Ecological Applications, 21(1), 2011, pp. 75–84

Modern tree species composition reflects ancient Maya "forest gardens" in northwest Belize

NANCI J. ROSS[1]

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269 USA

Abstract. Ecology and ethnobotany were integrated to assess the impact of ancient Maya tree-dominated home gardens (i.e., "forest gardens"), which contained a diversity of tree species used for daily household needs, on the modern tree species composition of a Mesoamerican forest. Researchers have argued that the ubiquity of these ancient gardens throughout Mesoamerica led to the dominance of species useful to Maya in the contemporary forest, but this pattern may be localized depending on ancient land use. The tested hypothesis was that species composition would be significantly different between areas of dense ancient residential structures (high density) and areas of little or no ancient settlement (low density). Sixty-three 400-m^2 plots (31 high density and 32 low density) were censused around the El Pilar Archaeological Reserve in northwestern Belize. Species composition was significantly different, with higher abundances of commonly utilized "forest garden" species still persisting in high-density forest areas despite centuries of abandonment. Subsequent edaphic analyses only explained 5% of the species composition differences. This research provides data on the long-term impacts of Maya forests gardens for use in development of future conservation models. For Mesoamerican conservation programs to work, we must understand the complex ecological and social interactions within an ecosystem that developed in intimate association with humans.

Key words: canonical correspondence analysis, CCA; El Pilar Archaeological Reserve, Belize; ethnoecology; forest gardens; historical ecology; Maya; Mesoamerica; tree species composition.

INTRODUCTION

The Maya peoples lived under the canopy of the Mesoamerican forests for millennia (Gomez-Pompa and Kaus 1999, Gill 2000, Ford 2005). The relationship of the Maya with their environment led to management practices utilizing natural biodiversity to support all aspects of Maya life, from food and medicines to spiritual practices (Gomez-Pompa et al. 2003). Biodiversity governs the provision of ecosystem services that directly relate to the preservation of human well-being (Naeem 2002). Ecosystem services, therefore, often lie at the interface between the social and natural sciences. The need for the integration of ecology and ethnobotany to address preservation of ecosystem services has been suggested numerous times in terms of both modern ethnoecological studies (Prance et al. 1995, Salick 1995, Begossi 1996, Chazdon and Coe 1999, Ticktin 2004) and historical ecology approaches (Balée and Erickson 2006), but there are still few quantitative studies. To preserve Mesoamerican biodiversity, we must address the complex ecological and social interactions within an ecosystem that developed in intimate association with humans. The present study integrated ecology and ethnobotany to assess the lasting impact of ancient Maya home "forest gardens" on the tree species composition of a Mesoamerican forest.

When the Spanish arrived in Mesoamerica in the 16th century, they encountered the Maya living in villages filled with trees. The account of the Spanish priest Diego de Landa (1978 [1566]) describes the Maya homes surrounded by a diversity of tree species used for daily household needs: *forest gardens*. The Maya encountered by the Spanish were the remnants of a once much larger culture that had collapsed six centuries before. Modern archaeological and ethnobotanical studies, however, have documented extensive archaeological evidence of these forest gardens in the ruins of ancient (ca. 2000 BC to AD 1000) Maya urban centers (Wiseman 1978, Healy et al. 1983, Gomez-Pompa et al. 1987, Ford and Fedick 1992, Fedick 1995, Lentz et al. 2000, Campbell et al. 2006*a*). Both anthropological and archaeological studies provide us with a list of tree species commonly planted in ancient Maya forest gardens (Turner and Miksicek 1984, Gomez-Pompa et al. 1987, Lentz et al. 1996). The diversity of life-forms among the forest garden tree species indicates that the gardens mimicked the structure of the natural forest, utilizing all levels of the canopy. Researchers have argued that the ubiquity of these gardens throughout Mesoamerica, combined with intensive agricultural use of other land areas, have led to

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Manuscript received 16 April 2009; revised 9 December 2009; accepted 8 March 2010; final version received 17 April 2010. Corresponding Editor (ad hoc): K. A. Hibbard.

[1] Present address: Department of Biology, Drake University, 1344 27th Street, Des Moines, Iowa 50311 USA. E-mail: nanci.ross@drake.edu

FIG. 1. Map showing the location of the El Pilar Archaeological Reserve, northwestern Belize.

the dominance of Maya-useful species in the contemporary forest: the Mesoamerican forest is, in essence, a "feral garden" (Campbell et al. 2006*a*, Ford 2008). Postcolonial 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 postcolonial period. Analysis supported the theory that, in addition to forest gardens, these "feral pastures" also influenced the development of the modern forest.

There is evidence, however, that there is a localized pattern of species composition depending on precolonial Maya land use (Folan et al. 1979, Lentz et al. 2000). Fedick (1995) found a correlation between land resource variability and ancient Maya residential settlement. The ancient Maya selected locations for houses depending on soil resources. Residential spacing shows that even in densely settled areas, Maya households were sufficiently separated to provide space for home forest gardens (Fedick 1988, Fedick and Ford 1990, Ford and Fedick 1992). The Maya practiced intensive management and selection on Mesoamerican species for at least 3000 years until the Maya cultural collapse at the end of the first millennium AD, when significant population reductions and abandonment of major urban centers led to the virtual abandonment of the majority of forest gardens (deMenocal 2001). The tested hypothesis was that, due to centuries of intensive management, home forest gardens built by the ancient Maya altered the tree species composition of the forests in a way that can still be detected today. Furthermore, it was hypothesized that there is a localized pattern to the altered species composition, yielding a significant difference between densely settled areas and areas of little or no ancient settlement.

METHODS

Research location

The field research was conducted around the ancient Maya city of El Pilar, the largest Maya site in the Belize River area of northwest Belize (Ford 2005). The site spans the Belize–Guatemala border and is held within the 1620-ha El Pilar Archaeological Reserve for Maya Flora and Fauna, an absolute reserve (Fig. 1). The first evidence of human settlement in El Pilar dates to the middle pre-Classic period, around 1000 BC (Fedick and Ford 1990). The city reached its peak in the late Classic period (AD 600–900), but was abandoned after the Maya cultural collapse around AD 1000. Both archaeological and historical evidence indicate that the El Pilar area was only sparsely and intermittently populated after the collapse, by subsistence farmers whose ephemeral impact on the forest, as seen in many tropical regions, is difficult to detect (Ford 2008). 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 dry season extends from January to May, with an average rainfall of <25 mm/month, increasing to 250 mm/month in the wet season (Birchall and Jenkin 1979). The relatively young soils are composed of P-limited mollisols and ultisols (Birchall and Jenkin 1979).

Data collection

A major hurdle in historical ecological research is separating anthropogenic from edaphic factors that potentially impact the study. To this end, census data of the tree communities were collected, as well as data on edaphic characteristics of all study areas.

Plot censusing.—Two groups of 400-m^2 plots were located randomly within mature forest in and around the El Pilar reserve during three field seasons: May 2005, June–August 2006, and June–August 2007. "Mature" forest is the functional equivalent of "old-growth" forests in that evidence of modern human management of the forest (i.e., tree stumps, burning, farming, tree gardening, and so forth) was not found, with the following exceptions. Chicle (*Manilkara zapota*, Sapotaceae) tapping and mahogany (*Swietenia macrophylla*, Meliaceae) extraction were common throughout the region during the last century, as well as limited selective logging, mostly of *Sabal* palms, for use by villagers in the nearby Maya village of Bullet Tree Falls (N. J. Ross, *personal observation*).

Using previously conducted archaeological surveys of the El Pilar area (Ford 2005), sample plots were established in otherwise similar forest areas that contained either a "high density" (>100 archaeological structures/km^2) of ancient Maya residential remains, or a "low density" (<10 structures/km^2). High-density areas were not within temple or ceremonial areas and no monument construction was encountered in these areas; only archaeologically identified house mound remains were found. No archaeological structures were encountered in any of the low-density plots. In total, 31 high-density plots and 32 low-density plots were censused. All trees greater than 2.5 cm diameter at breast height (dbh) were identified, measured, and labeled with a unique identification number regardless of their ethnobotanical importance. Although the census was restricted to trees (naturally multistemmed shrub species were not included), when an individual was encountered that had a stem split at the base, the diameter of each branch was measured and summed for a total dbh. Such individuals represented <5% of the total individuals. Multiple vouchers of all species or morpho-species were collected for positive identification and deposited in the Belize National Herbarium (BZE) and the University of Connecticut Herbarium (CONN). Species names follow the nomenclature in the *Flora de Nicaragua* (Stevens et al. 2001). Names and authorities for species not found in the *Flora de Nicaragua* follow the names listed in the *Checklist of the Vascular Plants of Belize* (Balick et al. 2000). High- and low-density forest areas are ~4 km apart. Each plot was located randomly within each of the forest areas, ensuring that plots were separated by at least 30 m.

Species accumulation curves were generated to test the adequacy of the sampling effort. Several richness estimators were compared using the EstimateS statistical program (Colwell 2005), including Chao 1 and 2, ICE, ACE, and Jackknife. Curves from all estimators had overlapping standard deviations; therefore, only the Chao 1 was used for clarity (Chao 2005). Tree species richness, evenness ($\exp(H)/S$, as per Hill 1973), and Shannon diversity were compared between high- and low-density plots with ANOVA (SYSTAT 2004). For a comparison of overall vegetation structure between high- and low-density areas, tree basal area per hectare and stem density per hectare were assessed.

Tree species compositions of high and low ancient settlement density forest areas were compared using a nonparametric analysis of similarities (ANOSIM) test available in the PRIMER software package, version 6 (Clark and Warwick 2001). This test is a randomization-based analog to ANOVA. A resemblance matrix was built comparing the species compositions of the a priori defined sample groups, high and low settlement density plots. Due to the substantial diversity inherent in tropical forests, a Chao–Jaccard matrix was used to account for any species missed during sampling (Chao et al. 2005).

The ANOSIM analysis examines similarity in overall species composition; however, to consider the role of Maya forest garden species, a similarity percentage (SIMPER) analysis was used. SIMPER is a nonparametric analysis that identifies how much each species contributes to differences (the average Bray-Curtis value of dissimilarity) between groups and to similarities (the average Bray-Curtis value of similarity) within groups (Clark and Warwick 2001). A SIMPER analysis was run on the census data with high- and low-density plots defined as a priori sample groups. In addition, an indicator species analysis (Dufrene and Legendre 1997) was conducted using PC-Ord, version 4 (McCune and Mefford 1999) on all species in both high- and low-density plots. Based on fidelity and relative abundances, this test identifies species that are significant "indicators" of a priori defined sample groups.

To interpret the meaning of the SIMPER and indicator species analysis results, the relevant ethnobotanical literature was used. Extensive ethnobotanical work has been conducted on the tree species managed by both the ancient and modern Maya forest gardeners, including archaeobotanical remains (Turner and Miksicek 1984, Lentz 1991, Lentz et al. 1996), surveys of modern Maya forest gardens (Rico-Gray et al. 1991, Campbell et al. 2006*b*), and studies of tree use and management depicted in Maya art and iconography (database of C. Zidar, Foundation for the Advancement of Mesoamerican Studies, *available online*).[2]

Utilizing these resources, as well as interviews with local Maya forest gardeners, a subset of 32 tree species known to have been commonly utilized in forest gardens was identified and labeled as "forest garden" species (Table 1). These species are members of 19 different plant families and display a variety of life history characters including different pollination syndromes, life-forms (canopy vs. understory tree), and dispersal agents.

Edaphic characteristics.—Potential edaphic differences have been one of the major ecological criticisms of research on Maya plant relicts (e.g., Lambert and Arnason 1982). Tree species composition can vary significantly across soil types and topography within the same geographic area (Clark et al. 1999). Fedick tested the correlation between settlement patterns and

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[2] ⟨http://research.famsi.org/botany/index.php⟩

TABLE 1. Maya forest garden species previously identified as commonly utilized species in ethnobotanical literature.

Forest garden species	Family	Forest garden species	Family
Albizia niopoides	Mimosaceae	*Lonchocarpus castilloi*	Fabaceae
Alseis yucatanensis	Rubiaceae	*Malmea depressa*	Annonaceae
Annona primigenia	Annonaceae	*Manilkara zapota*	Sapotaceae
Aspidosperma spruceanum	Apocynaceae	*Pimenta dioica*	Myrtaceae
Attalea cohune	Arecaceae	*Piper amalago*	Piperaceae
Brosimum alicastrum	Moraceae	*Pouteria campechiana*	Sapotaceae
Bursera simaruba	Burseraceae	*Protium copal*	Burseraceae
Caesalpinia sp.	Caesalpiniaceae	*Prunus* spp.	Rosaceae
Ceiba pentandra	Bombacaceae	*Pseudolmedia spuria*	Moraceae
Chrysophyllum mexicanum	Sapotaceae	*Psychotria chiapensis*	Rubiaceae
Cryosophila stauracantha	Arecaceae	*Sabal morrisiana*	Arecaceae
Cupania belizensis	Sapindaceae	*Spondias radlkoferi*	Anacardiaceae
Dendropanax arboreus	Araliaceae	*Swietenia macrophylla*	Meliaceae
Hamelia axillaris	Rubiaceae	*Terminalia amazonia*	Combretaceae
Lacistema aggregatum	Lacistemataceae	*Vitex gaumeri*	Verbenaceae
Licania platypus	Chrysobalanaceae	*Zuelania guidonia*	Flacourtiaceae

Note: Sources include Turner and Miksicek (1984), Lentz (1991), Rico-Gray et al. (1991), Lentz et al. (1996), Campbell et al. (2006*b*), and the database of Charles Zidar, Foundation for the Advancement of Mesoamerican Studies ⟨http://research.famsi.org/botany/index.php⟩.

soils in the Belize River area (Fedick 1988). Using both previous soil survey data (Birchall and Jenkin 1979) and Fedick's own limited, finer-scaled soil survey of the Belize River area (Fedick 1988), both Fedick and Ford argue that ancient settlement patterns were significantly impacted by edaphic characteristics including soil texture, drainage, slope, and fertility (Ford and Fedick 1992, Fedick 1995). Fedick (1995) found that Maya home sites were preferentially located on well-drained upland soils. Effort was made to locate low-density plots in comparable forest areas to the high settlement density plots using field comparisons of soils and slope.

In each plot, four 20-cm soil cores were collected randomly and combined for a plot-wide sample. Slope (measured using a clinometer) and drainage (evaluated by mottling) were assessed in the field. Soils samples were air-dried for 72 h, sealed in airtight plastic bags, and shipped to Brigham Young University Soil and Plant Analysis Laboratory for analysis of available N and P, exchangeable cations (Ca, Mg, Na, K), pH, percentage organic matter, and soil texture.

Canonical correspondence analysis (CCA), a direct gradient analysis method, was used to look for patterns between edaphic characters, ancient Maya settlement density, and species compositions (ter Braak and Prentice 1988). CCA has been found to deal well with uneven species distributions and "noisy" data and it is not hampered by correlated species or environmental variables (Palmer 1993). Analysis was conducted using PC-Ord, version 4 (McCune and Mefford 1999).

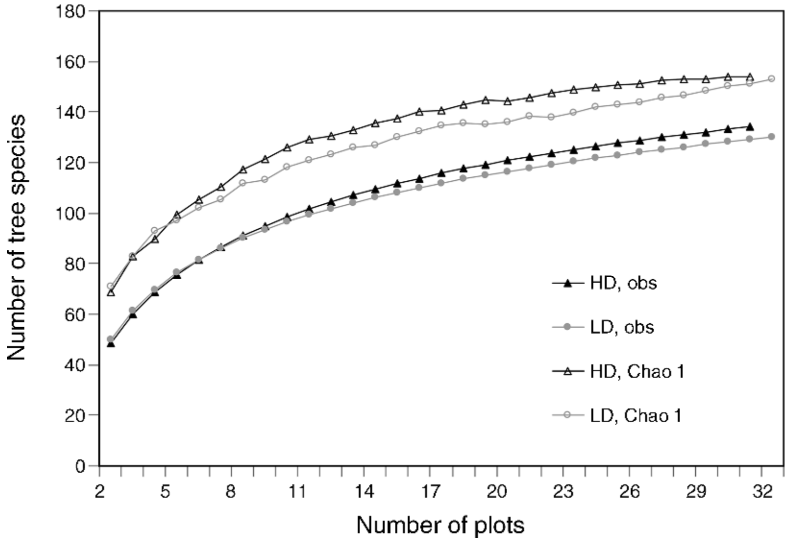

FIG. 2. Species accumulation curves for high-density (HD, black triangles) and low-density (LD, gray circles) ancient settlement plots. Mau Tau observed (obs) values (solid symbols) are compared to values calculated using the Chao 1 species richness estimator (open symbols).

TABLE 2. Comparison of vegetation structure of high- and low-density forest areas in the El Pilar Archaeological Reserve in northwestern Belize.

Area density	N	Tree basal area (m^2/ha)	Tree density (no./ha)
High density	31	46.6 ± 10.3	2539.5 ± 522.0
Low density	32	43.9 ± 12.6	2719.5 ± 653.1

Notes: Values are means ± SD. Area density refers to the density of ancient residential structures. Sample size (N) is the number of 400-m^2 plots. Differences between high- and low-density areas were not significant for either basal area (P = 0.361) or tree density ($P = 0.232$).

Edaphic character values were log-transformed for normality except for soil texture and slope. Texture was analyzed proportionally for percentage sand, clay, and silt; therefore, the arcsine square-root transformation was used (Sokal and Rohlf 1994). Texture values are linear combination values (percentage sand, clay, and silt equaling 100%) that cannot be present in the matrix analysis used in CCA. One of the texture variables, percentage silt, was therefore randomly chosen and removed from the analysis. Drainage was not found to vary between plots. Slope, however did differ significantly between high- and low-density plots ($F = 11.279$, df = 1, 58, $P = 0.001$). Therefore, slope was included in the ordination.

RESULTS

Species accumulation curves of high and low settlement density plots show that sampling effort was sufficient to account for the tree diversity of the forests around El Pilar (Fig. 2). Analysis of tree density and basal area showed no difference between high- and low-density forest plots (Table 2). There was also no significant difference in Shannon diversity indices, species richness, or evenness between high and low ancient settlement density forest areas (Table 3).

Despite the similar forest structure, the ANOSIM analysis confirmed that there was, in fact, a significant localized difference in species composition between high- and low-density ancient settlement areas (global $R = 0.241$, $P = 0.001$; Fig. 3). None of the randomized iterations produced a higher R value than the empirical data. A Mantel test showed that this difference was not due to spatial correlation between high and low ancient settlement density areas and species compositions (high, $r = 0.008602$, $P = 0.475$; low, $r = -0.1767$, $P = 1.000$).

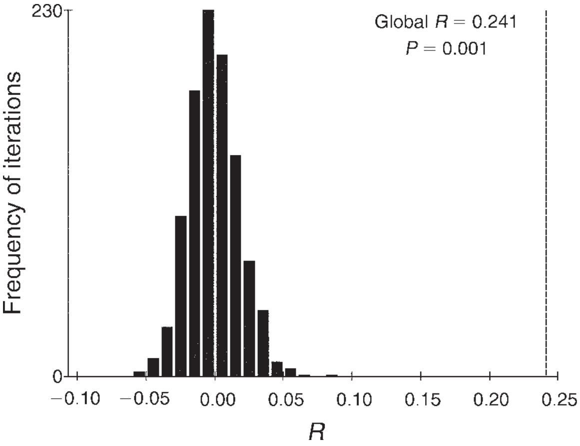

FIG. 3. ANOSIM (analysis of similarities) of tree species composition. There are no randomized iterations greater than the empirical global R value ($R = 0.241$). Species composition of ancient garden areas differs significantly from the composition of the forest matrix ($P = 0.001$). Analysis was conducted using PRIMER (Clark and Warwick 2001).

Analysis of edaphic characters showed that these did not explain the compositional differences either. CCA resulted in three axes of variation. Two-sample t tests (SYSTAT 2004) of the linear combination (LC) scores for edaphic variables showed that axis 1 scores differed significantly between high and low ancient settlement density sample groups ($t = 7.762$, df = 61.0, $P = 0.000$) (Fig. 4). Axes 2 and 3 did not differ significantly between high and low density ($P = 0.615$ and 0.957, respectively).

All three CCA axes, however, explained only 9.8% of the total variation in species composition: 5%, 2.6%, and 2.2%, respectively (Table 4). The standardized canonical coefficients for edaphic variables showed that high-density plots were characterized by greater available N, percentage organic matter, Ca, Mg, and Na. Low-density plots showed higher pH, available P, and K as well as greater percentages of sand and clay in the soils (Table 5). Despite the significant difference between high and low ancient settlement density forest areas identified by axis 1, the low eigenvalue of axis 1 (0.178)

TABLE 3. Comparison of high- vs. low-density ancient settlement plots: exponentiated Shannon-Weaver diversity index (H'), species richness, and species evenness, with ANOVA statistics.

Settlement density and ANOVA	N	exp(H')	Species richness	Species evenness
High-density plots	31	19.5 ± 4.1	31.7 ± 4.9	0.61 ± 0.07
Low-density plots	32	19.4 ± 5.6	32.7 ± 6.6	0.59 ± 0.1
ANOVA				
F		0.008	0.469	0.662
df		1, 61	1, 61	1, 61
P		0.931	0.496	0.419

Notes: Values are given as means ± SD. Richness of each plot is the number of species encountered in that plot; evenness is the exponentiated Shannon diversity [exp(H')] divided by richness. ANOVA was conducted using SYSTAT, version 11 (SYSTAT 2004).

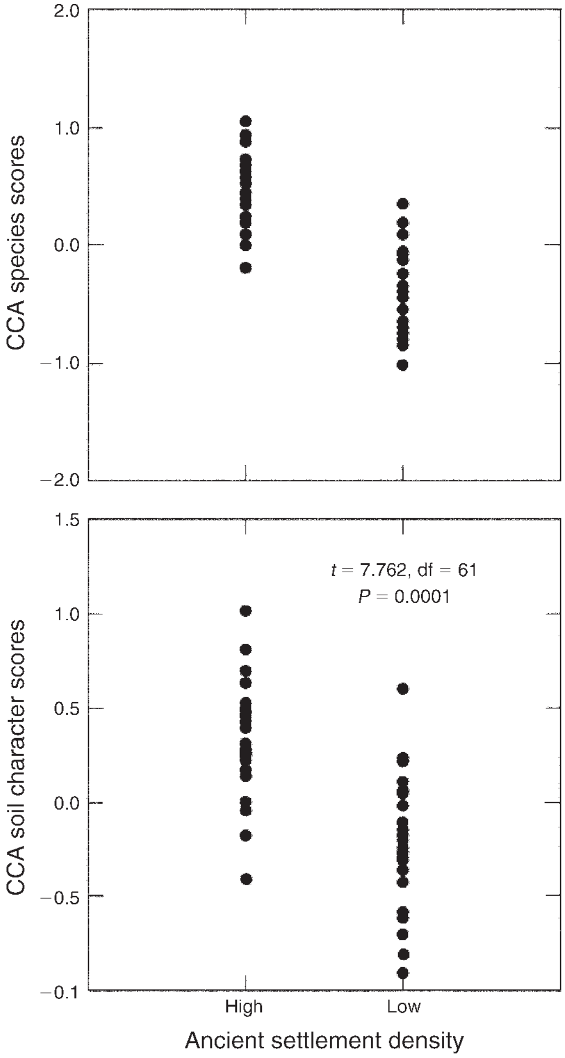

FIG. 4. Comparison of CCA axis 1 linear combination (LC) scores between high and low settlement density areas. The upper panel shows LC scores for species; the lower panel shows LC scores for tested edaphic characters. A two-sample t test identified a significant difference between high and low settlement density areas.

TABLE 4. Canonical correspondence analysis (CCA) axis summary statistics.

Statistic	Axis 1	Axis 2	Axis 3
Eigenvalue	0.178	0.090	0.079
Variance in species data			
Variance explained (%)	5.0	2.6	2.2
Cumulative % explained	5.0	7.6	9.8
Pearson correlation	0.799	0.786	0.836
Kendall (rank) correlation	0.616	0.571	0.662

Notes: Cumulative % is the cumulative percentage of the dissimilarity between groups. Axis 1 represents the greatest amount of variance explained by the edaphic variables; however, the eigenvalue (0.178) is low, indicating that it does not represent a strong gradient in species composition. The analysis was conducted using PC-Ord, version 4 (McCune and Mefford 1999). Total inertia in species data = 3.542 (a measure of the total amount of variance, related to the spread of species optima in ordination space).

signifies that the axis does not, in fact, represent a strong gradient in species composition (Table 4). Axes 2 and 3 do not represent differences between high- and low-density forest areas, so the 4.8% of variance explained by them most likely does not relate to the differences in species composition between these areas. Therefore, 90–95% of the total difference in species composition between high- and low-density plots is not explained by edaphic differences.

SIMPER analysis identified 28 species (of 171 total species) that explain the top 50% of the compositional dissimilarity between high and low ancient settlement density plot groups (Table 6). Of the 28 species identified, 17 species belong to the list of forest garden species (Table 1). SIMPER results show that 12 of those 17 forest garden species have a greater average abundance in high-density plots. Correspondingly, nine of the 11 non-garden species had a greater abundance in the low-density control plots. Indicator species analysis (Dufrene and Legendre 1997) further clarified this result. Not only did the majority of forest garden species have greater abundance in high-density plots, but eight of those species were identified as significant ($P < 0.05$) "indicators" of the high-density forest areas (Fig. 5).

That's just over half of the Mayan spp.

DISCUSSION

The data reveal a link between current forest compositional differences and density of ancient Maya occupation around El Pilar. After a millennium of abandonment, one might suggest that dispersal and mortality would have eliminated any sign of forest gardens, yet results of the SIMPER and indicator species analyses (Fig. 5) strongly indicate they did not. Economically important tree species (species known to have been commonly utilized in ancient forest gardens) play a major role in compositional differences between high and low ancient settlement density areas and show a definite trend of higher abundances in ancient forest garden areas. Chicle (*Manilkara zapota*), surprisingly,

TABLE 5. Standardized canonical coefficients from the multiple regression of plots in species space on edaphic characters for CCA axis 1.

Variable notation	Canonical coefficients (standardized)
ln(ppm P)	−0.100
ln(ppm NO_3-N)	0.202
ln(% organic matter)	0.056
ln(pH)	−0.144
Arcsine square-root(% sand)	−0.046
Arcsine square-root(% clay)	−0.121
ln(ppm Ca)	0.115
ln(ppm Mg)	0.011
ln(ppm K)	−0.319
ln(ppm Na)	0.128
Slope	0.040

TABLE 6. Species contributing the top 50% of dissimilarity in species composition between high- and low-density plots ordered by proportional contribution.

Species	Average abundance		Diss/SD	Contrib%	Cum%
	High	Low			
Pouteria reticulata	1.25	3.54	1.75	3.77	3.77
Pseudolmedia spuria†	2.03	3.44	1.41	3.21	6.98
Attalea cohune†	2.12	0.66	1.47	2.98	9.96
Alseis yucatanensis†	2.31	0.96	1.62	2.47	12.43
Lacistema aggregatum†	1.42	0.30	0.97	2.22	14.64
Ampelocera hottlei	2.08	2.12	1.27	2.14	16.78
Cryosophila stauracantha†	3.75	3.38	1.20	2.04	18.82
Malmea depressa†	0.34	1.46	1.37	1.98	20.8
Manilkara zapota†	0.36	1.41	1.35	1.89	22.69
Protium ravenii	1.29	1.08	1.32	1.77	24.47
Protium copal†	1.17	0.35	1.34	1.69	26.16
Pouteria campechiana†	0.99	1.11	1.23	1.68	27.84
Aspidosperma megalocarpon	0.49	1.13	1.29	1.58	29.42
Koanophyllon albicaule	0.92	0.33	0.89	1.57	30.99
Psychotria chiapensis†	1.04	0.61	1.23	1.53	32.51
Cupania belizensis†	0.79	1.00	1.21	1.53	34.04
Pouteria belizensis	0.72	0.85	1.18	1.48	35.52
Piper amalago†	1.05	0.48	1.24	1.44	36.96
Matayba apetala	0.30	1.00	1.13	1.43	38.39
Caesalpinia sp.†	0.84	0.16	0.73	1.42	39.81
Rehdera penninervia	0.21	0.94	1.00	1.42	41.23
Laetia thamnia	0.47	0.89	1.06	1.41	42.63
Zuelania guidonia†	0.91	0.86	1.19	1.32	43.96
Hamelia axillaris†	0.85	0.61	1.14	1.31	45.26
Acacia gentlei	0.78	0.84	1.19	1.28	46.55
Spondias radlkoferi†	0.83	0.30	1.12	1.25	47.8
Dracaena americana	0.63	0.47	0.92	1.25	49.04
Vitex gaumeri†	0.71	0.64	1.08	1.25	50.29

Note: Diss/SD is dissimilarity/SD; Contrib% is the proportional contribution to total dissimilarity between groups; Cum% is the cumulative percentage of dissimilarity between groups.

† Forest garden species.

did not show higher abundances in ancient residential areas, despite extensive evidence of ancient use by the Maya (Turner and Miksicek 1984, Lentz 1991, Lentz and Hockaday 2009). The effects of modern resin extraction, however, still visible in the forest today, make it difficult to analyze this result.

A major problem of historical ecological research is the lack of information on the environment before human settlement. Although it cannot be asserted unequivocally that the species composition differences detected here were the direct result of Maya forest management, the ubiquity of useful species in the high settlement density plots strongly suggests an anthropogenic effect, and one with considerable impact on persistence. In France, Dambrine et al. (2007) also discovered long-term impacts of ancient agriculture, Roman in that case, on the local biodiversity and species composition after more than 1500 years of abandonment. Dambrine et al. found that plant species richness increased as one approached the center of the ancient Roman settlement, with an increase in neutrophilous and nitrogen-loving species. Thus, it is not unreasonable to conclude that the importance of ancient historical land use has been generally underestimated (Tscharntke et al. 2005).

Explanation of the soil differences between ancient forest garden plots and the forest matrix is also hindered by the lack of pre-Maya data. Nonetheless, the vast majority of variation in species composition was independent of edaphic variables. Combined with the distribution of forest garden species, it can be argued that the soil differences are not of pre-forest garden origins. Tree species are affected by the soil on which they grow; but they also affect the soil in which they grow (Binkley and Giardina 1998, Finzi et al. 1998). The long-term continuation of the forest garden tree community could have resulted in the development of unique soil characteristics.

One significant factor that has not been addressed is the possible role of fire in controlling species composition. Could the differences in species composition between high and low ancient settlement density areas actually be an artifact of fire? Although fire has been an important disturbance factor in the Mesoamerican forest (Rico-Gray and García-Franco 1992, Otterstrom et al. 2006), there is no evidence of preferential burning in either high or low ancient settlement density forest areas around El Pilar that would explain the species composition differences found in this study. Failing that, data on the individual fire responses of the 28 species explaining the top 50% of compositional differences between high and low settlement density areas (Fig. 5) were sought. Unfortunately, due to the inherent diversity of tropical forests, information on fire resistance was located for only a few of the 28 species.

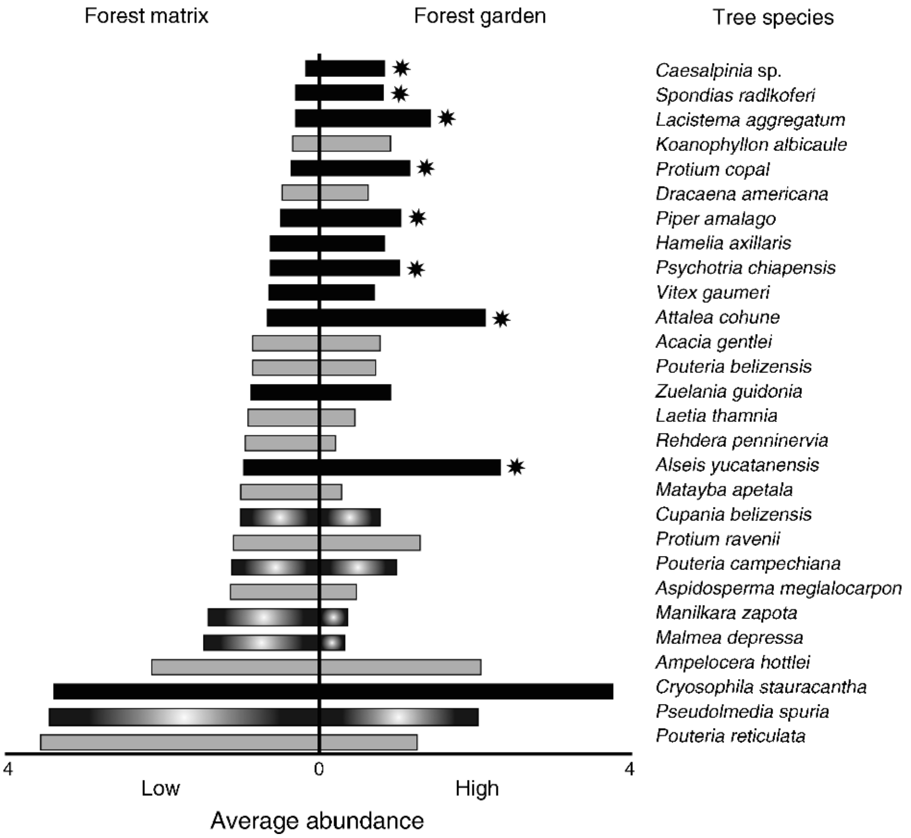

FIG. 5. Abundance of tree species (bars) in the forest matrix (ranked least to most abundant, left side of vertical axis) vs. abundance of the same species in ancient forest garden areas (right side of vertical axis). Included are those species accounting for 50% of dissimilarity in species composition between high and low settlement density areas, as identified by SIMPER analysis. Gray bars are species of no known cultural and economic importance (non-forest garden species). Variegated bars are forest garden species with higher abundance in low settlement density plots. Black bars are forest garden species having greater abundance in high-density plots (12 of 17 forest garden species). Of these 12 species, eight are significant ($P < 0.05$) "indicators" of forest located on ancient garden areas (marked by stars).

Attalea cohune, a significant indicator of high settlement density forest (as per Fig. 5), is known to be highly fire resistant (Ivanauskas et al. 2003). On the other hand, *Spondias radlkoferi*, another significant indicator species for high settlement density areas, has thin bark that makes it vulnerable to fire damage (Croat 1974, Uhl and Kauffman 1990). *Vitex gaumeri*, a characteristic species of mature forest in Mesoamerica (Rico-Gray and García-Franco 1992), also had greater abundance in high settlement density forest plots. This species does not tolerate fire and was found to be nearly absent from postburn secondary forests for decades (Rico-Gray and García-Franco 1992). Clearly, this is far from a complete investigation of the role that fire may play in determining the species composition of the forest around El Pilar, and further research is warranted. Yet, combined with the lack of evidence for preferential burning in either high- or low-density forest areas, the available information suggests that fire is not the driving force behind the compositional differences found in this study.

In a recent review, Chazdon et al. (2009) recognized two essential steps to understanding the current and future status of Neotropical diversity: understanding the patterns of biodiversity in actively managed lands and investigating how those patterns are affected by different practices. Historical ecology studies such as the Dambrine et al. (2007) paper and the study described herein provide us with a means to identify the long-term impacts of historical human activities. This would provide an understanding of the "baseline" biodiversity levels that conservationists are working from. In addition, it would help us to understand how the landscape adapts to those activities. Human modifications to a landscape can interact with the system to have unique and potentially valuable outcomes.

Modern Maya forest gardens are often highly diverse, with farmers maximizing the services harvested from their gardens (Campbell et al. 2006*b*). It is reasonable to assume that the ancient Maya would have done the same. Diversity can increase the opportunities for synergistic interactions between species that would enhance the stability and sustainability of the garden

(Altieri 1994). This study found no indication of a loss of diversity in ancient, intensively managed areas. This suggests that the methods utilized in forest gardening work within the precincts of the natural system. That, in turn, suggests that the preservation of forest gardening techniques can help to maintain ecosystem services beyond the economy of the household to the level of regional ecosystem protection.

Viable sustainable development models must have two essential components: data that policy makers and researchers trust, and practices that local people find credible based on their cultural perspectives (Cash et al. 2003). Forest gardens are an important part of the traditional ecological knowledge (TEK) system still practiced by a diminishing number of the descendants of the ancient Maya. TEK-based practices have the advantage of being adapted to a specific environment as well as being understood and accepted by local peoples. Therefore, such practices have the potential to form the basis of viable proposals for effective natural resource management (Davis and Wagner 2003). In areas of highly threatened biodiversity, an understanding of the historical development of the ecosystem is essential. Historical ecological studies can provide a baseline on which to design biodiversity recovery strategies and conservation goals. Maya forest gardens may prove a valuable aspect of Mesoamerican sustainable development models.

ACKNOWLEDGMENTS

Financial support was provided 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. My thanks go to Anabel Ford, UC–Santa Barbara, for contributing her extensive archaeological knowledge and logistical support. The fieldwork was made possible by the expertise and friendship of Leopoldo Romero and Don Heriberto Cocom. This project would have been impossible without them. At the University of Connecticut, I thank Gregory Anderson and Robin L. Chazdon, who provided considerable experience in methodologies and analysis; Felix Coe and Susan Letcher, for help with voucher identification; and Robert Colwell for analytical assistance. Thanks also go to the Belize Forestry Department, the Belize Department of Archaeology, the Instituto de Antropología e Historia de Guatemala, Colin Young (Galen University, Belize), and two anonymous reviewers.

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