem diameter at soil level equal to or larger than 3 cm (SMA 1997),

15  identifying them to species level. For each individual, we measured eight functional traits

16  related to nutrient cycling, according to Cornelissen *et al.* (2003): leaf size, specific leaf

17  area, leaf dry matter content, stem specific density, height, basal area, resprouting capacity,

18  and bark thickness. We collected the data from March 2009 to May 2010, measuring leaf

19  traits during the rainy season, when productivity was higher, as recommended by

20  Cornelissen *et al.* (2003). The way we measured each functional trait is described in detail

21  in Cornelissen *et al.* (2003).

22      We collected leaves recently shed, oven-dried them at 80°C for 24 h, and put 5 g in each

23  one of 2000 litterbags. In each plot, we placed 20 litterbags, in four sets of five bags. We

24  collected one bag of each set in each plot after 1, 2, 3, 6, and 12 months. In the laboratory,

1    we gently brushed the material to remove soil particles and other debris, oven-dried the

2    bags at 80°C for 24 h, and weighted them. Comparing the initial and the final masses, we

3    found the amount of litter that was decomposed. For each plot and each month, thus, we

4    found the average remaining amount of matter. Since the exponential model describes best

5    the loss of mass over time during litter decomposition (Wieder & Lang 1982), we adjusted

6    the values to an exponential equation ($y = ae^{kt}$), in which $k$ is the coefficient of

7    decomposition, $y$ is the remaining mass in time $t$, and $a$ is the initial mass. After collecting

8    the data in field, we obtained three matrices: the first one with individuals in rows,

9    functional traits in columns, and trait values in entries; the second one with species in rows,

10   functional traits in columns, and average trait values in entries; and the third one with

11   decomposition rates per plot.

12       To answer the first question, for each plot, we calculated species richness (s), Shannon

13   index (H'), and FD. To calculate FD (Petchey & Gaston 2002, 2006), we used the second

14   matrix, standardised the variables to zero mean and unit variance, converted it into a

15   distance matrix with Euclidean distances, produced a dendrogram by clustering the distance

16   matrix with unweighted pair group method with arithmetic averages, and calculated the

17   total branch length of the dendrogram necessary to connect all species in a given plot. We

18   tested whether the data were spatially autocorrelated by appling the Moran test (Legendre

19   & Legendre 1998). As long as they were not, we used simple linear regression analyses

20   (Zar 1999), in which the decomposition rate was the response variable and s, H', or FD

21   were the explanatory variable. We tested the relationships for significance and compared

22   their coefficients of determination ($R^2$), used as a measure of fit (Zar 1999).

23       To answer the second question, we included abundance in functional diversity using four

24   methods: (1) individual-based functional diversity (iFD; Cianciaruso *et al.* 2009), calculated

1     the same way as FD, but with the first matrix, with individuals in rows – with this index,

2     we included not only abundance, but also intraspecific variation; (2) a new index we called

3     "abundance-weighted functional diversity" ($_{aw}$FD), in which the second matrix, that with

4     species in rows, is weighted by a relative abundance vector – then we calculated it the same

5     way as FD; (3) a new index we called "branch-weighted functional diversity" ($_{bw}$FD),

6     calculated the same way as FD, but, when calculating the total branch length, we weighted

7     the terminal branches, which represent the unique contribution of a given species to FD, by

8     its relative abundance; (4) functional entropy (FE), calculated the same way as

9     phylogenetic entropy (Allen *et al.* 2009), but using a functional dendrogram produced from

10     the second matrix instead of a phylogenetic tree. We calculated Spearman's rank correlation

11     coefficient (Zar 1999) among all diversity measures.

12       To answer the third question, we did simple linear regression analyses (Zar 1999), in

13     which the decomposition rate was the response variable and $_i$FD, $_{aw}$FD, $_{bw}$FD, or FE were

14     the explanatory variable. We tested the relationships for significance and compared their

15     coefficients of determination (Zar 1999). We carried out all analyses in R (R Development

16     Core Team 2009), using the "ade4" (Dray & Dufour 2007), "ape" (Paradis *et al.* 2004), and

17     "vegan" (Oksanen *et al.* 2009) packages. We also wrote a code to calculate functional – or

18     phylogenetic – entropy, which is available online (cerradoecology.com).

19

20     **RESULTS**

21

22     We sampled 1995 individuals belonging to 60 species, for which we calculated mean

23     functional trait values (Table 1). Decomposition rate presented a coefficient of variation of

24     16.79 percent and was not significantly related to richness, Shannon index, or functional

1 diversity and, in all cases, explanatory power was very low (Table 2; Fig. 1). We

2 demonstrated that the inclusion of abundance in functional diversity is possible, even

3 though most indices were significantly correlated with each other (Fig. 2). When compared

4 to FD as usually calculated, the inclusion of abundance did not lead to an increased

5 predictive power. The decomposition rate was not significantly related to individual-based

6 functional diversity, abundance-weighted functional diversity, branch-weighted functional

7 diversity, or functional entropy and, in all cases, explanatory power was very low (Table 2;

8 Fig. 1).

9

10 **DISCUSSION**

11
12 We expected that functional diversity would be a better predictor than traditional diversity

13 measures, such as species richness and Shannon index (Díaz & Cabido 2001, Petchey

14 2004). However, this expectation was not corroborated, as we did not find any relationship

15 between decomposition and either traditional or functional diversity indices. The absence of

16 relationship between functional diversity and litter decomposition rates may be due to five

17 reasons (Petchey & Gaston 2006): (1) unimportant traits considered, (2) inappropriate

18 measures of functional diversity, (3) another process or factor more important than

19 functional diversity, (4) statistical power, or (5) absence of effect of functional diversity on

20 community functioning. The first reason is unlikely, since we chose traits directly related to

21 functioning (Cornelissen *et al.* 2003). So is the second reason, since FD and FE are

22 appropriate measures of functional diversity (Petchey & Gaston 2006, Allen *et al.* 2009),

23 and the extensions of the former, have the advantage of taking abundance into account. Our

24 sampling effort was high enough, with 100 plots and 1995 individuals. Thus, we postulate

1     that either other processes or factors are more important or that functional diversity has no

2     effect on decomposition rates.

3        Plant community influence decomposition processes and nutrient cycling either directly,

4     by litter quality, or indirectly, by creating unique micro-environment conditions (Scherer-

5     Lorenzen 2008, Vivanco & Austin 2008). Living plant functional traits are linked to litter

6     decomposability (Cornelissen & Thompson 1997, Cornwell *et al.* 2008), especially

7     considering that green and litter leaves traits are correlated with decomposition in

8     equivalent ways (Hättenschwiler *et al.* 2011). Although green leaf traits can predict even

9     better decomposition rates (Bakker *et al.* 2011), litter leaf traits are more associated to

10    decomposability (Cornwell *et al.* 2008, Zhang *et al.* 2008) due to emergent propreties and

11    synergistic efects among litter leaves from different species (Gartner & Cardon 2004,

12    Hättenschwiler *et al.* 2005). To assess plant functional diversity effects on decomposition

13    rate, we isolated the litter quality, homogenising the material in the litterbags. Maybe we

14    could not find a relationship, because indirect effects of plant traits on decomposition were

15    very low compared to effects of litter quality. Alternatively, the complementarity among

16    decomposers and detritivores may be more important to decomposition (David & Handa

17    2010, Gessner *et al.* 2010). The impacts of decomposer diversity on the stability of

18    essential functions differ between plant communities (Eisenhauer & Shäudler 2011) and are

19    dependent of several trophic levels (Gessner *et al.* 2010, Eisenhauer & Shäudler 2011).

20    Thus, indirect effects of plant traits in creating micro-habitats may not be linear to the

21    decomposer diversity.

22       If the functional role of a species depends on its relative abundance or productivity

23    (Whittaker 1965), then species effects should be weighted by its abundance to reflect its

24    contribution to the functioning (Villéger *et al.* 2008). As a consequence, many indices of

1 functional diversity that include abundance have been developed (Rao 1982, Mason *et al.*

2 2003; Mouillot *et al.* 2005, Botta-Dukát 2005). These indices are an improvement in

3 relation to those of functional richness, but they present some undesirable properties: some

4 are designed to work with only one trait at a time; others violate set monotonicity (Petchey

5 & Gaston 2006). As originally concepted, FD is a functional richness measure, since it does

6 not take abundances into account (Botta-Dukát 2005, Pechey & Gaston 2006).

7 Nevertheless, we demonstrated that it is possible to include species abundances into FD and

8 that is possible to do that in different ways. Even if in our study the inclusion of abundance

9 into FD did not increase its predictive power, there may be situations in which that

10 inclusion will increase it.

11     Each measure we applied required a similar sampling effort, except $_i$FD. To calculate

12 FD, $_{aw}$FD, $_{bw}$FD, and FE, it would be necessary to measure functional traits of 10

13 individuals per species (as indicated for FD; Cornelissen *et al.* 2003) and to count the

14 number of individuals present in each plot. For some species with less than 10 individuals

15 in the plots, an additional sampling effort could be necessary to find individuals outside the

16 plots. In the case of $_i$FD, all individuals should be measured, what could represent an

17 extremely higher effort in terms of time and money. For example, in our study, since we

18 found 60 species, one would have to sample only 600 individuals, instead of 1995, to

19 calculate FD, $_{aw}$FD, $_{bw}$FD, and FE. However, there may be situations in which sampling all

20 individuals is recommended. For example, when intraspecific variability is high, the

21 relationship between FD and $_i$FD becomes weak (Cianciaruso *et al.* 2009). In such a case,

22 including intraspecific variation should allow a more complete understanding of the

23 processes that link diversity and community functioning (Cianciaruso *et al.* 2009).

1    Most of the indices we proposed were correlated with species richness and FD, what is

2    supposed to happen when species are equally complementary (Pechey & Gaston 2006). If

3    one uses many functional traits and if they are uncorrelated, then there woud be potential

4    for separation of species in high-dimensional trait space (Petchey & Gaston 2002). The

5    high-dimensional trait space allows all species to differ equally, that is, all species can be

6    equidistant in trait space (Petchey & Gaston 2002). If so, one would expect a linear

7    relationship between species richness and FD (Petchey & Gaston 2002), as we found.

8    Conversely, the weak, albeit significant, correlation between FD and $_i$FD indicated a

9    relatively high intraspecific variability. Intraspecific variability highlights processes linking

10    individuals and community and may provide better predictions of the effects of

11    environmental changes on both biodiversity and community functioning (Cianciaruso *et al.*

12    2009, Jung *et al.* 2010). However, since the sampling effort necessary to calculate $_i$FD is

13    much higher than for any other indices, its use must be considered in a cost-benefit

14    analysis.

15    Different distribution of abundances will lead to different correlation coefficients among

16    the indices we proposed. When the most abundant species are also the most complementary

17    ones, there will be weak correlations between FD and the new indices. All indices would

18    help one to predict how the loss of one species influences functional diversity, since it

19    depends on how abundance is related to both the order species are lost and the functional

20    distances (Petchey & Gaston 2006). Thus, in a worst-case scenario, when a rare and

21    complementary species is lost, one could expect lower values of $_{aw}$FD, $_{bw}$FD, $_i$FD, and FE

22    than those predicted by FD.

1    We also expected that the inclusion of abundance in functional diversity would result in

2    more predictive measures of diversity (Petchey & Gaston 2006). However, the indices we

3    proposed did not increase our predictive capacity in the cerrado data set. Assuming that the

4    main criterion for the selection of an index is whether it accurately measures what it is

5    intended to describe (Schleuter *et al.* 2010), the new indices we applied brought no extra

6    advantage over FD and PE, because we did not find significant relationships between them

7    and litter decomposition. Nevertheless, there may be situations in which the new indices

8    will predict community functioning better. For instance, when one is working at larger

9    scales, with other vegetation types, or other descriptors of community functioning.

10    Depending on the characteristics of the community, an index can be more appropriate

11    than other. A good way to choose an appropriate index is by its response to loss or addition

12    of species and to changes in species abundances (Petchey & Gaston 2006). However, the

13    effects of changing species dominance in functional diversity and properties of

14    communities are much less investigated than effects of species loss (Hillebrand *et al.* 2008).

15    When any factor changes species distributions, functional trait distribution also changes.

16    Consequently, the magnitude of inter- and intraspecific relationships, community dynamics,

17    and processes dependent of abundance are also modified (Hillebrand *et al.* 2008). Since

18    species richness and evenness are not always positively correlated, one should consider

19    whether the prediction depends on species abundance distributions (Hillebrand *et al.* 2008).

20    Moreover, the data set in question, its dimensionality, and the type of variables available

21    are also important when choosing an index (Schleuter *et al.* 2010). Thus, by incorporating

22    species abundances into a dendrogram-based measure of diversity, we showed that it is

23    possible to combine the best of both worlds.

24

7

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14

1 TABLE 1. *Abundance and mean trait values for woody species sampled in a woodland*

2 *cerrado, southeastern Brazil (approximately, 21°58'05.3" S, 47°52'10.1" W). A=*

3 *abundances, LS = leaf size (cm$^2$), SLA = specific leaf area (cm$^2$/g), LDMC = leaf dry*

4 *matter content (mg/g), SSD = specific stem density (g/cm$^3$), H = height (m), BA = basal*

5 *area (cm$^2$), RC = resprouting capacity (resprout/ind), BT = bark thickness (mm).*

| Family | Species | A | LS | SLA | LDMC | SSD | H | BA | RC | BT |
|---|---|---|---|---|---|---|---|---|---|---|
| Anacardiaceae | *Tapirira guianensis* Aubl. | 1 | 125.2 | 80.8 | 384.4 | 0.4 | 3.9 | 22.0 | 0.0 | 0.2 |
| Annonaceae | *Annona coriacea* Mart. | 2 | 61.7 | 79.7 | 311.5 | 0.2 | 2.0 | 11.7 | 0.0 | 0.2 |
| Annonaceae | *Annona crassiflora* Mart. | 1 | 63.0 | 78.0 | 385.3 | 0.3 | 6.2 | 503.3 | 0.0 | 3.5 |
| Annonaceae | *Xylopia frutescens* Aubl. | 2 | 4.3 | 121.5 | 535.2 | 0.5 | 4.3 | 13.7 | 0.0 | 0.3 |
| Aquifoliaceae | *Ilex cerasifolia* Reiis. | 1 | 17.6 | 157.9 | 333.3 | 0.4 | 3.5 | 13.6 | 0.0 | 0.1 |
| Araliaceae | *Schefflera macrocarpa* (Cham. & Schltdl.) Frodin | 5 | 148.8 | 45.8 | 384.6 | 0.3 | 3.4 | 20.9 | 0.2 | 0.7 |
| Araliaceae | *Schefflera vinosa* (Cham. & Schltdl.) Frodin & Fiaschi | 62 | 93.5 | 70.0 | 386.2 | 0.4 | 3.2 | 23.8 | 0.1 | 0.3 |
| Asteraceae | *Gochnatia pulchra* Cabrera | 23 | 23.1 | 103.8 | 462.2 | 0.6 | 2.3 | 26.6 | 0.4 | 1.1 |
| Asteraceae | *Piptocarpha rotundifolia* (Less.) Baker | 97 | 52.8 | 101.3 | 364.8 | 0.3 | 2.5 | 42.2 | 0.0 | 4.6 |
| Bignoniaceae | *Tabebuia ochracea* (Cham.) Standl. | 87 | 134.7 | 81.6 | 324.0 | 0.3 | 1.9 | 20.6 | 0.0 | 4.3 |
| Celastraceae | *Plenckia populnea* Reissek | 10 | 43.8 | 108.6 | 390.3 | 0.5 | 4.5 | 73.3 | 0.0 | 2.1 |
| Clusiaceae | *Kielmeyera coriacea* Mart. & Zucc. | 51 | 67.2 | 76.0 | 291.9 | 0.3 | 2.5 | 80.2 | 0.0 | 6.1 |
| Clusiaceae | *Kielmeyera grandiflora* (Wawra) Saddi | 29 | 151.5 | 70.7 | 243.2 | 0.3 | 2.1 | 67.6 | 0.1 | 3.7 |
| Dilleniaceae | *Davilla elliptica* A. St.-Hil. | 4 | 31.1 | 137.4 | 315.0 | 0.5 | 2.1 | 93.0 | 0.8 | 2.2 |
| Dilleniaceae | *Davilla rugosa* Poir. | 1 | 12.3 | 133.5 | 381.3 | 0.6 | 3.1 | 13.6 | 0.0 | 0.1 |
| Ebenaceae | *Diospyros hispida* A. DC. | 35 | 124.5 | 73.1 | 355.1 | 0.3 | 1.6 | 17.2 | 0.0 | 4.1 |
| Erythroxylaceae | *Erythroxylum cuneifolium* (Mart.) O.E. Schulz | 6 | 2.5 | 146.1 | 408.5 | 0.7 | 4.2 | 10.0 | 0.2 | 0.2 |
| Erythroxylaceae | *Erythroxylum suberosum* A. St.-Hil. | 58 | 28.1 | 106.4 | 347.2 | 0.3 | 1.5 | 26.5 | 0.1 | 5.6 |

| Erythroxylaceae | *Erythroxylum tortuosum* Mart. | 51 | 52.2 | 99.2 | 328.7 | 0.3 | 1.3 | 32.8 | 0.0 | 6.4 |
|---|---|---|---|---|---|---|---|---|---|---|
| Euphorbiaceae | *Pera glabrata* Poepp. ex Baill. | 18 | 35.2 | 70.2 | 428.9 | 0.5 | 5.6 | 120.5 | 0.2 | 0.6 |
| Fabaceae | *Acosmium dasycarpum* (Vogel) Yakovlev | 19 | 99.5 | 105.2 | 299.4 | 0.3 | 1.8 | 26.5 | 0.1 | 7.9 |
| Fabaceae | *Acosmium subelegans* (Mohlenbr.) Yakovlev | 4 | 50.4 | 81.4 | 358.2 | 0.5 | 2.2 | 33.1 | 0.0 | 6.6 |
| Fabaceae | *Bauhinia rufa* (Bong.) Steud. | 26 | 66.3 | 86.7 | 424.6 | 0.5 | 3.1 | 10.6 | 0.0 | 0.8 |
| Fabaceae | *Dalbergia miscolobium* Benth. | 43 | 55.2 | 63.1 | 440.9 | 0.4 | 7.6 | 355.9 | 0.0 | 9.3 |
| Fabaceae | *Dimorphandra mollis* Benth. | 8 | 256.0 | 145.1 | 354.2 | 0.4 | 3.3 | 42.5 | 0.0 | 6.6 |
| Fabaceae | *Macherium acutifolium* Vogel | 4 | 82.7 | 90.4 | 419.1 | 0.5 | 3.5 | 60.4 | 0.0 | 7.4 |
| Fabaceae | *Stryphnodendron adstringens* (Mart.) Coville | 44 | 267.1 | 80.1 | 339.8 | 0.4 | 2.4 | 45.2 | 0.0 | 2.9 |
| Fabaceae | *Stryphnodendron obovatum* Benth. | 30 | 159.1 | 94.1 | 342.8 | 0.6 | 3.0 | 14.8 | 0.0 | 1.3 |
| Lauraceae | *Ocotea pulchella* (Nees) Mez | 43 | 12.9 | 77.0 | 462.9 | 0.5 | 4.3 | 55.8 | 0.2 | 0.5 |
| Malpighiaceae | *Banisteriopsis megaphylla* (A. Juss.) B. Gates | 1 | 3.7 | 123.6 | 256.1 | 0.4 | 5.6 | 42.7 | 0.0 | 0.5 |
| Malpighiaceae | *Byrsonima coccolobifolia* Kunth | 60 | 42.1 | 112.9 | 351.9 | 0.3 | 2.2 | 24.2 | 0.1 | 1.5 |
| Malpighiaceae | *Byrsonima verbascifolia* (L.) DC. | 2 | 148.7 | 68.5 | 377.4 | 0.3 | 3.0 | 118.1 | 0.0 | 3.2 |
| Malpighiaceae | *Heteropterys umbellata* A. Juss. | 4 | 5.8 | 125.4 | 379.2 | 0.7 | 2.5 | 12.8 | 0.3 | 0.4 |
| Melastomataceae | *Leandra lacunosa* Cogn. | 2 | 12.9 | 75.3 | 364.7 | 0.9 | 2.1 | 15.4 | 0.0 | 0.6 |
| Melastomataceae | *Miconia albicans* (Sw.) Triana | 117 | 28.3 | 74.6 | 453.7 | 361.3 | 2.8 | 97.8 | 1.0 | 1.1 |
| Melastomataceae | *Miconia ligustroides* (DC.) Naudin | 10 | 14.5 | 102.0 | 368.0 | 0.5 | 2.7 | 21.2 | 0.0 | 0.3 |
| Melastomataceae | *Miconia rubiginosa* (Bonpl.) DC. | 1 | 30.2 | 67.8 | 437.2 | 0.6 | 4.0 | 35.6 | 0.0 | 2.8 |
| Myrsinaceae | *Rapanea ferruginea* (Ruiz & Pav.) Mez in Urb. | 6 | 15.9 | 128.1 | 370.8 | 0.5 | 4.1 | 32.8 | 0.0 | 0.6 |
| Myrsinaceae | *Rapanea guianensis* Aubl. | 1 | 22.3 | 56.6 | 381.7 | 0.6 | 4.4 | 87.8 | 1.0 | 0.8 |
| Myrsinaceae | *Rapanea umbellata* (Mart.) Mez | 557 | 27.7 | 79.5 | 374.4 | 0.5 | 3.6 | 16.4 | 0.1 | 0.4 |
| Myrtaceae | *Campomanesia adamantium* (Cambess.) O.Berg | 22 | 25.8 | 108.8 | 383.9 | 0.5 | 2.1 | 11.2 | 0.1 | 0.9 |
| Myrtaceae | *Myrcia bella* Cambess. | 42 | 5.6 | 88.4 | 404.7 | 0.4 | 2.7 | 29.7 | 0.0 | 6.4 |
| Myrtaceae | *Myrcia fallax* DC. | 6 | 25.0 | 165.2 | 408.7 | 0.6 | 3.2 | 12.2 | 0.0 | 0.3 |
| Myrtaceae | *Myrcia* lingua (O.Berg) Mattos & D.Legrand | 129 | 14.5 | 101.6 | 355.7 | 0.4 | 2.6 | 37.1 | 0.0 | 4.8 |

| Myrtaceae | *Myrcia rostrata* DC. | 4 | 6.8 | 74.7 | 489.1 | 0.5 | 3.3 | 22.1 | 0.0 | 2.0 |
| Myrtaceae | *Myrcia tomentosa* (Aubl.) DC. | 4 | 15.5 | 113.2 | 382.0 | 0.5 | 3.5 | 29.5 | 0.3 | 0.2 |
| Myrtaceae | *Psidium lauroteanum* Cambess. in A.St.-Hil. | 2 | 16.1 | 66.7 | 480.4 | 0.5 | 4.2 | 12.7 | 0.0 | 3.4 |
| Nyctaginaceae | *Guapira noxia* (Netto) Lundell | 4 | 49.5 | 119.9 | 214.7 | 0.3 | 2.1 | 250.4 | 0.5 | 14.5 |
| Nyctaginaceae | *Guapira opposita* (Vell.) Reitz | 3 | 33.4 | 115.6 | 289.2 | 0.5 | 2.0 | 17.1 | 0.0 | 1.2 |
| Ochnaceae | *Ouratea spectabilis* (Mart. ex Engl.) Engl. | 3 | 28.0 | 56.5 | 430.5 | 0.4 | 2.4 | 49.7 | 0.0 | 4.4 |
| Phyllanthaceae | *Phyllanthus acuminatus* Vahl | 2 | 4.4 | 172.6 | 440.7 | 0.4 | 4.2 | 11.7 | 0.0 | 0.2 |
| Rubiaceae | *Palicourea rigida* (Cham.) K.Schum. | 1 | 161.3 | 86.1 | 301.2 | 0.2 | 1.8 | 35.6 | 0.0 | 6.8 |
| Rubiaceae | *Rudgea viburnoides* (Cham.) Benth. | 11 | 46.2 | 76.7 | 287.4 | 0.3 | 3.2 | 39.6 | 0.2 | 2.7 |
| Rubiaceae | *Tocoyena formosa* (Cham. & Schltdl.) K.Schum. | 41 | 116.9 | 96.9 | 335.2 | 0.4 | 2.5 | 17.9 | 0.0 | 0.4 |
| Rutaceae | *Zanthoxyllum rhoifolium* Lam. | 3 | 45.4 | 104.6 | 397.6 | 0.5 | 4.0 | 26.2 | 0.0 | 0.3 |
| Salicaceae | *Casearia sylvestris* Sw. | 6 | 11.3 | 144.1 | 342.7 | 0.3 | 1.9 | 16.1 | 0.2 | 4.2 |
| Styracaceae | *Styrax ferrugineus* Nees & Mart. | 9 | 27.5 | 81.3 | 433.4 | 0.3 | 3.0 | 77.0 | 0.1 | 7.0 |
| Thymelaeaceae | *Daphnopsis fasciculata* (Meissn.) Nevl. | 4 | 8.1 | 88.2 | 393.8 | 0.4 | 4.6 | 22.4 | 0.0 | 0.1 |
| Verbenaceae | *Aegiphilla lhotzkiana* Cham. | 8 | 123.7 | 168.6 | 210.0 | 0.2 | 2.9 | 28.2 | 0.0 | 5.7 |
| Vochysiaceae | *Vochysia tucanorum* Mart. | 165 | 19.9 | 116.8 | 274.6 | 0.4 | 3.2 | 46.1 | 0.1 | 0.7 |

1

1 TABLE 2. *Slope (b), coefficient of determination ($R^2$), and p-values (p) for simple linear*

2 *regressions between decomposition rate as response variable and richness (s), Shannon*

3 *index (H'), functional diversity (FD), individual-based functional diversity ($_iFD$),*

4 *abundance-weighted functional diversity ($_{aw}FD$), branch-weighted functional diversity*

5 *($_{bw}FD$), and functional entropy (FE) as explanatory variables. Data collected for woody*

6 *species in a woodland cerrado, southeastern Brazil (approximately, 21°58'05.3" S,*

7 *47°52'10.1" W).*

| Index | $B$ | $R^2$ | $p$ |
|---|---|---|---|
| S | 0 | 0.000 | 0.98 |
| H' | 0 | 0.001 | 0.71 |
| FD | 0 | 0.001 | 0.81 |
| $_iFD$ | 0 | 0.011 | 0.30 |
| $_{aw}FD$ | 0 | 0.004 | 0.55 |
| $_{bw}FD$ | 0 | 0.000 | 0.99 |
| FE | 0 | 0.000 | 0.93 |

8

9

1   FIGURE 1. Decomposition rate (k) in relation to (A) richness (s), (B) Shannon index (H'),

2   (C) functional diversity (FD), (D) individual-based functional diversity ($_i$FD), (E)

3   abundance-weighted functional diversity ($_{aw}$FD), (F) branch-weighted functional diversity

4   ($_{bw}$FD), and (G) functional entropy (FE). Data collected for woody species in a woodland

5   cerrado, southeastern Brazil (approximately, 21°58'05.3"S, 47°52'10.1"W).

6

7   FIGURE 2. Pairwise Spearman's rank correlation coefficients among richness (s), Shannon

8   index (H'), functional diversity (FD), individual-based functional diversity ($_i$FD),

9   abundance-weighted functional diversity ($_{aw}$FD), branch-weighted functional diversity

10  ($_{bw}$FD), and functional entropy (FE) for woody species sampled in a woodland cerrado,

11  southeastern Brazil (approximately, 21°58'05.3"S, 47°52'10.1"W). Tukey's running

12  median smoothing line in black. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.