BIOTROPICA 43(2): 141–148 2011 10.1111/j.1744-7429.2010.00666.x

BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

Ancient Maya Agroforestry Echoing Through Spatial Relationships in the Extant Forest of NW Belize

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ABSTRACT

Previous research has shown that ancient Maya 'forest gardens'—tree-dominated home gardens containing a diversity of tree species used for daily household needs—still resonate in the species composition of the modern forest. Centuries of positive interspecies interactions may enhance the reproductive and survival success of garden species selected and encouraged by experienced Maya forest gardeners. We hypothesized that such interaction may result in aggregated spatial patterns between 32 pre-selected, commonly utilized forest garden species. In this paper, we developed a novel randomization (Monte Carlo) method designed to measure and test if the spatial relationships among pairs of Maya 'forest garden' trees species differ between areas that experienced high and low ancient settlement density in northwestern Belize. A total of 28 high ancient settlement density and 27 low ancient settlement density plots containing a total of 2772 and 3134 trees, respectively, were used for this study. The analysis revealed that 58 pairs of forest garden species tended to 'cluster' together significantly more often in the high settlement density areas than would be expected in a random distribution. In low settlement density plots, only 12 pairs of species exhibited a significant clustered spatial relationship. The effect was not species specific, suggesting that some synergistic relationships, mediated by third-party agents such as dispersers, may occur at the community level. The impacts of ancient human land use, echoing across centuries of dispersal, colonization, disturbance, and biotic and abiotic interactions, can have important implications for understanding the current biodiversity patterns and processes.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: ancient land use; Maya; Monte Carlo; pairwise distances; synergisms; tropical forest community dynamics.

EFFECTS OF ANCIENT HUMAN ACTIONS ON EXTANT ECOSYSTEMS have recently been the focus of increased attention in the ecological literature (Balée & Erickson 2006, Dambrine *et al.* 2007, Heckenberger *et al.* 2007). The impacts of these actions, echoing across centuries of dispersal, colonization, disturbance, and biotic and abiotic interactions, can have important implications for understanding the current biodiversity patterns and processes (Chazdon *et al.* 2009) as well as providing lessons useful to conservation biodiversity. A recent study in Belize identified a persistent localized signal of ancient silviculture in the modern forest (Ross, in press). Previous research had suggested that the ancient Maya had permanently altered much of the Mesoamerican forest (Gomez-Pompa & Kaus 1990, Campbell *et al.* 2006a). Ross (in press) identified a localized signal of ancient 'forest gardens'—tree-dominated home gardens providing the Maya with food, medicines, tools, as well as spiritual and cultural services—where the species composition around ancient residential areas still reflects a higher abundance of forest garden species than forest with no evidence of ancient settlement.

The ancient Maya forest gardens, filled with a diversity of tree species and imitating the multi-level canopy structure of the natural forest, experienced intensive management throughout the millennia of Maya settlement in the area. The Maya cultural collapse at the end of the first millennium AD resulted in significant population reductions which, in turn, led to the virtual abandonment of the majority of forest gardens (deMenocal 2001). The extensive time period since the collapse of the Maya Classic Period populations (*ca* AD 1000), and the subsequent abandonment of the urban centers, would lead one to reasonably suspect that centuries of natural seed dispersal would eliminate any localized correlation between ancient forest garden sites and distribution of garden trees. Despite centuries of abandonment of the forest gardens, however, species composition at areas of high ancient settlement density (HSD) still carry a detectable signal of human management in the forest tree community, with a higher abundance of many commonly utilized forest garden tree species (Ross, in press). Conversely, using the nonparametric analysis of similarities (ANOSIM) test, Ross (in press) found that areas where there is little or no evidence of ancient settlement (low settlement density, LSD) have a significantly different species composition. HSD and LSD areas were found to show no significant edaphic or vegetation structure differences. The search for an explanation for the apparent long-term persistence of the forest garden species community led us to enquire whether pairs of garden tree species are spatially associated.

The question of spatial patterns in tropical forests has been a major ecological question because Wallace (1878) first noticed how the high diversity was associated with low densities of each species in a given area. Since that time, several theories have been proposed and tested to explain this pattern including the Janzen–Connell hypothesis (Janzen 1970, Connell 1971) and Hubbell's neutral theory (Hubbell 2001). These theories, however, are primarily focused on spatial patterns within individual species instead of patterns in the spatial association between pairs of different species, essentially viewing species as independent of one another. Notable exceptions are Simberloff and Connor (1981), who studied the differences in species composition between islands in an archipelago, Hubbell and Foster (1986), who looked at the role of chance and uncertainty in structuring tropical forest communities, and Lieberman

Received 10 September 2009; revision accepted 25 April 2010.

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and Lieberman (2007), who studied the relationships between nearest neighbors. The conclusions of these papers supported the idea that species are arranged independently of one another. As we show, the results from Belize run counter to this idea leading to the question: what ecological mechanism could explain the long-term persistence of the forest garden tree community composition?

The analysis of interspecies spatial relationships has often been limited to 'nearest-neighbor' relationships on the assumption that relationships between tree species would be limited by the ability of the trees to directly affect their physical surroundings (Lieberman & Lieberman 2007; for an exception, see Hubbell & Foster 1986). Spatial relationships, however, can extend beyond the physiological interaction with only the nearest neighbor. For example, due to variations in species composition, changes in pollinator or disperser behavior may impact spatial relationships between species (Fleming *et al.* 1977).

Taking a first step to investigate possible ecological interactions or relationships between pairs of species, we looked at the spatial relationships between species in the ancient forest garden areas and compared them with the forest matrix. The main hypothesis is that forest garden species grow in a more spatially 'clustered' pattern within areas of high ancient Maya settlement density (HSD) than expected by chance alone. While clustering does not directly imply a positive ecological interaction (*i.e.*, a synergism), centuries of positive interspecies interactions may enhance the reproductive and survival success of garden species selected and encouraged by experienced Maya forest gardeners. We hypothesized that such interaction may result in aggregated spatial patterns between forest garden species.

METHODS

A set of 400 m^2 (20×20 m) plots was established within forest containing a high density of ancient Maya residential structures (>100 archeological structures per km^2, HSD). This forest was protected within the El Pilar Archaeological Reserve for Maya Flora and Fauna (http://www.marc.ucsb.edu/elpilar). El Pilar lies within the Subtropical Moist Forest Life Zone (Holdridge *et al.* 1971). The natural vegetation is seasonal rain forest of deciduous broadleaf tree species covering limestone ridges (Wright *et al.* 1959). The reserve actually stretches across the Belize–Guatemala border within the eastern Petén rain forest (Campbell *et al.* 2006a; Fig. S1). A corresponding set of plots were established in and around the reserve in similar forest areas with little or no sign of ancient settlement (LSD) as determined in previous archeological examinations of the area (A. Ford, pers. comm.). A total of 28 HSD plots and 27 LSD plots were used for this study containing a total of 2772 and 3134 trees, respectively. Tests that looked at soil mottling (as an indicator of soil drainage) showed no difference in drainage between HSD and LSD plots (Ross, in press). In all plots, all trees >2.5 cm diameter at breast height (dbh) were measured, identified, and permanently marked. Species names and authorities were assigned using Stevens *et al.* (2001) and Balick *et al.* (2000). Vouchers were deposited in the University of Connecticut herbarium and the Belize herbarium. For this study, 'tree' was defined as a woody species having a single main trunk in order to eliminate shrubs from the analysis.

Following the census, the *x*–*y* location of each tree was determined to identify the empirical distance between every pair of individuals in each plot. At the time each plot was established, they were oriented with the first leg running directly north–south. For the mapping, the corner of origin of every plot was chosen to be the southeastern corner. The *x*–*y* coordinates were determined by setting up meter tapes at each 5 m along the *x*-axis and physically measuring the location of each tree in relation to the *x* and *y* axes (represented by the meter tape at $x = 0$ m). HSD and LSD forest areas were approximately 4 km distant. Within both HSD and LSD forest areas, all individual plots were separated by >30 m.

To evaluate if a given pair of species tend to be randomly spaced, clustered, or segregated, the *x*–*y* coordinates of the geographical location of all individuals of the two species were used to calculate pairwise distances. Pairwise distances were broken into seven equally spaced distance classes within the plot: 0–4, 4–8, 8–12, 12–16, 16–20, 20–24, and 24–28 m. This was done to allow the use of the χ^2 test to test for variation from randomness. For each two species, the number of pairwise distances between individuals that fall into each distance class describes the spatial relationship between the species (Fig. S2). In this study, we evaluated spatial relationship among pairs of 32 species (Table S1). Species pairs with <10 individual pairs were eliminated from the analysis. For each pair of species and each distance class, within each respective settlement density plot group (HSD or LSD), the number of pairs of individuals was summed across plots.

The observed spatial relationship between each pair of species was contrasted against the null expectation of full randomness in the geographical position of the individuals of each species. A null expectation of full randomness would be unrealistic within a species; yet if spatial patterning between species is determined by chance rather than biotic interactions (as per Hubbell 1979), then randomness is the logical null expectation. The null expectation was calculated using a computer-aided Monte Carlo procedure, which consisted of randomly assigning geographical position within a virtual 20×20 m plot. The number of individuals of each species was kept the same as in the observed data, for each plot. After randomizing the position of the individuals across all plots, the number of pairwise distances between individuals falling within each distance class was calculated. The procedure was replicated 5000 times, and the average number of pairwise distance between individuals, within each distance class, was calculated. Because of geometric shape of the plot, the probability of individuals being at intermediate distance apart is higher than the maximum distance within the plot (the maximum distance is 28.3 m, the hypotenuse of an isosceles triangle with 20 m legs). The Monte Carlo randomization approach used here, however, accounts for the geometric constraint in pairwise distances within the plot, because the shape and the area of observed and expected plots are the same. Also, it controls for unbalanced abundances between species, because the null expectation is calculated using the observed number of individuals. Finally, because not all species were present in all plots, it was not possible to directly analyze spatial relationships between most species pairs.

The null hypothesis was that the observed number of pairwise distances between individuals in the distance classes would not

1. Mostly fleshy and non-fleshy fruits
2. Seed size

differ significantly from the one calculated after randomizing the spatial position of the individuals. This hypothesis can be tested using a χ^2 test: $\chi^2 = \sum_{i=1}^{n} \frac{(\mathbf{o}_i - \mathbf{e}_i)^2}{\mathbf{e}_i}$, where χ^2 is the calculated chi square, i denotes a distance class, n is the number of distance classes, and $\mathbf{o}$ and $\mathbf{e}$ are, respectively, the vectors of observed and expected number of pairwise distances between individuals in each distance class. The P-value for χ^2 can be found using a χ^2 distribution with $n - 1$ degrees of freedom. Conservatively, α was set at 0.01, which means that a Type I error of 1 percent is considered acceptable. Thus, P-values > 0.01 denote random placement of individuals of a species in relation to another species. If the spatial relationship between a pair of species is significantly different from the null expectation ($P < 0.01$), we looked at the distribution of pairwise distance across distance classes to identify two possible spatial patterns: (1) 'clustered', pairs of individuals tend to be significantly closer together than was expected by chance alone and (2) 'segregated', pairs of individuals tend to be significantly farther apart than expected by chance alone. Clustered relationships were investigated using two different criteria levels. The relationship is considered clustered if the *observed* number of pairwise distances between individuals, summed across the first two distance classes (0–4 and 4–8 m), is larger than in the *expected* number of pairwise distances between individuals in the same first two distance classes; or the observed number of pairwise distances between individuals in the first two distance classes is at least 10 percent larger than in the expected number of pairwise distances. The second test is more conservative and designed to test the strength of the clustered relationship. A relationship was considered segregated if the observed number of pairwise distances between individuals in the first distance class ($0 - 4$ m) was > 50 percent less than expected by chance alone. This test was determined using the simulated results of the randomization method (Fig. S2).

In all plots, a total of 171 species were encountered. To identify the species of interest, we used previous ethnobotanical literature (Turner & Miksicek 1984, Lentz 1991, Rico-Grey *et al.* 1991, Lentz *et al.* 1996, Campbell *et al.* 2006b), from which a total of 32 tree species commonly utilized in ancient Maya forest gardens were pre-selected as 'garden' species (Table S1). The randomization algorithm was not, however, applied to all possible 992 pairs of these species because not all species were sufficiently abundant in all plots. In HSD plots, 22 species were included for a total of 462 possible species pairs. In LSD plots, 21 tree species were included in the analysis for a total of 420 possible species pairs.

RESULTS

For the analysis of species–species spatial relationships discussed in this paper, the meaningful unit of analysis is a pair of species, with the individual trees of each species being used to generate replicates of species pairs. Of the 30 species tested, 22 were members of at least one spatially significant clustered species pair (Table 1). The 22 species belong to 16 different families and were utilized by ancient Maya forest gardeners for a variety of services such as food, medicine, construction materials, and ritual/cultural uses (Table 1). The life-form of these species range from canopy emergents (*e.g.*, *Alseis yucatanensis*) to understory treelets (*e.g.*, *Piper amalago*) and do not cluster based on life-form characteristics.

TABLE 1. *Forest garden species that are members of at least one clustered species pair in either HSD or LSD forest. Also included are the families each species belongs to and reported uses (Balick* et al. *2000).*

Species	Family	Uses
Alseis yucatanensis	Rubiaceae	Wood
Aspidosperma spruceanum	Apocynaceae	Construction, medicine
Attalea cohune	Arecaceae	Food, construction, medicine
Bursera simaruba	Burseraceae	Medicine, ritual
Caesalpinia sp.	Caesalpiniaceae	Medicine, ritual
Cryosophila stauracantha	Arecaceae	Construction, medicine
Cupania belizensis	Sapindaceae	Fuel, medicine, food, construction
Dendropanax arboreus	Araliaceae	Food, ornamental, forage, medicine
Hamelia axillaris	Rubiaceae	Medicine
Lacistema aggregatum	Lacistemataceae	Construction, medicine
Malmea depressa	Annonaceae	Food, medicine
Manilkara zapota	Sapotaceae	Food, medicine, latex
Piper amalago	Piperaceae	Medicine
Pouteria campechiana	Sapotaceae	Food
Protium copal	Burseraceae	Ritual
Pseudolmedia spuria	Moraceae	Food
Psychotria chiapensis	Rubiaceae	Medicine
Sabal morrisiana	Arecaceae	Construction
Spondias radlkoferi	Anacardiaceae	Medicine, construction, food
Terminalia amazonia	Combretaceae	Construction
Vitex gaumeri	Verbenaceae	Ornamental, fuel, forage, construction
Zuelania guidonia	Flacourtiaceae	Fuel, medicine, food, forage, resin

To look at differences in clustering patterns between HSD and LSD forests, we first applied criterion 'a', under which clustering is determined by the number of *observed* pairwise distances from distances classes 1 and 2 being greater than the *expected* number of pairwise distances (by any amount). Within HSD forest, 58 pairs of forest garden species show clustered spatial relationship (Fig. 1A). Within LSD forest, on testing the same set of Maya forest garden species, only 12 pairs of species tended to cluster (Fig. 1B).

Certain species were more likely to be a member of a pairwise cluster. In HSD plots, the species that was a member of the greatest number of clustered pairs (12) was *Dendropanax arboreus* (Araliaceae). *Zuelania guidonia* (Flacourtiaceae), *Aspidosperma spruceanum* (Apocynaceae), *Cryosophila stauracantha* (Arecaceae), and *Cupania belizensis* (Sapindaceae) were members of 11 clustered species pairs. *Hamelia axillaris* (Rubiaceae) is a member of nine clustered pairs. *Pseudolmedia spuria* (Moraceae) and *Pouteria campechiana* (Sapotaceae) are members of eight pairs each and *Lacistema aggregatum* (Lacistemataceae) is found in seven pairs. The other species are members of five or fewer pairs with *Psychotria chiapensis* (Rubiaceae), *Bursera simaruba* (Burseraceae) and *Protium copal* (Burseraceae) being found in no clustered species pairs in

They tested whether garden species are more frequently
clustered in former gardens than in other areas.

Use Fst statistics treating species as alleles,
measuring species dispersal (allele migration)
within vs. among communities (populations)

A HSD

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Pseuspur																					
2	Attacohu																					
3	Alseyuca																					
4	Laciaggr																					
5	Malmdepr	-	-	-	-	-																
6	Manizapc	-	-	-	-	-																
7	Protcopa					-	-															
8	Poutcamp	C			C	-	-															
9	Psycchia					-	-															
10	Caessp.					-	-															
11	Zuelguid	C	C	C	C	-	-				C											
12	Hameaxil	C	C	C	C	-	-		C		C	C										
13	Sponradl					-	-															
14	Vitegaum					-	-					C										
15	Aspispru	C	C		C	-	-		C		C	C	C									
16	Sabamorr					-	-					C	C									
17	Burssima					-	-															
18	Termamaz					-	-															
19	Dendarbc	C	C	C	C	-	-		C			C	C	C	C	C						
20	Cryostau	C			C	-	-		C		C	C	C			C			C	C		
21	Pipeamal	C				-	-		C							C					C	
22	Cupabeli	C	C	C	C	-	-		C		C	C	C			C				C	C	

how do these patterns vary w size structure

B LSD

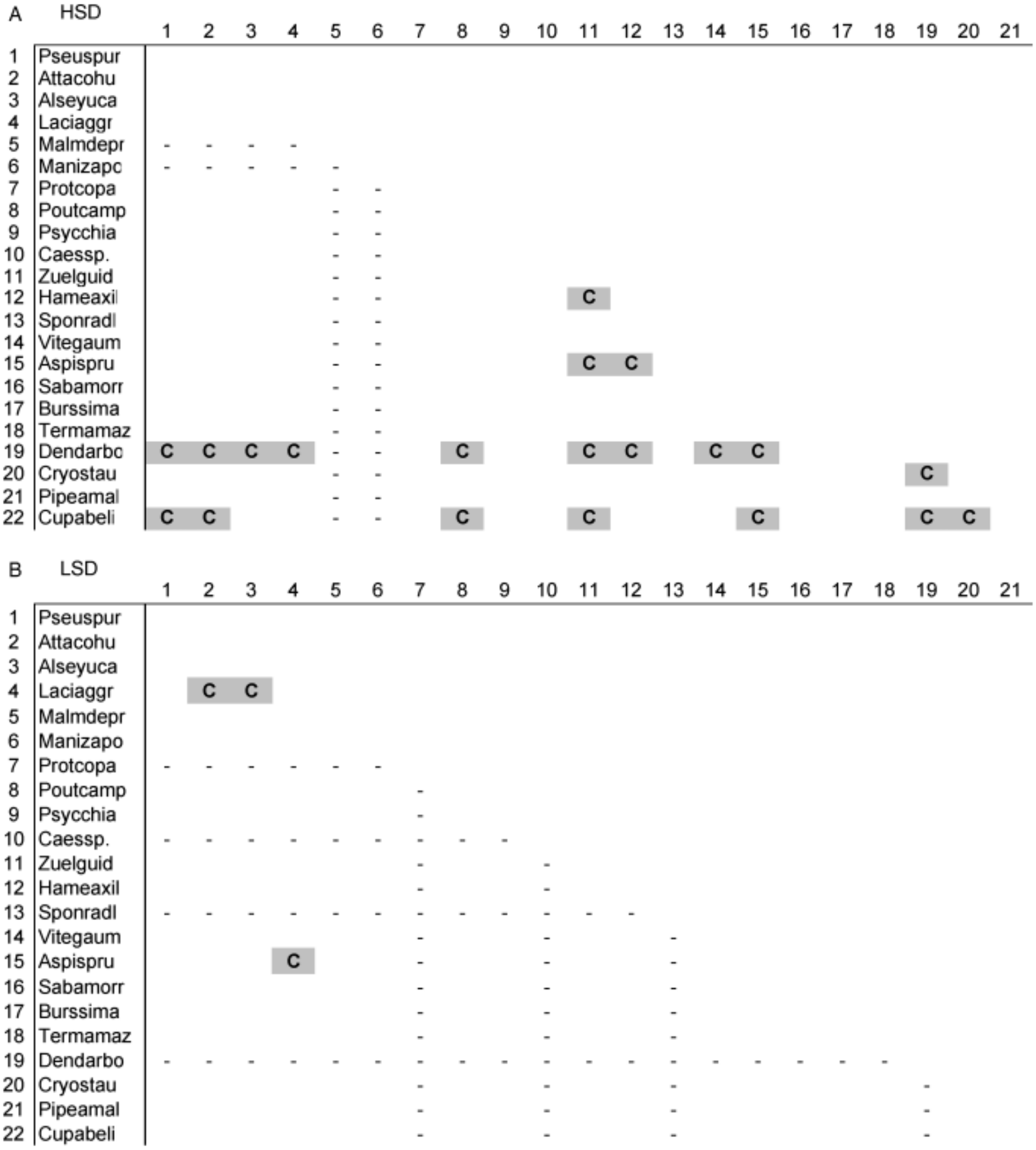
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Pseuspur																					
2	Attacohu																					
3	Alseyuca																					
4	Laciaggr	C	C	C																		
5	Malmdepr																					
6	Manizapo																					
7	Protcopa	-	-	-	-	-	-															
8	Poutcamp							-														
9	Psycchia					C		-														
10	Caessp.	-	-	-	-	-	-	-	-	-												
11	Zuelguid							-			-											
12	Hameaxil							-			-											
13	Sponradl	-	-	-	-	-	-	-	-	-	-	-	-									
14	Vitegaum							-			-			-								
15	Aspispru			C	C			-			-			-								
16	Sabamorr		C					-			-			-								
17	Burssima						C	-			-			-								
18	Termamaz							-			-			-								
19	Dendarbo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
20	Cryostau		C		C			-			-			-			C	C		-		
21	Pipeamal							-			-			-						-		
22	Cupabeli							-			-			-						-		

Why would a pair be clustered in HSD but not in LSD?
What would be the “community effect” mechanism?

FIGURE 1. Matrices showing the spatially clustered forest garden species pairs identified under criterion ‘a’ in both (A) HSD plots and (B) LSD plots. ‘Clustered’ means the observed number of pairwise distances in the first two distance classes is larger than the expected number of pairwise distances. For clarity, species not a member of any clustered species pair (HSD or LSD) are not included in the table. C, clustered; –, insufficient data; 1, *Pseudolmedia spuria*; 2, *Attalea cohune*; 3, *Alseis yucatanensis*; 4, *Lacistema aggregatum*; 5, *Malmea depressa*; 6, *Manilkara zapota*; 7, *Protium copal*; 8, *Pouteria campechiana*; 9, *Psychotria chiapensis*; 10, *Caesalpinia* sp.; 11, *Zuelania guidonia*; 12, *Hamelia axillaris*; 13, *Spondias radlkoferi*; 14, *Vitex gaumeri*; 15, *Aspidosperma spruceanum*; 16, *Sabal morrisiana*; 17, *Bursera simaruba*; 18, *Terminalia amazonia*; 19, *Dendropanax arboreus*; 20, *Cryosophila stauracantha*; 21, *Piper amalago*; 22, *Cupania belizensis*.

HSD plots. In LSD plots, *B. simaruba* is a member of two clustered pairs with *Manilkara zapota* (Sapotaceae) and *C. stauracantha* while *P. chiapensis* clusters with *Malmea depressa* (Annonaceae). Unfortunately, *M. zapota* and *M. depressa* have too few individuals in HSD plots to include in the analysis, and *P. copal* is also too rare in LSD areas for testing. Interestingly, only two of the 12 species pairs from LSD areas coincided with pairs from the HSD forest plots, *L. aggregatum*/*A. spruceanum* and *L. aggregatum*/*C. stauracantha*. In LSD plots, the species belonging to the greatest number of clustered pairs was *L. aggregatum* (five pairs). Segregated relationships were not found in either HSD or LSD areas.

The randomization method was ran a second time using a more conservative criterion ‘b’, under which the relationship is considered clustered if the observed number of pairwise distances in the first two distance classes (0–4 and 4–8 m) is at least 10 percent larger than in the expected number of pairwise distances in those same two distance classes. In HSD, this test revealed 20 clustered pairs (Fig. 2A) while in LSD, the number of clustered



A HSD

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Pseuspur																					
2	Attacohu																					
3	Alseyuca																					
4	Laciaggr																					
5	Malmdepr	-	-	-	-																	
6	Manizapo	-	-	-	-	-																
7	Protcopa					-	-															
8	Poutcamp					-	-															
9	Psycchia					-	-															
10	Caessp.					-	-															
11	Zuelguid					-	-															
12	Hameaxil					-	-					C										
13	Sponradl					-	-															
14	Vitegaum					-	-															
15	Aspispru					-	-					C	C									
16	Sabamorr					-	-															
17	Burssima					-	-															
18	Termamaz					-	-															
19	Dendarbo	C	C	C	C	-	-		C			C	C		C	C						
20	Cryostau					-	-													C		
21	Pipeamal					-	-															
22	Cupabeli	C	C			-	-		C			C				C				C	C	

B LSD

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Pseuspur																					
2	Attacohu																					
3	Alseyuca																					
4	Laciaggr		C	C																		
5	Malmdepr																					
6	Manizapo																					
7	Protcopa	-	-	-	-	-	-															
8	Poutcamp							-														
9	Psycchia							-														
10	Caessp.	-	-	-	-	-	-	-	-	-												
11	Zuelguid							-			-											
12	Hameaxil							-			-											
13	Sponradl	-	-	-	-	-	-	-	-	-	-	-	-									
14	Vitegaum							-			-			-								
15	Aspispru				C			-			-			-								
16	Sabamorr							-			-			-								
17	Burssima							-			-			-								
18	Termamaz							-			-			-								
19	Dendarbo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
20	Cryostau							-			-			-						-		
21	Pipeamal							-			-			-						-		
22	Cupabeli							-			-			-						-		

FIGURE 2. Matrices showing the spatially clustered forest garden species pairs in (A) HSD plots and (B) LSD plots identified under criterion 'b'. 'Clustered' means the observed number of pairwise distances in the first two distance classes is ≥ 10 percent larger than the expected number of pairwise distances (criterion b). For clarity, species not a member of any clustered species pair (HSD or LSD) are not included in the table. C, clustered; –, insufficient data 1, *Pseudolmedia spuria*; 2, *Attalea cohune*; 3, *Alseis yucatanensis*; 4, *Lacistema aggregatum*; 5, *Malmea depressa*; 6, *Manilkara zapota*; 7, *Protium copal*; 8, *Pouteria campechiana*; 9, *Psychotria chiapensis*; 10, *Caesalpinia* sp.; 11, *Zuelania guidonia*; 12, *Hamelia axillaris*; 13, *Spondias radlkoferi*; 14, *Vitex gaumeri*; 15, *Aspidosperma spruceanum*; 16, *Sabal morrisiana*; 17, *Bursera simaruba*; 18, *Terminalia amazonia*; 19, *Dendropanax arboreus*; 20, *Cryosophila stauracantha*; 21, *Piper amalago*; 22, *Cupania belizensis.*

pairs dropped to only three (Fig. 2B). All the three LSD clustered pairs include *L. aggregatum*, but none of these pairs are found in the 20 HSD pairs. There are no shared clustered species pairs between HSD and LSD plots under criterion b.

In HSD plots under criterion b, *D. arboreus* is again the species with the greatest number (11) of pairwise clusters. On application of the more strict definition of clustered, only the pair *D. arboreus*/*Spondias radlkoferi* was eliminated from the previous list of clustered pairs which included *D. arboreus*. In contrast, *Caesalpinia* sp. is not represented in a single clustered pair in HSD using criterion b (Fig. 2). *Cupania belizensis* is still represented in seven clustered pairs. *Zuelania guidonia* and *A. spruceanum* are members of four clustered pairs each. *Hamelia axillaris*, *C. stauracantha*, and *P. campechiana* complete the HSD clustered pairs with two pairs each. As previously, no segregated relationships were identified.

DISCUSSION

Within a diverse tropical forest, chance and uncertainty have been found to exert a profound influence on species composition such that 'evolution will reflect the temporal and spatial average of the selective conditions created by a suite of ever changing and diffuse competitors' (Hubbell & Foster 1986). This leads to the mosaic theory of species composition with composition continually shifting over time (Watt 1947, Chazdon & Denslow 2002). Hubbell and Foster (1986) suggested that the effect of unpredictability in biotic neighborhoods could have profound influence on the nature of selection and the resulting species composition of tropical forest communities. In the case of forest gardens, however, the long-term intensive management by the Maya controlled the suite of available 'competitors', limiting the power of chance. After nearly a millennium of abandonment, despite the sporadic disturbances and environmental fluctuations that affect tropical forests, many forest garden species display a nonrandom spatial relationship around ancient forest garden sites. This is not to suggest that the Maya altered the evolutionary relationships between species, but rather that they may have, unknowingly or not, exploited already existing niche relationships that allowed for heightened facilitative interactions within forest garden communities.

Modern Maya forest gardens exhibit a high diversity of species because farmers, both modern and ancient, work to maximize the utility of their gardens (Campbell *et al.* 2006b). Altieri and Nicholls (1999) suggest that creating a functionally diverse agroecosystem can initiate synergistic relationships that would provide ecological services such as pollinator or disperser fidelity or nutrient recycling. The ancient Maya may not have known the mechanism behind such positive interspecific relationships, but centuries of familiarity would have allowed them to recognize that such species grow better together than apart. Agroecology strategy exploits the complementarities and synergisms that result from various combinations of crops, tree, and animals in spatial and temporal arrangements (Anderson 1952, Altieri 1994). Future ethnobiological research with modern Maya forest gardeners investigating their perceptions of interorganism and interspecies relationships could help us to bring this idea beyond mere speculation and give us an intriguing new perspective on how human cultures and ecosystems interact.

Researchers have found the impacts of Maya land use and management throughout the Mesoamerican forest. Beyond forest gardens, the Maya would have impacted other areas through hunting, medicinal plant harvesting, and myriad other land uses. The dominance of Maya useful species in the contemporary forest has led to the perception of the Mesoamerican forest as a 'feral garden' (Campbell *et al.* 2006a, Ford 2008). Post-colonial land use has also been found to have impacted the species composition of the extant forest. Campbell *et al.* (2008) investigated the role of remnant shade trees left standing in land cleared for pastures during the post-colonial period. Analysis supported the theory that, in addition to forest gardens, these feral pastures also influenced the development of the modern forest, further emphasizing the long-term effects of human land use. The results of the study herein, however, looked within this feral forest and found that pre-colonial forest gardening may have an even stronger influence on forest development, allowing the garden communities to persist partially independent from the forest surrounding them.

As has been mentioned previously in the literature, either environmental variations or species interactions could result in species distributions diverging from randomness (Simberloff & Connor 1981). The edaphic and vegetation structure analyses performed on the plots included in this study suggest that environmental variations are not a significant factor in this study (Ross, in press); however, these analyses were conducted at the plot level. A more intensive, localized analysis of the soils could provide a different perspective. Lieberman and Lieberman (2007) state that interactions between species should result in 'substantial, systematic, and repeated departures from random mixing'. In ancient Maya forest garden areas (HSD plots) included in this study, the randomization method described above identified 58 pairs of species, 12.6 percent of all 462 possible species pairs. Compare this with the results for the LSD forest plots where only 12 species pairs, or 2.8 percent of all 420 possible pairs, exhibited a clustered relationship. These results could be due to significant interspecies interactions within the HSD forest area. Even using the more conservative definition of clustered described herein as criterion b, 20 clustered pairs were found, 4.3 percent of all possible species–species pairs, in HSD plots vs. only three species pairs (< 1% of possible pairs) in LSD. The consistent departure from randomness in the spatial arrangement of forest garden species in ancient high-density residential areas suggests that species interactions could be affecting the localized species compositions of the forest around El Pilar. To further investigate this, studies on growth rates and reproductive success, for example, on forest garden species under clustering and nonclustered conditions would be needed.

The negative results for segregated relationships may not be due to a real spatial pattern, but rather in difficulties on the definition of segregation. Initially, we attempted to arbitrarily define segregation by looking at increases in the observed pairwise distances in distance classes four (12–16 m) and five (16 – 20 m). Unfortunately, the results of this test were unreliable. Therefore, the results from the simulation (Fig. S2) were used to define segregation. The randomization method described in this paper should allow for the analysis of segregated relationships, but we need more data to calibrate the approach. A parameterization data set created using species known to have an over-dispersed relationship would provide a model to test the data against.

We attempted to assess intraspecies clustering using Ripley's K analysis (Ripley 1976). Unfortunately, despite the high diversity of the forest (a total of 171 species were identified in all plots), there were too few occurrences of individuals of each species in each plot. Therefore, we were unable to analyze intraspecies spatial distributions. To fully test segregated relationships, an experimental approach, perhaps utilizing larger plots that contain a sufficient number of individuals per species, designed to investigate spatial relationships in high diversity systems is needed.

Of course, other possible explanations beyond synergistic interactions exist for the patterns observed in this study. Because of the long life spans of many tropical forest tree species, the results could simply be due to the fact that there has not been enough time for random dispersal to eliminate the forest gardens completely. On the other hand, this area has experienced significant disturbance from hurricanes (such as Hurricane Hattie in 1961) that penetrated far inland (Friesner 1993). With such extreme disturbances occurring with some regularity, it can be argued that tree life spans alone would not be sufficient to explain the slow rate of change in species composition around former forest gardens. Fire has also been found to be a profound selective agent in tropical forests (Otterstrom *et al.* 2006). Several forest garden species have been found to be highly fire tolerant (*e.g.*, *Attalea cohune*, see Ivanauskas *et al.* 2003). Conversely, *Metopium browneii*, not a forest garden species, is also highly fire tolerant (Sánchez-Sánchez & Islebe 2002), yet is completely absent from ancient forest garden areas. Without research specifically investigating the question of fire in this area, fire as a selective agent cannot be ruled out, yet there is no evidence currently that fire has occurred consistently in either HSD or LSD areas and not in the other that could lead to consistent compositional differences.

The great diversity of species in tropical forests presents a common problem in spatial analysis in tropical forests. High species richness results in most possible species pairs never being found adjacent to one another (Lieberman & Lieberman 2007). Using the randomization method described in this paper, we were able to analyze distances between the majority of forest garden species pairs. The prevalence of clustered relationships between forest garden species in forest growing on ancient Maya residential lands where forest gardens were intensively managed for centuries provides a fascinating puzzle to be solved. Did the ancient Maya, in fact, learn to recognize synergistic relationships between useful tree species? If so, the data in this study suggest that these relationships are not primarily at the individual species level, but rather function as part of a group-level mechanism for community stability. Relationships between trees through direct chemical or physical alterations to their immediate environment (that extend little farther than their individual root systems) have been demonstrated (Janzen 1970); however, synergistic interactions between tree species mediated by third-party dispersal agents or pollinators could have even more significant impact than previously expected.

ACKNOWLEDGMENTS

We thank A. Ford for providing NJR access to the El Pilar Reserve. Field data collection was made possible by the work of L. Romero, H. Cocom, M. Manzanero, M. Humes, and I. Windsor. G. Anderson and R. L. Chazdon provided considerable experience in methodologies and analysis. Our thanks go to R. Colwell for analytical assistance and F. Coe and S. Letcher for help with voucher identification. We also thank the Belize Forestry Department, the Belize Institute of Archaeology, the Instituto de Antropología e Historia de Guatemala, D. G. Campbell, and C. Young. The text was greatly improved by the help of two anonymous reviewers and the subject editor, T. Gillespie. NJR is funded by the Society for Economic Botany, Garden Club of America, Center for Environmental Sciences and Engineering (University of Connecticut), Center for Conservation and Biodiversity (University of Connecticut), and the Ronald Bamford Endowment to the University of Connecticut Department of Ecology and Evolutionary Biology. TFR is funded by a CAPES/Fulbright fellowship and the University of Connecticut.

SUPPORTING INFORMATION

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

TABLE S1. *Maya forest garden species.*

FIGURE S1. Map showing the location of HSD (H) and LSD (L) experimental plots.

FIGURE S2. Simulated scenarios that illustrate: (A) random; (B) clustered; and (C) segregated species–species spatial relationships for two species.

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TABLE S1. *Maya forest garden species. Species had been previously identified as commonly utilized species in ethnobotanical literature (Turner & Miksicek 1984, Lentz 1991, Rico-Gray* et al. *1991, Lentz* et al. *1996, Campbell* et al. *2006a).*

'Garden' Species	Family	Common / Yucatec Maya name
Albizia niopoides	Mimosaceae	jesmo
Alseis yucatanensis	Rubiaceae	wild mamey
Annona primigenia	Annonaceae	wild custard apple
Aspidosperma spruceanum	Apocynaceae	my lady
Attalea cohune	Arecaceae	corozo
Brosimum alicastrum	Moraceae	ramón
Bursera simaruba	Burseraceae	gumbo limbo, cha-ca
Caesalpinia sp.	Caesalpiniaceae	warrie stick
Ceiba pentandra	Bombacaceae	kapok
Chrysophyllum mexicanum	Sapotaceae	wild star apple, tzik-i-ya
Cryosophila stauracantha	Arecaceae	give-and-take
Cupania belizensis	Sapindaceae	grandy betty, chac pom
Dendropanax arboreus	Araliaceae	lion's paw, mano de león
Hamelia axillaris	Rubiaceae	ix-canan, sac-te-much
Lacistema aggregatum	Lacistemataceae	wild coffee
Licania platypus	Chrysobalanaceae	succotz
Lonchocarpus castilloi	Fabaceae	black cabbage bark, man-chich
Malmea depressa	Annonaceae	sufrecaya
Manilkara zapota	Sapotaceae	chicle, chic ibul
Pimenta dioica	Myrtaceae	allspice
Piper amalago	Piperaceae	cordoncillo, queen of piper
Pouteria campechiana	Sapotaceae	sapotillo rojo
Protium copal	Burseraceae	copal, pomte
Prunus spp.	Rosaceae	john crow wood, shu-yuk

Pseudolmedia spuria	Moraceae	manax
Psychotria chiapensis	Rubiaceae	wild ix-canan
Sabal morrisiana	Arecaceae	botán
Spondias radlkoferi	Anacardiaceae	hog plum, rum-p'ok
Swietenia macrophylla	Meliaceae	mahogany
Terminalia amazonia	Combretaceae	nargusta, canxun
Vitex gaumeri	Verbenaceae	fiddlewood, yax nik
Zuelania guidonia	Flacourtiaceae	tamai

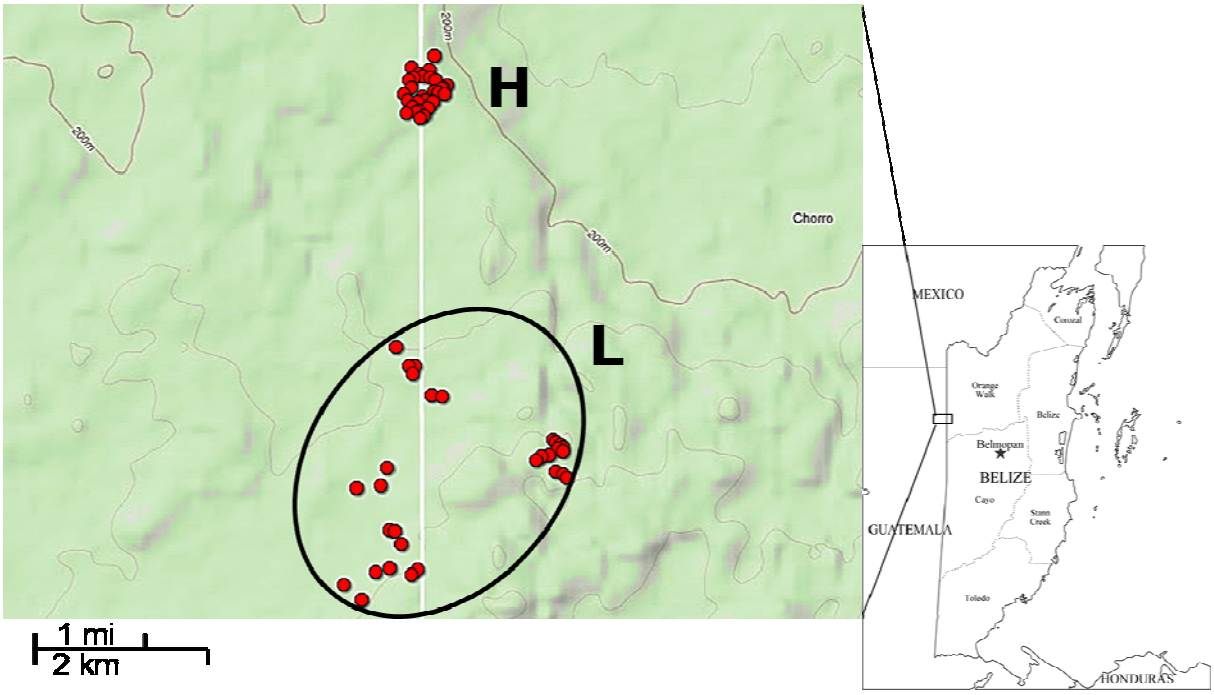

FIGURE S1. Map showing the location of HSD (H) and LSD (L) experimental plots. Map data ©2009 LeadDog Consulting, Europa Technologies.

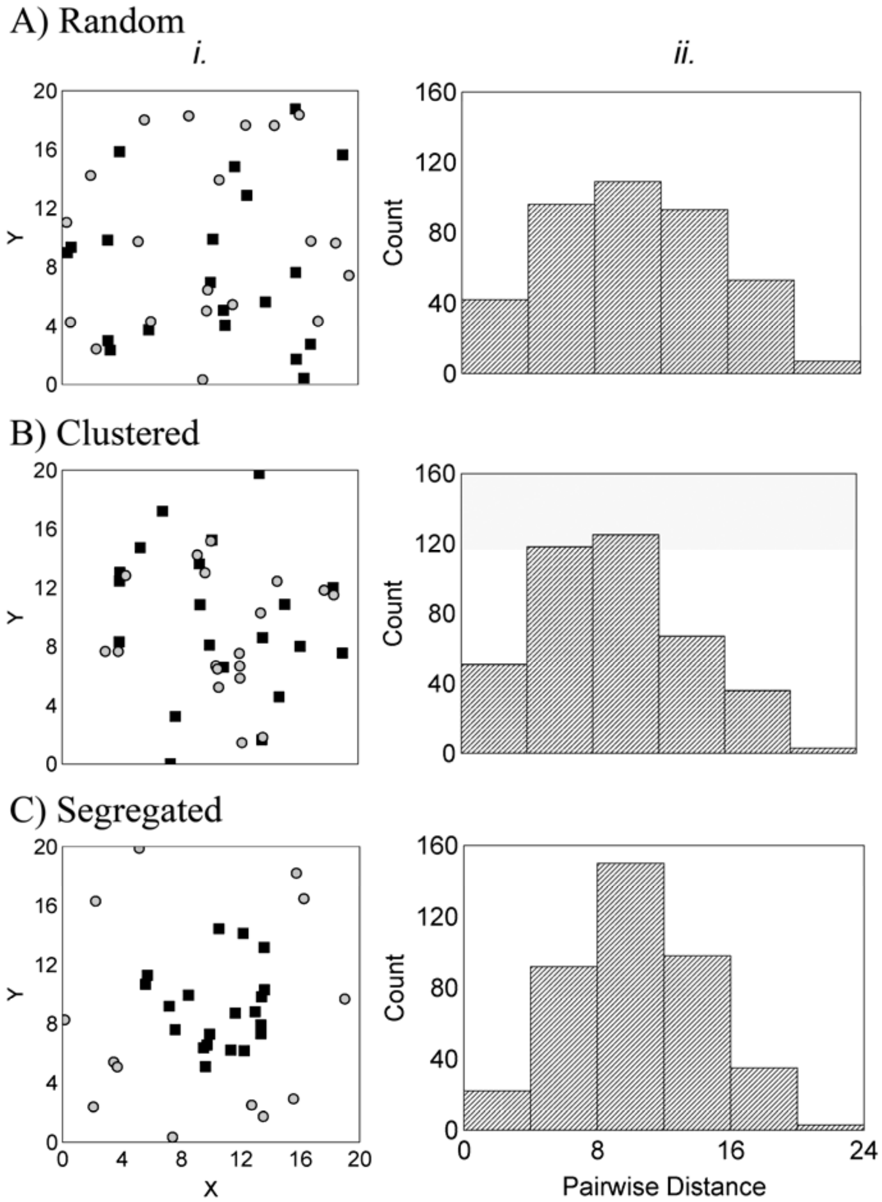

FIGURE S2. Simulated scenarios that illustrate: (A) random; (B) clustered; and (C) segregated species–species spatial relationships for two species. In column *i.* simulated maps of the relative positions of individuals of species 1 (squares) and species 2 (circles) are shown. Column *ii.* shows the distribution of potential square-circle pairs per each distance class.