

## LETTER

# Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly

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### Abstract

Site-to-site variation in species composition ( $\beta$ -diversity) generally increases from low- to high-diversity regions. Although biogeographical differences in community assembly mechanisms may explain this pattern, random sampling effects can create this pattern through differences in regional species pools. Here, we compared assembly mechanisms between spatially extensive networks of temperate and tropical forest plots with highly divergent species pools (46 vs. 607 species). After controlling for sampling effects,  $\beta$ -diversity of woody plants was similar and higher than expected by chance in both forests, reflecting strong intraspecific aggregation. However, different mechanisms appeared to explain aggregation in the two forests. In the temperate forest, aggregation reflected stronger environmental correlations, suggesting an important role for species-sorting (e.g. environmental filtering) processes, whereas in the tropics, aggregation reflected stronger spatial correlations, more likely reflecting dispersal limitation. We suggest that biogeographical differences in the relative importance of different community assembly mechanisms contribute to these striking gradients in global biodiversity.

### Keywords

Amazonia, beta-diversity, community assembly, dispersal limitation, environmental filtering, intraspecific aggregation, metacommunity, Ozarks, species pool, species sorting.

*Ecology Letters* (2013) 16: 151–157

## INTRODUCTION

Patterns of site-to-site variation in species composition, known as  $\beta$ -diversity, can provide fundamental insights into the processes that create and maintain biodiversity (e.g. Condit *et al.* 2002; Tuomisto *et al.* 2003; Gilbert & Lechowicz 2004; Dornelas *et al.* 2006; Dyer *et al.* 2007; Chase 2010; Anderson *et al.* 2011; Kraft *et al.* 2011).  $\beta$ -diversity describes not only the scaling relationship between local ( $\alpha$ ) and regional ( $\gamma$ ) diversity, but also how communities respond to anthropogenic influences (e.g. Passy & Blanchet 2007; Vellend *et al.* 2007), climate change (Leprieur *et al.* 2011) and environmental gradients (e.g. Cottenie 2005; Anderson *et al.* 2011). At the global scale,  $\beta$ -diversity generally increases from low-diversity (e.g. temperate) to high-diversity (e.g. tropical) regions (Koleff *et al.* 2003; Qian & Ricklefs 2007; Soininen *et al.* 2007; Korhonen *et al.* 2010; Cáceres *et al.* 2012). One possible explanation for this pattern is that local community assembly processes might differ in their relative importance among biogeographical regions (Harms *et al.* 2000; Dyer *et al.* 2007; Schemske *et al.* 2009; Chisholm & Pacala 2011; Freestone & Osman 2011; Johnson *et al.* 2012). These include dispersal limitation (e.g. Hurtt & Pacala 1995; Hubbell *et al.* 1999; Condit *et al.* 2002), deterministic processes such as environmental or habitat filtering (e.g. Pitman *et al.* 2001; Tuomisto *et al.* 2003; John *et al.* 2007; Kraft *et al.* 2008), and stochastic processes that generate ecological drift (Hubbell 2001; Chase 2010; Chisholm & Pacala 2011). Alternatively, larger scale processes that create differences in the size of regional

species pools (i.e.  $\gamma$ -diversity) may drive biogeographical gradients in  $\beta$ -diversity (Ricklefs 1987; Kraft *et al.* 2011; Cáceres *et al.* 2012).

In a recent study, Kraft *et al.* (2011) used a null-model approach to examine  $\beta$ -diversity of tree communities across elevational and latitudinal gradients that include strong variation in the size of the regional species pool. First, they showed that observed patterns of  $\beta$ -diversity will increase as  $\gamma$ -diversity increases owing simply to random sampling effects. In regions with higher  $\gamma$ -diversity, a smaller proportion of the species pool is expected (by chance) to occur in any one community, resulting in higher expected  $\beta$ -diversity or random ‘spill over’ of species among local communities. Second, they used this null expectation to discern whether  $\beta$ -diversity varied systematically across elevational and latitudinal gradients after controlling for sampling effects owing to variation in regional pool size. Small deviations of  $\beta$ -diversity from the null expectation (hereafter ‘ $\beta$ -deviations’) would suggest an overriding role for biogeographical and evolutionary processes that determine the size of species pools (Ricklefs 1987), whereas larger positive  $\beta$ -deviations would indicate that species are more spatially aggregated than expected from sampling alone (Kraft *et al.* 2011). Importantly, absence of systematic variation in  $\beta$ -deviations along ecological gradients may imply that similar mechanisms underlie patterns of community assembly across these widely divergent types of forests (Kraft *et al.* 2011). For example, density-dependent mortality of seeds or seedlings could have similar influences on patterns of tree diversity at temperate and tropical latitudes (Hille Ris Lambers *et al.* 2002). However, because aggregated distributions of species that

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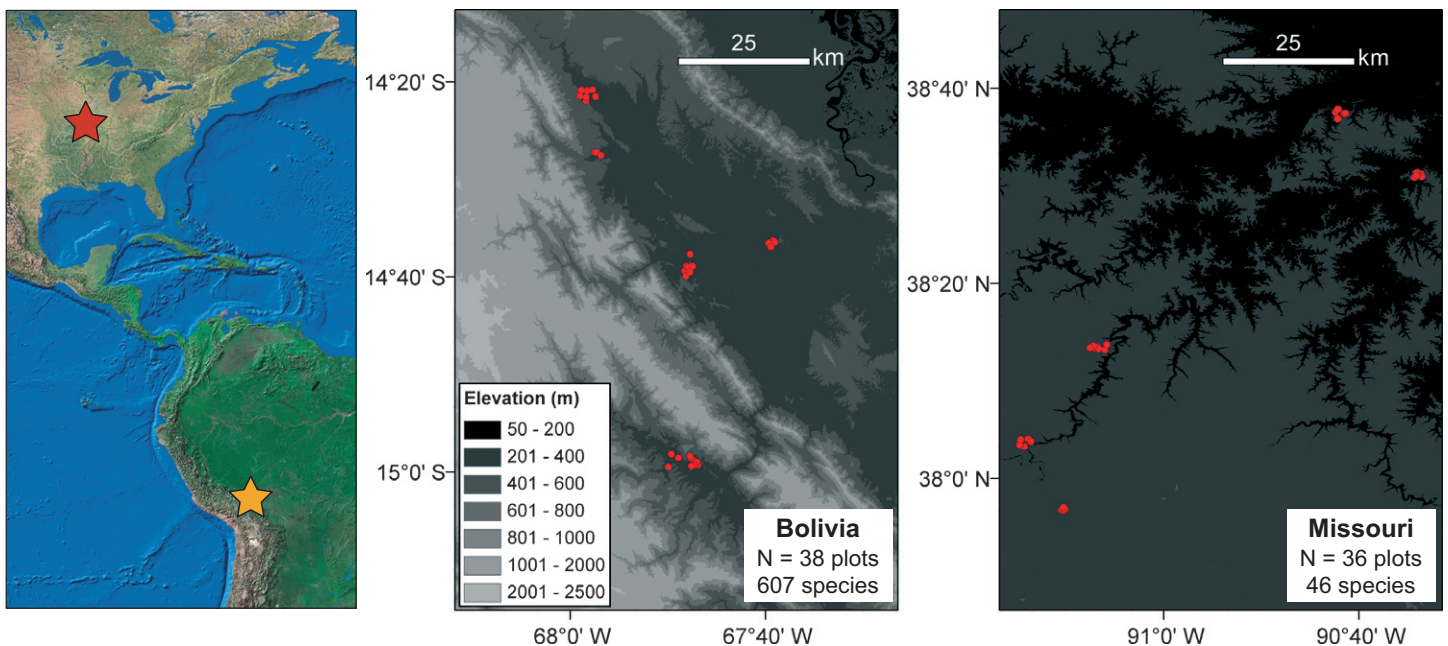
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lead to high  $\beta$ -deviations could result from dispersal limitation, environmental filtering or a combination of both processes (e.g. Condit *et al.* 2000, 2002; Tuomisto *et al.* 2003), similar non-random patterns could reflect dissimilar processes underlying community assembly.

Variation-partitioning analyses of community composition across environmental and spatial gradients provide insights into mechanisms underlying community assembly (e.g. Gilbert & Lechowicz 2004; Cottenie 2005; Legendre *et al.* 2009). If  $\beta$ -diversity is strongly correlated with environmental variation, processes associated with ‘species-sorting’ (e.g. environmental filtering) models of meta-community structure (e.g. Chase & Leibold 2003) are likely operating, whereas if  $\beta$ -diversity is strongly correlated with spatial variation, processes associated with ‘dispersal-assembly’ models (Hubbell 2001) are likely playing a stronger role. The proportion of variation in  $\beta$ -diversity that is unexplained by environment and space – representing the ‘error’ term – may be influenced by local stochasticity due to ecological drift (Legendre *et al.* 2009), regional sampling effects (Chase & Myers 2011) or unmeasured environmental and spatial variables (Borcard *et al.* 2004). Because the unexplained variation in  $\beta$ -diversity is expected to be much higher in high-diversity regions simply due to a sampling effect (Kraft *et al.* 2011), a null-model analysis is needed to compare the relative importance of environmental and spatial processes among regions that vary in the size of the species pool (Chase & Myers 2011). Using a global network of spatially contiguous (25–50 ha), stem-mapped forest plots that vary in the size of the regional species pool, Cáceres *et al.* (2012) used this null-model analysis to show that regional pool size explained much of the difference in local (within-plot)  $\beta$ -diversity among forests. Among plots, however, there were strong differences in local topographic gradients, and within plots, almost all of the variation in  $\beta$ -diversity explained by topographic variables was also explained by spatial variables (Cáceres *et al.* 2012), making it difficult to explicitly disentangle

whether environmental and spatial processes vary among temperate and tropical forests with highly divergent species pools.

In this study, we explicitly tested the hypothesis that similar assembly mechanisms give rise to similar  $\beta$ -deviations in low- and high-diversity forests. We compared  $\beta$ -diversity of woody plant species between temperate and tropical forest plots that span a 13-fold difference in the size of the species pool. In contrast to previous studies conducted at relatively small spatial scales (e.g. < 1 km; Kraft *et al.* 2011; Cáceres *et al.* 2012), we compared  $\beta$ -deviations between two spatially extensive networks of forest plots (0.03–82 km) sampled explicitly for comparative purposes. Using standardised sampling methods, we censused 38 plots in lowland western Amazonia and 36 plots in oak–hickory forest in central North America (Fig. 1). In both regions, plots were located in a single forest type (western Amazonia or oak–hickory), thereby encompassing environmental gradients within a single biogeographical region. Furthermore, because variation in elevational gradients among forests strongly influences  $\beta$ -diversity (e.g. Cáceres *et al.* 2012), we compared plots across a similar range of elevations in both regions (190 and 124 m in Bolivia and Missouri respectively). The spatial arrangement of plots was also similar between regions, thereby allowing us to compare the potential influence of environmental and spatial processes on  $\beta$ -diversity across similar spatial scales. We first compared  $\beta$ -diversity among the regions, and asked whether it differed from a null model based on random sampling from the regional species pool. Consistent with previous studies (Kraft *et al.* 2011; Cáceres *et al.* 2012), we show that  $\beta$ -diversity in the two forest types is higher than expected by the null model. Second, we show that these positive  $\beta$ -deviations reflect strong intraspecific aggregation in both temperate and tropical communities. Third, because intraspecific aggregation could result from a combination of processes, such as dispersal limitation and environmental filtering, we used variation-partitioning analyses to show that after controlling for differences in the unex-



**Figure 1** Geographical location and spatial distribution of 0.1-ha plots (red points) in lowland western Amazonia forests in Madidi National Park, Bolivia (orange star) and temperate oak–hickory forests in the Missouri Ozarks, USA (red star).

plained variation due to sampling effects, spatial processes due to dispersal limitation appear to play a relatively stronger role in the tropical forest, whereas environmental processes due to species sorting appear to play a relatively stronger role in the temperate forest.

## MATERIALS AND METHODS

### Forest plot networks in Bolivia and Missouri

To disentangle the mechanisms that give rise to  $\beta$ -diversity in regions with divergent species pools, we compared two spatially extensive networks of forest plots: one from a hyper-diverse tropical forest in lowland western Amazonia (607 species; Madidi National Park, Bolivia), and one from a lower diversity temperate oak–hickory forest (Missouri Ozarks, USA, 46 species). In both regions, we censused woody plants in 0.1-ha (20 × 50-m) plots using identical field methods. From Bolivia, we selected a subset of 38 plots (from a total of 442) in five localities established as part of The Madidi Project (Friedman-Rudovsky 2012; [www.mobot.org/MOBOT/Research/madidi/](http://www.mobot.org/MOBOT/Research/madidi/)): Eslabón-Chalalán ( $n = 3$  plots), Río Hondo ( $n = 6$ ), Río Hondo-Arroyo Negro ( $n = 10$ ), Río Rudidi ( $n = 7$ ) and Río Quendeque ( $n = 12$ ) (Fig. 1). The five localities encompass a wide range of environmental conditions within this biogeographical region (see Figure S1, S4 & S5 in Supporting Information). Similarly, in Missouri, we established 36 plots across five localities (Fig. 1) including three state parks (Babler, Meramec, Onondaga Cave) and two research stations (Reis Biological Station, Saint Louis University; Tyson Research Center, Washington University in St. Louis). As in Bolivia, we established plots in locations that span a wide range of environmental conditions in the Ozarks (Fig. S1, S4 & S5). At the state parks and Tyson Research Center, we established two plots in each of four habitat types: bottomlands/ravines, northeast-facing slopes, ridge tops/plateaus and southwest-facing slopes ( $n = 8$  total plots/locality), whereas at Reis Biological Station, we established one plot in each of the same four habitat types ( $n = 4$  total plots).

In both regions, the plots span similar geographical distances (range = 0.03–81 and 0.05–82 km for Bolivia and Missouri respectively), elevations (median = 330 and 246 m, range = 280–470 and 171–295 m respectively) and were established outside of floodplains and areas with recent anthropogenic or natural disturbance. When establishing plots on slopes, we positioned the plot centreline perpendicular to slopes to minimise elevational gradients within plots. In addition, because sampling in both regions included similar numbers of plots spanning small and large geographical distances (Fig. 1), we were able to compare the potential influence of dispersal limitation between regions at similar scales, including scales that encompass typical dispersal distances (seed shadows) of temperate and tropical trees (Clark *et al.* 1999). In each plot, we measured the abundance of each species (or morphospecies)  $\geq 2.5$ -cm diameter at breast height (1.3 m), yielding 8127 total stems and 607 species in Bolivia, and 4513 total stems and 46 species in Missouri.

### Null-model and statistical analyses

We used a null-model approach to compare the observed  $\beta$ -diversity to the  $\beta$ -diversity expected from random sampling of the regional species pool. We first defined the species pool as the total number of species and the total abundance of each species observed across all plots within a region. Next, we measured

observed  $\beta$ -diversity as the dissimilarity between each pair of plots within a region using both an abundance-based (Bray–Curtis) and incidence-based (Jaccard's) metric. We then applied the null model to simulate species assemblages in each plot by randomly sampling individuals from the regional species pool while preserving the relative abundance of each species in the regional pool and the total number of individuals in each plot (Crist *et al.* 2003; Kraft *et al.* 2011). From 2000 iterations of the null model, we calculated a standardised effect size ( $\beta$ -deviation) as the difference between the observed and mean expected dissimilarity, divided by the standard deviation of expected values. A  $\beta$ -deviation of zero indicates that observed  $\beta$ -diversity does not differ from random sampling, a positive  $\beta$ -deviation indicates higher  $\beta$ -diversity than expected by chance and a negative  $\beta$ -deviation indicates lower  $\beta$ -diversity than expected by chance.

We tested for differences in observed  $\beta$ -diversity, expected  $\beta$ -diversity and  $\beta$ -deviations between Bolivia and Missouri using a nonparametric analysis of variance designed to examine the homogeneity of multivariate dispersions based on distance-to-centroid values (Anderson 2006; Anderson *et al.* 2011). We obtained distance-to-centroid values using the 'betadisper' function in the R vegan package (Oksanen *et al.* 2012). In this test,  $\beta$ -diversity is defined as the average distance-to-centroid, measured as the average distance (or compositional dissimilarity) from an individual plot to the centroid of the group of all plots within a region. We obtained similar results using separate-sample bootstrap tests on distance-to-centroids (Anderson *et al.* 2011). In our data sets, the average distance-to-centroids and average Bray–Curtis and Jaccard's dissimilarities show the same regional patterns. In our figures, we therefore present overall summary statistics (box plots) for Bray–Curtis and Jaccard's dissimilarities, rather than average distance-to-centroids, because these measures of  $\beta$ -diversity have been used in relevant recent articles (e.g. Kraft *et al.* 2011) and provide an intuitive way to graphically represent  $\beta$ -deviations.

To compare environmental and spatial influences on  $\beta$ -diversity, we used distance-based redundancy analysis (dbRDA) to partition variation in observed  $\beta$ -diversity and  $\beta$ -deviations into fractions explained by environmental and spatial variables (Peres-Neto *et al.* 2006; Legendre *et al.* 2009). Our initial analyses included a range of environmental variables that vary at both local (e.g. soils, topography) and regional (e.g. climate) scales (Table S1, Figure S1), including: (1) 16 soil variables measured from field samples at soil testing laboratories in Bolivia (Environmental Quality Laboratory, Universidad Mayor de San Andres, La Paz) and Missouri (Soil and Plant Testing Laboratory, University of Missouri, Columbia), (2) 5 topographic variables (eastern and northern aspect, elevation, habitat type, slope) obtained from GIS or field measurements and (3) 19 bioclimatic variables obtained from WorldClim (Hijmans *et al.* 2005; [www.worldclim.org/](http://www.worldclim.org/)). Although the relatively coarse spatial resolution of bioclimatic variables ( $\sim 1$  km) often resulted in identical climate data for plots within sampling localities, climate varied substantially among localities within both regions (Fig. S1, S4). Spatial variables included plot geographical coordinates (latitude and longitude) and spatial eigenfunctions obtained from Principal Components of Neighbor Matrices (PCNM) (Borcard *et al.* 2004; Griffith & Peres-Neto 2006; Legendre *et al.* 2009). PCNM eigenfunctions with positive eigenvalues were used as explanatory variables, yielding four eigenfunctions for Bolivia and one eigenfunction for Missouri.

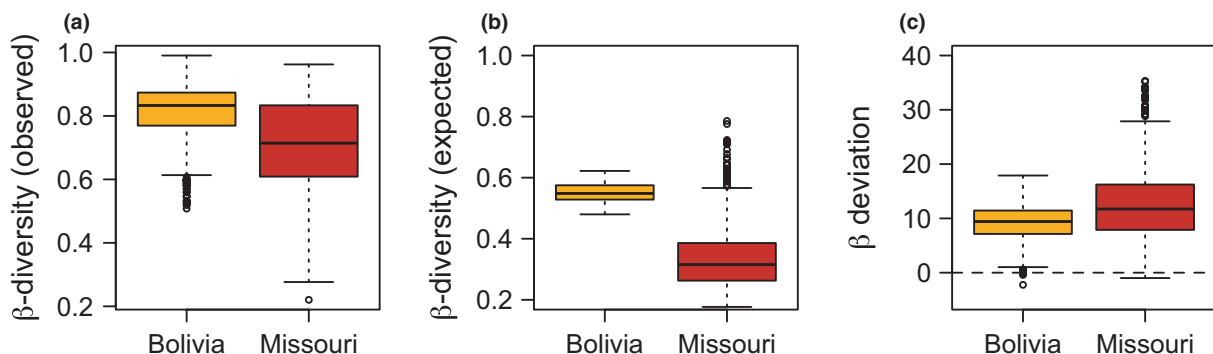


We accounted for collinearity among environmental variables using two separate analyses. First, from the initial set of all environmental variables, we removed variables that were highly correlated with other variables (Pearson  $r \geq 0.80$ ), yielding a total of ten to eleven soil, four to five topographic and five to seven bioclimatic variables for the dbRDA ( $n = 21$  total environmental variables per region) (Table S1). Second, we performed a principal component analysis (PCA) on the 25 environmental variables measured in both regions, and used the orthogonal PCA axes as explanatory variables. Both analyses yielded similar results, so for ease of interpretation, we present the results based on analyses using original variables (Table S1).

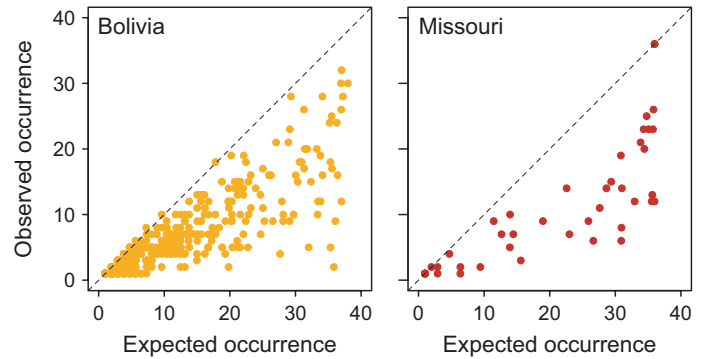
Following Blanchet *et al.* (2008), we used dbRDA to partition variation in  $\beta$ -diversity in two ways. First, we began with a full model that included the complete set of environmental and spatial variables for each region (Table S1). After confirming that the full models were statistically significant ('global tests'), we used the full models to calculate the total amount of variance explained by the combination of environmental and spatial variables for both the observed  $\beta$ -diversity and  $\beta$ -deviations. Second, we performed forward-model selection ('ordiR2step' function in the R *vegan* package) to examine in more detail the relationship between explanatory variables and  $\beta$ -diversity, yielding five to seven significant variables for each region (Table S1). We then used the explanatory variables retained in forward-model selection to partition variation in observed  $\beta$ -diversity and  $\beta$ -deviations into individual fractions explained by environmental, spatial and spatially structured environmental variables. Finally, we tested for differences between regions in the total variance explained (from the full model), the fraction explained by environmental variables (after forward-model selection) and the fraction explained by spatial variables (after forward-model selection) using bootstrap tests (Peres-Neto *et al.* 2006) based on 999 iterations. Because similar results were obtained for Bray–Curtis and Jaccard's metrics of  $\beta$ -diversity, we focus on results for Bray–Curtis and present results for Jaccard's in the Supporting Information. All analyses were performed using R (R Core Development Team 2012).

## RESULTS

Observed  $\beta$ -diversity was higher in Bolivia than in Missouri (Fig. 2a; homogeneity of multivariate dispersion test on average



**Figure 2**  $\beta$ -diversity in Bolivia and Missouri. (a) Observed  $\beta$ -diversity (Bray–Curtis dissimilarity). (b) Expected  $\beta$ -diversity from a null model based on random sampling from the regional species pool. (c)  $\beta$ -deviations, a standardised effect size of  $\beta$ -diversity that controls for sampling from the regional species pool. Boxes represent the median and 25th/75th percentile, and whiskers extend to 1.5 times the interquartile range. Note that  $\beta$ -deviations in both regions are strongly positive, indicating higher  $\beta$ -diversity than expected by chance. Similar results were obtained using an incidence-based (Jaccard's) metric of  $\beta$ -diversity (Figure S2).

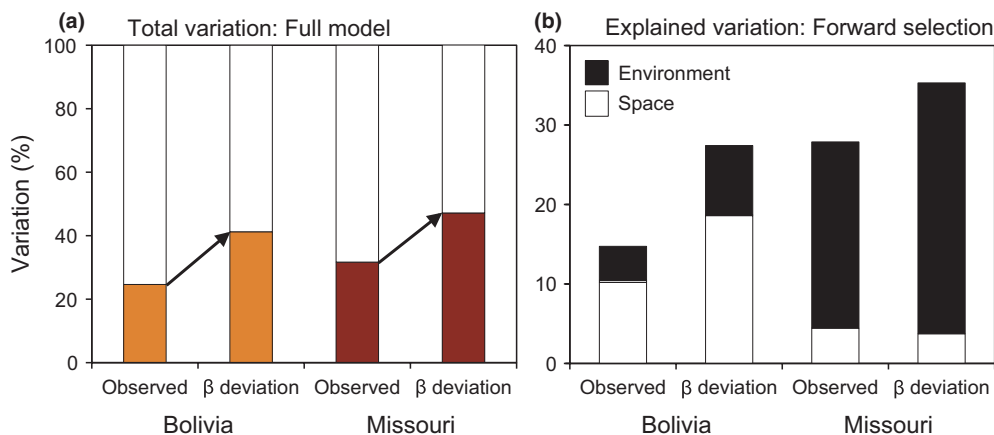


**Figure 3** Intraspecific aggregation in Missouri and Bolivia, measured as the relationship between the observed number of plots in which a species was present (occurrence) and the expected (simulated) number of plots from the null model. Note that most points fall below the dashed line (1 : 1 relationship), indicating that most species occurred in fewer plots than expected by chance.

distance-to-centroids,  $F = 18.47$ ,  $P = 0.0002$ ). Because of differences in species pools, this was expected by sampling (Fig. 2b;  $F = 101.08$ ,  $P = 0.0001$ ). Consequently, the  $\beta$ -deviation was similar between regions, and even slightly higher in Missouri (Fig. 2c;  $F = 4.63$ ,  $P = 0.03$ ). Moreover, the  $\beta$ -deviations were strongly positive in both forests, reflecting strong intraspecific aggregation of most species (Fig. 3).

To disentangle whether intraspecific aggregation may have resulted from dispersal limitation, environmental filtering or a combination of both processes, we examined the extent to which  $\beta$ -diversity varied across environmental and spatial gradients within each network of sites. The total amount of variation in the  $\beta$ -deviations explained by the combination of environmental and spatial variables was similar in the two regions (bootstrap test of combined fractions,  $P = 0.67$ ; Fig. 4a). The unexplained variation in observed  $\beta$ -diversity was high, and ranged from 68 to 75% in Missouri and Bolivia respectively. After accounting for sampling from the species pool, however, the unexplained variation decreased in both regions (53–59%) (Fig. 4a).

Although  $\beta$ -diversity was similarly non-random among forest communities within Bolivia and Missouri, reflecting a high degree of intraspecific aggregation in both regions (Fig. 3), the relative importance of environmental and spatial variables differed between regions (Fig. 4b). Spatial variables explained a larger fraction of the



**Figure 4**  $\beta$ -diversity explained by environmental and spatial variables in Bolivia and Missouri. (a) Total variation in observed  $\beta$ -diversity (Bray–Curtis dissimilarity) and deviations from the null-model ( $\beta$ -deviation) explained by the full redundancy analysis model. The arrows indicate the increase in the total variation explained in each region after accounting for random sampling effects. (b) Variation in observed  $\beta$ -diversity and  $\beta$ -deviations explained by environmental and spatial variables after forward-model selection. Spatially structured environmental variables explained a negligible fraction of observed  $\beta$ -diversity and  $\beta$ -deviations (0.1–1.4% in Bolivia and Missouri respectively; not visible in figure). Note the difference in the scale of the y-axis in (a) and (b). Environmental and spatial variables are listed in Table S1.

$\beta$ -deviations in Bolivia (bootstrap test of spatial fractions,  $P = 0.001$ ), whereas environmental variables explained a larger fraction of the  $\beta$ -deviations in Missouri (bootstrap test of environmental fractions,  $P = 0.003$ ) (Fig. 4b). The relative importance of different environmental variables also varied between regions. Soil (e.g. pH) and topographic (e.g. elevation) variables explained  $\beta$ -deviations in both regions (Table S1). In contrast, after controlling for elevation, climate variables explained  $\beta$ -deviations in Bolivia but not in Missouri (Table S1). In both regions, spatially structured environmental variables explained a negligible fraction of the  $\beta$ -deviations (0.1–1.4% in Bolivia and Missouri respectively). Similar results were obtained for observed  $\beta$ -diversity (Fig. 4b).

## DISCUSSION

Our results do not support the hypothesis that similar assembly mechanisms give rise to similar patterns of  $\beta$ -diversity in low- and high-diversity forests. Although biogeographical and evolutionary processes that determine the size of the regional species pool strongly influence large-scale gradients of  $\beta$ -diversity (Kraft *et al.* 2011; Cáceres *et al.* 2012), we show that this does not imply that local ecological processes operate in a consistent way in low- and high-diversity regions. Our results indicate that although both forests were similar in their overall structure (Figs 2 and 3), different mechanisms appear to underlie these emergent patterns (Fig. 4), indicating a shift in the relative importance of community assembly mechanisms between these largely divergent forest types. Specifically, among temperate forest plots spanning local to intermediate spatial scales (0.05–82 km), we found that environmental variables explained a larger proportion of the variation in  $\beta$ -deviations than spatial variables, whereas spatial variables had a stronger influence on  $\beta$ -deviations in tropical plots. By explicitly comparing  $\beta$ -diversity while controlling for differences in species pools using spatially extensive networks of forest plots, our study provides some of the first direct evidence that dissimilar ecological mechanisms underlie community assembly in temperate and tropical forests.

Even though most previous studies have not been able to directly compare the relative importance of environmental vs. spatial controls on community composition between high- and low-diversity regions, some of the variable results observed in other studies parallel our findings. For example, Gilbert & Lechowicz (2004) found a stronger influence of environment relative to space on  $\beta$ -diversity at local scales (0.1–3.5 km) in a relatively low-diversity temperate forest understory, whereas Condit *et al.* (2002) found that a purely spatial model of community assembly predicted observed  $\beta$ -diversity at intermediate scales (e.g. 0.5–50 km) in tropical tree communities. Similarly, in a global comparison of stem-mapped forest plots (25–50 ha), Cáceres *et al.* (2012) found that spatial factors explained more variation in local  $\beta$ -diversity in the tropical-forest plot with the largest species pool compared with the temperate-forest plot with the smallest species pool, and among all plots, the variation explained by spatial factors showed a negative, but non-significant relationship with latitude.

Biogeographical comparisons of  $\beta$ -diversity across environmental gradients may be strongly influenced by the degree of environmental heterogeneity within regions. Among tree communities, for example,  $\beta$ -diversity may be positively correlated with topographic heterogeneity within communities (Cáceres *et al.* 2012). To minimise the influence of coarse-scale environmental heterogeneity on our results, we compared  $\beta$ -diversity among plots that span a similar range of elevations and geographical distances in the two regions. Even so, the stronger environmental correlations in Missouri relative to Bolivia could reflect stronger environmental gradients in Missouri, assuming tree species in temperate and tropical regions respond similarly to the same level of environmental heterogeneity. Our analyses, however, revealed no systematic regional differences in variances across the 25 environmental variables measured in both regions (e.g. ~50% of the variances were larger in Bolivia; Fig. S4). Moreover, using a multivariate analysis, we found that overall environmental variation was larger in Bolivia than in Missouri (bootstrap test for homogeneity of covariance matrices,  $P = 0.001$ ; Fig. S5), suggesting that our analyses conservatively estimated differences in the strength of environmental correlations between the two regions.

Although caution is needed when using variation partitioning alone to evaluate the strength of specific assembly processes (Smith & Lundholm 2010; Stegen & Hurlbert 2011), our results are consistent with the hypothesis that dispersal limitation has a strong influence in species-rich communities that harbour extremely large numbers of rare species (Hurtt & Pacala 1995; Hubbell *et al.* 1999; Hubbell 2001). Even though environmental gradients such as soil resources play an important role in tropical tree community assembly (e.g. Tuomisto *et al.* 2003; John *et al.* 2007; Table S1), especially at large spatial scales (Higgins *et al.* 2011), pervasive dispersal limitation will reduce the likelihood that many rare species reach all suitable habitats (Hubbell *et al.* 1999), resulting in strong intraspecific aggregation (Condit *et al.* 2000) (Fig. 3). At local scales (e.g. < 0.5 km), for example, seeds of most tropical tree species often fail to reach most local sites within a community (Clark *et al.* 1999; Hubbell *et al.* 1999) and poorly dispersed tree species are often more spatially aggregated than well-dispersed species (Condit *et al.* 2000). Tree species in temperate forests, in contrast, are relatively more common than in the tropics (Pitman *et al.* 2001; Gilbert *et al.* 2010). Consequently, intraspecific aggregation in temperate tree communities may be influenced more by environmental filtering (Gilbert & Lechowicz 2004; Qian & Ricklefs 2007; Gilbert *et al.* 2010).

Unexplained variation in  $\beta$ -diversity reflects a combination of local stochastic processes underlying community assembly (e.g. ecological drift; Cottenie 2005; Legendre *et al.* 2009), regional sampling effects due to variation in the sizes of species pools (Chase & Myers 2011; Kraft *et al.* 2011; Cáceres *et al.* 2012) and unmeasured environmental and spatial variables (Borcard *et al.* 2004). Initially, we found that a large proportion of the variance was unexplained by measured environmental and spatial variables, and that this proportion was higher in Bolivia than in Missouri. After accounting for the regional sampling effect with our null model, however, we found that explained variation increased in both regions, but with a larger increase in explained variation in Bolivia relative to Missouri (Fig. 4, Fig. S3). Collectively, these results suggest that raw comparisons of observed  $\beta$ -diversity among regions with different species pools may overestimate the overall importance of stochastic processes relative to environmental or spatial factors, particularly in tropical regions with large species pools.

We conclude that differences in the size of the species pool alone cannot account for differences in  $\beta$ -diversity between temperate and tropical forests (Kraft *et al.* 2011). Instead, our results suggest that in hyper-diverse regions such as tropical forests, intraspecific aggregation leading to high  $\beta$ -diversity reflects strong dispersal limitation, whereas in lower diversity forests with fewer rare species, aggregation is more strongly influenced by species sorting across environmental gradients. Biogeographical differences in the strength of these aggregation mechanisms, as well as local biotic interactions, are often invoked to explain large-scale diversity gradients (Harms *et al.* 2000; Dyer *et al.* 2007; Qian & Ricklefs 2007; Schemske *et al.* 2009; Chisholm & Pacala 2011; Freestone & Osman 2011; Johnson *et al.* 2012), but often without explicit consideration of how regional species pools and local ecological mechanisms interactively shape gradients of  $\beta$ -diversity. By simultaneously disentangling regional, environmental and spatial influences on  $\beta$ -diversity, our study suggests that biogeographical variation in community assembly mechanisms underlie some of the most striking differences in biodiversity observed across the planet.

## ACKNOWLEDGEMENTS

We thank the *Dirección General de Biodiversidad*, the Bolivian Park Service (SERNAP), the Madidi National Park and local communities for permits, access and collaboration in Bolivia, where field work was supported by the National Science Foundation (DEB 0101775). For assistance with fieldwork in Madidi National Park, we thank Sergio Apana, Hector Cabrera, Miki Calzadilla, Leslie Cayola, Alfredo Fuentes, Juan Kuqui, Erick Makuapa, Gilder Makuapa, Carla Maldonado, Tatiana Miranda, Diego de la Quintana and Jhonny Sevillano. For permits, access and assistance in Missouri, we thank Missouri State Parks, Reis Biological Station (Saint Louis University), Tyson Research Center (Washington University), Travis Mohrman, Merrill Rudd and Loren Sackett. For discussions, ideas and comments, we thank Brian Allan, Amber Burgett, Kerri Crawford, Simon Hart, Allen Hurlbert, Nathan Kraft, Manuel Macía, Emma Moran, Eleanor Pardini, Kristin Powell, Robert Ricklefs, Andrew Rypel, Matthew Schuler, Kevin Smith, Alexander Strauss, Sebastian Tello, Mark Vellend, Lauren Woods and the Beta-diversity Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant EF-0553768), the University of California, Santa Barbara and the State of California. We thank the editor and anonymous referees for helpful comments on the manuscript. Financial support for J.A.M. was provided by Washington University's Tyson Research Center.

## AUTHORSHIP

J.A.M., J.M.C., I.J. and P.M.J. designed the study; A.A.M., J.A.M., N.P.Z. and R.S. collected data; I.J. and J.A.M. analysed the data; J.A.M. wrote the first draft of the manuscript; J.M.C., I.J. and P.M.J. contributed substantially to revisions.

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Editor, Howard Cornell

Manuscript received 12 June 2012

First decision made 17 July 2012

Manuscript accepted 23 September 2012