

Seed Rain in a Tropical Dry Forest and Adjacent Home Gardens in the Yucatan

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Abstract

Tropical home gardens are widely recognized as reservoirs of biodiversity. Typically, Maya home gardens have an area of intensive management and one of extensive management. In the latter, some wild plant species may find safe sites for establishment, since they exhibit a high degree of similarity (in terms in plant species composition) to the surrounding forest and are dominated by plants with fleshy fruit. Therefore, this may attract frugivorous animals, which in turn may generate some seed rain. The objective of our study was to compare seed rain in the extensively managed areas of home gardens and in the surrounding forest during the fruiting peak in a rural landscape in the Yucatan. We assessed seed rain using seed traps in two habitats: the extensively managed areas of home gardens and an adjacent tropical forest. Seed rain was more abundant, denser and more diverse in the home gardens than in the adjacent forest. Approximately one quarter of the seeds recorded are from species shared between the forest and home gardens, suggesting there is notable seed exchange between these habitats. Also 50% of the seed species exclusively found in home gardens are allochthonous, likely rare species from the forest. In general, our results suggest that home gardens—particularly their extensively managed areas—are effective seed traps for forest species.

Keywords

forest regeneration, nucleation, seed dispersal, traditional agroecosystem, plant management, Yucatan Peninsula

In fragmented forests, seed exchange between forest patches and the surrounding matrix is highly relevant because it increases the chance of matrix recovery and, in the long term, the expansion of forest patches (Duncan & Chapman, 1999; Kupfer et al., 2006; Laborde et al., 2008; Reid et al., 2015; Vespa et al., 2018). However, the extent of this exchange partially depends on the quality of the matrix in which forest patches are embedded (Herrera & García, 2009; Jules & Shahani, 2003). For example, flying vertebrates are the main seed dispersers in tropical forests (Fleming et al., 1987; Herrera, 2002; Howe & Smallwood, 1982), but venturing beyond forest patches may be risky or energetically unprofitable for them (e.g. Charles et al., 2017; Chetan et al., 2019; Holl, 1999). Nevertheless, the availability of perches (e.g. the branches of standing dead trees; Holl, 1998), feeding resources (e.g. fleshy fruit; Galindo-González et al., 2000) and other elements in the matrix such as artificial resting places (La Mantia

et al., 2019) may attract frugivores and generate seed rain (Cavallero et al., 2013; Cubiña & Aide, 2001; Galindo-González et al., 2000; Holl, 1998). The positive effects of these elements in the matrix may increase with the density (de la Peña-Domene et al., 2017) and diversity of the resources offered (Cavallero et al., 2013), and

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as a function of the degree of environmental contrast between habitats (i.e. forest vs. matrix; Vespa et al., 2014). As occurs with animal-dispersed seeds, those of wind-dispersed plants can also accumulate beneath the canopies of trees and shrubs in the matrix, which may act as seed traps by interrupting wind flow (Cavallero et al., 2013).

Passive vegetation recovery after the abandonment of agricultural land occurs by two main (non-exclusive) strategies: (i) on-site regeneration, such as plants sprouting from living vegetative tissue or the germination of seeds present in the seed bank and (ii) colonization by newly dispersed seeds from surrounding forested areas (Norden et al., 2009; Runkle, 1985). However, on-site tissue from which sprouts could emerge are often removed from the matrix during moderate to intensive or prolonged anthropic land use. Similarly, the seeds of native tropical plant species often form transient seed banks that only last a few months (Baskin & Baskin, 1998), or seeds in the soil can be damaged by anthropogenic activities such as agriculture (Cubiña & Aide, 2001; López-Toledo & Martínez-Ramos, 2011). Therefore, the recovery of these agricultural habitats after abandonment relies on allochthonous seed rain from the surrounding vegetation, which is in turn influenced by habitat quality (e.g. use intensity) and the availability of resources (e.g. perches and food) to seed dispersers (Cavallero et al., 2013; González-Varo et al., 2017; Herrera & García, 2009). In these regenerating habitats, seed rain may provide a useful predictor of future community structure (de la Peña-Domene et al., 2017; Perini et al., 2019).

Home gardens are conspicuous elements in several rural areas in the tropics, and are often surrounded by forest (Kumar & Nair, 2006; Ordóñez, 2018; Webb & Kabir, 2009). However, to the best of our knowledge, no previous study has addressed their potential as seed traps for forest species. Tropical home gardens have been recognized as a repositories of biological diversity owing to their high diversity of wild and domesticated plants, structural complexity and ecological similarity to the surrounding forest (Caballero et al., 2010; Galluzzi et al., 2010; Idohou et al., 2014; Webb & Kabir, 2009). The home gardens of the Yucatec Maya are among the most studied (Caballero, 1992; Caballero et al., 2010; Castañeda-Navarrete et al., 2018). Their mean size ranges from 500 to 2,000 m² and the mean number of species is 50–100 per garden with up to 200 species per location, 80% of which are native species (Caballero, 1992; Caballero et al., 2010). Typically, a large proportion of the plants (70–85%) in these gardens produce fleshy fruits which are available year round (Castañeda-Navarrete et al., 2018; Salinas-Peba & Parra-Tabla, 2007). In terms of management, two main areas have been identified in Maya home gardens: one

where management is intensive and one where it is extensive (Caballero, 1992; Caballero et al., 2010). The former is closer to the house and therefore where most social activities take place. It is subjected to more intensive plant management, which can be classified as ex situ cultivation (sensu González-Insuasti & Caballero, 2007). The area of extensive management is further from the house, some of the plants growing there established naturally and therefore, this area is similar to the forest in terms of species composition, density and structure (Caballero, 1992; Caballero et al., 2010; Castañeda-Navarrete et al., 2018). The management intensity of this area can be classified as incipient with selective gathering, plant tolerance and tree pruning as the most common management practices (Caballero, 1992; González-Insuasti & Caballero, 2007).

The objective of this study was to compare seed rain between the area of extensive management of home gardens and the surrounding forest during the fruiting peak in a rural landscape in the Yucatan. We predicted that the seed rain in this area of the home gardens would be similar in composition and density to that of the forest owing to the ecological similarity between these habitats.

Methods

Study System

The study area was the village of San Bernardo and the surrounding forest (20° 35'–42' N, 89° 47'–57' W, 10–16 m a.s.l.) in the municipality of Kopomá, Yucatan, Mexico (Fig. 1). The weather is tropical sub-humid with summer rains (June–October), mean annual rainfall is 1,000–1,100 mm and mean annual temperature is 26–28°C. San Bernardo is a small rural village inhabited by people of Maya ethnicity. The main economic activities are small-scale agriculture, raising cattle, apiculture and low-scale production of charcoal (Secretaría de Desarrollo Social, 2018). All of the dwellings have home gardens with an average area of 1,034 m² (range: 600–1,650 m²), in which fleshy-fruited trees such as *Brosimum alicastrum* (Moraceae), *Annona squamosa* (Annonaceae), *Melicoccus bijugatus* (Sapindaceae), *Spondias purpurea* (Anacardiaceae) and *Cordia dodecandra* (Boraginaceae) are the dominant species (Unpubl. Res.). As in other rural areas of the Yucatan Peninsula (Caballero, 1992; Caballero et al., 2010), all of the home gardens in San Bernardo had an area of intensive management and one of extensive management. In the former, the understory is frequently cleared and only commonly used plant species are cultivated. These plants are watered and protected from herbivores and competitors. In the extensively managed area, some plant species established naturally and are incipiently managed (sensu González-Insuasti & Caballero, 2007).

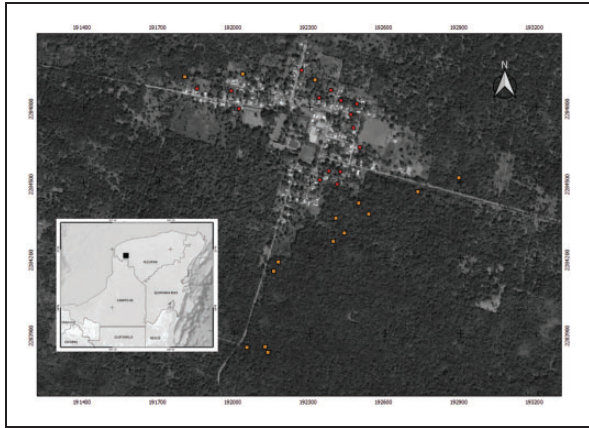


Figure 1. Location of the Study Area and Spatial Distribution of Seed Traps. Red circles and orange squares represent home garden and forest traps, respectively. The insert shows the location of the study area (black square) on the Yucatan Peninsula. The image was taken in January 2017.

The main management practices of this vegetation are selective gathering (wood and edible fruit) and tree pruning. The understory vegetation of extensively managed areas typically is not cleared. Management practices and their intensity were similar among all of the home gardens sampled.

San Bernardo is surrounded by a mixture of primary and secondary tropical dry forest, the latter resulting from the abandonment of henequen plantations (*Agave fourcroydes*: Agavaceae) 40–50 years ago (Villanueva-Mukul, 2012). The secondary forest shows clear signs of recovery (complete canopy closure, trees with a DBH of up to 80 cm and the presence of late successional species such as *Plumeria rubra*: Apocynaceae), likely favored by the presence of patches of mature forest in the region (González-Iturbide et al., 2012) (Fig. 1). Dominant species in the forest are *Bursera simaruba* (Burseraceae), *Ehretia tinifolia* (Boraginaceae), *Piscidia piscipula* and *Lysiloma latisiliquum* (Fabaceae). The matrix around the forest is primarily agricultural, plus the village of San Bernardo itself, where the main vegetation cover is the home gardens (Fig. 1). Our research group has identified bat (e.g. *Artibeus jamaicensis*, *Glossophaga soricina* and *Sturnira lilium*) and bird (e.g. *Pitangus sulphuratus*, *Icterus gularis*, *Cyanocorax yucatanicus*) species as the main seed dispersers of zoochorous plants in the study area.

Seed Rain

Seed rain was assessed between May and October 2019, which covers the end of the dry season and the rainy season, and coincides with the peak in fruiting in the study area (Unpubl. Res.). Fifteen traps of the same size

(1 m²) were placed in two habitats: the extensively managed area of home gardens (for simplicity, also referred as home garden hereafter) and forest, for a total of 30 traps covering a sampling area of 30 m² (Fig. 1). Some previous studies have set up a similar number of traps (12–33) or a similar area covered by traps (4.5 – 30 m²) (César et al., 2017; da Silva et al., 2016; Labatore et al., 2017; Piña-Rodrigues & Aoki, 2014;); therefore, sampling efforts are comparable. All traps were placed in the areas of extensive management of the selected home gardens because they offer better conditions for plant establishment than intensively managed area does. The traps were set up over an area of 389 hectares, 41% of which is covered by agricultural land and human settlements, the other 59%, a forest with varying degrees of disturbance (Fig. 1). We used funnel-shaped traps made with PVC piping for the frame. The interior was permeable fabric with a < 0.2 mm opening, with a 40 cm² insert of mosquito netting (opening: 1 mm) in the center to improve water drainage. In both habitats, traps were hung 0.50–1.00 m above ground with a rope. A heavy rock was placed in the center of each trap to avoid disturbance by the wind. Trap allocation was not completely random because home gardens are privately owned, so the permission of owners was required, and the specific position of traps had to be negotiated. In the forest, some of the random points were inaccessible owing to the density of the vegetation and the absence of paths; therefore, traps were installed as close as possible to the random points. The minimum distance between traps was 300 m, and for the home garden traps, contiguous gardens were avoided. To standardize sampling, no traps were placed beneath fruiting trees in either habitat. The mean distance from home garden traps to the nearest forest edge was 70.53 ± 10.62 m.

Trap contents were collected daily, put in paper bags, and taken to the laboratory where the seeds were separated from litter and/or debris, and counted. For animal-dispersed seeds, both partially eaten fruit and completely clean seeds were counted. Seeds were checked for viability either by cutting (n = 1384 seeds) or germination (n = 335 seeds) tests. Cutting is an indirect test of seed viability consisting of cutting the seed longitudinally to observe the endosperm. If the latter is normal in color and morphology and has a well developed embryo, the seed is presumed viable (Food and Agricultural Organization [FAO], 1985). Seeds were identified to the finest taxonomic category using a reference collection obtained from vegetation in the home gardens sampled and around the traps set up in the forest (within a 10 m radius of each trap), and by consulting the seed collection curated by the germplasm bank of the Centro de Investigación Científica de Yucatán (CICY) and the experts in local flora at CICY. Seeds that could not be identified by comparison were germinated and

Table 1. Seeds of Plant Species Found Only in the Seed Traps in the Forest Interior (Forest) and Only in the Extensively Managed Areas of Home Gardens (Home gardens), as well as the Species Shared Between the Forest and the Extensively Managed Areas of Home Gardens (Shared).

Forest	Shared	Home gardens
<i>Machaonia lindeniana</i> (37) ^a	<i>Ehretia tinifolia</i> (443) ^b	Morph 5 (92)^b
<i>Lysiloma latisiliquum</i> (32) ^a	<i>Maclura tinctoria</i> (309) ^b	<i>Tecoma stans</i> (73) ^a
<i>Morinda royoc</i> (9) ^b	<i>Piscidia piscipula</i> (159) ^a	Morph 3 (14)^b
<i>Diospyros anisandra</i> (7) ^b	Morph 9 (125) ^b	<i>Annona squamosa</i> (13) ^b
<i>Sideroxylon obtusifolium</i> (4) ^b	<i>Bursera simaruba</i> (103) ^b	<i>Byrsonima crassifolia</i> (11) ^b
<i>Bourreria pulchra</i> (3) ^a	<i>Karwinskia humboldtiana</i> (74) ^b	<i>Hylocereus undatus</i> (10) ^b
<i>Senna atomaria</i> (3) ^a	Morph 10 (53) ^b	<i>Gossypium barbadense</i> (9) ^a
Morph 2 (2) ^b	<i>Brosimum alicastrum</i> (38) ^b	<i>Guazuma ulmifolia</i> (9) ^b
Morph 8 (1) ^b	<i>Melicoccus bijugatus</i> (38) ^b	<i>Azadirachta indica</i> (7) ^b
Morph 14 (1) ^b	Morph 6 (21) ^b	Morph 12 (5)^b
Morph 18 (1) ^a	<i>Sabal yapa</i> (10) ^b	<i>Cocos nucifera</i> (4) ^a
		<i>Cordia dodecandra</i> (4) ^b
		<i>Sapranthus campechianus</i> (4)^b
		<i>Spondias purpurea</i> (4) ^b
		<i>Terminalia catappa</i> (4) ^b
		Morph 15 (3)^b
		Morph 16 (3)^b
		<i>Caesalpinia mollis</i> (1)^a
		Morph 1 (1)^b
		Morph 4 (1) NI
		Morph 7 (1)^b
		Morph 11 (1)^b
		Morph 13 (1)^b
		Morph 17 (1)^b

Note. Seed species in bold are allochthonous. The number of seeds collected is given in parentheses. Symbols represent dispersal mode.

NI Unidentified dispersal agent.

^aAbiotically dispersed.

^bAnimal dispersed.

kept in a controlled environment chamber (Binder KBW240E5.1) at 28 °C with a 12 h dark/light photoperiod until they developed the first pair of true leaves. Only two species were identified without ambiguity to the species level (*Maclura tinctoria* and *Tecoma stans*) and one to the family level (Solanaceae, shown as Morph 12 in Table 1). Unidentified species were classified as morphospecies for the analyses. All seed species except one were categorized as either animal dispersed or abiotically dispersed (anemochorous + hydrochorous + autochorous) based on the literature and morphology. All seed species in the abiotically-dispersed category were anemochorous, except three: one hydrochorous and two autochorous species. We recognize that we could have missed a few seeds smaller than 1 mm during our sampling owing to the size of the openings of the mesh insert in the traps. However, the fact that these seeds are usually dispersed in clumps embedded in animal feces or fruit pulp lead us to think that it was not a frequent occurrence.

Data Analysis

Seed density (number of seeds per m²) and seed species richness per trap were compared between habitats (two levels: forest and home gardens) using generalized linear models (GLM) with a Poisson error distribution and the log link function. The proportion of seeds and seed species dispersed by animals per trap were compared between habitats using GLMs with a binomial error distribution and a logit link function. For each trap, Shannon-Weaver's diversity index (H') was calculated and compared with Wilcoxon's non-parametric test. We calculated the observed statistical power of all these variables for the habitat factor by model simulation after 1,000 randomizations. In all cases power was 100%, except for the proportion of seed species dispersed by animals for which it was 60%, suggesting that the number of traps was in general suitable for assessing habitat differences in our study system. However, because power was lower than optimal (80%) for the proportion of seed species dispersed by

animals, the results for this particular variable should be interpreted with caution.

An ordination of seed species composition was conducted for each trap using nonmetric multidimensional scaling (NMDS) based on a Bray-Curtis dissimilarity matrix. We identified the centroid for each habitat using the convex hull approach and showed this graphically with spiders connecting the traps in each habitat with the centroids of the hulls. Seed species composition was also compared between habitats using a permutational analysis of variance (PERMANOVA) with 999 permutations.

All analyses were run in R.6.3.2 (R Core Team, 2019). Data are available online in Appendix S1.

Results

In total, 1,749 seeds belonging to 46 different taxa were caught in the 30 traps, 18 of which were identified as morphospecies. The species identified belonged to 19 families, and the most speciose families were Fabaceae (four species) and Boraginaceae (three species) along with Annonaceae, Malvaceae, Moraceae, Rubiaceae, each with two species. Of the 1,719 seeds tested, 47% were viable. The most abundant species were *Ehretia tinifolia* representing 25% of the total seeds (Boraginaceae, 443 seeds), *Maclura tinctoria* representing 17.49% (Moraceae, 309 seeds) and *Piscidia piscipula* representing 9.09% (Fabaceae, 159 seeds). *E. tinifolia* and *M. tinctoria* are dispersed by animals, while *P. piscipula* is dispersed by wind. Six hundred and seventy-six (38.65%) seeds were collected in the forest traps and 1,073 (61.34%) in home gardens. All (15) of the traps caught seeds in home gardens, while 86% (13) of the traps in the forest had seeds. Of the 46 identified taxa, 24 and 11 seed species were found exclusively in the home garden and forest traps, respectively. The remaining 11 species were shared by both habitats (Table 1). All shared seed species were animal-dispersed except one (91%). Also, 80% of seed species exclusively found in home gardens and 54% in the forest were dispersed by animals (Table 1). Of the 24 seed species exclusively found in home gardens, 13 species (54%) were allochthonous (i.e. no adults of these species were growing in the home gardens) while, in the forest, no allochthonous seed species were captured.

Home garden and forest traps overlapped to a moderate degree in species composition, but had clearly differentiated centroids in the 2D ordination plot, suggesting that these two habitats had a relevant proportion of distinctive seed species (Fig. 2). The results of the PERMANOVA confirmed that seed species composition was statistically different between the forest and the home gardens ($F_{1,23} = 1.57$, $P = 0.04$).

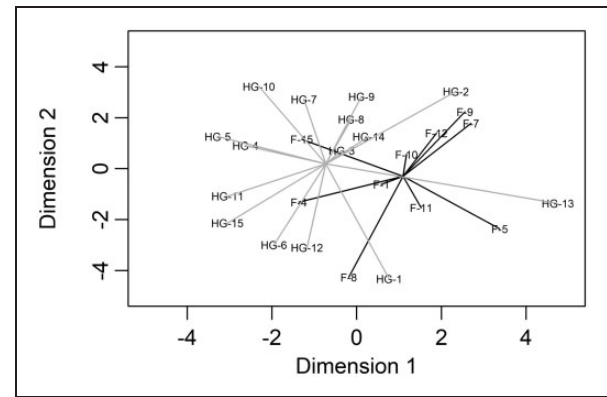


Figure 2. Ordination Plot of Seed Rain Composition Observed in Seed Traps Placed Within a Forest (F1-15) and the Extensively Managed Areas of Home Gardens (HG1-15) in Central Yucatan, Mexico. The two dimensions (axes) were obtained using non-metric multidimensional scaling. The spiders indicate the distance from each trap to the centroids of a convex hull for each habitat: forest (black) and the areas of extensive management of home gardens (gray).

Seed density (1.8 times), the proportion of animal-dispersed seeds (1.48 times), seed species richness (2.38 times), the proportion of animal-dispersed seed species (1.5 times) and seed species diversity (3.77 times) were all significantly greater in home gardens than in the forest (Table 2).

Discussion

Our results clearly show that home gardens, particularly their area of extensive management, are highly effective seed traps. Seed rain was more abundant, denser and more diverse in home gardens than in the adjacent forest. Approximately one quarter of the seeds caught belong to species that are shared between the forest and home gardens, suggesting that there is an important degree of seed exchange between these habitats. Also, a half of the seed species exclusively found in home gardens were allochthonous, probably rare species from the forest. Therefore, the extensively managed areas of home gardens, in addition to being an important reservoir for agrobiodiversity, play an important role as seed traps and potentially as regeneration nuclei for forest vegetation.

We found that the seed rain in home gardens was 183% denser and 238% richer in species than in the adjacent forest. This result contrasts with those of previous studies, which have often reported less or similar seed rain in agroecosystems compared to that of adjacent forests. For example, Charles et al. (2017) found that seed rain in an abandoned pasture represented only 40% of the seed abundance observed in the Australian moist forest. Similarly, de la Peña-Domene

Table 2. Seed density, Proportion of Animal-Dispersed Seeds, Seed Species Richness, Proportion of Animal-Dispersed Species and Seed Species Diversity (Shannon-Weaver: H') in a Tropical Dry Forest (Forest) and the Extensively Managed Areas of Home Gardens (Home gardens) in Yucatan, Mexico.

Response	Forest	Home garden	Statistics
Seed density (seeds / m ²)	41.13 ± 24	75.46 ± 24	$\chi^2_1 = 153^{**}$
Proportion of animal dispersed seeds	0.58 ± 0.10	0.86 ± 0.08	$\chi^2_1 = 7.24^{**}$
Seed species richness	3.33 ± 0.24	7.93 ± 0.32	$\chi^2_1 = 29.01^{**}$
Proportion of animal-dispersed species	0.56 ± 0.09	0.84 ± 0.06	$\chi^2_1 = 4.04^*$
Seed species diversity (H')	0.27 ± 0.03	1.02 ± 0.03	$W = 26^{**}$

Note. The statistics in the last column are comparisons between the forest and home gardens, all carried out using generalized linear models with a Poisson (seed density, seed species richness) or binomial (proportion of animal dispersed seeds and species) error distribution, except for H' , which was assessed with a non-parametric Wilcoxon's test. Values are means ± SE per trap.

* $p < 0.05$. ** $p < 0.01$.

et al. (2014) found that the number of seed species in an intensively used pasture represents 79% of that found in a primary tropical forest in Mexico. More recently, Chetan et al. (2019) found similar seeds in the soil of an abandoned tea plantation and an adjacent tropical forest in India. The diversity of the plants that are present and the availability of feeding resources in home gardens (Caballero et al., 2010; Salinas-Peba & Parra-Tabla, 2007) are likely to be more attractive to dispersers than those available in the monocultures/pastures assessed in previous studies (Charles et al., 2017; Chetan et al., 2019; de la Peña-Domene et al., 2018). Additionally, the low degree of contrast (in terms of structure and species composition) between the extensively managed area of home gardens and the forest may facilitate seed exchange between these habitats, as observed in other system (temperate forest patches embedded in an agricultural matrix) in Argentina (Vespa et al., 2014). Most of the shared seed species are dispersed by animals (91%), and this was likely because seed dispersers such as birds and bats can find suitable perches or feeding sites in home gardens.

The vast majority of seeds and seed species that arrived in the home gardens were dispersed by animals. In contrast, on abandoned agricultural lands, wind-dispersed seeds are far more common than seeds dispersed by animals (Zimmerman et al., 2000). Also, in these degraded habitats, animal-dispersed plants are more often seed-limited than wind-dispersed plants (de la Peña-Domene et al., 2014). The difference between the results of previous studies and ours may be due to the fact that the area of extensive management of home gardens offer more feeding resources and a more suitable habitat to dispersers than other intensively-used agroecosystems where a high degree of matrix openness not only limits animal seed dispersal but also favors seed dispersal by wind (San-José et al., 2019). Another explanation is that the proportion of animal-dispersed seeds was higher in home gardens because this habitat is dominated by animal-dispersed plants, but seeds are not

removed or are moved within the same habitat (Guevara et al., 1986; Holl, 1999). Although this is the case for some cultivated plants with large seeds such as *Annona squamosa* (seed size =1 cm), *Cordia dodecandra* (2.5 cm), *Spondias purpurea* (1.50 cm), and *Terminalia catappa* (3 cm), whose mesocarp is consumed *in situ* by frugivorous birds and who drop the seeds beneath mother trees; however, these species represent less than the 25% of home garden plants. In fact, more than 50% of the seed species found exclusively in home garden traps are allochthonous seeds. Of these, there were 11 animal-dispersed morphospecies that we could not identify even with the reference collection, which included all of the species present in the home gardens we sampled and within a 10 m radius around the traps in the forest. Therefore, it is highly likely that these seeds belong to rare plant species in the forest. Rare-biased frugivory and seed dispersal has been reported for flying vertebrates and the seed rain of these species may be directed to habitats where feeding resources for frugivores are abundant, such as home gardens (Morán-López et al., 2018).

An undesirable by-product of seed exchange between natural and transformed habitats is the introduction of exotic/invasive species into the forest (Bonilla & Pringle, 2015). However, in our study we did not find any allochthonous seed species in the forest traps, suggesting that seed dispersal from home gardens to the forest is limited. Even though the fleshy fruits of crops may have a positive effect (facilitation) on co-fruited plants in the forest (Carlo, 2005; Preciado- Benítez et al., 2015), we cannot rule out the possibility of a competitive effect, particularly considering that feeding resources are more spatially concentrated and are available for longer periods of time in home gardens than in the forest (Carlo, 2005).

An important question to address is whether the seeds that arrive in home gardens reach safe sites for germination and seedling establishment. Home gardens offer a suitable habitat for the recruitment of several forest

species, particularly in the areas of extensive management. Typically, the ground and understory in this area of home gardens is not cleared and this allows for the natural recruitment of some wild and semidomesticated species (Caballero, 1992; Caballero et al., 2010; Castañeda-Navarrete et al., 2018; Rico-Gray et al., 1990). This may be the situation for at least some of the species found in the seed traps. However, a worrisome trend observed in home gardens in other areas of the Yucatan Peninsula is the reduction in the area of extensive management (Cruz-Cortés et al., 2019), which may limit the establishment of forest species. We also acknowledge that the success of home gardens as seed traps may also have a negative impact, for example, if home gardens generate a seed rain of species that do not find safe sites there, this may contribute to seed limitation in the forest, a risk that deserves further attention.

The Maya and other ancestral cultures in the Neotropics often tolerate and protect naturally established plant species including crop wild relatives in their home gardens (Caballero et al., 2010; Casas et al., 2007; Fausto & Neves, 2018; Rival & McKey, 2008). In fact, home gardens are recognized as experimental areas where new plant uses are discovered and plant domestication takes place (Casas et al., 2007; Fausto & Neves, 2018). Therefore, seed exchange between the forest and home gardens not only contributes to the conservation of biodiversity, but also is relevant for the conservation of biocultural processes (Galluzzi et al., 2010; Idohou et al., 2014). We conclude that home gardens, particularly their extensively managed areas, play an important role as seed traps of forest species.

Implications for Conservation

Home gardens are conspicuous elements in tropical landscapes and are important seed traps for forest species. In fragmented forests, where the matrix is dominated by rural settlements, the inclusion of home gardens in management practices offers a means of increasing landscape connectivity. Particularly important for this purpose are those gardens with proportionally larger areas of extensive management, where forest species may find safe sites for their establishment. Home garden owners could be considered potential recipients of payment for environmental services and actively participate in management strategies.

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References

- Baskin, C. C., & Baskin, J. M. (1998). *Seeds: Ecology, biogeography, and evolution of dormancy and germination* (666 pp.). Academic Press.
- Bonilla, N. O., & Pringle, E. G. (2015). Contagious seed dispersal and the spread of avian-dispersed exotic plants. *Biological Invasions*, 17(12), 3409–3418.
- Caballero, J. (1992). Maya homegardens: Past, present and future. *Etnoecologica*, 1, 35–54.
- Caballero, J., Cortés, L., & Martínez-Ballesté, A. (2010). El manejo de los huertos familiares. In Toledo, V. M. (Ed.), *La Biodiversidad de México: Inventarios, Manejos, Usos, Informática, Conservación e Importancia Cultural* (pp. 220–234). Fondo de Cultura Económica.
- Carlo, T. A. (2005). Interspecific neighbors change seed dispersal pattern of an avian-dispersed plant. *Ecology*, 86(9), 2440–2449.
- Casas, A., Otero-Arnaiz, A., Pérez-Negrón, E., & Valiente-Banuet, A. (2007). In situ management and domestication of plants in mesoamerica. *Annals of Botany*, 100(5), 1101–1115.
- Castañeda-Navarrete, J., Lope-Alzina, D. G., Ordoñez, M. J. (2018). Los huertos familiares de la Península de Yucatán. In M. J. Ordoñez (Ed.), *Atlas biocultural de huertos familiares en México: Chiapas, Hidalgo, Oaxaca, Veracruz y Península de Yucatán* (pp. 331–389). UNAM, CRIM.
- Cavallero, L., Raffaele, E., & Aizen, M. A. (2013). Birds as mediator of passive restoration during early postfire recovery. *Biological Conservation*, 158, 342–350.
- César, R. G., Rother, D. C., & Brancalion, P. H. S. (2017). Early response of tree seed arrival after liana cutting in a

- disturbed tropical Forest. *Tropical Conservation Science*, 10, 194008291772358–194008291772357.
- Charles, L. S., Dwyer, J. M., & Mayfield, M. M. (2017). Rainforest seed rain into abandoned tropical Australian pasture is dependent on adjacent rainforest structure and extent. *Austral Ecology*, 42(2), 238–249.
- Chetan, H. C., Ganesan, R., & Ganesh, T. (2019). Seed and seedling establishment in abandoned tea plantations role of ecological and edaphic factors, Southern Western Ghats, India. *Tropical Ecology*, 60(4), 566–580.
- Cruz-Cortés, J. J., Fraga, J. E., & Munguía-Rosas, M. A. (2019). Effects of changes in traditional agroecosystems on vernacular dwellings: The occupants' perspective. *Human Ecology*, 47(4), 553–563.
- Cubiña, A., & Aide, M. (2001). The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica*, 33, 260–267.
- da Silva, E. P., Figueiredo, F. G., Fernandes, S. S., & Pereira, Z. V. (2016). Evaluation of the potential of seed rain as an alternative for forest restoration in permanent preservation areas. *Revista Árvore*, 40(1), 21–28.
- de la Peña-Domene, M., Howe, H. F., Cruz-León, E., Jiménez-Rolland, R., Lozano-Huerta, C., & Martínez-Garza, C. (2017). Seed to seedling transitions in successional habitats across a tropical landscape. *Oikos*, 126(3), 410–419.
- de la Peña-Domene, M., Martínez-Garza, C., Palmas-Pérez, S., Rivas-Alonso, E., & Howe, H. F. (2014). Roles of birds and bats in early tropical-Forest restoration. *PLoS One*, 9(8), e104656.
- Duncan, R. S., & Chapman, C. A. (1999). Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications*, 9(3), 998–1008.
- FAO. (1985). *A guide to forest seed handling with special reference to the tropics* (392 pp.). FAO.
- Fausto, C., & Neves, E. (2018). Timeless gardens: Deep indigenous history and the making of biodiversity in the amazon. In N. Sanz (Ed.), *Tropical Forest conservation: Integration natural and cultural diversity for sustainability. A global perspective* (pp. 150–178). UNESCO.
- Fleming, T. H., Breitwisch, R., & Whitesides, G. H. (1987). Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics*, 18(1), 91–109.
- Galindo-González, J., Guevara, S., & Sosa, V. J. (2000). Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rain forest. *Conservation Biology*, 14, 1693–1703.
- Galluzzi, G., Eyzaguirre, P., & Negri, V. (2010). Home gardens: Neglected hotspots of agro-biodiversity and cultural diversity. *Biodiversity and Conservation*, 19(13), 3635–3654.
- González-Insuasti, M. F., & Caballero, J. (2007). Managing plant resources: How intensive can it be? *Human Ecology*, 35(3), 303–314.
- González-Iturbide, J. A., Olmstead, I., & Tun-Dzul, F. (2012). Tropical dry Forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in Northern Yucatan, Mexico. *Forest Ecology and Management*, 167, 67–82.
- González-Varo, J. P., Carvalho, C. S., Arroyo, J. M., & Jordano, P. (2017). Unravelling seed dispersal through fragmented landscapes: Frugivore species operate unevenly as mobile links. *Molecular Ecology*, 26(16), 4309–4321.
- Guevara, S., Purata, S. E., & van der Maarel, E. (1986). The role of remnant forest trees in tropical secondary succession. *Vegetatio*, 66, 77–84.
- Herrera, C. M. (2002). Seed dispersal by vertebrates. In C. M. Herrera & O. Pellmyr (Eds.), *Plant-animal interactions: An evolutionary approach* (pp. 175–208). Blackwell Science.
- Herrera, J. M., & García, D. (2009). The role of remnant trees in seed dispersal through the matrix: Being alone is not always so sad. *Biological Conservation*, 142(1), 149–158.
- Holl, K. D. (1998). Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? *Restoration Ecology*, 6(3), 253–261.
- Holl, K. D. (1999). Factors limiting tropical rain forest regeneration in abandoned pasture: Seed rain, seed germination, microclimate, and soil. *Biotropica*, 31(2), 229–242.
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13(1), 201–228.
- Idohou, R., Fondohan, B., Salako, V. K., Kassa, B., Gbédomon, R. C., Yédomonhan, H., Kakaï, R. L. G., & Assogbadjo, A. P. (2014). Biodiversity conservation in homegardens: Traditional knowledge, use patterns and implications for management. *International Journal of Biodiversity Science, Ecosystem Services & Management*, 10, 89–100.
- Jules, E. S., & Shahani, P. (2003). A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. *Journal of Vegetation Science*, 14(3), 459–464.
- Kumar, B. M., & Nair, P. K. R. (2006). Introduction. In B. M. Kumar & P. K. R. Nair (Eds.), *Tropical homegardens. Advances in agroforestry* (pp. 1–10). Springer.
- Kupfer, J. A., Malanson, G. P., & Franklin, S. B. (2006). Not seeing the ocean for the islands: The mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*, 15(1), 8–20.
- Labatore, A. C., Spiering, D. J., Potts, D. L., & Warren, I. I., R. J. (2017). Canopy trees in an urban landscape-viable forests or long-lived gardens? *Urban Ecosystems*, 20(2), 393–401.
- Laborde, J., Guevara, S., & Sánchez-Ríos, G. (2008). Tree and shrub seed dispersal in pastures: The importance of rainforest trees outside forest fragments. *Écoscience*, 15(1), 6–16.
- López-Toledo, L., & Martínez-Ramos, M. (2011). The soil seed bank in abandoned tropical pastures: Source of regeneration or invasion? *Revista Mexicana de Biodiversidad*, 82(2), 663–678.
- Mantia, T. L., Rül, J., Massa, B., Pipitone, S., Lo Verde, G., & Bueno, R. S. (2019). Vertebrate-mediated seed rain and artificial perches contribute to overcome seed dispersal limitation in a Mediterranean old field. *Restoration Ecology*, 27, 1393–1400.
- Morán-López, T., Carlo, T. A., & Morales, J. M. (2018). The role of frugivory in plant diversity maintenance—A simulation approach. *Ecography*, 41(1), 24–31.

- Norden, N., Chazdon, R. L., Chao, A., Jiang, Y. H., & Vilchez-Alvarado, B. (2009). Resilience of tropical rain forests: Tree community reassembly in secondary forests. *Ecology Letters*, *12*(5), 385–394.
- Ordóñez, M. J. (2018). *Atlas biocultural de huertos familiares en México: Chiapas, Hidalgo, Oaxaca, Veracruz y Península de Yucatán* (430 pp.). UNAM, CRIM.
- Perini, M., Dias, E. M., & Kunz, S. H. (2019). The role of environmental heterogeneity in the seed rain pattern. *Floresta e Ambiente*, *26*(spe1), e20180406.
- Piña-Rodríguez, F. C. M., & Aoki, J. (2014). Seed rain as indicator of forest fragment conservation in Sorocaba, São Paulo state. *Ciencia Forestal Santa Maria*, *24*, 911–923.
- Preciado-Benítez, O., Gómez y Gómez, B., Navarrete-Gutiérrez, D. A., & Horváth, A. (2015). The use of commercial fruits as attraction agents may increase the seed dispersal by bats to degraded areas in Southern Mexico. *Tropical Conservation Science*, *8*(2), 301–317.
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. www.R-project.org/
- Reid, J. L., Holl, K. D., & Zahawi, R. A. (2015). Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications*, *25*(4), 1072–1082.
- Rico-Gray, V., García-Franco, J. G., Chemas, A., Puch, A., & Sima, P. (1990). Species composition, similarity and structure of Maya homegardens in Texpeul and Tixcacatuyub, Yucatán, México. *Economic Botany*, *44*(4), 470–487.
- Rival, L., & McKey, D. (2008). Domestication and diversity in manioc (*Manihot esculenta* Crantz ssp. *esculenta*, Euphorbiaceae). *Current Anthropology*, *49*(6), 1119–1125.
- Runkle, J. R. (1985). Disturbance regimes in temperate forests. In: S. T. A. Pickett & P. S. White (Eds.), *The ecology of natural disturbance and patch dynamics* (pp. 17–34). Academic Press.
- Salinas-Peba, L., & Parra-Tabla, V. (2007). Phenology and pollination of *Manilkara zapota* in forest and homegardens. *Forest Ecology and Management*, *248*(3), 136–142.
- San-José, M., Arroyo-Rodríguez, V., Jordano, P., Meave, J. A., & Martínez-Ramos, M. (2019). The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor. *Landscape Ecology*, *34*(5), 1069–1080.
- Secretaría de Desarrollo Social. (2018). *Catálogo de microrregiones*. www.microrregiones.gob.mx/catloc/contenido.aspx?refnac=310450002.
- Vespa, N. I., Zurita, G. A., Gatti, G., & Bellocq, M. I. (2018). Seed movement between the native forest and monoculture tree plantations in the Southern Atlantic Forest: A functional approach. *Forest Ecology and Management*, *430*, 126–133.
- Vespa, N. I., Zurita, G., & Bellocq, M. I. (2014). Functional responses to edge effects: Seed dispersal in the Southern Atlantic Forest, Argentina. *Forest Ecology and Management*, *328*, 310–318.
- Villanueva-Mukul, E. (2012). *Yucatán: Historia y cultura henequenera* (417 pp.). Secretaría de la Cultura y las Artes.
- Webb, E. L., & Kabir, E. (2009). Homegardening for tropical biodiversity conservation. *Conservation Biology*, *23*(6), 1641–1644.
- Zimmerman, J. K., Pascarella, J. B., & Aide, T. M. (2000). Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology*, *8*(4), 350–360.