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Population structure of *Eschweilera coriacea* (DC.) S. A. Mori in forest fragments in eastern Brazilian Amazonia

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ABSTRACT – (Population structure of *Eschweilera coriacea* (DC.) S. A. Mori in forest fragments in eastern Brazilian Amazonia). The population structure of a common canopy tree was examined in three sites to investigate the possible effects of forest fragmentation in eastern Amazonia. Evidence for the escape hypothesis of differential seed/seedling survival was evaluated. Two 1 ha plots were established at each site and all individuals of *Eschweilera coriacea* (DC.) S. A. Mori over 1 m tall were tagged, measured and mapped. Smaller individuals were recorded in the same way within subplots. Mature individuals were abundant at all sites with densities of 32-52 ha^{-1}. The species exhibited substantial regeneration, although total population density varied fourfold among sites (1,256-4,805 individuals ha^{-1}). Overall, juveniles were clumped while adults were randomly distributed. The difference between the dispersion pattern of adults and juveniles supported the escape hypothesis. However, no difference in population structure among sites could be related to the forest fragmentation.

Key words - dispersion pattern, escape hypothesis, forest fragmentation, Neotropical forest, population density

RESUMO – (Estrutura populacional de *Eschweilera coriacea* (DC.) S. A. Mori em fragmentos florestais no leste da Amazônia brasileira). A estrutura populacional de uma árvore de dossel comum na Amazônia oriental foi examinada em três áreas para investigar possíveis efeitos da fragmentação da floresta. Evidências para a hipótese de escape referente à sobrevivência diferenciada de sementes/plântulas foram avaliadas. Duas parcelas amostrais de um hectare foram estabelecidas em cada área e todos os indivíduos de *Eschweilera coriacea* (DC.) S. A. Mori acima de um metro de altura foram marcados, medidos e mapeados. Indivíduos menores foram registrados da mesma maneira em subparcelas. Indivíduos maduros foram abundantes em todas as áreas com densidades de 32-52 ha^{-1}. A espécie exibiu regeneração substancial, embora a densidade populacional tenha variado quatro vezes entre as áreas (1.256-4.805 indivíduos ha^{-1}). Em geral, jovens apresentaram-se agregados enquanto adultos eram distribuídos aleatoriamente. A diferença no padrão de dispersão de adultos e jovens deu suporte à hipótese de escape. Entretanto, nenhuma diferença na estrutura da população entre as áreas pôde ser relacionada à fragmentação da floresta.

Palavras-chave - densidade populacional, floresta neotropical, fragmentação de floresta, hipótese de escape, padrão de distribuição

Introduction

In the past half century, development in the tropics has led to large-scale deforestation at unprecedented rates in the evolutionary context of tropical rain forests, which will have profound effects on these ecosystems (Bierregaard Junior *et al*. 1992). Although large undisturbed areas of tropical rain forest can still be found, only small patches remain in many regions, and these patches may constitute the only possibility of preserving these ecosystems (Turner & Corlett 1996).

An increasing number of studies have demonstrated that human-induced changes to natural ecosystems, particularly deforestation and habitat fragmentation, result in significant alterations of distribution and abundance of organisms. The susceptibility of a particular species to habitat disturbance is highly variable, however, and while many species decline or disappear, others remain unaffected or are even benefited (Tabarelli *et al*. 1999, Laurance *et al.* 2002, Lindenmayer *et al.* 2002).

Understanding ongoing processes in forest remnants may be of crucial importance for the management and conservation of natural systems (Bierregaard Junior *et al*. 1992). The processes involved in the regeneration of tree populations, including many plant-animal interactions, may be of particular interest, since they will ultimately determine the floristic composition of the remnants (Laurance *et al*. 1998). For instance, the recruitment of many tree species is animal-mediated, and the loss of seed-dispersal agents is likely to endanger tree species and affect community structure and dynamics (Cordeiro & Howe 2001, Wright & Duber 2001). However, the net effect of fragmentation on plant-animal interactions may have opposite outcomes,

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since it may disrupt beneficial relationships such as pollination and seed dispersal, and decrease antagonistic relationships such as seed predation at the same time (García & Chacoff 2007).

The data presented here are part of a study that investigated the possible consequences for a common canopy tree (*Eschweilera coriacea* (DC.) S. A. Mori, Lecythidaceae) of the loss of potential seed dispersers due to forest fragmentation in eastern Brazilian Amazonia. A natural experimental approach was used in which the structure and dynamics of *E. coriacea* populations were compared at three sites.

Recruitment shortfalls in a tree population can occur at different life history stages, including the arrival of the seeds on the ground, which depends, in turn, on the density and dispersion of adults, adult fecundity, and seed dispersal distances (Clark *et al*. 1998). In this paper, I describe the density, dispersion and population size structure of *E. coriacea* at the three sites, and test the escape hypothesis which postulates disproportionate mortality of progeny near parent plants, caused by distance- or density-responsive seed predators, herbivores, or pathogens (Janzen 1970, Connell 1971, Howe & Smallwood 1982, Clark & Clark 1984, Nathan & Casagrandi 2004). Data on other life stages and population processes are reported elsewhere.

I aim to answer the following questions: 1) Do the dispersion patterns of juveniles, adults and the population as a whole differ among themselves? 2) How do the densities of adults and juveniles vary with distance from individual trees? 3) Are dispersion and abundance patterns in the small forest fragment significantly different from those at the other sites? In addition to characterising the population structure of *E. coriacea* at the three sites, questions 1 and 2 evaluate the escape hypothesis, whereas among-site comparisons (question 3) are relevant to investigate possible effects of habitat fragmentation on population structure of *Eschweilera coriacea*.

Material and methods

Study sites – The three study sites are located in the Brazilian state of Pará, in the easternmost extreme of the Amazonian biome (figure 1). The climate of the three sites is relatively similar (Köppen's Am category), although there is a north-south gradient of decreasing precipitation, which correlates

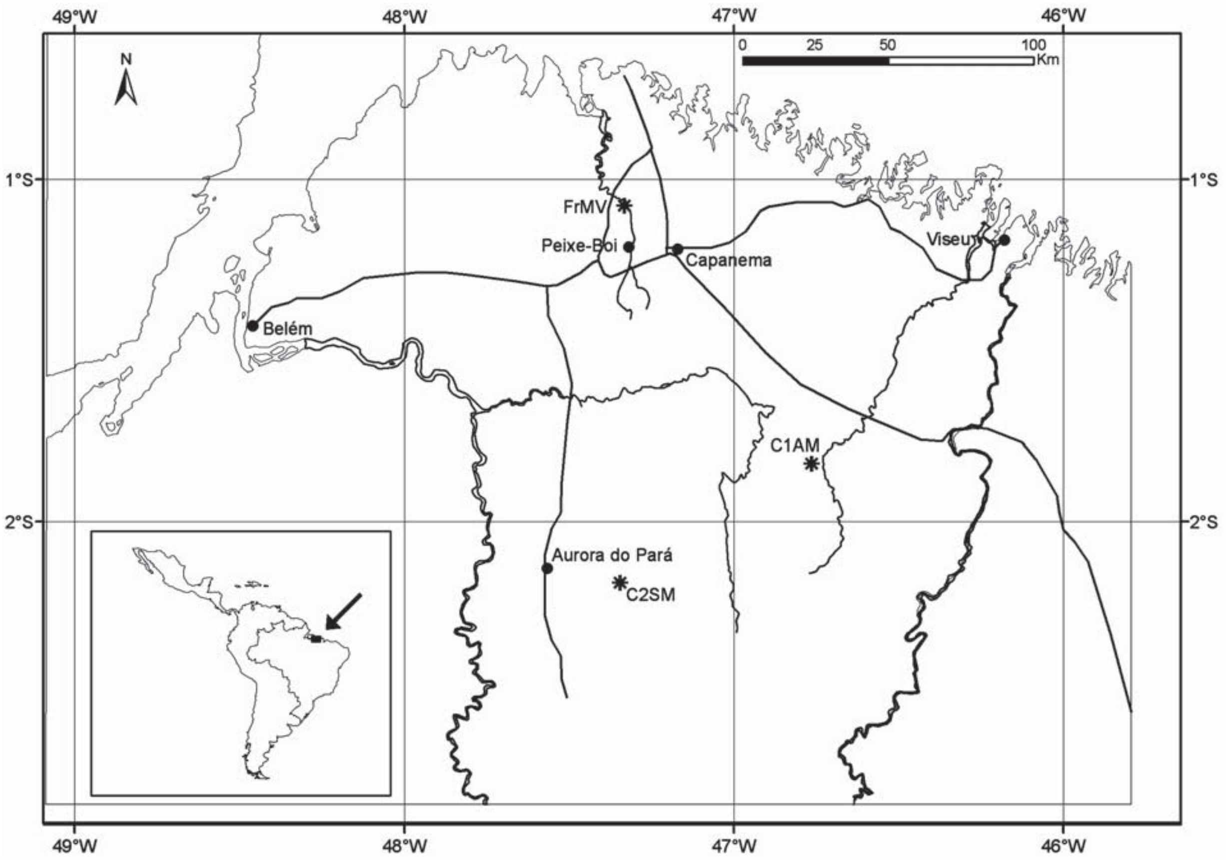

Figure 1. Location of the study sites in eastern Brazilian Amazonia.

with increasing distance from the coast (SUDAM 1984, Diniz 1986, Guimarães *et al*. 2001). Mean annual temperature at all three sites is 25-27 °C, mean annual precipitation is 2,000-2,500 mm and average relative humidity is 80%-85% (Oliveira *et al*. 2002). The rainiest trimester is February to April and the driest is September to November (Guimarães *et al*. 2000). The predominant soil type is yellow latosoil (Silva & Carvalho 1986), and the original vegetation was primarily lowland "terra firme" rainforest (Prance 1989, Veloso *et al*. 1991).

The site at the "Fazenda Monte Verde" (FrMV) in the municipality of "Peixe-Boi" (1°11' S, 47°19' W) is a 200 ha forest fragment of prevailing "terra firme" forest that has been isolated for at least forty years. The region has already lost at least eighty five percent of its original forest cover, resulting in a mosaic landscape of pastures, cultivated fields, secondary forest and remnant patches of primary forest, of which FrMV is the largest (Alencar *et al*. 1996, Vieira *et al*. 1996). FrMV has lost most of its larger mammalian fauna, including three medium-sized primates and all of its ungulates (Lopes & Ferrari 2000).

The second study site, a 1,200 ha forest reserve at the "Fazenda Amanda" (C_1AM) in the municipality of Viseu (1°50' S, 46°45' W), is part of a fragment of approximately 3,500 ha of predominantly "terra firme" forest. Viseu contains a similar mosaic landscape to that observed at "Peixe-Boi", although there are relatively large forest remnants in its southern extreme, where "Fazenda Amanda" is located. The diurnal mammal community at the site appears to be relatively intact (Pereira 2002).

The third area is a reserve of approximately 3,600 ha of "terra firme" forest at the "Fazenda São Marcos" (C_2SM), in the municipality of "Aurora do Pará" (2°13' S, 47°20' W). Until 1993, this reserve was part of a forest fragment of 10,000 ha, the majority of which was felled for agriculture, leaving only the study site and a separate 1,000 ha fragment. Prior to fragmentation, the mammalian fauna at this site was apparently intact (Lopes & Ferrari 2000), and recent observations indicate that most species are still present. Given their characteristics, these two larger fragments are considered to be control sites in the present study, for comparisons with FrMV.

Study species – *Eschweilera coriacea* is a common canopy tree up to 37 m tall, widely distributed in the Amazon basin, and occurs at high densities in eastern Amazonia (Nelson & Oliveira 2001, and references therein). It is most abundant in "terra firme" forest, but is also found in seasonally-flooded "várzea" and "igapó" up to 1000 m above sea level (Pires & Prance 1977).

The species's fruit is a medium-sized woody *pyxidium* measuring 5-7 × 3.5-8 cm that contains one to several large – 25-30 × 15-20 mm – seeds (Mori & Prance 1990). As in most lecythid species, the fruit remains fixed to the tree until the seeds are released. There is no fleshy pulp, but seeds have well-developed lateral funicle-arils that may attract some frugivorous animals, such as large birds and bats. Seeds are dropped in large numbers directly under parent trees. Gravity plays a role in their dispersal and vertebrate consumers such as rodents and primates may also disperse seeds (Prance & Mori 1978, Mori & Prance 1990, personal observation).

Sampling design – Two randomly selected one hectare plots (100 × 100 m) were established at each study site to estimate the abundance, size class structure and dispersion patterns of *E. coriacea*. Each plot was divided into one hundred 10 × 10 m quadrats demarcated with wooden stakes at each corner. All individuals of *E. coriacea* with a stem height of at least one metre were tagged, measured (stem diameter) and mapped to the nearest centimeter. Distances to the two closest grid stakes were measured and used to locate each plant on a map of the plot. Stem diameter was measured at soil level (das) for plants < 2 m in height, and at breast height (dbh: 1.3 m), or above buttresses, for those > 2 m.

All individuals < 1 m in height were sampled in eleven 2 × 100 m transects per plot. Each of these transects was divided into 1 × 5 m quadrats to which individuals were assigned. For mapping, the location of each individual was considered to be the centre of the quadrat to which it was assigned.

The minimum size of adults was determined by monitoring flowering and fruiting of 499 trees (dbh ≥ 10 cm) for two years in the six study plots and three other one-hectare plots, two at FrMV and one at C_1AM. Only individuals with dbh ≥ 14 cm fruited during the study.

Data analyses – Structural characteristics (size class structure, dispersion and density) were determined and compared among sites. To visualise the size class structure at each site, the number of individuals in transect samples (individuals < 1 m in height) was scaled to 1 ha and combined with individuals with dbh < 1 cm. The rest of the population was grouped in doubling size classes (dbh up to 2 cm, 4 cm, 8 cm…), following Preston (1948, in Hubbell 2001). Differences among sites in size class population structure were evaluated using the Kolmogorov-Smirnov goodness-of-fit test (Sokal & Rohlf 1995, Ayres *et al*. 2005).

Dispersion patterns were evaluated using standardised Morisita's index of dispersion (I_p) (Krebs 1999). The effect of quadrat size on the spatial distribution patterns detected was examined by calculating the index for different quadrat sizes. For individuals ≥ 1 m tall, quadrat sizes of 100, 200, 400, 900, 1,600 and 2,500 m^2 were tested. Quadrat sizes tested for individuals < 1 m tall – 5, 10, 20, 40, 50, 100 and 200 m^2 (an entire transect) – were different due to the alternative sample design for this size class. Differences in dispersion patterns between plots within a site and among sites were tested with the Kruskal-Wallis nonparametric analysis of variance. To determine which of the samples differed significantly, multiple comparisons were performed following Dunn's procedure (Zar 1999, Ayres *et al*. 2005).

Spatial patterns of *E. coriacea* at the three sites were also evaluated using Condit *et al*. (2000) relative neighbourhood density or Ω, which examines the distribution of conspecifics around each individual within the plots. Ω was used to compare dispersion patterns of *E. coriacea* among plots and sites, and to examine neighbourhood differences between juveniles (≥ 1 m tall) and adults. All calculations were run in a Matlab program written by L. Sternberg (unpublished).

Distance intervals were 5 m-wide concentric rings (0 to 5 m, 5 to 10 m, and so on), a value chosen based on the mean crown radius recorded for a sample of adult trees (13 individuals, 4 measurements for each tree [$n = 52$], mean crown radius = 5.3 m, range: 3.6-9.4 m). Around each individual, the number of conspecifics (N_i) within ring *i* was counted and the area of the ring within the plot measured (A_i). Densities were computed for each ring (D_i) as $\Sigma N_i / \Sigma A_i$. The density of conspecifics could then be examined as a function of distance from the average individual. Density values were standardised by dividing them by the average population density at each site, giving Ω.

A value of $\Omega = 1$ represents a perfectly random distribution, whereas values greater than one indicate clumping, and those less than one reflect hyperdispersion. Statistical significance of aggregation or overdispersion was determined by checking whether confidence limits (estimated following Condit *et al*. 2000) included 1.0, and estimates were compared by checking whether confidence limits overlapped. Because the sample plots were relatively small, complicating the calculation of ring area, only distance intervals of ≤ 50 m were examined.

In a slightly different approach, changes in the distribution of adults and juveniles (grouped in two classes: < 1 m and ≥ 1 m in height) with distance from the nearest adult were examined. Any individual that was closer to a boundary of the plot than to its nearest adult was excluded from the analysis, since it might have been closer to an adult outside the plot. If mortality is a random thinning process independent of distance from adults, the distribution of adults along distance intervals should be the same as the distribution of juveniles. In other words, the proportion of adults in a certain distance interval should be equivalent to that of juveniles in the same distance interval. Distance from nearest adult was measured for all individuals that were grouped in concentric 5 m rings around adult trees, as above. The distribution of the individuals of different size classes among rings was compared using χ^2.

Results

As expected, *Eschweilera coriacea* was relatively common in all sites (table 1), although population density varied considerably among sites (1,256-4,805 individuals ha^{-1}). Differences between sites in the density of individuals were less apparent when considering the larger size classes compared to smaller individuals. Mature individuals were abundant at all sites with densities of 32-52 ha^{-1}. Site C$_1$AM had the largest overall population, more than double that of FrMV, and more than three times that of C$_2$SM. Much of this difference was due to the smallest size class (dbh < 1 cm), although in the case of C$_2$SM, numbers were consistently low in most size classes with the exception of the three largest ones. Individuals in the largest size classes (dbh > 32 cm) were around twice as abundant at C$_1$AM as at the other two sites.

Table 1. Population size structure at each site. Values are the number of individuals sampled in two 1 ha plots per site. The < 1 cm class includes all individuals < 1 m in height recorded in transects, scaled to plot size (FrMV = "Fazenda Monte Verde"; C$_1$AM = "Fazenda Amanda"; C$_2$SM = "Fazenda São Marcos").

Size class – dbh (cm)	FrMV	C$_1$AM	C$_2$SM
≥ 14 (adults)	91	99	72
< 1	3721	8993	2256
≥ 1 and < 2	111	177	95
≥ 2 and < 4	118	206	52
≥ 4 and < 8	108	84	27
≥ 8 and < 16	72	62	18
≥ 16 and < 32	59	42	36
≥ 32 and < 64	21	45	27
≥ 64	2	2	1
Total	4212	9611	2512

Comparing size class structure among the three sites (figure 2), FrMV exhibited a more even distribution than either C$_1$AM or C$_2$SM. The latter two sites also exhibited similar between-plot variation in the smallest size class, which produced significant between-plot differences (C$_1$AM: $\chi^2_2 = 8.600$, $P = 0.014$; C$_2$SM: $\chi^2_2 = 16.237$, $P < 0.001$), which disappeared when this class was omitted (C$_1$AM: $\chi^2_2 = 0.034$, $P = 0.983$; C$_2$SM: $\chi^2_2 = 1.216$, $P = 0.545$). One additional pattern was observed at C$_2$SM, where there was a dip in the abundance of the intermediate size classes (both plots exhibited the same pattern) (figure 2). Given these differences, size structure distribution patterns differed significantly among all sites (FrM *vs.* C$_1$AM: $\chi^2_2 = 25.736$, $P < 0.0001$; FrM *vs.* C$_2$SM: $\chi^2_2 = 14.156$, $P < 0.001$; C$_1$AM *vs.* C$_2$SM: $\chi^2_2 = 8.134$, $P = 0.017$).

The standardised Morisita's index of dispersion tended to vary irregularly with quadrat size, irrespective of size class (figures 3, 4). In general, adults were less clumped in their distribution than juveniles and the population as a whole at all three sites, although the pattern was least clear at C$_2$SM. Small juveniles (< 1 m tall) were more aggregated than larger individuals (*cf*. figures 3, 4), and patterns were relatively consistent across sites. There were no significant differences among plots ($H_5 = 8.00$, $P = 0.156$) and sites ($H_2 = 5.145$, $P = 0.076$) in the dispersion pattern indices for total population (≥ 1 m), while a significant difference appeared when analysing juveniles of < 1 m (table 2). In this case, C$_1$AM was statistically different from FrMV and C$_2$SM.

Values of Ω were relatively close to 1.0 for most distance intervals in all three populations (figure 5). At

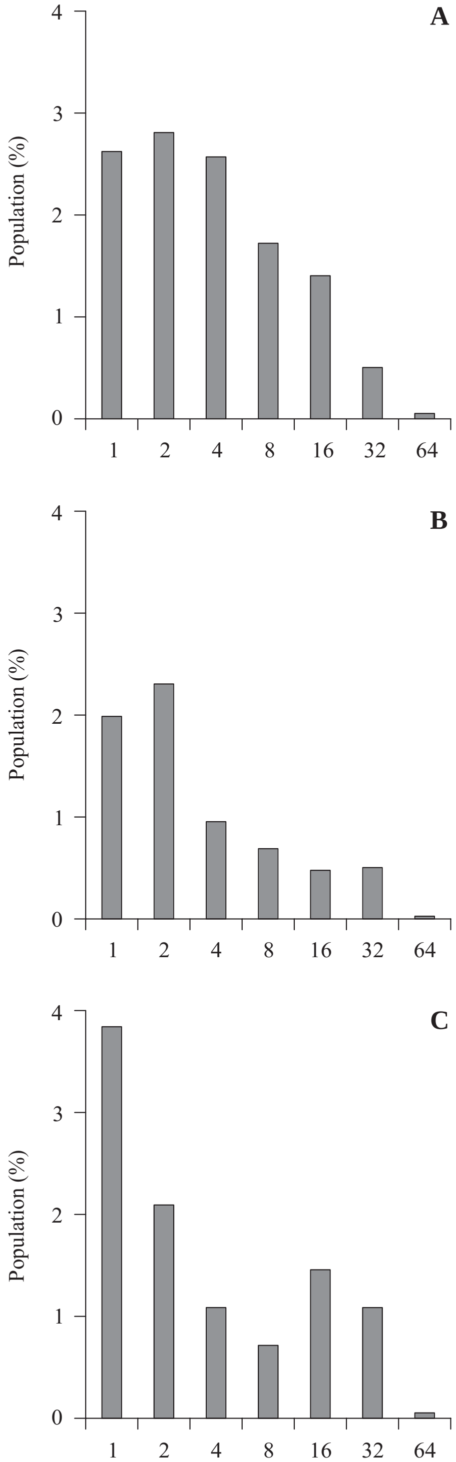

Figure 2. Size structure (percentage of individuals per size class) at the three sites. In order to facilitate visualization, only individuals with dbh ≥ 1 cm were plotted, given that smaller individuals constitute 88.3%, 93.6% and 89.8% of the sample populations at FrMV (A), C_1AM (B) and C_2SM (C), respectively. The rest of the population was grouped in doubling size classes (dbh up to 2 cm, 4 cm, 8 cm…), following Preston (1948, *apud* Hubbell 2001).

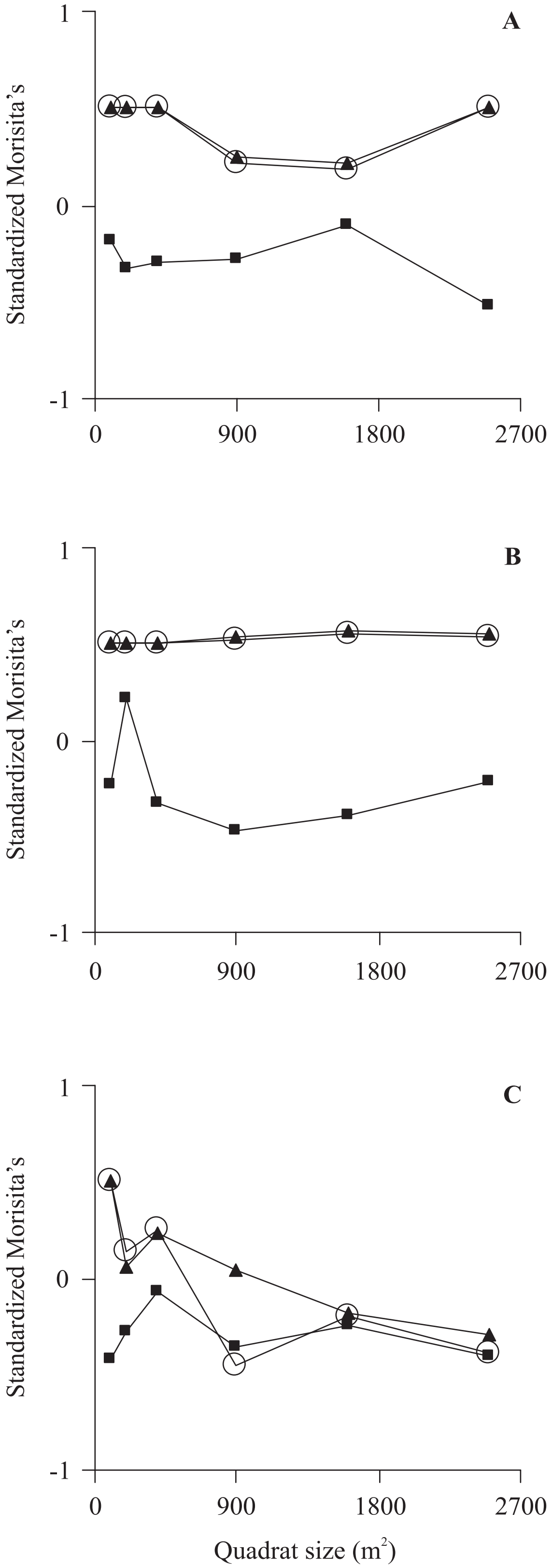

Figure 3. Variation in standardised Morisita's index of dispersion (I_p) with quadrat size for juveniles (≥ 1 m tall), adults and total populations at each site: FrMV (A) , C_1AM (B) and C_2SM (C) (▲ = juveniles; ■ = adults; ○ = total population).

Table 2. Statistical comparison of standardised Morisita's index for juveniles (< 1 m tall) among sites and plots (two per site), based on 5-m^2 quadrats within transects[1] (FrMV = "Fazenda Monte Verde"; C_1AM = "Fazenda Amanda"; C_2SM = "Fazenda São Marcos"; H = Kruskal-Wallis value; P = probability).

	Plots	Sites
H	18.052	18.046
Degrees of freedom	5	2
P	0.003	< 0.001
z for pairwise comparisons:		
FrMV *vs.* C_1AM		3.444*
FrMV *vs.* C_2SM		0.428
C_1AM *vs.* C_2SM		3.872*
FrMV$_1$ *vs.* FrMV$_2$	0.067	
FrMV$_1$ *vs.* C_1AM$_1$	2.421	
FrMV$_1$ *vs.* C_1AM$_2$	2.382	
FrMV$_1$ *vs.* C_2SM$_1$	0.344	
FrMV$_1$ *vs.* C_2SM$_2$	0.328	
FrMV$_2$ *vs.* C_1AM$_1$	2.488	
FrMV$_2$ *vs.* C_1AM$_2$	2.449	
FrMV$_2$ *vs.* C_2SM$_1$	0.278	
FrMV$_2$ *vs.* C_2SM$_2$	0.261	
C_1AM$_1$ *vs.* C_1AM$_2$	0.039	
C_1AM$_1$ *vs.* C_2SM$_1$	2.766	
C_1AM$_1$ *vs.* C_2SM$_2$	2.749	
C_1AM$_2$ *vs.* C_2SM$_1$	2.727	
C_1AM$_2$ *vs.* C_2SM$_2$	2.710	
C_2SM$_1$ *vs.* C_2SM$_2$	0.017	

[1] Critical values of z for the multiple comparison test are 2.936 and 2.394 for $\alpha = 0.05$ and $k = 6$ and $k = 3$, respectively. Statistical significance is indicated by asterisks.

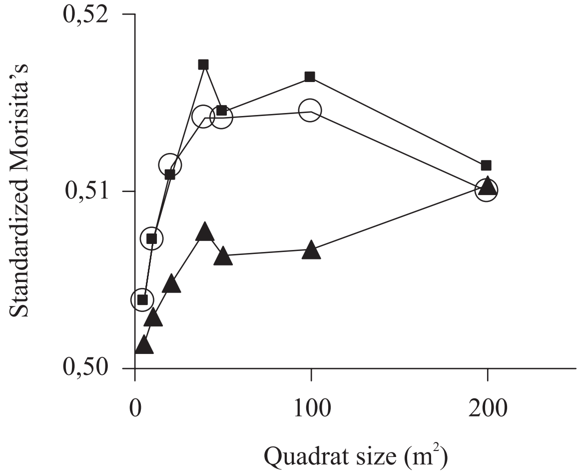

Figure 4. Variation in standardised Morisita's index of dispersion (I_p) with quadrat size for juveniles < 1 m tall. (▲ = FrMV; ○ = C_1AM; ■ = C_2SM)

FrMV and C_2SM, Ω_{0-5} was significantly greater than 1.0 for the total population and significantly less than 1.0 for adults, but oscillated around 1.0 in more distant intervals. At C_1AM, Ω was significantly greater than 1.0 for the total population in all distance intervals up to 30 m, whereas for adults, Ω again oscillated around 1.0. Overall, then, dispersion patterns tend towards randomness, with the most marked differences between adults and total population being found in the first distance interval at all sites. One difference between sites was a tendency towards a more clumped distribution in the population as a whole at C_1AM, in intervals up to 30 m.

Juveniles and adults had different distribution patterns in relation to nearest adults. At FrMV and C_1AM, the smallest juveniles (< 1 m tall) exhibited a steady decline in abundance from the nearest to the farthest distance interval (figure 6), while at C_2SM, this pattern was obscured by an increase in numbers in the second interval (5-10 m). For the larger juveniles and adults, there was an overall tendency for the number of individuals to peak in this second interval, although once again, there was variation, in particular, a sharp increase in adults in the 15-20 m interval at C_1AM. Distribution patterns were significantly different when small juveniles were compared with both larger juveniles and adults (table 3), with the exception of the latter comparison at C_2SM, although even here, $P < 0.10$.

Two patterns were clear from these results. Firstly, there did not appear to be a minimum recruitment distance; the smallest juveniles were found in all intervals, together with larger individuals. Secondly, mortality appeared to be higher closer to adults, based on the difference in the distribution of adults and juveniles within distance intervals (figure 6).

Discussion

Although *E. coriacea* was a common species at all three study sites, its population density varied up to fourfold among sites. The size class structure of *E. coriacea* at all sites is typical of a species with good regeneration (Hartshorn 1980), although each population exhibited a different structure, reflecting the inherent natural variability resulting from both historical and random factors (Hubbell 2001, Valencia *et al*. 2004). This population structure patterns, with many individuals in smaller size classes and relatively few in large diameter classes was also found in many of the more common tree species in floodplain forest, Peru (Gentry & Terborgh 1990), and characterized shade-tolerant species in closed-canopy forest in Barro Colorado Island (BCI), Panama

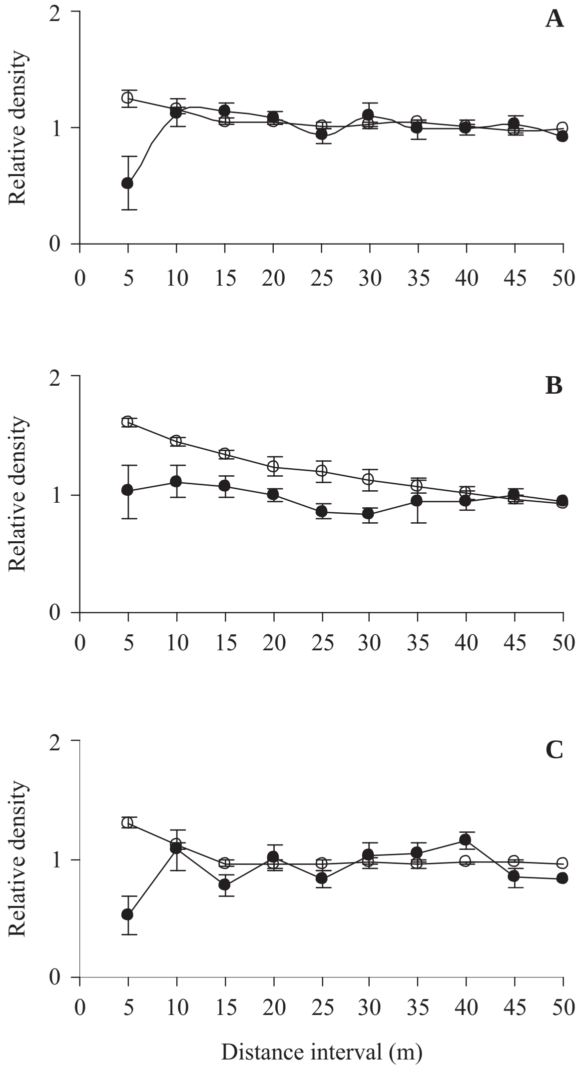

Figure 5. Relative neighbourhood density (Ω) as a function of distance (i) from the average individual: FrMV (A), C_1AM (B) and C_2SM (C). Distance intervals were 5 m-wide concentric rings (0 to 5 m, 5 to 10 m, and so on). Vertical bars represent 95% confidence limits (see Methods).
(○ = total population; ● = adults)

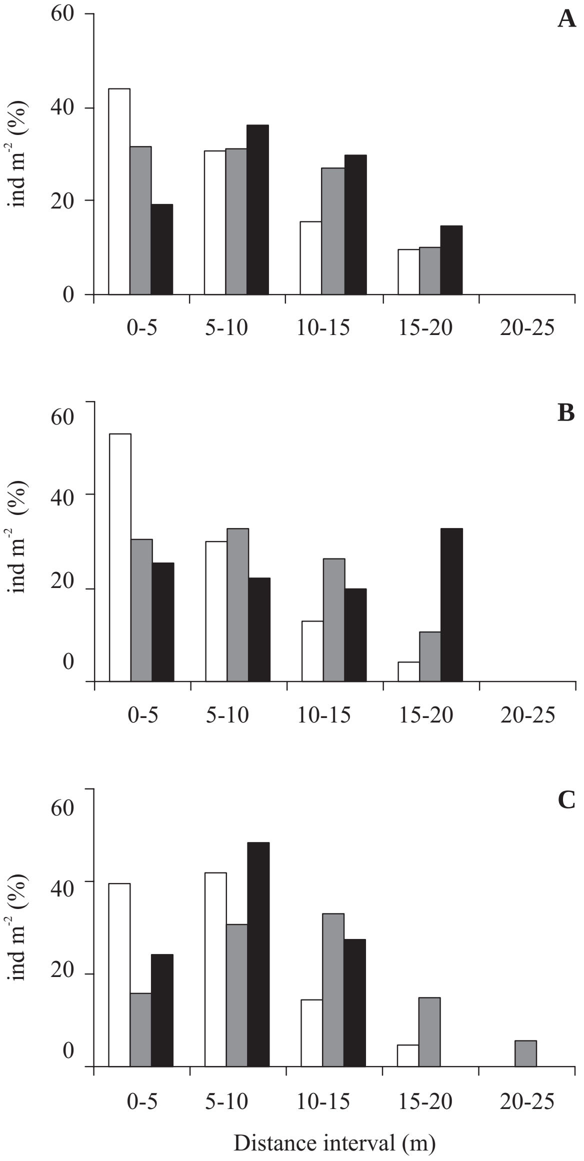

Figure 6. Relative density of individuals of a given size class at different distance intervals in relation to the nearest adult: FrMV (A), C_1AM (B) and C_2SM (C).
(□ = juv < 1 m; ▨ = juv > 1 m; ■ = adults)

(Wright *et al.* 2003). The cause of the dip in abundance in the medium-size classes at C_2SM (figure 2) is unknown, but it might be related to past logging events, decreasing the number of reproductive individuals by that time. The species has low-quality timber, but is sometimes exploited for fence posts.

Overall, juveniles presented a relatively clumped distribution pattern, whereas adults tended to be randomly distributed. Clumped distribution and relatively short distances among adults were also found in populations of several of the most common species in a dry forest in Costa Rica (Hubbell 1979, 1980), and this was the prevalent pattern found in a study of a Caribbean semi-evergreen forest (Forman & Hahn 1980). Other studies of tree species, at least two in Neotropical forests (Henriques & Sousa 1989, Oliveira Filho *et al*. 1996) and two in Asia (He *et al*. 1997, Bunyavejchewin *et al.* 2003) have also reported decreasing aggregation and increasing randomness from smaller to larger size classes.

The relatively low neighbourhood density (Ω) values recorded in the present study are similar to those reported by Condit *et al*. (2000) for the common tree species studied at a number of tropical forest sites such as BCI, in Panama. Hubbell (1979) also found a negative correlation between clumping and population density in Costa Rica. In the present study, however, clumping was stronger

Table 3. Results of pairwise χ^2 tests for comparisons of distribution patterns in relation to nearest adults[1] (FrMV = "Fazenda Monte Verde"; C_1AM = "Fazenda Amanda"; C_2SM = "Fazenda São Marcos"; *P* = probability).

Small juveniles[2] *vs.*	χ^2 (*P*) at:		
	FrMV	C_1AM	C_2SM
Adults	15.913 (0.001)	28.169 (< 0.0001)	47.225 (< 0.0001)
Large juveniles[2]	16.746 (< 0.001)	82.374 (< 0.0001)	4.758* (0.093)

[1] Degrees of freedom = 3 in all cases, except for *, where d.f. = 2.

[2] Small juveniles < 1 m tall; large juveniles ≥ 1 m tall.

where population density was highest, *i.e.* at C_1AM. Aggregation was also relatively less intense among larger individuals, once again agreeing with Condit *et al*. (2000). The evidence points to differential mortality in relation to the distance from conspecific adults, supporting the escape hypothesis. Hubbell (1979) did not find evidence of such a difference between adults and juveniles, however.

The most marked differences between adults and the population as a whole were found in the 0-5 m interval at all sites. At both FrMV and C_2SM, adults were significantly hyperdispersed in this interval, compared to significant aggregation in the population as a whole. In the 5-10 m interval, however, the two classes were remarkably similar (figure 5). This pattern is slightly different at C_1AM, where population density was highest overall. This would appear to further support the escape hypothesis. As in the present study, Condit *et al*. (1992) used 5 m distance intervals, rather than 10 m, as in Condit *et al*. (2000). With this smaller distance interval, the authors found the repelled distribution extended for just one crown width for 14 of the 15 species that were repelled from the vicinity of conspecific adults, which is the same pattern I observed for *E. coriacea*, particularly at FrMV and C_2SM.

Conclusions about the randomness of adult dispersion must be regarded as tentative, however. The adult population of *E. coriacea* may be randomly distributed at the three sites, but it could also be randomly distributed within clumps too large to be detected with the sample plot size used in this study.

Since the youngest plants are mainly the result of recruitment from seeds after the isolation of the forest fragment, the density and dispersion patterns of young juveniles should provide evidence to possible effects of fragmentation on tree regeneration (Harrington *et al*. 1997). However, none of the differences in abundance and dispersion patterns recorded among sites appears to be related to the forest fragmentation. If the missing mammal species played a significant role in the dispersal of *E. coriacea*, in their absence young juveniles should be relatively more aggregated. In contrast, young juveniles in plot 2 at FrMV were significantly less aggregated than those at C_1AM (table 2). It seems either that the original dispersal system of *E. coriacea* did not include the agents that have disappeared from FrMV, or that other agents have taken over their role at this site. Given the abundance and the dispersion pattern of *E. coriacea* at the three study sites, one could suppose that seeds are dispersed virtually by gravity. Nonetheless, I found evidence of seed dispersal by small rodents at FrMV that deserves future investigations (*e.g.* seeds of *E. coriacea* far from any fruiting tree around the entrance of a rodent's burrow on the forest floor).

About a third of the tree species at FrMV have less than one individual per hectare and may not be recruiting (Vieira *et al*. 1996), which may have resulted in an increased availability of regeneration sites for *E. coriacea*. Terborgh (1992) has suggested that escaping predation due to the absence of medium-sized mammals enables large-seeded trees to out-compete other species on small islands in Gatun Lake, Panama. A similar process might be occurring at FrMV.

As the density of new recruits generally tends to be higher closer to adults, the effects of distance and density are correlated (Schupp 1992) and could not be separated in the present analysis. Distance- and density-dependence can regulate populations through intraspecific processes, such as allelopathy or competition, or interspecific interactions, such as seed predation, herbivory and pathogen attack (Howe and Smallwood 1982, Augspurger 1983). Although many studies have found negative effects of population density on different life stages of tropical trees (Harms *et al*. 2000, Wright 2002), the role of density dependence in the maintenance of the high species diversity in tropical forests remains unclear (Peters 2003). Nevertheless, the identification of density-dependent processes in the present study will hopefully help us to understand the population structure and dynamics of *E. coriacea*.

Overall, *E. coriacea* was a common species at all study sites, although population density varied considerably among sites. Regeneration was apparently adequate for the maintenance of populations at all sites, although each population exhibited differences reflecting its specific history, as well as random factors. The dispersion patterns observed at all three sites were relatively clumped for juveniles but random for adults. This suggests differential mortality, in particular in close proximity to adult trees, which lends reasonable support to the escape hypothesis (questions 1 and 2). By contrast, differences in juvenile abundance and dispersion patterns among sites could not be related to forest fragmentation (questions 3).

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