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Flower and Fruit Availability along a Forest Restoration Gradient

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ABSTRACT

Frugivores and pollinators are two functional groups of animals that help ensure gene flow of plants among sites in landscapes under restoration and to accelerate restoration processes. Resource availability is postulated to be a key factor to structure animal communities using restoration sites, but it remains poorly studied. We expected that diverse forests with many plant growth forms that have less-seasonal phenological patterns will provide more resources for animals than forests with fewer plant growth forms and strongly seasonal phenological patterns. We studied forests where original plantings included high tree species diversity. We studied resource provision (richness and abundance of flowers and fruits) of all plant growth forms, in three restoration sites of different ages compared to a reference forest, investigating whether plant phenology changes with restoration process. We recorded phenological data for reproductive plant individuals (351 species) with monthly sampling over 2 years, and found that flower and fruit production have been recovered after one decade of restoration, indicating resource provision for fauna. Our data suggest that a wide range of plant growth forms provides resource complementarities to those of planted tree species. Different flower phenologies between trees and non-trees seem to be more evident in a forest with high non-tree species diversity. We recommend examples of ideal species for planting, both at the time of initial planting and post-planting during enrichment. These management actions can minimize shortage and periods of resource scarcity for frugivorous and nectarivorous fauna, increasing probability of restoring ecological processes and sustainability in restoration sites.

Abstract in Portuguese is available in the online version of this article.

Key words: Atlantic forest; enrichment planting; pollination; resource complementarity; seed dispersal; seasonal semideciduous forest; seasonality; tropical forests.

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RE-ESTABLISHMENT OF FOREST DYNAMICS IN RESTORATION SITES IS directly related to reproductive success of planted species (Castro *et al.* 2007). This success makes recruitment of future individuals possible; consequently, assessing reproduction is an important tool in restoration and management. Nevertheless, because estimating self-sustainability of ecosystems and population dynamics requires long-term studies, few studies have addressed this in restoration sites despite relevance of recovering biological interactions (Ruiz-Jaen & Aide 2005).

When designing restoration projects for tropical ecosystems, one must often deal with a high diversity of native species and a lack of basic biological information (Parrotta & Knowles 2001). In the tropics, there is often limited knowledge of plant reproductive biology, including fruit and seeding phenology, as well as information about when to obtain seeds of key species (Lamb 2005, Rodrigues *et al.* 2009). This limited knowledge is a barrier that makes planting native seedlings difficult (Viani *et al.* 2007). Because data from growth forms such as herbs are particularly limited, herbaceous species are often underused in restoration plantings (Vieira & Silveira 2010).

A diverse plant community is likely to include species that differ in resource partitioning and the proportion of niche space occupied (Whittaker 1972, Grubb 1977, Loreau 1998). How ecosystem functions are influenced by species diversity is not always understood, but increased plant diversity often enhances ecosystem functioning (Hooper *et al.* 2005, Nadrowski *et al.* 2010, Brittain *et al.* 2013). Consequently, the diversity of plant phenological strategies is often positively influenced by species diversity (Bullock & Soli-Magallanes 1990, Vamosi *et al.* 2006). Although recovery of tree and shrub species in ecosystems being restored is often rapid, the colonization of growth forms such as epiphytes and climbers may be much slower (Garcia 2012). Because different growth forms have dissimilar phenological patterns (Morellato & Leitão Filho 1996, Ramírez 2002, Frenedozo 2004, Marques *et al.* 2004), monitoring phenology can help identify resource bottlenecks and keystone species in locations undergoing restoration (Wallace & Painter 2002).

Planting nursery-grown tree seedlings is the most commonly used restoration technique in Brazil’s rainy and dry forests (Sampaio *et al.* 2007, Rodrigues *et al.* 2009). Initial plantings of large numbers of species are important to provide resources to local fauna. These initial plant/animal interactions should catalyze subsequent regeneration more quickly than with natural regeneration,

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and if more species are planted, the chances are greater that resources will be available throughout the year owing to variations in phenology. Therefore, recognizing which plant species attract different dispersal agents at different times can enhance natural succession and will promote restoration efforts (Muscarella & Fleming 2007; Garcia *et al.* 2009). This will be especially important in the Atlantic forest biome considered the fourth 'hottest' hotpot in the world, which has a high level of habitat loss and also of endemic species (Myers *et al.* 2000).

Our objective was to investigate how temporal abundance of resources develops in restoration sites, using as a natural remnant forest site. Our hypotheses are (1) climatic variables influence the number of species flowering or fruiting, but will affect tree and non-tree species differently; (2) planting tree seedlings ensures tree regeneration but not that of other growth forms. As a result, restored communities with more species, and hence growth forms, provide more resources for pollinations and seed dispersers than communities with lower species diversity.

METHODS

STUDY AREA AND STUDY SITES.—We surveyed four riparian forest sites in the same watershed in São Paulo state, Brazil. The sites, located between 554 and 711 m elevation, were located in the seasonal semideciduous forest domain in the highly fragmented Atlantic forest biome. The restoration sites, all formerly sugarcane plantations, were plantations of different ages: 12, 23, and 55 years old. The 12-yr-old site was 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 23-yr-old site was 50 ha in size and 70 m from nearest fragment (22°34′36.84″ S, 47°30′ 29.92″ W) and the 55-yr site was 30 ha in size and 180 m from the nearest fragment (22°40′18.84″ S, 47°12′21.64″ W; WGS 84).

The initial restoration was done with a combination of pioneer and non-pioneer species in 12- and 23-yr sites and random heterogeneous planting in the 55-yr site. These sites were restored via planting of a high diversity of tree species (>70 species in each case) chosen according to availability of seedlings from commercial sources, as well as from seeds collected in the surrounding landscapes, using mostly native but also some exotic species (species list available in Nogueira 1977, Rodrigues *et al.* 1992, Siqueira 2002, Vieira & Gandolfi 2006). We compared phenology data from these restoration sites to data for a reference forest that was the second largest natural remnant in the municipality of Campinas (244.9 ha, in size, 403 m from the nearest forest remnant, 46°55′37.48″ W, 22°50′4.86″ S, WGS 84; Santos 2003, Santos *et al.* 2009). The four study sites are located with 27–65 km from each other (Amazonas *et al.* 2011).

At each site, we selected a 2.5-ha stand following the sampling design of Cielo-Filho *et al.* (2007), who established the plots in the reference forest. To reduce environmental variation among plots, they were located randomly in forest areas lacking signs of recent anthropogenic disturbances (*e.g.*, charcoal on the ground, soot on trunks, and the presence of stumps or coppiced trees). Stands were located near watercourses, but we were careful not to use areas that undergo cyclic flooding. Within stands we then randomly established 30 (10 × 10 m) plots.

PLANT SAMPLING METHODS.—In each plot, we marked all individual of all angiosperm growth forms except graminoids and recorded if they were flowering or fruiting in monthly surveys conducted between May 2008 and April 2010. We referred to growth forms other than trees collectively as 'non-trees' (subshrubs, shrubs, herbs, vascular epiphytes, hemi-parasitics, and climbers). Species were identified with the help of the vouchers of the UNICAMP herbarium (UEC), keys, and consulting by taxonomists. Vouchers were deposited in the herbarium at the Universidade Estadual de Campinas (UEC) and at the Escola Superior de Agricultura 'Luiz de Queiroz', Universidade Estadual de São Paulo (ESA).

PLANT PHENOLOGY.—The presence and intensity of flower and fruit production (*i.e.,* how many flowers and fruits each site supported per hectare per month) were recorded in plots monthly over 2 years for all sampled species, *i.e.*, we sampled only individuals that were reproducing. To avoid observer variation, observations were performed by the same person (LCG) throughout the study. We considered the following reproductive phenophases: flowers and ripe fruits. For all species studied, the percentage of the phenophase over the whole crown area was estimated for a given individual, and percentages were converted to intensity scores: 0 = 0 percent; 1 = 1–25 percent; 2 = 26–50 percent; 3 = 51–75 percent, and 4 = 76–100 percent (Fournier 1974). We measured diameter at breast height (dbh, 1.3 m aboveground) of reproductive tree individuals, as well as diameter at soil height (dsh, on the soil) for shrubs and sub-shrubs. We classified fruits according to dispersal syndromes (see Table S1).

DATA ANALYSES: PHENOLOGY AND CLIMATE FACTORS.—We performed Spearman's correlation analysis in Statistica 6.0 (StatSoft 2001) to determine if climatic variables such as rainfall, mean temperature, and day-length influenced the number of species in flower or fruiting (total number per month per site). Climatic data were provided by the *Centro Integrado de Informações Agrometeorológicas* (CIIAGRO), from the nearest meteorological station to each study sites (Santa Bárbara D′Oeste city for the 12-yr site, Limeira city for the 23-yr site, Paulínia city for the 55-yr site, and Campinas city for the reference forest).

DATA ANALYSES: TESTING FOR SEASONALITY: ZOOCHOROUS SPECIES FRUITING AND SPECIES FLOWERING.—We examined the potential seasonality of zoochorous species, which are key resources for frugivores, using circular statistics (*e.g.*, Morellato *et al.* 2010). To assess whether fruiting of zoochorous tree and non-tree species showed periodicity, we used Watson's U^2 test (Uniform, U^2), as our data were nonparametric, bimodal, or multimodal (Zar 1996). Hence, we evaluated all zoochorous species at the beginning and peak of ripe fruit phenophase, examining the first month that at least one individual of a given species presents ripe fruit (beginning) and the month when most individuals of a given species present fruiting (peak). As recommended by Morellato *et al.* (2000), we used averages when peak or beginning occurred in two consecutive months or were different between years. Because Watson's U^2 tests were significant for each community, we used this test to compare zoochorous ripe fruit availability among sites to determine whether different sites exhibit similar seasonal patterns for beginning of ripe fruit phenophase and for peak fruiting. In addition, we used Watson's U^2 tests to determine if different growth forms (trees and non-trees) exhibit seasonal patterns for beginning of zoochorous ripe fruit phenophase and for peak fruiting. We performed these analyses in the ORIANA package (Kovach 2002). Focusing on flower resources for pollination, we used the same statistical procedures that were carried out for zoochorous fruit phenophase.

Data analyses: comparing flower and fruit production among sites.—Although phenological scores provide information on reproductive intensity, they do not consider plant size, which is crucial to estimate resource availability. For instance, shrubs with a score of 4 are not equivalent in terms of food provisioning to large trees with the same score. To solve this problem, we considered plant sizes on the basis of stem diameter in the phenology assessment. According to Chapman *et al.* (1992), using of dbh as estimators of fruit abundance is a time-efficient and precise methodology, compared with crown volume and visual estimates. Accordingly, to estimate individual monthly flower and fruit production, we associated dbh or dsh with the phenological scores following Wallace and Painter (2002). We multiplied phenological intensity scores by the corresponding basal areas, yielding a value per hectare by which to compare flower and fruit production among sites (Wallace & Painter 2002). We calculated how many flowers and fruits each site supported per hectare per month. Because it was not possible to measure diameter of herbs, epiphytes, hemi-parasitics, and climbers, we used only dbh data for tree species and dsh for shrub and sub-shrub species. Although circular analyses are useful for detecting cycles, they are not appropriate for assessing phenophase intensity throughout the year (Chapman *et al.* 1999). Hence, to assess differences in flower and fruit production over months and among sites, we used nonparametric analysis of variance (Friedman test). When significant differences were detected, Wilcoxon pairwise post-hoc comparison tests were used to identify sources of the difference, performed in BioEstat 5.0 (Ayres *et al.* 2007). For this fruit production test, we grouped all species in fruit because they attract a broad diversity of animal species in addition to frugivores (*e.g.*, ants, rodents, beetles).

RESULTS

Phenology and climate factors.—The number of tree species in flower was significantly correlated with all climatic variables in the 23-yr site, as were number of flowering non-tree species in the 55-yr and reference sites. The highest significant correlation value was found between mean temperature and numbers of non-tree species in flower in the 55-yr site (0.68; Table 1). Numbers of tree species fruiting were significantly negatively correlated with all analyzed climatic variables only in the reference forest. The highest correlation value found for fruiting species was between day-length and numbers of non-tree species in the reference forest (−0.60; Table 1). Both numbers of tree and non-tree species in flower and fruiting were significantly correlated with day-length and mean temperature in the reference forest.

TABLE 1. *Spearman rank correlation tests between climatic variables and number of species in flower and fruiting at three sites under restoration (12-yr, 23-yr, and 55-yr old) and a reference forest. Values with asterisks indicate significance at the* P < *0.05 level.*

		Flower		Ripe fruit	
Study sites	Climatic factor	Tree	Non-tree	Tree	Non-tree
	Rainfall				
12-yr		0.13	0.30	−0.39	−0.46
23-yr		0.49*	0.06	−0.48*	−0.57*
55-yr		0.10	0.43*	0.11	−0.33
reference		0.30	0.57*	−0.57*	−0.36
	Day-length				
12-yr		0.19	0.47*	−0.25	−0.39
23-yr		0.56*	0.04	−0.41*	−0.29
55-yr		0.37	0.57*	−0.12	−0.27
reference		0.46*	0.60*	−0.55*	−0.60*
	Mean temperature				
12-yr		−0.05	0.39	−0.39	−0.40
23-yr		0.54*	0.10	−0.29	−0.33
55-yr		0.31	0.68*	−0.46*	−0.12
reference		0.40*	0.55*	−0.57*	−0.53*

Testing for seasonality: zoochorous species fruiting and species flowering.—Over 2 years, we recorded phenological data on 351 species (Table S1). Most species in the 55-yr site were zoochorous (52–56%), and richness of this group increased along the restoration age gradient (Table 2). Ripe fruit phenology of zoochorous species among sites was, in general, similar among sites (*i.e.,* zoochorous ripe fruit availability among sites had similar seasonal patterns for beginning of ripe fruit phenophase and for peak fruiting). The exception was initiation of ripe fruit phenophase in zoochorous species, which was earlier in the reference forest (main tendency pointed to beginning of April) and later in the 12-yr site (end of May) ($U^2 = 0.302$; $P < 0.005$). Analyzing zoochorous species of all growth forms together of each site, the reference forest showed marked seasonality in initiation of fruiting (bimodal trend pointed to early April and October) and the 55-yr site for initiation and peak fruiting (middle of May and middle of January, respectively) (Fig. S1).

We did not find differences in seasonality of tree and non-tree zoochorous species in each site (Table 2). Despite that, we identified significant differences in periodicity related to zoochorous tree and non-tree species in some situations, such as the initiation of fruit phenophase for tree and non-tree species in the 55-yr site,

TABLE 2. *Total number of species sampled, zoochorous species sampled, and results of circular statistics:mean date, Watson's* U^2 *Tests (Uniform,* U^2*), which is a test of periodicity in each site, length of mean vector, which is an index ranging from 0 (complete asynchrony of the event) to 1 (highest possible synchrony) for ripe fruit phenology of zoochorous species, and pairwise comparisons of tree and non-tree species seasonality (via Watson's* U^2 *Tests) at three sites under restoration (12-yr, 23-yr, and 55-yr old) and a reference forest. Values with one asterisks indicate significance at the* $P < 0.05$ *level and two asterisks indicate no results.*

	Years since restoration:						Natural forest:	
	12-yr-old		23-yr-old		55-yr-old		Reference	
	Santa BárbaraD'Oeste city		Iracemápolis city		Cosmópolis city		Campinas city	
	Tree	Non-tree	Tree	Non-tree	Tree	Non-tree	Tree	Non-tree
Total number of species	27	53	45	33	45	58	55	116
Zoochorous species								
Total number of zoochorous species	8	19	17	16	25	30	34	38
Relative number of zoochorous species (%)	30	36	38	48	56	52	62	33
Initiation of zoochorous ripe fruit phenophase								
Watson's U^2 tests (periodicity in each site)	**	0.161	0.098	0.044	0.232*	0.226*	0.086	0.494*
Mean date					Early of Jun*	End of Apr*		Early Apr
Length of Mean Vector (r)					0.429*	0.313*		0.517*
Watson's U^2 tests (seasonality comparison of trees and non-trees)	2.176		0.025		0.119		0.167	
Peak zoochorous fruiting								
Watson's U^2 tests (periodicity in each site)	**	0.178	0.216*	0.048	0.140	0.189*	0.110	0.111
Mean date			end of Feb*			end of Dec*		
Length of Mean Vector (r)			0.502*			0.301*		
Watson's U^2 tests (seasonality comparison of trees and non-trees)	3.631		0.150		0.124		0.053	
Species in flower								
Initiation of flower phenophase								
Watson's U^2 tests (periodicity in each site)	0.127	0.415*	0.094	0.116	0.374*	0.218*	0.217*	0.490*
Mean date		early April			early March*	middle March*	end of Feb*	early April*
Length of Mean Vector (r)		0.325*			0.382*	0.196*	0.167*	0.301*
Watson's U^2 tests (seasonality comparison of trees and non-trees)	0.035		0.049		0.060		0.153	
Peak flowering								
Watson's U^2 tests (periodicity in each site)	0.081	0.412*	0.186	0.179	0.105	0.209*	0.200*	0.583*
Mean date		end of April*				end of March*	early March*	early April*
Length of Mean Vector (r)		0.340*				0.231*	0.193*	0.279*
Watson's U^2 tests (seasonality comparison of trees and non-trees)	0.057		0.104		0.034		0.224*	

non-trees in the reference forest, peak of fruiting for trees in the 23-yr, and peak of fruiting for non-trees in the 55-yr (Table 2).

We found a significant difference for the peak flowering periods of tree and non-tree species only in the reference forest ($U^2 = 0.224$; $P < 0.05$; Table 2), with tree species flowering peak before early March and non-tree species in early April. We also identified some significant differences in periodicity related to species in flower, including the initiation and the peak of flower phenophase for non-tree species in the 12-yr site, initiation of flower phenophase for trees and initiation and peak flowering for non-trees in the 55-yr site, and initiation and peak flowering for trees and non-trees in the reference forest (Table 2).

Peak and decay of flower and fruit phenology were similar between tree and non-tree species (Figs. 1 and 2), except during the peak flowering period of the reference forest ($U^2 = 0.224$; $P < 0.05$; Table 2). We found higher numbers of non-tree species in flower and in fruit, however, except in the 23-yr site (Figs. 1 and 2). We observed pronounced periods of complementarity between non-tree and tree species in flower (Figs. 1 and 2), in which numbers of tree species fruiting decreased at the same time that numbers of non-tree species fruiting increased (Figs. 1 and 2). We detected periods of complementarity between non-tree species and tree species in flower in the reference forest, in particular during the peak flowering period (Table 2); in general, the main period of fruiting was similar in the different strata (*i.e.*, trees and non-trees) (Figs. 1 and 2).

COMPARING FLOWER AND FRUIT PRODUCTION AMONG SITES.—Overall monthly flower output showed significant differences in production across months among sites ($Fr = 10.05$, $P = 0.0181$, Fig. 3), with the early forest (12-yr) producing fewer flowers than the 23-yr and 55-yr sites (Fig. 3). Despite the differences among restored sites, flower production of tree, shrub, and sub-shrub species together in these sites was not distinguishable from that of the reference forest (Wilcoxon, $P > 0.05$ for all pairs, except between 12-yr and 23-yr and 12-yr and 55-yr sites, $P < 0.05$, Fig. 3). Numbers of species in

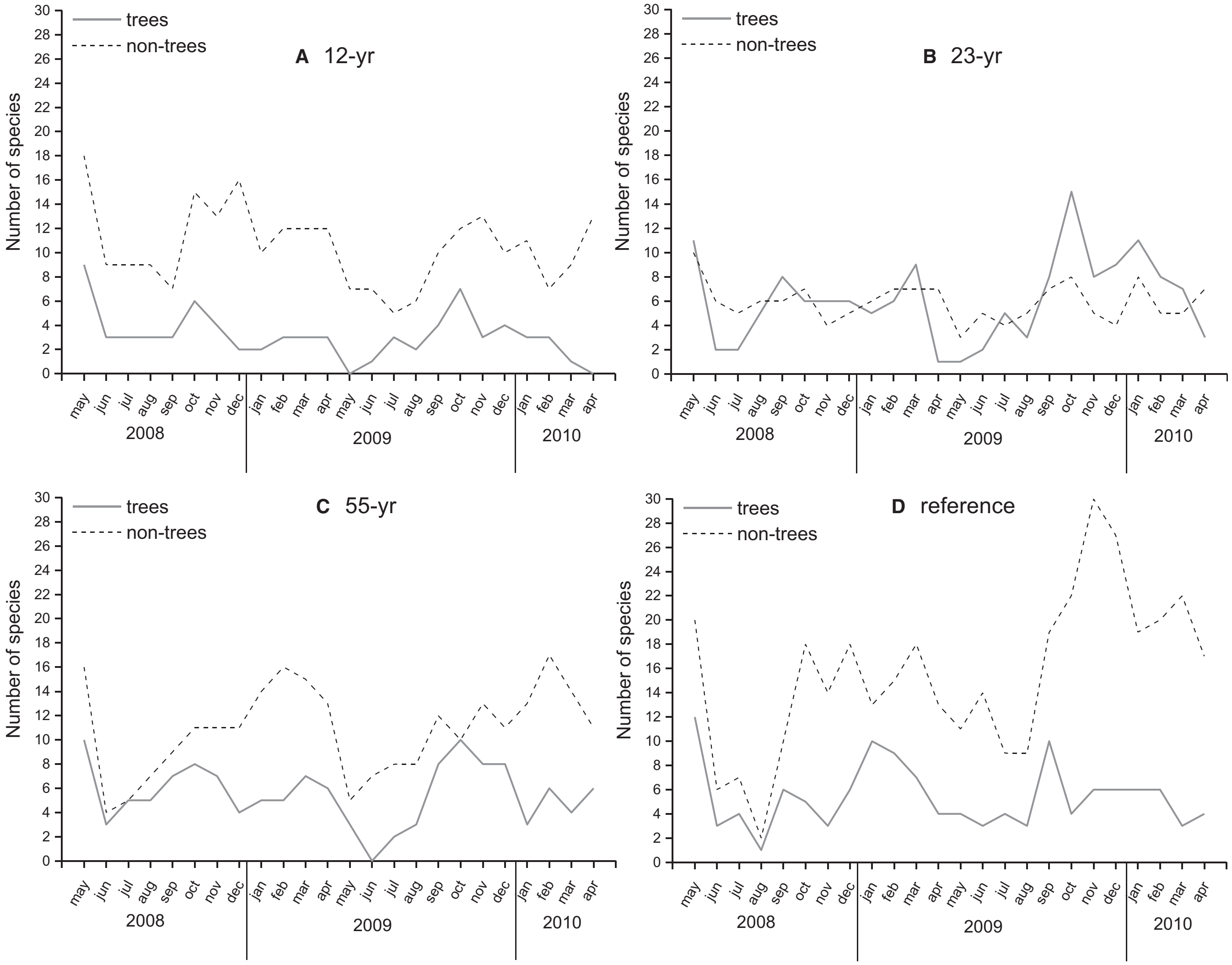

FIGURE 1. Flowering of tree and non-tree (semi-shrubs, shrubs, herbs, epiphytes, hemi-parasitics, and climbers) species at three restoration sites: (A) 12-yr, (B) 23-yr, (C) 55-yr old, and (D) a reference forest. Tree and non-tree species data are for all individuals sampled in reproduction from May 2008 to April 2010.

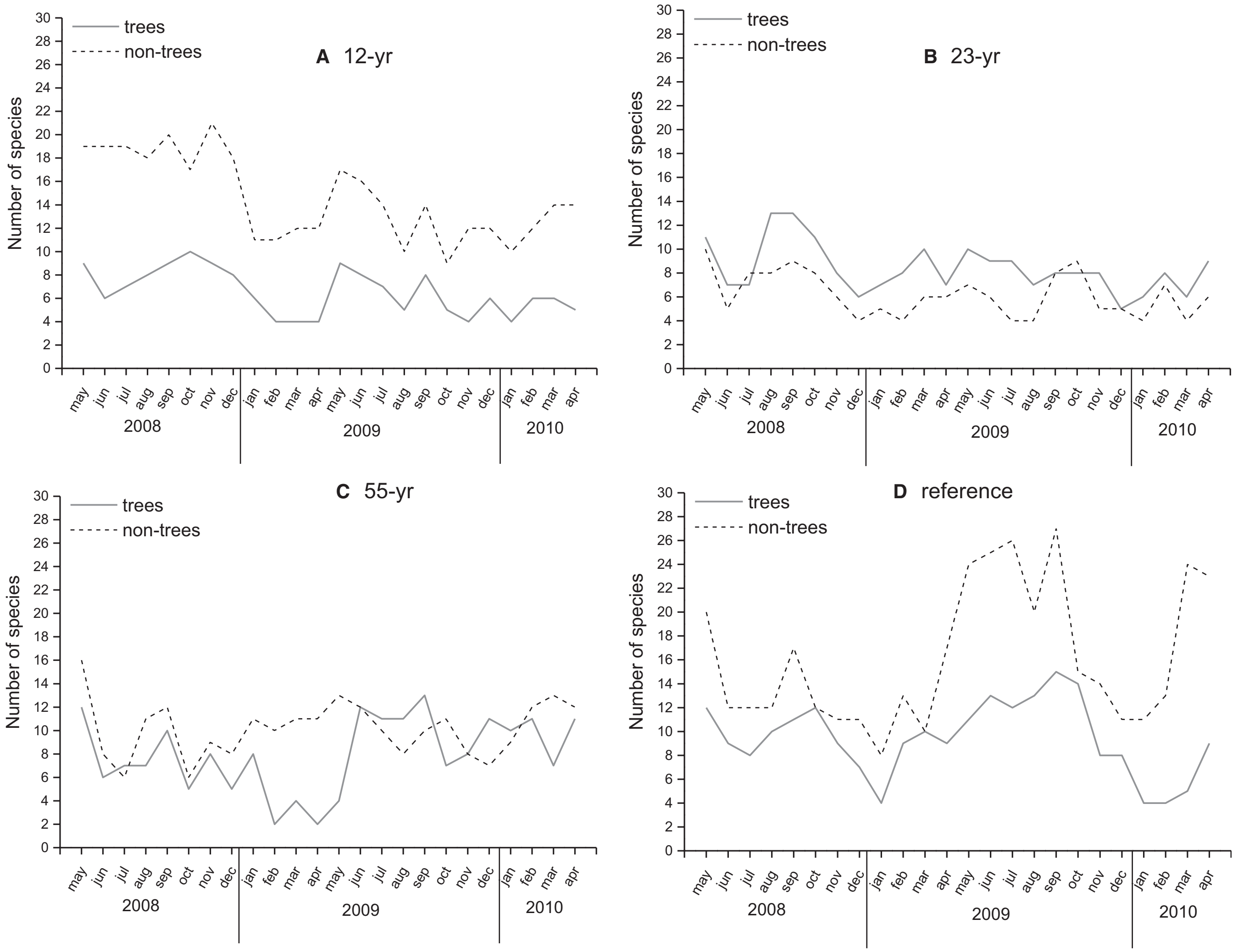

FIGURE 2. Ripe fruit phenology of tree and non-tree (semi-shrubs, shrubs, herbs, epiphytes, hemi-parasitics, and climbers) species at three restoration sites: (A) 12-yr, (B) 23-yr, (C) 55-yr old, and (D) a reference forest. Tree and non-tree species data are for all sampled individuals in reproduction from May 2008 to April 2010.

flower did not necessarily increase total flower production in the 12-yr site and in the reference forest (Fig. 3). For the oldest restoration site (55-yr), we could identify the same numbers of species supporting a completely different flower production between years (*e.g.*, 18 species in October 2008 and October 2009; Fig. 3).

In terms of ripe fruit output, significant differences were found in production across months, indicating seasonality (*Fr* = 16.65, $P = 0.0008$, Fig. 4), with the intermediate-age site (23-yr) showing higher fruit production than the 12-yr-old site and the reference forest. On the other hand, 12-yr and 55-yr forests showed ripe fruit production similar to that of the reference forest (Wilcoxon, $P > 0.05$ for all pairs, except between 12-yr and 23-yr and 23-yr and reference forest, $P < 0.05$, Fig. 4). The numbers of species with ripe fruits did not translate into in an increased overall fruit production in the 12-yr site (*e.g.*, over the period between May and November/2008; Fig. 4). In this site, we detected the same number of species supporting markedly different fruit production (*e.g.*, 18 species in September 2008 and May 2009; Fig. 4). In the 23-yr site, a small number of species in June–August 2009 produced more ripe fruits than larger numbers of species between September and November 2008 (Fig. 4). Likewise, in the 55-yr site, similar numbers of species produced three times more ripe fruits in February 2010 compared with September 2008. In the reference forest, highest numbers of species with ripe fruits occurred in April and May; however, the month with the greatest production was October 2009 (Fig. 4).

DISCUSSION

We recognize the limitations of both the chronosequence approach used here and the lack of replication of site ages. Restoration sites of similar ages are limited in the study region and sites for comparison with older restoration areas are scarce. Our study, however, provides useful information with which to assess longer term trends in restoration sites; such insights are virtually impossible to obtain in any other way. We showed that tree and non-tree species

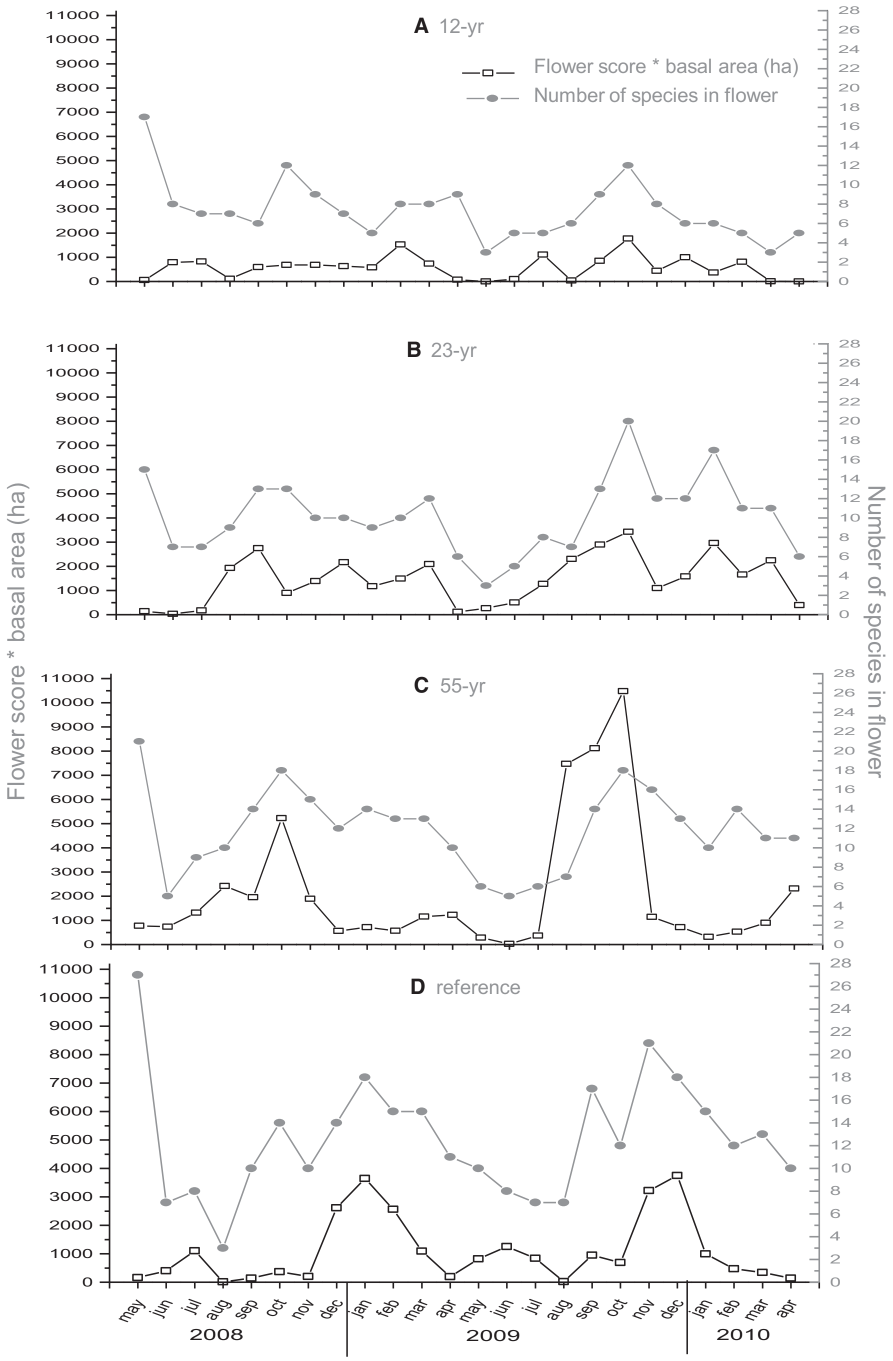

FIGURE 3. Number of species in flower (gray line with closed circles) and flower production (*i.e.,* flower score * basal area (hectares); black line with open squares) of tree, shrub, and semi-shrub species at three restoration sites: (A) 12-yr, (B) 23-yr, (C) 55-yr old, and (D) a reference forest, from May 2008 to April 2010.

differ in reproductive phenology, and suggest that failure to include different growth forms with complementary phenologies could have a direct impact on fauna that depend on fruits and flowers.

Seasonality and Restoration Sites.—Analysis of the relationship between phenology and climate factors indicated that flower production was positively correlated with climatic factors in some cases (*e.g.*, tree species in the 23-yr site and non-tree species in the 55-yr site and in the reference forest), whereas ripe fruit production was negatively correlated (*e.g.*, tree species in the reference forest). Highest flower production coincided with the highest temperatures and hottest periods with longest days, whereas the highest ripe fruit production was found in the opposite. As a result, seed dispersal may be mostly concentrated soon after the dry and cold winter period. Although this could restrict seedling establishment for species without dormancy, in seasonal

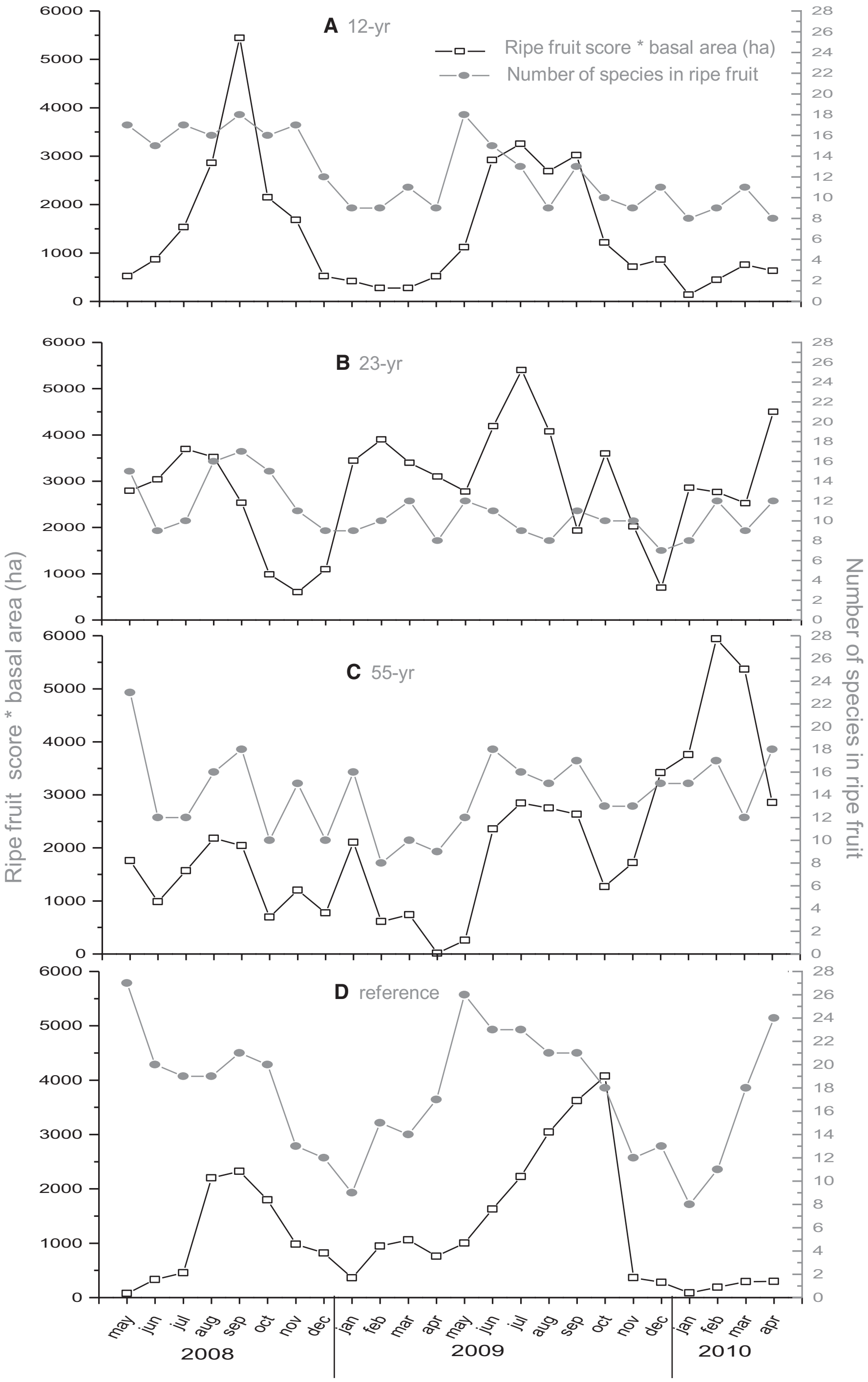

FIGURE 4. Number of species with ripe fruit (gray line with closed circles) and flower production (*i.e.*, ripe fruit score * basal area (hectares); black line with open squares) of tree, shrub, and semi-shrub species at three restoration sites: (A) 12-yr, (B) 23-yr, (C) 55-yr old, and (D) a reference forest, from May 2008 to April 2010.

Neotropical environments, most species fruiting at the end of the dry season produce dormant seeds (Salazar *et al.* 2011, Silveira *et al.* 2012). Conversely, seed dispersal during this period also brings an advantage for seed and seedlings, namely the avoidance of seed predators and herbivores, as they emerge from diapause after the first rains (Wright 1996). Early germination may enhance seedling regeneration success due to avoidance of herbivore attack (Hanley 1998), which can be an important influence in sites under restoration.

When considering zoochorous species of all growth forms, only the oldest restoration site showed significant seasonality for peak fruit availability. This means that fruit availability can be seasonally concentrated in some periods and scarce in others. On the other hand, the lack of seasonality at other sites allows a better availability of fruits to fauna through time. Similar, less-seasonal patterns for animal-dispersed fruits have been observed by other studies in seasonal forests (Morellato *et al.* 1990, Spina *et al.* 2001, Santos & Kinoshita 2003). Although we did not detect significant seasonality in the early restoration forest, we noted a month of fruit scarcity in this 12-yr site: in August 2009, only the climber species *Smilax fluminensis* Steud. (Smilacaceae) provided zoochorous fruits. We recommend the inclusion of zoochorous species that were fruiting in the same month in the other restoration sites (Table S1). Although these 'keystone-species' could be very useful for restoration projects in the Atlantic forest biome, we emphasize that they could be especially important in early stages rather than in older sites.

DISSIMILAR PHENOLOGY PATTERNS AMONG GROWTH FORMS.—Trees contributed an important component of the overall output of flowers and fruits. However, climbers, herbs, shrubs, and other growth forms often provided substantial complementary fruit and flower resources. In particular, peak flowering was different between tree and non-tree species in the reference forest, which had more than double the number of non-tree species reproducing compared with restored sites. This demonstrates that growth forms other than trees can display different periodicity in their phenology, but is only apparent in sites with high diversity of non-tree species. A wide range of phenological patterns can have an important effect on plant–animal interactions by attracting a broader diversity of consumers, which can be an important component of both restoration and conservation strategies.

In several periods, flower and fruit production was low in the reference forest, but the number of species flowering or fruiting was high. However, the percentage of tree species in reproductive stages was smaller in the reference forest (54%) compared with sites under restoration (generally >70% of tree species). In general, negative relationships exist between reproductive effort and successional maturity (Hancock & Pritts 1987), often attributed to changes of ecological species groups present through time (Garcia 2012). Another possible constraint on this greater proportion of trees in reproduction is dense canopy cover, as tropical trees are light limited, which affects their phenology (Wright 1996). Ultimately, this interspecific and intersite variation in patterns of phenology, as well as within- and among-year fluctuations in fruit and flower abundance, may affect the behavior and movement patterns of fauna in restoration sites.

IMPLICATIONS FOR RESTORATION.—Our results have two important implications for efforts to restore tropical forests and future studies addressing their efficacy. First, it is important to ensure that one is including tree species with complementary phenologies to ensure constant fruits and flowers to consumers. Second, although no planning was done regarding which species would provide resource availability to fauna in the restoration sites we studied, there was wide variation in resource provisioning. This is likely owing to the large number of species used on these projects (> 70 species). Future studies should evaluate the extent to which the initial number of species is critical to ensuring sustainability of restoration efforts; specifically, the extent to which greater initial plant species diversity results in a more diversified fauna.

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SUPPORTING INFORMATION

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

FIGURE S1. Ripe fruit phenology of zoochorous species at three restoration sites.

TABLE S1. *Sampled species and their growth forms, origin, dispersal syndromes, location, flowering and fruit phenology.*

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