

Dispersal modes affect tropical forest assembly across trophic levels

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We examined assemblages of trees and two major groups of vertebrate seed dispersers, birds and primates, in Ugandan protected areas to evaluate the roles of dispersal limitation and species sorting in community assembly. We conducted partial Mantel tests to investigate relationships between community similarity, environmental distance and geographic distance. Results showed that environmental factors, specifically temperature and rainfall, significantly and more strongly structured tree assemblages than geographic distance. Analysis of tree dispersal modes revealed wind-dispersed tree guilds were significantly dispersal limited but trees dispersed by animals were not. For assemblages of vertebrate seed dispersers, dispersal limitation significantly and more strongly structured assemblages of primates than species sorting whereas environmental factors significantly and more strongly structured assemblages of birds than dispersal limitation. We therefore examined whether trees dispersed by primates were more dispersal limited than trees dispersed by birds. We found consistent trends that primate fruit trees were more dispersal limited than bird fruit trees using three definitions of dispersal syndromes based on fruit color. Our results suggest that the dispersal abilities of primary consumers may affect the distribution of primary producers at large spatial scales.

For the past century, ecologists have been interested in understanding how communities are assembled and why their compositions differ. A considerable amount of early ecological research focused on plant communities (Gleason 1926, Braun-Blanquet 1964) and in recent decades there has been growing interest in understanding the assembly of highly diverse tropical plant communities (Hubbell 2001, Tuomisto et al. 2003, Kraft et al. 2008). Most attempts to explain the composition of tropical plant communities have focused on understanding how the ecological characteristics of sites and the abilities of individuals to disperse among sites influence plant distributions. These major factors underlie two central perspectives on community assembly. From a niche-assembly perspective, a community is expected to consist of species that are best suited to the ecological conditions at the site and are therefore the superior competitors, which results in species sorting predictably along environmental gradients; from a dispersal-assembly perspective, a community is expected to consist of the individuals that reach the site and persist. It has become increasingly clear that both perspectives explain aspects of community assembly (Cottenie 2005, Soininen et al. 2007). Disentangling the relative contributions of niche-based processes and dispersal limitation to community assembly is of fundamental importance to ecological theory and practice.

To tease apart these processes, recent efforts have focused on how the relative importance of niche-based processes

and dispersal limitation varies across taxonomic groups, ecological systems and spatial scales (Cottenie 2005, Soininen et al. 2007, Chase and Myers 2011, Siefert et al. 2012). Moreover, there has been a growing movement to investigate functional traits rather than examining species-specific differences or assuming functional equivalence among species (McGill et al. 2006, Götzenberger et al. 2012).

One type of functional trait that likely has consequences for community assembly is the way in which species disperse. Despite considerable variation within dispersal modes, a recent meta-analysis of species-specific dispersal distances in plants has shown that both maximum and mean dispersal distances are strongly associated with dispersal mode. For example, unassisted species show the shortest dispersal distances, wind dispersed species are intermediate and seeds that are ingested by animals and passed through the gut show the longest dispersal distances (Thomson et al. 2011). Other reviews have also shown that vertebrate-dispersed plant species have greater dispersal distances than wind-dispersed plants (Willson 1993, Vittoz and Engler 2007). These patterns are not universal, however; an almost opposite conclusion for North American spruce-fir forests was made by Nekola and White (1999).

In this study we investigate the effects of dispersal modes on tree community composition in tropical forests across Uganda. In doing so, we quantify the observed effects of dispersal and recruitment limitation on plant assemblages in the major protected areas of Uganda. Our study complements

research on species-specific dispersal distances and dispersal modes by examining the net result of these factors on assemblages of adult trees. Moreover, we also investigate the relative importance of dispersal limitation on assemblages of vertebrate seed dispersers. We are thus able to evaluate the relative importance of dispersal limitation and species sorting in structuring assemblages and guilds with very different dispersal modes living in these forests.

While the existence of tightly coupled co-evolutionary dispersal syndromes between seed dispersers and seed producers has been debated (Fischer and Chapman 1993, Burns 2006), a number of studies have documented covariation between seed dispersers and traits of the seeds they disperse (Seidler and Plotkin 2006, Klinger and Rejmánek 2010, Valido et al. 2011), including several local-scale studies of African primates and birds (Knight and Siegfried 1983, Gautier-Hion et al. 1985). In addition, Lomascolo and Schaefer (2010) demonstrated that frugivorous primates and birds can identify primate and bird dispersed fruits using fruit color as a reliable signal.

At the macroecological scale, a comparison of frugivores in Madagascar and South Africa revealed that fruit colors in these two geographic regions reflected the fruit-color preferences of their respective frugivore communities (Voigt et al. 2004), which suggests that at large spatial scales there are strong associations between frugivores and fruit trees that are mediated by fruit color. Assessment of the importance of birds and mammals as dispersal agents in Brazilian Atlantic forests also revealed that there may be strong associations in the distribution of seed-dispersal agents and fruit characteristics (Almeida-Neto et al. 2008). We expand on these approaches by using dispersal syndromes based on fruit color to classify seed dispersal agents of Ugandan trees. We then examine the relative importance of dispersal limitation in structuring plant communities based on the dispersal limitation of the dispersal agents, thereby integrating community-level data from two trophic levels.

If dispersal limitation has strongly structured communities, then community similarity will depend heavily on geographic distance. Dispersal limitation will cause the species composition of communities that are close together to be more similar than the composition of communities that are far apart, regardless of ecological similarity. On the other hand, if communities have been primarily assembled through species sorting along environmental gradients, then environmental similarity between sites will strongly determine community composition, regardless of geographic distance. We therefore test predictions emerging from two hypotheses that are not mutually exclusive (Chase et al. 2005). If dispersal limitation structures assemblages, we expect a negative correlation between community similarity and geographic distance. We evaluate the relative strength of dispersal limitation based on the strength of the correlation value between community similarity and geographic distance. If niche-based species sorting along environmental gradients structures assemblages, then we expect a negative correlation between community similarity and environmental distance. We emphasize that our approach seeks to quantify the relative importance of these two processes by comparing the magnitude of the effect sizes because it is

likely that both species sorting and dispersal limitation structure assemblages to some degree (Qian and Ricklefs 2012).

We assume that there is likely variation in assembly processes within communities based on variation in functional traits and we test whether the processes governing the assembly of tropical plant communities are mediated by dispersal abilities. Following Fauth et al. (1996) we define a community as a group of organisms living in the same area at the same time; an assemblage as a subset of a community in the same taxonomic division or class and a guild as a subset of a community that utilizes a common class of resources, or dispersal mode in this study.

We begin by assessing the relative importance of dispersal limitation and species sorting in tree assemblages and then specifically investigate the role of tree dispersal modes. Next, we investigate dispersal limitation, or the lack of dispersal ability, in assemblages of two major tropical seed dispersing taxa: primates and birds. Lastly, we test whether the relative strength of vertebrate dispersal limitation can help explain the distribution of trees dispersed by primates and by birds. We predict that 1) tree assemblages will show more dispersal limitation than animal assemblages, 2) guilds of trees dispersed by wind (anemochory) will show more dispersal limitation than guilds of trees dispersed by animals (endozoochory), 3) primate assemblages will exhibit more dispersal limitation than bird assemblages, and 4) guilds of trees dispersed by primates will show more dispersal limitation than guilds of trees dispersed by birds.

Material and methods

Data collection

We analyzed data from a published survey of Ugandan protected areas (Howard 1991). The data consist of presence-absence records for trees, diurnal primates and birds in 12 Ugandan protected areas (Fig. 1) that vary in size and environment (Supplementary material Appendix 1). Although the sites are located non-randomly, the survey provides a remarkable dataset on biotic communities because efforts of its magnitude and methodological standardization are rare in the tropics, particularly because the sites were systematically and simultaneously surveyed for all three taxonomic groups. Data collection was conducted by teams of biologists and trained staff who sampled sites in proportion to forest size. Detailed survey methods have been described elsewhere (Howard 1991, Howard et al. 1998, 2000).

To investigate seed dispersal, we assigned each tree species to one of three primary dispersal modes: anemochory (wind dispersal), endozoochory (dispersal via ingestion by animals) or other. We used published data to categorize dispersal modes when available and otherwise inferred dispersal modes from plant morphology (e.g. anemochory from fruit with wings or pappi, endozoochory from fleshy fruit).

For each tree species dispersed via endozoochory, we compiled data on fruit color(s) from published sources (Eggeling and Dale 1952, Polhill et al. 1952–2011, Bloesch et al. 2009). We then categorized each tree species as a bird

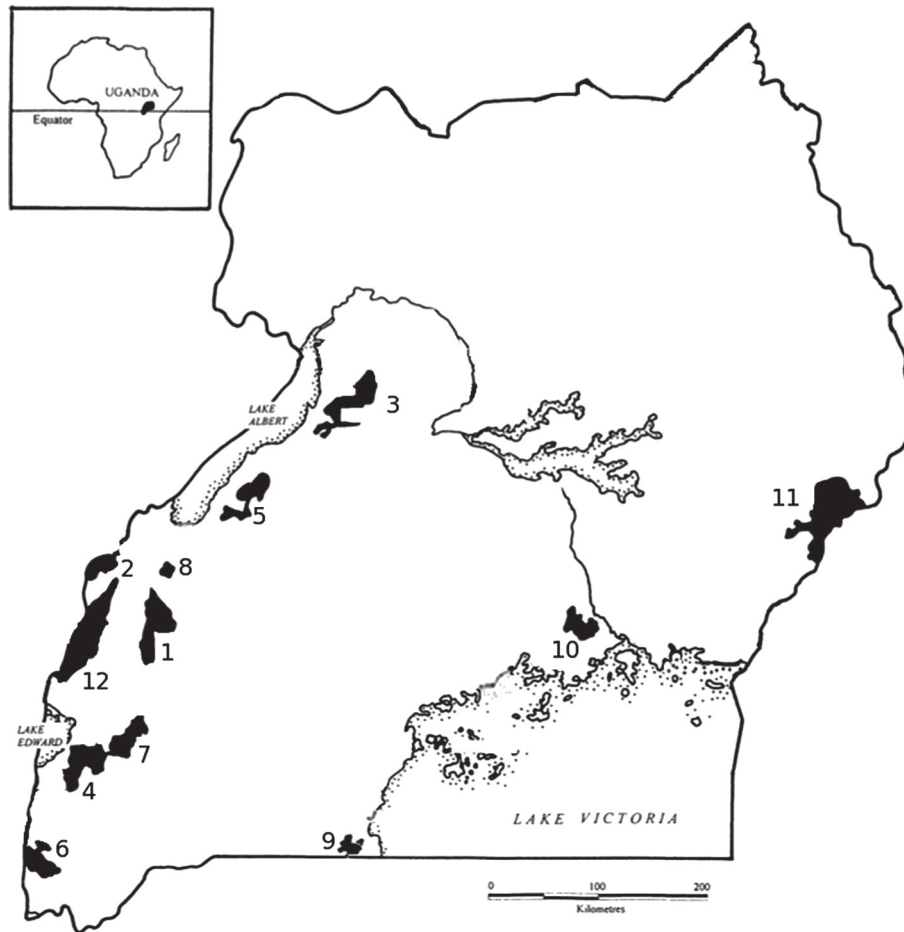


Figure 1. Locations of protected areas in Uganda. 1 – Kibale National Park, 2 – Semliki National Park, 3 – Budongo Forest Reserve, 4 – Kalinzu-Maramagambo Forest Reserve, 5 – Bugoma Forest Reserve, 6 – Bwindi Impenetrable National Park, 7 – Kasyoha-Kitomi Forest Reserve, 8 – Itwara Forest Reserve, 9 – Sango Bay Forest Reserve, 10 – Mabira Forest Reserve, 11 – Mount Elgon National Park, 12 – Rwenzori National Park. See Supplementary material Appendix 1 for additional information on site area and vegetation cover. Figure adapted from Howard et al. (2000).

or primate fruit tree using published dispersal syndrome definitions based on fruit colors (Knight and Siegfried 1983, Gautier-Hion et al. 1985, Lomascolo and Schaefer 2010) (Table 1). Studies of dispersal syndromes have considered various traits in addition to fruit color, such as husk thickness, reflectance, and odor. However, the inclusion of such traits varies across studies and data were not available for these traits for the large number of species included in this study. We therefore include only fruit color in the analysis based on dispersal syndromes.

Because we were primarily interested in birds as dispersers of seeds of fleshy-fruited trees, we compiled data on bird diets (Brown et al. 1982) and excluded species whose diets did not contain fruits. All primate species included in

this study consume fruits. Unlike primates in the Neotropics and Madagascar, all diurnal African primates have trichromatic vision. We therefore restricted our analysis to dispersal syndrome definitions based on African flora to control for variation in primate visual systems across geographic regions. We report the number of species included in each analysis (Table 2).

Community similarity

We calculated the Jaccard community dissimilarity index using the 'vegdist' function in the Vegan community ecology package in R (R Development Core Team) and used the

Table 1. Definitions of published African bird and primate fruit dispersal syndromes based on fruit color. We limited analyses to fruit colors classified as unique to either birds or primates. Parentheses indicate colors common to both bird and primate dispersal syndromes that were excluded from analyses. As such, the trees included as bird dispersed fruit trees are entirely independent from the trees included as primate dispersed fruit trees for each definition.

Definition	Author	Bird tree fruit colors	Primate tree fruit colors
1	Gautier-Hion et al. (1985)	black, purple, (red)	yellow, orange, (red)
2	Knight and Siegfried (1983)	black, red, (orange)	yellow, green, (orange)
3	Lomascolo and Schaefer (2010)	blue spectrum (i.e. blue, purple, (black))	green spectrum (i.e. yellow, green, brown, (black))

Table 2. Results of partial Mantel tests. Correlation values (r) and significance values (p) are given for each test. Results significant at the $\alpha \leq 0.05$ level are indicated in bold. For each community (defined as a taxon, dispersal mode or dispersal syndrome definition), we evaluated the independent effects of environmental distance and geographic distance on community similarity. The relative strength of the relationship is given by the partial Mantel (r) value while the significance of the relationship is given by p .

Assemblage or guild	No. species	R^2	Environmental distance		Geographic distance	
			r	p	r	p
Taxon (primates)	12	0.30	-0.27	0.15	-0.49	0.04
Taxon (birds)	153	0.32	-0.57	0.02	+0.06	0.52
Taxon (trees)	426	0.57	-0.73	<0.01	-0.33	0.10
Mode (Anemochory)	40	0.61	-0.74	<0.01	-0.41	0.05
Mode (Endozoochory)	262	0.53	-0.70	<0.01	-0.27	0.15
Mode (other)	107	0.56	-0.72	<0.01	-0.36	0.08
Definition 1 (bird)	38	0.36	-0.54	<0.01	-0.30	0.09
Definition 1 (primate)	61	0.50	-0.67	<0.01	-0.36	0.10
Definition 2 (bird)	87	0.51	-0.69	<0.01	-0.25	0.16
Definition 2 (primate)	77	0.58	-0.73	<0.01	-0.38	0.08
Definition 3 (bird)	20	0.39	-0.60	<0.01	-0.17	0.23
Definition 3 (primate)	119	0.53	-0.69	<0.01	-0.32	0.12

complement for similarity. For presence-absence data, the Jaccard index of similarity is defined as $J = a/(a + b + c)$ where a is the total number of species occurring in both sites, b is the number of species occurring in the first site but not the second and c is the number of species occurring in the second site but not the first.

It has previously been noted that the Jaccard index typically underestimates similarity between sites because of unseen species that result from comparison of sites of very different sizes or incomplete sampling (Chao et al. 2005). We investigated the effect of variation in site size on community similarity by calculating the Preston index of community dissimilarity, which was designed to accommodate differences in site size and thus species richness in site comparisons (Preston 1962). We found, however, that the Preston index is not applicable when communities contain low numbers of species (Supplementary material Appendix 2). We also considered implementing recent advances in similarity index estimation for incidence data to account for unseen species, but unfortunately these developments require replicates of presence-absence data for each site (Chao et al. 2005), which are not available in the data set analyzed here. We therefore recognized that although the use of the classical Jaccard index is subject to the shortcomings noted elsewhere, it is the most appropriate of the available measures.

Ecological and geographic distance

We incorporated environmental data for each site from Howard (1991), which included area, minimum altitude, maximum altitude, minimum temperature, maximum temperature, and mean annual rainfall. For two sites, temperature data were not available from Howard (1991)

and we therefore extracted the values from the WorldClim 2.5 arc-minutes temperature layers available online (Hijmans et al. 2005).

We selected the environmental variables with the highest rank correlation with community data for each taxon. We did this with the 'bioenv' function from the 'vegan' package in R (Clarke and Ainsworth 1993). The variables contained in the best fit models were: trees: minimum and maximum temperature; primates: maximum temperature; birds: maximum temperature and mean annual rainfall. In order to compare the effects of environmental variables on community composition across taxa, we included minimum temperature, maximum temperature and mean annual rainfall because these variables best predicted community data for the three taxa overall. Because environmental values were correlated, we calculated Mahalanobis distances to accommodate this correlation. We calculated a matrix of environmental distances within each pair of communities following published methods (Beaudrot and Marshall 2011) using R 2.14.0 (R Development Core Team).

We calculated geographic distances using the 'pairdist' function in the spatstat package in R. We used the mean latitude and mean longitude of each site. Pairdist computes a matrix of Euclidean distances between latitude and longitude values for all pairs of sites.

Analyses

We performed partial Mantel tests to investigate correlations of 1) community similarity with environmental distance while accounting for geographic distance and 2) community similarity with geographic distance while accounting for environmental distance. We performed these tests in R and constructed added variable plots to display the correlation values of the partial Mantel tests using the Jaccard index of community similarity following published methods (Beaudrot and Marshall 2011).

To evaluate differences between the dispersal limitation signals of trees dispersed by different modes and to evaluate differences between the dispersal limitation signals of trees dispersed by primates and trees dispersed by birds, we tested for significant differences between the Mantel correlation values using the function 'r.test' in the 'psych' package in R. The test uses the z transformation and estimates the variance based on sample size. Because the sample size using a matrix correlation is the number of pairwise distances, this significance test is more likely to produce a significant result than if the data points were independent and is thus prone to false positives. However, we found no significant results using this test.

We present path diagrams to display partial Mantel results that account for intermediate variables (e.g. tree community composition) between environmental or geographic distance and primate or bird community composition. However, we note that the correlation values produced by partial Mantel tests are not equivalent to the standardized b coefficients typically used in path analysis. Mantel tests only provide point estimates and significance values whereas traditional path analysis incorporates error estimates

in the standardized b coefficients. As a result, we use the diagrams as a method for visual presentation only, following others who have previously combined path diagrams with partial Mantel tests (Hausdorf and Hennig 2005). We used the 'mantel' function with the Pearson method and 10 000 permutations from the 'ecodist' package in R for partialling out multiple matrices.

While significance values are reported for all results and discussed based on an $\alpha = 0.05$ cutoff, we note the movement away from null hypothesis testing and frequentist inference in ecology. We therefore place emphasis on the effect size for each partial Mantel test, which is represented by the Mantel r value (Nakagawa and Cuthill 2007).

Results

Partial Mantel tests

When we examined overall tree assemblages, there was a significant negative relationship between community similarity and environmental distance while controlling for geographic distance in trees ($r = -0.73$, $p < 0.01$), but not between community similarity and geographic distance while controlling for environmental distance ($r = -0.33$, $p = 0.10$) (Table 2). This suggests that species sorting along environmental gradients significantly determines tree community composition and that temperature and rainfall are much stronger predictors of tree community composition than geographic distance.

For the three categories of seed dispersal (anemochory, endozoochory, and other), all three dispersal modes showed significant negative relationships between environmental distance and community similarity after geographic distance was removed (Table 2), which supports the hypothesis that species sorting strongly affects tree species distribution irrespective of seed dispersal method. However, wind dispersed species, unlike the animal dispersed and other modes, also exhibited a significant negative relationship between community similarity and geographic distance ($r = -0.41$, $p = 0.05$) (Table 2; Supplementary material Appendix 3). Moreover, wind dispersed species exhibited a more negative correlation with geographic distance than animal dispersed ($r = -0.27$, $p = 0.15$) or other species ($r = -0.36$, $p = 0.08$), although the differences were not significant (wind–animal: $z = 0.89$, $p = 0.19$; wind–other: $z = 0.33$, $p = 0.37$). These results suggest that guilds of wind dispersed tree species may experience greater dispersal limitation than guilds of trees dispersed by other mechanisms.

Among assemblages of vertebrate seed dispersers, there was a significant negative relationship between community similarity and environmental distance when controlling for geographic distance in birds ($r = -0.57$, $p = 0.02$), but not primates ($r = -0.27$, $p = 0.15$). Moreover, there was a significant negative relationship between community similarity and geographic distance when controlling for environmental distance for communities of primates ($r = -0.49$, $p = 0.04$), but not birds ($r = 0.06$, $p = 0.52$) (Table 2; Fig. 2). This suggests that dispersal limitation more strongly determines primate community composition than species

sorting, whereas species sorting along environmental gradients more strongly determines bird community composition than dispersal limitation.

Further analysis of animal-dispersed trees showed that all three definitions of primate and bird dispersal syndromes exhibited a significant negative relationship between community similarity and environmental distance, suggesting that tree dispersal guilds are significantly and strongly structured by species sorting along environmental gradients irrespective of dispersal mode (definition 1: birds $r = -0.54$, $p < 0.01$; primates $r = -0.67$, $p = 0.01$; definition 2: birds $r = -0.69$, $p < 0.01$; primates $r = -0.73$, $p < 0.01$; definition 3: birds $r = -0.60$, $p < 0.01$; primates $r = -0.69$, $p < 0.01$; Table 2).

In the analysis of dispersal limitation across the three fruit dispersal syndrome definitions, two of the tests exhibited z values of 0.7 or greater but none were statistically significant (definition 1: $z = 0.19$, $p = 0.42$; definition 2: $z = 0.7$, $p = 0.24$; definition 3: $z = 0.73$, $p = 0.23$). In comparison with bird dispersed fruit trees, primate dispersed fruit trees exhibited a stronger negative correlation (r) between community similarity and geographic distance and thus a greater degree of dispersal limitation (definition 1: primate trees $r = -0.36 < \text{bird trees } r = -0.30$; definition 2: primate trees $r = -0.38 < \text{bird trees } r = -0.25$; definition 3: primate trees $r = -0.32 < \text{bird trees } r = -0.17$) (Fig. 3). Moreover, bird fruit trees showed less evidence of dispersal limitation than the overall analysis of animal dispersed trees ($r = -0.27$) in two of the three analyses (definition 2: $r = -0.25$; definition 3: $r = -0.17$) while primate fruit trees showed more evidence of dispersal limitation than the analysis of animal dispersed trees for all three definitions (definition 1: $r = -0.36$, definition 2: $r = -0.38$; definition 3: $r = -0.32$; Table 2). Taken together, these results suggest that guilds of tree species with fruits consumed and dispersed by primates may experience more dispersal limitation than guilds of tree species with fruits consumed and dispersed by birds.

We report summaries of the multiple regression models of community similarity with environmental distance and geographic distance as predictors (Smouse et al. 1986) (Table 2). For all models, the sample size was the number of observations in the pairwise distance matrix for each community ($N = (12 \times (12 - 1))/2 = 66$). The R^2 values can be interpreted as the percent of variance in community similarity explained by ecological and geographic distance. Model summaries for the taxonomic analysis were: trees, $R^2 = 0.57$; birds, $R^2 = 0.32$; primates, $R^2 = 0.30$. We therefore were able to explain the most variance for trees (57%), followed by birds (32%) and primates (30%). We note that there was no relationship between the number of species included in a community similarity index and the R^2 value for the overall model fit using the results from Table 2 (linear regression: $DF = 10$, $p = 0.263$, $R^2 = 0.04$).

We used path diagrams to display the direct and indirect relationships between environmental distance and geographic distance as predictor variables and community similarity of trees, birds and primates as response variables. The diagrams indicate that environmental distance is a significant predictor of tree assemblages, which are in turn a significant predictor of bird assemblages. Primate assemblages,

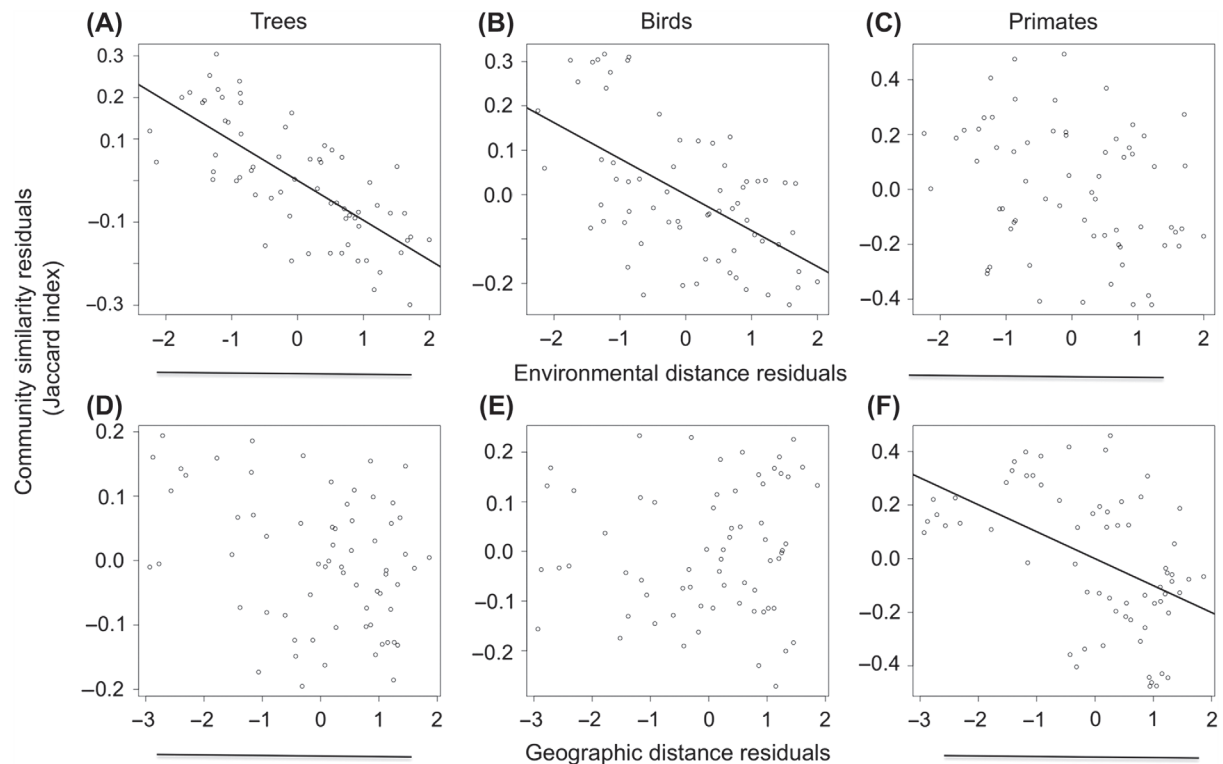


Figure 2. Added variable plots depicting correlations produced by partial Mantel tests. We plotted community residuals against environmental residuals (having accounted for geographic distance) for (A) trees (B) birds and (C) primates. We plotted community residuals against geographic residuals (having accounted for environmental distance) for (D) trees (E) birds and (F) primates. Lines depict significant correlations. Environmental distance is significantly negatively correlated with community similarity in birds and trees, but geographic distance is only significantly correlated with community similarity in primates (Table 2). The results suggest species sorting more strongly than dispersal limitation structures assemblages of birds and trees, but that dispersal limitation more strongly than species sorting structures primate assemblages.

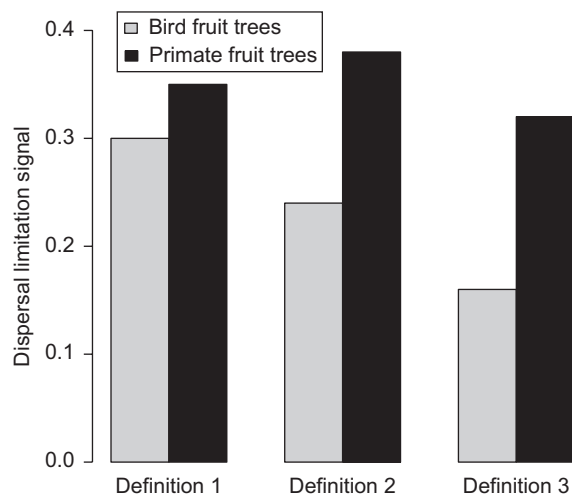


Figure 3. Dispersal is more limited in guilds of trees with fruits dispersed by primates than in guilds of trees with fruits dispersed by birds. Absolute values of partial correlations between community similarity and geographic distance are shown as the signal of dispersal limitation. Under all three definitions of bird and primate dispersal syndromes based on fruit color (Table 1), primate dispersed fruit trees exhibit a stronger negative correlation between community similarity and geographic distance than bird dispersed fruit trees. This consistent trend suggests that dispersal limitation may be stronger in guilds of trees whose fruits are consumed and dispersed by primates than guilds of trees whose fruits are consumed and dispersed by birds.

on the other hand, are most strongly, but not significantly, predicted by geographic distance and to a lesser extent are predicted by tree community composition (Fig. 4). The path diagrams also show the low correlation between environmental and geographic distance (-0.10). This suggests that the dataset contains environmentally similar sites that are both close together and far apart, which is necessary for teasing apart the effects of geographic and environmental distances on community assembly.

Discussion

We examined assemblages of trees and two major groups of vertebrate seed dispersers with very different dispersal modes living in protected areas across Uganda. This allowed consideration of plant–animal interactions at a macroecological scale, which is rather unusual. Our objective was to evaluate the relative importance of dispersal limitation and species sorting along environmental gradients in structuring these assemblages and to test whether dispersal modes mediate the processes governing the assembly of tropical plant communities. Overall tree assemblages were strongly structured by species sorting along environmental gradients. Analysis of tree dispersal modes revealed that wind-dispersed trees also exhibited evidence of significant dispersal limitation but that trees dispersed by animals and other methods did not. There were major differences in the

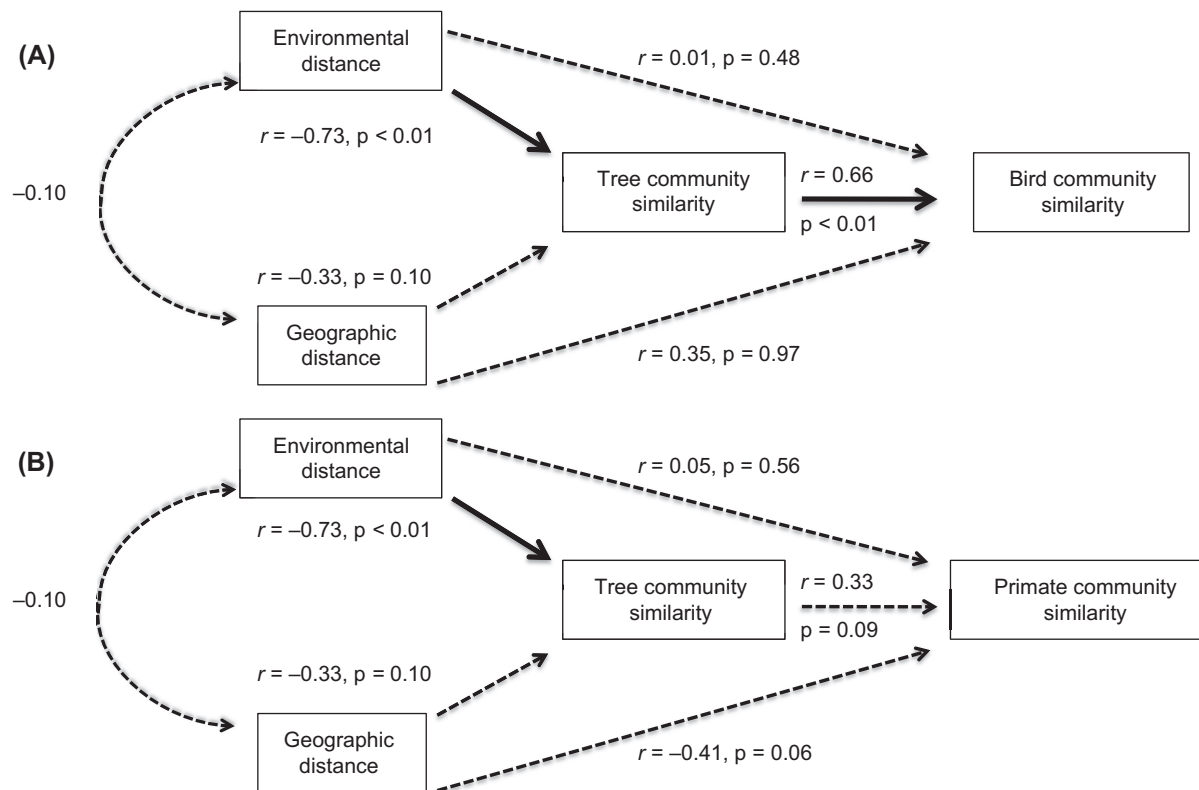


Figure 4. Path diagrams displaying the direct and indirect relationships between endogenous and exogenous variables for (A) bird communities and (B) primate communities. Partial Mantel correlation and significance values are shown. Significant relationships are indicated by bold arrows. Environmental distance significantly predicts tree community similarity, which in turn significantly predicts bird community similarity, but not primate community similarity.

assembly processes governing assemblages of seed dispersers: while dispersal limitation significantly structured assemblages of primates, species sorting significantly structured assemblages of birds. We therefore sought to determine if dispersal limitation of seed dispersers influenced tree community composition. Specifically, we examined whether guilds of trees dispersed by primates, which were strongly dispersal-limited, were more dispersal limited than guilds of trees dispersed by birds, which were not dispersal limited. There were consistent trends across three definitions of dispersal syndromes based on fruit color that primate dispersed fruit trees exhibited greater dispersal limitation than bird dispersed fruit trees, which suggests that the relative dispersal limitation of vertebrate seed dispersers may influence plant community composition across Ugandan protected areas.

Limitations

Despite its novelty, the study was subject to several limitations. The study would have benefitted from relative abundance data rather than presence-absence data to account for the influence of propagule pressure on dispersal and recruitment limitation. However, obtaining standardized abundance data across such a large scale in the tropics would require considerably more resources than the substantial investment used to collect the present data.

We did not account for potential barriers to dispersal, which likely vary by taxonomic group and individual

species, but may include bodies of water, variation in topography, and breaks in forest cover from historical climate change or anthropogenic disturbance. Analyzing dispersal syndromes based on fruit color was a simple approximation of which tree species birds and primates actually disperse and the rates at which they disperse them. In addition, in contrast to the trichromatic visual systems of African primates, birds have tetrachromatic vision (Vorobyev et al. 1998). Birds can therefore perceive UV wavelengths, which may alter their perception of fruit color. Moreover, the breakdown into bird and primate fruits omitted other seed dispersers, particularly bats and fruit-eating carnivores that play important ecological roles in tropical forests (Corlett and Primack 2011). It is also likely that long-distance dispersal from rare events and atypical mechanisms has contributed to the distributions of the tree species examined here and thus to community composition (Nathan 2006). Additionally, this study did not take into account the potential influence of phylogeny on dispersal (Valido et al. 2011) or community composition (Webb et al. 2002, Graham et al. 2009, Kamilar and Guidi 2010). Using a snap-shot approach, we were unable to detect alternative mechanisms for generating patterns consistent with dispersal limitation as have recently been identified through mesocosm experiments (Verreydt et al. 2012). Finally, many tropical forests traditionally considered old-growth forests have been disturbed and are in different stages of recovery (Chapman et al. 2010), but due to limited availability of study site histories, we were unable to examine the effects of

anthropogenic activity on community composition prior to or following the protected area surveys.

Variation in dispersal limitation across taxonomic groups

The finding that assemblages of trees are structured more by environmental characteristics than by dispersal limitation is consistent with other studies (Condit et al. 2002, Tuomisto et al. 2003, Gilbert and Lechowicz 2004) and the replication of this result across all dispersal modes and syndromes examined emphasizes the importance of environmental variables in determining plant community composition. This study complements existing research on dispersal by demonstrating the community level effects of plant dispersal abilities documented elsewhere at the dispersal-mode level (Willson 1993, Vittoz and Engler 2007, Thomson et al. 2011), particularly the greater dispersal limitation of wind dispersed trees in comparison with other dispersal modes.

Less research has addressed the potential role of dispersal limitation structuring bird assemblages. A continental-level analysis of South American birds found that the ecological underpinnings of habitat types played a more important role in bird distributions than dispersal (Graves and Rahbek 2005). In addition to Janzen's (1967) argument that mountain passes are more difficult barriers for organisms to cross in the tropics, the role of mountain passes as potential dispersal barriers for birds specifically has received attention (Graham et al. 2010). It has recently been argued that constraints on avian dispersal are stronger in the tropics because of increased specialization (Salisbury et al. 2012). Mechanistically, some birds may exhibit behavioral inhibition to dispersing across variation in the landscape and it has been suggested that such inhibition is likely more severe for tropical birds (Harris and Reed 2002). However, frugivorous birds tend to move over larger scales than insectivorous birds in the Neotropics (Levey and Stiles 1992), and this may explain the absence of dispersal limitation in our study. The finding that bird assemblages are significantly environmentally structured is consistent with several macroecological studies of birds (Graves and Rahbek 2005, Gotelli et al. 2010, Ozkan et al. 2013).

Primate assemblages were the only assemblage with a significant negative relationship between community similarity and geographic distance and where this relationship was stronger than the relationship between community similarity and environmental distance. These results are consistent with a recent comparison of primate dispersal limitation across biogeographic regions (Beaudrot and Marshall 2011) and suggest that more than the other communities examined in this study, community composition in primates is structured by dispersal limitation. Although long-lived and highly mobile, many species of primates spend the majority of their lives in an area of only few square kilometers. While individual primates may emigrate from their natal groups and groups of some species may range quite widely (e.g. mandrills (White et al. 2010)) no primates exhibit the large-scale migrations found in some bird species.

Moreover, breaks in forest cover may particularly hamper the ability of primates to disperse between forest patches (Schwarzkopf and Rylands 1989).

Although the negative relationship between primate community similarity and environmental distance was not significant, there was nevertheless a moderate negative relationship that suggests that ecological factors may play a role in structuring primate community composition even if to a lesser extent than the other taxonomic groups. The typically generalist feeding behaviors of many primate species may enable them to cope well with variation in resources whereas other more specialized taxonomic groups may exhibit higher turnover in response to resource availability at this scale. Their large body sizes relative to other organisms may allow them to better withstand seasonal food shortages (Boyce 1979) and allow them to live in a wider variety of environmental conditions because of relatively lower costs of thermoregulation in cooler habitats (Bergmann 1847).

An alternative interpretation is that our environmental measures failed to account for the ecological variables relevant to primate communities. This seems unlikely, however, given the success of these variables in predicting the other groups, particularly trees, which comprise the basis of most primate diets. Indeed, the path diagrams demonstrate that primate communities do not respond significantly to tree community composition. Finally, our result may be an artifact of scale as a result of variation in species geographic ranges (Steinbauer et al. 2013) or if the scale of the ecological gradients on which primate species sort is larger than the area examined in our analyses. It is well known that primate species are generally adapted to particular ecosystems (e.g. tropical rain forest, savannah) (Fleagle et al. 1999). If our analyses had included primate communities across a continent-level scale, for example, environmental distance may have been a stronger predictor of primate community composition (Kamilar 2009).

Two meta-analyses have attempted to tease apart the relative importance of functional traits on dispersal limitation (Cottenie 2005, Soininen et al. 2007). Not surprisingly, both found that as the spatial scale considered increases, the importance of dispersal limitation for structuring communities also increases. Soininen et al. (2007) found that dispersal limitation was more important for structuring communities of organisms dispersed as seeds than communities of mobile species. Moreover, dispersal limitation was less important for structuring communities of large-bodied species than communities of small-bodied species. In addition, a recent study of bromeliad fauna concluded that the role of environmental factors in structuring communities increased with organism size and that the extent of environmental determinism can be estimated using body size (Farjalla et al. 2012). Based on these studies, our results for primates become even more surprising. Given that none of these studies has included tropical vertebrates, we question the extent to which primates may be outliers.

Conservation implications

It is widely recognized that anthropogenic activity has cascading effects throughout forest communities and that

the loss of vertebrate seed dispersers will have major ramifications for tropical forest plant communities (Terborgh and Feeley 2010). Indeed, several recent studies have demonstrated effects of hunting on plant community composition due to a reduction in abundances of endozoochorous species and thus seed dispersal. These include alterations in the seedling bank on Barro Colorado Island (Wright et al. 2007), reduced recruitment of primate-dispersed trees in the Amazon (Nunez-Iturri et al. 2008), and reduced recruitment of large-seeded trees dispersed by game animals in central Africa and Uganda (Babweteera and Brown 2010, Vanthomme et al. 2010). Moreover, landscape-level changes due to anthropogenic activity may erode the abilities of tropical plant communities to respond to other threats. For example, hunting and habitat fragmentation may reduce the dispersal of endozoochorous plants at the very time that their persistence under human-induced climate change will require the ability to disperse to more suitable environments (Malcolm et al. 2002). Based on our results, we expect an increase in primate dispersal limitation as landscapes undergo increasing fragmentation (Junker et al. 2012) and a concomitant increase in the dispersal limitation of plant species dispersed by primates, threatening the composition of plant communities in forest fragments. Conservation efforts aimed at maintaining connectivity between protected areas may be particularly important for primate-dispersed plants.

Conclusions

In conclusion, like other studies, we found that assemblages of birds and trees are largely structured by environmental factors (i.e. temperature and rainfall). We demonstrated at the community level that trees dispersed by wind exhibit greater dispersal limitation than animal-dispersed species. Contrary to prior expectations, however, we found that primate assemblages are strongly structured by dispersal limitation and are apparent outliers in the context of meta-analyses to date. Moreover, we found consistent trends that guilds of trees dispersed by primates exhibit greater dispersal limitation than guilds of trees dispersed by birds. Given the numerous factors contributing to plant community composition, we find this pattern noteworthy. We suggest that investigating the consequences of variation in dispersal abilities on community assembly warrants further study.

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