

RESEARCH ARTICLE

The restoration of tropical seed dispersal networks

Fernanda Ribeiro da Silva^{1,2,3}, Daniel Montoya⁴, Rafael Furtado⁵, Jane Memmott⁴, Marco A. Pizo⁵, Ricardo R. Rodrigues²

Human activities have led to the loss of habitats and biodiversity in the Atlantic Rain Forest in Brazil. Ecological restoration aims to rebuild this biome and should include not only the reinstatement of species but also the reestablishment of complex ecological interactions and the ecological functions that they provide. One such function is seed dispersal, which is provided by the interactions between animal frugivores and plants. We studied seed dispersal networks in 3 different tropical forest sites restored 15, 25, and 57 years ago; temporal scales rarely observed in restoration studies. We investigated changes in network structure (nestedness, modularity, and network specialization) in these communities over restoration time. Although network size and the number of interactions increased with time since restoration, the networks were composed of generalist birds, and the large frugivores remained absent. Contrary to our expectations though, species richness was highest in the 25-year-old site, maybe due to the higher number of species used in the planting. Nestedness values were low in all 3 networks, but the highest nestedness was observed in the intermediate-aged site. However, the oldest network was significantly modular and showed higher complementary specialization. These results suggest that 57 years after restoration, the complexity of mutualistic interactions in seed dispersal networks has increased, this enhancing ecosystem function in the Atlantic forest.

Key words: Atlantic forest, birds, ecosystem function, network structure, restoration age

Implications for Practice

- Restoring the interactions between species is an excellent starting point for rebuilding a community structure.
- Bird-seed dispersal networks can be used as an indicator of restoration of ecosystem function.
- Measures of network structure could be used as an indicator of restoration success, and frugivorous birds can be used as a model for evaluating the influence of restoration in the ecological process in fragmented landscapes.

Introduction

It is increasingly evident that restoration efforts should focus not only on recovering species diversity and physiognomic traits of the vegetation but also on the complex ecological interactions involved in the provision of ecosystem functions that ultimately allow ecosystem reconstruction and perpetuation over time (SER 2004; Rodrigues et al. 2009; Devoto et al. 2012). For instance, the reestablishment of mutualistic networks between animal seed dispersers and plants is essential for the long-term ecological restoration of tropical forests, where the majority of plant species rely on animals for seed dispersal (Forup et al. 2008; Devoto et al. 2012). Analyzing the architecture of mutualistic networks between animals and fruit trees in restored areas of forest can provide a useful tool for evaluating and monitoring the restoration of the ecosystem function of seed dispersal (Tylianakis et al. 2010).

The Atlantic rainforest is a biodiversity hotspot with high levels of endemism (Myers et al. 2000). Nowadays,

less than 12% of the original forest remains distributed mostly in small and isolated fragments (Ribeiro et al. 2009). In 2009, NGOs, governments, and research institutions combined forces and started a restoration program called the “Atlantic Forest Restoration Pact” (AFRP, <http://www.pactomataatlantica.org.br/index.aspx?lang=en>), which aims to restore 15 million hectares of degraded land in the Brazilian Atlantic Forest by 2050 (Calmon et al. 2011; Melo et al. 2013). However, whether these restoration actions recover forest communities remains largely unknown, and a general limitation of restoration projects worldwide is that monitoring the outcomes of long-term restoration projects is rarely done. The goal of this study is to analyze restored Atlantic forest sites using a network approach, whereby species and their interactions are recorded and the community is described in terms of community-level properties. To understand changes in network

Author contributions: FRS, RRR, MP, JM, DM designed the research; FRS, RF performed the field work; FRS, DM designed analytical methods and analyzed the data; FRS wrote the first draft; all authors contributed substantially to revisions.

¹Departamento de Biologia Vegetal, Universidade Estadual de Campinas, Rua Monteiro Lobato, 970, Caixa-postal 6109, Cep 13083-970, Campinas, São Paulo, Brazil

²Departamento de Ciências Biológicas, Laboratório de Ecologia e Restauração Florestal (LERF), Escola Superior de Agricultura “Luiz de Queiroz”, Universidade de São Paulo, Avenida Pádua Dias, 11, Cep 13418-900, Piracicaba, São Paulo, Brazil

³Address correspondence to F. Ribeiro da Silva, email feribs@hotmail.com

⁴School of Biological Sciences, Life Sciences Building, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

⁵Departamento de Zoologia, UNESP—Universidade Estadual Paulista, Cep 13506-900, Rio Claro, São Paulo, Brazil

© 2015 Society for Ecological Restoration

doi: 10.1111/rec.12244

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.12244/supinfo>

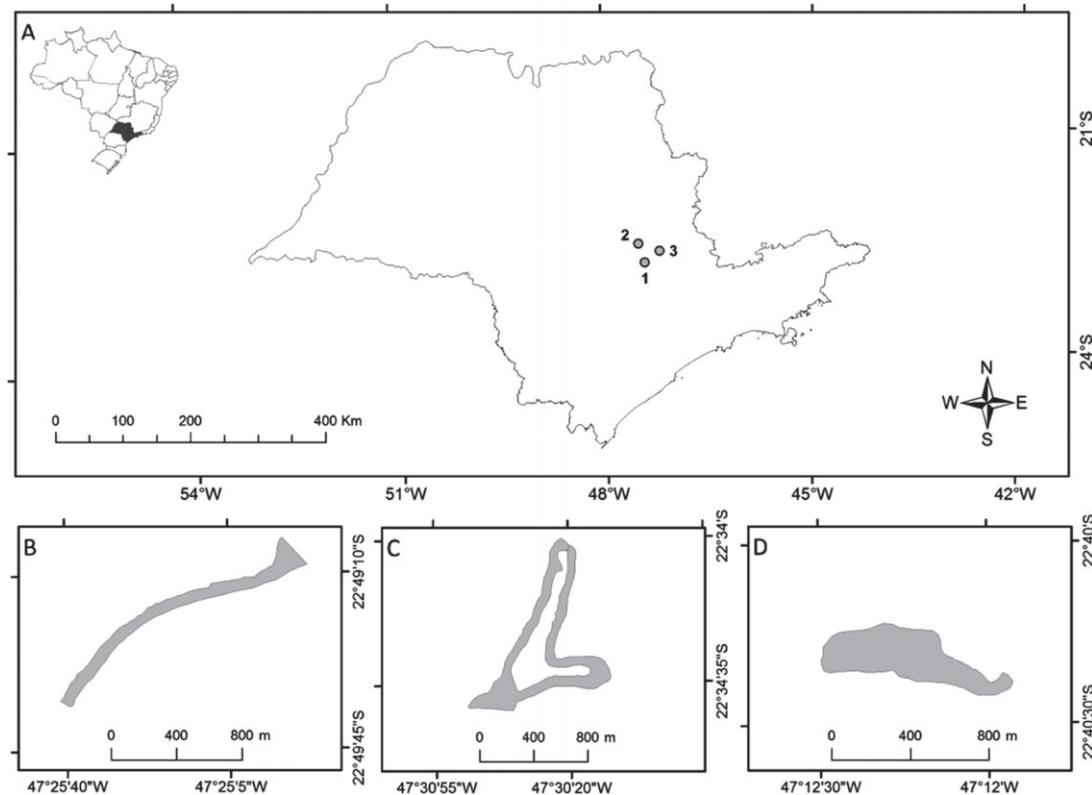


Figure 1. The field site: (A) Brazil and São Paulo state; (B) 15-year-old restored area, in Santa Bárbara D'Oeste city; (C) 25-year-old restored area, in Iracemápolis city; (D) 57-year-old restored area, in Cosmópolis city.

composition and structure following restoration, we studied seed dispersal networks in three different tropical forest sites that were restored 15, 25, and 57 years ago, a timescale that is rarely observed in restoration studies. We used this dataset to address three questions: (1) How does restoration age affect species richness and connectance? Older sites have been available for colonization by species for a longer time, and therefore we expect a positive correlation between restoration age and species richness. Given that connectance is negatively related to network size (Allesina & Tang 2012), we predict a reduction in the connectance of seed dispersal networks following time since restoration; (2) What are the effects of age on the structure of seed dispersal communities? Network structure affects network stability (May 1972; Tylianakis et al. 2010), and network metrics such as nestedness and modularity have been shown to increase community stability (Bascompte et al. 2006; Olesen et al. 2007). Because restoration seeks to increase the stability of restored communities, we predict that the older sites will be more nested and more modular; (3) Does restoration age affect the level of specialization of the seed dispersal community? High specialization is associated with a greater diversity of resources in mutualistic networks, which in turn allows for higher consumer diversity and more coexisting species (Fründ et al. 2010). We predict that, with restoration time, more niches will be available and, consequently, communities in older areas will be more specialized.

Methods

Study sites are riparian forest areas in the seasonal semi-deciduous forest domain (part of the Atlantic Forest biome) in São Paulo state, Brazil. They were restored by replanting a high plant species diversity (70–140 species) 15, 25, and 57 years ago. Both pioneer and nonpioneer species were planted, initially with good weed control (Rodrigues et al. 2009, 2011). Seedlings used in planting were chosen according to availability from commercial sources and also from native seeds collected from the surrounding landscapes. Some alien plants were used and others invaded (e.g. *Cordia absynnica*, *Melia azedarach*, *Callicarpa reevesii*; see species list in Garcia et al. 2014). The 15-year-old area is 30 ha in size and 1,435 m from the nearest forest remnant of comparable size (22°49'43.87"S, 47°25'57.71"W). The 25-year-old area is 50 ha in size and 70 m from nearest fragment (22°34'36.84"S, 47°30'29.92"W), and the 57-year site is 30 ha in size and 180 m from the nearest fragment (22°40'18.84"S, 47°12'21.64"W; WGS 84) (Garcia et al. 2014) (Fig. 1). All areas are located in a highly degraded landscapes with sugarcane matrixes and low habitat cover.

Constructing Seed Dispersal Networks

Sites were sampled from January 2011 to December 2012 at least once a month. At each site, we selected a plot 3 × 1,000 m comprising almost entirely of 1.2 km of preestablished trails.

Within these plots, we collected the data to construct the seed dispersal networks. Within each plot, fleshy fruited plants were tagged and we observed fruit consumption by birds in those plants monthly; we observed every plant that fruited on the plots, although not all tagged plants fruited. We consider all plants with fleshy fruits as potential ornithochorous plants, and a species list for each site is provided in the Table S1, Supporting Information. We built qualitative and quantitative networks for each site, the former being used to calculate modularity and the latter for nestedness and specialization degree. We built both qualitative and quantitative networks because for some feeding observations, the number of fruits consumed was not clear. Qualitative networks were constructed using direct observations of feeding birds made while walking transects through the plots, and also by sampling bird feces. Five mist nets (3×12 m) were used to capture birds with a sampling effort of 450 hours per site; mist nets were moved around within each plot monthly. Seeds were identified by comparison with reference collection and consultation with specialists. Quantitative networks were constructed using focal-tree observations for 11 tree species totaling 132.4 hours (mean \pm SD = 12 ± 11.4) in the 15-year plot, 21 species with 196.1 hours (8.9 ± 6.3) in the 25-year plot, and 16 species with 114.8 hours (7.2 ± 6.2) in the 57-year plot. In total, we undertook 443.3 hours of focal-tree observations. Whenever possible, we undertook observations on more than one individual plant per species. We recorded the number of visits, feeding time, and number of fruits eaten per visit, and we used number of visits to build the quantitative networks. There were differences in species numbers and observation efforts among the three sites due to differences in plant species richness.

We used null models to determine whether the differences in species richness in the three restored sites were larger than expected by chance. To do this, we assigned to each species a random number between 1 and 900 and then counted how many species fell into three equal-sized classes. These simulations were repeated 1,000 times. Then, we plotted the three classes at 95% confidence intervals (CI) to see if the observed differences in species richness are significantly different from random expectations.

Network Descriptors

To characterize the structure of the seed dispersal networks, we used descriptors identified as important in establishing the conservation value of ecological networks (connectance, nestedness, and modularity; Tylianakis et al. 2010), along with specialization degree that provides an insight on ecosystem functionality (Vazquez et al. 2009; Montoya et al. 2012). Each metric is described below.

Connectance. It measures the proportion of realized interactions among the possible ones. Connectance decreases with increasing network size (Jordano 1987).

Nestedness. It has been repeatedly observed that mutualistic networks are often nested, meaning that (1) there is a “core” of

generalist species that interact with each other and are responsible for most of the interactions, (2) specialist species tend to have few interactions and interact preferably with generalist species, and (3) specialist species rarely interact with each other (Bascompte et al. 2003, 2006). This architecture not only minimizes competition and enables more species to coexist (Bastolla et al. 2009; Thébault & Fontaine 2010) but also implies an interaction asymmetry (Bascompte et al. 2006) and provides robustness to the random loss of species (Memmott et al. 2004). Evaluating nestedness patterns in restored communities thus reveals aspects of their stability. We calculated nestedness using the index WNODF (Almeida-Neto & Ulrich 2011), which provides a weighted nestedness, measured on scale of 0–100, with high values representing high nestedness.

Modularity. The extent to which species interactions are organized into modules is termed the modularity of the network (Olesen et al. 2007), whereby modules comprise species that are more tightly connected with each other than to species in other modules. Modules are useful for separating functional groups and guilds (Guimerà & Amaral 2005; Mello et al. 2011), and as such they provide information on which species are likely to be important for network function in restored ecosystems (Krause et al. 2003; Teng & McCann 2004). Furthermore, modular networks are considered more stable as they can retain the impacts of a perturbation (e.g. species extinction) within a single module and thereby minimize impacts on other modules (Krause et al. 2003; Teng & McCann 2004). Moreover, it has been suggested that the restoration of modules may be a more successful approach than restoring individual species (Corbet 2000).

Modularity (M) was quantified with the software Netcarto (Guimerà & Amaral 2005). M varies from 0 (no modules) to 1 (totally separated modules). To test whether the restored networks were significantly more modular than expected by random, we generated 100 networks for each restored site based on our three seed dispersal networks (keeping connectance and number of species constant) and compared modularity of these randomly generated networks with the real seed dispersal networks (Olesen et al. 2007; Emer et al. 2013). In addition, we calculated each species “functional role” within the networks (Guimerà & Amaral 2005) by classifying each species according to Olesen et al. (2007) into peripherals, connectors, module hubs, and network hubs. Because connectors and hubs keep communities from breaking apart and initiating cascade extinctions, the identification of species serving as connectors and hubs could provide useful information for restoration practitioners.

Specialization Degree. The specialization of seed dispersal communities was measured as complementary specialization ($H2'$, Blüthgen et al. 2006). $H2'$ is a network-level measure of differentiation that describes the exclusiveness of interactions within the network considering the species degree (i.e. how connected a species is) and how these interactions differ among species (Blüthgen & Klein 2010). The index $H2'$ is useful for comparisons across different networks as it is unaffected by community size or sampling intensity (Blüthgen

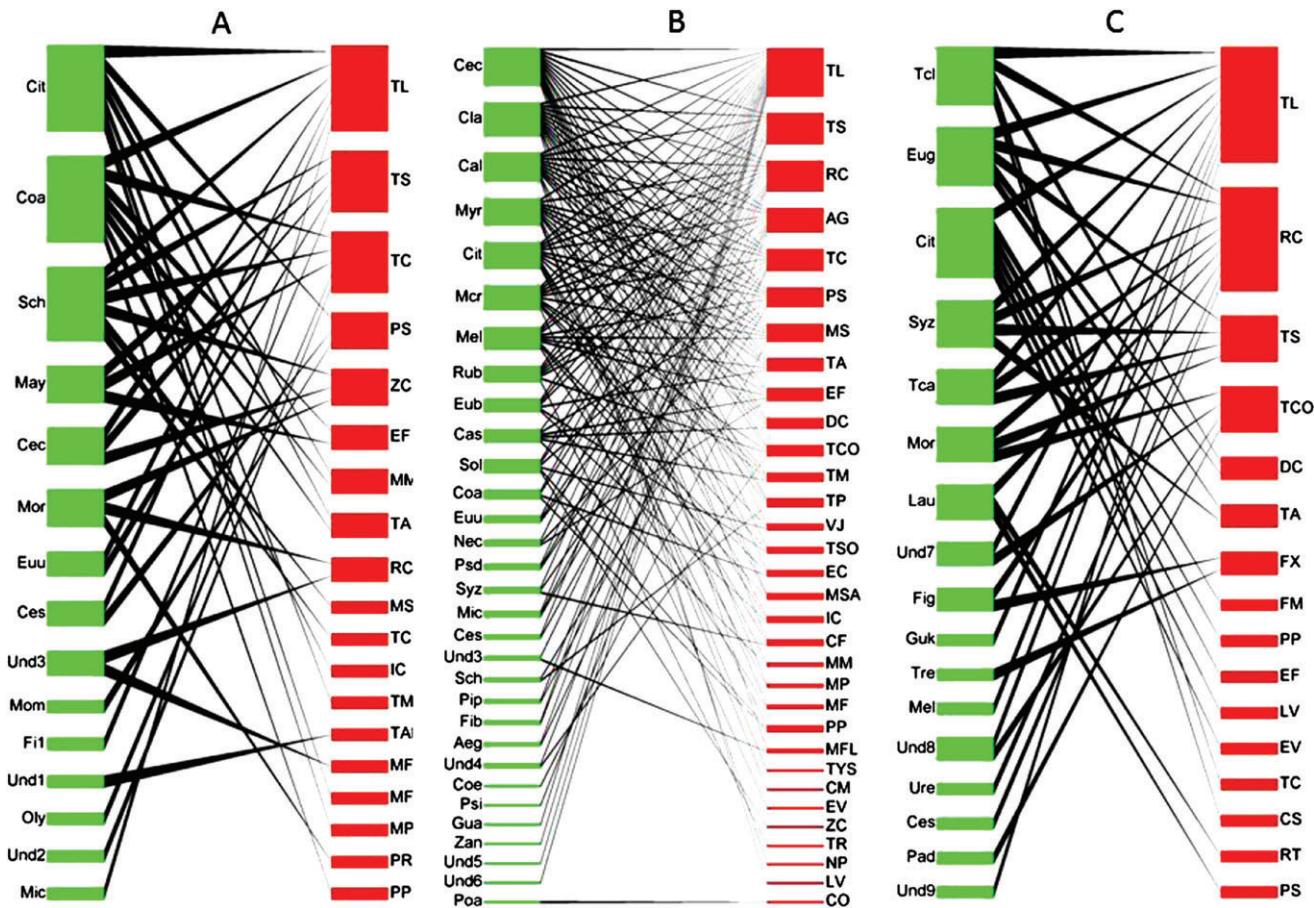


Figure 2. Quantitative bird-seed dispersal networks in three restored sites in São Paulo state, Brazil. In each panel, the left green boxes represent seed species, the right red boxes bird species, and the links represent the interactions. (A) 15-year-old restored plot, (B) 25-year-old restored plot, (C) 57 year-old plot. Bird species: AG, *Antilophia galeata*; CF, *Coereba flaveola*; CM, *Colaptes melanochloros*; CP, *Columbina talpacoti*; CS, *Conirostrum speciosum*; DC, *Dacnis cayana*; EC, *Euphonia chlorotica*; EF, *Elaenia flavogaster*; EV, *Empidonax varius*; FN, *Fluvicola nengeta*; FX, *Forpus xanthopterygius*; IC, *Icterus cayanensis*; LV, *Leptotila verreauxi*; MF, *Myiarchus ferox*; MFL, *Myiothlypis flaveola*; MM, *Myiodynastes maculatus*; MP, *Megarynchus pitangua*; MS, *Myiozetetes similis*; MSA, *Mimus saturninus*; NP, *Nemosia pileata*; PP, *Patagioenas picazuro*; PR, *Pyrrhocoma ruficeps*; PS, *Pitangus sulphuratus*; RC, *Ramphocelus carbo*; RT, *Ramphastos toco*; TA, *Turdus amaurochalinus*; TAL, *Turdus albicollis*; TC, *Tangara cayana*; TCO, *Tachyphonus coronatus*; TL, *Turdus leucomelas*; TM, *Tyrannus melancholicus*; TP, *Thraupis palmarum*; TS, *Thraupis sayaca*; TSO, *Thlypopsis sordida*; TYS, *Tyrannus savana*; VJ, *Volatinia jacarina*; ZC, *Zonotrichia capensis*; Plant species: Aes, *Aegiphila sellowiana*; Cal, *Callicarpa reversa*; Cas, *Casearia sylvestris*; Cec, *Cecropia pachystachya*; Ces, *Cestrum mariquitaense*; Cit, *Citharexylum myrianthum*; Cla, *Clausena excavata*; Coa, *Cordia abyssinica*; Coe, *Cordia ecalyculata*; Eub, *Eugenia brasiliensis*; Eug, *Eugenia sp1*; Euu, *Eugenia uniflora*; Fi1, *Ficus sp1*; Fib, *Ficus benjamina*; Fig, *Ficus guaranitica*; Gua, *Guarea sp1*; Guk, *Guarea kunthiana*; Lau, *Lauraceae sp1*; May, *Maytenus aquifolia*; Mel, *Melia azedarach*; Mic, *Miconia sp1*; Mcr, *Miconia rubiginosa*; Mom, *Momordica charantia*; Mor, *Morus nigra*; Myr, *Myrsine coriacea*; Nec, *Nectandra megapotamica*; Oly, *Olyra sp.*; Pad, *Piper aduncum*; Pip, *Piper sp1*; Poa, *Poaceae sp1*; Psd, *Psidium guajava*; Psi, *Psychotria carthagenensis*; Rub, *Rubus rosifolius*; Sch, *Schinus terebinthifolius*; Sol, *Solanum granulosoleprosum*; Syz, *Syzygium cumini*; Tca, *Trichilia catigua*; Tel, *Trichilia clausenii*; Ure, *Urera baccifera*; Und, *plant species not determined*; Zan, *Zanthoxylum sp.*

et al. 2006). H^2 ' values range from 0 (all species interacting with the same partner, i.e. low specialization) to 1 (high specialization).

To determine whether the empirical data display patterns that are significantly different from random, we generated 1,000 random networks using the *vaznull* model (Dormann et al. 2008), doing this for the network metrics described above. This model is conservative because it preserves marginal totals (i.e. takes account of interaction abundance) and keeps network connectance constant. All analyses, except for modularity, were carried out using the package *bipartite* in R (Dormann et al. 2008).

Results

We collected 51 plant species and 39 bird species in the three restored sites. The 25-year-old plot had more species than the 15- or 57-year-old ones for both plants and animals (Fig. 2).

Question 1: Does Restoration Age Affect Species Richness and Connectance?

There were differences in species richness (i.e. network size) among the restored sites (Fig. 3). There were 34 (15 plants + 19 birds), 63 (31 plants + 32 birds), and 33 (16 plants + 17 birds) species in the 15-, 25-, and 57-year-old plot, respectively. The

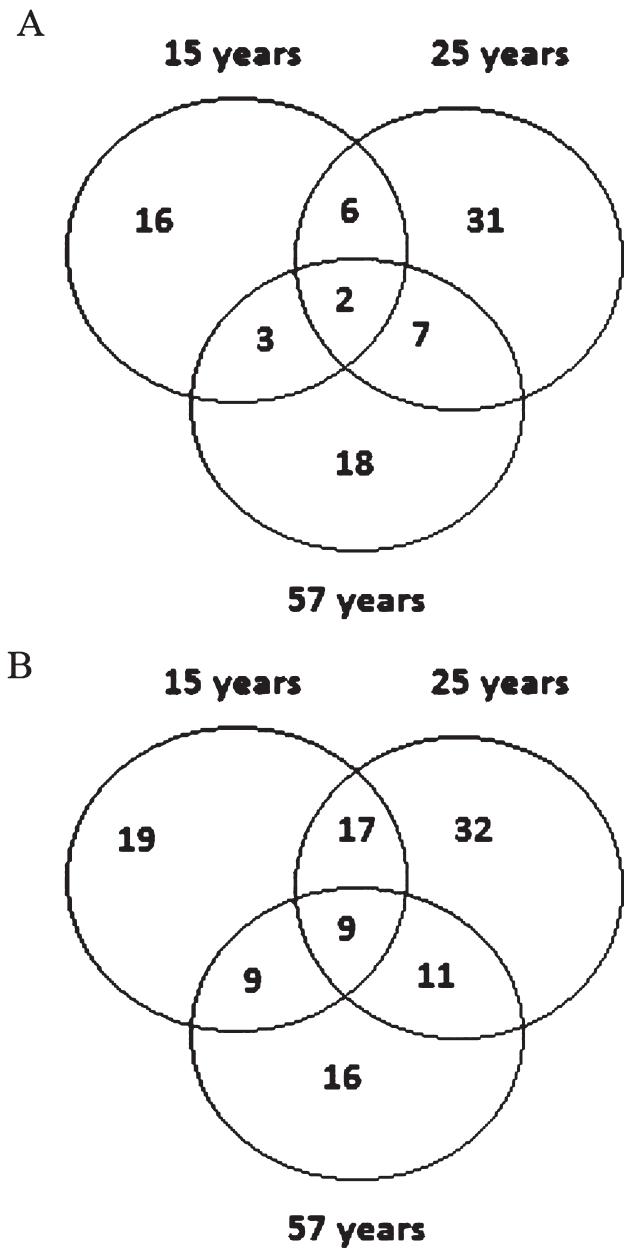


Figure 3. (A) Plant species; and (B) bird species richness showing the number of species in the 15-, 25-, and 57-year-old restoration areas, along with the overlap between and among them.

number of species in the 25-year-old plot was significantly different from random (95% CI = 21–37).

Although network complexity increased with time since restoration at all sites, in terms of number of species and interactions, only generalist birds (i.e. species that eat many different kinds of food and utilize forest and other habitats with trees) were recorded. Obligate frugivores (i.e. species that rely heavily upon fruits and normally are strongly associated with closed forest habitats; Snow 1981), as well as large fruit-eating birds such as guans, chachalacas, aracaris, and cotingas, were absent from all three sites. The largest bird found in the 15- and 25-year sites

was the pale-breasted thrush (*Turdus leucomelas*, Turdidae). In the 57-year plot, we had a single record of a large frugivore, the toucan (*Ramphastos toco*, Ramphastidae). Most of the interactions were made by small frugivores belonging to Turdidae and Thraupidae families.

Each plant species interacted on average with 2.7 ± 1.7 (mean \pm SD), 4.9 ± 4.7 , and 2.5 ± 2.8 birds in the 15-, 25-, and 57-year-old sites, respectively (Fig. 2). Each bird species interacted on average with 2.7 ± 2.1 , 4.8 ± 4.8 , and 2.65 ± 2.8 plant species in these plots. Only two plant species were found in all three plots (*Cestrum mariquitense*, a shrub in the Solanaceae family, and *Citharexylum myrianthum*, a tree in Verbenaceae family), and there was relatively little overlap in plant species between pairs of plots. Seed dispersers showed higher overlap, with nine species found in all plots and substantial overlap between pairs of plots (Fig. 3). For the quantitative networks, we found 21 (plants + birds = 7 + 14), 47 (19 + 27), and 23 (9 + 14) species in 15-, 25-, and 57-year-old sites, respectively. Although there were differences in species richness among plots, there was no difference in connectance between them (0.21, 0.22, and 0.28 for the 15-, 25-, and 57-year-old sites, respectively).

Question 2: Does Restoration Age Affect Nestedness and Modularity of Seed Dispersal Networks?

The networks from the three sites had low nestedness. Contrary to expectation, the highest nestedness value was not observed in the oldest site but in the intermediate-aged site (15 years: WNODF = 13.6, $p = 0.006$; 25 years: WNODF = 26.9, $p = 0.003$; 57 years: WNODF = 15.4, $p = 0.001$). In contrast to the older site, the networks from the two younger sites were not modular ($M = 0.51$, $p = 0.01$; Fig. 4). In the older site, we found six modules with most links occurring among species within the same module (76.2%, Fig. 4). None of the species in the 57-year network were connectors, but two species (the silver-beaker tanager *Ramphocelus carbo*, and the plant *Trichilia clausseni*) were identified as module hubs. The pale-breasted thrush *T. leucomelas* was a network hub, whereas the remaining bird species were peripherals.

Question 3: Does Restoration Age Influence Specialization Degree?

The specialization degree of the seed dispersal network in the youngest site was not significantly different from random ($H2' = 0.51$, $p = 0.07$). However, with the increase in restoration age, the seed dispersal communities begin to show significant differences in specialization from random communities in the 25-year-old site ($H2' = 0.3$, $p = 0.001$) and in the 57-year-old site ($H2' = 0.42$, $p = 0.009$).

Discussion

To our knowledge, this is the first restoration study that combines long-term restoration with an ecological networks approach. Restoration data become scarce or absent beyond 14 years after restoration in the temperate zone (Forup et al.

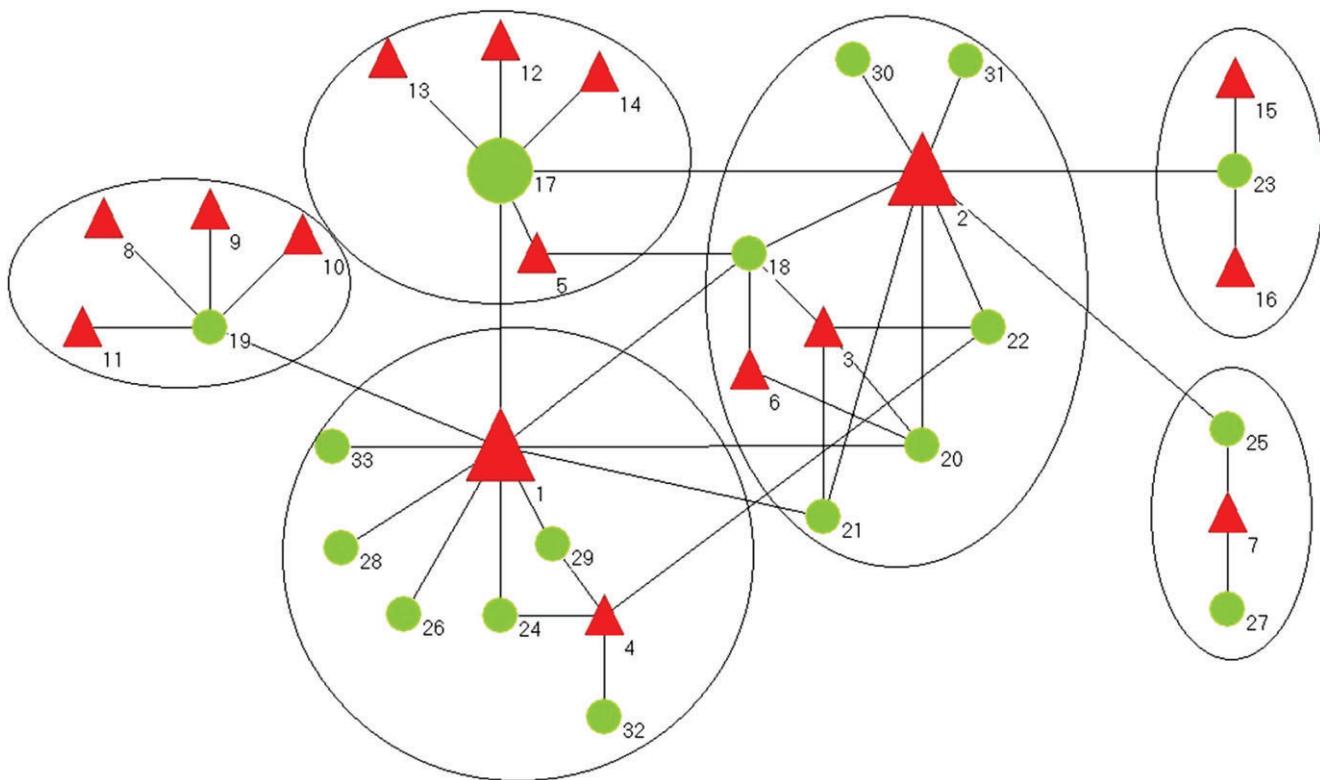


Figure 4. Modules in the seed dispersal network from the 57-year-old plot. The network has six modules; in this figure, the vertices represent species and links between vertices represent interactions of frugivorous birds. Red triangles represent birds (1–16) and green circles plants (17–33). The larger vertices represent hubs (i.e. species that connect modules; 1, *Turdus leucomelas*; 2, *Ramphocelus carbo*; 17, *Trichilia clausseni*). Birds: 1, *T. leucomelas*; 2, *Ramphocelus carbo*; 3, *Thraupis sayaca*; 4, *Tachyphonus coronatus*; 5, *Dacnis cayana*; 6, *Turdus amaurochalinus*; 7, *Forpus xanthopterygius*; 8, *Fluvicola nengeta*; 9, *Patagioenas picazuro*; 10, *Elaenia flavogaster*; 11, *Leptotila verreauxi*; 12, *Empidonax varius*; 13, *Tangara cayana*; 14, *Conirostrum speciosum*; 15, *Ramphastos toco*; 16, *Pitangus sulphuratus*. Plants: 17, *Trichilia clausseni*; 18, *Eugenia* sp1; 19, *Citharexylum myrianthum*; 20, *Syzygium cumini*; 21, *Trichilia catigua*; 22, *Morus nigra*; 23, Lauraceae sp.; 24, undetermined 7; 25, *Ficus guaranitica*; 26, *Guarea kunthiana*; 27, *Trema micrantha*; 28, *Melia azedarach*; 29, undetermined 8; 30, *Urera baccifera*; 31, *Cestrum mariquitense*; 32, *Piper aduncum*; 33, undetermined 9.

2008), a pattern probably more accentuated in the tropics. We provide evidence to suggest that active habitat restoration increases network complexity in restored areas of the Atlantic Forest. In line with our expectations, we found a significant increase in modularity and specialization degree in seed dispersal networks with restoration age. Contrary to our expectations though, species richness was highest in the 25-year-old plot, and nestedness was low in all three networks. In this section, we first present the limitations of this study and then discuss our results with respect to our original predictions, ending by considering the use of networks in restoration ecology more generally.

Limitations

The main limitation of this study, and of most restoration studies, is the lack of site replication (Montoya et al. 2012). Although the lack of replication is starting to be addressed in restoration studies, replicated datasets are still rare, and nonexistent at long temporal scales even in the Atlantic forest, where the earliest restoration projects started in 1862 but became more

common after the 1970s (Rodrigues et al. 2009; Calmon et al. 2011). However, although there are no long-term replicated datasets, decisions still need to be made concerning the best restoration practices in a seriously endangered habitat such as the Atlantic forest. We overcome this limitation to some extent by randomly generating seed dispersal networks at each of the three restored sites and comparing the observed patterns in the network structure of empirical seed dispersal networks versus the patterns observed in 1,000 simulated networks with identical species richness and connectance. Therefore, our results provide some much needed insight concerning the likely changes in the structure of mutualistic networks following restoration. A further limitation is the variation in plant species composition among the plots. This is mitigated in part by the fact that complexity is more a function of richness of species and functional groups than of individual species composition.

The Restoration of Seed Dispersal Networks

A key finding of this study is that seed dispersal communities became more modular and specialized over time relative

to recently restored communities. This is an important result as modular networks are likely to be more stable because they can retain the impacts of a perturbation within a single module and minimize further impacts on other modules (Krause et al. 2003; Teng & McCann 2004; Thébault & Fontaine 2010). Consequently, modularity hinders the propagation of extinctions through the network and increases the robustness of the community (Fortuna et al. 2010; Stouffer & Bascompte 2011).

Modular structures are associated with complex communities, which take time to assemble. This is a possible explanation for the lack of modularity in the younger sites. Therefore, the younger sites might be experiencing a period of transient dynamics where complexity has not yet built up again. Another nonexclusive explanation is that different species are found in younger versus older sites, and that species in the younger sites are more generalist (likely after perturbations), thus preventing the formation of modules in the community.

Modules are also useful for distinguishing different functional groups and guilds (Guimerà & Amaral 2005; Mello et al. 2011), and therefore modularity analysis provides information on which species are likely to be important for network function and stability in restored ecosystems. In particular, species serving as connectors and hubs keep communities linked and prevent extinctions (Olesen et al. 2007) and, therefore, the identification of these structurally most important species and their functional roles can provide guidelines for restoration actions. For example, the pale-breasted thrush *Turdus leucomelas* is a network hub in the 57-year-old network, connecting the six modules present in the community. Aside from the effects on plant reproductive ability, losing this bird species would break the community apart and divide the community into individual modules with fewer species and more vulnerability to perturbations. Restoration projects could use this information and make a particular effort to encourage this bird species in restored sites, e.g. by planting its favorite food plants (Table S1), thus accelerating the rebuilding of the mutualistic network. Similarly, looking at the plant species, *Trichilia clausenii* is a module hub (i.e. it is visited by many birds within the same module) and its planting should be strongly encouraged in restored sites to attract birds and recover the seed dispersal network.

The results reported in this study can also be used to target species relevant for landscape scale restoration (e.g. highly connected bird species like the pale-breasted thrush (*T. leucomelas*), burnished-buff tanager (*Tangara sayaca*), and silver-beaker tanager (*Ramphocelus carbo*)). The former two species are able to fly long distances, connecting fragments of forest at the landscape scale and dispersing seeds between them (Pizo & Santos 2011). These are important attributes (Montoya et al. 2008), and these bird species are thus fundamental in maintaining habitat connectivity between forest fragments and in ensuring the persistence of bird-dispersed plant species at the landscape scale. The restored sites are located within a highly fragmented landscape where less than 20% of original forest cover remains; this is less than the ideal of 30% original forest cover (Tambosi et al. 2014). Although not ideal, this level of forest cover is the reality in our study region and makes the restoration of good dispersers particularly important. Similarly, plants

that are particularly important to restored communities are *Cestrum mariquitense* (a shrub) and *Citharexylum myrianthum* (a tree), being the only plants found in all three plots. The latter is a highly connected species that produces a high number of fruits and receives a very large number of visits by birds in the three restored communities.

The 25-year-old plot supports more bird species than we would expect by chance, and hosts more bird species than the other two sites. This area is close to a natural forest and this is likely to influence its colonization rate along with the fact that it had the highest number of species used during the restoration planting. At this site, the plant species most important for birds in terms of visitation frequency were *Cecropia pachystachya*, a native species, along with *Clausena excavata* and *Callicarpa reevesii*, both alien species. The higher richness of birds in the intermediate-aged site could be directly linked to resource (i.e. plants) richness at this site, and the importance of individual plant species to frugivorous birds should be explored in the future.

Whether or not an alien plant should be used in a restoration project is a contentious point, but one of the practical implications from our results is that different plant species have different values in restoration projects, and choosing the right plants could effectively jump start restoration projects. Ideally, plants with a high value to multiple taxa—not just birds—should be identified. Although the highest bird species richness was seen in the 25-year-old site, interactions with large frugivorous species—here the toucan, *Ramphastos toco*—was seen only in the 57-year-old site. Toco toucans are open-country species, rather than forest species and this could have been a chance observation. That said, large frugivores are the key dispersers of large-fruited plant species as they have a larger gape (e.g. Galetti et al. 2013). Furthermore, large frugivore birds disperse seeds over longer distances than small birds and play a stabilizing role at the landscape/metacommunity scale by connecting habitats in space and time (Lundberg & Moberg 2003; Staddon et al. 2010). We observed a low frequency of visitation by toucan (only one visit) and it fed on Lauraceae fruits, a family that is characteristic of advanced successional stages. Toucans are a key disperser in Atlantic forest (Galetti et al. 2000), and their absence, together with the absence of other large birds in the more recently restored sites, suggests that there are not enough animals in the landscape for colonization. Another explanation is that the forest does not yet have the right food resources for these large frugivores, a problem that could be addressed by planting of plant species known to be favored by large birds (e.g. Lauraceae, Myristicaceae; Galetti et al. 2000). Ideally, experiments with replicate plots, with and without the addition of these plant families, would be used to determine the key factors important to these bird species.

Seed dispersal communities became more specialized over time in our three forests. Because specialization is related with resource complementarity, high levels of specialization mean a high degree of niche differentiation (Blüthgen 2010), and a likely decrease in competition, which facilitates species coexistence (Blüthgen & Klein 2010). Hence, the expectation is that as species differ in their functional roles (more complementarity),

there is an increase in functionality and biodiversity (Blüthgen & Klein 2010). In keeping with this expectation, we found the 57-year-old site more specialized (higher H^2), suggesting that after five decades of restoration there is an effective increase in ecosystem function in tropical restored forest.

The greatest challenge in ecological restoration is to recover stable, fully functional communities. Ecological restoration requires both ecosystem structure and function to be reinstated. This will be particularly challenging when restoring tropical forest, given its species richness and complexity. Ecologists and land managers need a better understanding of how network metrics change both as habitats degrade and as they are restored. Indeed, one of the most practical things restoration ecologists and restoration practitioners can do is to establish up long term, replicated study plots for the next generation of restoration ecologists. These experiments need levels of replication suited to both the inherent variability of natural communities and the practical considerations like site loss over the long term. Our results showed that restoration efforts in Atlantic forest are increasing complexity of mutualistic interactions involving seed dispersers and plants, and consequently enhancing ecosystem function in this important threatened biome. Ecological networks provide a powerful tool to evaluate the return of ecosystem functionality, and future studies should focus on understanding how this approach can be used to accelerate restoration of tropical forest.

Acknowledgments

F.R.S. was supported by a grant from FAPESP (2010/01861-1). M.A.P. is supported by a research grant from the Brazilian Research Council (CNPq), and D.M. was supported by the European Commission (MODECORESTORATION-FP7 Marie Curie Intra-European Fellowship for Career Development [301124]). We are very thankful to J. Tamashiro for plants and seeds identification and all the field work volunteers.

LITERATURE CITED

Allesina S, Tang S (2012) Stability criteria for complex ecosystems. *Nature* 483:205–208

Almeida-Neto M, Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling & Software* 26:173–178

Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences* 100:9383–9387

Bascompte J, Jordano P, Olesen JM (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312:431–433

Bastolla U, Fortuna MA, Pascual-García A, Ferrera A, Luque B, Bascompte J (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458:1018–1021

Blüthgen N (2010) Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. *Basic and Applied Ecology* 11:185–195

Blüthgen N, Klein AM (2010) Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology* 12:282–291

Blüthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interactions networks. *BMC Ecology* 6:9

Calmon M, Brancalion PHS, Paese A, Aronson J, Castro P, Silva SC, Rodrigues RR (2011) Emerging threats and opportunities for large scale ecological restoration in the Atlantic Forest of Brazil. *Restoration Ecology* 19:154–158

Corbet SA (2000) Conserving compartments in pollination webs. *Conservation Biology* 14:1229–1231

Devoto M, Bailey S, Craze P, Memmott J (2012) Understanding and planning ecological restoration of plant–pollinator networks. *Ecology Letters* 15:319–328

Dormann CF, Gruber B, Fründ J (2008) The bipartite package. Version 0.73. R Project for Statistical Computing, Vienna, Austria

Emer C, Venticinque EM, Fonseca CR (2013) Effects of dam-induced landscape fragmentation on amazonian ant–plant mutualistic networks. *Conservation Biology* 27:763–773

Fortuna MA, Stouffer DB, Olesen JM, Jordano P, Mouillot D, Krasnov BR, Poulin R, Bascompte J (2010) Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology* 79:811–817

Forup ML, Henson KSE, Craze PG, Memmott J (2008) The restoration of ecological interactions: plant–pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology* 45:742–752

Fründ J, Linsenmair KE, Blüthgen N (2010) Pollinator diversity and specialization in relation to flower diversity. *Oikos* 119:1581–1590

Galetti M, Guevara R, Cortés MC, Fadini R, Von Matter S, Leite AB, et al. (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340:1086–1090

Galetti M, Laps R, Pizo MA (2000) Frugivory by toucans at two altitudes in the Atlantic forest of Brazil. *Biotropica* 32:842–850

Garcia LC, Hobbs RJ, Santos FAM, Rodrigues RR (2014) Flower and fruit availability along a forest restoration gradient. *Biotropica* 46:114–123

Guimerà R, Amaral LAN (2005) Cartography of complex networks: modules and universal roles. *Journal of Statistical Mechanics: Theory and Experiment* 2:P02001

Jordano P (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *American Naturalist* 129:657–677

Krause AE, Frank KJ, Mason DM, Ulanowicz RE, Taylor WW (2003) Compartments revealed in food web structure. *Nature* 426:282–285

Lundberg P, Moberg F (2003) Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6:87–98

May R (1972) Will a large complex system be stable? *Nature* 238:413–414

Mello MAR, Marquitti FMD, Guimarães PR Jr, Kalko EKV, Jordano P, Aguiar MAM (2011) The modularity of seed dispersal: differences in structure and robustness between bat– and bird–fruit networks. *Oecologia* 161:131–140

Melo FP, Pinto SR, Brancalion PHS, Castro PS, Rodrigues RR, Aronson J, Tabarelli M (2013) Priority setting for scaling-up tropical forest restoration projects: early lessons from the Atlantic Forest Restoration Pact. *Environmental Science & Policy* 33:395–404

Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London* 271:2605–2611

Montoya D, Rogers L, Memmott J (2012) Emerging perspectives in the restoration of biodiversity-based ecosystem service. *Trends in Ecology & Evolution* 27:666–672

Montoya D, Zavala MA, Rodríguez MA, Purves DW (2008) Animal versus wind dispersals and the robustness of tree species to deforestation. *Science* 320:1502–1504

Myers N, Mittermeier RA, Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858

Olesen J, Bascompte J, Dupont YL, Jordano P (2007) The modularity of pollination networks. *Proceedings of the National Academy of Sciences* 104:19891–19896

Pizo MA, Santos BTP (2011) Frugivory, post-feeding flights of frugivorous birds and the movement of seeds in a Brazilian fragmented landscape. *Biotropica* 43:335–342

Ribeiro MC, Metzger JP, Martensen AC, Ponsoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142:1141–1153

Rodrigues RR, Gandolfi S, Nave AG, Aronson J, Barreto TE, Vidal CY, Brancalion PH (2011) Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. *Forest Ecology and Management* 261:1605–1613

Rodrigues RR, Lima RAF, Gandolfi S, Nave AG (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biological Conservation* 142:1242–1251

Snow DW (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13:1–14

Society for Ecological Restoration International, Science and Policy Working Group (2004) The SER International Primer on ecological restoration. Society for Ecological Restoration International, Tucson, Arizona. www.ser.org (accessed 22 Apr 2015)

Staddon P, Lindo Z, Crittenden PD, Gilbert F, Gonzalez A (2010) Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecology Letters* 13:543–552

Stouffer D, Bascompte J (2011) Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences* 108:3648–3652

Tambosi LR, Martensen AC, Ribeiro MC, Metzger JP (2014) A framework to optimize biodiversity restoration efforts based on habitat amount and landscape connectivity. *Restoration Ecology* 22:169–177

Teng J, McCann KS (2004) Dynamics of compartmented and reticulate food webs in relation to energetic flow. *American Naturalist* 164:85–100

Thébaud E, Fontaine C (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853–856

Tylianakis JM, Laliberté E, Nielsen A, Bascompte J (2010) Conservation of species interaction networks. *Biological Conservation* 143:2270–2279

Vazquez DP, Chacoff NP, Cagnolo L (2009) Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology* 90:2039–2046

Supporting Information

The following information may be found in the online version of this article:

Table S1. Avian species observed consuming fruits in three restored areas in São Paulo, Brazil. *Alien plant; #naturalized plant. Bird species names follow the checklist of the International Ornithological Congress (available at <http://worldbirdnames.org/names.html>) and plant species names follow APG III (2009).

Coordinating Editor: José Marcelo Torezan

Received: 12 December, 2014; First decision: 12 January, 2015; Revised: 22 May, 2015; Accepted: 22 May, 2015; First published online: 14 July, 2015