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ARTICLE



The role of recruitment and dispersal limitation in tree community assembly in Amazonian forests

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ABSTRACT

Background: Species composition of plant communities is shaped by the interplay between dispersal limitation, environmental filters and stochastic events.

Aims: The aim of this work was to investigate the effects of dispersal limitation and environmental filtering on tree recruitment. To accomplish this, we employed the unified neutral theory of biodiversity and biogeography to examine migration within the metacommunity, defined as a set of interacting local communities linked by the dispersal of multiple potentially interacting species.

Methods: We sampled 12,975 individuals with dbh \geq 1 cm in 26 1-ha permanent plots, including habitats of *terra firme*, transitional forests, *várzea* and *campinarana*, on the upper Madeira River, Brazilian Amazon.

Results: *Campinarana* drew individuals from outside the metacommunity species pool at a mean probability of recruitment of 0.06, a much lower probability than *terra firme* (0.31), transitional (0.21) and *várzea* forests (0.22). Environmental variables, such as water table depth, soil texture and fertility, were related to differences in community assembly.

Conclusions: Species abundance distribution and diversity patterns of plant assemblages in a large river landscape in the Amazon highlight the importance of environmental heterogeneity that conditions beta-diversity. The high variation in recruitment probabilities from the metacommunity species pool to local communities suggests high habitat variability in the process of maintaining patterns of local diversity.

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Introduction

Natural communities are mixtures of species. Generally, only a few species, the dominants, exceed all others in their biomass and biological activity (Whittaker 1965; ter Steege et al. 2013). The patterns of rarity and dominance of species are expressed in terms of the species rank abundance distribution (RAD), which indicates how common or rare a species is relative to other species in a defined location or community. The RAD in local communities often approaches a concave curve or hyperbolic ‘J-reverse’, indicating very few abundant species and many rare species (the tail of this distribution). This pattern occurs in different communities with low and high species richness, ranging from marine benthos to Amazon rainforest (Tokeshi 1993; Hubbell 2001; McGill et al. 2007).

Some empirical and theoretical studies have examined the predictive ability of RAD models, as

well as the variation of RADs along environmental gradients and the integration of RADs with other biodiversity patterns (e.g. McGill et al. 2007). An example is the ‘unified neutral theory of biodiversity and biogeography – UNTB’, which proposes to explain the origin, maintenance and loss of diversity (richness and abundance) in communities (Hubbell 2001). The UNTB assumes that ecological communities of sessile organisms are structured by demographic stochasticity, random immigration and random speciation. Species abundance distributions (SAD) are predicted as a function of two parameters, θ and m , where θ is a measure of the diversity of the metacommunity, defined as a set of interacting local communities which are linked by the dispersal of multiple potentially interacting species (Leibold et al. 2004); and m stands for the probability that an individual selected at random in the local community was recruited from the metacommunity

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species pool. Within the same metacommunity (same θ), m determines how ‘isolated’ the local community is in relation to the complete species pool. In the original theoretical concept, ‘isolation’ is related to dispersal limitation alone, assuming the ecological equivalence of all individuals, irrespective of species identity.

Until Chave and Jabot (2008), the analytical solution to understand SAD based on UNTB has neglected the fact that environmental filters occur post-dispersal and are, therefore, a crucial factor in community assembly (Ricklefs 1987; Hurtt and Pacala 1995; Nathan and Muller-Landau 2000). Jabot et al. (2008) suggested that the parameter m also represents the recruitment rate and, thus, reflects the sum of two processes shaping SAD: dispersal limitation and establishment limitation post-dispersal in response to environmental filters in the local community. Species composition of local communities poorly represents the metacommunity if the environment filtered out many species. Consequently, the estimation of parameter m for a given local community is expected to decrease as the environmental filter increases (Jabot et al. 2008).

Integrating the predictions of the UNTB with niche theory has been challenging and has led to a hotly debated controversy about the merits of neutral theory, compared with alternative methods to predict SAD (McGill et al. 2006; Chisholm and Pacala 2010; Purves and Turnbull 2010), including prospective integration with niche models (Leibold and McPeck 2006; Matthews and Whittaker 2014). More specifically, many studies have supported the alternative hypothesis that environmental heterogeneity is a determinant of spatial structure in biological communities (Wright 2002; Tuomisto et al. 2003; Richard et al. 2006). Communities at the same trophic level have been analysed by ordination where eigenvalues summarise the variation of structure (abundance) or species composition (presence/absence). The community metrics are correlated with environmental filters to infer the dominant mechanisms explaining variation in species assemblages of trees (John et al. 2007), ferns (Zuquim et al. 2012) and broad spectrum of distinct taxa (Cottenie 2005).

Numerous studies have attempted to disentangle the respective roles of dispersal limitation and environmental filtering in the assembly of tropical plant communities (Tuomisto et al. 2003; Jirka et al. 2007; Damasco et al. 2012; Garibaldi et al. 2014). Most of them have used

various types of variation partitioning techniques. The statistical approach used in our study is more original in that it is based on a fit of a model of community dynamics. This approach has been far less employed, except in the study by Jabot et al. (2008). Here, we have report an innovative way of applying UNTB concepts by creating distinct theoretical species pools (the metacommunity pool and the habitat pool) to evaluate tree recruitment, dispersal and environmental filtering.

From these theoretical species pools, we estimated the recruitment probabilities (parameter m) and assessed how dispersal and environmental filtering shaped tree communities in distinct habitats comprising plots of *terra firme*, transitional forest, *várzea* and *campinarana*. Throughout the study, we asked the following questions. (i) How the habitats sampled differ in their SAD? (ii) How do the estimated probabilities of recruitment from metacommunity to local communities express the dispersal limitation and environmental filtering? We hypothesised that habitats with relatively harsh conditions such as the seasonally flooded and nutrient-poor soils of *campinarana* would require specific adaptations leading to highly filtered tree communities with low recruitment from other habitats and the metacommunity.

Materials and methods

Study area

The study area covered the landscape in the upper Madeira River (9° 9' 35"- 9° 50' 25" S and 65° 28' 8"- 64° 35' 21" W), near Porto Velho, Rondônia, south-western Brazilian Amazon. The elevation was less than 360 m asl, and the climate tropical humid, type hyperthermic (Cochrane and Cochrane 2011). The mean minimum and maximum annual temperatures were 21.1°C and 32.2°C, respectively, and the mean annual precipitation ranged from 1700 to 2000 mm (Sombroek 2001). The Matinguari National Park (MNP) is a large conservation unit of ca. 1.7 M ha (data provided by the Chico Mendes Institute of Biodiversity Conservation – ICMBio) in 2017, and is located on the left bank of the river (north-northeast), where the landscape is hilly and relatively well preserved. On the right bank, outside of the MNP, the landscape is more fragmented as a result of more intensive land use and includes

farms, pastures, roads and Highway BR-364 (Ferraz et al. 2005).

The predominant vegetation type of the region is a lowland open rainforest (IBGE 2012; Perigolo et al. 2017) associated with oxisols (Quesada et al. 2011). Most of the area does not experience flooding during the rainy period ('*terra firme*'). Some areas are classified as transitional forests that have been subject to occasional disturbances such as logging and burning and also include areas with high bamboo abundance. Other vegetation types include *campinarana*, a low-stature forest where the water table reaches the surface during the rainy season (entisols-aquents) and which forms extensive and contiguous patches located in the lowlands south of the Madeira River. Despite the high silt content in the soils of the *campinarana*, their floristic composition and structure resemble the vegetation type described on white sand in the Amazon (Adeney et al. 2016; Perigolo et al. 2017). Finally, narrow strips of *várzea* forests, associated with fluvisols (young soil alluvial deposits), on the banks of the Madeira River (Quesada et al. 2011), are seasonally flooded by the rise of the mainstream channel and tributaries.

Sampling design

In 2011, we sampled palms and trees with diameter at breast height (dbh) ≥ 1 cm in 26 1-ha plots comprising four habitat types: *terra firme* (7 plots), transitional forests (6), *várzea* (6) and *campinarana* (7), encompassing 12,945 individuals and 947 species. We allocated the plots following the RAPELD protocols (Costa and Magnusson 2010) in transects perpendicular to the upper Madeira River (Figure S1). For more details of site description and sampling procedures, see Moser et al. (2014), who conducted a study involving 19 plots of the 26 used here. We sampled the soil to analyse physical and chemical properties in each plot and measured the mean annual depth of ground water (details in Appendix I).

Rank-abundance distributions

We compared the SAD among habitats using the log-series distribution (Fisher et al. 1943), which is the most common statistical model for estimating species abundance in a community. We

represented observed and estimated SAD in a rank-abundance diagram (RAD), where log-abundance was plotted on the y-axis vs. species rank on the x-axis (McGill et al. 2007). This model was fitted to the empirical SAD with a custom R script (courtesy Daniel Sabatier) using the R statistical environment (R Development Core Team 2015). We also calculated Fisher's alpha and associated confidence intervals for *terra firme*, transitional forests, *várzea* and *campinarana*, using the functions '*fitsad*' and '*confint*' in the '*sads*' R package (Prado et al. 2017).

We carried out an indicator species analysis to examine the indirect effect of particular environmental conditions associated with each vegetation habitat on species selection and the assembly of communities (Dufrene and Legendre 1997). This analysis was carried out using the '*labdsv*' R package (Roberts 2015).

Metacommunity model

The original immigration parameter m of UNTB reflects only pure dispersal limitation and is the probability that a dispersal event from the metacommunity will occur, resulting in establishment of a new individual in the local community. Etienne (2005) has estimated an analytical expression for the likelihood function associated with Hubbell's dispersal-limited neutral theory, making it possible to estimate the parameters m and θ based on species abundance datasets. We used the multi-sample inference to analytically estimate m as recruitment limitation of n samples belonging to the same metacommunity, including cases where neutrality was not met at the regional scale (Jabot et al. 2008). This method, based on UNTB, uses regional species abundance as parameter instead of summarising them by neutral parameter θ , the fundamental biodiversity constant that governs species richness (details in Appendix I). Hereafter, we consider parameter m as synonymous with recruitment limitation (Jabot et al. 2008), which, in turn, reflects the sum of two processes shaping SAD: dispersal limitation and establishment limitation post-dispersal in response to environmental filters in the local community.

The inference of the parameters m_i for each ' i ' community sampled within the same metacommunity was based on maximising the likelihood function of the inferred parameters from the empirical SAD of the 26 local communities

sampled. We used the freeware programme TeTame (Chave and Jabot 2008) to estimate m_i for each sample, assuming that the pooled abundances of all species in the observed samples would reflect the regional species pool, i.e. the metacommunity (Jabot et al. 2008). We calculated m for different subsets of metacommunity/local communities, allowing us to assess how local RAD differs from metacommunity RAD and thus infer how the dispersal and environmental filter components would limit recruitment of a local community (Jabot et al. 2008).

Because of unequal number of trees sampled within each plot, we standardised the sample size of local communities using rarefaction and bootstrap procedures. For each local community, we created 20 theoretical local communities, resampling the original dataset with replacement until reaching the smallest number of individuals observed in empirical communities ($n = 220$). Then, we calculated the multi-sample m for each simulated community considering the metacommunity as the sum of species abundances pooled from all theoretical communities and calculated the mean values and standard deviation.

Recruitment

We examined the recruitment probabilities by calculating the regional species pool for complete assemblages; therefore, the metacommunity was considered here as the pooled species abundance occurring in all 26 communities in the four habitats sampled. Parameter m , calculated with this approach, represents total recruitment limitation from regional pool to local communities and was indicated here after as metacommunity/local community. We associated m with some diversity parameters, including species richness, Fisher's alpha, abundance of singletons and maximum species abundance. Soil silt content, exchangeable bases and mean annual water table depth (Table S1) were related to recruitment by using linear regression.

Dispersal limitation

The role of dispersal limitation in recruitment from metacommunity pool to local communities within forest habitats was investigated by applying the metacommunity concept to the 'habitat species pool', defined as a set of

interacting local communities of a given habitat linked by the dispersal of multiple potentially interacting species on the habitat. We calculated m for each locality per habitat, but here we built four metacommunities, with pooled data from all sites from each habitat, thus excluding the effect of establishment limitation. This approach is indicated here in after as habitat metacommunity/local community. A theoretical 'habitat species pool' can be useful as an additional way of estimating dispersal limitation. In this case, the habitat is considered more homogeneous in environmental terms and is suitable for the establishment of species from the same 'habitat species pool'. The absence of any given species from the habitat species pool in a local community may result from failed dispersal with no relationship to environmental filters (Mota de Oliveira and ter Steege 2015).

If dispersal limitation is a determinant of the assembly of communities, it has been suggested that similarity in species composition should decrease with an increase in geographic distance between pairs of samples (Condit et al. 2002). We examined this simple proxy of dispersal limitation by regressing similarity among pairs of plots (Bray–Curtis distance on relative abundances) and Euclidian distance on geographic coordinates of plots within each vegetation type.

Environmental filtering

Evidence of post-dispersal environmental filtering on the recruitment of species from the metacommunity to each forest habitat (vegetation types) was examined using theoretical habitats of local communities. We pooled data for all sites within each habitat and used the metacommunity (all species pooled) to calculate one m value per habitat, thus excluding the effect of dispersal limitation on parameter m by eliminating geographic distance from the calculation of m . Calculating the parameter m using this approach represents the environmental filter and is indicated here in after as metacommunity/habitat community. Thus, we estimated the relative effect of dispersal and post-dispersal environmental filtering on the recruitment of local communities by the estimates of parameter m calculated based on two metacommunity sources – habitat metacommunity/local

community and metacommunity/habitat community, respectively.

Results

Rank-abundance distributions

Clear contrasts among habitats were indicated by the log-series models fitted to standardised observed RADs (Figure 1(a)), with wide variation of the mean alpha parameter (2.5–97.5% CI) among habitats: 209.9 (175.9–248.0) in *terra firme*, 154.6 (125.4–188.0) in *várzea*, 129.2 (103.5–158.7) in transitional forests and 44.0 (30.8–60.2) in *campinarana*. High incidence of rare species was found in *terra firme* forests, whereas higher dominance occurred in *campinarana*. *Várzea* and transitional forests had intermediate levels of rarity and a similar RAD. Estimated Fisher's alpha of the metacommunity was 235.0 (201.8–271.5, 95% CI). Lack of fit of the log-series to the metacommunity RAD (Kolmogorov–Smirnov, $D = .08$, $P < .01$) resulted in an overestimation of a number of individuals of species with intermediate abundances (Figure 1(b)).

We found that 72% of individuals belonged to indicator species in *campinarana*, 51% in transitional forests, 37% in *várzea* and 25% in *terra firme*. The ratio between the number of indicator species and the total species was similar in all vegetation types, 8.2%, 13.6%, 8.9% and 10% (Table 1). Species richness in well-preserved *terra firme* forests was almost twice as that in *várzea* forests and three times as that in *campinarana*.

Recruitment

The probability of recruitment (m) calculated with multi-sample inference correlated well with Fisher's alpha, abundance of singletons, species richness and maximum abundance (Figure 2). The values of m were correlated with environmental gradients, mainly silt content and depth of the water table (Figure S3). At one extreme of the environmental gradient with high silt content and shallow water table, the *campinarana* consistently had lower mean recruitment probabilities (m) compared with other forest types.

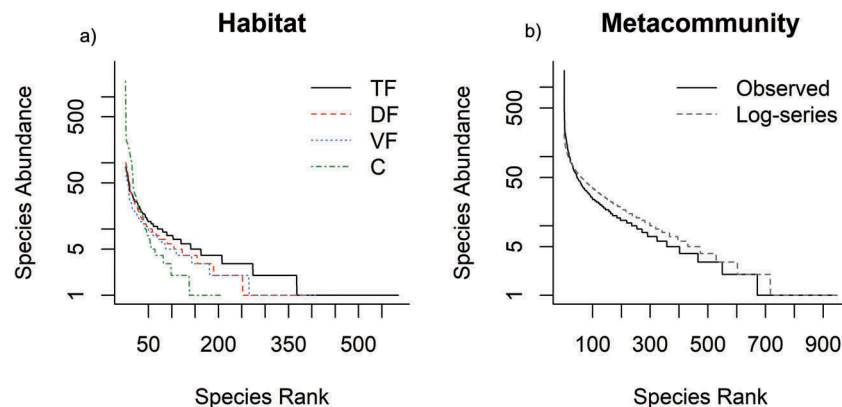


Figure 1. (a) Species RADs (log scale) of tree communities observed in four habitats: TF = *terra firme* forest ($n = 3196$ individuals), DF = transitional forest ($n = 2533$), VF = *várzea* ($n = 2095$) and C = *campinarana* ($n = 5151$) on the upper Madeira River, Brazilian Amazon. (b) Observed species RAD of tree individuals ($n = 12,975$) in the metacommunity with all species pooled and the associated log-series model.

Table 1. Number of species, individuals and relative proportions of indicator species and individuals belonging to indicator species in four vegetation types in a landscape on the upper Madeira River, Brazilian Amazon.

Parameter	TF	DF	VF	C
Total number of species	585	391	414	210
Indicator species	48	53	37	21
Proportion of indicator species	0.082	0.136	0.089	0.100
Total number of individuals	3196	2533	2095	5151
Total number of individuals of indicator species	811	1302	769	3703
Proportion of individuals of indicator species	0.254	0.514	0.367	0.719

TF = *terra firme* forest; DF = transitional forest; VF = *várzea*; C = *campinarana*.

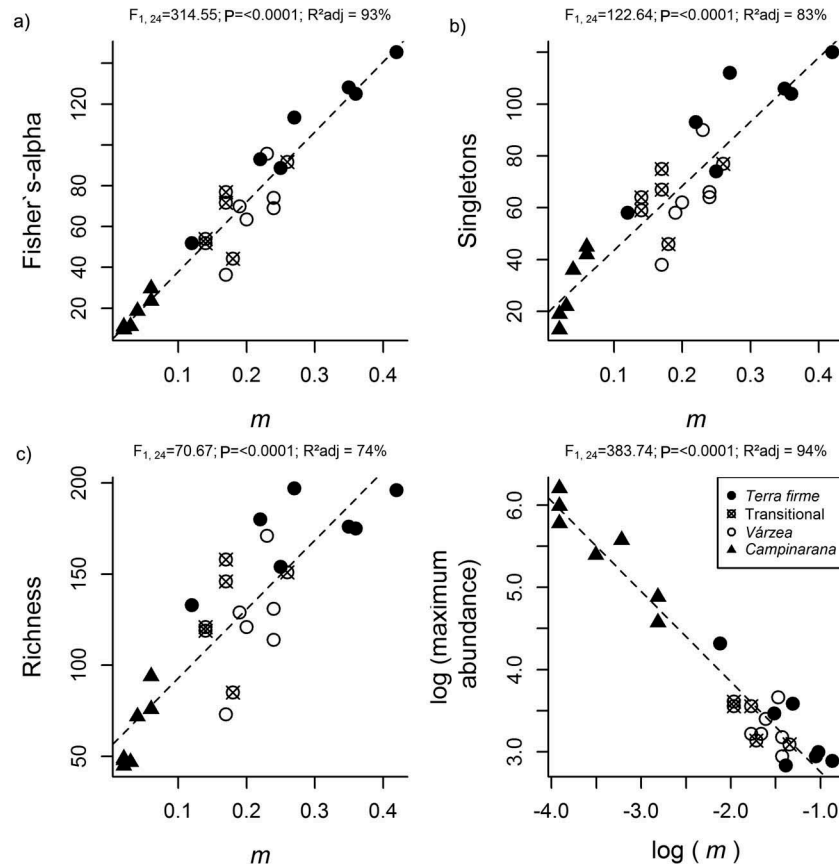


Figure 2. Recruitment probability (m) of tree individuals from the metacommunity to local communities associated with diversity metrics in four habitat types on the upper Madeira River, Brazilian Amazon. Response parameters: (a) Fisher's- α ; (b) number of singletons; (c) species richness; (d) number of individuals of the most abundant species.

Local tree communities of *campinarana* received individuals from outside the meta-community species pool at a mean (\pm sd) recruitment probability of 0.06 ± 0.03 , significantly lower ($F_{3,516} = 524.6$, $P < .00001$) compared to *terra firme* (0.31 ± 0.07), transitional (0.21 ± 0.05) and *várzea* (0.22 ± 0.05) (Figure 3(a)). The mean probability of recruitment of transitional and *várzea* forests was also lower compared to well-preserved *terra firme* forest (*post hoc* Tukey HSD with 95% confidence level; Figure 3(a)).

Dispersal limitation

The dispersal limitation in recruitment from 'habitat species pool' to local communities was variable (mean \pm sd) within *terra firme* (0.27 ± 0.07 , ANOVA: $F_{6,133} = 218.1$, $P < 0.0001$), transitional forests (0.32 ± 0.09 , $F_{5,114} = 90.0$, $P < 0.0001$) and *várzea* (0.31 ± 0.08 , $F_{5,114} = 120.2$, $P < 0.0001$) (Figure 3(c-e)). Some of this variation could be explained by plots that shared compositional and

structural similarities with those of the other adjacent forests analysed. In contrast, local *campinarana* communities had the strongest dispersal limitation from their habitat species pool (0.07 ± 0.03 , $F_{6,133} = 320.5$, $P < 0.0001$), and most recruitment originated from within the locality, as shown by the lower values of m (Figure 3(f)).

Dissimilarities in tree structure between *terra firme* and transitional forests were positively correlated with geographic Euclidian distances; however, this was not observed for *várzea* and *campinarana* (Figure S4). The differences in environmental conditions between pairs of plots were associated with geographical distance for sum of bases, but were not significant for silt content and mean annual depth of ground water (Figure S5).

Environmental filtering and establishment limitation

The recruitment probability of individuals from the total species pool (metacommunity) into the habitat species pool suggested that environmental

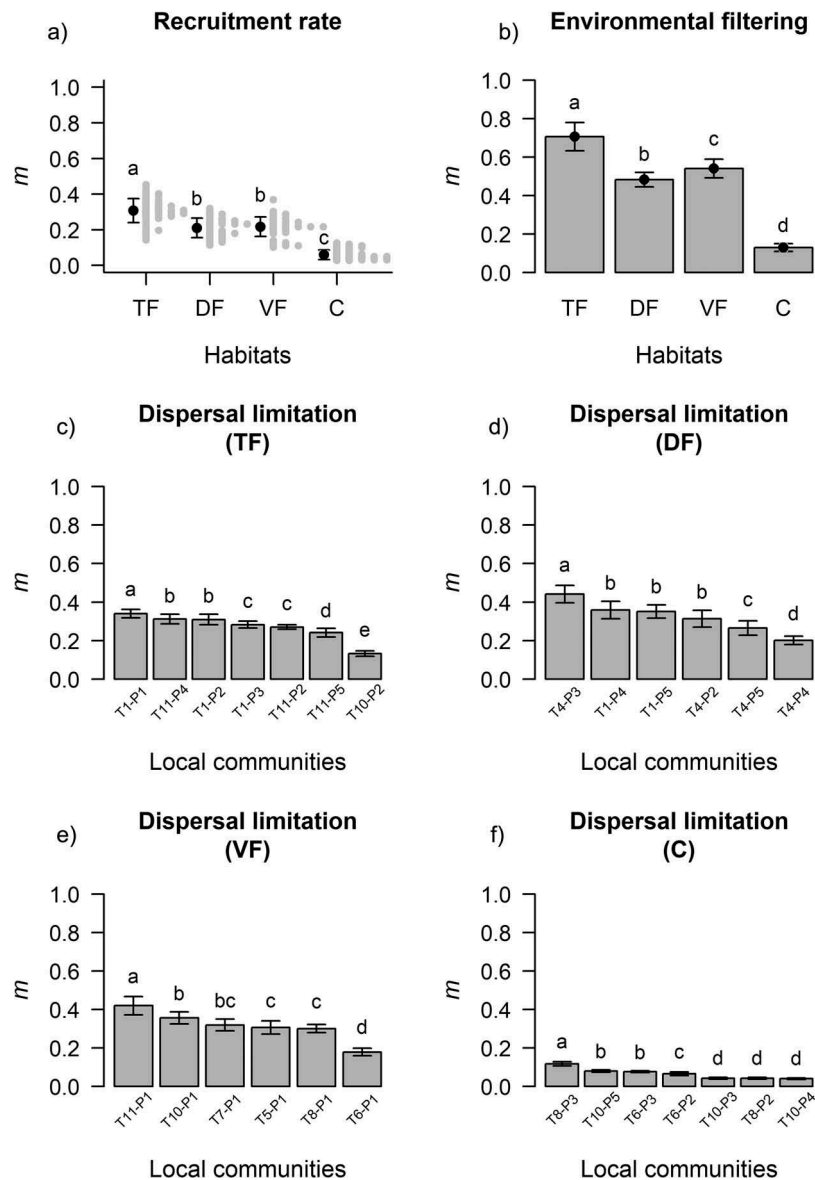


Figure 3. Estimates of recruitment probability (m). (a) Mean (black symbols) and standard deviation (vertical bars) of the recruitment from the metacommunity into local communities obtained with 20 bootstrap pseudoreplicates (grey symbols) in habitats of *terra firme* (TF), transitional forest (DF), *várzea* (VF) and *campinarana* (C), on the upper Madeira River, Brazilian Amazon. (b) The environmental filter component of m , given by the proportion of individuals recruited from the total species pool into the habitat species pool. The dispersal component of m , given by the proportion of individuals recruited from the habitat species pool into local communities within each habitat: (c) *terra firme*; (d) transitional forest; (e) *várzea*; and (f) *campinarana*. Values of m are only comparable within analysis, where different letters show statistical significance ($P < 0.05$).

filtering was variable (ANOVA: $F_{3,76} = 487.5$, $P < 0.0001$) and also higher in *campinarana* by lower m values (0.13 ± 0.02), contrasting with *terra firme* (0.71 ± 0.07), transitional forests (0.48 ± 0.04) and *várzea* (0.54 ± 0.05) (Figure 3(b)).

Discussion

SAD of the tree communities sampled, as described by the log-series distribution, were distinct for each habitat type in our study. Simulations have suggested that relative abundance distributions are more even in systems

where niche differentiation between species and conspecific density dependence is present than for those in which all species are competitively equivalent (Chave et al. 2002). However, surprisingly similar RAD patterns have appeared in communities in which different ecological processes operated, suggesting that the shape of community-level distributions cannot, in general, be used to distinguish among mechanisms that maintain diversity (Chave et al. 2002). We observed evidence of this in two out of four habitats, namely, transitional forests and *várzea*, which showed nearly the same shape of RADs, despite

having distinct environmental characteristics and underlying ecological processes. The RAD curve found in *terra firme* is typical of habitats with high species richness and high incidence of rare species (Pitman et al. 2002; ter Steege et al. 2013). This contrasts with the high dominance found in the species-poor *campinarana* communities, which resulted in a higher proportion of individuals belonging to indicator species. Such discrepancies in diversity and abundance metrics between *terra firme* and *campinarana* have also been reported for other areas within the Amazon (Stropp 2011).

The steep RAD curve for *campinarana* indicated a strong dominance of a few species. This may reflect the interacting effects of dispersal limitation and environmental filtering on specialist species that occur in this habitat. We expected that communities assembled on flooded habitats have a stronger environmental filtering and that communities stimulated by stressful conditions would have a high proportion of individuals belonging to indicator species (Phillips et al. 2003). Although the relative proportion of indicator species in each vegetation type was similar (8–14%), *campinarana* had the highest number of individuals of indicator species (73%). High incidence of indicator species in transitional forests (51%) could be attributed to past disturbances, such as fires and selective logging. Pioneer and fast-growing species, such as those belonging to the genera *Miconia* (Melastomataceae), *Protium* (Burseraceae), *Tachigali* (Fabaceae) and *Virola* (Myristicaceae), were abundant indicator species in the transitional forests. While not classified as an indicator, species of Hypericaceae, such as *Vismia guianensis* (Aubl.) Pers., were more abundant in some of the transitional forests sampled, most likely owing to their fire resistance and resprouting capability (Rocha et al. 2016).

Overall, our estimates of parameter m , which indirectly show the degree of similarity between local communities and the metacommunity, were highly correlated with diversity parameters, both among and within habitats. The most diverse habitat within the study site was *terra firme*, and as such, tree composition of plots in *terra firme* tended to look more like the metacommunity than plots in other forest types evaluated. As the number of sample plots and trees per habitat was similar, we did not expect plots in *terra firme* be more similar to the metacommunity than to plots of other forest types, just by

chance. Rather, we expected that plots in *campinarana* would resemble the metacommunity more than plots of other habitats, in particular because *campinarana* plots comprised the largest number of sampled individuals in total. This could bias the inferred m values in *campinarana* towards larger values, but we found very low m values in this habitat, further supporting that our results did not arise from statistical artefacts. These findings suggest that diversity has a stronger influence on estimates of m and assembly of local communities than abundance (Liu and Zhou 2011; May et al. 2011).

As hypothesised, our analyses consistently estimated lower values of parameter m for *campinarana*. Contrary to other habitats sampled, *campinarana* had a shallower and less variable water table, in addition to being flooded for several months, longer lasting than the flood pulse associated with the Madeira River in the *várzea*. Flooding represents a strong environmental filter by decreasing oxygen supply to the roots and may lead to severe anoxia and a complete absence of oxygen in the rhizosphere (Parolin 2009). This condition tends to reduce the otherwise possible recruitment of non-adapted species from the metacommunity. It has been reported that particular morphoanatomical and physiological traits associated with flood tolerance can improve plant oxygen supply which would, in turn, lead to individual acclimation by increasing water absorption by the roots and maintenance of photosynthesis (Herrera 2013). Under these conditions, tolerant or adapted *campinarana* tree species would grow as if flooding placed no stress at all on their physiology. Therefore, one possible focus of future investigation might involve the study of functional traits to better understand the mechanics of environmental filters, especially in the *campinarana* and *várzea* habitats. Comparative analyses of functional traits can use phylogenetically independent contrasts with congeneric pairs of species present on one of these habitats with a flood stressor and the *terra firme* forest. One goal of our study was to use our data to evaluate if m can be considered as a pure measure of dispersal limitation. Supporting the findings of Jabot et al. (2008), who studied tree communities in Panama, we found that our data did not support such an interpretation.

Low recruitment from the *campinarana* species pool to local communities suggests a strong dispersal limitation of non-dominant species. On the other hand, dominant species of

campinarana, such as *Ruizterania retusa* (Spruce ex Warm.) Marc.-Berti (average 247 ind/ha) and *Euterpe precatoria* Mart. (47 ind/ha), could have competitive advantages related to niche constraints. The analysis of recruitment from the habitat species pool was more efficient in detecting dispersal limitation within *campinarana*, as opposed to similarity based on distance analysis (see below). This can be explained by the fact that the first analysis is based on the total species pool within the habitat, and not based on paired comparisons between pairs of plots within the same habitat.

Our analyses provided little evidence of a decay in similarity with distance in *terra firme*, *várzea* or *campinarana*, habitats that occurred as continuous and well-defined patches of vegetation at the scale of our study area. The only exception was found in transitional forests, the most fragmented habitat, for which similarity among plots decreased with distance. Turnover in species composition and structure among communities within the same vegetation type was not strongly correlated with spatial distance between pairs of plots at the scale of our study site. This possibly reflects the natural limitations of the spatial scale because periodicities in the environment could be responsible for the absence of distance decay at some scales (Pansonato et al. 2013). In fact, distance decay in tree species similarity has been well documented at regional scales for *terra firme* (Condit et al. 2002), *várzea* (Albernaz et al. 2012) and *campinarana* (Ferreira 2009; Stropp 2011) within the Amazon basin.

The main drivers of community assembly in *campinarana* involve both dispersal limitation and environmental filters, but they could also be related to the distribution of *campinarana* in the Amazon basin. Regional diversity and habitat size of *campinarana* in the Amazon are much smaller compared to *terra firme* habitats (Adeney et al. 2016), and this is reflected in their species–area relationships (Stropp et al. 2011). The low diversity of trees in *campinarana* is also a likely result of reduced habitat species pool driven by limited size. Therefore, one can expect a larger regional tree species pool in *terra firme* forests compared with *campinarana* (ter Steege et al. 2000; Stropp et al. 2011), as we found here. This prediction can be explained by large-scale and long-term evolutionary processes that lead to higher speciation rates in larger areas, as well as the species–area effect, where large areas support more species (Rosenzweig and

Ziv 1999). A limitation of our estimate of regional species pool is the unequal size of the habitats considered here. Although our sampling was well-balanced across habitats, habitat size varied widely in the studied region, with *várzea* clearly occupying a much smaller area in the study site compared to other habitats (Perigolo et al. 2017).

We think that obtaining a reliable species pool in this kind of study is challenging, and further work should take into account the size of different habitats in a field sampling strategy (stratified sampling across habitats). We tried to partially overcome this sampling issue, which is recurrent in tropical forests with high habitat heterogeneity, by using rarefaction based on the bootstrap procedure to standardise the number of individuals and provide a baseline for comparisons between habitats, preventing numerous samples taking disproportionate importance. Habitat representativeness on the study sample design might bias m estimates downwards for the larger habitats with high heterogeneity, and maybe this was reflected in the estimates of m for *campinarana* and between local communities of *terra firme* associated with the habitat species pool. In spite of that, indeed, we provided evidence of contrasting effects of dispersal and environmental filtering on structure and composition of tree communities for four distinct habitats of Amazon rain forest.

Conclusions

While not necessarily positing an alternative hypothesis to the neutral process, as described by Matthews and Whittaker (2014), we used a multi-inference approach to estimate tree community recruitment and examine its environmental controls. The reconciliation of niche assembly and dispersal assembly is a non-trivial issue. In fact, this is one of the most fundamental unsolved problems in ecology today, and this debate has persisted so long because each perspective has strong elements of support at different spatio-temporal scales (Rosindell et al. 2011). As shown by us and elsewhere (Jabot et al. 2008), models incorporating neutral framework can be useful to investigate dispersal limitation and environmental filtering, which are key parameters that lead to an understanding of tree community assembly.

We found that *campinarana* plots were both more dispersal limited and more strongly environmentally filtered than the other habitats examined. Observed *campinarana* communities with

restricted recruitment had a greater number of species filtered by environmental factors, resulting in the recruitment and establishment of fewer species. Thus, in landscapes that comprise different habitat types, it cannot be assumed that tree species are ecologically equivalent since sites may limit establishment in different ways.

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