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Flower functional trait responses to restoration time

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Nomenclature

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Abstract

Questions: (1) Do species richness, flower functional diversity and redundancy of tree and non-tree species increase with restoration age; (2) are the flower traits of the reference forest similar to those found in restored sites; and (3) does species originality, in terms of unique combinations of different set of flower traits, differ among sites?

Location: Forests restored by planting a high diversity assemblage of tree species, within the Atlantic Rain Forest, Brazil.

Methods: We sampled all reproductive individuals (353 species) and classified them in terms of floral type, colour, size, generalization level and openness. As most trees were planted and non-tree species (sub-shrub, shrub, herbs, epiphytes, climbers and hemi-parasitic plants) were mostly naturally established, we analysed them in separate analyses. We compared species richness, functional diversity, redundancy and originality among sites. Moreover, we identified optimal subsets of flower traits to describe vegetation succession trends.

Results: (1) Flower functional diversity of tree species could be achieved after two decades of restoration, but remained far from reference values for non-tree species. The same gap regarding reference values occurred with species richness, which increased over restoration periods, although were far from the reference values. Redundancy and functional diversity are not related to restoration age. (2) Red/burgundy colour, gullet and bell-funnel shape and large size were identified as indicators of the reference forest flowers. Different indicator traits were found for each restoration sites. (3) Sites were similar regarding originality for tree and for non-tree species.

Conclusion: A highly diverse species pool seems to promise to increase richness and functional diversity of tree species, but not of non-tree species. Trait analyses have important implications for restoration projects and can be used instead of species taxonomic identity, especially for highly diverse tropical forests. Such functional diversity may be advanced through *a priori* definition of which species from the regional pool can be used in plantings for forest restoration, with special attention to functional traits of non-tree species. Otherwise, restoration sites in highly fragmented landscapes will not reach functional diversity of reference sites, even after a five-decade period.

Introduction

Focus on functional diversity can be a promising approach both in restoration projects and in species enrichment of sites undergoing restoration. In boreal and temperate forests, studies of reforestation and comparisons with undisturbed forests have focused on restoring original biodiversity (Fries et al. 1997; Flinn & Vellend 2005). However, few studies have used functional approaches (Gachet et al. 2007), and very few have used such approaches in tropical contexts. A recent study has proposed that structural development during forest succession could imply increasing functional diversity (Lohbeck et al. 2012). Functional groups are defined as sets of species that either have similar roles in ecosystems or respond to common environmental factors, regardless of phylogenetic

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relationships (Gitay & Noble 1997; Díaz & Cabido 2001; Lavorel & Garnier 2002; Rusch et al. 2003; Franks et al. 2009). By assuming that different plant functional groups have different functions, a higher functional diversity could be crucial for supporting ecosystem functions that had been lost during degradation (e.g. seed dispersal, primary production, nutrient cycling, etc.).

A large variety of plant traits are actually relevant to ecosystem functioning, but the particular process of selection among them must be clear (Ricotta & Moretti 2011). In such a framework, plant characteristics related to types of resources offered to wildlife, such as flowers, could be important (Mayfield et al. 2006). As we considered that tropical plants depend on animals as movement vectors for pollen or fruits, and consequently for gene flow, we focused on reproductive traits because they directly affect plant fitness (Aguilar et al. 2008). Recovery of species interactions is a target for archiving restoration success; hence, pollination is a paramount consideration in restoration planning (Dixon 2009). We focus on flower traits because flower form and function are related to specific animal interactions and (via pollination) contribute to a fundamental ecosystem process (Faegri & Pijl 1979; Machado & Lopes 2004; Olesen et al. 2007).

Functional diversity can affect the dynamics of ecosystem resources and their long-term stability (Díaz & Cabido 2001). However, 'diversity' is often regarded in terms of species richness; other diversity components, such as functional redundancy and functional diversity, are neglected despite their importance in ecosystem processes (Walker 1992; Díaz & Cabido 2001). Exclusive reliance on the simpler, traditional diversity indices may omit other valuable information. For instance, disturbance can reduce pollinator diversity of a plant community, thus becoming dependent on a single pollinator vector. Within such a scenario, the number of species and their abundance distributions might be the same, with functional changes not reflected in simple species diversity indices (Cianciaruso et al. 2009), but related to functional diversity and redundancy. In this example, functional redundancy increased in the group with the common pollinator and decreased in other groups that had different pollinators. Functionally redundant species play essential roles in ecosystem stability as an 'insurance policy' against function loss (Wohl et al. 2004).

In the present study, we aimed to (1) identify flower trait descriptors of vegetation succession trends at forest sites undergoing restoration, and (2) understand whether functional recovery could be completely achieved. We assumed that: recovery of flower diversity implies advancement in ecosystem restoration towards sustainability in supporting plant–pollinator relationships, and that species showing diverse flower traits can enhance plant community functionality via their species originality (i.e. species uniqueness), as species with high originality values represent unique combinations of different sets of flower traits. Our main questions were: (1) do flower functional diversity and redundancy of tree and non-tree species increase with restoration ages; (2) are there indicating flower traits characteristic of the reference forest, and if yes, do these traits relate to the age of restored sites? Finally, (3) does flower originality differ among sites? Our hypotheses were: (1) species richness, functional diversity and functional redundancy increase over restoration periods, faster for tree species and slower for non-tree species as study sites were restored by planting a high diversity assemblage of only tree species. (2) There are optimal subsets of flower traits that may describe vegetation succession trends in restoration sites. (3) Flower originality is higher in older sites, as we expect that these areas have more species and higher functional diversity rates.

Methods

Study area

Four forest sites were surveyed in the same watershed in São Paulo State, Brazil (App. S1). These sites lie in the seasonal semi-deciduous forest domain, within the Atlantic forest biome. Their climate is classified as Cwa according to Köppen; there is little elevation variation (554–711 m a.s.l.). Sites have different ages of restoration (12, 23 and 55 yr old), and were all formerly cultivated for sugarcane (Table 1). They were located with a maximum separation distance of 65 km (Amazonas et al. 2011). They were restored via plantation of a highly diverse tree species pool (>70 species in each site) chosen according to the availability of seedlings from commercial sources, as well as from seeds collected within surrounding landscapes; native species were used mostly, although some exotic species were employed as well (see species lists in Nogueira 1977; Rodrigues et al. 1992; Siqueira 2002; Vieira & Gandolfi 2006). The main goal of the projects was to reach maximum possible species numbers and to use native species as much as possible. There was no planning regarding which species traits should be prioritized. Sites were located in highly fragmented landscape, where autogenic restoration would rarely take place (Rodrigues et al. 2010).

We compared the restoration sites to a reference forest that is the second largest natural remnant of the formerly continuous forest in the Campinas municipality (Santos 2003; Santos et al. 2009) to evaluate functional recovery. Currently, 97% of Atlantic forest fragments are <250 ha; such tiny forest patches account for almost 42% of the remaining total forest area of this biome (Ribeiro et al. 2009).

We recognize the limitations of the lack of site age replication, which is simply impossible in this particular

Table 1. Characteristics of the study sites. Distance from the nearest remnant forest was considered as any remnant forest with at least similar size to the given site.

	Early[1]	Intermediate[2]	Old[3]	Reference natural remnant[4,5]
Name	Dam of São Luis	Supply Reservoir	Ester Sugar Mill	Ribeirão Cachoeira
Location	22°49′43″S, 47°25′57″W	22°34′36″S, 47°30′29″W	22°40′18″S, 47°12′21″W	22°50′4″S, 46°55′37″W
County	Santa Bárbara d' Oeste	Iracemápolis	Cosmópolis	Campinas
Size Area (ha)	30	50	30	245
Year of Planting	1998	1987/1992	1955/1960	–
Age After Restoration (yr)	12	23	55	–
Restoration Model	50% of pioneers and 50% of non-pioneers alternately on the same planting line	Modules of planting (6 pioneers and 2 early secondary, 1 late secondary or climax)	Random and heterogeneous planting, which includes pioneer and non-pioneer species	–
Distance from the Nearest Remnant Forest (m)	1435	70	180	403

Source: [1]Andé Nave-ESALQ/USP, pers. com.; [2]Rodrigues et al. (1992); Siqueira (2002); Vieira & Gandolfi (2006); [3]Nogueira (1977); [4]Santos (2003); [5]Cielo-Filho et al. (2007).

landscape; however, we hope our study will provide useful information with which one may assess longer-term trends in restoration sites. We highlight that such insights are virtually impossible to obtain in any other way, because of the limited number of restoration sites in this region, in particular those that are over four decades old.

Sampling methods

At each restoration site, we selected a 2.5-ha area without signs of recent anthropogenic disturbance (e.g. charcoal on ground, soot on trunks or presence of stumps or coppiced trees), following Cielo-Filho et al. (2007). Within each area, we randomly located 30 plots (10 × 10 m in size).

Within plots, every month from May 2008 to April 2010, we searched intensively for individual plants in flower and/or fruit for all angiosperm plants except graminoids, including trees, sub-shrub, shrub, herbs, epiphytes, hemi-parasitic plants and climbers (the latter six groups are collectively referred to as 'non-trees'). We identified plants to the species level by comparing specimens deposited at the UNICAMP herbarium (UEC), consulting literature and with aid from specialists to confirm identifications. Botanical material collected was deposited at UEC at Universidade Estadual de Campinas and at the Escola Superior de Agricultura 'Luiz de Queiroz,' Universidade Estadual de São Paulo herbarium (ESA).

Flower traits

We classified species into flower categories following Machado & Lopes (2004), adapted from Faegri & Pijl (1979). These categories included (1) shape (tubular, gullet, brush, dish, chamber, flag, bell-funnel or inconspicuous; the latter was defined for flowers <4 mm), and (2) colour (white, red/burgundy, greenish/beige/cream, yellow, orange, lilac/violet/blue and rose); and (3) size (small <10 mm, medium 10–20 mm, large 20–30 mm and very large >30 mm).

Given the hypothesis that specialist plant species restrict rewards to certain groups of pollinators, we also used an openness classification adapted from Olesen et al. (2007). Hence, flowers were classified as (1) closed blossoms (flag, tubular, gullet and chamber shapes) and (2) open blossoms (inconspicuous, dish, bell-funned and brush shapes). In addition, following the same authors, we classified flower generalization as (1) specialists (flag-, gullet-, chamber- and brush-shaped flowers) vs (2) generalists (tubular-, bell- or dish-shaped or inconspicuous flowers).

Data analysis

Since most trees were planted and non-tree species were mostly naturally established, we analysed tree and non-tree species in separate analyses.

Species richness, flower functional diversity and redundancy

We used rarefaction curves to compare species richness among sites (Magurran 2004), using Past (version v.1.82b, http://palaeo-electronica.org/2001_1/past/issue1_01.htm). We calculated functional diversity for each plot using the functional diversity index of Petchey & Gaston (2002, 2006). Flower colour and shape were used as nominal traits, generalization level and flower openness as binary traits, and flower size as an ordinal trait. We used Gower distances, as modified by Pavoine et al. (2009), to convert trait matrices into distance matrices. These analyses were carried out using the vegan, picante, FD and ade4 packages in R (R Foundation for Statistical Computing, Vienna, AT). We used null models to test whether functional diversity of tree and non-tree species in each site was different from chance expectations, based on 1000 null functional diversity (FD) values for each plot derived from an independent swap algorithm (Gotelli & Entsminger 2001). The assumption for these null models is that any species observed at a site could occur in any of the sampled plots. Therefore, we maintained the observed species richness and occurrence frequency among plots when generating null functional diversity values. We calculated standardized effect sizes (SES): SES = (FD–rdn FD)/sd.rdn FD, where FD is the observed functional diversity in a given plot, rdn FD is the mean functional diversity from the respective null distribution, and sd.rdn FD is the SD of the null distribution. Thus, SES indicates whether functional diversity is larger or smaller than expected by chance (Cianciaruso et al. 2012). Furthermore, from SES values, we examined functional redundancy: higher SES values indicate higher functional diversity than expected by chance (positive values); lower SES values (negative values) indicate lower functional diversity than expected by chance, indicating more redundant assemblages.

Flower traits and species originality

We adapted the indicator value (IndVal) method of Dufrene & Legendre (1997), which detects indicator species for groups of sites and combines species' relative abundances with species' relative frequencies of occurrence across multiple sites. Instead of species abundances or frequencies, we used flower traits as values in our analyses. Flower traits were defined as the most characteristic features of each group, found mostly in a single plot age, and present in most plots of the same age. Statistical significance of indicator values was evaluated with a randomization procedure (Dufrene & Legendre 1997). We tested over all sites to detect indicators for the reference site, whereas only restoration sites were used to analyse changes during the restoration process. To evaluate flower traits similarity among plots of different ages (all 30 plots per site), as well as for which flower traits are related to sites similarity, we performed a principal components analysis using the number of species with each flower trait per plot with Fitopac (version v.2.1, http://pedroeisenlohr.webnode.com.br/fitopac/).

We evaluated originality measured as species' relative contributions to functional diversity (Pavoine et al. 2005; Isaac et al. 2007), using the picante, ape and ade4 packages in R, and compared originality values found for all species per site with ANOVA (e.g. for trees in the 12-yr site, we used the 53 originality values for its 53 non-tree species, compared with 33 species found at the 23-yr site, 58 species at the 55-yr site and 118 species at the reference site). When significant differences were detected, Tukey *post-hoc* comparison tests were used to identify sources of differences, performed in Past (version v.1.82b, http://palaeo-electronica.org/2001_1/past/issue1_01.htm).

Despite differences in the composition of the species pool planted and planting methods, we assume that they do not influence the issues addressed in the present study. In spite of the fact that we found differences in proportions of ecological successional groups among restoration ages, all successional groups were similar regarding their species originality index; moreover, we did not find increasing flower specialization as a result of successional group changes over time (L.C., Garcia, F.A.M., Santos. & R.R. Rodrigues, in prep.).

Results

Species richness, flower functional diversity and redundancy

We sampled 353 species, including 134 tree and 219 non-tree species in total (App. S2). Both tree species number and functional diversity slightly increased with planting age (Figs 2, 3). A higher number of tree species was found in the reference forest, whereas the two older restoration sites showed functional diversity values close to those of the reference forest. However, the lowest functional diversity values for non-tree species were encountered in the restoration sites that were far from reference values (Fig. 3). While older restoration sites resembled the reference site in tree species richness, non-tree species richness was markedly lower in restored sites compared to the reference forest (Fig. 1).

Functional redundancy of trees was high in the reference forest (i.e. high numbers of tree species with small, white or greenish flowers), while functional diversity of tree species was high in restoration sites. On the other hand, restoration sites presented low SES values (i.e. redundancy) for non-tree species, whereas the reference forest showed higher functional diversity (i.e. trait overdispersion; Fig. 2).

Flower traits and species originality

Four indicator flower traits (i.e. red/burgundy colour, gullet shape, very large size and bell-funnel shape) showed an IndVal score >50% only for the reference site ($P < 0.01$; Table 2). Tubular flowers were an indicator trait for the 12-yr site, and bell-funnel, greenish, inconspicuous and flag flowers were indicator traits for the 55-yr site (Table 2). No indicator traits had IndVal scores >50% for the 23-yr site.

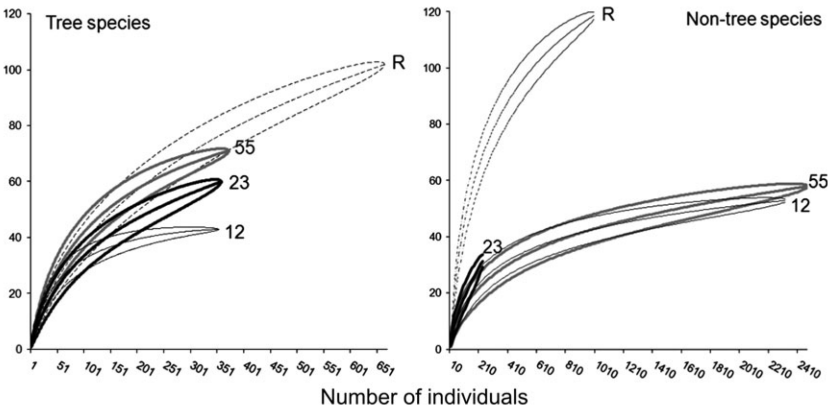

Fig. 1. Rarefaction curves (middle line) and 95% confidence intervals (upper and lower second lines) for total community species richness of tree and non-tree species in the three restoration sites (12, 23 and 55 yr old) and the reference forest (R).

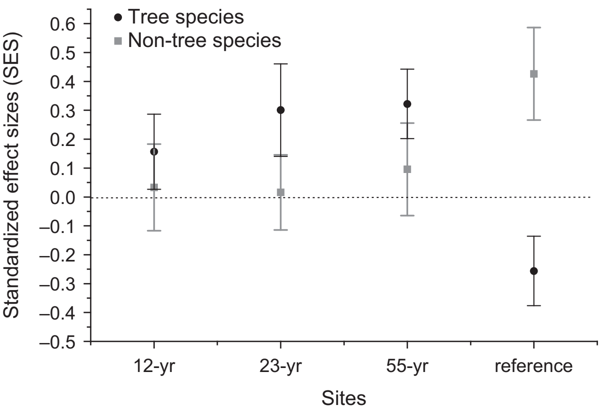

Fig. 2. Standardized effect sizes (SES) (mean ± SD) in three restoration sites and a reference forest based on functional diversity of flower traits of non-tree (grey square) and tree species (black circle). SES indicates whether functional diversity is higher (positive values) or lower (negative values) than expected by chance. Higher SES values mean larger functional diversity for positive values and redundancy for negative values.

Table 2. Flower traits showing an indicator value (IndVal) ≥ 50 ($P \leq 0.001$). Means and SD are for the maximum scores in each group.

Indicator Flower Trait	Site	IndVal	Mean	SD
Comparing All Sites				
Red/Burgundy	Reference	74.4	16.2	3.09
Gullet	Reference	71.3	17.9	3.42
Very Large, >30 mm	Reference	63.5	20.6	3.38
Bell-Funnel	Reference	56.7	24.5	2.84
Comparing Restoration Sites				
Tubular	12 yr	61.8	37.8	3.22
Bell-Funnel	55 yr	61.4	28.2	3.64
Greenish	55 yr	58.0	34.8	2.73
Inconspicuous	55 yr	51.4	28.2	3.64
Flag	55 yr	50.0	33.3	2.67

The four sites were separated by flower traits in the ordination analysis (Fig. 3). The reference forest correlated strongly with almost all flower traits along the first axis (48.0%), whereas the 12-yr forest was mostly negatively correlated with the second axis (9.49%). Traits most positively correlated with the first axis were generalist, small and open flowers (App. S3). On the other hand, traits most negatively correlated with the second axis were lilac, tube and orange flowers.

Sites were similar regarding originality for tree ($F = 1.929$, $P = 0.1268$) and for non-tree species ($F = 1.889$, $P = 0.1319$). At all sites, we detected some species that had high scores in terms of flower originality (App. S4).

Discussion

A highly diverse species pool seems to promise to increase richness and functional diversity of tree species. However, species richness and functional diversity of non-tree species remained lower than the reference forest, even after a 55-yr restoration period. Flower traits such as red colour, gullet shape, very large size and bell-funnel shape were indicators of the reference forest. Although species with such traits were present in the restoration sites, their richness and abundance were markedly lower than those of the reference forest. Flower functional redundancy in tree species did not recover even 55 yr after restoration. However, if the surrounding landscapes held large natural areas that were close enough to restoration sites, recovery of flower functional redundancy of tree species should happen over time. However, given the level of fragmentation of this landscape, the process may require several years for current patches to recover redundancy. Programmes aiming at large-scale ecological restoration, such as the Atlan-

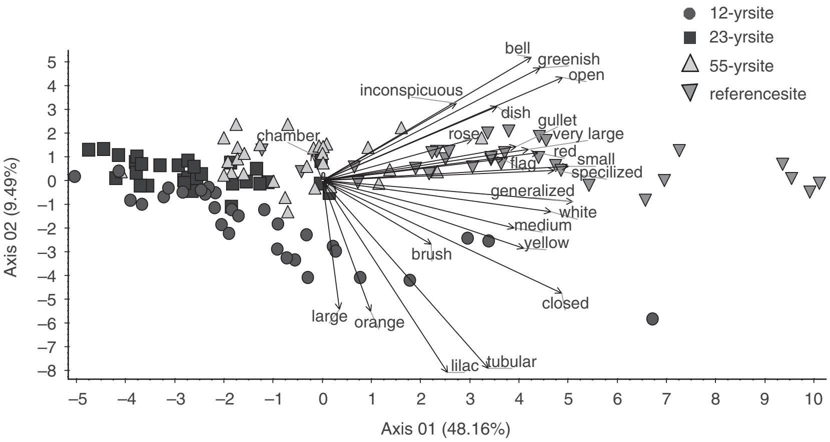

Fig. 3. Principal components analysis with biplot of total plant community species abundance and flower traits for three sites undergoing restoration and one reference forest. Circles, squares, triangles and inverted triangles represent plots (i.e. data as the number of species with each flower trait per plot) of 12, 23, 55 yr and reference sites, respectively.

tic Forest Restoration Pact (Calmon et al. 2011), may create scenarios where redundancy and functional diversity would recover faster than in the current context. On the other hand, with recent changes in the Brazilian Environmental Law, which regulates conservation, restoration and clearing of natural vegetation clearing in privately owned lands, significant decreases in restoration areas are expected (Garcia et al. 2013), which may have opposite effects, and retard functional recovery. The new law effectively reduces the extent of mandatory restoration areas as well as excluding a significant portion of previously protected areas.

We found that planting a highly diverse tree species assemblage promotes high levels of species richness and flower functional trait diversity of trees to similar levels achieved in the reference forest; such enhancement occurs at intermediate ages (23 yr). In this scenario, the idea of 'how little' redundancy is necessary to recover or sustain ecosystem functions (Walker 1992) may be dangerous and may bring a negative connotation, as species might play different roles; moreover, overall ecosystem functions are multivariate, and species' functions may also vary in space and time (Naeem 1998; Hector & Bagchi 2007; Petchey et al. 2007; Nadrowski et al. 2010). Nevertheless, functional redundancy is also important to maintain all ecosystem functions in case of species loss.

Our results show low functional diversity and redundancy of non-tree species, and suggest that enrichment of functional groups other than trees should be encouraged as part of restoration efforts. Flower traits may be a useful criterion by which to not only target species for forest restoration, but also to enrich natural forests for recovery of ecosystem functions. Addition of poorly represented non-tree species could also have benefits in enhancing functional diversity. Simultaneously, such management could enhance other features, such as the development of complementary phenologies among species, to assure constant flower and fruit availability to nectarivorous and frugivorous fauna species (Garcia et al. 2014). Likewise, improved species richness likely will improve multi-functionality, which is also a requirement for the provision of multiple ecosystem services (Maestre et al. 2012).

Species richness, flower functional diversity and redundancy

The restored sites showed lower non-tree richness than the reference forest (Garcia et al. 2014), as was the case for functionality. This result suggests that restoring with a highly diverse species pool may enhance functional diversity to similar levels of the reference forest for tree species, but not necessarily for non-tree species.

Only tree species of the reference site presented negative SES values, indicating the occurrence of trait under-dispersion and lower functional diversity than chance expectations. Filtering factors may result in flower trait convergence of tree species in this forest, leading to many species with small, white or greenish flowers. Functional diversity of pollination networks may be critical to ecosystem sustainability (Fontaine et al. 2006). As a result, recovery of functional diversity and redundancy is a crucial consideration in forest restoration. Overlap in ecological function leads to functional redundancy, whereas redundancy increases the system's ability to resist disturbance or further species exclusion (Peterson et al. 1998).

Functional diversity is usually driven by species richness (Poos et al. 2009) and, as shown in the present study, similar patterns were found for functional diversity in trees and non-trees. For example, higher non-tree species richness enhanced functional diversity in the reference forest. On the other hand, because planting included a high diversity of tree species, these forests reached near-reference values of flower functional diversity for tree species, and can be considered a reasonably rich forest with wide diversity of tree flower types. These results strengthen evidence that planting high-diversity species pools may contribute to increased functionality and possibly self-sustainability. Moreover, as Brancalion et al. (2010) and Aronson et al. (2011) commented, if the restoration practitioner decides to plant 30 vs 80 species, the cost of restoration will often not change as average seedling prices are usually similar among different species. However, availability of seedling diversity from commercial sources may be the only possible large obstacles to plant high-diversity species pools.

Flower traits and species originality

Some flower traits were particularly abundant in the reference forest; these traits seem to represent significant changes in flower traits. Through succession, selection of expensive multiple floral adaptations is likely to occur toward attracting a wider variety of flower visitors (Kay 1987). These characteristics, such as very large gullet-shaped red flowers, are typical of the bird syndrome (Faegri & Pijl 1979). Red flowers are mostly related to bird pollination (Kevan & Baker 1983), and indeed red colouring can reduce bee visits because of the difficulty of background detection, providing a less competitive nectar source for hummingbirds (Forrest & Thomson 2009; Lunau et al. 2011). However, some butterflies have red-sensitive vision and can also visit red flowers (Kevan & Baker 1983). Gullet shaping closely associates with bumblebee pollination; these animals tend to increase in diversity during succession, indicating specialization (Nakano & Washitani 2003; Alanen et al. 2011). The presence of *Adenocalymma*, a New World genus that exhibits floral adaptive radiation including species pollinated by bees, birds and possibly moths and bats (Machado & Vogel 2004), which was found chiefly in the reference forest, can reflect wide pollinator interactions. In particular, Hoffmann (1974) found that gullet was one of the most specialist flower shapes, such as flag flowers. Very large flowers were more related to hawk moths, hummingbirds, bats and bees in a study in a Brazilian tropical dry forest (Machado & Lopes 2004). Finally, bell-shaped flowers are mostly pollinated by bees (Faegri & Pijl 1979).

Lilac or orange tube flowers were concentrated in the youngest site (12 yr old), probably due to several tubular flower species mainly composed of herbs of the Asteraceae family. The high species diversity of this functional group was evident during the first restoration decade. Tubular flowers have an exclusive visitor fauna of long-tongued animals (Olesen et al. 2007), an animal group that will be remarkably favoured during the first restoration decade. On the other hand, a trend of enhancing species diversity of generalists with small and open flowers was noted over time.

Reproductive success is affected by resource costs (e.g. water, carbon and nutrient consumption), which in turn is influenced with flower size and shape (Galen 1999). As for size, despite potentially high energetic costs of maintaining large flowers because of decreased longevity, positive effects on hummingbird attraction may be reached (Mitchell 1994; Doorn & Schröder 1995). Cost of colour production is also related to pigment development: anthocyanins are pigments found in red, blue and purple flowers, and differences in intensity involve distinct biochemical mechanisms (Streisfeld & Rausher 2011). Regarding shape, tubular flowers have high light interception that may optimize pollinator attractiveness, but large corolla areas increase the proportion of flowers damaged by ants (Galen 1999).

Implications for forest management and restoration

One question arises from our results regarding restoration planning. Are there trees that could be used for planting that would enhance flower functionality of other growth forms? In future restoration projects, these flower traits should be emphasized by including species sets chosen for restoration planting. We recommend focusing on tree species at first, because planting some growth forms, such as lianas and epiphytes, at the beginning of the restoration process is not feasible as both need tree structure for support. However, sub-shrub individuals, shrub vegetation and herbs can also be planted. An alternative method could be planting tree species that have flower traits similar to those present in non-trees of the reference sites. For instance, the tree species *Erythrina* sp. has red and very large flowers, a mixture of flower traits lacking in restoration sites. By considering that species richness is correlated with multi-functionality (Maestre et al. 2012), we recommend the inclusion of as many species with a particularly important functional trait as possible, instead of high numbers of individuals of fewer species. We detected some species with high originality values, which can be considered as a measure of irreplaceability (Isaac et al. 2007). Planting these species may increase flower functional diversity of restoration areas. Our study draws attention to species richness and functional considerations as an essential objective, not only for planning and implementing restoration efforts, but also for forest management: if a functional group is lacking, it may be introduced.

Functional diversity is increasing and the next step would be the verification of plant animal interactions. The fruit-feeding butterfly community has been recovered at these same sites, where abundance of forest butterfly species could be used as an indicator of forest restoration success (Sant'Anna et al. 2014). We have no data about other taxa. However, because butterflies occurrence is affected by vegetation structure (Ribeiro & Freitas 2012; Ribeiro et al. 2012) as in many other groups (Gardner et al. 2007), we could expect that some components of original fauna (e.g. pollinators and frugivores) have re-colonized these sites. Moreover, their resources (e.g. flower and fruit production) have been recovered after one decade of restoration (Garcia et al. 2014). Thus, further investigations are needed to confirm fauna return.

For other ecosystem types, such as non-forest ecosystems, our adaptation of the indicator value (IndVal) method from Dufrene & Legendre (1997) may be used not only for flower traits, but also for vegetative traits. Moreover, we believe that originality, functional diversity and redundancy analyses can be widely applied to assess restoration success.

Trait analyses have important implications for restoration and can be used instead of species taxonomic identity (Pywell et al. 2003; Díaz et al. 2007; Clark et al. 2012), in particular for tropical areas, where species are numerous and can be hard to recognize. Besides species-rich plantings, actions should also be carried out to ensure targets and additional functions in forest restoration (Doherty et al. 2011). In human-dominated ecosystems or agricultural landscapes, prioritizing relevant ecological, social and technical criteria to select species for restoration is crucial for restoration sustainability (Meli et al. 2014). In fact, the most important ecological processes that should be manifested during restoration changes over time could be prioritized. For instance, the success of pollination and dispersal is not the initial aim at the beginning of restoration processes, as plant establishment and growth are the initial goals. In a second stage, a key factor to enhance sustainability of restoration areas is to provide fauna with wide resource diversity. As a result, the target should be the definition of trait requisites for each restoration stage success. Therefore, ecological restoration planning of functional traits should include all desirable functional sets in a comprehensive plan.

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References

Aguilar, R., Quesada, M., Ashworth, L., Herrerias-Diego, Y. & Lobo, J. 2008. Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches. *Molecular Ecology* 17: 5177–5188.

Alanen, E.L., Hyvonen, T., Lindgren, S., Harma, O. & Kuussaari, M. 2011. Differential responses of bumblebees and diurnal Lepidoptera to vegetation succession in long-term set-aside. *Journal of Applied Ecology* 48: 1251–1259.

Amazonas, N.T., Martinelli, L.A., Piccolo, M.D.C. & Rodrigues, R.R. 2011. Nitrogen dynamics during ecosystem development in tropical forest restoration. *Forest Ecology and Management* 262: 1551–1557.

Aronson, J., Brancalion, P.H.S., Durigan, G., Rodrigues, R.R., Engel, V.L., Tabarelli, M., Torezan, J.M.D., Gandolfi, S., Melo, A.C.G., (…) & Scarano, F.R. 2011. What role should government regulation play in ecological restoration? Ongoing debate in São Paulo state, Brazil. *Restoration Ecology* 19: 690–695.

Brancalion, P.H.S., Rodrigues, R.R., Gandolfi, S., Kageyama, P.Y., Nave, A.G., Gandara, F.B., Barbosa, L.M. & Tabarelli, M. 2010. Instrumentos legais podem contribuir para a restauração de florestas tropicais biodiversas. *Revista Árvore* 34: 455–470.

Calmon, M., Brancalion, P.H.S., Paese, A., Aronson, J., Castro, P., Silva, S.C.D. & Rodrigues, R.R. 2011. Emerging threats and opportunities for large-scale ecological restoration in the Atlantic Forest of Brazil. *Restoration Ecology* 19: 154–158.

Doi: 10.1111/avsc.12163

Carvalho, G.H., Cianciaruso, M.V. & Batalha, M.A. 2010. Plantminer: a web tool for checking and gathering plant species taxonomic information. *Environmental Modelling and Software* 25: 815–816.

Cianciaruso, M.V., Silva, I.A. & Batalha, M.A. 2009. Diversidades filogenética e funcional: novas abordagens para a ecologia de comunidades. *Biota Neotropica* 9: 93–103.

Cianciaruso, M.V., Silva, I.A., Batalha, M.A., Gaston, K.J. & Petchey, O.L. 2012. The influence of fire on phylogenetic and functional structure of woody savannas: moving from species to individuals. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 205–216.

Cielo-Filho, R., Gneri, M.A. & Martins, F.R. 2007. Position on slope, disturbance, and tree species coexistence in a seasonal semideciduous forest in SE Brazil. *Plant Ecology* 190: 189–203.

Clark, D.L., Wilson, M., Roberts, R., Dunwiddie, P.W., Stanley, A. & Kaye, T.N. 2012. Plant traits – a tool for restoration? *Applied Vegetation Science* 15: 449–458.

Díaz, S. & Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16: 646–650.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the USA* 104: 20684–20689.

Dixon, K.W. 2009. Pollination and restoration. *Science* 325: 571–573.

Doherty, J.M., Callaway, J.C. & Zedler, J.B. 2011. Diversity–function relationships changed in a long-term restoration experiment. *Ecological Applications* 21: 2143–2155.

Doorn, W.G. & Schröder, C. 1995. The abscission of rose petals. *Annals of Botany* 76: 539–544.

Dufrene, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Faegri, K. & Pijl, L.V.D. 1979. *The principles of pollination ecology*. Pergamon Press, Oxford, UK.

Flinn, K.M. & Vellend, M. 2005. Recovery of forest plant communities in post-agricultural landscapes. *Fronteries in Ecology and Environment* 3: 243–250.

Fontaine, C., Dajoz, I., Meriguet, J. & Loreau, M. 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology* 4: 129–135.

Forrest, J. & Thomson, J.D. 2009. Background complexity affects colour preference in bumblebees. *Naturwissenschaften* 96: 921–925.

Franks, A.J., Yates, C.J. & Hobbs, R.J. 2009. Defining plant functional groups to guide rare plant management. *Plant Ecology* 204: 207–216.

Fries, C., Johansson, O., Pettersson, B. & Simonsson, P. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. *Forest Ecology and Management* 94: 89–103.

Gachet, S., Leduc, A., Bergeron, Y., Nguyen-Xuan, T. & Tremblay, F. 2007. Understory vegetation of boreal tree plantations: differences in relation to previous land use and natural forests. *Forest Ecology and Management* 242: 49–57.

Galen, C. 1999. Why do flowers vary? *BioScience* 49: 631–640.

Garcia, L.C., Santos, J.S., Matsumoto, M., Silva, T.S.F., Padovezi, A., Sparovek, G. & Hobbs, R.J. 2013. Restoration challenges and opportunities for increasing landscape connectivity under the new Brazilian forest act. *Natureza & Conservação* 11: 181–185.

Garcia, L.C., Hobbs, R.J., Santos, F.A.M. & Rodrigues, R.R. 2014. Flower and fruit availability along a forest restoration gradient. *Biotropica* 46: 114–123.

Gardner, T.A., Barlow, J., Araujo, I.S., Avila-Pires, T.C.S., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., (...) & Peres, C. 2007. The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters* 11: 139–150.

Gitay, H. & Noble, I.R. 1997. What are functional types and how should we seek them? In: Smith, T.M., Shugart, H.H. & Woodward, F.I. (eds.) *Plant functional types*, pp. 3–19. Cambridge University Press, Cambridge, UK.

Gotelli, N.J. & Entsminger, G.L. 2001. Swap and fill algorithms in null model analysis: rethinking the Knight's Tour. *Oecologia* 129: 281–291.

Hector, A. & Bagchi, R. 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448: 188–190.

Hoffmann, F. 1974. *Biodiversity and pollination: flowering plants and flower-visiting insects in agricultural and semi-natural landscapes*. Rijksuniversiteit Groningen, Enschede, NL.

Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C. & Baillie, J.E.M. 2007. Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS One* 29: 6.

Kay, Q.O.N. 1987. The comparative ecology of flowering. *New Phytologist* 106: 265–281.

Kevan, P.G. & Baker, H.G. 1983. Insects as flower visitors and pollinators. *Annual Review of Entomology* 28: 407–453.

Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.

Lohbeck, M., Poorter, L., Paz, H., Pla, L., van Breugel, M. & Martínez-Ramos, M. & Bongers, F., 2012. Functional diversity changes during tropical forest succession. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 89–96.

Lunau, K., Papiorek, S., Eltz, T. & Sazima, M. 2011. Avoidance of achromatic colours by bees provides a private niche for hummingbirds. *Journal of Experimental Biology* 214: 1607–1612.

Machado, I.C. & Lopes, A.V. 2004. Floral traits and pollination systems in the caatinga, a Brazilian tropical dry forest. *Annals of Botany* 94: 365–376.

Machado, I.C. & Vogel, S. 2004. The north-east-Brazilian liana, *Adenocalymna dichilum* (Bignoniaceae) pollinated by bats. *Annals of Botany* 93: 609–613.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., Garcia-Gomez, M., Bowker, M.A., Soliveres, S., (...) & Zaady, E. 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335: 214.

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

Mayfield, M.M., Ackerly, D. & Daily, G.C. 2006. The diversity and conservation of plant reproductive and dispersal functional traits in human-dominated tropical landscapes. *Journal of Ecology* 94: 522–536.

Meli, P., Martínez-Ramos, M., Rey Benayas, J.M. & Carabias, J. 2014. Combining ecological, social and technical criteria to select species for forest restoration. *Applied Vegetation Science* 17: 744–753.

Mitchell, R.T. 1994. Effects of floral traits, pollinator visitation, and plant size on *Ipomopsis aggregata* fruit production. *The American Naturalist* 143: 870–889.

Nadrowski, K., Wirth, C. & Scherer-Lorenzen, M. 2010. Is forest diversity driving ecosystem function and service? *Current Opinion in Environmental Sustainability* 2: 75–79.

Naeem, S. 1998. Species redundancy and ecosystem reliability. *Conservation Biology* 12: 39–45.

Nakano, C. & Washitani, I. 2003. Variability and specialisation of plant–pollinator systems in a northern maritime grassland. *Ecological Research* 18: 221–246.

Nogueira, J.C.B. 1977. Reflorestamento heterogêneo com essências indígenas. *Boletim Técnico do Instituto Florestal* 24: 1–71.

Olesen, J.M., Dupont, Y.L., Ehlers, B.K. & Hansen, D.M. 2007. The openness of a flower and its number of flower-visitor species. *Taxon* 56: 729–736.

Pavoine, S., Ollier, S. & Dufour, A.B. 2005. Is the originality of a species measurable? *Ecology Letters* 8: 579–586.

Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S. & Daniel, H. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118: 391–402.

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

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

Petchey, O.L., Evans, K.L., Fishburn, I.S. & Gaston, K.J. 2007. Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology* 76: 977–985.

Peterson, G., Allen, C.R. & Holling, C.S. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1: 6–18.

Poos, M.S., Walker, S.C. & Jackson, D.A. 2009. Functional diversity indices can be driven by methodological choices and species richness. *Ecology* 90: 341–347.

Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L., Walker, K.J. & Rother, P. 2003. Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* 40: 65–77.

Ribeiro, D.B. & Freitas, A.V.L. 2012. The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. *Journal of Insect Conservation* 16: 733–744.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. 2009. The Brazilian Atlantic forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142: 1141–1153.

Ribeiro, D.B., Batista, R., Prado, P.I. Jr, Brown, K.S. & Freitas, A.V.L. 2012. The importance of small scales to the fruit-feeding butterfly assemblages in a fragmented landscape. *Biodiversity and Conservation* 21: 811–827.

Ricotta, C. & Moretti, M. 2011. CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia* 167: 181–188.

Rodrigues, R.R., Leitão Filho, H.F. & Crestana, M.S.M. 1992. Revegetação do entorno da represa de abastecimento de água do município de Iracemápolis/SP. In: Balensiefer, M. (ed.) *Anais do Simpósio Nacional de Recuperação de Áreas Degradadas*. pp. 406–414. Fundação de Pesquisas Florestais do Paraná, Curitiba, BR.

Rodrigues, R.R., Gandolfi, S., Nave, A.G., Aronson, J., Barreto, T.E., Vidal, C.Y. & Brancalion, P.H.S. 2010. Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. *Forest Ecology and Management* 261: 1605–1613.

Rusch, G.M., Pausas, J.G. & Lepš, J. 2003. Plant functional types in relation to disturbance and land use: introduction. *Journal of Vegetation Science* 14: 307–310.

Sant'Anna, C.L., Ribeiro, D.B., Garcia, L.C. & Freitas, A.V.L. 2014. Fruit-feeding butterfly communities are influenced by restoration age in tropical forests. *Restoration Ecology* 22: 480–485.

Santos, K. 2003. Caracterização floristica e estrutural de onze fragm*entos de mata estacional semidecidual da area de proteção ambiental do municipio de Campinas-SP*. PhD Thesis, Universidade Estadual de Campinas, Campinas, BR.

Santos, K., Kinoshita, L.S. & Rezende, A.A. 2009. Species composition of climbers in seasonal semideciduous forest fragments of southeastern Brazil. *Biota Neotropica* 9: 175–188.

Siqueira, L.P. 2002. *Monitoramento de áreas restauradas no interior do Estado de São Paulo, Brasil*. PhD Thesis, Escola Superior de Agricultura "Luiz de Queiroz," Universidade de São Paulo, Piracicaba, BR.

Streisfeld, M.A. & Rausher, M.D. 2011. Population genetics, pleiotopy, and the preferential fixation of mutations during adaptive evolution. *Evolution* 65–3: 629–642.

Vieira, D.C.M. & Gandolfi, S. 2006. Chuva de sementes e regeneração natural sob três espécies arbóreas em uma floresta em processo de restauração. *Revista Brasileira de Botânica* 29: 541–554.

Walker, B.H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6: 18–23.

Wohl, D.L., Arora, S. & Gladstone, J.R. 2004. Functional redundancy supports biodiversity and ecosystem function in a closed and constant environment. *Ecology* 85: 1534–1540.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. View of the study sites.
Appendix S2. Sampled species and their traits.
Appendix S3. Flower traits and eigenvectors of the first two principal component axes.
Appendix S4. Species originality value scores based on flower traits with scores of >0.55.