

# Does spatial heterogeneity blur the signature of dispersal syndromes on spatial patterns of woody species? A test in a tropical dry forest

Andrea Jara-Guerrero, Marcelino De la Cruz, Carlos I. Espinosa, Marcos Méndez and Adrián Escudero

*A. Jara-Guerrero (akjara@utpl.edu.ec) and C. I. Espinosa, Depto de Ciencias Naturales, Univ. Técnica Particular de Loja, CP: 11-01-608, Loja, Ecuador. – M. De la Cruz, Depto de Biología Vegetal, E.U.I.T. Univ. Politécnica de Madrid, ES-28040 Madrid, Spain. – MDC, M. Méndez and A. Escudero, Área de Biodiversidad y Conservación, Univ. Rey Juan Carlos, ES-28933 Móstoles, Spain.*

Spatial patterns of adult plants are a consequence of several ecological processes related to seed dispersal and recruitment. Dispersal limitation, mediated by dispersal syndrome, is considered a key factor in the formation of adult plant spatial patterns. Although this initial pattern determined by dispersal has been thoroughly studied, the subsequently modification by the effect of additional ecological factors, such as habitat heterogeneity is less understood. We explored the relative importance of dispersal syndrome and spatial heterogeneity on the realization of spatial patterns of adult trees in an Ecuadorian tropical dry forest. The spatial distribution of 28 species was modeled with four different spatial point processes each: homogeneous Poisson (HPP), inhomogeneous Poisson (IPP), homogeneous Poisson cluster (HPCP), and inhomogeneous Poisson cluster process (IPCP). These models allowed us to discern between effects of random processes, habitat heterogeneity, limited dispersal, and joint effects of habitat heterogeneity and limited dispersal. We employed Akaike's information criterion (AIC) to select the model which best fit the spatial pattern of each species. The best model of each species was used to analyze differences in cluster size and degree of aggregation, between dispersal syndromes. Seventy-five percent of the species showed inhomogeneous patterns. IPCP yielded the best fit for the spatial distribution of 50% of species in the studied forest and was the prevalent model for the three dispersal syndromes. Thus, the effect of spatial heterogeneity was prevalent in the distribution of most species in this dry tropical forest. Only 21% of species had spatial patterns compatible with random mechanisms associated to limited dispersal around parent sources. Clearly, ignoring habitat heterogeneity could bias the analysis of relationships between dispersal syndrome and species patterns.

Seed dispersal is a critical life process determining not only persistence but also the spatial structure of populations and communities (Wang and Smith 2002, Cousens et al. 2008). Initial dispersal pattern sets the scene for subsequent ecological processes – such as depredation, germination, growth – modulated by plant–plant interactions and herbivory, that lead to the realized distribution of seedlings and adults (Schupp and Fuentes 1995, Nathan and Muller-Landau 2000). Several recent studies have advanced our understanding about how seed dispersal processes are affecting spatial patterns of plants (Hubbell 1979, Schupp and Fuentes 1995, Condit et al. 2000, Nathan and Muller-Landau 2000, Seidler and Plotkin 2006), and determined that dispersal syndromes are important attributes in the formation of those patterns (Hubbell 1979, Condit et al. 2000, Seidler and Plotkin 2006).

In agreement with these expectations, a concordance usually exists between the spatial patterns of seed arrival and those of seedlings (emergence) and adults (recruitment) (Schupp and Fuentes 1995, Seidler and Plotkin 2006). In particular, in tropical rain and dry forests the spatial aggregation of conspecific adults at different spatial scales has

been related to limited seed dispersal (Hubbell 1979, Condit et al. 2000, Nathan and Muller-Landau 2000, Hardesty and Parker 2002, Seidler and Plotkin 2006, Wiegand et al. 2009). If this relationship between dispersal and realized recruitment were universal, it could be thought that, ahead of other ecological processes, dispersal syndrome would be the main determinant of the adult realized distribution at fine spatial scales. Hubbell (1979) pioneered this idea by showing such a relationship between dispersal syndromes and the spatial pattern of adult tree species in tropical dry forests, and this evidence contributed to develop his neutral theory (Hubbell 2001). More recently, Seidler and Plotkin (2006) also found a strong correlation among seed dispersal syndromes and spatial patterns of trees in two tropical rainforests. They showed that the adults of zoochorous or anemochorous species, capable of relatively long-distance dispersal, appeared in larger clusters than those of autochorous species with more limited dispersal.

Although there is an almost general consensus that dispersal is critical for explaining the realized distribution of adults (Hubbell 1979, Condit et al. 2000, Seidler and Plotkin 2006, Wiegand et al. 2009, Jara-Guerrero et al.

2011), a number of biotic and abiotic mechanisms can blur such relationships (Schupp and Fuentes 1995, Seidler and Plotkin 2006). Among the biotic processes, the existence of facilitative interactions on early life stages (Callaway and Walker 1997), or perch effects (i.e. the increased recruitment around some trees or other objects employed as perches by dispersal agents; Herrera et al. 1994, Schupp and Fuentes 1995, Webb and Peart 2001) could distort the initial dispersal pattern. For instance, negative density-dependent processes (Janzen 1970) lead to higher survival and germination of those seeds falling further away from the parent plant. In addition, environmental heterogeneity with continuous variation in topography, aspect or soil properties, can influence not only seed shadows but also germination and recruitment of dispersed seeds (Grubb 1977, Schupp and Fuentes 1995, Lin et al. 2011). This could lead to a mismatch between the spatial patterns of dispersed seeds and that of recruited seedlings or adults (Comita et al. 2007, Cousens et al. 2008). Furthermore, even if dispersal were not limited, environmental heterogeneity could generate virtual aggregation (Schiffers et al. 2008), i.e. spatial patterns indistinguishable from those resulting from limited dispersal (Wiegand et al. 2007a). All in all, spatial patterns offer another exciting arena where to test a major question in ecology, namely the relative role of biotic versus abiotic factors in structuring ecological communities (Hubbell 2001).

We explored the relative importance of both dispersal syndrome and spatial heterogeneity on the realization of the spatial pattern of adult trees in an Ecuadorian tropical dry forest. Our working hypothesis is that the realized pattern is the result of a two-step process where dispersal syndrome (Hubbell 1979, Seidler and Plotkin 2006) first sets the initial spatial template and later ecological processes linked to environmental heterogeneity (Webb and Peart 2001) blur the original pattern of seed dispersal and determine the realized pattern of adult trees. As we work in a dry tropical forest, we expect that the tight relationship between dispersal syndrome and spatial pattern of adult trees found in tropical rainforests (Seidler and Plotkin 2006) would be less evident because of the stronger filter exerted by harsher environmental conditions.

We used spatial point pattern analysis, and a set of a priori hypotheses to discern those processes responsible for the realized pattern of trees (McIntire and Fajardo 2009). Specifically, we fitted four kinds of spatial point process models that can be easily interpreted in terms of biological processes and environmental conditions (Shen et al. 2009, Lin et al. 2011). The processes tested consider purely random processes (homogeneous Poisson process), random processes in heterogeneous habitat (inhomogeneous Poisson process), limited dispersal (Poisson cluster process), and the joint effect of habitat heterogeneity and limited dispersal (inhomogeneous Poisson cluster processes). Thus, if the final distribution of adults is the consequence of dispersal alone we would expect; 1) zoochorous plants to show patterns compatible with a homogeneous Poisson process (at the spatial scales considered in this study), because seeds are carried by very mobile dispersers and can reach any point in the territory; 2) autochorous plants to show patterns compatible with a homogeneous Poisson cluster process, in which adults are source for other recruits in a nested process (Cousens et al.

2008), because seeds are dispersed in the vicinity of mature plants, and 3) anemochorous species, depending on dispersal efficiency (i.e. plant architecture, aerodynamic properties of diaspores: Muller-Landau et al. 2008), to show patterns compatible with either homogeneous Poisson in more efficiently dispersed species, or homogeneous Poisson cluster processes (but with larger clusters than autochorous species) in those of more limited dispersal. On the contrary, if environmental heterogeneity matters, we would expect most adult patterns to be adequately described by inhomogeneous processes as a consequence of the environmental filter exerted on the seed pattern after primary dispersal (i.e. inhomogeneous Poisson or inhomogeneous Poisson cluster, depending on the relative importance of dispersal limitation).

## Material and methods

### Study area

The study was conducted in the Arenillas Ecological Reserve (REA, from its Spanish name), located in southwestern Ecuador (03°34'15.44''S; 80°08'46.15''E, 30 m a.s.l.). This area belongs to the Tumbesian biogeographic region, one of the most important areas of endemism in the world, but at the same time, one of the most threatened by increasing agriculture and livestock activities, which are leading to a decrease in forest remnants in this region (Best and Kessler 1995). Climate is characterized by a rainy season extending from January to May and a dry season extending from June to December. Annual mean precipitation at REA is 667 mm, and annual mean temperature is 25°C (Huaquillas weather station, with 45 years record period).

Vegetation corresponds to a transitional formation between dry deciduous forests and dry scrubs of lowlands. The most conspicuous tree species in the area are *Tabebuia chrysantha* and *Tabebuia billbergii* (Bignoniaceae), together with other species like *Colicodendron scabridum* (Capparaceae) and *Croton* spp. (Euphorbiaceae), which become more important in the dry scrub formation. The topography in the plot is relatively flat. Altitude varies between 31 to 39 m a.s.l., with an average of 35.4 m. The plot is traversed by a seasonal creek, with water only for very short periods during the intense rainfalls of the wet season. Soil is mostly sandy loam. The mean pH value is  $5.3 \pm 0.081$ . Organic matter content is low, and variable between dry and rainy season ( $31.3 \pm 3.1$  mg g<sup>-1</sup> and  $22.5 \pm 1.6$  mg g<sup>-1</sup>, respectively) (A. P. Castillo-Monroy pers. comm). Similarly values of organic carbon vary between dry ( $18.2 \pm 1.8$  mg g<sup>-1</sup>) and rainy ( $13.1 \pm 0.9$  mg g<sup>-1</sup>) season (A. P. Castillo-Monroy pers. comm). Although the community of seed dispersers has not been extensively studied, the REA hosts a high diversity of vertebrates (Best and Kessler 1995), some of which are potential seed dispersers (Tirira 2007). For example, at least three bat species (*Artibeus fraterculus*, *Carollia brevicauda*, *Sturnira lilium*) are considered frugivorous (Tirira 2007). Tinoco (2009) cites the presence of six frugivorous and ten omnivorous bird species in the REA. Two deer species that inhabit the REA (*Odocoileus peruvianus* and *Mazama americana*) have been reported feeding fruits (Tirira 2007), and we have found seeds of up to 11 species (and

not all of them from zoochorous species) in their droppings (Jara-Guerrero unpubl.). Other omnivores feeding on fruits are fox *Lycalopex sechurae* and some rodents (e.g. *Sciurus* spp. and *Proechimys* spp) (Tirira 2007).

## Data collection

Between January 2010 and September 2011, we located a 9-ha (300 × 300 m) permanent forest plot in a well conserved area of this forest. All trees and shrubs exceeding 5 cm diameter at breast height were mapped, measured, and identified to species. Individuals with multiple stems were counted as a single individual (Condit et al. 2000). Coordinates (x, y) and elevation (z) were measured using a computerized total surveying station with a resolution of 5 cm.

## Score of dispersal syndromes

We collected diaspores for all species in the REA forest during 2010 and 2011. Following Van der Pijl (1969), species were classified into three major dispersal syndromes: zoochory, anemochory and autochory. Zoochory was defined by the presence of fleshy and edible structures that promote the ingestion and transport of seeds by animals. Species having diaspores with membranous wings, or other aerodynamic structures that affect the rate of fall, were scored as anemochorous. Autochory group included species with diaspores propelled explosively, passive ballistics (triggered by passing animals, wind or raindrops), and those so-called barochorous (released and falling to the ground).

## Statistical models

We employed Ripley's K function to characterize the spatial pattern of each species (Ripley 1976, Illian et al. 2008). For a homogeneous point pattern where  $\lambda$  is pattern intensity (i.e. density),  $\lambda K(r)$  is the expected number of points within a circle of radius  $r$  around an arbitrary point.

We compared the spatial pattern of each species (as characterized by the K-function) and the expected pattern for four different spatial point processes (Shen et al. 2009, Lin et al. 2011; Table 1): 1) a homogeneous Poisson process (HPP), which assumes that the spatial location of points (i.e. standing individuals) is independent from each other and their intensity is constant in the whole area: it is the simplest process and considers the pattern as the result of purely random processes (Shen et al. 2009, Lin et al. 2011); 2) an inhomogeneous Poisson process (IPP), which still assumes independence between points but recognizes the existence of variations in intensity throughout the study area; it is usually

assumed that this variation is related to habitat heterogeneity (Wiegand et al. 2007b); 3) a homogeneous Poisson cluster process (HPCP) assumes constant intensity and considers aggregation of points as a result of limited dispersal (Shen et al. 2009); it assumes that the aggregated pattern is generated in a two-step process: first, a HPP of cluster centers (i.e. parent points) with intensity  $\rho$  is created and, afterwards, each parent produces a number of offspring according to a Poisson distribution which are located around the parents according to a radially symmetric Gaussian distribution with mean zero and standard deviation  $\sigma$  (Seidler and Plotkin 2006, Shen et al. 2009, Lin et al. 2011); 4) an inhomogeneous Poisson cluster process (IPCP), which assumes that the spatial pattern is created by dispersal limitation (i.e. like a HPCP), but with intensity varying in response to habitat heterogeneity (Wiegand and Moloney 2013). Note that following current literature (Seidler and Plotkin 2006, Shen et al. 2009, Lin et al. 2011, Wang et al. 2013) we are considering only simple two-step Poisson cluster processes whereas real populations can be structured by multiple cluster processes, which in some cases could be best fitted by some inhomogeneous (cluster) model.

We employed Akaike's information criterion (AIC) based on the sum of residuals and the number of parameters in different models (Webster and McBratney 1989, Shen et al. 2009) to select the model which best fitted the spatial pattern of each species. Mathematical details about the fitted models are provided in Supplementary Material Appendix 1.

We tested differences in the frequency of spatial patterns (HPP, IPP, HPCP and IPCP) among the three dispersal syndromes by means of an extension of the Fisher's exact test for larger than  $2 \times 2$  tables (function *fisher.test* in R package stats). The p-value for this extension was obtained by Monte Carlo simulation using the *simulate.p.value* option in the package stats of R.

Additionally, for those species which were best described by an HPCP or IPCP, we tested the existence of differences in the parameter  $\sigma$  among syndromes. This parameter is related to the average cluster size of each species (Seidler and Plotkin 2006). For this, we used Kruskal–Wallis tests. All statistical analyses were carried out with R (< [www.R-project.org/](http://www.R-project.org/) >). Computation of K functions, model fitting and selection were accomplished in R, using functions from of the R packages spatstat (Baddeley and Turner 2005) and ecespa (De la Cruz 2008). We have automated all the process in the new R package selectspm (available on the usual CRAN servers, e.g. < <ftp://cran.r-project.org> >).

## Results

In the period from July 2010 to November 2011 a total of 5296 individuals with DBH > 5 cm were tagged and georeferenced in the 9-ha plot. These individuals accounted for a total of 37 species but we only considered 28 species with more than 10 individuals, belonging to 19 families. The most common families were Mimosaceae (four species), Caesalpinaceae and Fabaceae (three species respectively). Zoochory was the dominant syndrome (50%, 14 species), followed by autochory (36%, 10 species) and

Table 1. Percentage of species (and number of species in parenthesis) in each dispersal syndrome described by each of the four point pattern processes considered. HPP: homogeneous Poisson process; IPP: inhomogeneous Poisson process; HPCP: homogeneous Poisson cluster process; IPCP: inhomogeneous Poisson cluster process.

Syndrome	HPP	IPP	HPCP	IPCP
Zoochory	7% (1)	36% (5)	14% (2)	43% (6)
Anemochory	0	25% (1)	25% (1)	50% (2)
Autochory	0	10% (1)	30% (3)	60% (6)
Total	4% (1)	25% (7)	21% (6)	50% (14)

anemochory (14%, four species) (Table 1). Most individuals in the plot belonged to zoochorous species (43.7%, 2300 individuals), while autochory represented 30.8% (1621 individuals), and anemochory 25.5% (1345 individuals) of the total.

### Spatial patterns and their relationship to dispersal syndrome

Inhomogeneous Poisson cluster process yielded the best fit for the spatial distribution of 50% of the species in the studied forest (Table 1; Supplementary material Appendix 1 Table A1). Inhomogeneous Poisson process was the best model for 25% of species, while other 21% of species was best fitted by homogeneous Poisson cluster process (Table 1). Only the spatial distribution of one species, the zoochorous shrub *Vasconcellea parviflora*, was best fitted by a homogeneous Poisson process (Table 1).

There was no significant association between dispersal syndrome and the process that yielded the best fit ( $4 \times 3$  Fisher's exact test,  $p = 0.739$ ). Inhomogeneous Poisson cluster process was the prevalent model for the three dispersal syndromes (Table 1).

### Spatial signature of dispersal syndromes

The  $K(r)$  functions for the three dispersal syndromes showed clear spatial aggregation within the range of the studied distances, between 1 and 75 m (Fig. 1). Aggregation was stronger at short scales and decreased with distance. Aggregation patterns decreased from autochorous, through

zoochorous, to anemochorous species (Fig. 1). At short scales (1–30 m) zoochorous and autochorous were more aggregated than anemochorous, and at medium scales (31–75 m) only autochorous species showed aggregation (Fig. 1).

We failed to detect a significant relationship between spatial cluster size and dispersal syndromes for the 28 studied species (Kruskal–Wallis,  $\chi^2 = 2.674$ ,  $DF = 2$ ,  $p = 0.263$ ), although a tendency to increase the size of the cluster from autochory to zoochory was evident (Fig. 2).

## Discussion

### Heterogeneity effects are prevalent among species

Within community ecology, the relative importance of biotic and abiotic factors in determining community patterns has been a topic of major interest (Hubbell 2001). Our results, obtained with a new methodological approach which allows discerning between 'pure' and virtually aggregated patterns, indicated an important role of environmental heterogeneity in spatial patterns, alone or in combination with dispersal limitation (75% species showed inhomogeneous patterns). This effect was prevalent irrespective of dispersal syndrome, and even *Senna mollissima*, an autochorous species which should show a clustered pattern, was in fact best described by an IPP.

Initial studies in rainforests have suggested that the aggregated patterns of species are just generated by limited dispersal (Plotkin et al. 2002, Seidler and Plotkin 2006), whereas environmental gradients would control species

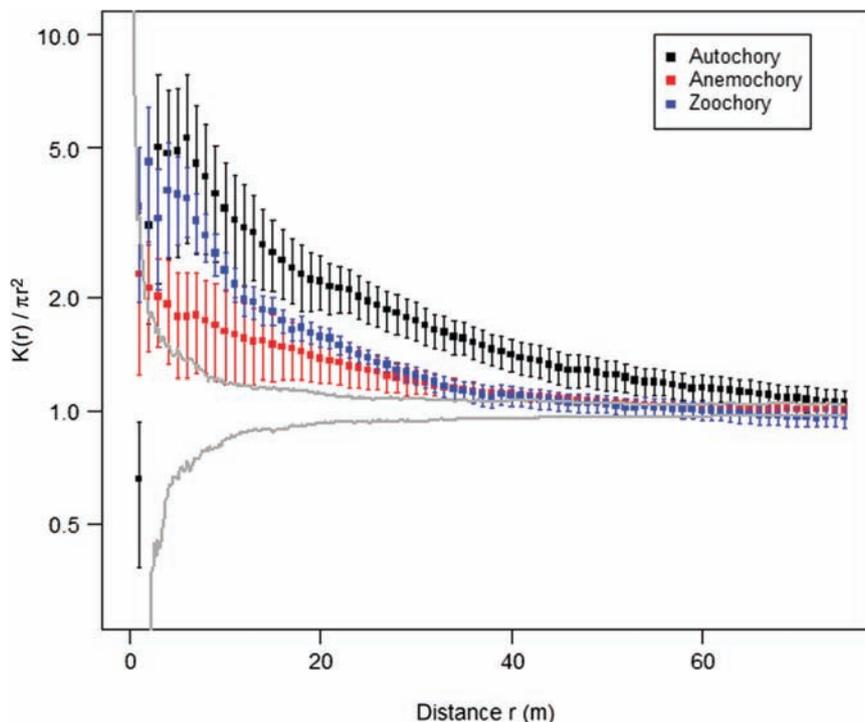


Figure 1. The function  $K(r)$  evaluated at a range of distances  $r$  for tree species in the three dispersal syndromes. The curves represent the average  $K(r)$  function value  $\pm$  standard error for each considered  $r$  distance. For a clearer interpretation, we show  $K(r) / \pi r^2$ . Values  $> 1$  indicate spatial aggregation. Grey lines represent confidence envelopes for a homogeneous Poisson pattern. Homogeneous and inhomogeneous Poisson processes should have values  $K = 1$  at all spatial scales. Homogeneous and inhomogeneous Poisson cluster processes would show values significantly  $> 1$  at the spatial scales where maximum aggregation occurs.

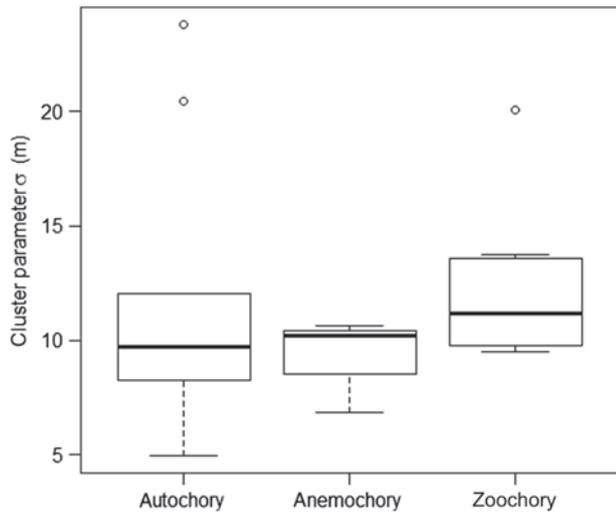


Figure 2. Relationship between dispersal syndrome and spatial aggregation of 20 woody species fitted by homogeneous or inhomogeneous Poisson cluster models. The figure shows the mean spatial cluster size ( $\sigma$ ) obtained from the best fitted model to each species. Thick lines indicate the median value of cluster size for each dispersal syndrome (anemochory,  $n = 3$ ; autochory,  $n = 9$ ; zoochory,  $n = 8$ ).

patterns only at large scales (Beaudrot et al. 2013). However, the joint effects of habitat heterogeneity and dispersal limitation at plot scale have been reported also for other tropical (Comita et al. 2007, Shen et al. 2009) and subtropical forests (Shen et al. 2009, Lin et al. 2011), suggesting that both are critical factors in structuring a wide array of megadiverse forest communities. Shen et al. (2009) and Lin et al. (2011) proposed that these two factors act sequentially. First, seed dispersal generates the basal template pattern on which seedlings will develop. Afterwards, this pattern is altered by the effects of habitat heterogeneity on survival rates and growth of seedlings. Our study suggests that the effects of environmental heterogeneity on spatial patterns may be especially important in tropical dry forests, where water availability has been shown to strongly affect the performance at different life stages of many trees (Espinosa et al. 2011, 2012). As seen here, heterogeneity effects could modify the original dispersal pattern in opposite directions: either diluting the (theoretically) clustered pattern of autochorous species (as in the case of *Senna mollissima*) to generate virtual aggregation, or restricting the (theoretically) wider dispersal of zoochorous and anemochorous species.

### Spatial patterns and their relationship to dispersal syndrome

Our results revealed a large variation in spatial patterns, even among species with the same dispersal syndrome (Table 1).

In the case of zoochorous species, only a 43% showed patterns compatible with the existence of unlimited dispersal (i.e. did not show or showed only virtual aggregation and were described by HPP or IPP models), whereas a large proportion of them (57%) showed spatial patterns compatible with limited dispersal (HPCP or IPCP). This could be explained by effects of other processes not explicitly considered here, such as perch effects mediated by

non-random movement of dispersers (Herrera et al. 1994, Schupp and Fuentes 1995). Previous studies have suggested perch effect as a cause of aggregated spatial patterns of some particular zoochorous species (Godoy and Jordano 2001, Muller-Landau et al. 2008). Moreover, in many cases, movements of dispersers occur over short distances from the parent plant (Godoy and Jordano 2001, Muller-Landau et al. 2008). Foraging distances can be related to fruit phenology. Dispersal distances and quantity of dispersed seeds are expected to be shorter for species fruiting in times of relative fruit abundance (Muller-Landau et al. 2008). In the study area, a large proportion of zoochorous species overlap fruiting time, restricted to the short period of rains (A. Jara-Guerrero unpubl.) which could explain this discrepancy in the results for some zoochorous species. This hypothesis is supported by a difference in the best fitting models for species fruiting during the rainy season (Poisson cluster processes) compared to species with long fruiting periods during the dry season (i.e. *Colicodendron scabridum*, *Jacquinia sprucei*, *Randia aurantiaca* and *Pisonia aculeata*) (Poisson processes).

We also found significant deviations from expected patterns in the case of anemochorous species. The two species of *Tabebuia* and *Eriotheca ruizii* showed patterns compatible with limited dispersal (IPCP and HPCP, respectively) while *Cochlospermum vitifolium* showed a pattern compatible with virtual aggregation (IPP). These patterns seem contradictory with dispersal potential based on aerodynamic considerations (Augsburger 1986) because winged propagules of *Tabebuia* are expected to show higher dispersal potential than floater propagules (*C. vitifolium* and *E. ruizii*). Thus, pure aerodynamic considerations seem to be poor predictors of spatial patterns for these anemochorous species. Other plant traits such as plant height, seed mass and their relationships have been shown to be closely related to dispersal distance in anemochorous plants (Muller-Landau et al. 2008, Wright et al. 2008, Thomson et al. 2011); however, those traits do not seem to explain the patterns observed here. Instead, environmental conditions during the dispersal season could affect the potential dispersal distance (Muller-Landau et al. 2008, Wright et al. 2008). In this respect, *Tabebuia* trees are expected to have low dispersal efficiency because they fruit early in the rainy season (A. Jara-Guerrero unpubl.), when wind circulation is lower and wet atmospheric conditions drastically reduce seed uplifting (Wright et al. 2008). In the case of *E. ruizii*, limited dispersal may be due to the fact that seeds are released in groups, which reduces propagule aerodynamic performance (Linares-Palomino 2005).

Even in the case of autochorous species, where nine out of ten showed aggregated spatial patterns (which was consistent with our hypotheses) one species (*Senna mollissima*) was best described by an IPP. In this case, lower aggregation could be explained by secondary dispersal events, since seeds of *S. mollissima* have been registered in deer droppings within the study area (A. Jara-Guerrero unpubl.).

### Signature of dispersal syndromes in spatial aggregation patterns

All the species showed spatial aggregation, with an increase of this spatial signal at short distances and independently

of the dispersal syndrome type (Fig. 1). According to our expectations, autochorous species showed the greater aggregation, which is consistent with previous studies (Condit et al. 2000, Seidler and Plotkin 2006). However, the lower aggregation of anemochorous in relation to zoochorous species did not match our expectations. Although this could be a spurious result due to the small number of anemochorous species in our sample (four species); similar results have been obtained in other studies (Muller-Landau et al. 2008).

The variation of cluster sizes among dispersal syndromes, with zoochorous species showing larger cluster sizes than anemochorous and autochorous species (Fig. 2) is consistent with previous studies (Seidler and Plotkin 2006, Thomson et al. 2011). However we did not detect statistically significant differences among syndromes. This result may be explained by the large variation within each dispersal syndrome. For instance, the large cluster size variation in zoochorous species could be explained by the different behavior of dispersers (Muller-Landau et al. 2008). According to Howe (1989), zoochory may result in two contrasting seed deposition patterns depending on disperser. Birds and bats deposit single seeds, resulting in isolated recruits, while large frugivores, such as mammals, usually defecate masses of seeds and may cause aggregated spatial patterns (Howe 1989, Wiegand et al. 2009). In fact, Seidler and Plotkin (2006) distinguished several types of animal dispersed species in tropical forests and found significant differences among them. In anemochorous species, dispersal distance depends on the rate of fall, given by the interaction between diaspore morphology (which affects aerodynamics) and the structure of the patch (which affects air currents) (Schupp and Fuentes 1995, Muller-Landau et al. 2008). Thus, although some species can disperse their seeds far away from the parent plant, other species can only attain a few meters. In general, autochorous species had the smaller cluster sizes, which is consistent with their limited dispersal, and as has also been reported in other studies (Seidler and Plotkin 2006, Muller-Landau et al. 2008). However, we found the largest variation in cluster size within this group, with some species such as *Pithecellobium excelsum* and *Mimosa acantholoba* showing cluster sizes even larger than all the zoochorous species. These outlier species could be caused by of accidental dispersal events, or secondary dispersal events. For example, in *M. acantholoba*, although it lacks specialized dispersal mechanisms, mature pods may become stiffly papery and often densely hispid-setose, which may promote dispersal away from the parent plant by wind or ectozoochory respectively (Barneby 1991). It has also been suggested that their lustrous seeds might be taken up by birds and dispersed undamaged (Barneby 1991). In fact, *M. acantholoba* is considered a pioneer species (Lebrija-Trejos and Bongers 2008) which suggests that these 'accidental' or secondary events should be usual in the species. In the case of *P. excelsum*, seeds do not fall from the pod immediately after dehiscence but instead remain suspended from a colored spongy aril, attractive to birds (Barneby and Grimes 1997), which might disperse them. It is important to note that the absence of significant differences between syndromes could be due to the small spatial scale of the study. In fact, when large scales have been considered, significant patterns have emerged. For example, Beaudrot et al. (2013) using a large-scale, almost macro-ecological, framework found significant

evidence that wind-dispersed trees had significant dispersal limitation but trees dispersed by animals did not. Thomson et al. (2011) in their meta-analysis of maximum and mean dispersal distances unequivocally showed that unassisted species had the shortest dispersal distances, wind dispersed ones were intermediate and species dispersed by animals reached the longest dispersal distance. The dimensions of our plot (300 × 300 m) are probably shorter than the mean and maximal dispersal distance for zoochorous species and this could cause the overlap between their fitted cluster and those of the rest of species. On the other hand, these small dimensions prevent confusion of multiple clustering processes (if present) with inhomogeneous processes, but care should be taken in larger plots.

In summary, predictions about spatial patterns of tree species and relations to dispersal syndrome can be improved by selecting the best model for each species from a set of models with well known biological links, instead of using a fixed model for all species. Our work enlightens the academic debate about the prevalence of different mechanisms in the formation of realized assemblages in tropical dry forests (Hubbell 1979, Leibold 1995, López-Martínez et al. 2013). On one hand, findings support the hypothesis that local spatial patterns are not independent of the biological attributes of plant species (Seidler and Plotkin 2006, Shen et al. 2009, Lin et al. 2011) and biological interactions. Differences in seed dispersal abilities, which are related to morphological attributes but also to phenological differences within a dispersal syndrome, may contribute to structuring and maintain the assemblage of species in the studied tropical dry forest. On the other hand, the fact that 75% of species were controlled by environmental heterogeneity let us conclude that spatial heterogeneity, and not only dispersal limitation, affected species realized spatial patterns in the studied dry tropical forest. Moreover, this finding shows that not only large scale environmental gradients (Beaudrot et al. 2013) but also small environmental heterogeneity filters the effects of dispersal limitation. Thus, ignoring habitat heterogeneity could bias the analysis of relationships between dispersal syndrome and species patterns.

*Acknowledgements* – This study was partially supported by projects CGL2009-13190-C03-02 (ISLAS ESPACIO), 293 CGL2012-38427 (MOUNTAINS), REMEDINAL3, PROY\_IECOLOGIA\_0018 and PROY\_IECOLOGIA\_0035 funded by Universidad Técnica Particular de Loja. The authors thank Ministerio del Ambiente del Ecuador and Ministerio de Defensa del Ecuador for facilities and operational support during field work.

## References

- Augspurger, C. 1986. Morphology and dispersal potential of wind-dispersed diaspores of Neotropical trees. – *Am. J. Bot.* 73: 353–363.
- Baddeley, A. and Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. – *J. Stat. Softw.* 12: 1–42.
- Barneby, R. C. 1991. *Sensitivae censitae: a description of the genus Mimosa* Linnaeus (Mimosaceae) in the New World. – *Mem. N. Y. Bot. Gard.* v. 65.
- Barneby, R. C. and Grimes, J. W. 1997. Silk tree, Guanacaste, monkey's earring: a generic system for the synandrous

- Mimosaceae of the Americas. – *Mem. N. Y. Bot. Gard.* v. 74, part II.
- Beaudrot, L. et al. 2013. Dispersal modes affect tropical forest assembly across trophic levels. – *Ecography* 36: 984–993.
- Best, B. J. and Kessler, M. 1995. Biodiversity and conservation in Tumbesian Ecuador and Peru. – *BirdLife Int.*
- Callaway, R. and Walker, L. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. – *Ecology* 78: 1958–1965.
- Comita, L. S. et al. 2007. Developmental changes in habitat associations of tropical trees. – *J. Ecol.* 95: 482–492.
- Condit, R. et al. 2000. Spatial patterns in the distribution of tropical tree species. – *Science* 288: 1414–1418.
- Cousens, R. et al. 2008. Dispersal in plants. A population perspective. – Oxford Univ. Press.
- De la Cruz, M. 2008. Métodos para analizar datos puntuales. – In: Maestre, F. T. et al. (eds), *Introducción al análisis espacial de datos en ecología y ciencias ambientales: métodos y aplicaciones*. Asociación Española de Ecología Terrestre, Universidad Rey Juan Carlos y Caja de Ahorros del Mediterráneo, pp. 76–127.
- Espinosa, C. I. et al. 2011. What factors affect diversity and species composition of endangered tumbesian dry forests in southern Ecuador? – *Biotropica* 4: 15–22.
- Espinosa, C. I. et al. 2012. Bosques tropicales secos de la región Pacífico Ecuatorial: diversidad, estructura, funcionamiento e implicaciones para la conservación. – *Ecosistemas* 21: 167–179.
- Godoy, J. and Jordano, P. 2001. Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. – *Mol. Ecol.* 10: 2275–2283.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. – *Biol. Rev.* 52: 107–145.
- Hardesty, B. and Parker, T. 2002. Community seed rain patterns and a comparison to adult community structure in a West African tropical forest. – *Plant Ecol.* 164: 49–64.
- Herrera, C. M. et al. 1994. Recruitment of a mast-fruited, bird-dispersed tree – bridging frugivore activity and seedling establishment. – *Ecol. Monogr.* 64: 315–344.
- Howe, H. F. 1989. Scatter and clump-dispersal and seedling demography: hypothesis and implications. – *Oecologia* 79: 417–426.
- Hubbell, S. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. – *Science* 203: 1299–1309.
- Hubbell, S. 2001. *The unified neutral theory of biodiversity and biogeography*. – Princeton Univ. Press.
- Illian, J. et al. 2008. Statistical analysis and modelling of spatial point patterns. – Wiley.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – *Am. Nat.* 104: 501–527.
- Jara-Guerrero, A. et al. 2011. Seed dispersal spectrum of woody species in south Ecuadorian dry forests: environmental correlates and the effect of considering species abundance. – *Biotropica* 43: 722–730.
- Lebrija-Trejos, E. and Bongers, F. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. – *Biotropica* 40: 422–431.
- Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. – *Ecology* 76: 1371–1382.
- Lin, Y. C. et al. 2011. Point patterns of tree distribution determined by habitat heterogeneity and dispersal limitation. – *Oecologia* 165: 175–184.
- Linares-Palomino, R. 2005. Spatial distribution patterns of trees in a seasonally dry forest in the Cerros de Amotape National Park, northwestern Peru. – *Rev. Peru Biol.* 12: 317–326.
- López-Martínez, J. O. et al. 2013.  $\beta$ -Diversity of functional groups of woody plants in a tropical dry forest in Yucatan. – *PLoS ONE* 8(9): e73660.
- McIntire, E. and Fajardo, A. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. – *Ecology* 90: 46–56.
- Muller-Landau, H. C. et al. 2008. Interspecific variation in primary seed dispersal in a tropical forest. – *J. Ecol.* 96: 653–667.
- Nathan, R. and Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. – *Trends Ecol. Evol.* 15: 278–285.
- Plotkin, J. B. et al. 2002. Cluster analysis of spatial patterns in Malaysian tree species. – *Am. Nat.* 160: 629–644.
- Ripley, B. D. 1976. The second-order analysis of stationary point processes. – *J. Appl. Probabil.* 13: 255–266.
- Schiffers, K. et al. 2008. Dealing with virtual aggregation a new index for analyzing heterogeneous point patterns. – *Ecography* 31: 545–555.
- Schupp, E. and Fuentes, M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. – *Écociencia* 2: 267–275.
- Seidler, T. and Plotkin, J. 2006. Seed dispersal and spatial pattern in tropical trees. – *PLoS Biol.* 4: 2132–2137.
- Shen, G. et al. 2009. Species–area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. – *Ecology* 90: 3033–3041.
- Tinoco, B. 2009. Estacionalidad de la comunidad de aves en un bosque deciduo tumbesino en el sur occidente de Ecuador. – *Ornitol. Neotrop.* 20: 157–170.
- Tirira, D. 2007. *Guía de campo de mamíferos del Ecuador*. – Editorial Murciélago Blanco.
- Thomson, F. J. et al. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. – *J. Ecol.* 99: 1299–1307.
- Van der Pijl, L. 1969. *Principles of dispersal in higher plants*. – Springer.
- Wang, B. and Smith, T. 2002. Closing the seed dispersal loop. – *Trends Ecol. Evol.* 17: 379–385.
- Wang, X. et al. 2013. Phylogenetic and functional diversity area relationships in two temperate forests. – *Ecography* 36: 883–893.
- Webb, C. and Peart, D. 2001. High seed dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications. – *Ecol. Lett.* 4: 491–499.
- Webster, R. and McBratney, A. B. 1989. On the Akaike information criterion for choosing models for variograms of soil properties. – *J. Soil Sci.* 40: 493–496.
- Wiegand, T. and Moloney, K. A. 2013. *Handbook of spatial point-pattern analysis in ecology*. – Chapman and Hall/CRC.
- Wiegand, T. et al. 2007a. Species associations in a heterogeneous Sri Lankan dipterocarp forest. – *Am. Nat.* 170: E77–E95.
- Wiegand, T. et al. 2007b. How individual species structure diversity in tropical forests. – *Proc. Natl Acad. Sci. USA* 104: 19029–19033.
- Wiegand, T. et al. 2009. Recruitment in tropical tree species: revealing complex spatial patterns. – *Am. Nat.* 174: E106–E140.
- Wright, S. J. et al. 2008. Understanding strategies for seed dispersal by wind under contrasting atmospheric conditions. – *Proc. Natl Acad. Sci. USA* 105: 19084–19089.

Supplementary material (Appendix oik.02098 at <[www.oikosjournal.org/readers/appendix](http://www.oikosjournal.org/readers/appendix)>). Appendix 1. Mathematical details about fitted models. Table A1. Results of model fitting. Table A2 Number of parameters fitted for each model.