

Structural patterns and floristics of a seasonally dry forest in Reserva Ecológica Chaparri, Lambayeque, Peru

REYNALDO LINARES-PALOMINO^{1,2*} & SUSANA I. PONCE-ALVAREZ²

¹*Department of Systematic Botany, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073-Göttingen, Germany*

²*Herbario Forestal, Universidad Nacional Agraria La Molina, Lima, Peru*

Abstract: To obtain floristic and forest structural data from the threatened seasonally dry forests in northwestern Peru, part of the Tumbes-Chocó-Magdalena biodiversity hotspot, we inventoried all plants with dbh \geq 1 cm in one hectare of forest in the Chaparri Ecological Reserve. We recorded 1255 individuals, representing 24 species, 19 genera and 12 families. The most abundant species was *Cordia lutea* (Boraginaceae, 249 individuals), the most diverse genus *Capparis* (Capparaceae) and the most diverse family Leguminosae. These results show that the forest plot in Chaparri represents an impoverished version of the seasonally dry forests in the region and is most similar, compositionally and in structure, to the seasonally dry forests located on the lower western slopes of the northern Peruvian Andes. Exploratory spatial pattern analyses of the most abundant species suggest that their dispersal properties were primarily responsible for the different observed patterns.

Resumen: Con el fin de obtener datos florísticos y de estructura del bosque de los bosques estacionalmente secos amenazados en el noroeste del Perú, los cuales forman parte del punto candente de biodiversidad de Tumbes-Chocó-Magdalena, elaboramos un inventario de todas las plantas con un dap \geq 1 cm en una hectárea de bosque en la Reserva Ecológica Chaparri. Registramos 1255 individuos que representaron a 24 especies, 19 géneros y 12 familias. La especie más abundante fue *Cordia lutea* (Boraginaceae, 249 individuos), el género más diverso fue *Capparis* (Capparaceae) y la familia más diversa fue Leguminosae. Estos resultados muestran que la parcela de bosque en Chaparri constituye una versión empobrecida de los bosques estacionalmente secos en la región y que es más similar, tanto en composición como en estructura, a los bosques estacionalmente secos localizados en las pendientes bajas occidentales de los Andes del norte del Perú. Análisis exploratorios de los patrones espaciales de las especies más abundantes sugieren que sus propiedades de dispersión fueron las principales responsables de los diferentes patrones observados.

Resumo: Para obter dados florísticas e estruturais das florestas sazonalmente secas ameaçadas no noroeste do Peru, parte da área crítica de biodiversidade no Tumbes-Chocó-Magdalena, inventariaram-se todas as plantas com DAP \geq 1 cm num hectare de floresta na Reserva Ecológica de Chaparri. Foram registados 1255 indivíduos, representando 24 espécies, 19 géneros e 12 famílias. A espécie mais abundante foi a *Cordia lutea* (Boraginaceae, 249 indivíduos), o género mais diverso foi o *Capparis* (Capparaceae) e a família mais diversa foi a Leguminosae. Estes resultados mostram que a parcela florestal em Chaparri representa uma versão empobrecida da floresta sazonal seca na região e que é a mais similar, do ponto de vista da composição e estrutura, à floresta sazonalmente seca localizada nas vertentes ocidentais baixas do norte do Andes Peruvianos. A análise exploratória do padrão espacial das espécies mais abundantes sugere que as suas propriedades de dispersão foram primariamente responsáveis para os diferentes padrões utilizados.

* Corresponding Author; e-mail: r.linaresp@yahoo.co.uk

Key words: Dispersal strategy, floristic relationships, Lambayeque, Pacific Equatorial dry forest, Peru, plant inventory, Ripley's K.

Introduction

More than half of the world's remaining seasonally dry forests are located in South America, concentrated in two large contiguous areas in northeastern Brazil and in southeastern Bolivia, Paraguay and northern Argentina (Miles *et al.* 2006). West of the Andes, however, the largest remaining area of seasonally dry forest is located in southwestern Ecuador and northwestern Peru. This area, known as the Equatorial Pacific region, is one of the outstanding biodiversity hotspots of the world, both in terms of species richness, as well as in terms of endemism levels (BirdLife International 2008; Davis *et al.* 1997; Mittermeier *et al.* 2005). Despite these recognitions, little information exists for much of the vegetation in the area, particularly for the seasonal forest and dry open scrub vegetation. This lack of information is even more pressing in the face of the severe threats seasonally dry forests face globally (Maas 1995; Miles *et al.* 2006; Mooney *et al.* 1995) and in the Equatorial Pacific region particularly (Dodson & Gentry 1991; Parker & Carr 1992).

The information resulting from forest inventories not only provides data about the floristic composition and abundances of individual species, it also provides important structural attributes of the vegetation. In this paper, we report results from a forest inventory in the seasonally dry forests of Chaparri, located near the southern extreme of the Equatorial Pacific region in Peru. This region has been shown to constitute a separate biogeographical dry forest unit with little floristic affinities to the other major Neotropical seasonally dry forest areas (i.e., those in the Caribbean/Mesoamerican area, in southern South America and in Brazil) (Linares-Palomino *et al.* 2003). Thus, we aimed to produce botanical and structural information in order to compare the Chaparri forests to the other seasonally dry forests in the Equatorial Pacific region. In turn, we used this information to explore the potential processes that might have influenced the spatial assembly of the most abundant woody species in the Chaparri

seasonally dry forest and to assess the relative importance of their dispersal mechanisms.

Material and methods

Our study site was located in the Reserva Ecológica Chaparri, department of Lambayeque (northwestern Peru), a private reserve of 34412 ha established in 2000 by the Santa Catalina community. The reserve covers an altitudinal range from 150 m to 1533 m and contains a range of seasonally dry forest variations, including semi-deserts, sparse dry forest, lowland *Prosopis*-dominated forest and foothill dry forest (BirdLife International 2008). Former intensive grazing and uncontrolled timber extraction activities have degraded many areas of the reserve. Nowadays, under protection, the natural vegetation is recovering. Rainfall and temperature data for the region are scarce. Data from the Olmos meteorological station (67 km north of our study area and at 367 m altitude) taken over 19 years show low annual precipitation (mean of 160 mm) and mean temperatures of 24°C (CDC UNALM 1992).

We established one hectare plot (100 m x 100 m) in a homogeneous area of forest (6° 31'S, 79° 27' W, 714 m altitude) with no evidence of recent major soil, topographical or human disturbances. We subdivided the plot into 25 adjacent 20 m x 20 m quadrats and inventoried all plants with diameter at breast height (dbh) equal or above 1 cm. For each of these individuals we recorded dbh and its spatial position on a local coordinate system (in metres and to the nearest decimetre) that had its origin in the SW corner of the hectare plot. We calculated relative density, relative dominance (using basal area) and relative frequency for each species in order to estimate the importance value index (IVI) (Curtis & McIntosh 1951).

Common and well-known plants in the region were identified directly in the field. We photographed the rare and unknown plants and collected voucher specimens for later identification using local (e.g., Ríos 1989) and regional taxonomic

works (e.g., Gentry 1993). The collected voucher specimens have been deposited at the Forestry Herbarium of the Universidad Nacional Agraria La Molina, Lima, Peru. Plants for which we were unable to assign species rank, were treated as morphospecies (i.e., morphologically similar specimens that are lumped together and treated as one single species for subsequent analyses). Nomenclature follows the Missouri Botanical Garden Tropicos online database (www.tropicos.org).

We explored univariate spatial point patterns by using the $K(r)$ function for point patterns of second-order neighbourhood. We calculated $K(r)$ and plotted the linearized version of $K(r)$: $L(r)$ as $L(r) = \sqrt{K(r)/\pi} - r$. $L(r)$ has an expectation of zero under the null hypothesis of Complete Spatial Randomness (CSR). $L(r)$ becomes positive when the pattern tends to clustering (or aggregation) and negative when it tends to regularity. We did the univariate analyses only for species with 30 or more individuals. We explored bivariate spatial patterns by using the linearized version of the intertype $K_{12}(r)$ function of second-order neighbourhood: $L_{12}(r) = \sqrt{K_{12}(r)/\pi} - r$, which has an expectation of zero under population independence. $L_{12}(r)$ becomes positive when the two population show attraction and negative when they show repulsion. The bivariate analysis was done to detect interaction between (i) adults and juveniles of the same species (we arbitrarily defined adults as all individuals with dbh ≥ 10 cm, juveniles had a dbh < 10 cm) and (ii) between all individuals of two different species. For the former case, we only used species with both a minimum of 30 adult individuals and a minimum of 30 juvenile individuals; for the latter case, we only used pairs of species in which both had each a minimum of 30 individuals. The null hypothesis for both bivariate analyses corresponded to an absence of interaction between the studied groups, i.e., $H_0 =$ the locations of type 1 and type 2 points (either adults and juveniles, or species 1 and species 2) result from two a priori independent spatial point processes (Goreaud & Pélissier 2003).

We performed univariate and bivariate analyses using Ripley's isotropic edge correction, because it is highly recommended when comparing point patterns or when using $K(r)$ values (or its modified $L(r)$ form) for ecological interpretations (Goreaud & Pélissier 1999). We used 10000 simulated point patterns to estimate local Monte Carlo confidence limits at each distance r . Spatial

analyses were done using the R software (R Development Core Team 2008) and package `ads` (Pelissier & Goreaud 2007).

Results

Floristics and diversity

We recorded 24 species (19 genera and 12 families), of which ten were trees, 12 were shrubs and two were erect (shrub - or treelike) cacti. Two species (Indet 4 and Indet 5, the latter known by the local common name "naranjita de monte") for which we were unable to collect fertile specimens could not be assigned to any taxonomic rank and were treated as morphospecies. Number of species per 20 m x 20 m quadrat ranged from seven to 17 species. The rate at which new species were encountered as the survey progressed increased slowly and the sample-based species accumulation curve showed that our inventory was fairly complete after surveying 20 quadrats (Fig. 1). The most diverse genus was *Capparis*, with three species. The most diverse family was Leguminosae with five species, followed by Capparaceae and Boraginaceae, both with three species.

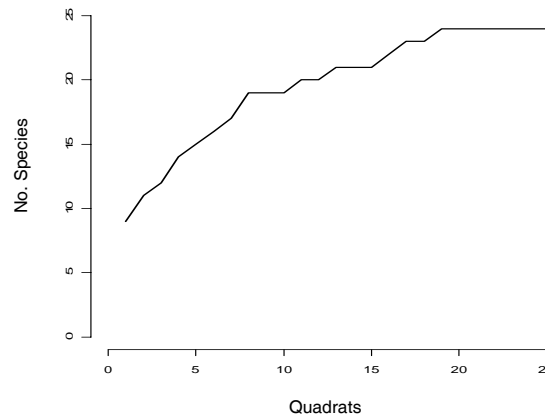


Fig. 1. Sample-based species accumulation curve for 1-ha of seasonally dry forest in Lambayeque, Peru.

Forest structure and dominance

The plot contained 1255 individuals, with 26 to 79 individuals per quadrat. We measured 425 trees stems, 676 shrub stems and 155 erect cacti stems with dbh ≥ 1 cm, with a total basal area of 11.74 m². The majority of the individuals (57%) fell within the 1 - 4.9 cm dbh class, but contributed

less than 3% of total basal area (Fig. 2). Thirteen individuals with dbh ≥ 40 cm accounted for the bulk of the basal area (27%). Mean dbh in the plot.

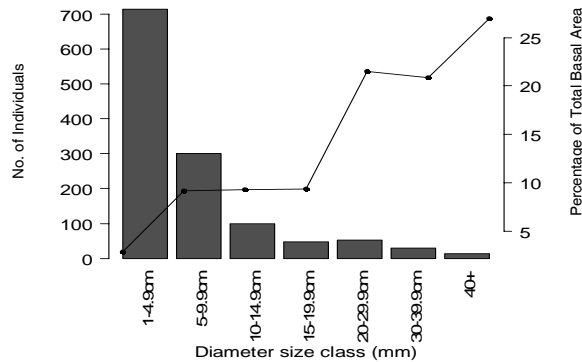


Fig. 2. Number of individuals per size class (bars) and percentage contribution of each size class to total basal area (line).

was 6.8 cm and the maximum diameter attained by any individual in the plot was 76 cm (by a *Loxopterygium huasango* tree). Mean woody plant height of the forest plot was 3.6 m and the tallest individual was another *L. huasango* tree with 14.8 m.

The most abundant species was *Cordia lutea* (Boraginaceae, 249 individuals), followed by *Ditaxis doica* (Euphorbiaceae, 177 individuals) and *Eriotheca ruizii* (Malvaceae-Bombacoideae, 151 individuals). Other common species were *Bursera graveolens* (Burseraceae, 125 individuals) and *Praecereus euchlorus* (Cactaceae, 100 individuals) (Table 1). These five species contributed to 64% of the total number of individuals and 58% of total basal area.

The species with the highest IVI were *E. ruizii*, *L. huasango*, *C. lutea*, *B. graveolens* and *D. dioica*. These five species contained 59% of the number of individuals and more than 90% of the total basal area (Table 1).

Table 1. Dominant species ranked by Importance Value Index (IVI).

Family	Species (Life Form)	N	RDen	BA	RDom	F	RF	IVI
Malvaceae	<i>Eriotheca ruizii</i> (T)	151	12.02	4.40	37.45	25	8.74	58.22
Anacardiaceae	<i>Loxopterygium huasango</i> (T)	36	2.87	4.12	35.07	20	6.99	44.93
Boraginaceae	<i>Cordia lutea</i> (S)	249	19.82	0.61	5.19	25	8.74	33.76
Burseraceae	<i>Bursera graveolens</i> (T)	125	9.95	1.42	12.09	23	8.04	30.08
Euphorbiaceae	<i>Ditaxis dioica</i> (S)	177	14.09	0.06	0.51	25	8.74	23.34
Cactaceae	<i>Praecereus euchlorus</i> (AC)	100	7.96	0.32	2.71	20	6.99	17.67
Nyctaginaceae	<i>Bougainvillea</i> sp. (T)	68	5.41	0.07	0.59	22	7.69	13.70
Cactaceae	<i>Armatocereus laetus</i> (AC)	55	4.38	0.41	3.53	15	5.24	13.15
	Indet 5 (S)	69	5.49	0.03	0.28	19	6.64	12.41
Boraginaceae	<i>Tournefortia</i> sp. (S)	67	5.33	0.02	0.16	19	6.64	12.13
Euphorbiaceae	<i>Croton</i> sp. (S)	55	4.38	0.01	0.10	19	6.64	11.12
Leguminosae	<i>Caesalpinia glabrata</i> (T)	29	2.31	0.21	1.81	16	5.59	9.72
Boraginaceae	<i>Cordia macrocephala</i> (S)	39	3.11	0.01	0.05	11	3.85	7.00
Caricaceae	<i>Carica</i> sp. (T)	6	0.48	0.01	0.05	6	2.10	2.62
Capparaceae	<i>Capparis guayaquilensis</i> (T)	5	0.40	0.00	0.03	5	1.75	2.17
Leguminosae	<i>Mimosa</i> sp. (S)	9	0.72	0.00	0.02	3	1.05	1.79
Asteraceae	Indet 6 (S)	6	0.48	0.00	0.00	3	1.05	1.53
Leguminosae	<i>Pithecellobium multiflorum</i> (T)	2	0.16	0.03	0.28	2	0.70	1.14
Capparaceae	<i>Capparis crotonoides</i> (S)	2	0.16	0.00	0.03	2	0.70	0.88
Leguminosae	<i>Acacia macracantha</i> (T)	2	0.16	0.00	0.01	2	0.70	0.87
Leguminosae	<i>Pithecellobium excelsum</i> (T)	1	0.08	0.01	0.04	1	0.35	0.47
Capparaceae	<i>Capparis aviceniifolia</i> (S)	1	0.08	0.00	0.00	1	0.35	0.43
	Indet 4 (S)	1	0.08	0.00	0.00	1	0.35	0.43
Solanaceae	<i>Solanum</i> sp. (S)	1	0.08	0.00	0.00	1	0.35	0.43
Total		1256	100	11.74	100	286	100	300

Life-Form: T: tree, S: shrub, AC: arborescent cactus. N: number of individuals, RDen: relative density, BA: basal area (m²), RDom: relative dominance, F: frequency, RF: relative frequency.

Spatial patterns within and between species

General spatial patterns for each species

We analysed 12 species represented by a minimum of 30 individuals. Of these, *Armatocereus laetus*, *B. graveolens*, *Cordia macrocephala*, Indet 5 and *P. euchlorus* showed an aggregated pattern at distances beyond 3 m. At shorter distances, the patterns for these species were not significantly different from complete spatial randomness (CSR). *Ditaxis dioica* was similar in this overall pattern, except that it returned to a CSR pattern at distances beyond 20 m. *Bougainvillea* sp. and *L. huasango* showed patterns mostly or completely not significantly different from CSR, respectively. *Cordia lutea*, *Croton* sp. and *E. ruizii* showed a mostly aggregated pattern at distances shorter than 15 m, beyond 15 m the spatial pattern was not significantly different from CSR. *Tournefortia* sp. showed aggregation at short (1.4 m - 5.5 m), intermediate (8.8 m - 12.9 m) and long (15.5 - 25 m) distances (Fig. 3).

Spatial patterns within species: is there any association between adults and juveniles?

We were able to analyse only two species with at least 30 juvenile and 30 adult individuals: *Bursera graveolens* and *Eriotheca ruizii*. We did not find evidence for any kind of association between the populations of adults and juveniles of *B. graveolens* (i.e., their populations were independent). *Eriotheca ruizii*, in contrast, showed statistically significant association between adults and juveniles at very short distances (between 2.4 m and 3.9 m). Adults and juveniles were spatially independent for the rest of the distances (Fig. 3).

Spatial patterns between species: is there any association between species?

Of the 66 possible pair wise comparison among the 12 species with 30 or more individuals, we detected 11 cases with statistically significant spatial attraction and two cases with statistically significant spatial repulsion among the populations of the analyzed species, the latter involving in both cases *C. macrocephala* (Fig. 4). Most of these cases, however, showed attraction/repulsion over very short distance intervals. Exceptions were the patterns shown by *B. graveolens* - *D. dioica* and *B. graveolens* - *E. ruizii* (significant attraction within the first 8 m),

B. graveolens - Indet 5 (significant attraction at distances between 17 m and 25 m), Indet 5 - *E. ruizii* (significant attraction at distances between 20 m and 25 m) and especially by Indet 5 - *L. huasango* (significant attraction at distances between 10 m and 25 m).

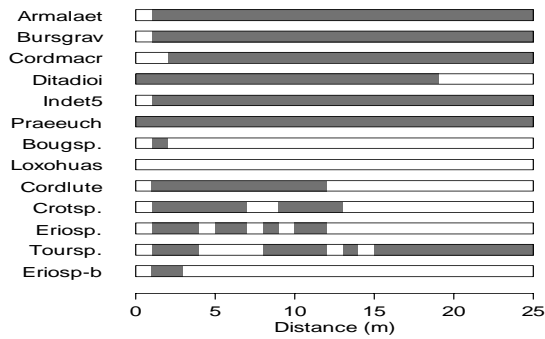


Fig. 3. Univariate (top 12) and bivariate (bottom one) spatial patterns of plant species in a seasonally dry forest using Ripley's K function. White areas indicate that the distribution does not differ from CSR for that distance interval, grey that it is aggregated in the univariate case. In the bivariate case, white areas indicate that the spatial distribution between adults and juveniles is independent, grey that there is significant statistical evidence for spatial attraction between adults and juveniles. Species' abbreviations correspond to the four first letters of the Latin binomial.

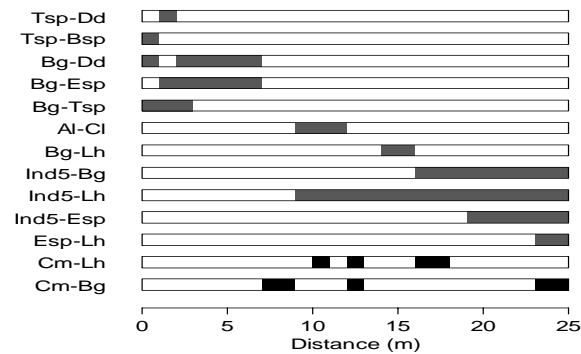


Fig. 4. Bivariate spatial patterns of plant species in a seasonally dry forest using Ripley's K function. White areas indicate that the spatial distribution between species is independent, grey that there is significant statistical evidence for spatial attraction between species and black that there is significant statistical evidence for spatial repulsion between species. Species' abbreviations correspond to the first letters of the Latin binomial.

Discussion

Forest structure and floristic diversity

Direct comparison with other seasonally dry forest inventories in the region is difficult because of unequal sampling methodologies. Some have been done using a smaller survey area (e.g., 0.1-ha transects or plots as in Gentry 1982 and Serván-Mori & Angulo-Pratolongo 2006) and some using a higher dbh cut-off (usually inventorying trees of 10 cm and above). The latter methodology, however, has usually been applied to 1-ha square plots like the one in the present study, allowing us to scale-up our results for comparison purposes. Leal-Pinedo & Linares-Palomino (2005), for example, obtained species richness values between 5 and 37 and densities between 31 and 458 for 16 one-hectare plots in the seasonally dry forest of Tumbes and Piura departments in Peru (north of our study area). If we consider these parameters for Chaparri, i.e., only considering plants with dbh equal to or above 10 cm, our plot would rank among the least diverse seasonally dry forests in the region (with 9 species and 242 individuals). Weberbauer (1945) already mentioned a north to south gradient of decreasing species richness of woody species on the western slopes of the Peruvian Andes attributing it to the increasing xerophytic conditions away from the equator.

There is little additional hectare plot information from the seasonally dry forests in adjacent Ecuador. Granda & Guamán (2006) report 24 species, 14 families, 1106 individuals and a basal area of 17.38 m² for trees with dbh \geq 5 cm in Macará. Josse & Balslev (1994) report 37 species, 22 families, 655 individuals and 7.5 m² of basal area for trees with dbh \geq 5 cm in Manabí. Madsen *et al.* (2001) report 28 species, 19 families, 451 individuals and 15.6 m² of basal area for trees with dbh \geq 5 cm in the thorn forest of Puná island, off Guayaquil. Again, using these same parameters for Chaparri (dbh \geq 5 cm), would result in a count of just 14 species and 543 individuals, making it very poor in terms of species richness.

In the 16 plots reported in Leal-Pinedo & Linares-Palomino (2005), Leguminosae was the most important family, including 34% of all species in them, although individual plots showed other families (especially Bombacaceae) as equally or more important in terms of number of individuals and species diversity. The Chaparri plot was similar in this respect. The Ecuadorean plots also show these characteristics, where Leguminosae is among the three most important families (Granda

& Guamán 2006; Josse & Balslev 1994; Madsen *et al.* 2001). In fact, this family has been identified as the most important of most Neotropical seasonally dry forests (Pennington *et al.* 2006). There was more variation with respect to the most abundant species. The Ecuadorean plots reported *Ampelocera* sp. (Ulmaceae, 35% of all individuals in Pechice, Josse & Balslev 1994), *Simira ecuadorensis* (Rubiaceae, 25% of all individuals in Macará, Granda & Guamán 2006) and *Jacquinia sprucei* (Theophrastaceae, 19% of all individuals in Puná Island, Madsen *et al.* 2001) as the most abundant species. The Peruvian plots, including Chaparri, showed that *Caesalpinia glabrata*, *Geoffroea spinosa*, *E. ruizii*, *B. graveolens*, *Terminalia valverdeae* and *C. lutea* were among the most abundant species. This variation of the most abundant species reflects the variation in the composition of the seasonally dry forests in the region.

Sørensen similarity comparisons with the other 1-ha seasonally dry forest inventories in northern coastal Peru show that Chaparri (nine species with dbh \geq 10 cm) is different in terms of floristic composition and individual species abundances. Sørensen similarity indices with the other 16 plots are well below 50% (range = 3% - 41%). The highest similarity of 41% is with the El Sauce plot (17 species with dbh \geq 10 cm), sharing four species with similar abundances (*L. huasango*, *E. ruizii*, *B. graveolens* and *Pithecellobium multiflorum*). A Nonmetric Multidimensional Scaling analysis using species abundances of each plot, however, shows that Chaparri is peripheral to the other 1-ha seasonally dry forest inventories in northern coastal Peru (Fig. 5), with closer relationships to the plots in El Cardo (eight species), Uña de Gato (six species) and Quebrada Maná (15 species), the latter three all located on the lower western slopes of the southern tip of the Amotape Cordillera. All these Amotape plots have low species richness values and densities below ca. 220 individuals, similar to those in Chaparri.

Exploring the spatial structure: patterns and potential causes

Hubbell (1979) found that all species he analysed in a Costa Rican dry forest were either aggregated or showed a CSR pattern. The study by Linares-Palomino (2005) found more cases of CSR than aggregation. In the present study, seven species showed aggregated spatial patterns over much of the analysed distances. Two additional species

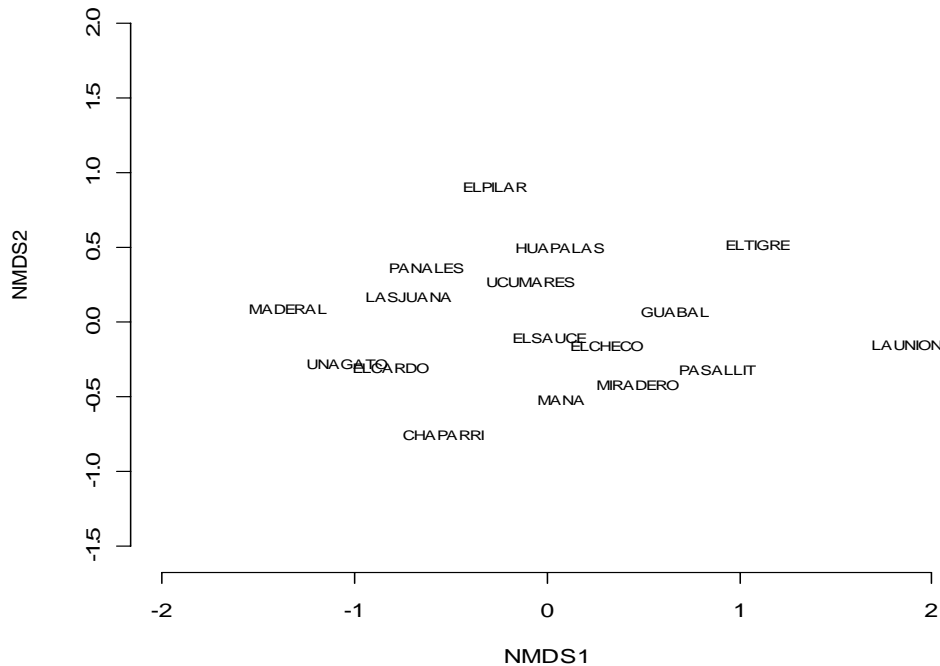


Fig. 5. Nonmetric Multidimensional Scaling analysis (using species abundances of each plot and the Sørensen index) comparing the Chaparri plot with 16 other 1-ha plots in northwestern Peru (data from Leal-Pinedo & Linares-Palomino 2005).

showed a mostly CSR pattern over much of the analysed distance, agreeing with the widely held notion that tropical trees show a mostly aggregated pattern at small spatial scales (Condit *et al.* 2000).

In a previous study of the spatial patterns of four characteristic Peruvian seasonally dry forests species in six 1-ha plots, where only trees with dbh ≥ 10 cm were measured, 11 out of 17 cases (65%) showed patterns not significantly different from CSR (Linares-Palomino 2005). Of these, we found three species at Chaparri (*E. ruizii*, *B. graveolens* and *C. glabrata*), but only two with enough individuals for a spatial analysis. In said study, *E. ruizii* showed a pattern not significantly different from CSR at all scales in all plots. Only *B. graveolens* showed variation in its spatial structure, with aggregated, regular and random patterns.

In the present study, *E. ruizii* showed aggregation at short and CSR at larger distances, and *B. graveolens* showed a strong aggregated pattern. Linares-Palomino (2005) argued that the dispersal properties of these species were

primarily responsible for the observed patterns and the results from Chaparri seem to confirm this. For *E. ruizii*, two events appear important in producing aggregated patterns at spatial scales below 15 m, and CSR beyond. First, the small seeds embedded in abundant kapok (Robyns 1963) are released shortly before the onset on rains. Clumps of kapok and seeds cover the ground underneath the tree (pers. obs.) and little material can be found further away. Second, a higher germination rate of the Brazilian *E. pentaphylla* (Vell.) A. Robyns was shown by Fischer (1997) when the kapok was still adhered to the seeds, as compared to seeds without kapok. This would suggest that seeds carried away from the mother trees by animal dispersers or stripped from the kapok by the wind, would have much lower survival and germination possibilities. The spatial attraction between juveniles and adults of *E. ruizii* at short distances would provide additional evidence for the importance of the two mechanisms in producing aggregated patterns. The strongly aggregated pattern of *B. graveolens* over all the studied distance range (25 m) can also be potentially explained by two events. First, *B.*

graveolens seeds have no structures to facilitate wind dispersal and whilst no disperser has been reported, birds, iguanas and rodents have been assumed to feed on them (Clark & Clark 1981). Second, that same study found that 90% of the young *B. graveolens* trees were within 20 m of a *Bursera* tree, corresponding well with the overall *B. graveolens* pattern found at Chaparri, but contradicting our bivariate analysis of juveniles and adults, which showed spatial independence between both populations. Careful study of isolated mother-tree individuals and seedlings, as well as larger scale inventories might provide additional information on this subject.

Unfortunately, little information exists about the dispersal ecology of the other analysed species at Chaparri. But from what is known about the dispersal mechanisms of some of them, they seem to correspond well with the observed spatial patterns. For instance, the aggregated patterns in *A. laetus*, *P. euchlorus*, *C. macrocephala* and *C. lutea*, all with relatively big or abundant fleshy fruits, suggest that in the absence of animal dispersers most fruits will fall near the mother-tree. The randomly wind-dispersed fruits of *Bougainvillea* sp. (a leathery fruit) and *L. huasango* (a dry samara) could have produced the observed CSR pattern.

There is little evidence for any kind of association in the seasonally dry forests of Chaparri. Only a third of the bivariate species interactions we analysed showed some kind of association (spatial attraction or repulsion), usually over short distances (less than 5 m), making it difficult to make general conclusions. *Cordia macrocephala*, a small shrub, showed repulsion with the large trees of *L. huasango* and *B. graveolens* at several distance intervals. It remains to be seen if this behaviour is a response of the competition for similar ecological requirements (light, soils nutrients) or some kind of allelopathic interaction on part of the two trees, as there is some evidence for growth inhibition of roots and seedlings of other species by several genera in the Anacardiaceae and Burseraceae (e.g., Fujii *et al.* 2003; Morgan & Overholt 2005). Nevertheless, these results contrast with the attraction at short distances found between *B. graveolens* and several other species in the SDF plot.

Although our results provide excellent structural and floristic data for this little known vegetation type in northwestern Peru, the spatial

scale of the study plot is too small to give conclusive results about the assembly mechanisms of this community. However, our data do suggest that species-specific dispersal mechanisms, seedling development and establishment are playing an important role in shaping some of the observed spatial patterns. In order to adequately assess these preliminary hypotheses, we need to work at greater temporal and spatial scales, mirroring successful studies elsewhere (e.g., the STRI forest dynamics plot network, Losos & Leigh 2004).

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