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Spatial distribution and habitats of useful plants: an initial assessment for conservation on an indigenous territory, Panama

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Abstract. In order to examine the spatial distribution of forest resources on local territories and to understand the factors controlling such distributions, we studied the spatial patterns of a group of 23 useful plant species on the territory of a Kuna community in the province of Darien, Panama. A stratified random sampling scheme was used to survey the distribution and abundance of the species across a 3500 ha area around the village. Data on the physical environment as well as the geographic coordinates of the sample plots were also obtained. A series of canonical analyses was conducted to evaluate the species–environment relationships and to identify spatial structures in the species distributions left unexplained by the environmental variables. Four distinct distribution patterns were identified among the species; these were most strongly explained by land-use, the degree of canopy closure and topography. Significant spatial structures, independent of the measured environmental variables, were related to anthropogenic pressure and an edaphic gradient, and the habitat associations of the individual species were described. The results obtained from this case study suggest that land-use dynamics may play a predominant role in structuring inhabited landscapes, and that diversity in distribution patterns and habitat associations will require a combination of spatially explicit management strategies to ensure the local resource base.

Key words: conservation, Darien – Panama, habitat, indigenous territory, partial canonical analysis, spatial distribution, useful plants

Abbreviations: CCA – canonical correspondence analysis; eq. – equation; field obs. – field observation; GIS – geographical information system; GPS – geographical positioning system; NGO – non-governmental organization; PCA – principal component analysis; RDA – redundancy analysis

Introduction

A large proportion of forested landscapes in the tropics are cultural landscapes, being inhabited, used and modified by people. Recognition of this human component of forest landscapes and of the traditional ecological knowledge held by the resident cultures has led to a model of 'community-based' conservation (Gadgil et al. 1993). As a result, the involvement of local communities in the planning and management

of protected areas has increasingly been sought (Western et al. 1994). For some indigenous peoples, this conservation strategy has provided a new legal framework in which to assert their land claims (Davis and Wali 1994).

One of the priorities for local people in establishing territorial rights is to ensure access to the plant and animal forest resources essential to their subsistence and cash economies. Wild plant resources are harvested by local people for a variety of purposes including construction materials, household tools, medicine, food, income generation and rituals. Although a large body of literature attests to the detailed traditional knowledge held by forest people on the use, natural history, and management of these resources (i.e. Posey and Balée 1989; Redford and Padoch 1992), it has become evident that problems of resource deterioration and over-exploitation are not uncommon on traditional territories (Coomes 1995; Ventocilla et al. 1995). The problem has been thought to be most severe with commercially oriented products; however, there is growing awareness that resource depletion is occurring even in villages removed from markets (Godoy and Bawa 1993). The undermining of subsistence and commercial resource bases may be one of the main management issues of importance to local communities and can provide an incentive for local initiation of conservation efforts (Pinedo-Vasquez et al. 1992; Coomes and Barham 1997).

When considering the management of the resource base of a given community, it is often desirable to conduct an initial evaluation of the status of local resources and then subsequently establish conservation strategies. Demographic models have been used to determine sustainable levels of harvest (i.e. Peters 1990; Pinard 1993; Boot and Gullison 1995; Nantel et al. 1996) or to evaluate local knowledge or management systems (Joyal 1996; Velasquez Runk 1998; Ticktin 2000). It has also been suggested that the assessment of the effects of harvest practices on the structure of plant populations could provide a rapid alternative (Hall and Bawa 1993). Although population trends cannot always be predicted from static data (Condit et al. 1998), in the absence of long-term monitoring, such studies can give preliminary indications of how plant populations may be affected by extractive activities or other land-uses. Murali et al. (1996), for example, identified species with under-representation in the small size classes in sites close to a local village, in opposition to distal sites, whereas Lykke (1998) used a similar approach to evaluate the size class distributions of useful plants in severely disturbed savanna ecosystems. The size class structure, community composition and diversity of forest communities under different harvest intensities were examined by Daniels et al. (1995) and Uma Shankar et al. (1998). Similarly, community analysis has been used to evaluate the impact of timber extraction, sylvicultural treatments (Salick et al. 1995), and other agricultural land-uses (Fujisaka et al. 1998) on useful plants.

Land management, however, requires an understanding not only of the impacts of different land-uses but also of the spatial patterns of the landscape. In conservation planning, for example, the distribution patterns of diversity and endemism have been important in identifying priority regions for protected areas (i.e. ter Steege 1998; de

Oliveira and Daly 1999). In cultural landscapes, several studies have mapped landuses (Sirait et al. 1994) and forest communities (Smith et al. 1999) for management purposes. Variability in the composition and/or density of useful plants has also been compared among forest types (Kohn 1992; Voeks 1996; Johnston 1998; Chazdon and Coe 1999; Salick et al. 1999; Frei et al. 2000). The latter group of studies, however, has tended to focus on inventories of a few representative plots, precluding analysis at larger spatial scales (but see Salick et al. 1999). Spatial patterns of tropical biodiversity at larger scales have been addressed in more detail by a growing number of studies which aim to identify factors explaining these patterns (i.e. Clark et al. 1995, 1999; Duivenvoorden 1995; Tuomisto et al. 1995; Condit 1996; Terborgh and Andresen 1998). Yet little comparable work is available for landscapes inhabited and managed by people.

The present study aims to characterize the distribution and habitat requirements of a group of useful plant species on the territory of a Kuna village in Panama. Specifically, the goals of the study were to: (1) examine the distribution patterns of some of the most important plant species on the territory, and evaluate factors explaining these distributions; (2) describe the habitat associations of the species; and (3) evaluate the potential implications of these findings for management. A second paper (Dalle and Potvin submitted) examines the conservation status and use of these species.

Study area

The research was conducted in collaboration with the Kuna village of Nurna in the 'Comarca Wargandi', and with Fundación Dobbo-Yala, a non-governmental organization (NGO) working in the region (see Lopez and Dalle in press). Our assessment of forest product use will contribute to a management plan for the Comarca. The territory, located in the province of Darien in eastern Panama, extends from the San Blas mountains (approx. 600 m above sea level), through hilly terrain down to the flat Pacific lowlands in the south. The longest river in Darien, the Chucunaque, originates in the northwestern corner of the territory and flows southeast towards the border of Colombia. The region up to approximately 300 m above sea level is covered by forests classified as 'humid tropical' in the Holdridge life zone system, with 'wet premontane' and 'wet tropical forests' being located at higher elevations (Instituto Geográfico Nacional 1988). Large-bodied vertebrates, such as jaguar (Panthera onca), tapir (Tapirus bairdii) and the harpy eagle (Harpia harpyia), endangered throughout the country, are still reported in the region by local people (pers. comm.). Annual precipitation in the area is approximately 2500 mm, and annual temperature averages at 25 °C (Instituto Geográfico Nacional 1988). There is a pronounced dry season from December to the end of April (Tosi 1971).

The village of Nurna is the first of the three villages of Wargandi located along the Chucunaque river. Although the village's traditional lands are more extensive, the



Figure 1. Map of the study area showing topography, major trails (dashed lines), and distribution of sampling sites (circles). The elevation surface was interpolated from altimeter readings at each of the sampling sites, using the kriging function in Arcview. The trails and sample plots were mapped using a GPS. Note that the sample sites are not shown to scale here.

present study focuses on a 7×5 km area (3500 ha) surrounding the village where most of the hunting and gathering activities take place. This area varies in elevation from approximately 50 to 300 m above sea level (Figure 1).

According to oral history, the village was established approximately 70-100 years ago when a fire destroyed the previous settlement located higher up in the mountains. The population of 200 people is predominantly Kuna-speaking. The local economy is based on swidden/fallow agriculture complemented by permaculture agroforestry along the riverbanks, hunting and to a lesser degree fishing. Forest products are still regularly harvested for construction, household tools, medicine, and rituals. Since approximately 1995, cash income has been obtained almost exclusively through contracts established with national logging companies for the commercial extraction of valuable timber species, including Swietenia macrophylla. Currently, income derived from timber sales is distributed equally among family heads and is used to obtain guns, bullets, plastic containers, cloth and sewing materials, some basic food items such as sugar, salt, as well as a number of 'luxury' items including radios, etc. As the upper reaches of the Chucunaque are unnavigable through most of the year, villagers access outside markets along the Panamerican highway by foot in the rainy season (8 h away at the time of this study), or via the logging roads in the dry season. Previously, cash income was much more limited and was derived from occasional timber sales, as well as that of Ipecac (Psychotria ipecacuanha) in the medicinal herb markets in Panama city.

Methods

Research agreement with the community

Before initiation of the field work, the objectives, methodology and desired outcomes of the research were discussed in the traditional village congress (*onmaket nega*), a forum in which the entire community meets nightly to discuss village politics or to listen to traditional chants. Subsequently, a written agreement was drawn up, outlining the respective responsibilities of the researchers, the community, and the NGO in the carrying out of the research. Two young men who were literate in Spanish were nominated by the community to participate as research assistants in the field work. The Agriculture Committee, a group of four men whose function is to coordinate community projects with Fundación Dobbo-Yala, were charged with overseeing the initial stages of the research project.

Species selection

Since the goal of the study was to sample extensively across a large territory, it was necessary to focus on a subset of useful plants. Plants chosen were all readily identified in the field by our informants avoiding the need for an intensive voucher collection. Twenty-three plant species were selected for this purpose, based on their perceived importance to the local community in each of five use categories (construction, weaving/utility, edibles, firewood, ritual). The species were selected from an initial list of 70 species obtained by free-listing interviews with two men and two women, as well as a group of five young men, who volunteered as informants. This list was reviewed for accuracy with the Agriculture Committee who were asked to prioritize species in each category according to their perceived importance. The final 23 species were selected among the 'priority' species by maximizing diversity in uses, life form and use by men/women. Voucher specimens for unknown species were collected (Table 1). For the remainder of the article, the species are referred to by their genus name only. Where a scientific identification is lacking, the species is referred to by its Kuna name.

Ecological inventory

Data on the distribution and abundance of the 23 species were collected using a stratified random sampling design. A base map of the study area (approx. 3500 ha) was developed from a 1:50000 topographic map of the area onto which trails and other landmarks were mapped using a Garmin 12 XL global positioning system (GPS) (Garmin International, Kansas, USA). The study area was then divided into a grid of 54 800 × 800 m blocks (64 ha each), and the coordinates of a point within each of the grid blocks was selected using a random number generator. These points were plotted

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Kuna name	Scientific name	Family	Voucher	Life form	Use
I. Construction					
Caoban	Swietenia macrophylla King	Meliaceae	$236^{a,b}$	Tree	Construction, commerical timber
Koibur	Dalbergia retusa Hemsley	Fabaceae	$205^{a,b}$	Tree	Construction, house post
Puarsip	unidentified	Rutaceae	$233^{a,b}$	Tree	House post
Baila-uar	Myroxylon balsamum (L.) Harms	Fabaceae	$200^{a,b}$	Tree	House post, adornment
Uichur-sichit	Oxandra sp.	Annonaceae	$201^{a,c}$	Tree	Roof framework
Па	Socratea exorrhiza (Mart.) H. Wendl.	Arecaceae	NS	Palm	House wall
Soso	Sabal mauritiiformis (H. Karst.) Griseb. H. Wendl.	Arecaceae	NS	Palm	Thatch, adornment
Sargi	Heteropsis oblongifolia Kunth	Araceae	$210^{a,b}$	Hemi-epiphyte	Latching
II. Utility/weaving					
Siler	Oenocarpus mapora H. Karst	Arecaceae	206^{a}	Palm	Weaving, house wall
Nai-uar	Carludovica palmata Ruiz & Pav.	Cyclanthaceae	238^{a}	Herb	Weaving
Dubsip	<i>Apeiba tibourbou</i> Aubl.	Tiliaceae	$229^{a,b}$	Tree	Bark rope, weaving
Alar-uar	Bactris coloradonis L.H. Bailey	Arecaceae	$204^{a,d}$	Palm	Pot holder
Bunur-sapi	Unidentified	Sterculiaceae	$207^{a,b}$	Tree	Hand beater
Mutu	Symphonia globulifera L. f.	Guttiferae	234 ^{a,b}	Tree	Sewing tool
III. Firewood					
Ugar-uar	Cordia alliodora (Ruiz & Pav.) Oken	Boraginaceae	227^{a}	Tree	Firewood
Ipup	Peltogyne purpurea Pittier	Fabaceae	223 ^b	Tree	Firewood
IV. Edible					
Naba	Astrocaryum standleyanum L.H. Bailey	Arecaceae	NS	Palm	Edible, house wall
Tupu-uar	Gustavia superba (Kunth) O. Berg	Lecythidaceae	$239^{\mathrm{a,b}}$	Tree	Edible
V. Ritual					
Sianele	Theobroma sp.?	Sterculiaceae	NS	Tree	Ritual, edible
Oa	<i>Aechmea magdalenae</i> André ex Baker	Bromeliaceae	NS	Herb	Ritual
Ukur-uar	Ochroma lagopus Sw.	Bombacaceae	NS	Tree	Ritual, staircase
Magep	Arrabidaea chica (Bonpl.) B. Verl.	Bignoniaceae	237 ^{a,b}	Vine	Ritual
Sabdur	Genipa americana L.	Rubiaceae	235^{a}	Tree	Ritual
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Table 1. Species selected for the study: listed according to each of the five use categories.

Voucher numbers are S. Dalle's collection number, unless otherwise indicated; ^a deposited at PMA; ^b deposited at F; ^c deposited at U; ^d deposited at NY; NS = no specimen collected.

on the base map and served to indicate the estimated starting point for a transect which was laid out in each block. In the field, the starting point for each transect was located by pacing the distance from a recognizable landmark (usually a trail intersection or farm) estimated using the base map. Two blocks were not sampled due to the extreme inaccessibility of the terrain (boulders and steep cliffs). The transects were 575 m in length and were oriented with a compass at 45° (the direction of the prevailing topographic gradient). Three pairs of circular plots, each separated by 25 m, were located at 250 m intervals along each transect, using a 'hip chain' measuring device (Chainman Industries, British Colombia, Canada). The plots were 12 m in radius (452 m^2) , and distances between plots were measured from the centre of each circle. Here we denote the plots of each pair as 'A' and 'B', such that the 'A' plot occurred first along the transect. The presence/absence of the species under study was recorded in both the 'A' and 'B' plots; for analyses of species distributions, data from the 'A' and 'B' plots were pooled to get a better estimate of occurrence at each sampling site. In the 'A' plots, the abundance of each species was recorded. For the trees and palms, abundance was recorded separately for each of five size classes (SC). SC for the trees were defined as follows: SC1 <0.5 m height; SC2 >0.5 m height and <10 cm dbh; SC3: 10-20 cm dbh; SC4: 20-40 cm dbh; and SC5 > 40 cm dbh. For the palms, size classes were SC1 < 0.5 m height; SC2 > 0.5 m height, trunkless; SC3: trunk < 3 m height; SC4: 3-7 m height; SC5 >7 m height. In the case of Socratea, which has trunk development from the seedling stage, SC2 was defined as palms 0.5-1 m tall, and SC3 as 1-3 m tall. For the present analyses, data on only the established SC (2-4) were employed. For a few species whose girth does not generally reach 40 cm dbh, only three SC were used. In the case of the clustered palms Oenocarpus and Bactris, it was generally possible to delineate individual clones, and thus abundance was recorded as the number of genets; size class was determined by the height of the tallest stem in the clonal group, following De Steven (1989). The delineation of individual clones was not possible for Carludovica and Aechmea, whose abundance was recorded as the number of ramets.

For all plots, data on the topography, land-use, forest structure, drainage and soils were recorded. To ensure rapid data collection, most variables were scored on an ordinal scale or as categories (Table 2). These variables were always scored by the same person (S. Dalle) to maintain consistency. A rating of the redness of soil colour was calculated from the Munsell soil colour chart classifications (Munsell Color 1990), according to the formula:

redness rating =
$$((10H)C)/V$$
 (1)

where *C* and *V* represent the chroma and value of the soil colour classification, and *H* is the figure preceding the yellow–red (YR) hue, such that for 5YR, H = 5 and for 10R, H = 0 (Torrent et al. 1983; Duivenvoorden and Lips 1998). A GPS was used to obtain the geographic coordinates of each plot, where canopy cover was not too dense. The waypoint with the highest internal accuracy reading for each transect was

	Ironnental variables.		
Type of environmental factor	Variable name	Descriptor type	Data collection
Topography	Elevation Position Slope	Quantitative Ordinal Ordinal	Altitude measured in meters above sea level, with an altimeter Position in the landscape: $1 = \text{valley}$, $2 = \text{slope}$, $3 = \text{hilltop}$ Steepness of slope: $1 = \text{flat} (<5^{\circ})$, $2 = \text{medium} (5-35^{\circ})$, $3 = \text{steep} (>35^{\circ})$
Land-use ^a	Farm Fallow Secondary forest Disturbed forest Intact forest Trail	Binary Binary Binary Binary Binary Binary	Field or farm Early secondary regeneration (less than 5 years) Later secondary forest (more than 5 years) Disturbed primary forest (from harvesting or windthrows, often with a mix of primary and invasive species; in some cases may be old secondary forest, >20 years) Intact primary forest in plot Trail or footpath present in plot
	Stumps	Binary	Stumps present in plot
Forest structure	Herb Understory Canopy Gap	Ordinal Ordinal Ordinal Binary	Density of herb layer (less than 1 m height): $1 = \text{open}$, $2 = \text{medium}$, $3 = \text{dense}$ Density of understory layer $(1-10 \text{ m})$: $1 = \text{open}$, $2 = \text{medium}$, $3 = \text{dense}$ Canopy cover: $1 < 25\%$ cover, $2 = 25-50\%$ cover, $3 = 50-75\%$ cover, $4 > 75\%$ cover Presence of treefall gap in plot
Drainage	Upland Stream Seasonal stream River	Binary Binary Binary Binary	Upland site, no stream present Presence of stream in plot Presence of seasonal stream in plot River or riverbank in plot
Edaphic	Clay Sand Loam Redness	Binary Binary Binary Quantitative	Soil texture clayey Soil texture sandy clay Soil texture loamy clay Redness rating of top 5 cm of soil profile, calculated from Munsell soil colour chart, using Equation (1)
	Limestone Rocks	Binary Binary	Limestone rocks or outcrops present in plot Other rocks present in plot
Other	Burn98	Binary	Plot burned in forest fires during El Niño in early 1998

^a We use the term 'land-use' to refer to anthropogenic uses (i.e. agricultural) as well as to successional stage of the forest since successional processes are often manipulated in traditional forest management systems (i.e. Balée and Gely 1989).

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ental variables Table 2 Definition of enviro chosen, and the coordinates for the remaining plots on the transect were calculated from this reference point. The average accuracy of the reference points was ± 16 m.

Field work was conducted between September 1998 and April 1999. To control for seasonal and/or temporal differences, the sampling order of the transects was randomized. A total of 52 transects were surveyed, comprising 154 sampling sites. The total sampling effort across the territory was approximately 14 ha or 0.4% of the territory. Data from four additional transects (12 sampling sites), positioned in areas rich in particular species, were included for analyses of size class–habitat relationships, but not for those of distribution using partial canonical analysis, reported below.

Data analysis

The determinants of species distributions were examined by means of partial canonical analysis, following Borcard et al. (1992), Borcard and Legendre (1994) and Legendre and Legendre (1998, pp 769–779). This method allows a partitioning of the variability of the species data with respect to environmental and spatial components. Here two sets of explanatory variables were investigated: (1) environmental variables describing the abiotic and biotic environment, and (2) the geographic coordinates of the sampling plots, expressed as a third-order polynomial. The use of the latter is related to trend surface analysis and is intended to model the spatial structure of the species distributions. The aim of the analysis was to partition the variance explained by these two sets of variables in order to (1) evaluate the extent to which the species distributions were related to the environmental factors and (2) identify spatial structures which remained unexplained by the recorded environmental variables.

Canonical ordinations were performed to relate the species data to each of three explanatory matrices: a matrix containing the environmental variables, a second one with the terms of the spatial polynomial, and finally a matrix that includes both the environmental and spatial variables. Based on these three analyses, the variation in the species matrix can be partitioned into four fractions: (a) non-spatially structured variation explained by environmental factors, (b) spatially structured variation explained by environmental factors, (c) spatially structured variation not explained by the environmental variables, and (d) unexplained variation. The interest in the present study was to identify fractions (a + b) and (c).

For this analysis, the species presence/absence data, pooled from the 'A' and 'B' plots at each sampling site, was related to the explanatory data matrices using redundancy analysis (RDA). RDA is a linear form of canonical analysis which produces an ordination based on principal component analysis (PCA), in which the axes are constrained to be linear combinations of the explanatory variables. Although RDA is generally not appropriate for the analysis of species presence/absence or abundance data which contain many zeroes, Legendre and Gallagher (2001) have recently proposed a series of transformations for species data which permits the application of RDA to such data.¹ RDA on transformed species data provides an alternative to the unimodal method of canonical correspondence analysis (CCA), which has the disadvantage of weighting species according to the inverse of their frequency such that rare or uncommon species tend to dominate the analysis. In the present study, each of the five transformations proposed by Legendre and Gallagher was calculated to determine which transformation yielded the best representation of the species data, as judged by the explanatory power of the RDA. The 'Hellinger distance' transformation served this purpose and was employed for all RDAs involving the presence/absence data matrix.

To make the explanatory data matrices (environmental and spatial) compatible with the pooled presence/absence species data, one of either the 'A' or 'B' plot at each sampling site was randomly selected (using the random number function in Excel) for inclusion in the analysis. The categories of nominal environmental variables were coded as dummy variables. The spatial data matrix was constructed using the terms of a third-degree polynomial calculated from the centred X and Y variables obtained from a PCA rotation of the geographic coordinates, as in Legendre and Legendre (1998, p 767). To reduce the large number of environmental variables to a subset which could be more easily interpreted in the biplots, the forward selection procedure available in the program CANOCO was employed. In this procedure, the explanatory variables are listed in terms of the increase in explained variation (called 'extra fit') which would be obtained by adding the variable to the ordination (in this case RDA), and the significance of the extra fit is evaluated with a Monte Carlo permutation test. The best variable is added to the model and the procedure is repeated until no significant extra fit is obtained by adding more variables. For this study, all environmental variables with $P \le 0.10$ were included in the analysis. When one category of a nominal variable was selected, some of the other categories were included to aid interpretation of the species' associations with the variable. Forward selection was also used for the RDA of species vs. the spatial variables in order to determine the combination of polynomial terms which best related to the species data. In this case the total α -level was maintained at 0.05, such that the global *P*-value for all selected terms of the polynomial did not exceed this level.

In addition to the partial canonical analysis, several other RDAs were performed to investigate habitat associations and spatial structure in more detail. For habitat associations, two additional analyses were conducted. In the first one, the most dominant variables in the original species vs. environment analysis were set as covariables in order to examine more subtle species–environment relations. In the second analysis, differentiation in habitat preferences among SC was investigated, using the species abundance data from the 'A' plots. In this case, the species matrix was prepared in such a way that the SC for each species were included as separate columns or descriptors; only species with more than five individuals per size class were included in the matrix. For this data matrix, the Legendre and Gallagher's 'distance between species profiles' transformation was found to be the most efficient. Forward selection of the environmental variables was applied to both of these analyses, using the same criteria as described above. Finally, in order to examine the spatial structures identified in the

partial canonical analysis, the RDA of species vs. the spatial polynomial was repeated, this time setting the environmental variables as covariables in order to partial out their effect. The fitted site scores along the first two canonical axes of this RDA were calculated for a 100×100 m grid of geographical coordinates covering the study area, and mapped as a contour plot in the program SigmaPlot version 4.

RDAs and PCAs were performed with the program CANOCO version 4 for Windows (ter Braak and Smilauer 1998). Monte Carlo tests (with 999 random permutations) were used to evaluate the statistical significance of the first ordination axis, as well as that of all canonical axes together using the trace statistic, for all RDAs performed. For the forward selection procedures 199 permutations were used. Maps of species distributions were prepared using the GIS program ArcView version 3.1 (ESRI, California, USA).

Results

Patterns of distribution and abundance

Of the 154 sampling sites, 50% were found in intact forest and 26% in disturbed forest, while the remaining 24% were located in farms (1.3%), fallows (11.7%) and secondary forest (11.0%). Farms and fallows tended to be concentrated in the regions within 1 h walking distance (4–5 km) from the village, and especially in low areas near the Chucunaque river.

The visualization of the species occurrences revealed several distinct distribution patterns, which can be characterized as (1) widespread, (2) predominantly southwestern, (3) absent in the centre (near the village), and (4) rare (Figure 2). In part, the accuracy of our representation of the distribution patterns depends on each species' relative occurrence, which varied greatly among species (Table 3). *Astrocaryum, Bac-tris, Gustavia, Oxandra* and *Sabal*, for example, were found in more than 50% of the sites ('A'+ 'B' plots pooled). Since less than 5% of the sites contained *Swietenia, Peltogyne, Genipa, Symphonia Dalbergia* and *Arrabidaea*, the distribution patterns of these species may not be as well characterized. 'Puarsip' and 'Sianele' were not encountered in the survey. Abundance followed the same general trends as occurrence, with the exception of *Aechmea*, whose clonal habit makes it the most abundant species although it was found in only about half of the plots.

Factors controlling species distributions

The results from the partial canonical analysis, summarized in Table 4, reveal that the distribution patterns of the species exhibit both significant species–environment relations and non-random spatial structures independent of the measured environmental variables. For the RDA of species occurrences vs. environment, 10 environmental



Figure 2. Distribution maps of species occurrences. Four distribution types are recognized: (A) widespread across territory, (B) skewed towards southwestern part of the study area, (C) absent in centre, near village, (D) rare. 'Puarsip' and 'Sianele' were not encountered in the survey and may also be considered rare. The location of the village is indicated with a black square.

variables were retained by the forward selection procedure; these plus five others of interest were included in the analysis. Five of the spatial polynomial terms were significant in the RDA of species occurrences vs. spatial polynomial (Table 5). Both the first canonical axis and the trace of these ordinations were significant (P = 0.001). The total variation in the species data explained by the combination of the two sets of variables was 33.5% (Table 4). Partitioning this explained variation into its components, we find that 60.6% is related to non-spatially structured environmental factors, 17.0% to spatially structured environmental factors, and the remaining 22.4% to the spatial structure independent of the measured environmental variables. The environmental variables most correlated to spatial structure (i.e. spatially structured environmental factors) were elevation, land-use, slope, and canopy closure.

At the level of individual species, the overall fit ranged from 6.8 to 46.9% of variance explained; species differed widely in the relative contributions of the three components in explaining their distributions (Figure 3). Overall, the environmental fraction (including the spatially structured component) accounted from 43.9 to 98.1%



Figure 2. Continued.

of species fit, while the proportion related to spatial structure alone ranged from 1.9 to 56.2%. The nature of individual species' habitat associations and spatial structures are described in more detail below.

Habitat associations

The habitat associations of the species can be derived from the RDA of species vs. environmental variables, conducted as part of the partial canonical analysis reported above. Among the 15 explanatory variables included in the analysis, canopy closure, land-use (fallows and intact forest) and elevation had the highest correlations with the ordination of the sites along the first canonical axis (r = -0.64, 0.62, -0.61, and -0.53, respectively), and therefore are most important in explaining the species distributions. Examining the biplot of this ordination (Figure 4A), the species' habitat associations can be divided into three main groups. Related to intact forest, closed canopy and higher elevations are *Socratea, Oenocarpus, Bactris, Heteropsis* and *Bunur*. This group is also associated with seasonal streams. The second group, located in the bottom left part of the biplot includes *Oxandra, Aechmea, Myroxylon*

		Abund	lance			
Species	Occurrence	SC2	SC3	SC4	SC5	Total
Astrocaryum standleyanum	89	411	16	12	16	455
Bactris coloradonis	69	53	173	110	2	338
Gustavia superba	63.9	776	73	16	0	865
Oxandra sp.	63.2	296	25	6	1	328
Sabal mauritiiformis	50.3	281	31	12	49	373
Aechmea magdalenae	49.7	-	-	-	-	2380
Myroxylon balsamum	42.6	177	11	6	10	204
Apeiba tibourbou	36.1	130	27	12	3	172
Carludovica palmata	32.3	-	-	-	-	337
Oenocarpus mapora	29.7	38	28	9	27	102
Heteropsis oblongifolia	26.5	-	-	-	-	71
Socratea exorrhiza	20.6	76	63	32	34	205
Cordia alliodora	18.1	45	12	4	0	61
Ochroma lagopus	14.8	194	3	2	0	199
'Bunur-sapi'	14.2	28	2	1	2	33
Swietenia macrophylla	5.8	20	0	0	2	22
Peltogyne purpurea	2.6	0	0	0	1	1
Genipa americana	1.9	1	0	0	1	2
Symphonia globulifera	1.9	10	0	0	2	12
Dalbergia retusa	1.3	0	0	0	1	1
Arrabidaea chica	0.6	-	-	-	-	2

Table 3. Occurrence (% sampling sites where present) and abundance by size class (total no. of individuals).

Listed in order of decreasing occurrence. SC - size classes.

Table 4. Variance partitioning results from the partial canonical analysis.

Fractions of variation ^a	Proportion of species variation (trace)	F-ratio (P-value)	Eigenvalue, first canonical axis	F-ratio (P-value)
(a + b)	0.26	3.497 (0.001)	0.135	21.750 (0.001)
(b + c)	0.132	4.487 (0.001)	0.067	10.662 (0.001)
(a+b+c)	0.335	3.546 (0.001)	0.136	21.066 (0.001)
Fractions	Proportion of	<i>F</i> -value	% of total explained	
(a)	0.203	(P-value) 2.919 (0.001)	(a + b + c) 60.6	
(b)	0.057	_	17	
(c)	0.075	2.982 (0.001)	22.4	
(d)	0.665	-	-	

Significance of the trace and the first canonical axis were assessed using Monte Carlo tests based on 999 permutations.

^a The fractions are: (a) non-spatially structured variation explained by environmental factors, (b) spatially structured variation explained by environmental factors, (c) spatially structured variation not explained by the environmental variables and (d) unexplained variation.

and *Astrocaryum* and is associated with disturbed forests, streams, and steeper slopes in valley bottoms. *Gustavia* is also associated with disturbed forests, as well as secondary forests and trails at low elevations. Finally, *Ochroma, Apeiba, Cordia* and

		Variance		
Analysis	Variable	explained (%)	F-ratio	P-value
Species vs. spatial	Y	0.05	8.41	0.005
structure	XY	0.02	3.26	0.005
	X^2	0.02	3.2	0.005
	X	0.02	2.51	0.01
	XY^2	0.02	4.23	0.005
		Sum of P	-values $= 0.03$	
Species vs. environment	Fallow	0.08	14.05	0.005
	Intact forest	0.05	8.03	0.005
	Canopy	0.02	4.12	0.005
	Elevation	0.02	3.24	0.005
	Upland ^a	0.01	2.32	0.01
	Herb	0.02	2.17	0.02
	Slope	0.01	1.8	0.045
	Rocks	0.01	1.91	0.025
	Trail	0.01	1.58	0.08
	Burn	< 0.01	1.76	0.04
	Farm	0.01	1.54	0.07
	Secondary forest	-	_	_
	Disturbed forest	-	-	_
	Position	-	_	_
	Stream	-	-	_
	Seasonal stream	-	_	_
Species vs. environment,	Elevation	0.02	3.1	0.01
controlling for light	Herb	0.01	2.15	0.005
	Slope	0.01	1.91	0.035
	Seasonal stream	0.01	1.87	0.03
	Burn	0.01	1.96	0.02
	Position	0.01	1.43	0.11
	Rocks	0.01	1.54	0.06
	Trail	-	-	-
	Redness	-	_	-

Table 5. Variance explained by each selected explanatory factor in the forward selection procedure of the partial canonical analysis.

Explained variance is expressed in terms of conditional effects (i.e. the extra fit attributed to the variable). Significance was assessed using Monte Carlo tests (199 perumutations under the reduced model). ^a The variable 'upland' had a large variance inflation factor (thus unduly biasing the analysis) when the other 'drainage' categories 'stream' and seasonal stream' were included in the analysis. The 'upland' category was therefore removed, since interpretation of drainage could more easily be made with the other categories.

Carludovica are early successional species found primarily in farms and fallows. *Sabal* is also positioned near this group but this association is much weaker, as indicated by the shortness of its vector in the figure. This species, as well as *Ochroma* and *Apeiba* are also associated with sites burned in early 1998. In general, the habitat associations of the rare species are not well characterized by this analysis. The environmental variables slope, position, and seasonal streams, while shown in the biplot, are better represented by the third canonical axis of this ordination. Examination



Figure 3. Percentage of species fit by component, from the partial canonical analysis. Percentage fit is for all canonical axes together. (a) Black – environment only, (b) light grey – spatially structured environment, (c) dark grey – spatial structure only. The spatially structured environment component is negative when the variance explained by the spatial and environmental variables combined is less than that explained by the sum of the components.

of biplots with the third axis (data not shown) reveals that *Heteropsis*, *Oenocarpus* and *Sabal* are most related to high topographic positions, whereas *Bactris*, *Aechmea*, *Gustavia* and *Apeiba* are associated with steep slopes in low valley positions.

In order to investigate more subtle species–environment relations, a partial RDA was performed, controlling for variables related to light environment (canopy closure and land-use) which dominated the previous ordination. In this analysis, seven environmental variables were significant in the forward selection procedure (Table 5). The resulting ordination accounted for 10.8% of the species variation, after controlling for the covariables (P = 0.001, 999 permutations); species fits ranged from 2.7 to 14.8%. The topographic variables had the highest explanatory power, the first axis being mostly related to elevation (r = 0.33), while the second axis was most strongly correlated with topographic position and slope (r = 0.29 and -0.22, respectively) (Figure 4B). For several species, new habitat associations are evident after controlling for light environment. In this analysis, *Oenocarpus* and *Bactris*, for example, which were previously related to high elevations, exhibit closer associations with high topographic positions and seasonal streams, respectively. The variable burn98 is not



Figure 4. Correlation biplots from RDAs of species presence/absence constrained by (A) 16 environmental variables, and (B) environmental variables, controlling for canopy closure and land-use. The species, as well as the quantitative and semi-quantitative environmental variables, are represented by vectors (arrows). The nominal environmental variables are represented by points (circles) at the centroids of the sites where they occur. Species with low percentages of variance explained were removed from the biplots. Correlation biplots may be interpreted as follows: the angles between species and quantitative environmental variables reflect their correlations; the distance between centroids, however, is meaningless; the projection at right angle of a centroid on either species vectors or canonical axes approximates the value of the variable on that axis.

well represented in this biplot; however, examination of axes 3 and 4 (data not shown) reveals close associations of *Apeiba* and *Astrocaryum*, and to a lesser degree *Ochroma* and *Carludovica* with this variable. This distinguishes *Cordia*, which was unrelated to burned sites, from the other early successional species. *Sabal* appears strongly related to flat slopes and somewhat to higher topographic positions, as opposed to *Aechmea* which is often found in steep ravines and valley bottoms. *Myroxylon* and *Oxandra* are not necessarily related to valleys as could be interpreted in Figure 4A (i.e. before controlling for light), but do appear associated with redder soils at lower elevations.

Habitat differentiation by life stage

The habitat associations described above were based on occurrence data for all individuals >50 cm in height. To what extent might these associations differ according to life stage? To explore this question, an RDA was conducted with each species' abundance separated by size class. To maximize the representation of pioneer and shade-tolerant species, separate analyses were conducted for each of these guilds. Forward selection results for the two ordinations are shown in Table 6. As expected for pioneers, size class 2 of all three species are associated with more early successional habitats than larger SC (Figure 5A). Large individuals of *Cordia* and in

Analysis	Variable	Variance explained (%)	<i>F</i> -ratio	P-value
Pioneer species	Canopy	0.03	4.77	0.005
*	Seasonal stream	0.08	3.23	0.01
	Slope	0.04	2.48	0.035
	Farm	0.03	1.97	0.115
	Fallow	0.05	2.42	0.035
	Burn	0.02	2.18	0.045
	Elevation	0.02	2.13	0.03
Shade-tolerant species	Canopy	0.07	12.63	0.005
-	Fallow	0.03	5.28	0.005
	Farm	0.02	2.89	0.025
	Understory	0.02	2.78	0.02
	Elevation	0.01	2.59	0.015
	Position	0.01	2.33	0.04
	Secondary forest	0.01	1.98	0.11
	Burn	0.01	2.06	0.055
	Stump	0.02	1.95	0.105
	Seasonal stream	0.01	1.97	0.065
	Rocks	< 0.01	1.62	0.01
	Redness	-	-	-

Table 6. Variance explained by each selected explanatory factor in the forward selection procedure of the analysis of size class–environment relationships.

Explained variance is expressed in terms of conditional effects (i.e. the extra fit attributed to the variable). Significance was assessed using Monte Carlo tests (199 perumutations under the reduced model).



Figure 5. Correlation biplots from RDAs of size class abundances constrained by environment, for (A) light demanding species, and (B) shade tolerant species. To improve representation in B species are represented by points (triangles) rather than arrows, positioned where the tips of the vectors would be. In addition, the vector lengths were divided by their standard deviations. Therefore, the length of a species' vector is not indicative of the % fit of that species. Otherwise, interpretation of the biplot is the same as in Figure 4.

particular *Apeiba* remain in more closed forests, which explains the broader distribution patterns of these two species as opposed to *Ochroma* (Figure 2). Size class 2 of *Cordia* is better represented in the fourth canonical axis, where it is found to be unrelated to burned sites, which is consistent with Figure 4B, above. In the case of the shade-tolerant species (Figure 5B), *Gustavia* and *Sabal* both exhibit associations of their smallest size class with more open sites and in fallows and secondary forest. In addition, *Sabal*'s regeneration appears closely related to burned sites. *Socratea*, *Myroxylon*, 'Bunur' and *Oxandra* all show close associations among all SC. All these species were observed to frequently regenerate in large patches around adult trees, possibly reflecting some form of dispersal limitation. *Astrocaryum* exhibits an interesting pattern with size class 4 being associated with farms, in direct opposition to size class 2.

Unexplained spatial structures

Examination of the spatial structures identified in the partial canonical analysis (above) can serve to illuminate the nature of additional processes which might influence species distributions. Maps of the fitted site scores for the first two canonical axes of the RDA of species vs. spatial polynomial, controlling for the environmental variables, are shown in Figure 6. The first canonical axis (Figure 6A) exhibits a gradient from negative values in the southwest to positive values in the north and northeast. The structure associated with the second axis (Figure 6B) is more complicated with peaks in the northwest and southeast corners, separated by a trough from southwest to northeast. Interestingly, the four palm species, Sabal, Socratea, Astrocaryum and Oenocarpus were the best represented by these spatial structures with 22.6, 13.8, 10.6, 9.6% of their total variation being explained, respectively. Aechmea had 10.4% of its variation explained. Examination of the RDA biplot (Figure 7), in combination with the maps of canonical components 1 and 2 (Figure 6), reveals that Sabal, Oenocarpus, Heteropsis and Myroxylon are all associated with the southwestern portion of the gradient in axis 1, while Astrocaryum and Gustavia are more closely related to the northern, positive portion. Similarly, Aechmea and Oxandra are related to the peaks in the axis 2 map, whereas *Socratea* is associated with its northeastern trough.

Discussion

Studies of species distributions and habitat associations may contribute to efforts to develop sustainable management strategies for indigenous communities. It has indeed been suggested that wild harvests of forest products may need to be supplemented with agricultural or sylvicultural management of key resources to ensure sustainable yields (Gunatilleke et al. 1993; Ocampo 1994; Boot 1997). In fact, domestication



Figure 6. Maps of spatial structure left unexplained by the 16 environmental variables in the partial canonical analysis. Surfaces are interpolated from the fitted site scores along (A) the first canonical axis, and (B) the second canonical axis, from the RDA of species presence/absence constrained by spatial polynomial, controlling for environment.

of wild plants are common management strategies employed by indigenous people (Caballero 1994a; Casas et al. 1996); in some cases domestication may be preferred to reducing or modifying harvesting practices as a conservation strategy. Assessments



Figure 7. Correlation biplot from the RDA of species vs. spatial polynomial, controlling for the 16 environmental variables. The relationship of the species with each of the canonical axes (mapped in Figure 6) can be interpreted from this biplot.

of plant distribution and abundance can serve to identify preferred habitats as an initial step toward domestication (Coradin and Lleras 1988; Hall and Bawa 1993). For many species in the tropics this basic information is lacking or is restricted to casual observations from a few sites. Here we examined the distribution and ecology of 23 culturally important plant species over more than 3000 ha to provide guidelines for future conservation.

Spatial patterns on an inhabited landscape

The territory used and managed by the villagers of Nurna is a largely forested landscape. The plant resources that it harbors, however, occur in a variety of spatial patterns. Overall, much of the spatial structure was related to human influence on the landscape. This is evidenced by the dominance of canopy cover and land-use in the analyses of species distributions, which likely reflects the patterning of activities such as agriculture, mechanized logging, as well as smaller-scale disturbances such as trail

openings, tree fellings, collection of forest products. Such anthropogenic factors are likely more important than natural disturbances such as tree-falls in determining the dynamics of light regimes on Nurna's territory. Most studies of species distributions in tropical forests have focussed exclusively on non-inhabited primary forest sites. Our results suggest that it is important to recognize the importance of land-use dynamics as well as their variability. Land-use patterns are indeed likely to vary according to socio-cultural factors such as settlement patterns, land-tenure regimes and population density. A companion study led by one of us (CP) indicates that in Ipeti, an Embera village some 75 km from Nurna, early and late successional habitats are interspersed over the territory. This contrasts with Nurna where most farms and fallows were found closer to the village. We believe that the spatial patterns of these cultural landscapes are due to the land-tenure regimes. In Ipeti the territory has been divided among households and each plot is managed to maintain a mix of successional stages (Dalle and Potvin submitted). This is in contrast to Nurna where all of the forested land is communal. In another study (Frei et al. 2000), different habitat use for collection of medicinal plants was reported in relation to settlement pattern. In that study, the dispersed settlement pattern of Zapotec communities in Mexico permits increased access to a variety of habitat types. Conversely, the Mixtec who live in nuclear settlements rely more heavily on early successional habitats. Variation in land-use dynamics, thus, is likely to impact how resources are distributed across local territories. Clearly, 'community-based' conservation needs to consider local decisionmaking processes and land-use dynamics (i.e. Gilruth et al. 1995) as well as biological information.

Additional factors explaining species distributions

Our data suggest that light availability may be of greater importance in structuring species distributions in inhabited landscapes as compared to non-inhabited sites. When light availability has been considered in analyses of non-inhabited landscapes, its effect has generally been found to be secondary. For example, Svenning (1999) found that topography was more important than drainage or canopy height in explaining micro-habitat associations of palms in a 50 ha plot in Ecuador. A similar result was found for Pteridophytes and Melastomataceae in the Peruvian Amazon (Tuomisto et al. 1995). In our study, topography and drainage became important only after controlling for the effect of light. It is possible that our sample of useful plants may be biased towards species which thrive in high light environments. Some studies have indeed suggested that people may be more likely to use plants found in early successional habitats, due to their increased accessibility (Kohn 1992; Frei et al. 2000; Stepp and Moerman 2001).

In most studies of species distributions, environmental conditions usually only account for a fraction of the total variation in species distributions; in our data, 27% was accounted for by environment. We used a type of trend surface analysis in order

to characterize spatial structures which were left unexplained by the environmental variables measured in our study. Examination of these structures suggests several possible phenomena which might help to understand our species distributions. The spatial structure observed in Figure 6B, for example, suggests phenomena related to the distance from the village affect the distributions of several species. Possible explanations may include reduction of populations due to harvesting or pressure on dispersers due to hunting. People in Nurna have, in fact, observed declines in populations of *Socratea* and *Oxandra* (Dalle and Potvin submitted), two species related to this structure. The hypothesis of anthropogenic pressure on these species, therefore, seems consistent with local people's observations, although it seems less plausible for *Aechmea* which is not heavily used (Dalle and Potvin submitted).

The SW-NE gradient found in Figure 6A, on the other hand, suggests an abiotic cline, possibly related to edaphic factors, such as pH, which were not reflected in the variables measured (i.e. soil colour and texture). This hypothesis seems likely in the case of Sabal, the species most strongly related to this structure, which is reported by Zona (1990) to be 'common on soils derived from limestone'. Examination of the 1:250000 geological map of Darien province (Ministerio de Comercio e Industrias 1976) reveals, in fact, that Nurna lies at the boundary between the volcanic Maje formation from which the San Blas mountains (to the northeast) are derived, and sedimentary deposits (to the southwest), laid down in the late Eocene when the volcanic islands rose from the sea. These deposits are composed of sandstones and limestone, the latter of which is found in calcareous streams to the southwest of the study area. It appears, then, that Sabal may be strongly restricted to limestone-derived soils to the southwest. A similar hypothesis could also be proposed for Myroxylon which exhibits a distribution pattern similar to that of Sabal. In the case of Astrocaryum and Gus*tavia*, whose distributions are associated with the northwestern portion of the spatial structure in Figure 6A, it is possible that the association of these widespread species with wetter microsites may not have been completely captured by the 'drainage' variables used here which documented the presence/absence of hydrological features within the sample plots. This is suggested by the fact that many of the plots which have the highest scores along the first canonical axis are located in areas near the Chucunaque river and tributaries; a more adequate measure of hydrology may be the proximity to such watercourses.

Although the above hypotheses would require verification, this discussion illustrates the utility of trend surface analysis in studies of species distribution patterns. This method may be particularly helpful when working in remote regions where certain types of data and/or topographic maps may be difficult to obtain.

Habitat associations

Of the 23 species considered, we identified habitat associations for 15; the remaining seven occurred at low population densities and could not be adequately sampled in

the present study. It is interesting to note that most of these rare species appear to be poorly known in the literature, suggesting a sparsity of information for rare species in general. This emphasizes the need for improved sampling designs for species occurring at low densities; methods such as the point-quarter or other density estimation measure may serve this purpose (i.e. Lykke 1998).

Of the 15 for which we obtained sufficient data, our study provides new information for several species, such as Heteropsis, Myroxylon, Sabal (and potentially Oxandra and 'Bunur'), for which no formal studies exist in the literature. For other species which have been studied previously, our results generally concur with the habitat associations reported. For example, the association of Oenocarpus mapora to high topographic positions – which tends to be associated with gap openings and possibly high disturbance regimes (Poorter et al. 1994) - is consistent with this species' dominance on windblown environments in the Canal zone (Leigh et al. 1993). Similarly, Gustavia superba's regeneration has previously been found to rely on gap openings to reach maturity (Sork 1985), and Astrocaryum has often been reported to prefer imperfectly drained soils and to respond well to disturbance (Croat 1978; Pedersen 1994; Henderson et al. 1995). Socratea's observed restriction to undisturbed forest is consistent with Araus and Hogan (1994)'s findings that this species exhibits photo-inhibition in gap openings. In addition, Tosi (1971) describes Socratea as a common component of the wetter 'premontane forest' life zone; this is confirmed in our study by its association with higher elevations. More abundant in wetter microsites in freshwater swamps (Scariot et al. 1989), and being ubiquitous in tropical wet forest at La Selva (Clark et al. 1995), Socratea may prefer wetter environments, although does not seem to be restricted to them.

To a certain degree, our study provides some information which may be particular to Nurna or to cultural landscapes. For example, two species found to be rare in our study, Symphonia (ter Steege 1998) and Peltogyne (Perez et al. 1995) are reported to be abundant in swamp forests elsewhere, as may be the case also for *Socratea*. On the other hand, the associations of Astrocaryum and Cordia with burned sites (negative in the case of the latter) have not (to our knowledge) been reported previously in the literature. In this sense, it is important to recognize that rather than representing the ecological requirements of the species *per se*, our data are indicative of the association of individual species with the habitat *available* on the territory of Nurna. In a regional study of species distributions in the Peruvian Amazon, Pitman et al. (1999) found the majority of tree species to exhibit wide geographic ranges and to occur in several forest types (as determined by hydrological regimes). This indicates that more regional surveys, as they become available, may help improve our understanding of species habitat associations. For the purposes of land-management planning, however, an initial survey such as that conducted in the present study, is useful in identifying potential habitat in a given area. Yet it should be recognized that the habitat associations unveiled in a field survey do not necessarily reflect causal relationships. For example, the association of Sabal's regeneration with burned sites reported here may be due to resprouting from its underground stem (Zona 1990), rather than being a germination requirement. Because of the possibility of co-variation with other variables in field surveys, controlled experimental designs are necessary for elucidating causal relationships (Veenendaal and Swaine 1998), and may be particularly useful for identifying germination requirements.

Preliminary suggestions for land management and conservation

One of the objectives of our study was to explore how information on the distribution patterns and habitat associations of species can be used in land-use planning and conservation efforts. To understand the relevance of the results presented here, we can consider the case of the following five species Heteropsis, Sabal, Swietenia, Socratea and Puarsip. These have been identified as declining in abundance, based on local people's perceptions, (Dalle and Potvin submitted) and may be targets for future conservation actions in Nurna. Swietenia is the primary focus of commercial logging in Nurna, and is used for construction of canoes and other items. The other four species are used in different aspects of house construction. Our results here indicate that these five species vary both in terms of distribution patterns and habitat associations (Table 7), which in turn suggests that different conservation strategies will be needed if all five species are to be conserved. In the case of Socratea and Heteropsis, which are associated with intact forests, the conservation of this habitat type will be important. This, for example, might be achieved through the establishment of village reserves as has been reported in other sites (Breslin and Chapin 1988, Pinedo-Vasquez et al. 1992) and would require an understanding of land-use dynamics in the area. On the other hand, a species such as Sabal, which is relatively abundant and tolerant to various forms of disturbance, makes it an excellent candidate for management in agroforestry or other agricultural systems. This strategy has been adopted for related Sabal spp. by the Maya of Yucatan, Mexico in response to deforestation (Caballero 1994b). Although as a (presumably) slow-

8,	8			
Species	Distribution pattern	Habitat association	Other ecological characteristics	Characteristics of use
Swietenia	Southwestern	Intact forest	Hardwood, canopy species	Commercial timber extraction
Sabal	Southwestern	Ecologically variable	Fire/disturbance tolerant	Thatch – only species used
Socratea	Absent near village	Intact forest	Disturbance intolerant	Walls for house – preferred species
Heteropsis	Absent near village	Intact forest	Hemi-epiphyte	Lashing in house construction – only species used
'Puarsip'	Rare	Not known	Hardwood, lower canopy	House post – preferred species

Table 7. Summary of distribution patterns and habitat associations for the five species considered to be declining, according to local knowledge.

growing hardwood species occurring at very low densities 'Puarsip' exhibits very different ecological characteristics as compared to *Sabal*, this species might also benefit management in agroforestry systems through the sparing of adult trees. Sparing of some species is a traditional practice among the Kuna (Castillo and Beer 1983), but it is increasingly being overlooked by the younger generation in Nurna (field obs.). This can be seen in the case of *Astrocaryum* where adults were more closely associated with farms than juveniles, which was explained by the local research assistants to be a result of management practices which were more commonly practised in the past. These involved sparing and/or tending of *Astrocaryum* individuals in order to attract game animals which feed on the palm's fruits.

In terms of distribution patterns, it is interesting to note that the five 'priority' species represent all except for the 'widespread' distribution type described in the present study. Although we have not examined the entire plant community, these distributions likely reflect more general trends of β -diversity which would be important to consider in the establishment of land-use zones or village reserves (Menon and Bawa 1997; Eng 1998). The distribution of particular resources may also indicate the potential impact of new land-uses. This is the case for the commercial extraction of Swietenia, which, due to the dispersed distribution pattern (as well as the lack of adequate planning and monitoring operations), has been spreading quickly throughout the southwestern portion of the territory (field obs.). Logging and related practices (i.e. road construction etc.) may negatively impact populations of other species present in this southwestern zone. Even for species such as Sabal whose regeneration might be promoted by some effects of logging (such as canopy openings), this might be counteracted by the destruction of reproductive individuals which are often knocked down during road and trail construction. Investigations on the community structure and the population dynamics of key species are thus necessary to understand the actual effects of new land-uses.

In addition to providing preliminary suggestions for management strategies, our data may also be useful in order to design more detailed experimental field studies on individual species or land-uses (Clark et al. 1995). For example, the geological disjuncture which appears to restrict *Sabal*'s distribution may affect the population dynamics of other species in more subtle ways (i.e. growth rates or reproductive output might vary with nutrient status of these soils). This would not have been directly interpretable from the geological maps which are too coarse in scale. Pending verification with soil sampling, *Sabal* might be used as a bioindicator of these differing substrate conditions.

Note

¹A pre-print of the article and a program to perform the transformations are available online at www.fas. (umontreal.ca/BIOL/legendre/.)

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