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Full Length Research Paper

When ecological functions are more important than richness: A conservation approach

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In this work, we utilize the assessment of functional groups (FG) and functional diversity (FD) to evaluate and compare the ecological functions of two types of dry forest of South Eastern Brazil. Hence, we hypothesized that forests with different species richness could have similar FD and FG, but distinct ecological functions. The floristic composition from two physiognomies (deciduous and semideciduous forests) of six tree communities was carried out in the state of Minas Gerais, South-Eastern Brazil. The inventory was pooled together considering the traits of species such as: shade tolerance, deciduousness and desiccation tolerance of seeds; one structural feature: position on vertical strata; and two animal-plant interactions: dispersal syndrome and pollination syndrome. We chose two multivariate analyses to infer to the functional groups and used the one-way ANOVA to test differences between the abundance of the groups in the two physiognomies. The difference in FD between the two physiognomies was tested using the Shannon diversity index and the Hutcheson t-test. Both physiognomies had the same FG and FD. The most abundant group in the semi-deciduous forest was G1, which occupied lower communities (shade tolerant and perennial), whereas G4 for deciduous forest was anemochoric and autochoric of superior community strata that is light demanding. The functional diversity between the two physiognomies showed that semi-deciduous contains more species than the deciduous ones (75% more species) and are more diverse with the Shannon index of 3.3. Hence, the number of species alone had little importance when we analysed functions in ecosystems. The more abundant groups in each forest had completely different traits and were complementary in their functions to the ecosystem. In this case, a species-rich and less- species-rich system provided different key functions to the ecosystem despite their differences in species richness, diversity or physiognomic type. The use of species-rich and less- species- rich areas would present different key groups, and as such, this may be the best alternative to choose priority areas for conservation.

Key words: Complementarity, deciduous forest, dry forest, functional diversity, functional groups, semi-deciduous forest.

INTRODUCTION

The classification of functional groups (FGs) reduces a large number of species in a small group of functional types, which incorporate the same responses to perturbations or are similar with regard to dispersion, competition and survival processes (Hubbell, 2005; Skov, 2000). Groups of species may also reveal features of system functionality (Swaine and Whitmore, 1988) which would be difficult to detect when looking at the species separately.

The use of FGs is particularly important because the diversity of functional types is more important than the diversity of species for many aspects of ecosystem performance (Pendry et al., 2007) . For example, plant reproductive success tends to increase with the functional diversity of pollinators (Fontaine et al., 2006). Additionally, functional diversity increase plant

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productivity and light penetration in a grassland-savanna, but species diversity does not (Tilman et al., 1997). Thus, functional diversity (FD) can be defined as a variety of life-history traits presented by an assemblage of organisms (Fontaine et al., 2006; Mayfield et al., 2005) and it is critical for the maintenance of ecosystem processes and properties (Tilman et al., 1997).

The usual measure of FD is the number of functional groups in a community (Hooper and Vitousek, 1997; Tilman et al., 1997) and the number of species and traits that influence the functional groups (Petchey and Gaston, 2002b, 2006). A greater number of traits and species are associated with more functional groups and, therefore, more FD (Petchey, 2004; Petchey and Gaston, 2002a), although this is not always true. However, a greater number of species does not necessarily mean more traits (Petchey and Gaston, 2002a) or more FD and FG. Hence, we hypothesize that forests with differences in species richness could have similar FD and FG, but distinct ecological functions in the ecosystem.

For a good representation of ecological functions, we need to choose traits that represent important functions to systems. Most studies on functional diversity in plant communities have focused on the importance of traits associated with plant physiology, like sunlight interception or shadow tolerance (Girao et al., 2007). Little is still known with regards to the functional diversity of traits that affect ecosystem functioning, such as those related to plant- animal interactions (Fontaine et al., 2006; Mayfield et al., 2005), mainly on the tropical ecosystems with high diversity and complex interactions. Therefore, studies which associate plant physiology and plant-animal interactions are needed to better understand and compare forest systems.

To test the hypothesis we used a Brazilian seasonally dry tropical forest, one of the most threatened ecosystems in Brazil (Espirito-Santo et al., 2009). Also, dry forests are neglected by research and conservation efforts compared to the tropical rain forests (Sanchez-Azofeifa et al., 2005), maybe because they lower the diversity of plant species on the seasonal forests. Dry forests can be subdivided into seasonal deciduous and semi-deciduous forests (Oliveira-Filho and Ratter, 2002). Both are physiognomically identical in terms of structural parameters (height of canopy, density and basal area) and appear next to each other or are connected in the landscape, but the first one is less rich in species. However, we know little about the ecological functions in the ecosystem of these threatened forests, and as such, comparisons of ecological functions in similar physiognomic environments are still lacking. We aimed to answer the following questions to test our hypothesis: (1) Can less-species-rich forests have similar functional diversities as compared to species-rich forests? (2) Are the functional groups of these forests similar? (3) Do similar functional groups have the same value of the ecosystem? (4) Can the functional diversity in complementary forests justify different conservation efforts?

METHODS

The study was conducted in six fragments of seasonal forests in the state of Minas Gerais, South-eastern Brazil at coordinates 18°56’ S and 48°12’ W, 18°40’ S and 48°24’ W, 18°29' S and 48°22' W for semideciduous sites and 18°48’ S and 48°07’ W, 18°47’ S and 48°06’ W, 18°39’S and 48°25’ W for deciduous sites. The sites were in the same climatic zone, characterized by warm temperatures throughout the year with a rainy summer and a dry winter. The regional climate is Aw (tropical savannic) according to the Köppen classification (1948), with a mean annual precipitation of 228.5 mm in each wet month (October to march) and 35.5 mm in each dry month (April to September), and a mean annual temperature of 23.7°C available in a weather station called the 5° Meteorological District/Uberlândia Station, Brazil. A plant species list for three seasonal deciduous and three semi-deciduous sites was collected in arboreal community studies (Kilca et al., 2009; Siqueira et al., 2009; Vale et al., 2009). An area of one hectare was sampled at each site and all trees, with a circumference at breast height (CBH to 1.3 m above ground floor), that are equal to or larger than 15 cm were measured. Only species with at least five individuals in each site were analysed. The data of the three deciduous sites were united as one sample and the same was done with the data for the three semi-deciduous sites.

For each species, data were collected for three physiological traits: (1) shade tolerance, (2) deciduousness and (3) desiccation tolerance of seeds; one structural feature: (4) position on vertical strata; and two animal-plant interactions: (5) dispersal syndrome and (6) pollination syndrome. These characteristics are illustrated in Table 1. Information about these ecological attributes were researched in scientific articles and specialist books, field observations, specialist conferences and the analyses previously performed on the structure of tree communities (Table 1) . A total of 53 species in the deciduous forest and 93 species in the semi-deciduous forest were analysed. The complete list of species, with the occurrence, density, matrix of treats and group is shown in Appendix 1. The same species found in both forests were considered once in the matrix. Therefore, a matrix with 132 species and 19 traits (Table 1 and Appendix 1) was used for analysis. We converted the data into a presence/absence matrix with species and their ecological attributes. The columns were exclusive for each characteristic. Following this, a matrix of ecological distance was produced (Petchey and Gaston, 2002b). The functional groups were derived by the distance matrix, using the “cluster” and the “correspondence” analyses.

Cluster analysis

The groups were defined by euclidian distance and a dendrogram generated through the group average (UPGMA). Multivariate clustering methods were used to see which groups of plant species would emerge. These methods calculated the similarity or association measures based on the extent to which species have attributes in common (Leishman and Westoby, 1992). The cophenetic correlation for the generated dendrogram was calculated. The coefficient of cophenetic correlation (equivalent to the Pearson coefficient) was proposed as a measure of how a dendrogram maintains the original pair wise distances (Bussab and Morettin, 1990). The statistical analyses were performed using the FITOPAC SHELL 1.6.4 program (Shepherd, 2004).

Correspondence analysis (CA)

This exploratory technique could represent the correspondence

Table 1. Characteristics and their respective ecological functions used for the distance ecological matrix.

Trait	Classification	Categories	Ecological function
Dispersion syndrome	Diaspores dispersed by wind	Anemochory	Long dispersion, which is affected slightly by fragmentation.
	Free fall or ballistic mechanisms	Autochorory	Short distance dispersion, highly affected by fragmentation.
	Birds	Ornitochory	Medium distance of dispersion, affected by fragmentation and a resource for birds.
	Mammals	Mammaliochory	Short distance dispersion, highly affected by fragmentation and a resource for mammals.
Deciduousness	Species were all leaves		
	Fall off during some period of the dry station	Deciduous	High litter release and canopy opened to other plants.
	Remain during the entire year	Perennials	Shade and refuge for animals, increases shading to other plants.
Shadow tolerance	Light environment required for establishment		
	Tolerate shade under other trees	Shade tolerant	Low growing species and climax species, related to maturity of forest.
	Need direct sunlight to develop	Light demanding	Fast growing species, generally represent initial stages of regeneration.
Vertical strata	Based on the stature commonly reached by adult individuals		
	Always reaches the canopy	Typical canopy	Represents greater biomass accumulation and shades smaller species.
	Sometimes, it reaches the canopy	Intermediate strata	Integrate canopy and understory, generally representing some strata.
	Usually do not reach the upper layers of the forest	Typical understory	Low basal area but high density species, is a distinct habitat for animals than canopy.
Seed desiccation tolerance	Related to how seeds remain in the environment until the next season		
	Seeds are able to survive until the next season	Orthodox	Form seed banks in forest.
	Seeds are unable to survive until the next season	Non-orthodox	Form a "bank of seedlings" but not a seed bank

Table 1. Contd.

Pollination syndrome	Species were classified by animal pollinator		
	Body size under 5 mm	Very small insects	Prevent inbreeding, promotes genetic variability and a resource to very small insects.
	Small bees, wasps and flies (body size 5-12 mm)	Small insects	Prevent inbreeding, promotes genetic variability and a resource to bees, wasps and flies.
	Bees with large size body (more than 12 mm)	Large bees	Prevent inbreeding, promotes genetic variability and a resource to big, solitary bees.
	Beetles	Beetles	Prevent inbreeding, promotes genetic variability and a resource to beetles.
	Butterflies and moths	Lepidoptera	Prevent inbreeding, promotes genetic variability and a resource to moths and butterflies.
	Bats	Bats	Prevent inbreeding, promotes genetic variability and a resource to bats.

between species. We considered this technique appropriate for detecting functional groups because the ecological distance between the species is expressed graphically. This analysis was performed using FITOPAC SHELL 1.6.4 program (Shepherd, 2004).

To compare the functional diversity, we calculated Shannon diversity index (Brower et al., 1997) for the functional groups that is resultant from the cluster and correspondence analysis. Unlike the traditional Shannon index, the abundance of species is replaced by abundance of groups. Therefore we treat the Shannon index value for functional groups like functional diversity. Then we calculated and compared the significance of these indices with Hutcheson t-test for the deciduous and semi-deciduous forests (Brower et al., 1997).

One-way ANOVA was used to test differences in the abundance of groups between deciduous and semi-deciduous forests, and to test differences in group species number per plot. For these tests, we randomly selected 50 plots in the deciduous and semi-deciduous forests. The Bonferroni post-hoc procedure was applied to assess differences in group abundance among the sites. Abundance data were transformed into a logarithmic scale (base 10) for data standardization.

The intention of these analyses was to determine if the areas with lower species richness and diversity have priority for conservation and if these criteria are valid for dry forests. We think that these methods, using FD and FG, could help in prioritizing conservation by focusing on ecosystem functionality.

RESULTS

The 53 tree species analysed here represented 92% of the individuals found in the deciduous sites. The 93 tree species analysed in semi-deciduous sites represented 91% of the total of individuals in this physiognomy. These high values indicate the high representation of species analysed in these systems.

Appendix I shows the list of species used for the analysis of functional groups with the number of individuals and the respective attributes of each one.

The dendrogram formed five groups (Figure 1) with a high cophenetic correlation of 0.77, thus the dendrogram and species ecological differentiation showed a good correlation. Therefore the number of functional groups is the same for both forests (five). The Hutcheson t-test for the Shannon index value found between forests for the five groups was not significant ($p > 0.1$; df > 500). This means that these forests have the same functional diversity. However, in the correspondence analysis of ecological distances, we could only view four cohesive groups. This was because two of the groups formed in the dendrogram (G3a and G3b) were joined together in the CA (Figure 2). All four groups contained deciduous and semi-deciduous species. Therefore, the FG found in both analyses was strictly the same. The Hutcheson t-test for the Shannon index value found between the four groups in CA was not significant ($p > 0.1$; df > 500). This means that these forests have the same functional diversity for CA groups too, just like cluster analyses.

After it was found that there were no great differences between both multivariate techniques, we concluded that both techniques were satisfactory for showing FG in forests. As there were no major ecological differences between groups G3a and G3b in the cluster analysis, hence we chose to use the results of the CA for the remainder of the analysis. Table 2 shows the ecological characteristics of the four groups found

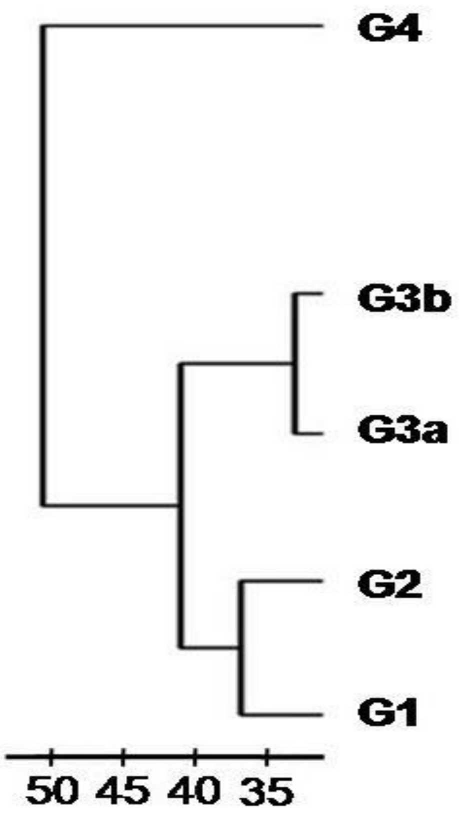

Figure 1. Functional groups based on ecological distance formed by clustering in six seasonal dry tropical forests in South-eastern Brazil. A cluster was defined by the Euclidian distance and UPGMA method. Group characteristics are shown in Table 2.

in the semi-deciduous and deciduous forests.

The abundance (number of individuals in each group) of the four groups varied between the forests. G1 was the most abundant group in semi-deciduous forests, while G4 was the most abundant in deciduous forests (Figure 3a), but both groups had the same abundance according to the Bonferroni test ($p > 0.05$; df = 7). The five other groups showed no significant differences for abundance. The Bonferroni test showed that G1D, G3D, G3S, G2D and G4S had the same weight to ecosystem in terms of the number of individuals ($p > 0.05$; df = 7) (D is for deciduous and S is for semi-deciduous forest). One group (G2S - species on lower layers of the community is shade tolerant, deciduous, ornitochoric and pollinated by small insects and lepidoptera) was underrepresented in the semi-deciduous forest. These results reflect the environmental differences between both forests. As such, deciduous forests have more water deficit in soil during the dry season (Oliveira-Filho and Ratter, 2002), which influences the deciduousness in these sites. However, this feature of water stress in soil clearly separated the two physiognomies, not only due to the deciduousness which interferes with floristic and structural variations, but also in the main functions of these forests (compares G1 and G4 in Table 2).

Unlike the abundance, the number of species per group showed different results. The two most species-rich groups were the same as the most abundant groups for the forests (G1S and G4D - Figure 3b). However, the other groups were significantly different according to the Bonferroni test. Group G4S had more species than the remaining five groups and G3S had more species than the other remaining four groups ($p < 0.01$; df = 7). Therefore, these four groups (G1S, G4D, G4S and G3S) were more redundant in the ecosystem than the others were. As such, the remaining groups had the same number of species ($p > 0.05$; df = 7). These results show that the number of species do not always have a relation with the abundance of the groups formed. G3 has the same abundance for both deciduous and semi-deciduous forests (Figure 3a), but is much richer in the species on semi-deciduous forest (Figure 3b). The inverse occur in G2, with same richness (Figure 3b), but more abundant on deciduous sites (Figure 3a).

When analysing the similar groups for both forests, we could see differences for groups per physiognomy. For example, G1 had more species and individuals in the semi-deciduous forest than in the deciduous forest (Figures 3a and 3b), and G4 was more abundant in the deciduous forest ($p < 0.01$; df = 7), but the number of species in both physiognomies was the same ($p > 0.05$; df = 7). Group G3 had the same number of individuals ($p > 0.05$; df = 7) in both forests, but the species number was much greater in the semi-deciduous forest ($p < 0.01$; df = 7) . Finally, G2 was more abundant in the deciduous forest ($p < 0.01$; df = 7), but the species number was the same in both physiognomies ($p > 0.1$; df = 7). This means that functional groups may have a greater influence on the floristic composition or structure in forests, depending on soil moisture. In the deciduous forest (drier) there was a greater variation in forest structure than in the number of species (greater abundance of G2 and G4 - Figure 3a, but no variation in the number of species in these groups - Figure 3b). Furthermore, the semi-deciduous forest was more rich in species (G3 - Figure 3b), but there was no variation in the abundance of this group (G3 - Figure 3a).

DISCUSSION

Can less-species-rich forests have similar functional diversities to species-rich forests?

Seasonal dry tropical forests (deciduous and semi-deciduous) are present in all tropical regions, but mainly in the neotropics (Miles et al., 2006). Deciduous forests are more associated with a water deficit in the dry season and are less rich in species (Oliveira-Filho and Ratter, 2002; Ratter, 1992). However, the functional diversity, or

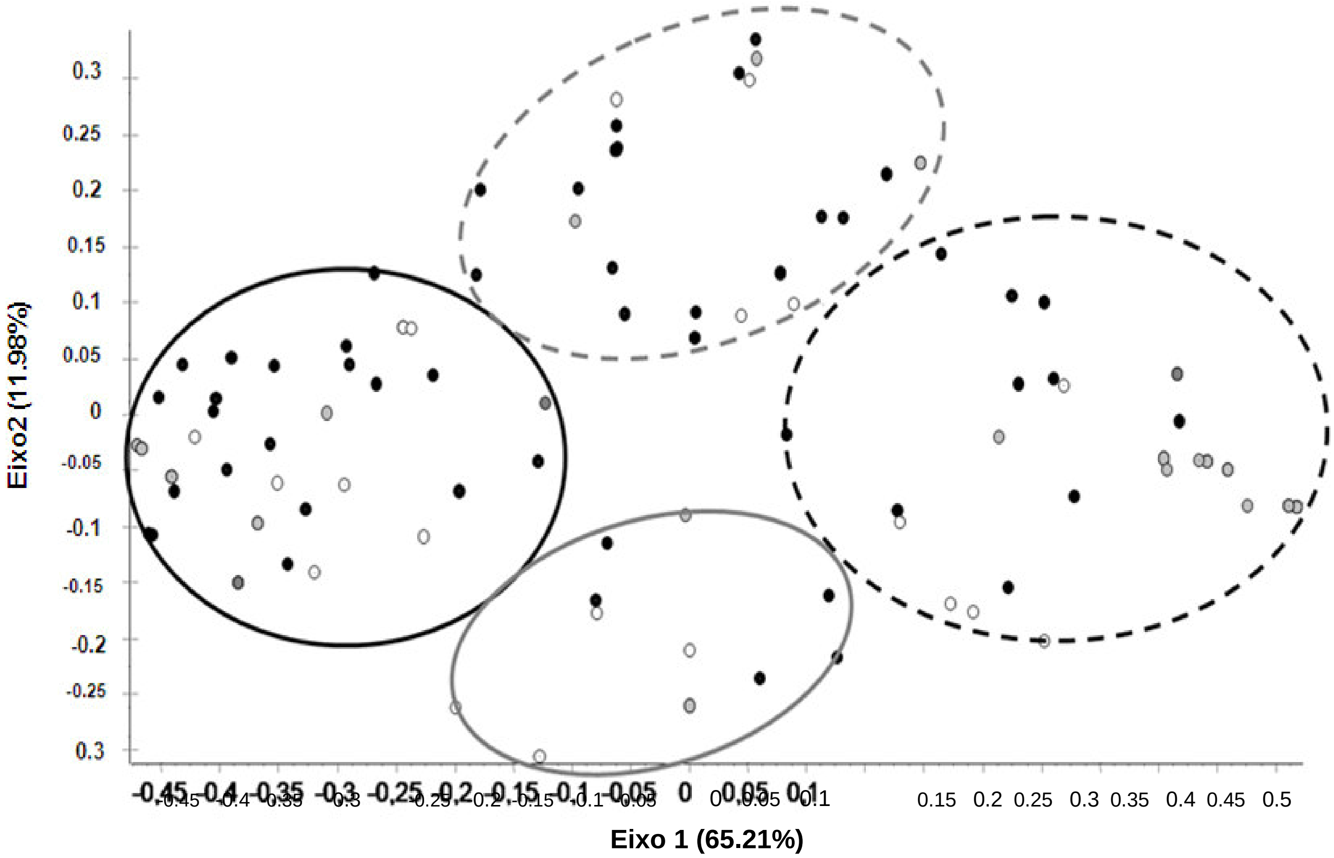

Figure 2. Functional groups based on ecological distance formed by correspondence analysis in six seasonal dry tropical forests in south-eastern Brazil. The black circles represent semi-deciduous species, the empty circles represent deciduous species and the grey circles represent species common to both physiognomies. The black solid lines show Group 1, the grey solid lines denote Group 2, the grey dotted lines denote Group 3 and the black dotted lines show Group 4. However, group characteristics are shown in Table 2.

Table 2. Functional groups formed by correspondence and cluster analysis and their respective characteristics for six seasonal dry forests in Minas Gerais, Brazil.

Functional groups	Main determinant characteristics of the functional groups
Group 1 (G1)	Occupies lower layers of the community and is shade tolerant and perennial. Provides fruit resources to birds. The pollination is performed by small insects, lepidoptera and very small insects. There are non-orthodox seeds.
Group 2 (G2)	Occupies lower layers of the community and is shade tolerant. Unlike G1, it is deciduous. This group provides fruit resources to birds. The pollination is performed by small insects and lepidoptera. There is no distinction in tolerance of desiccation of seeds.
Group 3 (G3)	This is a zoochoric group from higher layers providing resources to mammals and birds. This group is perennial and has shade-tolerant and light-demanding species. The greatest diversification of pollinators occurs in this group (small insects, very small insects, moths, butterflies and beetles). Most species are non-orthodox.
Group 4 (G4)	This is the only group that is abiotically dispersed (anemochoric and autochoric) and is fully deciduous. It occupies the superior community strata and is light demanding. This is the only group pollinated by large bees, but is still pollinated by small insects and lepidoptera. Most species in this group are orthodox.

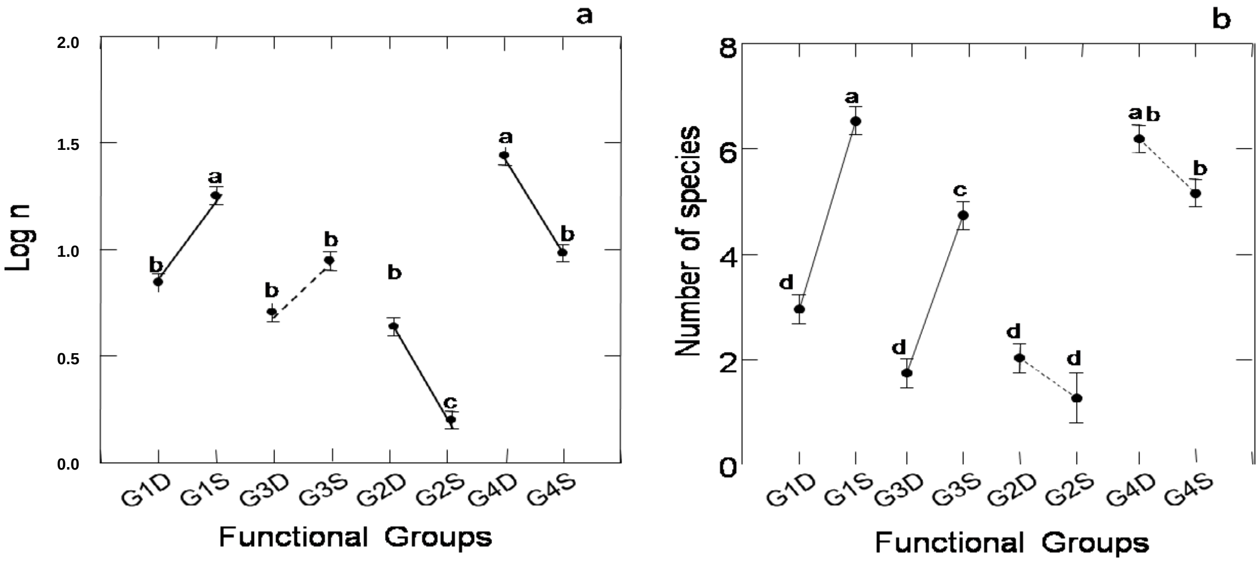

Figure 3. One-way analysis of variance for the log number of individuals “A” and number of species “B” per group (G1, G2, G3 and G4) for deciduous (D) and semi-deciduous (S) seasonal dry tropical forests with the Bonferroni post-hoc test. The same letters denote that there is no statistical difference and the different letters represent significant differences. The black points represent the means and the lines represent standard deviations.

the extent of functional differences among the species in a community (Tilman et al., 2001), could be the same in deciduous forests as in semi-deciduous ones, despite their difference in species richness. Our results exemplified this. Semi-deciduous forests contain more species than the deciduous ones (75% more species) and are more diverse (the Shannon index for semi-deciduous forests is above 3.3 and less than 2.8 in deciduous forests) (Kilca et al., 2009; Siqueira et al., 2009; Vale et al., 2009), but both have the same FD (four) as shown by the study’s results. Hence, the number of species alone has little importance when analysing functions in ecosystems. Other studies demonstrated FD having a greater impact on ecosystem processes than species diversity (Tilman et al., 1997) and addressing questions about ecosystem processes (Chapin et al., 2000; Diaz et al., 2001; Tilman et al., 2001). In some systems, a decrease in species richness can even lead to an increase in functional richness/diversity, increasing the number of ecosystem processes (Loreau et al., 2001; Micheli and Halpern, 2005). Thereby, less-species-rich systems could present similar FD to species-rich systems and both are important to ecosystem maintenance. Here, deciduous forest (a less rich system) has the same FD than semi-deciduous forest (a richer system). Thus we cannot neglect systems with lower species richness because, for some ecological attributes, they present the same number of functions systems with greater species richness. Many conservations efforts focus more on species-rich systems. However, we have demonstrated that systems with lower species richness could posses the same number of functions as species-rich systems, therefore having the same ecological importance.

Are the functional groups of these forests similar?

The functional groups in both forests were exactly the same in the attributes that were analysed. This was because the species in the deciduous forest had the same ecological functions than semi-deciduous species, even though there were fewer species. However, the number of species per group and number of individuals per group greatly varied. This could be observed in G1 and even more clearly in G3. G1 was more abundant and much richer in species in the semi-deciduous forest, while G3 was equally abundant in both forests but was much richer in species in the semi-deciduous forest. This variation in species richness between these forests could be important when considering the ecological redundancy of the species in a group. This is particularly important because a greater number of species with similar characteristics represents a greater ecological redundancy (Walker et al., 1999). The higher the redundancy, the lower the chance of one species’ loss, resulting in the loss of a function to the ecosystem (Micheli and Halpern, 2005). Many species in a group represents more species capable of occupying the niche of a species affected by a perturbation (Loreau, 2000; Walker, 1992). If a rare species becomes extinct, this can be compensated by the growth of a similar dominant species (Smith and Knapp, 2003). In the case of a low redundancy, the loss of a species with a determinate functional trait could have a great impact on the community, and the reverse is also true (Micheli and Halpern, 2005). In deciduous forests, some characteristics are more dangerous because fewer species do these functions (like G3). The study areas are in a threatened seasonal biome, in the Brazilian Savannas (Cerrado) (Myers et al., 2000). During the dry season in the savannas, the forests could be an important refuge for animals, particularly vertebrate dispersers. A greater number of plant species represents a greater capacity for maintaining vertebrate species (mainly for birds and mammals in this case) in the case of a disturbance. Species with ecological redundancy could not have the same tolerance to disturbance (Micheli and Halpern, 2005; Walker et al., 1999), and in deciduous forests, few species are available as resources for vertebrates. Here, climate changes may affect the high abundance of species which cannot be replaced by others with the same function. This could cause serious problems in supplying food to the animals in these forests and therefore alter the environmental relationships and functions.

Do similar functional groups have the same value in the ecosystem?

Despite the four groups being found in both physiognomies, the abundance of the groups or the value of each group in the ecosystem was clearly different. When the abundance of G1 and G4 are compared, it can be suggested that the major groups were different in both forests. Whilst these forests had the same FD, they had different weights for each group in the ecosystem and therefore distinct functions in the environment. This is very important because these two physiognomies are considered as the same “dry forest” in the literature. However, we demonstrated that these forests are complementary because they have different functions for the ecosystem. Semi-deciduous forests (dominated by G1) have more vertebrate resources. Birds and mammals have the preference to occupy different layers of the forest (Clark et al., 2001; Pearson, 1971). This preference could be linked to temperature, leaf density, luminosity and abundance of resources (Pearson, 1971; Richards, 1996; Walther, 2002; Walther et al., 1999). More perennials of lower strata groups like G1 could provide a different luminosity and temperature for vertebrates than the canopy. In this case, the vertebrates that forage in the canopy should be distinct than those that forage in the understory. Group G3, for example, had the same abundance in deciduous and semi-deciduous species, but it is a canopy group and should have the same function in both forests. Therefore the importance of G1 for the diversity of large animals, particularly those that forage in the understory, is a clear function to the ecosystem. This group also produces non-orthodox seeds. Non- orthodox seeds are linked to fresh fruit (Tweddle et al., 2003); therefore, G1 can provide constant shade and protection against insolation and also provide fresh fruit to animals in lower layers of vegetation. Pollinators do not respond clearly in groups because they do not form specific groups.

Nevertheless, we highlighted the presence of very small insects that are only found in the understory species of G1. These pollinators contrast with the large bees found only in the canopy species (G4), demonstrating niche differentiation for pollinators in these forests.

On the other hand, the deciduous forest (dominated by G4) could be considered as less affected by fragmentation processes because it is abiotically dispersed. The dispersion efficiency in superior strata is generally greater in anemochoric than zoocoric species (Clark et al., 2001) and species with a high dispersal capacity are less susceptible to fragmentation processes (Fahrig and Merriam, 1994; Frankie et al., 1974; Lord and Norton, 1990). Light demanding species, such as those in G4, can easily attain higher layers of communities having distinct colonization processes compared to G1. The occurrence of a group with tall heights dominating the deciduous forest is due to the diaspore dispersal distance increasing with plant height in wind dispersal (Deng et al., 2008; Howe and Smallwood, 1982; Wikander, 1984; Yamamoto et al., 2007), and deciduousness is related to this syndrome because leaves could hinder the dispersion. The orthodox seed of this group also provides the chance to form a seed bank for future seasons.

Deciduous forests could not even lose leaves, but twigs too (dry branches that fall from trees). Species which spend their lifetime under a closed canopy have more chances of being hit by debris (Deng et al., 2008). This could be a factor that favours the abundance of a higher group in a deciduous forest (G4) over the understory groups. The chance of a deciduous canopy recruit (G4 species) being hit by debris is small because deciduous species generally grow faster than perennials (Cornelissen et al., 1996) and live in fewer understory areas.

Also, light demanding species grow faster than shadow tolerant (Poorter and Bongers, 2006) species and the G4 abundance indicated that deciduous forests can accumulate more biomass and recover faster after perturbation events. On the other hand, the lower abundance of G4 species provided by the perennial canopy in the semi-deciduous forest could facilitate the presence of shadow- tolerant plants in the lower layers of a community. Shade tolerant species are more persistent in the environment because they have more protection against herbivores, less mechanical disturbance due to the greater wood density (Chave et al., 2006; Coley, 1983; Poorter et al., 2006; Swenson and Enquist, 2007) and they can provide a more stable understory in the semi-deciduous forest.

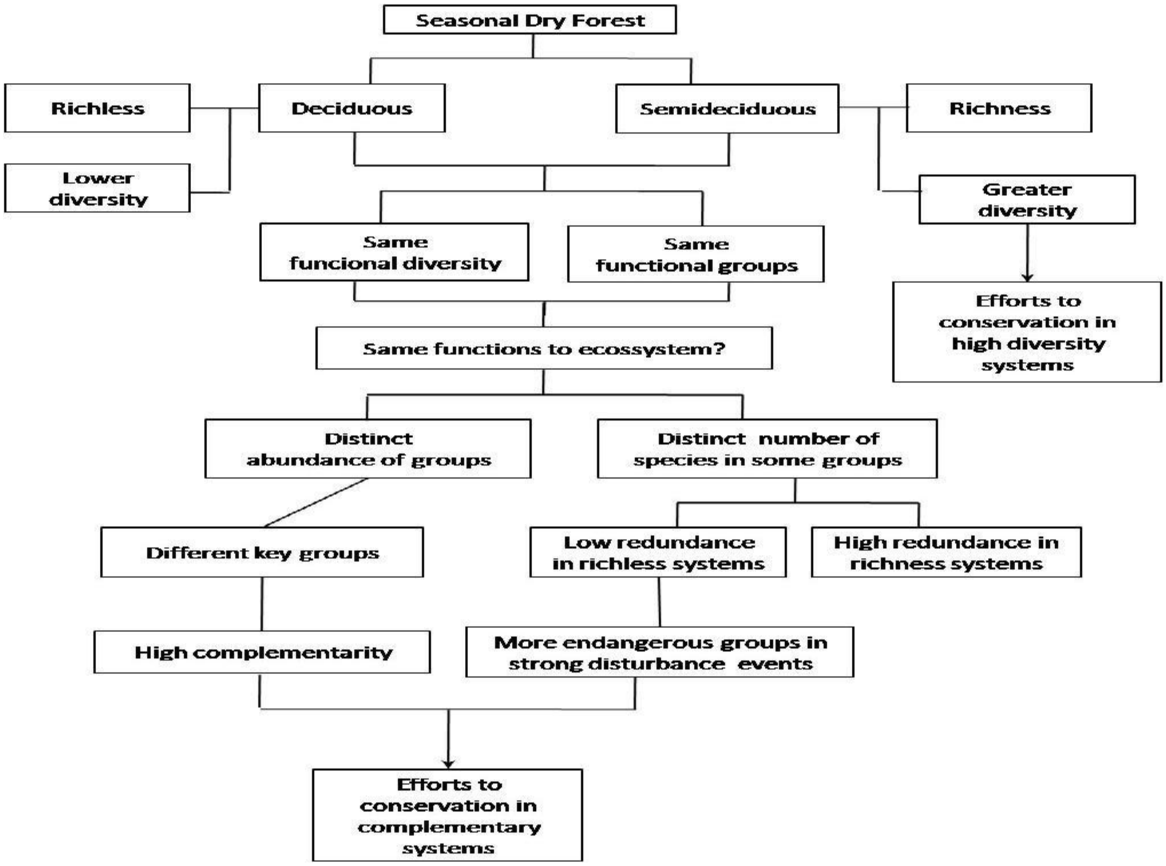

Figure 4. Fluxogram showing the steps in this work. Note that both forests, one with high species diversity and one with lower species diversity, are important to conservation. When two types of forest occur in the same environment, both need to be conserved to prevent the loss of ecological functions.

Can the functional diversity in both complementary forests justify different conservation efforts?

We argue that the so- called "dry forests" have different ecosystem functions. These forests are commonly classified according to the degree of deciduousness (Veloso et al., 1991; Scariot and Sevilha, 2005; Oliveira-Filho and Ratter, 2002). However, we think that semi-deciduous and deciduous forests have distinct traits and therefore distinct functions to the environment. Greater differences between species trait values represent greater trait complementarity independent of the number of species (Petchey and Gaston, 2002b). Species complementarity is related to species that occupy distinct spatial niches and thereby fulfil complementary functional roles (Loreau, 2000).

In the present study, the species rich and not too species rich “dry forest” had key functional groups with distinct traits. Here, deciduous forests have mainly group G4 and semi-deciduous have mainly group G1. These groups are different too, in terms of their functions to the ecosystem and the forest. The first one is a canopy light demanding deciduous abiotically dispersed group (G4) and the other is an understory shade-tolerant perenial animal dispersed group (G1) (Figure 4).

Furthermore, these forests are complementary in terms of functions. It is shown that the functions performed by one type of forest were not performed as often in the other type, hence the more abundant groups in these forests (G1 and G4) are distinct in several key features of a forest or even in an ecosystem. From a wider view of both types of forest co-occurring in the cerrado biome, the deciduous forest is considered as less species rich and the semi-deciduous forest is considered as species rich (Oliveira-Filho and Ratter, 2002). We think that the co-occurrence of a species rich and less species rich system could provide different key functions to an ecosystem and that both can be very complementary despite differences in species richness, diversity or physiognomic type. At least, this seems to be true for the dry forest. The functional group diversity is an important determinant of ecosystem functioning for some locations, but not for others (Petchey, 2004), and functional groups do not represent the same value to an ecosystem due to the differences in abundance of groups. For the dry forest, the most important factor is the abundance of key functional groups and thus their complementarity for the ecosystem (Figure 4). Some papers have shown the importance of complementarity (Loreau, 2000; Petchey and Gaston, 2002b) and we think this should be analysed in more detail to show its real importance to a system. In this work, deciduous and semi-deciduous forest is shown to be complementary (G1 and G4 differences in Table 2), so both forests are important for ecosystem in different ways despite their species richness. Henceforth, we should think in terms of a system rather than the kind of forest, number of species or species diversity alone, but we should also think in terms of the functions that a determinate area could provide for all "microsystems" existing there. On a broader scale, we can argue that less-species -rich systems, when co- occurring with systems of greater species richness, could provide different services to ecosystems and we need to pay more attention to this fact when determining conservations areas (Figure 4). The use of species rich and less-species-rich areas would present different key groups or high complementarity and may be the best alternative we have for choosing priority areas for conservation.

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REFERENCES

Brower JE, Zar JH,von Ende CN (1997). Field and laboratory methods for general ecology. The McGraw-Hill Companies, Massachusetts.

Bussab WO, Morettin PA (1990). Estatística Básica, São Paulo.

Chapin FS, Zavaleta ES, Eviner VT, Naylor, RL. Vitousek, PM, Heynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000). Consequences of changing biodiversity. Nature, 405: 234–242.

Chave J, Muller-Landau HC, Baker TR, Easdale TA, Steege HT, Weeb CO (2006). Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecol. Appl., 16: 2356–2367.

Clark CJ, Poulsen JR, Parker VT (2001). The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. Biotropica, 33: 606–620.

Coley PD (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol. Monogr. 53: 209–233.

Cornelissen JHC, Diez PC, Hunt R (1996). Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. J. Ecol., 84: 755–765.

Deng F, Zang R, Chen B (2008). Identification of functional groups in an old-growth tropical montane rain forest on Hainan Island, China. For. Ecol. Manage., 255: 1820–1830.

Diaz S, Noy-Meir I, Cabido M (2001). Can grazing response of herbaceous plants be predicted from simple vegetative traits? J. Appl. Ecol., 38: 497–508.

Espirito-Santo MM, Sevilha AC, Anaya FC (2009). Sustainability of tropical dry forests: Two case studies in southeastern and central Brazil. For. Ecol. Manage., 258: 922–930.

Fahrig L, Merriam G (1994). Conservation of fragmented populations. Conserv. Biol., 8: 50–59.

Fontaine C, Dajoz I, Meriguet J (2006). Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. Plos Biol., 4: 129–135.

Frankie GW, Baker HG, Opler PA (1974). Comparative phenological studies of trees in tropical wet and dry forests in lowlands of Costa-Rica. J. Ecol., 62: 881–919.

Girão LC, Lopes AV, Tabarelli M (2007). Changes in tree reproductive traits reduce functional groups in a riparian landscape. Plos One, 9: 1–12.

Hooper DU, Vitousek PM (1997). The effects of plant composition and diversity on ecosystem processes. Science, 277: 1302–1305.

Howe HF, Smallwood J (1982). Ecology of seed dispersal. Ann. Rev. Ecol. Syst., 13: 201–228.

Hubbell SP (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. Funct. Ecol., 19: 166–172

Kilca RV, Schiavini I, Araújo GM (2009). Edaphic and structural differences between two seasonal forests in the Cerrado biome. Neo. Biol. Conserv., 4: 150–163.

Koppen W (1948). Climatologia: com um estúdio de los climas de la terra. Fondo de Cultura Econômica, México.

Leishman MR, Westoby M (1992). Classifying plants into groups on the basis of associations of individual traits evidence from Australian semi-arid woodlands. J. Ecol., 80: 417–424.

Lord JM, Norton DA (1990). Scale and the spatial concept of fragmentation. Conserv. Biol., 4: 197–262.

Loreau M (2000). Biodiversity and ecosystem functioning: recent theoretical advances. Oikos, 91: 3–17.

Loreau M, Naeem S, Incheusti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001). Ecology - Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science, 294: 804–808.

Mayfield MM, Boni ME, Daily GC, Gretchen CD, Ackerly D (2005). Species and functional diversity of native and human-dominated plant communities. Ecology, 86: 2365–2372.

Micheli F, Halpern BS (2005). Low functional redundancy in coastal marine assemblages. Ecol. Lett., 8: 391–400.

Miles L, Newton AC, DeFries RS, DeFries RS, Corinna R, May I, Blynth S, Kapos V, Gordon JE (2006). A global overview of the conservation status of tropical dry forests. J. Biogeogr., 33: 491–505.

Myers N, Mittermeier RA, Mittermeier CG (2000). Biodiversity hotspots for conservation priorities. Nature, 403: 853–858.

Oliveira-Filho AT, Ratter JA (2002). Vegetation Physiognomies and Woody Flora of the Cerrado Biome. In: Oliveira PS and Marquis RJ (eds). The Cerrados of Brazil. Columbia University Press, New York.

Pearson DL (1971). Vertical stratification of birds in a tropical dry forest. Condor., 73: 46–55.

Pendry CA, Dick J, Pullan MR (2007). In search of a functional flora-towards a greater integration of ecology and taxonomy. Plant Ecol., 192: 161–167.

Petchey OL (2004). On the statistical significance of functional diversity effects. Funct. Ecol., 18: 297–303.

Petchey OL, Gaston KJ (2002a). Extinction and the loss of functional diversity. Proc. Royal Soc. B-Biol. Sci., 269: 1721–1727.

Petchey OL, Gaston KJ (2002b). Functional diversity (FD), species richness and community composition. Ecol. Lett., 5: 402–411.

Petchey OL, Gaston KJ (2006). Functional diversity: Back to basics and looking forward. Ecol. Lett., 9: 741–758.

Poorter L, Bongers F (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology, 87: 1733–1743.

Poorter L, Bongers L, Bongers F (2006). Architecture of 54 moist-forest tree species: Traits, trade-offs, and functional groups. Ecology, 87: 1289–1301.

Ratter JA (1992). Transitions between cerrado and forest vegetation in Brazil. In: Furley PA, Proctor J and Ratter JA (eds) Nature and Dynamics of Forest-Savanna Boundaries. Chapman and Hall, London.

Richards PW (1996). The tropical rain forest: An ecological study. Cambridge University Press, New York.

Sanchez-Azofeifa GA, Kalacska M, Quesada M (2005). Need for

integrated research for a sustainable future in tropical dry forests. Conserv. Biol., 19: 285–286.
Scariot A, Sevilha AC (2005). Biodiversity, structure and conservation of deciduous forests in the Cerrado. In: Scariot, A., Felfili, J. M., Souza-Silva, J. C. (Org.). Savannah: Ecology, Biodiversity and Conservation. Brasilia: Ministry of Environment.
Shepherd GJ (2004). FITOPAC-Shell 1.6.4. State University of Campinas, Campinas.
Siqueira AS, Araújo GM, Schiavini I (2009). Tree component structure and soil characteristics of two fragments of deciduous forest in the river valley Araguari, MG, Brazil. Acta Bot. Bras., 23: 10–21.
Skov F (2000). Distribution of plant functional attributes in a managed forest in relation to neighbourhood structure. Plant Ecol., 146: 121–130.
Smith MD, Knapp AK (2003). Dominant species maintain ecosystem function with non-random species loss. Ecol. Lett., 6: 509–517.
Swaine MD, Whitmore TC (1988). On the definition of ecological species groups in tropical rain forests. Vegetation, 75: 81–86.
Swenson NG, Enquist BJ (2007). Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. Am. J. Bot., 94: 451–459.
Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997). The influence of functional diversity and composition on ecosystem processes. Science, 277:1300–1302.
Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001). Diversity and productivity in a long-term grassland experiment. Science, 294: 843–845.
Tweddle JC, Dickie JB, Baskin CC, Baskin JM (2003). Ecological aspects of seed desiccation sensitivity. J. Ecol., 91: 294–304.
Vale VS, Schiavini I, Lopes SF, Dias Neto OC, Oliveira AP, Gusson AE (2009). Floristic composition and structure of the tree component in a remnant of primary forest in semideciduous Araguari, Minas Gerais, Brazil. Hoehnea, 36: 417–429.
Veloso HP, Rangel Filho AL, Lima JCA (1991). Classification of Brazilian vegetation adapted to a universal system. IBGE, Rio de Janeiro.
Walker B, Kinzig A, Langridge J (1999). Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosyst., 2: 95–113.
Walker BH (1992). Biodiversity and Ecological Redundancy. Conserv. Biol., 6: 18–23.
Walther BA (2002). Grounded ground birds and surfing canopy birds: Variation of foraging stratum breadth observed in neotropical forest birds and tested with simulation models using boundary constraints. Auk., 119: 658–675.
Walther BA, Clayton DH, Gregory RD (1999). Showiness of neotropical birds in relation to ectoparasite abundance and foraging stratum. Oikos, 87: 157–165.
Wikander T (1984). The dispersal mechanism of the distribution of life forms in a deciduous forest of Venezuela. Biotropica, 16: 276–283.
Yamamoto LF, Kinoshita LS, Martins FR (2007). Pollination syndromes and dispersal in fragments of tropical semideciduous forest, Brazil. Acta Bot. Bras., 21: 553–573.