Journal of Tropical Ecology

www.cambridge.org/tro

Research Article

Cite this article: Beaudrot L, and Marshall AJ (2019) Differences among regions in environmental predictors of primate community similarity affect conclusions about community assembly. *Journal of Tropical Ecology* **35**, 83–90. https://doi.org/10.1017/S0266467418000470

Received: 8 October 2018
Revised: 21 December 2018
Accepted: 22 December 2018
First published online: 25 January 2019

Keywords:
Community assembly; dispersal limitation; macroecology; soil characteristics; species sorting; tropical forest

Author for correspondence: *Lydia Beaudrot, Email: beaudrot@rice.edu

Differences among regions in environmental predictors of primate community similarity affect conclusions about community assembly

Lydia Beaudrot[1,*] and Andrew J. Marshall[2,3,4,5]

[1]Department of BioSciences, Program in Ecology & Evolutionary Biology, Rice University, 6100 Main St., Houston, TX, 77005-1892, USA; [2]Department of Anthropology, University of Michigan, 1085 S. University Ave., Ann Arbor, MI 48109-1107, USA; [3]Program in the Environment, University of Michigan, 440 Church St., Ann Arbor, MI 48109-1041, USA; [4]School for Environment and Sustainability, University of Michigan, 440 Church St., Ann Arbor, MI 48109-1041, USA and [5]Department of Ecology & Evolutionary Biology, University of Michigan, 1105 North University Ave., Ann Arbor, MI 48109-1085, USA

Abstract

Understanding why ecological communities contain the species they do is a long-standing question in ecology. Two common mechanisms that affect the species found within communities are dispersal limitation and environmental filtering. Correctly identifying the relative influences of these mechanisms has important consequences for our understanding of community assembly. Here variable selection was used to identify the environmental variables that best predict tropical forest primate community similarity in four biogeographic regions: the Neotropics, Afrotropics, Madagascar and the island of Borneo in South-East Asia. The environmental variables included net primary productivity and altitude, as well as multiple temperature, precipitation and topsoil variables. Using the best environmental variables in each region, Mantel and partial Mantel tests were used to reanalyse data from a previously published study. The proportion of variance explained increased for each region. Despite increases, much of the variation remained unexplained for all regions (R^2: Africa = 0.45, South America = 0.16, Madagascar = 0.28, Borneo = 0.10), likely due to different evolutionary and biogeographic histories within each region. Nonetheless, substantial variation among regions in the environmental variables that best predicted primate community similarity were documented. For example, none of the 14 environmental variables was included for all four regions, yet each variable was included for at least one region. Contrary to prior results, environmental filtering was an important assembly mechanism for primate communities in tropical forests worldwide. Geographic distance more strongly predicted African and South American communities whereas environmental distance more strongly predicted Malagasy and Bornean communities. These results suggest that dispersal limitation structures primate communities more strongly than environmental filtering in Africa and in South America whereas environmental filtering structures primate communities more strongly than dispersal limitation in Madagascar and Borneo. For communities defined by genera, environmental distance more strongly predicted primate communities than geographic distance in all four regions, which suggests that environmental filtering is a more influential assembly mechanism at the genus level. Therefore, a more nuanced consideration of environmental variables affects conclusions about the influences of environmental filtering and dispersal limitation on primate community structure.

Introduction

Understanding why ecological communities contain the species they do is a long-standing question in ecology. Dispersal limitation and environmental filtering are two mechanisms that can affect the species found in a community. Dispersal limitation occurs when a species that could persist in a location is absent because individuals of the species are unable to reach the site (Hurtt & Pacala 1995). Environmental filtering occurs when species occur in locations with the environmental conditions to which they are best adapted (Holyoak *et al.* 2005). Numerous studies have examined the relative roles of dispersal limitation and environmental filtering in structuring communities, to the extent that multiple meta-analyses have synthesized how environmental and organismal attributes affect these assembly processes (Astorga *et al.* 2012, Cottenie 2005, Soininen *et al.* 2007). However, the results of individual studies are likely contingent upon the quality of the environmental data used to quantify environmental filtering and the metrics used to quantify dispersal limitation (Chang *et al.* 2013).

Correctly identifying the relative influences of dispersal limitation and environmental filtering has important practical applications, such as spatial planning for reserve selection in conservation (Steinitz *et al.* 2005). This is particularly important for tropical systems where extinctions are occurring disproportionately (Pimm *et al.* 2014). Despite the fact that species richness is highest in the tropics, there is a significant disparity in the number of studies at large spatial scales that have been carried out in the tropics in comparison with higher-latitude regions (Beck *et al.* 2012). Currently, the majority of our knowledge about tropical community assembly comes from plants (Swenson 2013). However, the mechanisms that structure communities of tropical plants, which are sessile, may differ from the mechanisms that structure communities of large-bodied, mobile vertebrates. Primates are a key taxonomic group for understanding tropical regions because they are a major component of vertebrate biomass (Corlett & Primack 2006) and the most frequently studied tropical organisms (Marshall & Wich 2016, Marshall *et al.* 2016). Their distributions are well-studied because primates are more easily and accurately censused than other mammalian forest taxa due to their typically diurnal activity patterns, relatively large bodies and noisy group-living behaviour (Emmons 1999, Kamilar & Beaudrot 2013).

Here we use a variable selection approach (Clarke & Ainsworth 1993) to identify the environmental variables that best predict tropical forest primate community similarity in four biogeographic regions spanning the distribution of primates. We then analyse data from a previously published study on the relative influence of dispersal limitation and environmental filtering (Beaudrot & Marshall 2011). Specifically, we test the following two hypotheses. H1: If dispersal limitation is important for structuring communities, then sites that are close together are expected to share many species in common regardless of environmental characteristics. Community similarity is expected to decrease with increasing geographic distance. H2: If the environment determines community similarity, then sites with similar environmental conditions are expected to share more species in common irrespective of the geographic distance between them (hereafter 'environmental filtering'). Community similarity is expected to decrease with increasing environmental distance (Chase *et al.* 2005). While these two hypotheses are not mutually exclusive, their comparison can reveal the relative strengths of environmental and geographic influences on community composition.

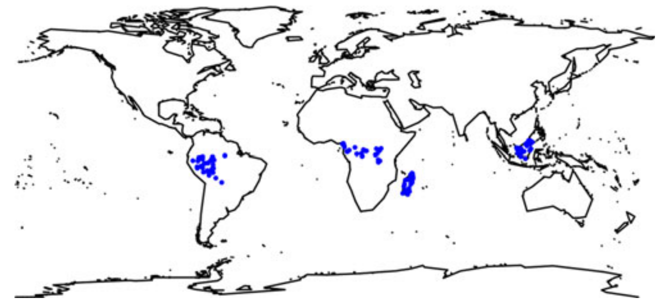

Figure 1. World map with blue points depicting locations of tropical forest primate communities in this study.

Methods

Our approach involved four steps. First, we used presence-absence data on primate community composition to calculate primate community similarity among sites within a region. Then we calculated the geographic distances between sites. Next, we quantified ecological distance between sites by applying a variable selection approach to select the best temperature, precipitation and soil variables for each region using the highest rank correlation values. Lastly, we applied Mantel and partial Mantel tests to examine the correlations between primate community similarity and the geographic and environmental distance predictor variables.

Data collection and distance matrix calculations

Primate community composition was defined using presence-absence data for species compiled from published sources following the taxonomy of Groves (2001). The data included 124 sites across Africa (N = 23), South America (N = 45), Madagascar (N = 28) and Borneo (N = 28) (Figure 1). Primate communities for each region were defined in three ways – by all species, by diurnal species only or by genera. We first examined all species of primates. We then examined diurnal species only to exclude any potential differences caused by the inclusion of solitary, nocturnal species (e.g. resulting from the fact that they are more difficult to detect when sampling during daylight hours and nocturnal sampling effort likely varied among sites). Lastly, we conducted additional tests at the genus level to exclude any potential results contingent on species designations. All data in this study were from Beaudrot & Marshall (2011). See Appendix S1 in Beaudrot & Marshall (2011) for species and site information.

We calculated pairwise primate community similarity between all sites in each region using the Jaccard Index with the vegdist function from the Vegan community ecology package in R. High values of the Jaccard community similarity index indicate that two sites share many species in common and few species are found only at one of the sites.

We collected geographic coordinates from the community composition site reference when available, or otherwise from the UNEP and IUCN Worldwide Database on Protected Areas (IUCN-UNEP 2009). We calculated geographic distances between all pairs of sites in each region using the pairdist function from the spatstat package in R. Pairdist computes the matrix of Euclidean distances between latitude and longitude.

It is likely that the plant species on which primates feed influence primate distributions. Because systematic information on plant community composition was unavailable for each site, we collected information on environmental variables known to affect plant distributions – temperature, precipitation and soil (Franklin 1995). We collected 14 variables for the geographic coordinates of each site from publicly available datasets using ArcGIS (Figure 2). The variables were: net primary productivity, altitude, annual mean temperature, mean diurnal temperature range, isothermality, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation of warmest quarter, topsoil sand fraction, topsoil clay fraction, topsoil organic carbon, topsoil pH and topsoil cation exchange capacity.

We used the 'bioenv' function from the 'vegan' package in R to select a subset of environmental variables with the highest rank correlation with community data. Specifically, the bioenv function uses a weighted Spearman rank coefficient that calculates the harmonic rank correlation between the community similarity matrix and the environmental variable matrix (Clarke & Ainsworth 1993). Thus, the rank order of the community similarity matrix is correlated with the rank order of the environmental variable matrix. The bioenv function tests all possible subsets of environmental variables and calculates the rank correlation for each combination. We then calculated a matrix of ecological distances with the subset of best-fit environmental variables for each region using a Euclidean distance calculation.

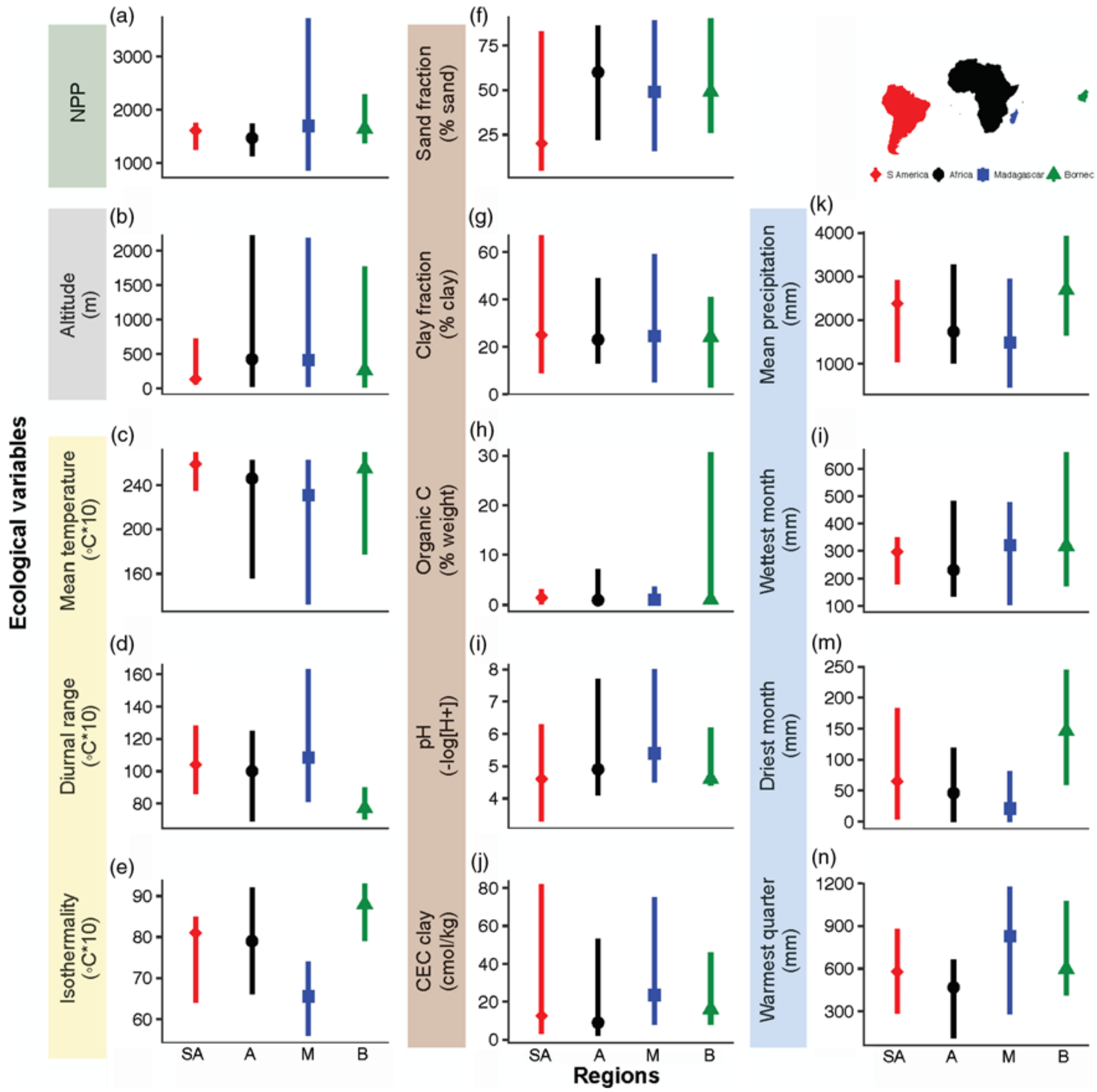

Figure 2. Summary of 14 ecological variables for the primate community sites in each of the four regions. Variable selection was used to identify the subset of these variables that best predicted primate community similarity for each of the four regions and three community definitions (Appendix 1). Lines denote the range of values for sites in each region. Points indicate the median. Red lines with diamond symbols represent South America (SA), black lines with circular point symbols represent Africa (A), blue lines with square point symbols represent Madagascar (M) and green lines with triangle point symbols represent Borneo (B). The ecological variables included an index of net primary productivity (a), altitude (b), three temperature variables, five topsoil variables and four precipitation variables. The temperature variables included mean temperature (c), the diurnal temperature range (d) and isothermality (e). The topsoil variables included the sand fraction (f), clay fraction (g), organic carbon content (h), pH (i) and cation exchange capacity (j). The precipitation variables included mean precipitation (k), precipitation in the wettest month (l), precipitation in the driest month (m), and precipitation in the warmest quarter (n).

Mantel tests

We conducted simple Mantel tests to investigate bivariate correlations of community similarity with ecological distance and geographic distance and partial Mantel tests (Smouse *et al.* 1986) to investigate partial relationships between these variables. The partial Mantel tests allowed us to examine the independent relationships between (1) community similarity and geographic distance (i.e. while accounting for their covariation with environmental distance) and (2) community similarity and environmental distance (i.e. while accounting for their covariation with geographic distance). For example, to examine the relationship between community similarity and geographic distance independently from environmental distance, we first regressed community similarity on environmental distance and saved the residuals. We then regressed geographic distance on environmental distance and saved the residuals. We were able to examine the relationship between community similarity and geographic distance independent of environmental distance by examining the correlation between these two sets of residuals. While concerns about the Mantel test have been raised (Bradburd *et al.* 2013, Steinbauer *et al.* 2013), use of the Mantel test was necessary for direct comparison with previous results.

All tests were performed in R using the 'mantel' and 'mantel.-partial' commands, the Pearson method and 10 000 permutations. We used a similarity matrix for community composition and dissimilarity matrices for ecological and geographic distance.

Spatial scale

Lastly, we calculated the spatial extent of the sampling area in each biogeographic region by measuring the area within the minimum convex polygon surrounding the outermost geographic coordinates for sites in each region. To do this we used the earth.poly function from the fossil package in R. A map of the sites is shown in Figure 1. We note that minimum convex polygon methods are prone to area overestimation and may therefore introduce measurement error.

Results

Environmental variables

There was considerable variation among regions in the ecological variables that best predicted primate community similarity. None of the regions retained all 14 environmental variables, yet each variable was included in at least one region. No single variable was retained for all four regions (Appendix 1). We report the minimum, maximum and median values for each variable in each region in Figure 2.

Some ecological variables were consistently retained for a region irrespective of whether all species, diurnal species or genera were considered. Africa consistently included precipitation of the wettest month; South America consistently included isothermality, precipitation of the warmest quarter, topsoil organic carbon and the topsoil sand fraction; Madagascar consistently included annual mean temperature, precipitation of the wettest month, precipitation of the driest month, and topsoil cation exchange capacity (clay); Borneo consistently included precipitation of the wettest month.

Three ecological variables were retained by the variable selection approach for only one region each: Africa was the only region to include altitude, South America was the only region to include the topsoil organic carbon content and Madagascar was the only region to include net primary productivity (Appendix 1).

Mantel tests

In both the Mantel and partial Mantel tests, ecological distance significantly predicted primate community similarity for all tests (Figure 3), which suggests an important role for environmental filtering for primate communities in all regions. Geographic distance significantly predicted primate community similarity for most tests, which suggests a significant role for dispersal limitation in most cases. The three exceptions were the partial Mantel test for South America and both the Mantel and partial Mantel test for Borneo based on communities defined by genera (Figure 3).

Communities defined by all species and by diurnal species had similar results using both the Mantel and the partial Mantel tests: geographic distance more strongly predicted African and South American communities whereas environmental distance more strongly predicted Malagasy and Bornean communities (Figure 3). These results suggest that dispersal limitation structures primate communities more strongly than environmental filtering in Africa and in South America whereas environmental filtering structures primate communities more strongly than dispersal limitation in Madagascar and Borneo. For communities defined by genera, environmental distance more strongly predicted primate communities than geographic distance in all four regions (Figure 3), which suggests that environmental filtering is a more influential assembly mechanism at the genus level.

Mantel tests accounted for the greatest amount of variation for primate communities in Africa, followed by Madagascar and then South America. For all regions, more variance was consistently explained at the species level than the genus level (Table 1).

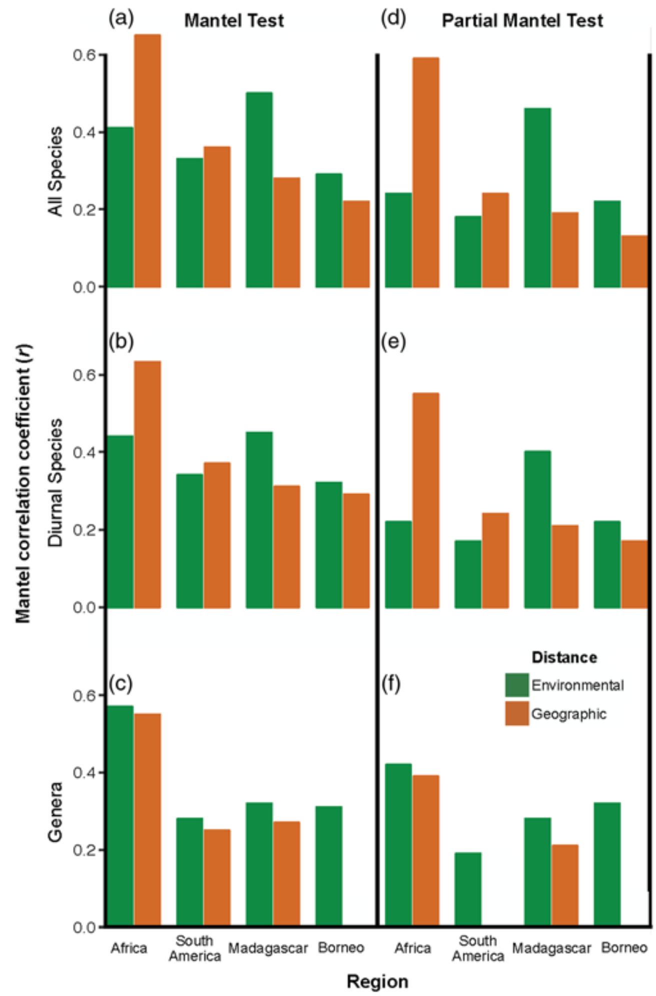

Figure 3. Barplots showing Mantel and partial Mantel results for significant predictors of primate community similarity. Results are shown for the three community definitions for each of the four biogeographic regions. Green bars depict the effects of environmental distance on community similarity based on environmental variables chosen by variable selection, which reflects the level of environmental filtering. Brown bars show the effects of geographic distance on community similarity, which indicate the strength dispersal limitation. Only results significant at the level of a = 0.05 are shown. Correlation coefficients from the Mantel tests are shown for communities defined by all species (a), diurnal species (b) and genera (c). Correlation coefficients from the partial Mantel tests are shown for all species (d), diurnal species (e) and genera (f).

Spatial scale

Based on the minimum convex polygon surrounding the sites in each region rounded to the nearest 100 km^2, the geographic extent of sampling was greatest for sites in South America (2 126 200 km^2) followed by Africa (1 590 100 km^2), Borneo (691 900 km^2) and Madagascar (475 000 km^2). The relationship between the sampling area of the four biogeographic regions and the strength of the partial correlation between diurnal primate community similarity and geographic distance was non-significant (linear regression: $R^2 = 0.199$, df = 2, P = 0.55; Appendix 2), suggesting the differences among regions were not importantly affected by spatial extent.

Discussion

This study examined the relative importance of dispersal limitation and environmental filtering for structuring tropical forest primate

Table 1. Model summaries providing the proportion of variance explained (i.e. R^2) for multiple regression models of primate community similarity with ecological and geographic distance as predictors. Primate communities were defined in three ways (i.e. by all species, diurnal species only or genera) for each of the four regions

Region	All species	Diurnal	Genera
Africa	0.45	0.44	0.42
South America	0.16	0.16	0.09
Madagascar	0.28	0.24	0.15
Borneo	0.10	0.13	0.11

communities worldwide. Unlike previously published research, this study used a variable selection approach to identify the set of environmental variables that best predict primate community similarity in South America, Africa, Madagascar and Borneo. Further analysis with these variables demonstrated that applying a variable selection approach can result in qualitatively different conclusions concerning the relative importance of community assembly mechanisms than results produced in the absence of variable selection. We discuss these two key findings in turn below.

Despite increases in variance explained by contemporary environmental conditions following the use of a variable selection approach, much of the variation in primate community composition remained unexplained for all regions. The different evolutionary and biogeographic histories of these regions likely account for much of the unexplained variation (Fleagle & Lehman 2006, Lawes & Eeley 2000).

Regional variation in environmental predictors of primate community similarity

The environmental variables that best predicted primate community similarity varied substantially among biogeographic regions. For example, Africa was the only region in which the variable selection retained altitude. It is likely that the change in altitude from the moist and wet forest areas of the Congo basin to the more mountainous regions near the border of Congo with Tanzania and Uganda spans environmental and habitat differences that contribute to faunal turnover (Holt *et al.* 2013) and spans geographic barriers that have prevented the dispersal of some primate species (Harcourt & Wood 2012). The retention of several precipitation variables indicates an important role of precipitation seasonality for variation in the species composition of African primate communities and further suggests that the transition from the wet tropical forests of the Congo basin to more seasonal forests to the east is associated with faunal turnover.

The island of Madagascar contains diverse ecological regions ranging from wet tropical forests in the east to dry deciduous forests in the west and spiny forests in the south. Accordingly, the Malagasy sites exhibited the greatest range in net primary productivity of the four regions (Figure 2). Madagascar was also the only region in which net primary productivity was retained, likely because net primary productivity captured the extensive variation in forest types. Habitat characteristics have been argued to be the primary determinants of mammal community composition in Madagascar (Muldoon & Goodman 2010). Variables associated with precipitation seasonality, specifically precipitation of the wettest and driest months, were also consistently retained. Multiple studies have highlighted the importance of rainfall variability on Madagascar for the evolution of species characteristics (Dewar & Richard 2007) and lemur diversity (Kamilar & Muldoon 2010). Lastly, topsoil cation exchange capacity was consistently retained for Malagasy sites, which suggests that there is important variation in nutrient retention across Malagasy soils. Heterogeneity in cation exchange capacity can cause variation in tropical fruit crop production (Kainer *et al.* 2007).

South American communities were consistently predicted by two topsoil variables that were not consistent predictors in other regions: the topsoil sand fraction and organic carbon content. Soil fertility and its effects on floristic diversity have been previously suggested to be determinants of primate community structure in western Amazonia (Haugaasen & Peres 2005, Peres 1997). Soil chemical composition varies significantly among major forest types in western Amazonia: topsoil deposition from annual flooding cycles maintains higher levels of macronutrients, which maintains greater floristic diversity in some forests (Haugaasen & Peres 2006). The fraction of both course and fine sand varies significantly between forest types (Haugaasen & Peres 2006) and both primate biomass and species richness vary significantly between habitat types (Haugaasen & Peres 2005).

Bornean primate communities showed the weakest response to environmental variables of the four regions and our models explained the least variance. Precipitation in the wettest month, an important predictor in three of the four regions we sampled (Appendix 1), was the only consistently retained predictor of Bornean primate communities. Borneo is characterized by the greatest variability and largest maximum value for precipitation in the wettest month of any of the regions we sampled (Figure 2), reflecting the substantial longitudinal gradient in weather and the intensity of El Niño–Southern Oscillation effects across Malesia (van Schaik *et al.* 2009, Wich & van Schaik 2000). The precise mechanisms by which this influences primate community composition are not clear, although they may differ in Borneo from other regions because unlike other regions, rainfall is not associated with either plant productivity or primate species richness in South-East Asia (Fleagle & Reed 1996, Kay *et al.* 1997). One possibility is the role that extremely high rainfall might play in leeching soil nutrients in Asian forests (Kay *et al.* 1997), a possibility consistent with the importance of several soil characteristics in predicting community composition in Borneo. Although there is limited research on how soil characteristics influence higher trophic levels in tropical forests (Corlett & Primack 2011), variation in soils across Malesia clearly has important ecological effects. For example, forests of low pH and with high sand content (e.g. peat swamps, heath forests) differ substantially from mineral soils in their plant diversity and species composition, temporal patterns of fruiting phenology and animal abundances (MacKinnon *et al.* 1996, Marshall *et al.* 2009, 2014; Paoli *et al.* 2010, Slik *et al.* 2009), all of which likely influence primate community composition.

Relative influences of environmental filtering and dispersal limitation

Beaudrot & Marshall (2011) previously concluded that dispersal limitation structured primate communities more strongly than environmental filtering in the tropical forests of Africa, South America and Borneo. The earlier study used all 14 environmental variables described herein for all regions in order to apply a standardized method for cross-continental comparison (Corlett & Primack 2006). While the previous environmental distance calculation provided a comparable baseline, it did not allow for meaningful ecological variation across biogeographic regions that could affect primate communities.

Exclusion of extraneous environmental variables improved the percentage of variance explained for all regions in this study. Moreover, this study found a significant negative relationship between primate community similarity and environmental distance for all community definitions in all regions, which suggests a consistent influence of environmental filtering on primate communities in all the biogeographic regions in which they occur.

In some cases, variable selection reversed the previously published finding that primate communities were structured more strongly by dispersal limitation than by niches. Tests at the genus level in this study produced qualitatively different results for primate communities in Africa, South America and Borneo than previously published. Incorporating the best-fit environmental predictors increased the predictive power of the environmental variables to the extent that the ecological distances became stronger predictors of primate community composition than geographic distances were. For South America and Borneo, geographic distance was no longer a significant predictor of primate community similarity, which suggests that dispersal limitation may not be an important assembly mechanism in these regions at the genus level.

We also found qualitatively different results for primate communities defined at the species level in Borneo. Given that only 8% of variation in community composition had previously been explained and this study explained 10% of variation, this difference was not dramatic. Factors not considered in either of the analyses may explain additional variation. For example, historical factors may be particularly important for Bornean communities given the complex biogeographic history of the Sunda Shelf (Slik *et al.* 2011). Competition with non-primates may also influence Bornean primate community composition (Beaudrot *et al.* 2013a, 2013b; Ganzhorn 1999).

We found that a more nuanced consideration of environmental variables affects conclusions about the influences of environmental filtering and dispersal limitation on primate communities, particularly at the genus level. Nevertheless, improvements to the geographic distance measure might further affect these conclusions. For example, using a least-cost path analysis and incorporating differences in forest cover or barriers, such as roads, rivers and mountains might produce a more ecologically realistic measure of dispersal costs that further affect results. Determining the relative importance of dispersal limitation and environmental filtering has important applications for biodiversity conservation. Given that conclusions are dependent on the quality of environmental data, a robust understanding of community assembly processes is necessary before management recommendations can be made.

Author ORCIDs. Lydia Beaudrot https://orcid.org/0000-0001-8135-7519; Andrew J. Marshall https://orcid.org/0000-0002-7703-8811

Acknowledgements. We thank several anonymous reviewers and Michael Lawes for feedback on previous manuscript versions.

Financial support. None.

Literature cited

Astorga A, Oksanen J, Luoto M, Soininen J, Virtanen R and Muotka T (2012) Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules. *Global Ecology and Biogeography* **21**, 365–375.

Beaudrot L and Marshall AJ (2011) Primate communities are structured more by dispersal limitation than by niches. *Journal of Animal Ecology* **80**, 332–341.

Beaudrot L, Struebig MJ, Meijaard E, Van Balen S, Husson S and Marshall AJ (2013a). Co-occurrence patterns of Bornean vertebrates suggest competitive exclusion is strongest in distantly related taxa. *Oecologia* **173**, 1053–1062.

Beaudrot L, Struebig MJ, Meijaard E, Van Balen S, Husson S, Young CF and Marshall AJ (2013b). Interspecific interactions between primates, birds, bats and squirrels may affect community composition on Borneo. *American Journal of Primatology* **75**, 170–185.

Beck J, Ballesteros-Meijia L, Buchmann CM, Dengler J, Fritz SA, Gruber B, Hof C, Jansen F, Knapp S, Kreft H, Schneider A-K, Winter M and Dormann CF (2012) What's on the horizon for macroecology? *Ecography* **35**, 673–683.

Bradburd GS, Ralph PL and Coop GM (2013) Disentangling the effects of geographic and ecological isolation on genetic differentiation. *Evolution* **67**, 3258–3273.

Chang L-W, Zeleny D, Li C-F, Chiu S-T and Hsieh C-F (2013) Better environmental data may reverse conclusions about niche- and dispersal-based processes in community assembly. *Ecology* **94**, 2145–2151.

Chase JM, Amarasekare P, Cottenie K, Gonzalez A, Holt RD, Holyoak M, Hoopes MF, Leibold MA, Loreau M, Mouquet N, Shurin J and Tilman D (2005) Competing theories for competitive metacommunities. In Holyoak M, Leibold MA and Holt RD (eds), *Metacommunities: Spatial Dynamics and Ecological Communities*. Chicago, IL: University of Chicago Press, pp. 334–354.

Clarke KR and Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**, 205–219.

Corlett RT and Primack RB (2006) Tropical rainforests and the need for cross-continental comparisons. *Trends in Ecology and Evolution* **21**, 104–110.

Corlett RT and Primack RB (2011) *Tropical Rain Forests: An Ecological and Biogeographical Comparison*. Hong Kong: Wiley-Blackwell.

Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters* **8**, 1175–1182.

Dewar RE and Richard AF (2007) Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences USA* **104**, 13723–13727.

Emmons LH (1999) Of mice and monkeys: primates as predictors of mammal community richness. In Fleagle JG, Janson C and Reed KE (eds), *Primate Communities*. Cambridge: Cambridge University Press, pp. 171–188.

Fleagle JG and Lehman SM, eds. (2006) *Primate Biogeography: Progress and Prospects*. New York, NY: Springer.

Fleagle JG and Reed KE (1996) Comparing primate communities: a multivariate approach. *Journal of Human Evolution* **30**, 489–510.

Franklin J (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* **19**, 474–499.

Ganzhorn JU (1999) Body mass, competition and the structure of primate communities. In Fleagle JG, Janson C and Reed KE (eds), *Primate Communities*. Cambridge: Cambridge University Press, pp. 141–157.

Groves CG (2001) *Primate Taxonomy*. Washington, DC: Smithsonian Institution.

Harcourt AH and Wood MA (2012) Rivers as barriers to primate distributions in Africa. *International Journal of Primatology* **33**, 168–183.

Haugaasen T and Peres CA (2005) Primate assemblage structure in Amazonian flooded and unflooded forests. *American Journal of Primatology* **67**, 243–258.

Haugaasen T and Peres CA (2006) Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower rio purus region of Central Amazonia, Brazil. *Acta Amazonica* **36**, 25–36.

Holt B, Lessard JP, Borregaard MK, Fritz S, Araujo MB, Dimitrov D, Fabre P-H, Graham CH, Graves GR, Jonsson KA, Nogues-Bravo D, Wang Z, Whittaker RJ, Fjeldsa J and Rahbek C (2013) An update of Wallace's zoogeographic regions of the world. *Science* **339**, 74–78.

Holyoak M, Leibold MA and Holt RD, eds. (2005) *Metacommunities: Spatial Dynamics and Ecological Communities*. Chicago, IL: University of Chicago.

Hurtt GC and Pacala SW (1995) The consequences of recruitment limitation–reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* **176**, 1–12.

IUCN-UNEP (2009) *World Database on Protected Areas (WDPA)*. Cambridge: UNEP-WCMC.

Kainer KA, Wadt LHO and Staudhammer CL (2007) Explaining variation in Brazil nut fruit production. *Forest Ecology and Management* **250**, 244–255.

Kamilar JM and Beaudrot L (2013) Understanding primate communities: recent developments and future directions. *Evolutionary Anthropology* **22**, 174–185.

Kamilar JM and Muldoon KM (2010) The climatic niche diversity of Malagasy primates: a phylogenetic perspective. *PLoS ONE* **5**, e11073.

Kay RF, Madden RH, Van Schaik CP and Higdon D (1997) Primate species richness is determined by plant productivity: implications for conservation. *Proceedings of the National Academy of Sciences USA* **94**, 13023–13027.

Lawes MJ and Eeley AC (2000) Are local patterns of anthropoid primate diversity related to patterns of diversity at a larger scale? *Journal of Biogeography* **27**, 1421–1425.

MacKinnon K, Hatta G, Halim H and Mangalik A (1996) *The Ecology of Kalimantan: Indonesian Borneo*. Singapore: Periplus Editions.

Marshall AJ, Ancrenaz M, Brearley FQ, Fredriksson GM, Ghaffar N, Heydon M, Husson SJ, Leighton M, McConkey KR, Morrough-Bernard HC, Proctor J, Van Schaik CP, Yeager CP and Wich SA (2009) The effects of forest phenology and floristics on populations of bornean and sumatran orangutans: are Sumatran forests more productive than Bornean forests? In Wich SA, Utami S, Mitra Setia T, and van Schaik C (eds), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. Oxford: Oxford University Press, pp. 97–117.

Marshall AJ and Wich SA (2016) Why conserve primates? In Wich SA and Marshall AJ (eds), *An Introduction to Primate Conservation*. Oxford: Oxford University Press, pp. 13–29.

Marshall AJ, Beaudrot L and Wittmer H (2014) Responses of primates and other frugivorous vertebrates to plant resource variability over space and time at Gunung Palung National Park. *International Journal of Primatology* **35**, 1178–1201.

Marshall AJ, Meijaard E, Van Cleave E and Sheil D (2016) Charisma counts: the presence of great apes affects the allocation of research effort in the paleotropics. *Frontiers in Ecology and the Environment* **14**, 13–19.

Muldoon KM and Goodman SM (2010) Ecological biogeography of Malagasy non-volant mammals: community structure is correlated with habitat. *Journal of Biogeography* **37**, 1144–1159.

Paoli GD, Wells PL, Meijaard E, Struebig MJ, Marshall AJ, Obidzinski K, Tan A, Rafiastanto A, Yaap B, Slik JWF, Morel A, Perumal B, Wielaard N, Husson S and D'Arcy L (2010) Biodiversity conservation in the redd. *Carbon Balance and Management* **5**, 7–15.

Peres CA (1997) Primate community structure at twenty Western Amazonian flooded and unflooded forests. *Journal of Tropical Ecology* **13**, 381–405.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM and Sexton JO (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752.

Slik JWF, Aiba S, Bastian M, Brearley FQ, Channon CH, Eichhorn KAO, Fredriksson G, Kartawinata K, Laumonier Y, Manson A, Marjokorpi A, Meijaard E, Morley RJ, Nagamasu H, Nilus R, Nurtjahya E, Payne J, Permana A, Poulsen AD, Raes N, Riswan S, Van Schaik CP, Sheil D, Sidiyasa K, Suzuki E, Van Valkenburg JLCH, Webb CO, Wich S, Yoneda T, Zakari R and Zweifel N (2011) Soils on exposed sunda shelf shaped biogeographic patterns in the equatorial forests of Southeast Asia. *Proceedings of the National Academy of Sciences USA* **108**, 12343–12347.

Slik JWF, Raes N, Aiba S, Brearley FQ, Cannon CH, Meijaard E, Nagamasu H, Nilus R, Paoli G, Poulsen AD, Sheil D, Suzuki E, Van Valkenburg JLCH, Webb CO, Wilkie P and Wulffraat S (2009) Environmental correlates for tropical tree diversity and distribution patterns in Borneo. *Diversity and Distributions* **15**, 523–532.

Smouse PE, Long JC and Sokal RR (1986) Multiple regression and correlation extensions of the mantel test of matrix correspondence. *Systematic Zoology* **35**, 627–632.

Soininen J, McDonald R and Hillebrand H (2007) The distance decay of similarity in ecological communities. *Ecography* **30**, 3–12.

Steinbauer MJ, Dolos K, Reineking B and Beierkuhnlein C (2013) Current measures for distance decay in similarity of species composition are influenced by study extent and grain size. *Global Ecology and Biogeography* **21**, 1203–1212.

Steinitz O, Heller J, Tsoar A, Rotem D and Kadmon R (2005) Predicting regional patterns of similarity in species composition for conservation planning. *Conservation Biology* **19**, 1978–1988.

Swenson NG (2013) The assembly of tropical tree communities– the advances and shortcomings of phylogenetic and functional trait analyses. *Ecography* **36**, 264–276.

Van Schaik CP, Marshall AJ and Wich SA (2009) Geographical variation in orangutan behavior and biology. In Wich SA, Utami S, Mitra Setia T and van Schaik C (eds), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. Oxford: Oxford University Press, pp. 351–361.

Wich SA and Van Schaik CP (2000) The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology* **16**, 563–577.

Appendix 1

Variable selection was used to identify the subset of 14 ecological variables that best predicted primate community similarity in four regions: Africa, South America, Madagascar and Borneo. Using the best environmental variables in each region, Mantel and partial Mantel tests were then used to reanalyse data from a previously published study to examine the relative influence of dispersal limitation and environmental filtering in structuring primate communities. Below are the results of the variable selection for each of the four regions and three primate community definitions (i.e. all species, diurnal species only, or genera). The letter o indicates a variable that was retained for only one region. Uppercase X indicates the consistent inclusion of a variable for a region across community definitions (i.e. all species, diurnal species, genera). All other retained variables are indicated with a lowercase x.

	Africa			South America			Madagascar			Borneo		
Variable	All	Diurnal	Genera	All	Diurnal	Genera	All	Diurnal	Genera	All	Diurnal	Genera
Net primate productivity							o		o			
Altitude	o	o										
Annual mean temperature			x				X	X	X			
Mean diurnal temperature range							x	x		x	x	
Isothermality	x		x	X	X	X						
Annual precipitation				x	x				x			
Precipitation of wettest month	X	X	X				X	X	X	X	X	X
Precipitation of driest month	x	x		x	x		X	X	X			
Precipitation of warmest quarter	x		x	X	X	X						
Topsoil sand fraction	x	x		X	X	X				x	x	
Topsoil clay fraction	x			x		x					x	
Topsoil organic carbon				X	X	X						
Topsoil pH							x			x		X
Topsoil cation exchange capacity (clay)							X	X	X		x	

Appendix 2

We tested whether the spatial extent of regions predicted primate dispersal limitation (i.e. the partial Mantel correlation between primate community similarity and geographic distance) using linear regression. We did not find a significant relationship; the dashed line shows a non-significant linear relationship. The lack of a significant relationship suggests that the spatial extent of a region is not the cause of dispersal limitation structuring primate communities in these four tropical forest regions.