

Temporal and spatial patterns of propagule deposition in the riparian zones of mountain rivers

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Abstract

Although the dispersal is important for riparian plants, few studies have evaluated the patterns in species richness and composition of propagules deposited by different dispersal types. In the present study we evaluate the temporal and spatial patterns in the diversity of propagules deposited by hydrochory and by other types of dispersal along mountain rivers. To do this, we sampled the propagules deposited in the riparian zone in a distance gradient with respect to the site of origin of the rivers in two seasons. Regarding the temporal analyses, we found no differences in the number of propagules between seasons. In the rainy season we observed a greater number of species deposited by hydrochory, while for other types of dispersal there was a greater number of species in the dry season. Differences in composition were observed for hydrochory but not for other types of dispersal. Regarding the spatial analyses, there were no changes in the number of propagules deposited along the river by hydrochory, while for other types of dispersal an increase was observed in the dry season. A lower number of species deposited by hydrochory along the river in the rainy season was observed. Finally, we observed that turnover increases by other types of dispersal in the dry season but not for hydrochory. The results underline the importance of types of dispersal other than hydrochory in the contribution of propagules dispersed and the temporal and spatial particularities of the hydrochory in mountain rivers.

1. Introduction

Dispersal is the transport of individuals from their site of origin to an establishment site (Cousens et al., 2008; Pijl, 1969). In plants this transport is generally driven by one or several dispersal vectors, for example, if the transport is by wind it's called anemochory, by an animal it's called zoochory and if the transport is by water it's called hydrochory (Boudell, 2016; Matthysen, 2012; Pijl, 1969). Given that for plants the transport of propagules depends on dispersal vectors, the dynamics of these vectors has important implications for plant communities since dispersal has been observed to be important for the patterns of species richness and composition of communities, the coexistence of species and the maintenance of metacommunities (Boudell, 2016; Levine & Murrell, 2003; Nilsson et al., 2010).

Hydrochory is an important source of propagules for riparian plant communities, since it transports the greatest number of different species' propagules to the riparian zones (Jansson et al., 2005; Leyer, 2006; Moggridge & Gurnell, 2010; Neff & Baldwin, 2005). For this reason, great efforts have been made to understand this dispersal mechanism in rivers (Hyslop & Trowsdale, 2012; Nilsson et al., 2010). These studies have shown that hydrochory has two important characteristics that determine the spatial distribution of dispersed propagules in the riparian zones along rivers: (i) the movement of propagules is unidirectional

and (ii) there is a downstream accumulation of the propagules (Andersson et al., 2000; Nilsson et al., 2010). This unidirectional movement and accumulation of species and propagules transported downstream by the river is related to the increase in species richness and the nesting of plant communities along rivers (Kuglerová et al., 2015). This has served as a basis to explain the diversity patterns of plant communities along rivers, synthesized in the "River Collector Hypothesis" (hereinafter referred to as RCH). The RCH suggests that the species richness increases along the river to a maximum point in the intermediate zones and then decreases towards the mouth of the rivers, in addition, it supposes the nesting of the upstream communities in the downstream ones (Nilsson et al., 2010).

In addition to these spatial changes, temporal variations in the dispersal of propagules by hydrochory have been observed. The most relevant pattern occurs in the season of greatest streamflow, which is correlated with a greater number of propagules and species dispersed along the rivers (Greet et al., 2011; Gurnell et al., 2008; Pettit & Froend, 2001). This increase in the number of dispersed propagules depends on a greater streamflow, but it is also the result of the synchronization of the reproductive phenology of the riparian species with the maximum flow peaks of the water, producing a greater number of propagules that can be dispersed (Pettit & Froend, 2001).

The plants of the riparian communities, also have other vectors of dispersal to move their propagules to other watersheds or riparian zones through anemochory and zoochory (Fraaije et al., 2017). These types of dispersal are important for the spatial distribution patterns of propagules in riparian zones because for some species they are the first dispersal vector that carries propagules from the parental plant to the riparian zone along the river (Esper-Reyes et al., 2018; Fraaije et al., 2017; Nilsson et al., 2010). These types of dispersal could be particularly important for propagule movement in intermittent rivers in which hydrochory propagule transport only occurs at certain times of the year (Boland, 2017; Drezner et al., 2001; Schwab et al., 2018) or in turbulent rivers where the disturbance of the floods limits the establishment of the propagules deposited by hydrochory (Hasselquist et al., 2015). However, there is little empirical studies on the patterns of richness and composition of dispersal types other than hydrochory along rivers and their temporal variations.

Another of the unknown aspects of dispersal in riparian zones is the study of variations in the richness, composition and number of propagules dispersed in rivers with specific geomorphological characteristics, such as mountain rivers. The geomorphological and hydrological characteristics of these rivers, such as the altitudinal gradients, the steep slopes, the large confining sections and the current velocity, increase their downstream transport capacity and reduce their deposition of matter towards the riparian zones (Jacobsen, 2008; Meyer et al., 2007; Wohl, 2010) and thus, it is possible that the deposition patterns of the propagules transported by hydrochory are different from what has been observed in other sections of the rivers.

In this study, we contrast spatial and temporal changes in the number of propagules, species, and species composition deposited by hydrochory and other types of dispersal with increasing distance to the site of origin of rivers in a mountainous system. For the temporal patterns we expect that: (i) the abundance and species richness of propagules deposited by hydrochory is greater in the rainy season than in the dry season, while no changes are observed for other types of dispersal and (ii) differences in composition between seasons for hydrochory but not for other types of dispersal. Regarding spatial patterns, we expect that: (iii) the number of species and propagules dispersed by hydrochory increases with distance to the site of origin of rivers while remaining constant for other types of dispersal, (iv) nesting pattern for hydrochory but not for other dispersal types and (v) the turnover remains constant for hydrochory-dispersed propagule communities and increases for other dispersal types.

2. Method

2.1. Study area

The study area is limited to the upper area of the Papaloapan River in the state of Oaxaca, southern Mexico. In this area the rivers drain from a maximum altitude of 3,216 m a.s.l. towards a minimum altitude of 1,833 m a.s.l. Strahler order of rivers ranges from 1 at sites in the smallest rivers (headwaters) to 5 at sites that are located on the largest rivers (downstream). The flow ranges from 0.01 l/s to 2.5 l/s and has a negative

relationship with altitude (Flores-Galicia et al., 2021). The climate in the upper part of the watershed corresponds to humid temperate with summer rains and in the lower and middle part it corresponds mainly to sub-humid temperate with summer rains. The upland forests are *Abies hickelii* and *Pinus hartwegii* forests in the upper areas and mixed forests of *A. hickelii* - *Pinus patula* and *Pinus pseudostrobus* var. *apulcensis* - *Quercus crassifolia* towards the middle and low areas of the watershed (Pina & Trejo, 2014). The vegetation of the riparian zone changes along the streams, in the headwaters arboreal elements of species such as *A. hickelii*, *Pinus* spp., *Quercus* spp., towards the intermediate parts *Alnus acuminata*, *Oreopanax xalapensis* and *Meliosma dentata*, while in the lower areas *A. acuminata* and *Salix humboldtiana* are observed (Flores-Galicia et al., 2021).

To evaluate the changes in the communities of propagules, nine sampling sites were established in two tributary rivers (Yavesia's river and Lachatao's river) that are part of the same drainage network in the basin, the location of the sites was determined based on a progressive criterion of distance with respect to the origin of the rivers (Fig. 1).

2.2. Sampling propagules

To characterize the communities of propagules dispersed by hydrochory and other types of dispersal in the riparian zone, generative propagules were collected, that is, those that are the product of the sexual reproduction of plants such as seeds or fruits (Pijl, 1969) in two types of traps that were placed in sediment deposition zones adjacent to the streams: (i) Leyer boxes to collect propagules dispersed by hydrochory and (ii) mesh traps to collect propagules dispersed by other types of dispersal. Leyer boxes (*sensu* Leyer, 2006) were boxes open at the bottom, covered by a 0.15 mm mesh size at the top and fastened by wires. The construction ensured the free flow of water, sediments, and propagules into the box, inside an artificial turf mat were placed (0.5x0.5 m) to retain the propagules. The boxes were tied to 75 cm long metal rods to prevent them from being dragged by the waterflood (Araujo et al., 2015). On the other hand, the mesh traps to collect propagules dispersed by other types of dispersal consisted of extended squares (1.5 x 1.5 m) of shade cloth (1.5 mm mesh) that were placed near the Leyer boxes. Leyer boxes were placed at the lowest line of perennial vegetation (greenline) (Fig. 1c).

In each of the nine sampling sites, two Leyer boxes and three mesh traps were placed to collect propagules dispersed by hydrochory and by other types of dispersal (Fig. 1b). The traps were visited every two or three months to collect the propagules trapped in them between January 2017 and January 2018 (they were visited five times: March, June, August, and November 2017 and January 2018). At each visit the traps were removed and new traps were placed, so that a total of 90 Leyer boxes and 135 mesh traps were placed throughout the sampling period. Due to river flooding and other events, 36% of the Leyer boxes (n=32) and 15% of the mesh traps (n=20) were lost. During this period, propagules in the dry season (March 2017 and January 2018) and in the rainy season (June, August, and November 2017) were collected.

The propagules were identified (to species level or otherwise assigned to a morphospecies), counted and removed manually. The propagules were compared with specimens deposited in the Collection of Fruits and Seeds of the National Herbarium (MEXU), of the Institute of Biology of the UNAM.

2.3. Data analysis

2.3.1. Temporal variations

To detect differences between seasons, a database was prepared differentiating the propagules collected in the dry season (propagules collected in March 2017 and January 2018) and the rainy season (propagules collected in June, August and November 2017), with which performed the following analyses in R ver. 4.0.3 (R Core Team, 2020).

Since differences in the number of propagules between seasons, a standardization of the sampling effort was first carried out by randomly selecting 52 traps for hydrochory (dry= 26 traps, rainy=26 traps) and 92 traps for other types of dispersal (dry= 46 traps, rainy= 46 traps). Subsequently, and because the data were not

normal, we performed a Mann-Whitney test to determine differences in the number of propagules between seasons.

To contrast species richness, a rarefaction analysis was performed using the *iNEXT* function (Hsieh et al., 2016) from the iNEXT package. We calculated the estimated species richness (q^0) and its 95% confidence intervals for the dry and rainy seasons considering the lower coverage that we recorded in the traps (traps for hydrochory in the rainy season=0.995) (Hsieh et al., 2016). Finally, to determine changes in species composition, a permutational multivariate analysis of variance (PERMANOVA) was performed, applying a Hellinger transformation to the abundance data using the *adonis* function from the vegan package in R (Oksanen et al., 2013). For the PERMANOVA, a distance matrix was used that was obtained with the Bray Curtis coefficient. To graphically evaluate the associations in the composition of the propagules dispersed by hydrochory and by other types of dispersal in the dry and rainy season, an NMDS was performed with the *metaMDS* function of the vegan package (Oksanen et al., 2013).

2.3.2. Longitudinal variations along the streams

To evaluate changes in the abundance and richness of species with the distance to the origin of the river, a Generalized Linear Mixed Effects Model (GLMM) with a negative binomial link function was performed using the *glmer.nb* function of the lme4 package (Bates, 2010). The number of propagules/m² and the number of species estimated at each site were used as a fixed effect and the stream in which the sites were established (Yavesia river or Lachatao river) as a random effect (Fig. 1).

To determine changes in the turnover and nesting of propagule communities with increasing distance to the origin of the river, values were obtained for the Simpson dissimilarity index ($\beta_{\Sigma\mu}$) and nesting between sites near the river origin (site one: 0.5 km and site two: 0.8 km) and the downstream sites, in this analysis the sites that were located in the Lachatao stream (sites six, seven and nine) were excluded because they are located in a different stream than the rest of the sites. The turnover and nesting values were obtained using the functions *vegdist* and *nestednodf* of vegan package (Oksanen et al., 2013). Subsequently, a Pearson correlation analysis was carried out to determine if there was a relationship between the distance to the origin of the river and the turnover and nesting values.

3. Results

3.1. Temporal variations in the propagules

During the study period and considering the traps for hydrochory and for other types of dispersal, a total of 43,025 propagules belonging to 106 species were collected. In the traps for hydrochory 5,435 propagules belonging to 46 species were collected and in the traps for other types of dispersal 37,590 propagules of 66 species were captured. No differences were observed in the number of propagules collected between the dry and rainy seasons in the hydrochory traps (rainy: $x = 152$, S.D. = 410, dry: $x = 57.38$, S.D. = 102.83, Mann-Whitney $U = 441$, $p = 0.06$) or in the traps for other types of dispersal (rainy $x = 513.85$, S.D. = 990.92, dry: $x = 173.39$, S.D. = 324.77, Mann-Whitney $U = 1157$, $p = 0.44$) (Fig. 2a). Regarding species richness, a higher estimated species richness was observed in the rainy season than in the dry season in the hydrochory traps (rainy: $q^0 = 37.82$, 95% C.I.: 31.60-44.34; dry: $q^0 = 10.12$, 95% C.I.: 7.93-12.31), while in the traps for other types of dispersal there is a higher species richness estimated in the dry season than in the rainy season (rainy: $q^0 = 17.79$, 95% C.I.: 16.88-18.72; dry: $q^0 = 27.89$, 95% C.I.: 25.33-30.32) (Fig. 2b).

Regarding the composition, the PERMANOVA shows that in the hydrochory traps the composition is different between the dry and rainy seasons (pseudo-F = 2.55, $p = 0.02$). Some of the species that were only observed in the rainy season were conifers (*Abies hickelli* y *Pinus* sp.), some composites (Asteraceae, Asteraceae 2 y Asteraceae 6) and a grass species (Poaceae), in the dry season *Rumex* sp. was a characteristic species and species such as *Alnus acuminata* and *Clematis dioica* were observed in both seasons (Fig. 3, Appendix 1). With respect to the propagules deposited by other types of dispersion, no differences were observed in the composition between the seasons (pseudo-F = 0.75, $p = 0.62$) (Fig. 3).

3.2. Spatial changes of propagule communities along the river

Regarding the number of propagules, no changes were observed with the increase in the distance to the origin of the river in the traps for hydrochory, while for other types of dispersal an increase in the number of propagules deposited in the dry season was observed (Fig. 4, table 1).

Regarding to the changes in species richness, a decrease in estimated species richness was observed with increasing distance from the river origin in hydrochory traps in the rainy season but not in the dry season. While for other types of dispersal, no changes were observed in the estimated species richness with the distance to the site of origin of the river in any of the seasons (Fig. 5, table 2).

Finally, nesting values were low and turnover was high in traps for hydrochory and for other types of dispersion in both seasons. No relationships of nesting or turnover values with increasing distance to sites near the river origin were observed in any of the seasons for propagules deposited by hydrochory. For other types of dispersion, a positive relationship was observed with the turnover of species in the dry season (Fig. 6, table 3).

4. Discussion

The temporal variations in the species richness of propagules deposited by hydrochory show similarities with what has been observed in other rivers and what we propose in our hypotheses. These temporary changes are determined by the increase in the level and volume of water in the rivers during the rainy season (or higher water flow) which in turn increase the number of species that are dispersed towards the riparian zones (Boedtelje et al., 2004; Fraaije et al., 2017; Moggridge et al., 2009). In contrast, the abundance of propagules dispersed by hydrochory towards the riparian zone did not increase during the rainy season. Previous work has found that there is a greater number of propagules during the season of higher water flow in rivers due to the greater capacity of propagule dispersal through water currents (Boedtelje et al., 2004; Esper-Reyes et al., 2018; Fraaije et al., 2017; Moggridge & Gurnell, 2010; Naiman et al., 2010). However, there is no temporal trend in the deposition of propagules by hydrochory and it has been suggested that this may be due to the great production of propagules of one species (e.g. *Veronica anagallis-aquatica*) throughout the year (Gurnell et al., 2008), a similar phenomenon could be occurring in the study area.

In our case, we observed that the dominant tree species in the riparian zone (*Alnus acuminata*) (Flores-Galicia et al., 2021) had a peak in propagule release that was detected in the traps for other types of dispersal at the end of the rainy season (November 2017). Subsequently, the increase was reflected in the hydrochory traps at the beginning of the dry season (January 2018) (Annex 1). The effect of *A. acuminata* propagule production on temporal variations in the number of propagules deposited by hydrochory is confirmed if this species is eliminated from abundance analyses. By doing this, the number of propagules deposited by hydrochory in the rainy season is greater than in the dry season (rainy: $x = 21.8$, S.D. = 44.3, dry: $x = 3.1$, S.D. = 6.3, $W = 502$, $d.f. = 45$, $p < 0.01$). The foregoing indicates that, in this system, the temporal patterns of abundance of propagules dispersed by hydrochory are not only determined by the temporal variations in the flow of water from the rivers, but also that the local production of propagules.

The differences in the composition of the propagules dispersed by hydrochory between the dry and rainy seasons were consistent with our hypothesis. These temporary changes in composition are related to differences throughout the year in the production of propagules of the species that make up the riparian communities or of the adjacent forests (Esper-Reyes et al., 2018), the accumulation of these in the riparian zones and their subsequent remobilization during river floods (Boedtelje et al., 2004; Fraaije et al., 2017; Gurnell et al., 2008). In our system we observed that some species with peaks of propagule production during the rainy season were only observed during the same season in propagules deposited by hydrochory, such as *A. hickelli*, *Pinus* sp., *Solanum* sp and some Asteraceae (Asteraceae 2 y Asteraceae 6).

For the spatial dimension, there are contrasts between what our hypotheses propose and what we observed in this study, specifically for the richness patterns, the number of propagules and the composition of the communities of propagules dispersed by hydrochory along the river. Contrary to what was expected, a greater number of species dispersed by hydrochory was not observed with increasing distance from the origin site of the river. The absence of a positive relationship between the number of species and the distance to

the origin of the river may be the result of the fact that downstream there was no accumulation of species from upstream, as has been observed in other rivers (Andersson et al., 2000; Andersson & Nilsson, 2002). The nesting analysis supports the above since the composition of the communities of the sites close to the origin of the river (sites one and two) is not a subset of the communities further away from the origin of the river. The low nesting indicates that the species near the origin of the river were not transported downstream (sites beyond 7 km) or if they did, the propagules were not deposited in the downstream riparian zones and continued their course in the column. of water beyond the study area.

Regarding the number of propagules deposited by hydrochory along the rivers, our results contrast with what we propose in our hypotheses and what has been observed in other studies (Andersson & Nilsson, 2002; Esper-Reyes et al., 2018). As occurs for the temporal variations in the number of propagules, the absence of an increase in the propagules deposited along the river could be related to the local production of *A. acuminata*. However, when *A. acuminata* is eliminated from the analyses, an increase in the number of propagules is observed along the rivers in the hydrochory traps in the dry season (estimated= 0.15, $z = 2.65$, $p = <0.01$) but not in the rainy season, where instead a decrease in the deposited propagules is observed (estimated= -0.14, $z = -2.46$, $p = 0.01$). This same analysis (exclusion of *A. acuminata*) in the traps for other types of dispersal yields similar results (rainy: estimated= -0.20, $z = -3.04$, $p = <0.01$; dry: estimated= 0.17, $z = 2.42$, $p = 0.01$). This could indicate that the production of propagules in the sites near the origin of the river is greater in the rainy season, which increases the deposition of propagules by hydrochory in the area, while in the dry season there is a greater production of propagules in the sites furthest from the origin of the river.

The results that we observed with respect to the spatial dimension (absence of relationship between the distance to the origin of the river with the estimated species richness or with the number of propagules, absence of nesting of the upstream communities in those of downstream), has important implications for theoretical frameworks such as RHC that hypothesize regarding longitudinal changes in diversity of riparian plant communities. The RHC postulate that the number of plant species increases to a maximum point in the intermediate zone of the rivers from which it decreases towards its mouth, these changes are associated with: (i) a linear increase in the disturbance in the riparian zones at along the river and (ii) a constant increase in the number of species and propagules dispersed by hydrochory (Nilsson et al., 1994, 2010). As there is no greater deposition of species and propagules deposited downstream, the patterns of diversity of the riparian plant communities that the RHC supposes could not be observed in rivers of mountainous systems (see for example Flores-Galicia et al., 2021; Pielech, 2021).

Some methodological limitations of this work did not allow us to conclude whether the contrasts between what we propose in our hypotheses with respect to the spatial distribution patterns of the propagules along the river (that is, a greater number of propagules and species deposited by hydrochory along the river, as well as nesting of the upstream communities in the downstream communities) and what we observed (absence of changes in the number of propagules, in the richness and decrease in the nesting of the communities). This is due to the fact that in this system: (i) the propagules transported in the water column travel a shorter distance than has been observed in other studies (Andersson et al., 2000; Boedeltje et al., 2003) or (ii) the propagules are effectively transported over long distances but due to the characteristic erosive capacity of mountain rivers (Wohl, 2010) the propagules deposited in the riparian zone are quickly remobilized to downstream and were not detected in our traps. Future studies could determine which of these hypotheses is correct through controlled propagule release experiments and the measurement of the distances they travel (Boland, 2017; da Cunha et al., 2017) or through sampling of propagules in the water column (Boedeltje et al., 2003).

Conclusion

Hydrochory in tropical mountain systems has characteristic deposition patterns that do not agree with what has been observed in rivers with different geomorphological characteristics or in complete rivers (origin-mouth). In tropical mountain rivers, the contribution of propagules by other types of dispersal and the spatial and temporal changes in the local production of propagules by the riparian plant species have a decisive

influence on the spatial and temporal patterns of deposition of the dispersed propagules by hydrochory. The dynamics of the transport of propagules in the water column remains unknown, so it is necessary to increase efforts to understand in depth the process of dispersion in mountain rivers.

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Data availability

Propagule sampling data will be accessible via Figshare data repository.

Tables

Table 1. Generalized mixed effects linear models to the association between the distance to the origin site of the river and the number of propagules collected in the traps for hydrochory and other types of dispersal. (*) Denotes significant effects. Var. = variance of the random effect (river), S.D. = standard deviation, Est. = estimate of the fixed effect (distance to the origin of the river), S.E. = standard error.

Type of trap	Season	Random effect	Random effect	Fixed effect	Fixed effect	Fixed effect
		Var.	S. D.	Est.	S. E.	z
Hydrochory	Rainy	<0.01	<0.01	0.01	0.11	0.12
	Dry	<0.01	<0.01	0.27	0.14	1.87
Other type of dispersion	Rainy	<0.01	<0.01	0.07	0.06	1.10
	Dry	<0.01	<0.01	0.16	0.07	2.42

Table 2. Linear generalized mixed effects models to the association between the distance to the origin site of the river and the richness of species in the traps for hydrochory and other types of dispersal. (*) Denotes significant effects. Var. = variance of the random effect (river), S.D. = standard deviation, Est. = estimate of the fixed effect (distance to the origin of the river), S.E. = standard error.

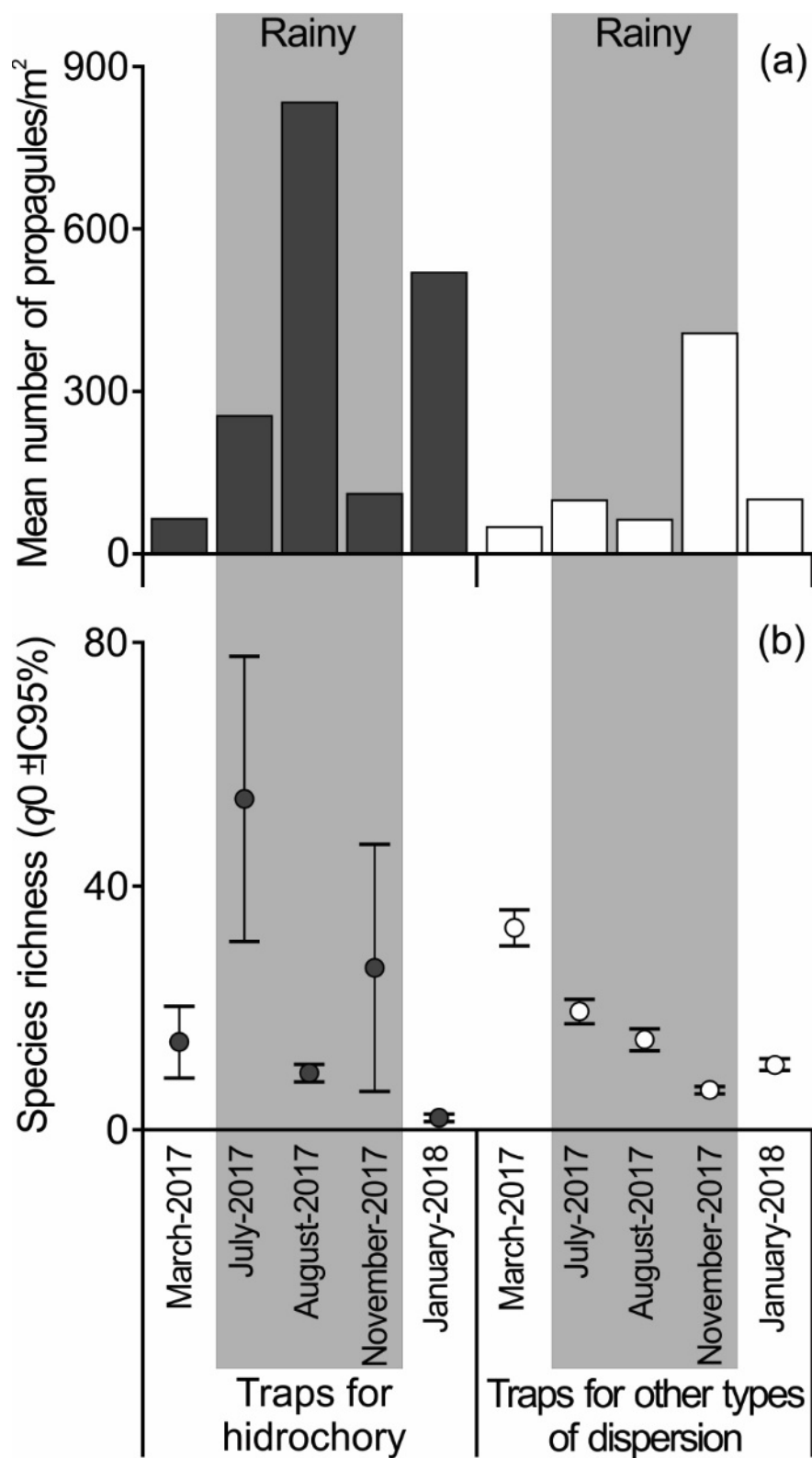


Figure 2. Mean number of propagules and species richness of propagules in the traps for

hydrochory and the traps for other types of dispersal . (a) No differences were observed between the rainy and dry seasons in the number of propagules for any of the traps. (b) For species richness, it was higher in the wet season than in the dry season in hydrochory traps, while for other types of dispersal it was higher in the dry season than in the rainy season. Shading indicates the rainy season.

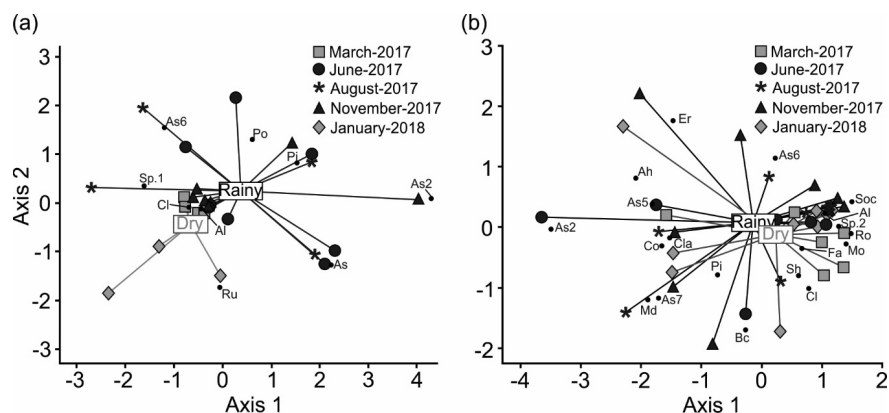


Figure 3. Ordination of seed traps collections during two seasons (rainy: June-2017, August-2017 and November-2017; dry: March-2017 and January-2018) in the hydrochory traps (a) and for other types of dispersion (b). Species with > 10 registered individuals are shown with a black dot (the names of the species are found in Appendix 1).

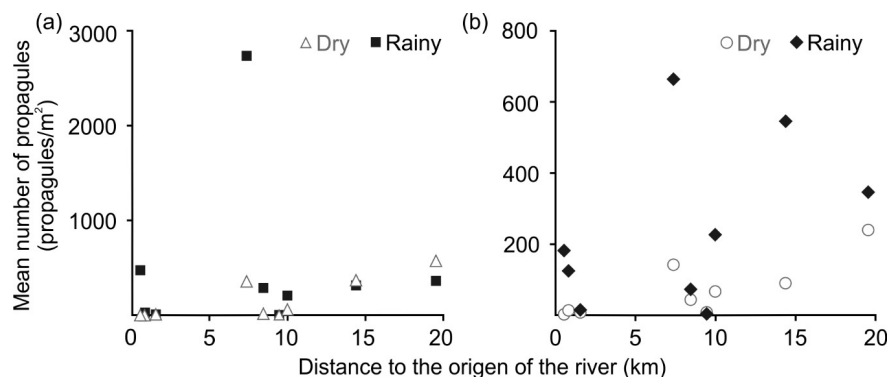


Figure 4. Changes in the number of propagules (propagules/m²) with increasing distance to the origin site of the river in the dry and rainy seasons. (A) propagules collected in traps for hydrochory, (B) propagules collected in traps for other types of dispersal.

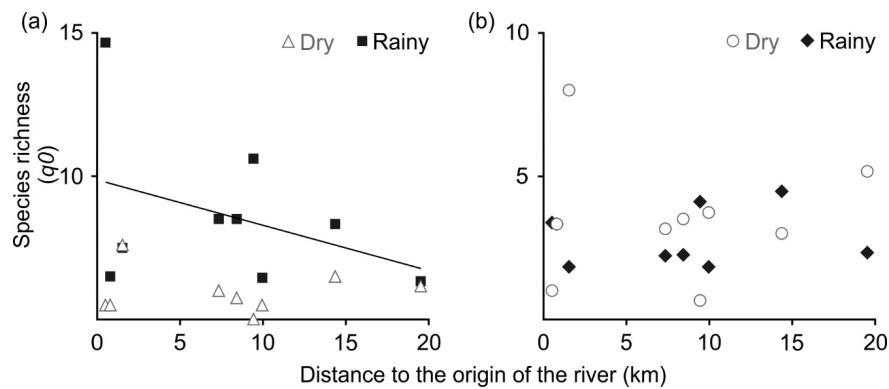


Figure 5. Changes in species richness with increasing distance to the origin site of the river in the dry and rainy seasons. (A) species richness in traps for hydrochory, (B) species richness in traps for other types of dispersal. Trend lines are shown for those significant relationships ($p < 0.05$).

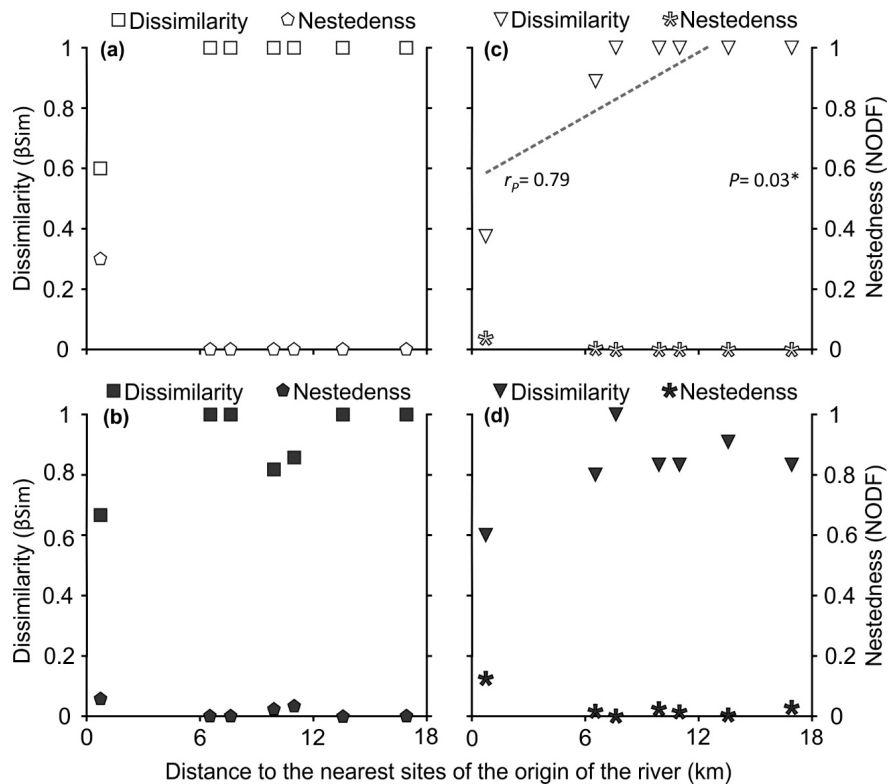


Figure 6. Changes in the turnover and nesting of the communities with the increase in the distance to the sites near the origin of the river. (a) Traps for hydrochory in the dry season, (b) traps for hydrochory in the rainy season, (c) traps for other types of dispersion in the dry season, (d) traps for other types of dispersion in the rainy season. Filled bullets correspond to nesting values, unfilled bullets correspond to replacement values. Trend lines are shown for significant relationships.

Appendices

Appendix 1. Abundance of propagules (log of number of propagules/m²) by species collected in traps for

hydrochory and in traps for other types of dispersal. Species that had more than 10 individuals are show. In parentheses, the code name of the species. The gray shade indicates the collections corresponding to the rainy season (July, August, and November 2017).

