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Regional and historical effects on the spatial distribution of Neotropical trees

by

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To my nephew, Matías

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CONTENTS

ABSTRACT

Regional and historical processes influence the present configuration of Neotropical tree floras. At the local scale, species assemblages depend on local conditions and the dispersal of propagules from surrounding regions. In turn, the biotic composition of these source regions is shaped by processes taking place at broad temporal and spatial scales such as speciation, extinction, and biotic interchange, as well as changes in the physiography and climate of the regions. This dissertation seeks to understand the effects of regional and historical processes on the diversity and spatial distribution of Neotropical tree species by examining their current distributions in the context of historic climate and physiography.

In *chapter 1*, I investigate regional enrichment of local species assemblages by testing two contrasting hypotheses: (1) that local species assemblages are enriched by unfiltered species pools, which are composed of all species that can disperse to a locality, regardless of the suitability of the local environment; (2) that local species assemblages are enriched by filtered pools, which are composed of all species that can disperse into a locality from similar environments. I found that Neotropical species assemblages are enriched by unfiltered species pools. This result suggests that populations of many species are decreasing locally at any given time, but can be rescued by propagules arriving from the surrounding region.

In *chapter 2*, I explore a hypothesis proposing two major legacies of the Great American Biotic Interchange (GABI) on Central American lowland and montane tree floras: (1) A major contrast in plant family composition between lowland and montane tree floras; (2) Lowland tree floras form a nested gradient of species diversity from the Darien (east) to the Tehuantepec region (west), whereas montane tree floras exhibit a nested gradient of species diversity running in the opposite direction. I found marked differences in the representation of families between lowland and montane tree floras, consistent with the first GABI legacy described above. However, lowland floras do not exhibit the hypothesized GABI legacy: Costa Rican lowland tree floras do not resemble more closely Darien floras than Tehuantepec floras. Moreover, the spatial structure of montane floras is opposite to the expected pattern: Costa Rican montane tree floras more closely resemble montane floras to the east, in the Darien region of eastern Panama, than to the west, in the Tehuantepec region of southern Mexico. These results suggest that the movement of species between the lowlands of Central and South America may have been too fast to leave any enduring spatial legacy and that lineages that occur in South

American montane floras are more important in Central American montane floras than previously thought.

In *chapter 3*, I focus on the effects of the Last Glacial Maximum (LGM) on the distribution of palms (Arecaceae) across Neotropical lowland moist forest, wet forest, and rainforest, collectively known as humid-to-superhumid forest. In particular, I explore the hypothesis of postglacial migration lags, which states that due to the effects of past glaciations species do not occupy all climatically suitable areas. To investigate this hypothesis I addressed the following questions: (1) Are there palm species restricted to climates suitable for tropical lowland humid-to-superhumid forest? (2) Did climate suitable for this forest expand to new areas since the LGM? And, (3) Do palm species occur more frequently in areas with stable climates, suitable for humid-to-superhumid forest, than in areas where climate became suitable for this forest after the LGM? I found that the LGM did not have a strong effect on the distribution of palm species. On one hand, a relatively small fraction of the palms species occurring in climates suitable for lowland humid-to-superhumid forest are restricted to these climates (196 out of 501 species); moreover, paleoclimate estimates based on three circulation models suggest that most of the area that currently has climate suitable for lowland humid-to-superhumid forest also had climate suitable for this forest at the LGM (88 - 99%). Thus, palms restricted to lowland humid-to-superhumid forest had little opportunity to experience postglacial migration lags. However, the distributions of some palm species, among those restricted to areas suitable for lowland humid-to-superhumid forest, tend to exclude areas where climate became suitable for humid-to-superhumid forest only after the LGM. Thus, despite the little opportunity, palms seem to exhibit postglacial migration lags.

This dissertation is based on analyses of large datasets documenting broad-scale geographic variation in species occurrences and environmental conditions. Yet, despite the substantial size of these datasets, assessments of Neotropical plant diversity patterns, and the processes that determine such patterns, are still limited by incomplete information on the current geographic distribution of species. It is important to adopt approaches that recognize and attempt to account for this deficiency, known as the “Wallacean Shortfall,” when analyzing currently available data. Each of the three chapters in this dissertation adopts such approaches to provide significant insight into the degree to which regional and historical events have shaped the present distributions of Neotropical tree floras. They illustrate how consideration of processes operating at different spatial scales (regional, local) in particular historical contexts contributes to a holistic understanding of current patterns and dynamics of species distributions, which in turn serves as the foundation for efforts directed at the conservation of biodiversity.

RESUMEN

Los procesos regionales e históricos influyen en la configuración espacial actual de las floras de árboles neotropicales. A una escala local, los ensambles de especies dependen de las condiciones locales y la dispersión de propágulos de las regiones circundantes. A su vez, la composición biótica de estas regiones está conformada por procesos que tienen lugar a escalas temporales y espaciales amplias, como la especiación, la extinción y el intercambio biótico, así como los cambios en la fisiografía y el clima de las regiones. Esta investigación busca comprender como los procesos regionales e históricos afectan la diversidad y distribución espacial de las especies de árboles neotropicales.

En el *capítulo 1*, se investigó el enriquecimiento regional de los conjuntos de especies locales poniendo a prueba dos hipótesis: (1) las comunidades locales se enriquecen con grupos de especies que no son filtradas por el ambiente, es decir que se componen de todas las especies que pueden dispersarse a una localidad, independientemente de la idoneidad de el ambiente local; (2) las comunidades locales se enriquecen por especies filtradas, es decir que se componen de todas las especies que pueden dispersarse en una localidad desde ambientes similares a esta. Se encontró, que las comunidades locales de arboles neotropicales se enriquecen por especies sin filtrar. Este resultado sugiere que las poblaciones locales de algunas especies disminuyen en un momento dado, pero estas pueden ser rescatadas por propágulos que llegan de la región circundante.

En el *capítulo 2*, se exploró una hipótesis que propone dos legados que dejo el Gran Intercambio Biótico Americano (GABI) en las floras de árboles de tierras bajas y montañosas de América Central: (1) Diferente composición de familias de plantas entre las floras de árboles de tierras bajas y montanas; (2) Las floras de árboles de tierras bajas forman un gradiente anidado de diversidad de especies desde el Darién (este) hasta la región de Tehuantepec (oeste), mientras que las floras de árboles montanos exhiben un gradiente anidado de diversidad de especies en la dirección opuesta. Se encontró marcadas diferencias en la representación de las familias entre floras de árboles de tierras bajas y montanas, lo cual esta deacuerdo con el primer legado descrito . Sin embargo, las floras de tierras bajas no exhiben el legado hipotético de GABI: las floras de árboles de tierras bajas de Costa Rica no se parecen más a las floras de Darién que a las floras de Tehuantepec. Además, la estructura espacial de las floras montanas es opuesta al patrón esperado: las floras de árboles montanos costarricenses se parecen más a las floras montanas al este, en la región del Darién del este de Panamá, que al oeste, en la región de

Tehuantepec del sur de México. Estos resultados sugieren que el movimiento de especies entre las tierras bajas de América Central y del Sur pudo haber sido demasiado rápido para dejar un legado espacial perdurable, y que los linajes en las floras montanas de América del Sur son más importantes en las floras montanas de América Central.

El *capítulo 3*, analiza los efectos del Último Máximo Glacial (UMG) en la distribución actual de las palmeras (Arecaceae) de bosques húmedos a superhúmedos tropicales de tierras bajas. En particular, se exploró la hipótesis de los retrasos en la migración posglacial, que establece que debido a los efectos de las glaciaciones pasadas, las especies no ocupan todas las áreas climáticamente adecuadas. Para investigar esta hipótesis, se analizó las siguientes preguntas: (1) ¿Hay especies de palmeras restringidas a climas adecuados de bosques húmedos a superhúmedos tropicales de tierras bajas? (2) ¿Se expandió el clima adecuado para este bosque a nuevas áreas desde el UMG? Y, (3) ¿Ocurren las especies de palmeras con mayor frecuencia en áreas con climas estables adecuados para bosques húmedos a superhúmedos tropicales de tierras bajas, que en áreas donde el clima se volvió adecuado para este bosque después de la UMG? Se encontró que el UMG no tuvo un fuerte efecto en la distribución de las especies de palmeras. Por un lado, una fracción relativamente pequeña de las especies de palmeras que se encuentran en climas adecuados para bosques húmedos a superhúmedos tropicales de tierras bajas están restringidas a estos climas (196 de 501 especies); Además, las estimaciones paleoclimáticas basadas en los tres modelos de circulación climatica usados, sugieren que la mayor parte del área que actualmente tiene un clima adecuado para bosques húmedos a superhúmedos tropicales de tierras bajas también tenía un clima adecuado para este bosque en el UMG (88 - 99%). Por lo tanto, las palmeras restringidas a bosques de tierras bajas húmedas a superhúmedas tuvieron pocas oportunidades de experimentar retrasos de migración posglacial. Sin embargo, las distribuciones de algunas especies de palmeras, entre aquellas restringidas a áreas adecuadas para bosques húmedos a superhúmedos tropicales de tierras bajas, tienden a excluir áreas donde el clima se volvió adecuado para estos bosques solo después de la UMG. Por lo tanto, a pesar de las pocas oportunidades, las palmas parecen exhibir retrasos en su migración despues de la ultima glaciacion.

Esta investigacion se basa en análisis de conjuntos de datos grandes que documentan la variación geográfica de las especies de arboles a una gran escala. Sin embargo, a pesar del tamaño sustancial de estos conjuntos de datos, las evaluaciones de los patrones de diversidad de plantas neotropicales y los procesos que determinan dichos patrones aún están limitados por la información incompleta sobre la distribución geográfica actual de las especies. Es importante adoptar enfoques que reconozcan e intenten identificar esta deficiencia, conocida como el "Wallacean shortfall", al analizar los datos disponibles actualmente. Cada uno de los tres capítulos de esta disertación adopta dichos enfoques para proporcionar una comprensión significativa del grado en que los eventos regionales e históricos han afectado las distribuciones actuales de las floras de árboles neotropicales. Los tres capítulos tambien ilustran cómo la consideración de los procesos que operan a diferentes escalas espaciales (regionales, locales) en contextos históricos particulares contribuye a una comprensión holística sobre los patrones actuales y la dinámica de las distribuciones de especies, que a su vez sirve de base para los esfuerzos dirigidos a la conservación de la biodiversidad.

CHAPTER 1.

Enrichment of local tree assemblages by unfiltered regional species pools in Neotropical forests

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ABSTRACT

Regional enrichment of local species assemblages occurs when the number of species at a given locality depends on diversity in the surrounding region. Here we examine two hypotheses with contrasting definitions of regional species pools, i.e., (i) all species that can disperse to a locality, regardless of the suitability of the local environment (unfiltered pool hypothesis); ii) all species that can disperse into a locality from similar environments (filtered pool hypothesis). For each hypothesis, we predicted the relationship between local assemblages and regional species pools for species richness and composition. We tested these predictions using a large dataset of local tree species assemblages from Costa Rica and regional species pools based on specimen records from Costa Rica, Panama, and Nicaragua. We found empirical support for all predictions derived from the unfiltered pool hypothesis, but not from the filtered pool hypothesis. These results question the seemingly common assumption that local assemblages reflect filtered regional species pools.

KEYWORDS: dispersion field, diversity anomalies, environmental filtering, regional effects, species richness, species composition.

INTRODUCTION

Regional enrichment of local species assemblages is said to occur when the number of species present at a given locality depends on the number of species within the larger surrounding region (Ricklefs 1987; Freestone and Harrison 2006; White and Hurlbert 2010). This relationship reflects the dispersal of propagules from the region to the locality (Harrison and Cornell 2008), which adds new species and prevents local extinction of existing populations (Rosenzweig 1995). In this way, regional diversity, itself determined by broad-scale processes such as speciation (Mittelbach and Schemske 2015; Schluter and Pennell 2017) and continental biotic interchange (Vermeij 1991; Donoghue 2008), may influence the diversity of local species assemblages. Thus, other factors (e.g., environment) being equal, sites embedded in regions with a high (low) species number would tend to display high (low) local species richness. These regional effects are known as "diversity anomalies" (Ricklefs and Latham 1993; Ricklefs 2004; Jiménez and Ricklefs 2014), which are deviations from the relationship between local species richness and the physical environment (Ricklefs and He 2016). If regional species pools enrich local species assemblages, such deviations should be explained by variation in the richness of regional species pools.

Crucial in this context is the idea of a regional species pool, which can be thought of as the set of species that potentially could colonize a particular locality (Srivastava 1999; Cornell and Harrison 2014). Even though this concept has played an important role in the development of community ecology, ecologists have found little consensus regarding its operational definition (Carstensen et al. 2013; Cornell and Harrison 2014). Regional species pools are mostly defined without regard to the processes that link regional and local species assemblages (Srivastava 1999; Loreau 2000; Lessard et al. 2012*a*; Carstensen et al. 2013; Cornell and Harrison 2014). Often they are simply based on the geographical coverage of the data analyzed (e.g., species lists delimited by habitat, geopolitical units, or areas delimited by natural geography). Yet, defining species pools in a manner that reflects relevant evolutionary and ecological processes is essential for understanding the regional enrichment of local species assemblages and, more generally, the dynamics of species assemblages at different temporal and spatial scales, including how they might respond to ongoing change in the physical environment (McGill 2011; Lessard et al. 2012*a*; Carstensen et al. 2013; Cornell and Harrison 2014).

Given uncertainty about an operational definition of the regional species pool, further understanding of regional enrichment of local species assemblages may require empirical examination of hypotheses that assume contrasting definitions. Previous analyses suggest two general working hypotheses. The first is enrichment by “unfiltered” regional species pools, which assumes that a regional species pool includes all the species that can disperse to a locality, regardless of the suitability of the local environment for the dispersing propagules. Under this hypothesis, the regional species pool influences the local community via mass effects (Shmida and Wilson 1985). Therefore, sink species, which cannot maintain populations locally, may contribute importantly to overall local community composition (Shmida and Wilson 1985; White and Hurlbert 2010). Sink species persist in a local community, despite a negative local balance between birth and death rates, because of immigrants (Pulliam 2000). This unfiltered pool hypothesis is consistent with the generally observed higher slopes of species-area relationships in archipelagos than within continents, where local extinction is more readily compensated by the influence of source populations (Rosenzweig 1995). Unfiltered regional species pools have been featured in several studies (see Cornell and Harrison 2014 for a review).

The second working hypothesis is enrichment by “filtered” regional species pools. Accordingly, a regional species pool includes all the species that can disperse into a locality from similar environments. Thus, the number of species occupying a local area of habitat should reflect the number of species occurring in that habitat in the surrounding area (Zobel 1997). For example, the regional species pool for a local community in a wetland habitat would be the species that could potentially disperse into that local community from surrounding wetlands (Pärtel et al. 1996, 2011). Under this hypothesis, not only dispersal but also environment (habitat) limit local species richness. Filtered regional species pools have been used broadly in ecology (see Cornell and Harrison 2014 for a review), and have even been regarded *a priori* as conceptually superior to unfiltered pools (Srivastava 1999; Cornell and Harrison 2014). Yet, we are unaware of empirical tests comparing the extent to which filtered and unfiltered regional pools explain variation in the species richness of local assemblages.

These two hypotheses provide two contrasting predictions by which one might evaluate their merit. The first prediction addresses the relationship between the species richness of local assemblages and the richness of regional species pools, after accounting for effects of the local environment on local richness. The unfiltered enrichment hypothesis predicts that deviations from the relationship between local species richness and variables representing the local environment are positively related to the richness of unfiltered regional species pools. In contrast, the filtered enrichment hypothesis predicts that such deviations are positively related to the richness of filtered regional species pools.

The second prediction focuses on the relationship between the composition of local species assemblages and regional species pools, after accounting for the effect of the local environment on local species composition. To the extent that regional enrichment of local species assemblages occurs, the species found in a local community are a sample of the respective regional species pool (McGill 2011; Cornell and Harrison 2014) and, therefore, local and regional species composition should be related. Thus, the unfiltered and filtered hypotheses predict that local species composition should be related to the species composition of the unfiltered and filtered regional species pools, respectively.

Here, we evaluate these two predictions to test the hypotheses of enrichment by unfiltered and filtered regional species pools. We used a dataset for tree species assemblages on 45 local forest plots in Costa Rica (Holdridge et al. 1971) and estimated regional species pools based on 135,822 herbarium specimen records from the Tropicos database (http://www.tropicos.org/), which extensively documents the tree floras of Costa Rica, Panama, and Nicaragua (Davidse et al. 2012, 2015, Hammel et al. 2003a, 2003b, 2004, 2007, 2010, Stevens et al. 2001). We represented each hypothesis by several models of regional species pools and examined each model in terms of the two predictions.

METHODS

Local species assemblages

We used plant species lists (presence/absence data) from 45 ca. 0.3-ha local sites widely distributed across Costa Rica (Figure 1) and summarized by Holdridge et al. (1971). Each site was located in relatively undisturbed, mature, natural forest, including dry forest, montane forest, and lowland rainforest. All plant individuals that reached a diameter at breast height (DBH) ≥ 10 cm (shrubs, lianas, tree palms, and tree ferns) were documented. We standardized species taxonomy using The Taxonomic Name Resolution Service (TNRS, Boyle et al. 2013).

We included only tree species in our analyses, because species with the same growth form presumably respond similarly to changes in their physical and biological environments (Duckworth et al. 2000; Voigt et al. 2007). Thus, we removed 28 species of shrubs and lianas from the data set, following Engerman et al.'s (2016) data on plant growth form for the New World in conjunction with a number of local floras (Davidse et al. 2012, 2015, Hammel et al. 2003a, 2003b, 2004, 2007, 2010, Stevens et al. 2001). Trees were defined as a woody plants rooted in the soil, usually with a single, erect, and persistent trunk of at least 10 cm of DBH and 5 meters height (Engemann et al. 2016). Under this definition, tree palms and tree ferns are considered trees, and were included in the data set representing 559 species distributed in 336 genera and 104 families. We calculated local species richness as the number of species in each site (Table S1).

Regional species pools models

We estimated regional species pools based on herbarium specimen records from Costa Rica, Panama, and Nicaragua, accessed from the Tropicos database during September 2017. All families and genera that do not contain trees (as defined above) were removed from the dataset. We considered only specimen records that were identified to species. The data set included ~135,000 herbarium specimen records (Figure 1; data will be uploaded to Dryad upon acceptance) of 3,736 tree species distributed in 144 families and 849 genera.

We used various models of regional species pools to represent each of the two working hypotheses of interest. The hypothesis of enrichment by unfiltered regional pools, which defines the regional species pool as all the species that can disperse to a locality regardless of local habitat suitability, was represented by four models: two "neighborhood" models and two "dispersion field" models (Table 1). The hypothesis of enrichment via filtered regional pools was represented by two models: a forest-type model and an elevation-band model (Table 1).

Neighborhood regional pool models− We developed two versions of the neighborhood model. The first included all species occurring within a 7,854-km^2 (50-km radius) circular neighborhood; the second included all species within a 1,963-km^2 (25-km radius) circular neighborhood. Both regional pools were centered at the geographical coordinates of a particular local site (Figure 2a and 2b). The 50-km and 25-km radii defining these two regional pool models correspond to the distances that the geographic boundary of a tree species could extend during ~602 and ~301 years, respectively, if the median displacement rate were 0.083 km/yr^{-1}. This is the estimated median rate of displacement for geographic ranges of tree species, based on reconstructed migration rates during the Holocene within both Temperate and Tropical areas (Settele et al. 2014). Thus, the neighborhood regional pool models are based on explicit reference to dispersal capabilities of organisms during ecological time, as suggested by Cornell and Harrison (2014).

Dispersion-field regional pool models− Following Graves and Rahbeck (2005), we constructed a dispersion field for each local site by overlapping the geographic ranges of all the species at the site. Dispersion fields provide asymmetric, unique spatial diagrams for each local site, which may reflect the regional source pool for local assemblages (Graves and Rahbek 2005; Carstensen et al. 2013). The rationale for dispersion fields is based on the idea that "if a site shares any species with the focal site, dispersal between the sites should also potentially be possible for other species" (Carstensen et al. 2013). However, one of the pitfalls of using dispersion fields is the impact that widespread species can have on their extent. To remove the impact of such species, we included only sites that shared at least 75% (Figure 2c), in one model, or 25% (Figure 2d) in a second model, of the species at the local site, to delineate the dispersion field (Carstensen et al. 2013). Then, the regional species pool was defined as all the species occurring within the contours of the dispersion field.

To delineate the dispersion fields we used the extent of occurrence of each of the species at each local site. Extent of occurrence is a measure of the geographic boundaries of a species and not of its occupancy within those boundaries (Gaston and Fuller 2009). We used all the specimen records available in the Tropicos database to determine the extent of occurrence of each species.

Forest type regional pool model– This model defined the regional species pool as all species occurring within the forest type where the site was located, and within 50 km of the site. Forest types for each site were defined according to the map of terrestrial ecoregions of the world (Olson et al. 2001) (Figure 2e).

Elevational band regional pool model– This model defined the regional species pool as all species within a 300-m elevational band centered on the elevation of a particular site, and within 50 km from the site (Figure 2f).

For all these models, regional species richness was estimated using rarefaction (Gotelli and Colwell 2001) to correct for differences in the number of specimen records available to estimate regional species pools. In particular, we repeatedly and randomly subsampled 283 specimen records from the total set of specimen records in a given regional species pool. The size of these subsamples equaled the minimum number of specimen records across all regional pools. We calculated species richness for each of 1,000 subsamples from a regional species pool and then calculated mean richness across subsamples (Table S2). Analyses based on larger subsamples yielded similar results.

Tests of predictions

We examined the relative merits of the hypotheses of enrichment by unfiltered and filtered regional pools by testing two predictions. To test each prediction, we represented each hypothesis by several *a priori* statistical models. In turn, each *a priori* statistical model was based on a single model of the regional species pool (described above). Thus, the hypothesis of enrichment by unfiltered regional pools was represented by four statistical models and the hypothesis of enrichment by filtered regional pools was represented by two statistical models (Table 1).

The first prediction regards the relationship between the species richness of local assemblages and that of regional species pools, after accounting for effects of the environmental variables on local richness. We used linear regression models where local species richness was the response variable, and regional species richness (according to a regional pool model), local plot area, and three variables describing the local environment were the explanatory variables. The first environmental factor was mean annual precipitation (Table S1). The second was represented by the first axis of a principal components analysis (PCA) based on elevation, mean annual temperature, and potential evapotranspiration (Table S1). This PCA axis accounted for 99% of the variation in the correlation matrix (Figure S1). Holdridge et al. (1971) estimated all the climate variables that we used here, based on data from the closest of 23 meteorological stations to each site. In fact, sites were chosen to be close to long-term meteorological stations (see Holdridge et al. 1971). Finally, the third explanatory variable was the first component of a PCA accounting for 56% of the variation in five variables describing soil properties within an area of 1 m^2 to a depth of 200 cm, including pH and concentration of K, Ca, Na, Mg, and P (Table S1, Figure S2, Holdridge et al 1971). Because concentrations of K, Na and P exhibited high kurtosis and skewness (Table S3), they were log-transformed before performing the PCA.

To examine multicollinearity among the variables, we used Pearson's correlations between predictor variables to assess multicollinearity. Only one pair of predictors exceeded the threshold for collinearity ($r \geq 0.7$; Dormann et al. 2013; Figure S2). We decided to keep both predictors and interpret the results with caution, because they only affect one of the regression models (dispersion field using 75% of species shared). We also examined the assumption of independent regression residuals by testing for spatial autocorrelation using a permutation test for Moran's *I* for each regression model (Legendre and Legendre 2012). No spatial autocorrelation was revealed by these tests (maximum Moran's $I = 0.16$, $p = 0.86$).

The second prediction concerns the relationship between the species composition of local assemblages and that of regional pools, after accounting for effects of the local environment. We tested this prediction using two approaches (Legendre et al. 2008). First, we performed a multiple regression on distance matrices to test whether species turnover (beta diversity) between local assemblages was positively related to species turnover between their respective regional species pools, after accounting for effects of differences in local environment on local species turnover. We evaluated the statistical significance of the regression coefficients using 1,000 permutations of the response variable (Legendre and Legendre 2012). The response in this analysis was species beta diversity between pairs of local species assemblages, measured as a dissimilarity incidence-based (Jaccard) metric (Legendre and Legendre 2012). The explanatory variables included species beta diversity between pairs of regional pools, quantified by Jaccard metric, and environmental dissimilarity between pairs of sites measured by the Euclidean distance based on three environmental variables (described above): i) the largest principal component of variables describing a temperature gradient (Figure S1); ii) annual precipitation; and iii) the largest principal component of variables describing soil properties (Figure S2).

To account for differences in the number of specimen records available to estimate regional species pools, we estimated regional beta diversity using rarefaction by randomly subsampling 283 specimen records (the minimum across all regional pools) for each regional pool model 1,000 times. Each time, a presence/absence species composition matrix was created to calculate beta diversity (Jaccard metric) among regional species pool pairs. In turn, these values were used to calculate a mean value for regional beta diversity for each regional species pool pair. Additionally, we estimated regional beta diversity based on higher numbers of specimen records when possible.

Second, we used a distance-based redundancy analysis (dbRDA, Legendre and Anderson 1999) to determine whether local species composition was related to the species composition of regional pools, after accounting for the effect of the local environment on local species composition. The response variables in this analysis were the 44 ordination axes representing the species composition of local species assemblages. The explanatory variables included the first two ordination axes representing the species composition of regional pools, and three variables describing the local environment (detailed above). To obtain the ordination according to species composition for local assemblages (response variable) and regional pools (explanatory variable), we performed a principal coordinates analysis (PCoA) on a matrix of species compositional dissimilarity based on a Jaccard metric. The dissimilarity matrix for regional pools was obtained through rarefaction, as explained above.

Selection of statistical models representing different hypotheses

Beyond testing the predictions set out above, we determined whether different statistical models were consistent with expected effects of local environmental variables according to theory and previous studies. We used the Akaike information criterion (AIC, Burnham and Anderson 2003) to examine empirical support for regression models used to test the first prediction. This was not possible for models used to test the second prediction, because no methods exist to calculate AIC for models based on regression of distance matrices or distance-based redundancy analysis. Therefore, in lieu of AIC values, we examined empirical support for models based on regression of distance matrices using the pseudo r^2. Likewise, we examined empirical support for dbRDA models using adjusted r^2. Admittedly, these latter assessments of model performance are not ideal (Burnham and Anderson 2003). However, given that all models have the same number of explanatory variables, and that models differ only in the identity of one variable (the variable representing a regional pool model), pseudo r^2 and adjusted r^2 values provide a reasonable assessment of the performance of models.

RESULTS

First, we tested whether species richness in local assemblages is positively related to the richness of regional species pools, as defined by each hypothesis, after accounting for effects of the local environmental variables. Only one model, representing enrichment by unfiltered regional pools, passed this test (Table 2). This was the neighborhood regional pool model defined by a 50-km radius, according to which there is a positive linear relationship between local and regional richness (Figure 3A). This model was also consistent with expected effects of local environmental variables on local richness: species richness was significantly related to the first principal component of temperature and elevation variables (Table 2), indicating a positive relationship between species richness and mean annual temperature and potential evapotranspiration, and a negative relationship between species richness and elevation (Figure S1). Similarly, species richness was positively and significantly related to the first principal component of the soil variables, although not to annual precipitation (Table 2). This model also had the highest empirical support as measured by AIC (all other models had $\Delta AIC \geq 6$, Table 2). These results held when we estimated regional species richness based on larger rarefaction subsamples (Table S4, Figure S4).

The second prediction was that local species composition is related to the species composition of the regional species pool, as defined by each hypothesis, after accounting for the effect of the local environment. We used two approaches to test this prediction. The first approach relied on distance matrix regression models. All such models representing the hypotheses of enrichment by unfiltered and filtered regional pools passed this test (Table 3, Figure 4). Moreover, all models were consistent with expected effects of differences in local environmental variables on species turnover between localities. In particular, in all models, local species turnover was positively and significantly related to differences between sites in the first principal component of variables related to mean annual temperature and elevation, the first principal component of soil variables, and annual precipitation (Table 3). However, pseudo r^2 values indicated that two models performed particularly well (Table 3). The neighborhood regional pool model defined with 25-km radii showed the highest pseudo r^2 value (0.37), exceeding by 0.06 − 0.07 all other models representing the unfiltered pool hypothesis. And, the elevation band-regional pool model had the highest pseudo r^2 value (0.39), which was 0.05 higher than the other model representing the filtered pool hypothesis. Differences in pseudo r^2 values between the best models representing each hypothesis did not seem large (0.02). These results held when we estimated regional species turnover using larger rarefaction subsamples (Table S5, Figure S5).

We used a second approach to test the second prediction, based on models of distance-based redundancy analysis (dbRDA). All dbRDA models, representing the hypotheses of enrichment by unfiltered and filtered regional pools, passed this test (Table 4). In all dbRDA models, all local environmental variables were significantly related to local species composition ($p < 0.001$, Table 4). Performance did not differ across dbRDA models, as all models explained approximately equal proportion of variation (0.22 − 0.24%, Table 4). These results held after we estimated regional species composition using larger rarefaction subsamples (Table S6).

DISCUSSION

The interplay between regional and local species assemblages is a central theme in ecology (Loreau 2000; McGill 2011; Lessard et al. 2012*a*). Our understanding of regional enrichment of local species assemblages is limited by the difficulty of defining regional species pools in biologically meaningful ways (Srivastava 1999; Carstensen et al. 2013; Cornell and Harrison 2014; Karger et al. 2016). To address this issue, we used an extensive tree survey and a comprehensive database of herbarium specimens from Central America, both of which encompass a wide range of habitats (dry forest, lowland rainforest, and montane rainforest) and elevations (0 − 3080 m), to empirically examine two hypotheses of species enrichment that assumed contrasting definitions of regional species pools: "unfiltered" and "filtered" (Table 1).

The first postulates that regional species pools include all the species that can disperse into a locality, regardless of the suitability of the local environment for the dispersing propagules. In contrast, “filtered” species pools include only species that can disperse into a locality from similar environments. We tested two predictions derived from each of these hypotheses. Our analysis supported the hypothesis that local species assemblages are influenced by "unfiltered" regional species pools, so that the number and composition of species occurring in a local site is related statistically to the number and composition of species occurring within a surrounding region of 50 km radius (Table 2, Figure 2). Below we explore implications of these findings for our understanding of the dynamics of species assemblages at different spatial scales, and examine potential caveats to our analyses.

The first prediction focused on the relationship between the species richness of local assemblages and that of regional species pools, after accounting for effects of the local environment on local richness. We found empirical support for the hypothesis of enrichment by unfiltered regional pools, but not for the hypothesis of enrichment by filtered regional pools (Table 2, Figure 3). In particular, only the neighborhood regional pool model defined with a 50-km radius (Figure 3A) was consistent with the first prediction. Previous tests of this prediction suffered from a series of shortcomings. First, the operational definition of regional species pools has been challenging for ecologists, mostly due to data limitation (Srivastava 1999; Loreau 2000; Cornell and Harrison 2014). We overcame this problem by using a well-sampled and intensively studied region (Nicaragua, Costa Rica, and Panama: Davidse et al. 2012, 2015, Hammel et al. 2003a, 2003b, 2004, 2007, 2010, Stevens et al. 2001). Second, regional species pools for different local species assemblages are not independent; indeed, because they overlap in space, they could be spatially autocorrelated, resulting in type I error (Srivastava 1999). However, our regression models did not exhibit spatial autocorrelation in the residuals, and so these models yielded valid statistical results. Third, local and regional species richness measures often are not independent (Srivastava 1999). Previous studies have estimated local and regional species richness from the same dataset, i.e., the latter as the sum of all species across all sampling locations, which could lead to spurious correlations (Srivastava 1999; Loreau 2000; Hillebrand and Blenckner 2002). Here, we used independent datasets to estimate regional and local species richness. Local species richness was estimated using species presence/absence data from 45 sites, while regional species richness was estimated separately using all tree specimen records from Costa Rica, Panama, and Nicaragua. Fourth, the statistical relationship between local and regional species richness depends on the spatial scale at which local and regional pools are defined (i.e., if the area of the local habitat is close to that of the region, then most of the species will be found in the local community, and a positive relationship between local and regional species richness would trivially reflect shared species due to extensive spatial overlap; Srivastava 1999; Loreau 2000; Hillebrand and Blenckner 2002). In our study, our local assemblages were defined to occur within areas of about 0.3 ha, which likely represents an area within which tree species in a local community can interact among themselves and potentially affect each other's abundances (Huston 1999). And, our regional species pools used different scales (i.e., the neighborhood regional pool models were defined according to 50- and 25-km radii, based on explicit dispersal abilities of trees during ecologically relevant periods of 300 – 600 years; Settele et al. 2014). Additionally, all our models were controlled for the effects of local environmental variables (soil and climatic factors), and local site area. Thus, these models should provide accurate estimates of regional enrichment (White and Hurlbert 2010).

When local and regional assemblages are defined to encompass very different spatial scales (as in our study), support for the first kind of prediction is not trivial. In these cases, a positive relationship between local and regional richness is not required. Indeed, lack of empirical support is possible, as illustrated by models that show how increasing the richness of regional species pools may have little, or no, effect on local species richness (Fox and Srivastava 2006). For example, an increase in regional species richness may be associated with a decrease in average population size across the region and, in turn, decreased propagule pressure over localities. Other models show how the number of species in a local assemblage may not exceed a level determined by local species interactions, regardless of propagule pressure from a regional species pool (Case 1990, 1991). Beyond the processes emphasized in these two examples, a wide range of potential mechanisms may prevent regional enrichment of local species assemblages (Harrison and Cornell 2008). Moreover, experimental studies show that increasing the diversity of propagules arriving at a locality does not always increase local richness (Fox et al. 2000; Shurin et al. 2000). Thus, our results, showing that only one of the models is consistent with our first prediction (i.e., the neighborhood regional pool enclosing the largest area), are biologically meaningful.

The second prediction we tested related the species composition of local assemblages to the species composition of regional pools, after accounting for effects of the local environment on local species composition. If the species occurring locally are a sample of the associated regional species pool, then local and regional species composition should be related. This is the case for all our regional species pool models: the species composition of local assemblages is strongly related to that of the species region (Table 3, 4, Figure 4). However, support for this second prediction is necessary, but not sufficient, to empirically support a given hypothesis about enrichment. In particular, local and regional species composition may be related in the absence of regional enrichment of local species assemblages (Fox et al. 2000). Therefore, although our results regarding the second prediction lend support to both hypotheses of interest, the first kind of prediction supports only the hypothesis of local enrichment via unfiltered regional pools.

Most studies that test regional enrichment of local assemblages define regional species pools as all the species that might disperse to a locality from places having similar environments, here referred to as the "filtered pool hypothesis" (see Cornell and Harrison 2014 for a review). This definition has been widely adopted because theory and previous studies emphasized that environmental conditions act as a filter that removes species lacking the traits required to persist under local conditions (Srivastava 1999; Cornell and Harrison 2014). Thus, species in the region that are poorly adapted to the local environment cannot contribute to the species richness/diversity and composition of those local communities (Keddy 1992; Belmaker and Jetz 2012). If local species assemblages are composed only of species well-adapted to the local environment, then regional species pools composed of well-adapted species will explain the variation in species richness and composition in local species assemblages. This does not seem to be the case for local species assemblages in Costa Rica, since all filtered regional species pools performed poorly in explaining variation in local species richness ($\Delta AIC \geq 6$, Table 2).

Regional enrichment of local species assemblages in Costa Rica is related to unfiltered regional pools (Table 2, Figure 2). Rosenzweig (1995) proposed that local assemblages within the mainland include two types of species: 1) "source species," which have an average net rate of reproduction sufficient to maintain positive population size because they are well-suited to the local habitat conditions, and 2) "sink species," which do not have sufficient net rates of reproduction locally to maintain a population. Sink species do, however occur intermittently in local assemblages through random colonization events, but they might fail to persist in the system if the rain of propagules from the region stops (MacArthur 1960; Magurran and Henderson 2003; Belmaker 2009). Sink species are constantly on the road to local extinction, but they can be rescued through mass effects (Shmida and Wilson 1985), meaning that the regional species pool is constantly sending propagules of these species to the local assemblage (Pulliam 2000). We suggest that this is the case for local species assemblages in Costa Rica, especially because of the heterogeneity of habitats in Costa Rica, where sink populations of a particular species could be maintained by dispersal to habitats where environmental conditions are outside of the species niche (Pulliam 2000). We believe that this insight is important to understanding the processes that shape local species assemblages; it also contrasts previous ideas about the definition of regional species pools. If sink species are more common than we previously thought, and play an important role in local assemblages, then we should rethink the operational definition of regional species pools. In particular, filtered regional species pools should not be regarded a priori as conceptually superior to unfiltered species pools (cf. Srivastava 1999; Cornell and Harrison 2014).

We found strong regional effects on local species richness and composition. However, both soil and climate variables also contribute complementarily to explaining variation in local species richness (Table 2) and composition (Table 3,4). In the case of species richness, our best model was strongly related to soil properties and temperature (Table 2). Soil properties provided the more significant effect ($p < 0.001$), which was negative, meaning that more species occur on soils with low pH and low concentrations of K, Ca, Na, Mg, and P. These results agree with previous studies across soil gradients (Huston 1980; Harrison et al. 2006) and across temperature gradients (Harrison et al. 2006; Ricklefs and He 2016). They also corroborate previous studies of plant species diversity across soil gradients (John et al. 2007; Jones et al. 2008) and climate gradients (Siefert et al. 2012). Most of these studies report a significant influence of soils, as we found in our analyses, suggesting that soil properties influence local species assemblages.

A major criticism of previous studies was uncertainty about the operational definition of the regional species pool (Srivastava 1999; Loreau 2000; Hillebrand and Blenckner 2002; Cornell and Harrison 2014). This definition is key to understanding the ecological and evolutionary processes that shape local species assemblages (Lessard et al. 2012*b*; Carstensen et al. 2013). Here, we used different definitions to test the predictions of two hypotheses (unfiltered and filtered) concerning the regional enrichment of local assemblages. We demonstrated that local assemblages in Costa Rica are enriched by unfiltered regional species pools, and that sink species, maintained by persistent immigration, might be more common than previously thought.

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FIGURE LEGENDS

Figure 1. Map of lower Central America showing the local communities (red dots) and tree specimen records (gray dots) used to estimate regional species richness. Red triangle is the reference site for Figure 2. Costa Rica lies between Nicaragua to the west and Panama to the east.

Figure 2. Regional species pool models for a given local community (red triangle) include either **A.** all species within a 50 km radii, **B.** all species within 25 km radii, **C.** all species in the dispersion field (25% of species shared), **D.** all species in the dispersion field (75% of species shared), **E.** all species within the forest type (1 = Costa Rican seasonal moist forest, 2 = Isthmian Atlantic moist forest and 3 = Talamancan Montane forest) where the site was located, and **F.** all species within a 300-m elevational band. In all six figures tree specimen records are represented by gray dots.

Figure 3. Partial regression plots for all regression models showing a linear relationship between local species richness and regional species richness after controlling for the other variables (precipitation, PC1 soil, and PC1 temperature). Regional richness was estimated by rarefaction based on 1,000 samples of 283 specimens. **A.** *Neighborhood regional pool* based on a circular area, having a radius of 50 km, centered on each local site. **B.** *Neighborhood regional pool* within a 25 km of radius around each local site. **C.** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes. **D.** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes. **E.** *Forest regional pool* based on the type of forest where the local site was located. **F.** *Elevational band regional pool* based on the elevational band where the local site was located.

Figure 4. Partial regression plots for all matrix regression models showing a relationship between local species turnover and regional species turnover after controlling for the other variables (precipitation, PC1 soil, and PC1 temperature); each gray dot represents a pair of sites. Species turnover was measured as the Jaccard dissimilarity index. Regional species turnover was estimated by rarefaction based on 1,000 samples of 283 specimens **A.** *Neighborhood regional pool* based on area of a circle, having a radius of 50 km, around each local site. **B.** *Neighborhood regional pool* the area of a 25-km radius circle around each local site. **C.** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes. **D.** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes. **E.** *Forest regional pool* based on the type of forest where the local site was found. **F.** *Elevational band regional pool* based on the elevational band where the local site was located.

Figure 1

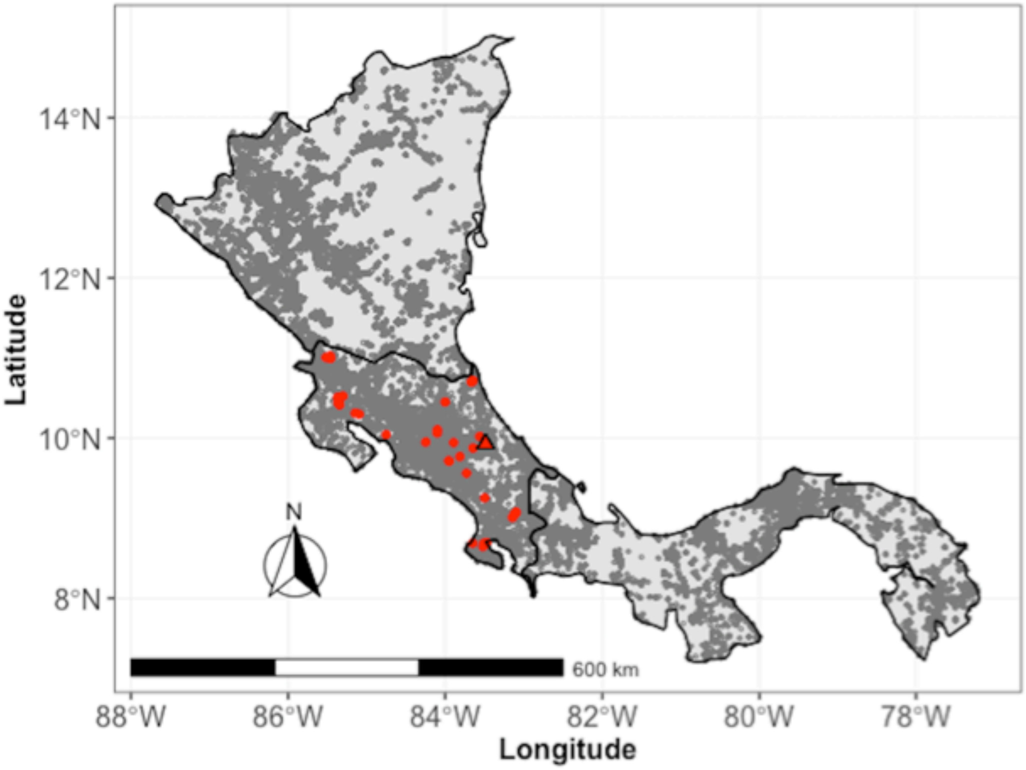

14°N
12°N
10°N
8°N
Latitude
N
600 km
88°W
86°W
84°W
82°W
80°W
78°W
Longitude

Figure 2

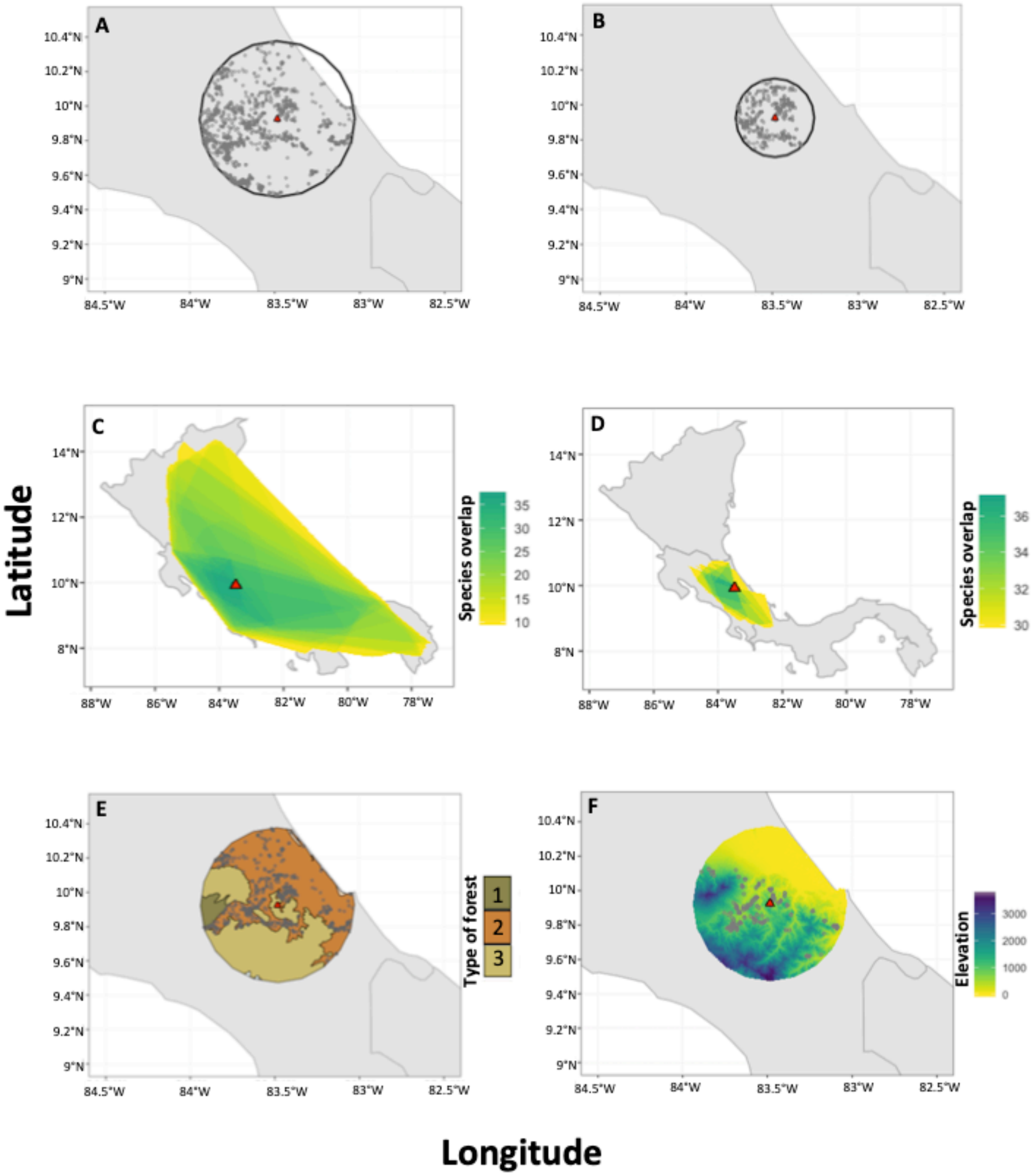

A
B
C
D
E
F
Latitude
Longitude
10.4°N
10.2°N
10°N
9.8°N
9.6°N
9.4°N
9.2°N
9°N
84.5°W
84°W
83.5°W
83°W
82.5°W
14°N
12°N
8°N
88°W
86°W
82°W
80°W
78°W
Species overlap
35
30
25
20
15
10
36
34
32
Type of forest
1
2
3
Elevation
3000
2000
1000
0

Figure 3

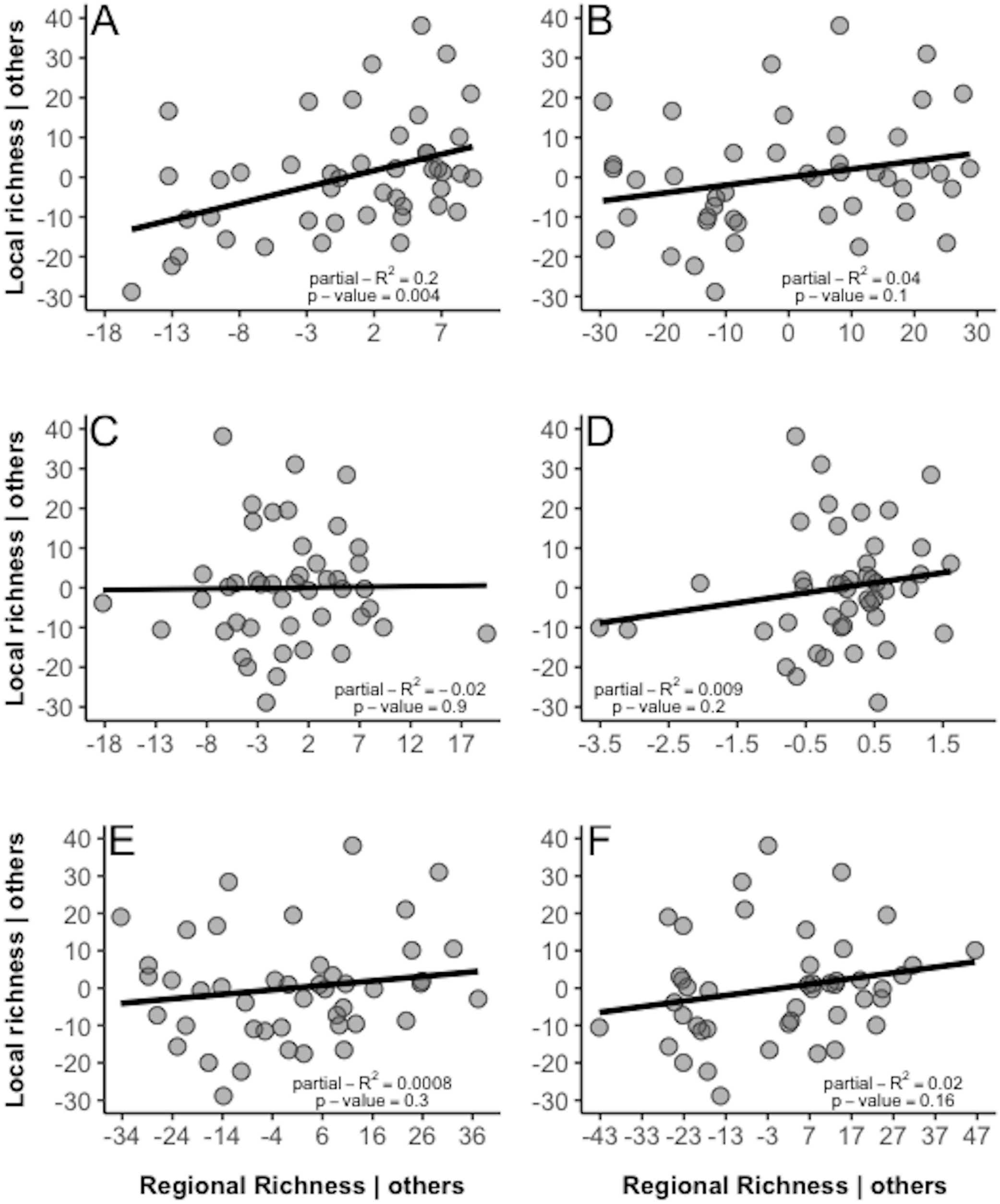
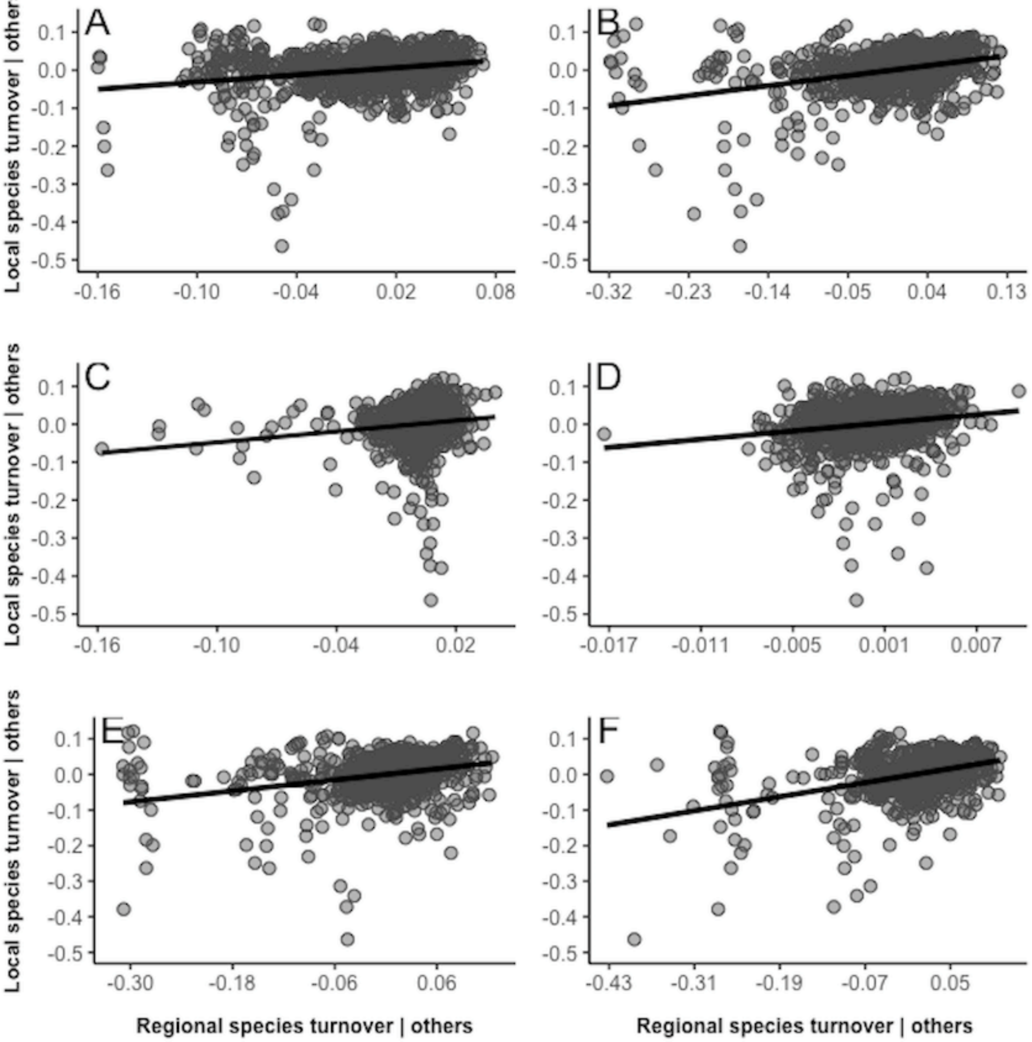

A
B
C
D
E
F
Local richness | others
Regional Richness | others
partial – R² = 0.2
p – value = 0.004
partial – R² = 0.04
p – value = 0.1
partial – R² = – 0.02
p – value = 0.9
partial – R² = 0.009
p – value = 0.2
partial – R² = 0.0008
p – value = 0.3
partial – R² = 0.02
p – value = 0.16
40
30
20
10
0
-10
-20
-30
-18 -13 -8 -3 2 7
-30 -20 -10 0 10 20 30
-18 -13 -8 -3 2 7 12 17
-3.5 -2.5 -1.5 -0.5 0.5 1.5
-34 -24 -14 -4 6 16 26 36
-43 -33 -23 -13 -3 7 17 27 37 47

Figure 4


A
B
C
D
E
F
Local species turnover | others
Regional species turnover | others
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.16
-0.10
-0.04
0.02
0.08
-0.32
-0.23
-0.14
-0.05
0.04
0.13
-0.017
-0.011
-0.005
0.001
0.007
-0.30
-0.18
-0.06
0.06
-0.43
-0.31
-0.19
-0.07
0.05

TABLES

TABLE 1. The hypotheses of enrichment by unfiltered and filtered regional pools with their respective regional species pool models and statistical models for each prediction.

Hypotheses	Regional species pool models	Statistical models prediction 1	Statistical models prediction 2
H1: Enrichment by unfiltered regional pools	*Neighborhood regional pool*	Local species richness~ environmental variables + neighborhood regional species richness (50 km radius)	Local species turnover~ environmental variables + neighborhood regional beta diversity (50 km radius)
		Local species richness~ environmental variables + neighborhood regional species richness (25 km radius)	Local species turnover ~environmental variables + neighborhood regional beta diversity (25 km radius)
	Dispersion-field regional pool	Local species richness~ environmental variables + dispersion field regional species richness (75% species shared with the local plot)	Local species turnover ~environmental variables + dispersion field regional beta diversity (75% species shared with the local plot)
		Local species richness~ environmental variables + dispersion field regional species richness (25% species shared with the local plot)	Local species turnover ~environmental variables + dispersion field regional beta diversity (25% species shared with the local plot)
H2: Enrichment by filtered regional pools	*Forest type regional pool*	Local species richness~ environmental variables + forest regional richness	Local species turnover ~ environmental variables + forest regional beta diversity
	Elevational band (300 m) regional pool	Local species richness~ environmental variables + elevation regional species richness	Local species turnover ~ environmental variables + elevation regional beta diversity

Note: Hypothesis 1 (H1): a regional species pool includes all the species that can disperse into a locality, regardless of the suitability of the local environment for the dispersing propagules. Hypothesis 2 (H2): a regional species pool has all the species that can disperse into a locality from similar environments. The environmental variables used in each statistical model were precipitation, PC1 temperature, and PC1 soil. For the first prediction, local species richness is the response variable and the area of the local plot is a co-variable in all models. For the second prediction, local beta diversity calculated with the Jaccard metric is the response variable.

Table 2. Linear regression models testing the prediction that the species richness of local assemblages are positively related to the species richness of regional species pools.

		Enrichment by unfiltered pools				Enrichment by filtered pools	
		H1.N.50km	**H1.N.25km**	**H1.DF.75%**	**H1.DF.25%**	**H2.F**	**H2.E.300m**
Parameters (SE)	Intercept	-159.7 (65.8)*	-6.2 (24.7)	23.6 (86.1)	-602 (559.9)	7.1 (26.2)	4.6 (21.1)***
	Precipitation	-0.0004 (0.001)	-0.003 (0.001).	-0.002 (0.002)	-0.002 (0.001)	-0.003 (0.001)	-0.003 (0.001)
	PC1 soil	-8.4 (1.5)***	-7.5 (1.6)***	-7.9 (1.7)***	-7.7 (1.6)***	-7.4 (1.7)***	-7.2 (1.7)***
	PC1 temperature	-5.1 (1.5)**	-3.3 (1.4)*	-2.8 (2.8)	-1.8 (1.8)	-3.1 (1.4)*	-1.3 (1.2)
	Regional Richness	0.8 (0.3)**	0.2 (0.1)	0.03 (0.3)	2.5(2.2)	0.1 (0.1)	0.1 (0.1)
Co-variable (SE)	Area (m^2)	0.002 (0.009)**	0.003 (0.001)**	0.003 (0.001)**	0.003 (0.001)**	0.003 (0.001)**	0.003 (0.001)**
Performance	AICs	371.2	377.2	380	378.6	379	378
	ΔAIC	0	6	8.8	7.4	7.8	6.8
	Adjusted r^2	0.60	0.54	0.51	0.53	0.52	0.53

Note: All the models are significant at $p < 0.0001$. Model names as in Table 1: **H1.N.50km =** *Neighborhood regional pool* based on a circular area, having a radius of 50 km, centered on each local site, **H1.N.25km =** *Neighborhood regional pool* within a 25 km of radius around each local site, **H1.DF.75% =** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes, **H1.DF.25% =** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes, **H2.F =** *Forest regional pool* based on the type of forest where the site was located, and **H2.E.300m =** *Elevational band regional pool* based on the elevational band within which the site occurred. PC1 temperature describes a temperature-related gradient (elevation, mean annual temperature, and potential evapotranspiration), PC1 soil describes soil properties (pH, K, Ca, Na, Mg, P). Regional richness was estimated by rarefactions based on 1,000 samples of 283 specimens. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, .$p < 0.1$.

Table 3. Distance-matrix-regression linear models testing the relationship between regional species composition and local species composition for different definitions of regional species pools in Costa Rica.

		Enrichment by unfiltered pools				Enrichment by filtered pools	
		H1.N.50km	**H1.N.25km**	**H1.DF.75%**	**H1.DF.25%**	**H2.F**	**H2.E.300m**
Parameters	Intercept	0.59	0.63	0.034	-3.05^{**}	0.65	0.60
	Precipitation	$8.2X10^{-6\,**}$	$3.6X10^{-6}$	$1.28X10^{-5***}$	$1.01X10^{-5***}$	$6.9X10^{-6**}$	$4.24X10^{-6*}$
	PC1 soil	0.01^{***}	0.01^{***}	0.01^{***}	0.01^{***}	0.01^{***}	0.01^{***}
	PC1 temperature	0.01^{***}	0.01^{***}	0.01^{***}	0.02^{***}	0.02^{***}	0.01^{**}
	Regional beta-diversity	0.33^{***}	0.31^{***}	0.62^{**}	4.4^{***}	0.27^{***}	0.34^{***}
Performance	Pseudo r^2	0.31	0.37	0.30	0.31	0.34	0.39
	p-value	0.001	0.001	0.001	0.001	0.001	0.001

Note: Local and regional species composition (beta diversity) was calculated as a Jaccard dissimilarity index. Model names as in Table 1: **H1.N.50km =** *Neighborhood regional pool* based on a circular area, having a radius of 50 km, centered on each local site, **H1.N.25km =** *Neighborhood regional pool* within a 25 km of radius around each local site, **H1.DF.75% =** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes, **H1.DF.25% =** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes, **H2.F =** *Forest regional pool* based on the type of forest where the site was located, and **H2.E.300m =** *Elevational band regional pool* based on the elevational band within which the site occurred. PC1 temperature describing a temperature gradient (elevation, mean annual temperature, and potential evapotranspiration); PC1 soil describing soil properties (pH, K, Ca, Na, Mg, P). The number of specimens to estimate regional richness for each definition was the same (283 specimens).$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$.

Table 4. Distance-based redundancy analysis testing the relationship between regional species composition and local species composition for different definitions of regional species pools in Costa Rica.

		Enrichment by unfiltered pools				Enrichment by filtered pools	
		H1.N.50km	**H1.N.25km**	**H1.DF.75%**	**H1.DF.25%**	**H2.F**	**H2.E.300m**
Sum of Squares	Precipitation	0.84^{***}	0.84^{***}	0.84^{***}	0.84^{***}	0.84^{***}	0.84^{***}
	PC1 soil	1.29^{***}	1.29^{***}	1.29^{***}	1.29^{***}	1.29^{***}	1.29^{***}
	PC1 temperature	1.15^{***}	1.15^{***}	1.15^{***}	1.15^{***}	1.15^{***}	1.15^{***}
	Regional beta-diversity (PCoA1)	0.71^{***}	0.77^{***}	0.56^{**}	0.68^{**}	0.80^{***}	0.72^{***}
	Regional beta-diversity (PCoA2)	0.68^{***}	0.72^{**}	0.56^{*}	0.53^{*}	0.56^{*}	0.61^{**}
Performance	Adjusted r^2	0.23	0.24	0.22	0.22	0.23	0.23
	p-value	0.001	0.001	0.001	0.001	0.001	0.01

Note: Model names as in Table 1: **H1.N.50km =** *Neighborhood regional pool* based on a circular area, having a radius of 50 km, centered on each local site, **H1.N.25km =** *Neighborhood regional pool* within a 25 km of radius around each local site, **H1.DF.75% =** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes, **H1.DF.25% =** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes, **H2.F =** *Forest regional pool* based on the type of forest where the site was located, and **H2.E.300m =** *Elevational band regional pool* based on the elevational band within which the site occurred. PC1 temperature describing a temperature gradient (elevation, mean annual temperature, and potential evapotranspiration); PC1 soil describing soil properties (pH, K, Ca, Na, Mg, P). The number of specimens to estimate regional richness for each definition was the same (283 specimens).$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$.

SUPLEMENTARY MATERIAL

Table S1. Plot local climate and soil variables for 45 Costa Rican forest sites.

Site	LR	Elev.	Temp.	PET	PRC	pH	K	Ca	Na	Mg	P
1A	61	70	27.3	1525	1600	5.5	0.2	6.9	0.44	1.7	1.9
1B	37	35	27.6	1533	1550	6.3	0.83	12.5	0.2	2.8	1.6
1C	2	4	27.8	1550	1525	7.6	0.17	34.3	2.5	11.56	1.7
1D	7	5	27.8	1550	1525	6.7	0.25	39.9	1.63	10.56	19.4
1E	10	3	27.8	1550	1525	6.5	0.68	17	0.77	6.87	4.6
1F	20	10	27.7	1550	1525	6.9	0.7	27.8	0.71	8.26	7.8
1G	13	27	27.6	1550	1525	6.9	0.92	24.5	0.42	9.38	5.1
2A	74	40	28.1	1580	2150	5.1	0.12	8.9	0.36	3.21	2.4
2B	49	240	26.3	1470	2250	5.5	0.41	16.3	0.27	13.39	1.1
2C	31	250	26.3	1470	2250	5.6	0.42	12.8	0.17	4.97	1
3	38	580	22.7	1325	2500	5.1	0.21	5.7	0.41	6.7	1.2
20A	57	380	24.5	1380	2400	5.3	0.11	1.8	0.28	1.37	1.2
20D	55	450	24.5	1380	2400	5.5	0.07	3.1	0.88	2.9	0.4
23	43	520	25	1410	2000	6.2	0.14	5.1	0.22	2.43	0.7
4	33	350	22.5	1290	4600	4.1	0.2	2.7	0.27	1.39	4.6
8A	99	600	26.4	1525	4300	5.2	0.05	0.3	0.17	0.59	0.8
8B	4	420	27.8	1580	4000	6.4	1.2	5.6	7.66	13.3	2.1
8C	2	2	27.8	1575	3900	5.6	3.01	5.1	12.8	13	9
8D1	19	1	27.7	1565	4200	6.6	0.12	19.9	0.38	7.98	2.2
8E	20	9	27.7	1555	4250	6.1	0.06	19.6	0.29	9.84	0.7
8F	47	10	27.5	1540	4350	6	0.17	7.5	0.43	24.8	1.2
19A	63	110	25.8	1480	5700	5.1	0.04	0.2	0.23	0.3	1
19B	25	40	25.7	1472	5700	5	0.04	0.1	0.14	0.2	1
19C	3	75	25.9	1482	5700	5.2	0.25	5.6	0.25	3.16	2.4
19E	11	4	25.9	1482	5700	4.9	0.1	6	0.3	2.05	2.7
19F	45	2	25.8	1480	5700	5	0.06	0.3	0.23	0.61	1.2
18	48	50	23.3	1355	1850	5.9	0.48	10.4	0.29	5.89	0.9
21	26	800	25.4	1425	1850	6.2	0.37	5.1	0.12	1.77	0.6
7	61	330	24.1	1365	3600	5	0.04	0.2	0.16	0.19	1.3
11	58	620	26.2	1500	3649	4.7	0.06	0.2	0.2	0.2	0.5
15A	36	110	21.5	1235	3300	5.4	0.04	0.4	0.14	0.19	1
15B	43	900	21.8	1255	3100	5.4	0.05	0.5	0.1	0.15	1
15C	33	825	22.4	1290	2950	5.5	0.03	0.3	0.1	0.09	1
16	32	710	22.5	1310	2900	5.7	0.22	5.8	0.59	2.74	0.5
5	23	675	19	1110	4900	6.2	0.21	31.2	0.21	1.46	3.5
22A	76	1275	21.8	1248	5500	5	0.05	0.1	0.12	0.09	1
22B	38	830	22.1	1265	5500	4.9	0.08	0.1	0.14	0.33	1
22D	44	770	22	1260	5500	4.7	0.07	0	0.13	0.28	1
22E	52	785	19.5	1120	5800	4.9	0.02	0.1	0.14	0.04	1
17	21	1100	13.7	806	1450	6.2	0.45	6.6	0.17	1.13	7.3
10	40	2360	17.5	1000	2900	5.7	0.31	4.2	0.39	1.95	0.9
9A	28	1700	13.5	795	3750	5.1	0.03	0.2	0.23	0.03	1
9B	22	2400	13.8	810	3650	4.6	0.13	0.1	0.31	0.1	6.5
12	60	2350	14.4	848	4400	5.5	0.07	0.2	0.13	0.26	1.7
6	13	3080	10.8	635	2941	4.1	0.26	0.4	1.06	0.29	7.1

Note: LR = local richness, Elev = elevation, Temp. = temperature, PET = potential evotranspiration, PRC = precipitation, K = potassium, Ca = calcium, Na = sodium, Mg = magnesium, P = available phosphorus.

Table S2. Mean regional species richness for 45 Costa Rican forest sites

Site	LR	RR.N.50km	RR.N.25km	RR.DF.75%	RR.DF.25%	RR.F	RR.E.300m
1A	61	223.985	164.001	249.087	251.937	167.355	171.31
1B	37	223.014	162.956	250.912	251.978	168.027	170.347
1C	2	218.226	157.948	242.561	247.844	161.425	162.112
1D	7	219.172	157.917	247.454	251.965	161.629	162.239
1E	10	219.323	158.349	250.08	252.244	165.927	162.188
1F	20	232.426	157.197	250.824	251.922	159.936	160.578
1G	13	232.89	174.102	250.603	251.998	158.616	161.946
2A	74	235.764	226.365	250.42	251.769	225.477	197.909
2B	49	232.505	204.156	248.937	251.974	228.419	207.992
2C	31	232.391	203.882	247.619	251.693	228.328	205.962
3	38	228.342	217.059	246.827	251.899	220.606	211.444
20A	57	225.959	218.935	245.035	251.651	208.244	210.882
20D	55	226.531	221.223	243.852	251.628	208.567	217.596
23	43	226.44	222.018	243.366	251.189	204.205	206.357
4	33	230.798	224.55	249.428	250.502	221.806	212.405
8A	99	228.552	223.496	246.446	250.915	227.532	214.226
8B	4	228.659	222.823	239.059	251.409	227.866	215.384
8C	2	228.41	222.926	250.96	251.02	184.227	210.264
8D1	19	226.285	222.725	246.343	250.501	226.31	216.825
8E	20	228.188	223.661	246.011	250.444	227.713	211.055
8F	47	228.166	224.229	248.79	250.711	227.51	215.459
19A	63	204.009	201.065	248.657	250.512	204.381	198.381
19B	25	204.207	200.963	247.713	250.222	204.383	198.351
19C	3	201.914	203.876	247.912	251.51	197.721	200.233
19E	11	204.099	201.076	249.258	250.289	203.933	198.709
19F	45	204.132	200.891	245.904	250.54	204.329	198.299
18	48	239.668	214.381	247.655	252.177	223.215	228.089
21	26	225.887	222.079	246.167	251.51	203.82	206.723
7	61	229.861	221.548	248.688	251.562	226.552	209.369
11	58	221.709	200.314	248.401	250.73	207.768	200.799
15A	36	231.269	197.119	249.05	250.59	224.677	214.34
15B	43	230.926	197.3	248.709	250.802	225.218	196.108
15C	33	230.88	199.493	247.772	250.497	225.676	192.52
16	32	226.494	221.401	239.923	251.202	208.539	211.556
5	23	233.739	203.751	232.566	251.301	208.765	206.028
22A	76	229.91	224.404	248.18	250.713	198.596	213.141
22B	38	230.268	224.425	248.905	250.404	226.846	210.897
22D	44	229.925	224.634	240.313	250.412	226.475	211.145
22E	52	229.343	224.139	243.827	250.421	194.894	205.504
17	21	232.456	212.764	209.444	247.039	210.764	144.541
10	40	235.214	215.868	218.432	250.997	214.611	193.982
9A	28	236.148	206.734	199.844	249.338	209.301	132.652
9B	22	234.785	207.288	237.831	250.611	206.511	136.659
12	60	233.643	216.195	226.244	250.357	204.193	154.326
6	13	228.447	203.041	195.463	245.316	206.5	91

Note: LR= Local richness**, RR.N.50km** = *Neighborhood regional pool* based on area of a circle with a radius of 50 km, **RR.N.25km=** *Neighborhood regional pool* based on area of circle with a radius of 25 km**, =** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes, **RR1.DF.25%=** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes, **RR.F =** *Forest regional pool* based on the type of forest where the site was found and **RR.E.300m =** *Elevational band regional pool* based on the elevational band where the site was found).

Table S3. Descriptive statistics for local and regional variables for 45 sites at Costa Rica.

Variable	Mean	STD	Kurtosis	Skewness
Local species richness	35.44	21.74	0.11	0.5
Elevation	615.04	781.78	1.69	1.58
Temperature	23.62	4.57	0.71	-1.26
Potential Evapotranspiration	1344.02	246.3	0.91	-1.34
Precipitation	3429.22	1484.02	-1.27	0.23
pH	5.57	0.75	-0.06	0.43
Potassium	0.3	0.49	19.21	4.08
Calcium	7.9	10.2	1.68	1.58
Sodium	0.83	2.17	21.01	4.6
Magnesium	4.01	5.23	3.85	1.86
Phosphorus (available)	2.62	3.37	11.95	3.16
Area local plot (m^2)	3777.78	2285.22	3.12	1.69
Neighborhood regional species richness (50 km)	226.33	9.25	1.49	-1.50
Neighborhood regional species richness (25 km)	205.67	21.32	0.38	-1.23
Dispersion field regional richness (75%)	242.48	12.84	5.43	-2.49
Dispersion field regional richness (25%)	250.81	1.31	6.45	-2.31
Forest regional richness	206.16	21.61	-0.06	-1
Elevation regional richness (300 m)	192.40	28.56	2.07	-1.53

Note: The number of specimens to estimate regional richness for each definition was the same (283 specimens)

Table S4. Linear models testing two hypotheses of regional enrichment of local species assemblages in Costa Rica.

		Enrichment by unfiltered pools				Enrichment by filtered pools	
		H1.N.50km	**H1.N.25km**	**H1.DF.75%**	**H1.DF.25%**	**H2.F**	**H2.E.300m**
Parameters (SE)	Intercept	-16.6 (25.8)	10.03 (14.7)	44.7 (30.7)	-22.8 (60.1)	16.2 (17.9)	4.6 (21.1)
	Precipitation	-0.001 (0.001)	-0.003 (0.001).	-0.002 (0.001)	-0.002 (0.001)	-0.002 (0.001)	-0.002 (0.001)
	PC1 soil	-7.9 (1.6)***	-7.5 (1.6)***	-8.2 (1.7)***	-7.6 (1.7)***	-7.4 (1.7)***	-7.3 (1.8)***
	PC1 temperature	-4.9 (1.7)**	-3.5 (1.4)**	-4.1 (2.8)	-2.1 (1.7)	-3.1 (1.4)*	-1.3 (1.9)
	Regional Richness	0.04 (0.02).	0.1 (0.03).	-0.01 (0.02)	0.02 (0.02)	0.04 (0.04)	0.2 (0.1)
Co-variable (SE)	Area (m^2)	0.003 (0.001)**	0.003 (0.001)**	0.003 (0.001)**	0.003 (0.001)**	0.003 (0.001)**	0.003 (0.001)**
Performance	AICs	375.9	376.7	379.8	379.1	379	377.9
	ΔAIC	0	0.8	3.9	3.2	3.1	2
	Adjusted r^2	0.56	0.55	0.52	0.52	0.52	0.53

Note: All the models are significant ($p < 0.0001$). Numbers in parentheses are standard errors of the estimates. Model names as in Table 1: **H1.N.50km =** *Neighborhood regional pool* based on a circular area, having a radius of 50 km, centered on each local site, **H1.N.25km =** *Neighborhood regional pool* within a 25 km of radius around each local site, **H1.DF.75% =** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes, **H1.DF.25% =** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes, **H2.F =** *Forest regional pool* based on the type of forest where the site was located, and **H2.E.300m =** *Elevational band regional pool* based on the elevational band within which the site occurred. PC1 temperature describing a temperature gradient (elevation, mean annual temperature, and potential evapotranspiration) PC1 soil describing soil properties (pH, K, Ca, Na, Mg, P). The number of specimens used to estimate regional richness differed for each definition (*n* = 3,104, *n* = 872, *n* = 3,782, *n* = 54,320, *n* = 601, and *n* = 283, respectively). ***p < 0.001, **p < 0.01, *p < 0.05, .p < 0.1.

Table S5. Matrix regression linear models testing the relationship between regional species turnover and local species turnover for different definitions of regional species pools in Costa Rica.

		Enrichment by unfiltered pools				Enrichment by filtered pools	
		H1.N.50km	**H1.N.25km**	**H1.DF.75%**	**H1.DF.25%**	**H2.F**	**H2.E.300m**
Parameters	Intercept	0.81^{***}	0.75	0.34	0.86^{***}	0.73	0.60
	Precipitation	$6.8X10^{-6\ **}$	$2.9X10^{-6}$	$1.2X10^{-5}$	$1.2X10^{-5***}$	$6.2X10^{-6**}$	$4.24X10^{-6*}$
	PC1 soil	0.01^{***}	0.01^{***}	0.01^{***}	0.01^{***}	0.01^{***}	0.01^{***}
	PC1 temperature	0.01^{***}	0.01^{***}	0.01^{***}	0.01^{***}	0.01^{***}	0.01^{**}
	Regional Beta Diversity	0.12^{***}	0.31^{***}	0.61^{**}	0.21^{**}	0.20^{***}	0.34^{***}
Performance	Pseudo r^2	0.33	0.39	0.30	0.29	0.35	0.39
	p-value	0.001	0.001	0.001	0.001	0.001	0.001

Note: Local and regional species composition (beta diversity or turnover) was calculated as a Jaccard dissimilarity index. Model names as in Table 1: **H1.N.50km =** *Neighborhood regional pool* based on a circular area, having a radius of 50 km, centered on each local site, **H1.N.25km =** *Neighborhood regional pool* within a 25 km of radius around each local site, **H1.DF.75% =** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes, **H1.DF.25% =** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes, **H2.F =** *Forest regional pool* based on the type of forest where the site was located, and **H2.E.300m =** *Elevational band regional pool* based on the elevational band within which the site occurred. PC1 temperature describing a temperature gradient (elevation, mean annual temperature, and potential evapotranspiration); PC1 soil describing soil properties (pH, K, Ca, Na, Mg, P). The number of specimens to estimate regional species turnover for each definition was different (*n* = 3,104 , *n* = 872, *n* = 3,782, *n* = 54,320, *n* = 601 and *n* = 283, respectively). ***p < 0.001, **p < 0.01, *p < 0.05.

Table S6. Distance-based redundancy analysis testing the relationship between regional species composition and local species composition for different definitions of regional species pools at Costa Rica.

		Enrichment by unfiltered pools				**Enrichment by filtered pools**	
		H1.N.50km	**H1.N.25km**	**H1.DF.75%**	**H1.DF.25%**	**H2.F**	**H2.E.300m**
Sum of Squares	Precipitation	0.84***	0.84***	0.84***	0.84***	0.84***	0.84***
	PC1 soil	1.29***	1.29***	1.29***	1.29***	1.29***	1.29***
	PC1 temperature	1.15***	1.15***	1.15***	1.15***	1.15***	1.15***
	Regional Beta Diversity (PCoA1)	0.71***	0.75***	0.55*	0.52*	0.79***	0.72**
	Regional Beta Diversity (PCoA2)	0.64***	0.71***	0.56*	0.58*	0.57**	0.61**
Performance	Adjusted r^2	0.23	0.24	0.22	0.22	0.23	0.23
	p-value	0.001	0.001	0.001	0.001	0.001	0.01

Note: Model names as in Table 1: **H1.N.50km =** *Neighborhood regional pool* based on a circular area, having a radius of 50 km, centered on each local site, **H1.N.25km =** *Neighborhood regional pool* within a 25 km of radius around each local site, **H1.DF.75% =** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes, **H1.DF.25% =** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes, **H2.F =** *Forest regional pool* based on the type of forest where the site was located, and **H2.E.300m =** *Elevational band regional pool* based on the elevational band within which the site occurred. PC1 temperature describing a temperature gradient (elevation, mean annual temperature, and potential evapotranspiration); PC1 soil describing soil properties (pH, K, Ca, Na, Mg, P). The number of specimens to estimate regional species composition for each definition differed (*n* = 3,104, *n* = 872, *n* = 3,782, *n* = 54,320, *n* = 601 and *n* = 283 respectively). ***p < 0.001, **p < 0.01, *p < 0.

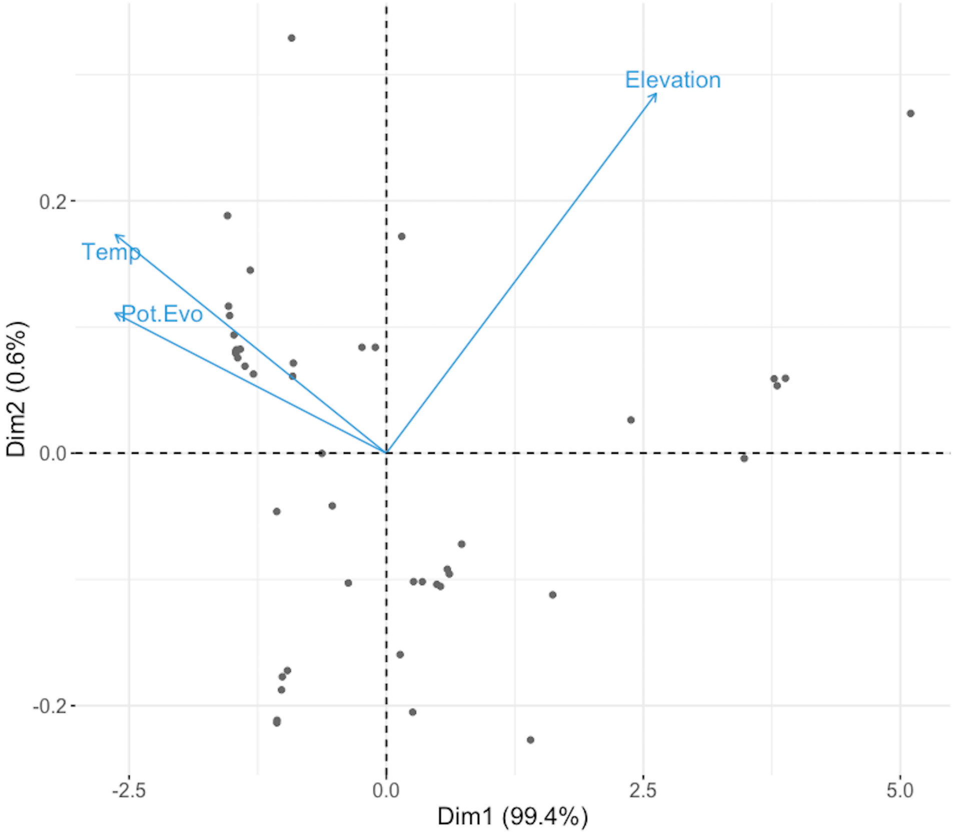


FIGURE S1. Principal component analysis for forty five local sites in Costa Rica, based on three climate variables (temperature, potential evapotranspiration, elevation) that reflect a temperature gradient.

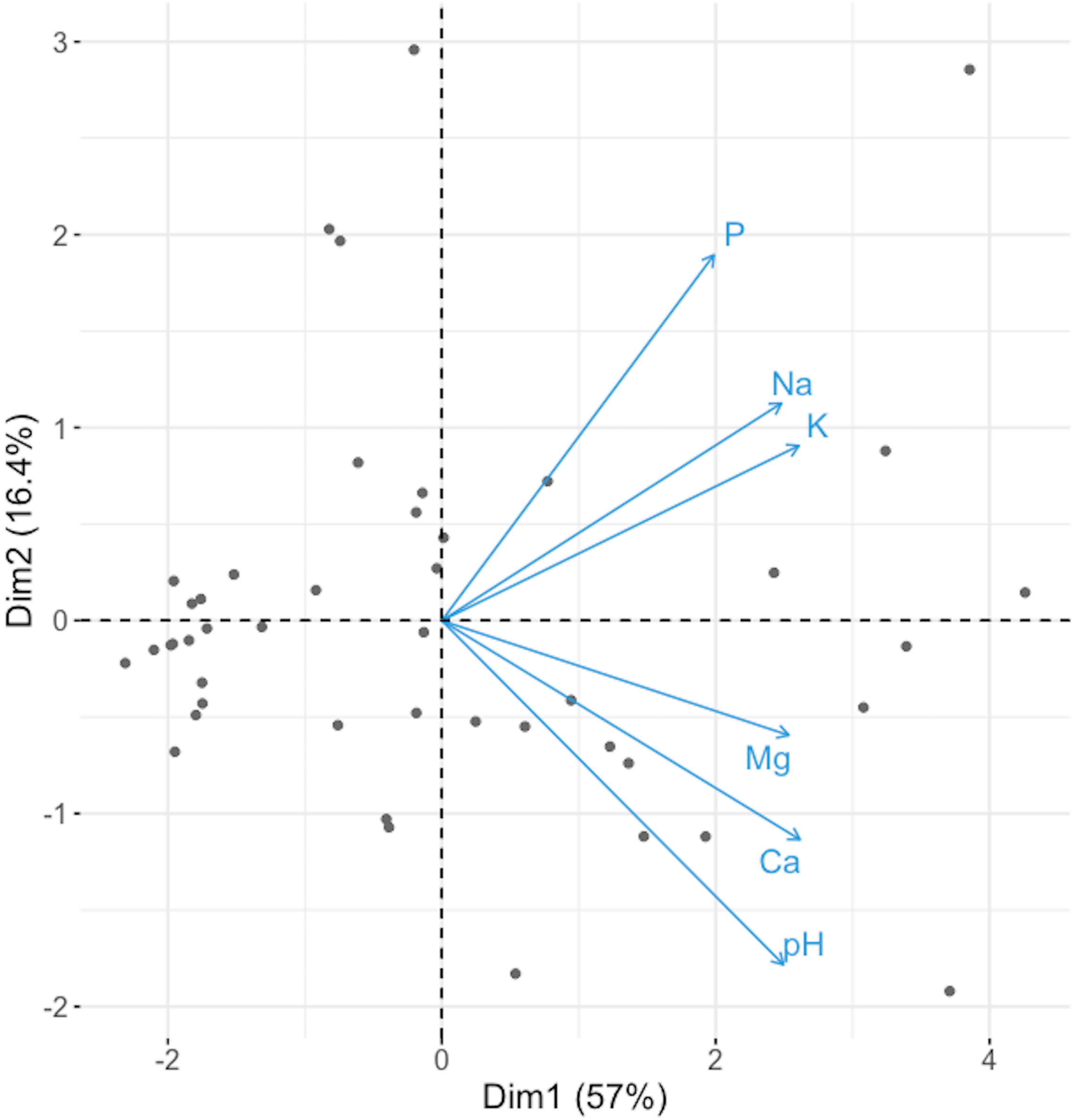
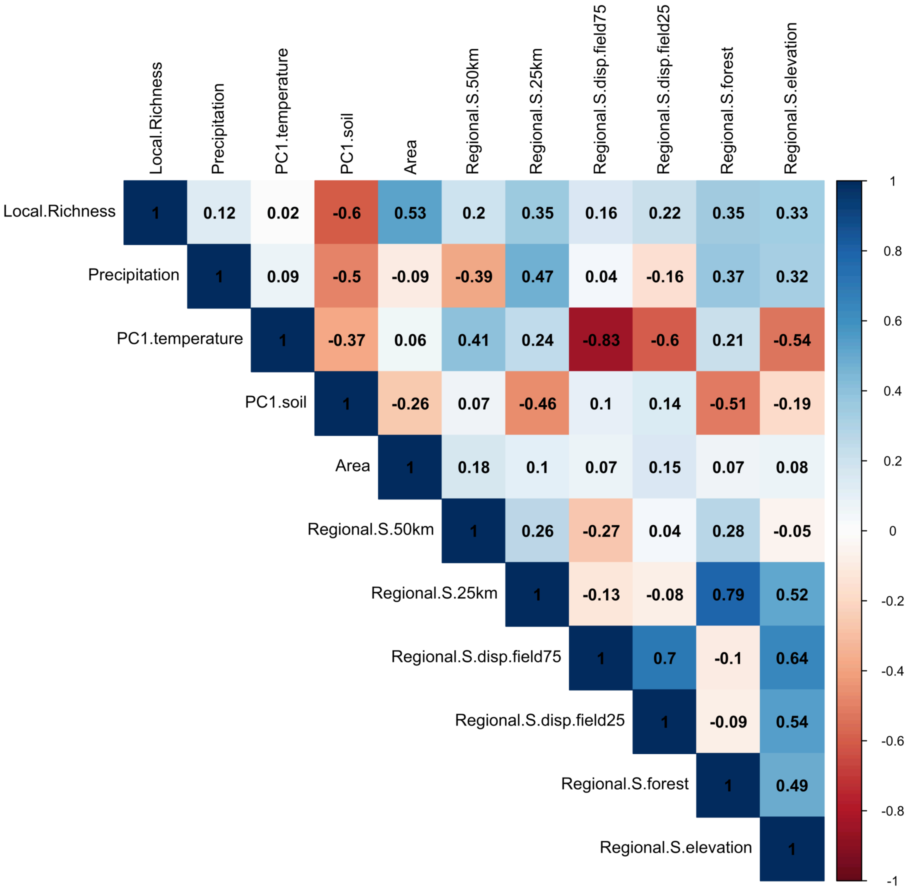


FIGURE S2. Principal component analysis for forty-five local sites at Costa Rica, based on six variables (pH, calcium, magnesium, potassium, sodium, and phosphorus) that reflect a soil gradient.



	Local.Richness	Precipitation	PC1.temperature	PC1.soil	Area	Regional.S.50km	Regional.S.25km	Regional.S.disp.field75	Regional.S.disp.field25	Regional.S.forest	Regional.S.elevation
Local.Richness	1	0.12	0.02	-0.6	0.53	0.2	0.35	0.16	0.22	0.35	0.33
Precipitation		1	0.09	-0.5	-0.09	-0.39	0.47	0.04	-0.16	0.37	0.32
PC1.temperature			1	-0.37	0.06	0.41	0.24	-0.83	-0.6	0.21	-0.54
PC1.soil				1	-0.26	0.07	-0.46	0.1	0.14	-0.51	-0.19
Area					1	0.18	0.1	0.07	0.15	0.07	0.08
Regional.S.50km						1	0.26	-0.27	0.04	0.28	-0.05
Regional.S.25km							1	-0.13	-0.08	0.79	0.52
Regional.S.disp.field75								1	0.7	-0.1	0.64
Regional.S.disp.field25									1	-0.09	0.54
Regional.S.forest										1	0.49
Regional.S.elevation											1

Figure S3. Bivariate correlations (Pearson correlation coefficient) between tree local richness and soil, climate, and regional species richness for forty-five Costa Rican forest sites.

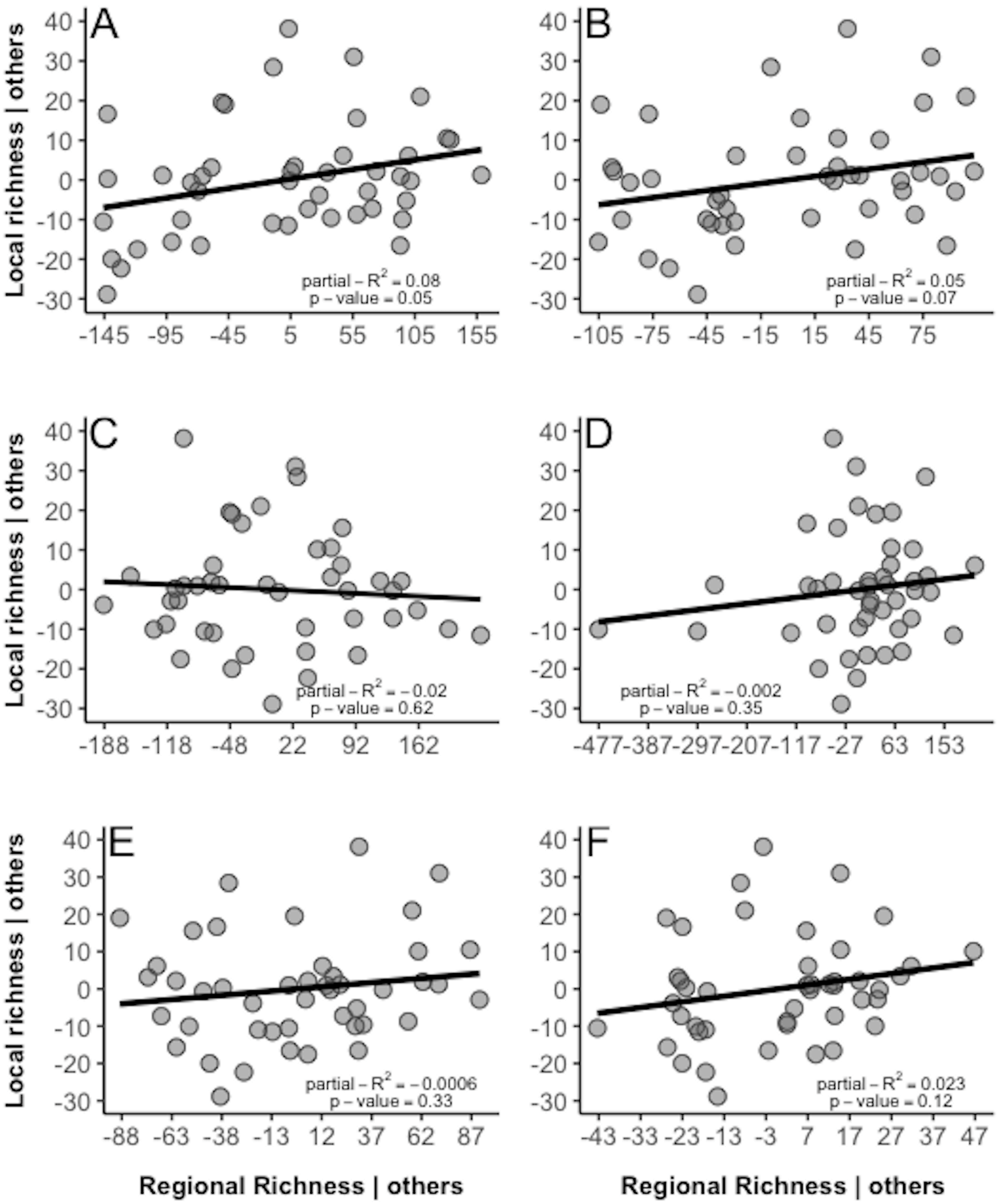


Figure S4. Partial regression plots for all regression models showing a linear relationship between local species richness and regional species richness after controlling for the other variables (precipitation, PC1 soil, PC1 temperature, area). **A.** *Neighborhood regional pool* based on a circular area having a 50-km radius, around each local site. **B.** *Neighborhood regional pool* within a 25-km radius around each local site. **C.** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic ranges. **D.** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic ranges. **E.** *Forest regional pool* based on the type of forest where the local site was located. **F.** *Elevational band regional pool* based on the elevational band within which the local site occurred. The number of specimens to estimate regional richness for each definition differed (*n* = 3,104, *n* = 872, *n* = 3,782, *n* = 54,320, *n* = 601, and *n* = 283, respectively).

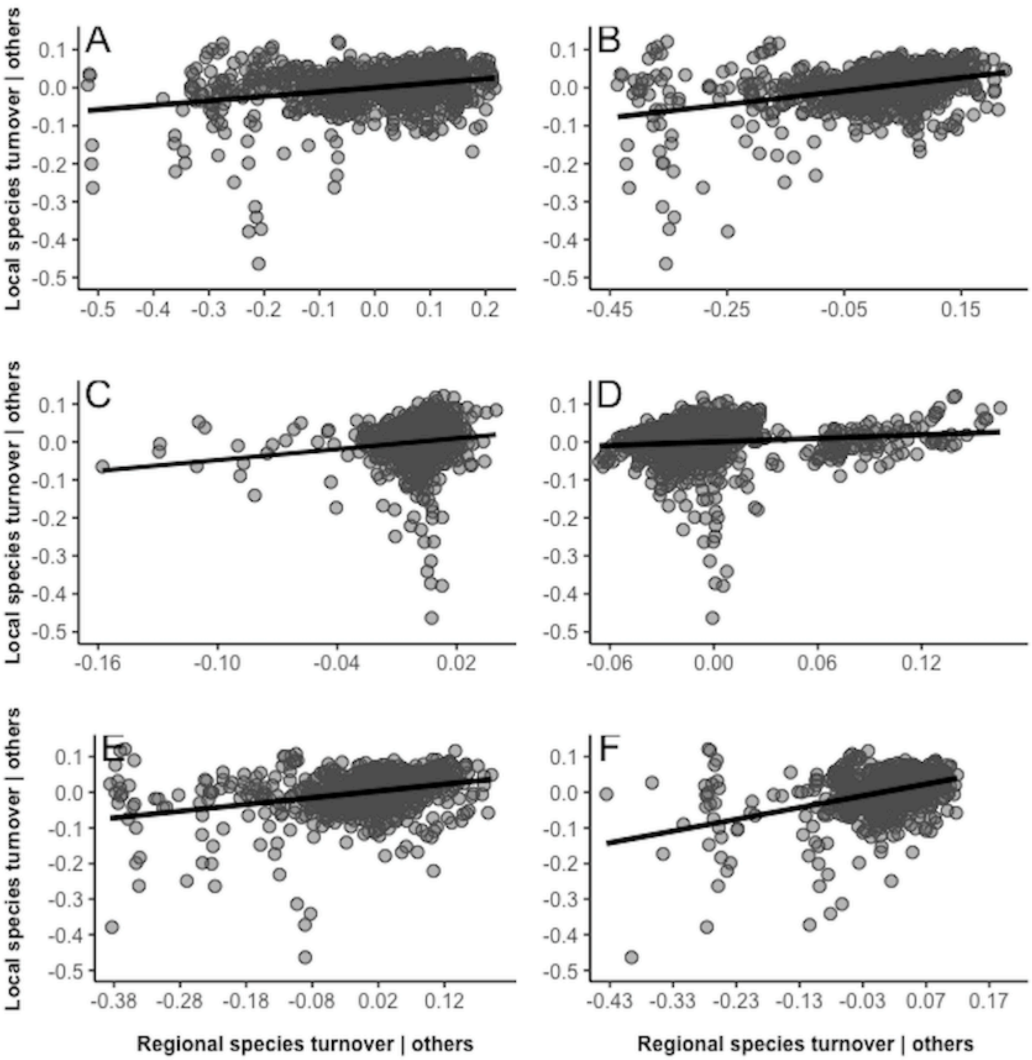


Figure S5. Partial regression plots for all matrix regression models showing a relationship between local species turnover and regional species turnover after controlling for the other variables (precipitation, PC1 soil, and PC1 temperature); each gray dot represents a pair of sites. Species turnover was measured as a Jaccard dissimilarity index. **A.** *Neighborhood regional pool* based on area of 50-km radius, around each local site. **B.** *Neighborhood regional pool* 25-km of radius around each local site. **C.** *Dispersion-field regional pool* based on 75% of shared overlap of species geographic range sizes. **D.** *Dispersion-field regional pool* based on 25% of shared overlap of species geographic range sizes. **E.** *Forest regional pool* based on the type of forest where the local site was located. **F.** *Elevational band regional pool* based on the elevational band where the local site occurred. The number of specimens to estimate regional species turnover differed among definitions (*n* = 3,104 , 872, 3,782, 54,320, 601, and 283, respectively)

CHAPTER 2.

Spatial legacies of the Great Biotic Interchange in Central American tree floras

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ABSTRACT

The Great American Biotic Interchange (GABI) began as the Isthmus of Panama was formed, ending the isolation of South America and permitting the migration of animals and plants between North and South America. Gentry (1982) hypothesized two major GABI legacies in the current spatial structure of Central America tree floras. First, Gentry (1982) suggested a major dichotomy between the composition of lowland and montane rainforest in terms of plant families, arguing that these rainforests were dominated by lineages of southern and northern origin, respectively. Second, Gentry (1982) hypothesized nested spatial gradients of species diversity in lowland and mountain rainforests across Central America. In particular, Gentry (1982) suggested that, due to the northward migration of plant lineages from South America during GABI, lowland rainforests of Central America currently form a nested gradient of decreasing species richness from the Darien region, near South America, westward and northward to the Isthmus of Tehuantepec. In contrast, Central American montane rainforests would have been more influenced by sources located towards North America than by migration of lineages from South America during GABI. Thus, according to Gentry (1982), these forests would currently form a nested gradient of decreasing species richness from the Isthmus of Tehuantepec towards the Darien region, opposite to that in the lowlands. Here, we tested these spatial patterns hypothesized by Gentry (1982) as legacies of GABI, using occurrence data from local species assemblages and tree occurrence records across Central America. Our results are partially in agreement with the pattern that Gentry (1982) described regarding the plant family composition of Central American lowland and montane tree floras. We found marked differences in the representation of plant families between lowland and montane rainforest, and the composition of Central American lowland rainforests was largely consistent with the description in Gentry (1982). However, plant families that Gentry (1982) assumed to be of northern origin did not dominate the composition of montane rainforests. In addition, we did not find empirical support for the nested spatial gradients of species diversity hypothesized by Gentry (1982) for the lowland or montane tree floras across Central America. That is, local species assemblages occurring in lowland rainforest in Costa Rica did not share more species with the sites toward Darien than with sites toward Tehuantepec, and, contrary to expectations, the species composition of montane rainforests in Costa Rica more closely resembled that of montane forests near the Darien area than of those by the Isthmus of Tehuantepec.

KEYWORDS: Lowland rainforest, montane rainforest, spatial legacies, species composition.

INTRODUCTION

Contemporary species assemblages at local, regional, and continental scales result in part from historical events and geographic configurations (Ricklefs and Schluter 1993, Donoghue 2008). At regional and continental scales, the legacy of such events is commonly described in terms of the spatial structure of biotas. For example, geographic regions delineated by patterns of biotic similarity are identified as biogeographic units, often though to result from a shared history of local origin and limited dispersal (Lomolino et al., 2010). Likewise, “transition zones” variously attributed to spatially nested patterns of species composition or relatively smooth spatial gradients of biotic similarity, have been proposed as legacies of the breakdown of barriers between biogeographic units (Williams 1999, Kreft and Jetz 2013) and the ensuing intermixing of previously independently evolving biotas, a phenomenon known as biotic interchange (Vermeij 1991, Riddle 1996).

The Great American Biotic Interchange (GABI), referring to the exchange of lineages between North and South America, has received much attention in biogeography as one of the major events structuring Neotropical biotas (Gentry 1982; Burnham and Graham 1999, Gentry 1982, Graham 2010, Lomolino et al 2010, Marshall et al., 1982, Simpson 1980, Stehli and Webb 1985, Webb 1985, Webb 2006). GABI began with the completion of the Isthmus of Panama at the end of Cenozoic Era (ca. 3 Ma, Coates and Obando 1996, Kirby et al., 2008) or perhaps even earlier (ca. 15 Ma, Montes et al., 2015, Bacon et al., 2015), ending the “splendid” isolation of South American mammals (Simpson 1980) and plants (Gentry 1982, Burnham and Graham 1999, Graham 2010). The new land connection between South and North America resulted in asymmetric exchange of biotas, as seems to often be the case in biotic interchanges (Vermeij 1991). In the case of mammals, southward geographic expansion of northern lineages into South America, and their subsequent diversification there, may have predominated. This is especially true for non-flying and non-marine groups, where about 40% of the South American mammal families and 50% of the genera and species derive from these northern lineages (Marshall et al., 1982, Webb, 1985). Conversely, few southern mammal lineages expanded their geographical ranges towards the north, where only 10% of the extant mammalian fauna of North America is ascribed to southern lineages (Webb 1991).

A more complex picture is drawn for plants. In contrast to mammals and montane plants, the norm for lowland plants seems to have been northward expansion of the geographic ranges of species of southern origin followed by diversification in Central America (Gentry 1982, Burnham and Graham 1999, Wendt 1993). This northward expansion of lowland plant lineages of southern origin may have left a major legacy of GABI in the current spatial distributions of the lowland tree floras of Central America. In particular, Gentry (1982) hypothesized that these floras form a nested gradient of decreasing species richness from the Darien region, near South America, westward and northward to the Isthmus of Tehuantepec. Thus, while many southern species of different lowland tree plant families would have reached lowland habitats in eastern Panama, fewer would have reached similar habitats in western Panama and Costa Rica and even fewer in Mexico (Gentry 1982). Nonetheless, lowland tree plant species of southern origin are thought to dominate, and account for most diversity in, lowland rainforests throughout Central America (Gentry 1982).

Conversely, Central American montane tree floras may have received relatively few immigrant lineages from the south during GABI (Gentry 1982, Graham 2010). The current structure of these montane tree floras may have been influenced more by the southern geographic range expansion of tree lineages of northern origin and, therefore, they may currently exhibit a nested gradient of decreasing species richness from the Isthmus of Tehuantepec towards South America, opposite to that in Central American lowland floras (Gentry 1982). Northern lineages such as Pinaceae, Fagaceae, Juglandaceae, Theaceae, Magnoliaceae, and Ulmaceae predominate ecologically in Central American montane forests in the Sierra Madre de Chiapas (Styles 1993, Gomez-Pompa and Dirzo 1995), which ranges from the southern part of the Isthmus of Tehuantepec across Guatemala into El Salvador and

Honduras. However, their presence gradually decreases toward the mountain ranges in the southern part of Central America, such as the Serrania de Darien, Serrania del Sapo, and Cordillera de San Blas. For example, Pinaceae lineages do not cross the San Juan river (Nicaragua-Costa Rica border), while representatives of the families Ulmaceae and Juglandaceae reach only montane habitats in Panama (Gentry 1982).

Gentry (1982) emphasized that, due to contrasting effects of GABI, there were important differences in the current taxonomic composition of Central American lowland and montane rainforest. In particular, largely based on Raven and Axelrod (1974) and distributional data from floras and taxonomic monographs, Gentry (1982) argued that a major feature of current Central American tree floras was a dichotomy between the families occurring in montane and lowland rainforest. According to this view, montane rainforests are largely composed of tree species that belong to plant families of northern origin (i.e., temperate or Laurasian origin) while lowland rainforests are dominated by trees that belong to plant families derived from the south (i.e., southern tropical or Gondwanan origin).

Recent empirical work has challenged previously accepted ideas about GABI, including the age of the Isthmus of Panama (Montes et al., 2015, Jaramillo et al., 2017, but see O'Dea et al., 2016) and the timing of dispersal between Central and South America (Cody et al., 2010, Bacon et al., 2015). However, we are unaware of studies critically examining putative spatial legacies of GABI (i.e., current spatial diversity patterns thought to be largely due to GABI) across Central American floras. Although Gentry (1982) hypothesized very particular spatial legacies of GABI, including contrasting nested spatial gradients of species diversity for lowland and mountain tree floras across Central America, as well as marked taxonomic differences between these two floras at the level of plant families, there do not seem to have been tests of the existence of such patterns. Gentry did not have sufficient information about the geographic distribution of species to conduct formal tests, a limitation known as the "Wallacean shortfall" that is particularly acute in the tropics and afflicts a wide range of studies of biogeography and macroecology (Hortal et al., 2015). Nevertheless, as more data is collected and made widely available, we are increasingly able to formally challenge long-held ideas about broad-scale spatial patterns of diversity (Serrano et al., 2018). We believe such tests are fundamental to our understanding of the current structure and historical assemblage of biotas in Central America and elsewhere.

Here, we examine two spatial patterns hypothesized by Gentry (1982) as legacies of GABI on Central American floras, using occurrence data from local species assemblages and tree occurrence records across Central America. First, we tested for taxonomic differences between lowland and mountain tree floras at the level of plant families, aiming to determine whether particular plant families show contrasting patterns of occurrence between these two floras, as proposed by Gentry (1982). Second, we tested for the particular nested spatial gradients of species diversity that, according to Gentry (1982), characterize lowland and mountain tree floras across Central America.

To carry out this second test, we derived two kinds of predictions from the hypothesis described by Gentry (1982). The first kind of prediction addresses the number of shared species between sites. If Central American lowland tree floras form a nested spatial gradient of decreasing species richness from the Darien region to the Isthmus of Tehuantepec (Figure 1A), then local species assemblages occurring in lowland forests between Darien and Tehuantepec would share more species with the sites toward Darien than with sites toward Tehuantepec (Figure 1C). Conversely, the opposite pattern would be observed for Central American montane tree floras (Figure 1B and D); according to Gentry (1982), these floras are more heavily influenced by the range expansion of tree lineages of northern origin. A second kind of prediction centers on the number of species that occur in local species assemblages in Costa Rica but not in other sites towards Darien and Tehuantepec. If the Central American lowland tree flora exhibits a nested spatial gradient, as proposed by Gentry (1982), then local species assemblages occurring in lowland forests between Darien and Tehuantepec would contain fewer unique species when compared to the sites towards Darien than when compared to the sites towards Tehuantepec (Figure 1E). For the Central American montane flora, we should expect the opposite pattern (Figure 1D).

Our results are partially in agreement with the pattern that Gentry (1982) described regarding the plant family composition of Central American lowland and montane tree floras. We found marked differences in the representation of plant families between lowland and montane rainforest, and the composition of Central American lowland rainforests was largely consistent with the description in Gentry (1982). However, the composition of montane rainforests was not dominated by plant families that Gentry (1982) assumed to be of northern origin. In addition, we did not find empirical support for the nested spatial gradients of species diversity hypothesized by Gentry (1982) for the lowland or montane tree floras across Central

America. That is, local species assemblages occurring in lowland rainforest in Costa Rica did not share more species with the sites toward Darien than with sites toward Tehuantepec, and, contrary to expectations, the species composition of montane rainforests in Costa Rica more closely resembled that of montane forests close to the Darien area than that of those at the Isthmus of Tehuantepec.

METHODS

Our study comprises the Central American subcontinent, taken to include the landmass between the Isthmus of Tehuantepec (17° 10'N, 94° 37'W), and the Darien region (7° 23'N, 77° 09'W, Figure 2A and B). At this broad geographic scale, there is large uncertainty about the spatial distribution of plant species (the "Wallacean shortfall", Hortal et al., 2015), so assessment of Gentry's (1982) hypothesis by simple observation of distributional maps is, plainly, not feasible. Instead, we used two datasets that provided information at different levels of spatial resolution and coverage. One of these datasets was tree plots characterizing local species assemblages. Each tree plot sampled ca. 0.3 hectares (ha) around the middle of the Central America (Costa Rica). These data provided accurate, high-resolution estimates of the composition of local assemblages in lowland and montane rainforest, but relatively poor geographic coverage across the Central American subcontinent. The second dataset was of species occurrences across Central America, compiled largely from herbarium specimen records. This second dataset had much more extensive geographic coverage than the former, but lower spatial resolution due to relatively low precision of the geographic coordinates for the collection localities. Thus, based solely on the second dataset, it was difficult to determine if particular species occurred in lowland or montane rainforest. However, we used the first dataset (tree plots) to determine which tree species occur in lowland or montane rainforests, and then described the broad scale distribution of those species using the second dataset. In particular, we used the second dataset to characterize assemblages of rainforest tree species within 25 × 25 km sampling units across the Central American subcontinent, and, thus, to test for the broad-scale patterns hypothesized by Gentry (1982).

Local species assemblages

We used 39 tree plots (ca. 0.3-ha) distributed in Costa Rican lowland, montane, and premontane rainforest (21, 8, and 10 tree plots respectively, data summarized by Holdridge et al., [1971]). Tree plots within lowland rainforest (Figure 2C) were at elevations below 600 m and contained 341 tree species distributed in 234 genera and 69 families. Tree plots within montane rainforest (Figure 2C) were above 1,000 m elevation and included 166 tree species distributed in 121 genera and 71 families. Tree plots within premontane forest were between 600 and 1,000 m elevation and included 232 tree species distributed in 164 genera and 61 families. Species taxonomy was standardized using The Taxonomic Name Resolution Service (TNRS, Boyle et al., 2013).

Broad-scale species assemblages

We described the composition of 25 × 25 km sampling units across Central America (Figure 2A) in terms of the 531 tree species found in the 39 Costa Rican tree plots. We used occurrence data compiled from the Botanical Information and Ecology Network (BIEN 4.1; Enquist et al., 2009) and Tropicos® (http://tropicos.org/). Records falling outside Central America, with missing geographic coordinates or uncertain species level determinations were excluded. We also ascertained that the geographic coordinates for each specimen record were consistent with the description of the collection locality. The final data set comprised 162,942 specimen records distributed across Central America.

We characterized the species composition of 25 × 25 km sampling units with at least 200 specimen records (Figure 2A, mean = 534; quartiles 25th = 251, 50th = 331 and 75th = 619). We chose this cut-off in the number of specimen records after considering the trade-off between the accuracy of estimates of species composition and geographic coverage. Increasing the minimum number of specimen records required per sampling unit increases the quality of the descriptions of the species assemblages in 25 x 25 km sampling units; but it also decreases the number of sampling units available for analysis and, therefore, the representation of different areas of the Central American subcontinent. We judged estimates based on samples of 200 specimen records to be a reasonable compromise (see cumulative number of sampling units as a function of specimen number in Figure S1).

We focused on sampling units located in lowland or montane rainforest. To do so we first identified sampling units located within wet, rainy, and moist ecoregions, based on the map of Terrestrial Ecoregions of the World (Olson et al., 2001). We then categorized the sampling units located in these ecoregions as lowland or montane according to whether they were located below 600 m or above 1,000 m of elevation, respectively, based on a 1-km resolution digital elevation map from CGIAR-SRTM (version 4.1; http://srtm.csi.cgiar.org/). This procedure identified 61 sampling units in lowland rainforest and 28 in montane rainforest (Figure 2B).

Test of taxonomic differences between lowland and mountain tree floras that Gentry (1982) hypothesized

To test if Central American floras are characterized by a dichotomy between the families occurring in montane and lowland rainforest, as suggested by Gentry (1982), we conducted a non-metric multidimensional scaling ordination (NMDS, Legendre and Legendre 2012) on the plant family composition of local species assemblages (tree plots) located in lowland, montane, and premontane rainforests. We performed a linear discriminant analysis on the NMDS axes, to test if local species assemblages (tree plots) could be confidently assigned to montane or lowland rainforest. Based on the NMDS ordination we further examined if particular plant families showed contrasting patterns of occurrence between lowland and montane tree floras, in the direction specified by Gentry (1982) according to presumed southern or northern origin. Thus, we used Gentry's (1982; Table S1) classification of plant families into presumed southern or northern in origin (which were largely based on Raven and Axelrod 1974) and examined: i) whether montane rainforest were mainly composed of tree species that belong to plant families of presumed northern origin (Laurasian origin). And, ii) whether lowland rainforests were dominated by trees that belong to plant families of presumed southern origin (Gondwanan origin). We stress that we used Gentry's classification of plant families according to presumed origin only to test the particular patterns of taxa distribution he advanced. We certainly do not claim or assume that such classification is accurate, an issue we address in the Discussion section.

Test of predictions derived from the spatial nested pattern that Gentry (1982) hypothesized

To test predictions about the number of shared species between sites (Figure 1C and D), we estimated species turnover between species assemblages, separately for lowland and montane rainforest. We used rarefaction (Gotelli and Colwell 2001) to account for heterogeneity in collection effort among the 25 × 25 km sample units of broad-scale species assemblages. In particular, we repeatedly subsampled 200 specimen records from each 25 × 25 km sample unit and calculated the number of species shared between each subsample and each local species assemblage (tree plot). We obtained 1,000 subsamples from each 25 × 25 km sampling unit and calculated the mean number of shared species with each local assemblage (tree plot) across subsamples.

To test whether the distance decay of the number of shared species between local and broad-scale species assemblages in the lowland rainforest had a more negative slope towards

Tehuantepec than towards the Darien region (Figure 1C), we used the following multiple regression model on distance matrices (Lichstein 2007, Legendre and Legendre 2012):

$$\textit{mean number of shared species} = b_0 + b_1 \times D + b_2 \times D \times Z + \varepsilon \qquad \text{equation (1),}$$

where any single value of the response matrix represents the mean number of shared species between a local (tree plot) and a broad-scale species assemblage (25 × 25 km sampling unit), both located within lowland rainforest, Z is a dummy variable taking a value of zero when the broad-scale species assemblage (25 × 25 km sampling unit) is closer to the Darien region than the local species assemblage (tree plot) and one otherwise (i.e., when the broad-scale species assemblage is closer to the Isthmus of Tehuantepec than the local species assemblage; Figure 2S). When the dummy variable Z takes a value of zero, D is the difference between the distance from the tree plot to the Darien region and the distance from the 25 × 25 km sampling unit to the Darien region (Figure 3A). When the dummy variable Z takes a value of one, D is the difference between the distance of tree plot to the Isthmus of Tehuantepec and the distance of the 25 × 25 km sampling unit to the Isthmus of Tehuantepec (Figure 3B). Finally, terms b_0 to b_2 are regression coefficients and ε is the error term.

Thus, when $Z = 0$, equation (1) simplifies to:

$$\textit{mean number of shared species} = b_0 + b_1 \times D + \varepsilon \qquad \text{equation (2),}$$

where coefficient b_1 is the rate of decay towards the Darien region in the number of shared species between local and broad-scale species assemblages within the lowland rainforest. In contrast, when $Z = 1$, equation (1) may be expressed as:

$$\textit{mean number of shared species} = b_0 + (b_1 + b_2) \times D + \varepsilon \qquad \text{equation (3),}$$

where $b_1 + b_2$ is the rate of decay towards the Isthmus of Tehuantepec in the number of shared species between local and broad-scale species assemblages within lowland rainforest. Thus, empirical support for the prediction that decay in the number of shared species is steeper towards Tehuantepec than towards the Darien region (Figure 1C), requires b_2 (equations 1 and 3) to be statistically significant and negative. To determine the statistical significance of the regression coefficients we used a null model that simultaneously randomized the order of the rows and columns in the response matrix, thus preserving any dependencies among all values involving a particular local or broad-scale species assemblage (Lichstein 2007, Legendre and Legendre 2012). We fitted the regression model in equation (1) to each of 1,000 iterations of the null model and thus constructed a null distribution of 1,000 values for each regression coefficient. We estimated p-values for each regression coefficient as the fraction of values in the null distribution that were at least as extreme as the observed coefficient.

To test if the distance decay of the number of shared species between local and broad-scale species assemblages in the montane rainforest had a more negative slope towards the Darien region than towards Tehuantepec (Figure 1D), we used the multiple regression model on distance matrices presented in equation (1), above, applied to comparisons between local (tree plot) and broad-scale species assemblages (25 × 25 km sampling units) located within montane rainforest. In this case, empirical support for the prediction requires $\boldsymbol{b_2}$ (equations 1 and 3) to be statistically significant and positive. We tested the statistical significance of these coefficients relying on 1,000 iterations of the null model described above.

To test predictions about the number of unique species in local assemblages (tree plots; Figure 1E and F) we estimated the number of species unique to a local assemblage in a comparison between local and broad-scale species assemblages, separately for lowland and montane rainforests. We used rarefaction (Gotelli and Colwell 2001) to account for differences in collection effort among the 25× 25 km sampling units used to describe broad-scale species assemblages. Then, we estimated the mean number of species unique to local assemblages in a similar manner as we did for the mean number of shared species (see above).

To test if in lowland rainforest the relationship between distance and the number of unique species to local assemblages had a more positive slope towards Tehuantepec than towards the Darien region (Figure 1E), we used the following multiple regression model on distances matrices (Lichstein 2007, Legendre and Legendre 2012):

$$\textbf{\textit{mean number of species unique to local assemblages}} = b_0 + b_1 \times D + b_2 \times D \times Z + \varepsilon \qquad \text{equation (4),}$$

where any single value of the response matrix is the mean number of species unique to a local (tree plot) assemblage in a comparison to a broad-scale species assemblage (25 × 25 km sampling unit), $\boldsymbol{Z}$ is a dummy variable taking a value of zero when the broad-scale species assemblage is closer to the Darien region than the local species assemblage (tree plot) and one otherwise (i.e., when the broad-scale species assemblage is closer to the Isthmus of Tehuantepec than the local species assemblage). When the dummy variable **Z** takes a value of zero, $\boldsymbol{D}$ is the difference between the distance of tree plot to the Darien region and the distance of the grid-cell to the Darien region (Figure 3A). When the dummy variable **Z** takes a value of one, $\boldsymbol{D}$ is the difference between the distance from the tree plot to the Isthmus of Tehuantepec and the distance from the grid-cell to the Isthmus of Tehuantepec (Figure 3B). Finally, terms b_0 to b_2 are regression coefficients and ε is the error term.

Thus, when $Z = 0$, equation (4) simplifies to:

$$\textbf{mean number of species unique to local assemblages} = b_0 + b_1 \times D + \varepsilon \quad \text{equation (5)},$$

where coefficient b_1 is the rate of increment towards the Darien region in the number of species unique to local assemblages within the lowland rainforest.

In contrast, when $Z = 1$, equation (1) may be expressed as:

$$\textbf{mean number of species unique to local assemblages} = b_0 + (b_1 + b_2) \times D + \varepsilon \quad \text{equation (6)},$$

where $b_1 + b_2$ is the rate of increment towards the Isthmus of Tehuantepec in the number of species unique to local assemblages within the lowland rainforest. Thus, empirical support for the prediction that increment in the number of species unique to local assemblages is steeper towards Tehuantepec than towards the Darien region (Figure 1E) requires b_2 (equations 4 and 6) to be statistically significant and positive. To determine the statistical significance of the regression coefficients we used the same null model approach as we did for the number of shared species (see above). Thus, we fitted the regression model in equation (4) to each 1,000 iterations of the null model and constructed a null distribution of 1,000 values for each regression coefficient. We estimated p-values for each regression coefficient as the fraction of values in the null distribution that were at least as extreme as the observed coefficient.

To test if the relationship between distance and the number of species unique to local assemblages in montane rainforest had a more positive slope towards Darien than towards Tehuantepec (Figure 1F), we used the multiple regression model on distance matrices presented in equation (4), above, applied to comparisons between local (tree plots) and a broad scale species assemblages located within montane rainforest. In this case, empirical support for the prediction requires b_2 (equation 4 and 6) to be statistically significant and negative. We tested the statistical significance of these coefficients relying on 1,000 iterations of the null model described above.

RESULTS

Tree family composition differed markedly between lowland and montane rainforests (Figure 4A and B). Central American lowland rainforest included a disproportionately high number of species belonging to families presumed to have southern origin. Conversely, families with presumed southern origin did not contribute as much to montane rainforest, which also included significant number of species belonging to families of presumed northern origin (Figure

4C and D). Additionally, other families (i.e., not presumed to have southern or northern origin) were present in both types of rainforests, although they seemed to contribute proportionally more to montane than lowland rainforest (Figure 4C and D). In addition, we found that premontane rainforest was more similar to lowland than montane rainforest in terms of tree family composition (Figure 4A and B). These results partially support Gentry's (1982) hypothesized pattern; species from families with presumed southern origin are important and dominant components in lowland forest. However, contrary to what Gentry (1982) hypothesized, species of presumed northern origin do not seem to dominate montane rainforest, at least in terms of species numbers.

In both lowland and montane rainforests, the number of shared species between local (tree plots) and broad-scale (25 × 25 km sampling units) species assemblages decreased with increasing geographic distance towards the Darien region or the Isthmus of Tehuantepec (Figure 5A and B). According to the predictions derived from Gentry’s (1982) hypothesis, in lowland rainforest the distance decay of the number of shared species between local and broad-scale species assemblages should be steeper towards Tehuantepec than towards Darien (Figure 1C). Despite a trend in the predicted direction, we only found a marginal significant difference between the rate of decay in the number of shared species towards Tehuantepec and Darien regions (Figure 4A and Table 1). For montane rainforest the prediction was that the distance decay of the number of shared species between local and broad-scale species assemblages should be steeper towards the Darien region than towards Tehuantepec (Figure 1D). Contrary to this expectation, we found that the distance decay was steeper towards Tehuantepec than towards the Darien region, and that this difference was statistically significant (Figure 5B and Table 1).

For lowland and montane rainforests, the number of species unique to local assemblages incremented with the distance towards the Isthmus of Tehuantepec or the Darien region (Figure 5C and D). According to the predictions derived from Gentry’s (1982) hypothesis, this increment should be higher towards Tehuantepec than towards Darien in lowland rainforests (Figure 1E), and higher towards Darien than towards Tehuantepec in montane rainforests (Figure 1F). Yet, for both, lowland and montane rainforests, the rate of increment in the number of species unique to local assemblages was similar towards Tehuantepec and Darien regions (Figure 5C, D and Table 1).

DISCUSSION

The Great American Biotic Interchange (GABI) is considered one of the major events that shaped current Neotropical biotas (Simpson 1980, Gentry 1982, Marshall et al., 1982, Stehli and Webb 1985, Webb 1985, Burnham and Graham 1999, Graham 2010, Lomolino et al., 2010). In this context, Gentry (1982) hypothesized contrasting GABI legacies for Central American lowland and montane tree floras, i.e. (i) marked taxonomic differences between these two floras at the level of plant families and (ii) particular nested spatial gradients of species diversity across Central America that run in opposing directions in lowland and mountain tree floras. According to Gentry (1982), Central American lowland tree floras form a nested spatial pattern of decreasing species richness from the Darien region toward the Isthmus of Tehuantepec; while Central American montane tree floras form a nested spatial pattern of decreasing species richness from the north to the south of Central America (opposite to lowland tree floras). Determining whether existing data support the existence of these contrasting broad-scale spatial legacies of GABI is fundamental to our understanding of Central America tree floras. However, we are unaware of studies that test this hypothesis empirically (but see Gentry 1982, Burnham and Graham 1999, Dick et al., 2005).

Here, we examined the two patterns hypothesized by Gentry (1982) as spatial legacies of GABI on Central American floras. To do so we used data on tree local assemblages (tree plots) distributed in Costa Rican rainforest, and an extensive database of tree herbarium specimens from Central American rainforests. Two main findings emerged from our analysis. First, we found partial support for Gentry's (1982) hypothesized pattern about the taxonomic composition of lowland and montane rainforest at the level of plant families. We found a marked difference in the family composition of lowland and montane rainforest, and that lowland rainforests were composed in its majority by species belonging to families of presumed southern origin. However, montane rainforest was not dominated by species belonging to families of presumed northern origin. Second, we did not find support for the predictions derived from Gentry's (1982) hypothesis regarding nested spatial patterns. Central American lowland and montane rainforest do not exhibit a nested spatial pattern as hypothesized by Gentry (1982). For lowland rainforest, the distance decay of the number of shared species was similar towards Darien and Tehuantepec. For montane rainforest we found a pattern opposite to the prediction: steeper distance decay of the number of shared species towards Tehuantepec than towards Darien. Thus, montane rainforest in Costa Rica seems to be more similar in composition to montane forest near South America. In addition, in both lowland and montane rainforest, the increment of species unique to local assemblages was similar towards Darien and Tehuantepec. Below we explore potential caveats in our analysis and the implications of these findings for our understanding of the structure of Central American floras.

Gentry (1982) discussed the assemblage of Central American floras in terms of the biogeographic origin of different lineages. Most of this discussion relied on the work by Raven and Axelrod (1974), which in turn was based on a combination of fossils and biogeographic evidence. Gentry (1982) emphasized that most species in Central American lowland forest come from lineages of presumed southern origin, and species occurring in Central American montane forest from lineages of northern origin. However, to be meaningful, such biogeographic origins must be discussed relative to an explicit time frame, because the assignment of species' origins may change as the reference time frame shifts farther away from the present (Ackerly 2009). In this context, the relevant question is: where did the lineages occur just before reaching Central America? Ideally, this question would be addressed by studies that reconstruct the ancestral geographic distribution of the lineages currently occurring in Central America. By example, studies based on fossil-calibrated phylogenies have examined the ancestral distribution of lineages in Bignoniaceae (Lohman et al., 2013), Burseraceae (Weeks et al., 2005), Meliaceae (Muellner et al., 2006), Annonaceae (Richardson et al., 2004), Moraceae (Zerega et al., 2005), Lauraceae (Chanderbali et al., 2001), Sapotaceae (Smedmark and Aderberg 2007) and Melastomataceae (Renner et al., 2001). In some cases these studies suggest different origins to those assumed by Gentry (1982). However, such analyses are not yet available for the majority of Central American tree lineages.

Gentry (1982) was partially correct regarding the family composition of lowland and montane rainforest. These forests are very distinctive based on the putative origin (following Gentry's (1982) classification) of the families that assembled them. Central America lowland forests are assembled predominantly by tree species that belong to families of putative southern origin (Figure 4D). Conversely, montane forests are assembled by tree species that belong to families of putative southern and northern origin, but are not dominated by the latter (Figure 4D). This last result is at odds with Gentry’s (1982) suggestion that montane forests have predominantly tree species belonging to families with northern origin. However, we emphasize that our findings reflect dominance in terms of the number of tree species per plant family. We did not have abundance data and, thus, did not examine dominance in terms of number of individual trees. Nevertheless, we still found that lowland and montane rainforest are different in plant family composition (Figure 4A and C), which indicates a clear separation in the lineages from which these forests were assembled. There are characteristic families present in each type of forest. A few plant families contain ca. 50% of species in Neotropical lowland rainforest (Jaramillo and Cardenas 2013), from most to least important: Fabaceae, Moraceae, Annonaceae, Lauraceae, Myristicaceae, and Arecaceae. Most of the species that belong to these families and that were included in our study occur in lowland forest (Table S1), which is in agreement with Gentry's 1982 observation regarding the composition of plant families in lowland rainforest. However, although Gentry (1982) was correct about some characteristic tree families occurring within montane rainforest, such as Actinidaceae, Betulaceae, Clethraceae, Cornaceae, Garryaceae, Papaveraceae and Rosaceae, there are also other characteristic families occurring in this type forest, some of presumed southern origin. These families are Ericaceae, Brunelliaceae, Cunoniaceae, Pentaphylacaceae, Podocarpaceae, Verbenaceae, Winteraceae among others (Figure 4C and Table S1).

The contrast in the family composition between lowland and montane Central American rainforests indicates a clear separation in the lineages from which these two forests were assembled. This may be surprising because angiosperm families are old clades (stem ages between 140 and 20 Ma; Magallón et al., 2015) and because lowland and montane rainforest are contiguous to each other. Thus, despite seemingly ample opportunity, colonization of montane areas by lineages characteristic of lowland rainforest appears uncommon. The same is true for colonization of lowland areas by lineages characteristic of montane forests. This observation could mean that lineages characteristic of lowland and montane rainforest are adapted to relatively narrow ranges of biotic and abiotic requirements, which may be constraining colonization of lowland or montane forests. In the case of species belonging to families that are characteristic to lowland rainforest, colonization of montane areas might require adaptation to frost and chilling.

Gentry (1982) hypothesized that the migration of lineages (north to south for lowland rainforest and south to north for montane rainforest) imprinted spatial patterns on present Central American lowland and montane rainforest. He described these patterns as a decrease in species richness from south to north for lowland rainforest, and north to south for montane rainforest, which reflected a nested spatial pattern of species composition. We did not find support for the spatial nested patterns that he described for lowland and montane rainforest (Figure 5A-D, Table 1). Dick et al. (2005) found that ca. 63% of the species occurring in the

Panama Canal watershed also occurred in Amazonia. However, only 21% of these species had a primarily Amazonian distribution, the rest being widely distributed. Most of these species seem to expand their ranges across South American and Central American lowland forests. The movement of species between Central America and South America may have been too fast to leave any enduring spatial legacy, thus the nested pattern that Gentry (1982) hypothesized may have never existed.

In the case of Central American montane rainforest, the Great American Biotic Interchange may have left a spatial legacy that differs from what previous authors proposed (Gentry 1982, Graham 2010). We found a pattern, different to the one predicted by Gentry (1982), whereby distance decay in the number of shared species was steeper from Costa Rica towards Tehuantepec than towards Darien region (Figure 5B). This result suggests that the Central American montane forest seems to form a nested gradient of species richness from Darien to the Tehuantepec region. Thus, lineages occurring in the South America montane rainforest appear to be important also in the Central American montane rainforest, for example, plant families such as Ericaceae, Cunoniaceae, Podocarpaceae are important components in both Central American and South American montane rainforest (Figure 4C, Gentry, 1995, Macía and Fuertes 2008).

Central American lowland and montane forests do not show the nested spatial structure that Gentry (1982) proposed as a GABI legacy. Lowland rainforests seem not to form a nested spatial gradient of species richness, and montane rainforests form a nested spatial gradient in the opposite direction to that proposed by Gentry (1982). These results have implications for our understanding of the spatial structure of Central American floras, especially if we want to propose useful hypotheses about processes responsible for the assembly of these floras. Similarly, understanding the spatial structure of biotas is fundamental for the identification of priority areas for biodiversity conservation (Serrano et al., 2018 and references therein). Ideally, conservation priorities would be based on complete information about the spatial distribution of species (Rodrigues and Brooks 2007); but for many groups of organisms, including plants, and many areas across Earth, particularly tropical ecosystems, our knowledge of species distributions and spatial patterns of diversity is extremely limited (the “Wallacean shortfall,” Hortal et al., 2015). Lack of empirical support for Gentry’s (1982) hypothesis illustrates this shortfall and points at the limits of expert opinion. Broad-scale patterns of tropical diversity, encompassing hundreds of thousands of square kilometers and hundreds of species, may be far too complex for informed guesses to be accurate, even if aiming only at general descriptions. To understand such patterns it is important to carry out explicit analysis of currently available data, while recognizing uncertainty and the need to collect further species occurrence data.

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FIGURES

Figure 1. Gentry's (1982) hypotheses about spatial legacies of the Great Biotic Interchange in Central American tree floras and predictions derived from them. **A.** Hypothesized nested spatial gradient of tree species in lowland rainforest of Central America, where richness decreases from the Darien region to the Isthmus of Tehuantepec. **B.** Hypothesized nested spatial gradient of tree species in montane rainforest of Central America, with decreasing richness from the Isthmus of Tehuantepec to the Darien region. **C.** Predictions about the number of shared species between a focal site and sites occurring towards Darien and Tehuantepec for lowland rainforest, in which the number of shared species should decrease at a faster rate towards Tehuantepec (red dots and line) than toward Darien (blue dots and line). **D.** Predictions about the number of shared species between a focal site and sites occurring towards Darien and Tehuantepec for montane rainforest, in which the number of shared species should decrease at a faster rate towards Darien (blue dots and line) than towards Tehuantepec (red dots and line). **E.** Predictions about the rate of change in the number of species unique to the focal site when comparing it with sites towards Darien and Tehuantepec within lowland rainforest. The increase in the number of unique species is higher towards Tehuantepec (red dots and line) than toward Darien (blue dots and line). **F.** Predictions about the rate of change in the number of species unique to the focal site relative to sites towards Darien and Tehuantepec within montane forest. The increase in the number of unique species is higher towards Darien (blue dots and line).

Figure 2. Geographic distribution of 25 × 25 km sampling units (broad-scale species assemblages) and ca. 0.3 ha tree plots (local species assemblages) across the Central American subcontinent, defined as the landmass between the Isthmus of Tehuantepec and the Darien region. **A.** Density of tree specimen records across 25 × 25 km sampling units; only sampling units with at least 200 specimen records were used to test Gentry's (1982) hypothesis. **B.** Distribution of 25 × 25 km sampling units with at least 200 specimen records (broad-scale species assemblages) between montane and lowland rainforests). **C.** Distribution of tree plots (local species assemblages) between lowland and montane rainforests.

Figure 3. Distance (*D*) estimates used in distance matrix regression models. **A)** Example for one local species assemblage (tree plot) and two broad scale species assemblages (25 x 25 km sampling units) that are closer to Tehuantepec than to Darien. Distance from the local and broad scale assemblages to Tehuantepec is shown by continuous and dotted black lines, respectively. **B.** Example for one local species assemblage (tree plot) and two broad scale

species assemblages (25 x 25 km sampling units) that are closer to Darien than to Tehuantepec. Distance from the local and broad scale assemblages to Darien is shown by continuous and dotted black lines, respectively. Both **A** and **B** show species assemblages in montane rainforests. Distance estimates (e.g. D_1, D_2, D_3 and D_4) were measured as the difference between the distance of the local species assemblage to Isthmus of Tehuantepec or Darien region and the distance of the broad-scale species assemblage to Isthmus of Tehuantepec or Darien region.

Figure 4. A. Non-metric multidimensional scaling ordination of lowland, montane and premontane rainforest local assemblages (39 tree plots) based on plant family composition. **B.** Distribution of local assemblages in the space defined by the first ordination axis. **C.** Loadings of plant families labeled according to presumed origin, following Gentry (1982). **D.** Distribution of plant families along the first ordination axis, labeled according to presumed origin.

Figure 5. Tests of predictions derived from Gentry's (1982) hypothesis. **A.** Distance decay in the mean number of shared species between pairs of local (tree plot) and broad-scale (25 × 25 km sampling units) assemblages in lowland rainforest. **B.** Distance decay in the mean number of shared species between pairs of local (tree plot) and broad-scale (25 × 25 km sampling units) assemblages in montane rainforest. **C.** Relationship between geographic distance and the number of species unique to a local assemblage in pairwise comparisons between local and broad-scale assemblages in lowland rainforests. **D.** Relationship between geographic distance and the number of species unique to a local assemblage in pairwise comparisons between local and broad-scale assemblages in montane rainforests.

Figure 1

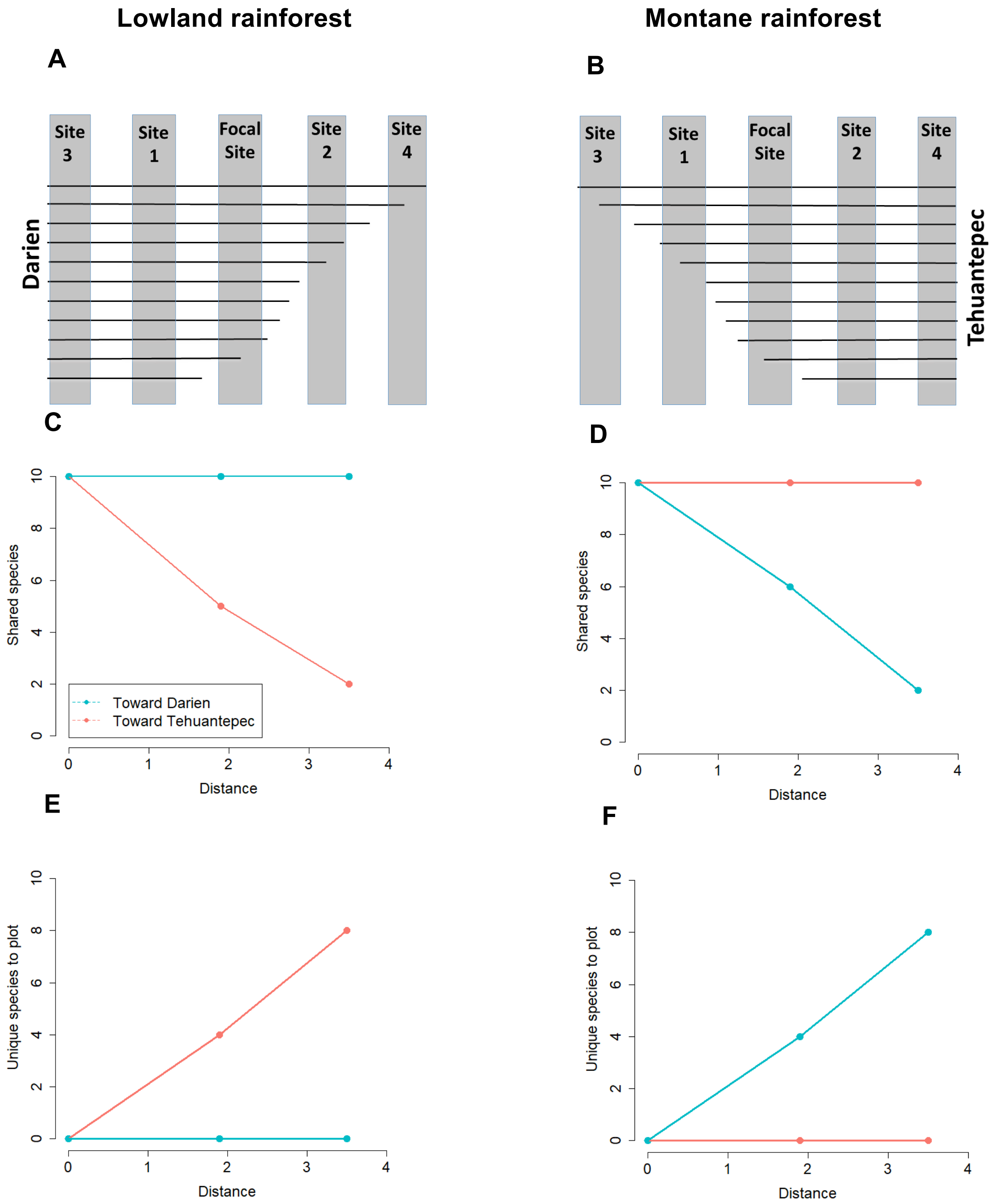
Lowland rainforest
Montane rainforest
A
Site 3
Site 1
Focal Site
Site 2
Site 4
Darien
B
Site 3
Site 1
Focal Site
Site 2
Site 4
Tehuantepec
C
Shared species
0
2
4
6
8
10
0
1
2
3
4
Distance
Toward Darien
Toward Tehuantepec
D
Shared species
0
2
4
6
8
10
0
1
2
3
4
Distance
E
Unique species to plot
0
2
4
6
8
10
0
1
2
3
4
Distance
F
Unique species to plot
0
2
4
6
8
10
0
1
2
3
4
Distance

Figure 2

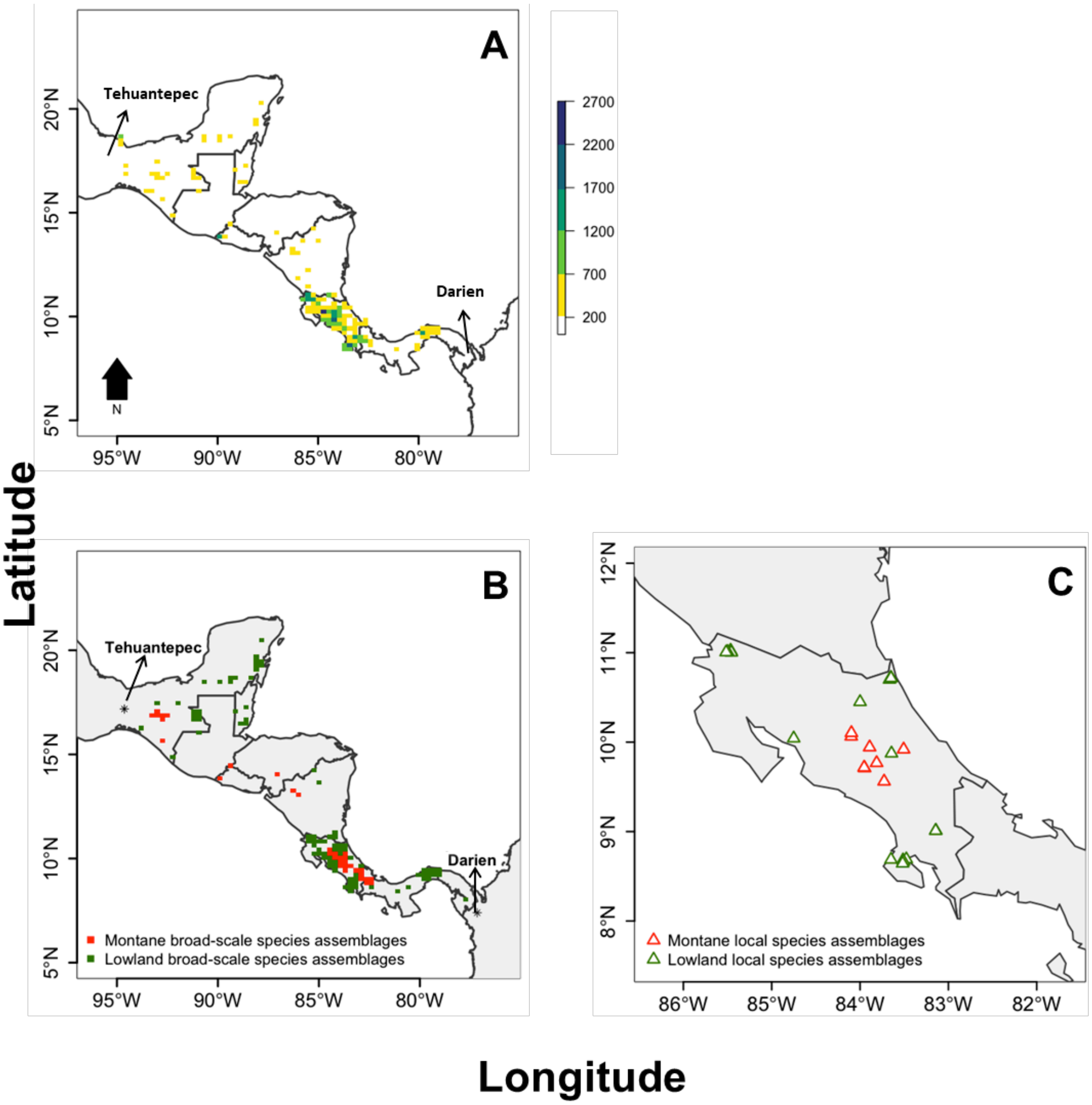
A
Tehuantepec
Darien
N
2700
2200
1700
1200
700
200
20°N
15°N
10°N
5°N
95°W
90°W
85°W
80°W
Latitude
B
Tehuantepec
Darien
🟥 Montane broad-scale species assemblages
🟩 Lowland broad-scale species assemblages
C
△ Montane local species assemblages
△ Lowland local species assemblages
12°N
11°N
10°N
9°N
8°N
86°W
85°W
84°W
83°W
82°W
Longitude

Figure 3

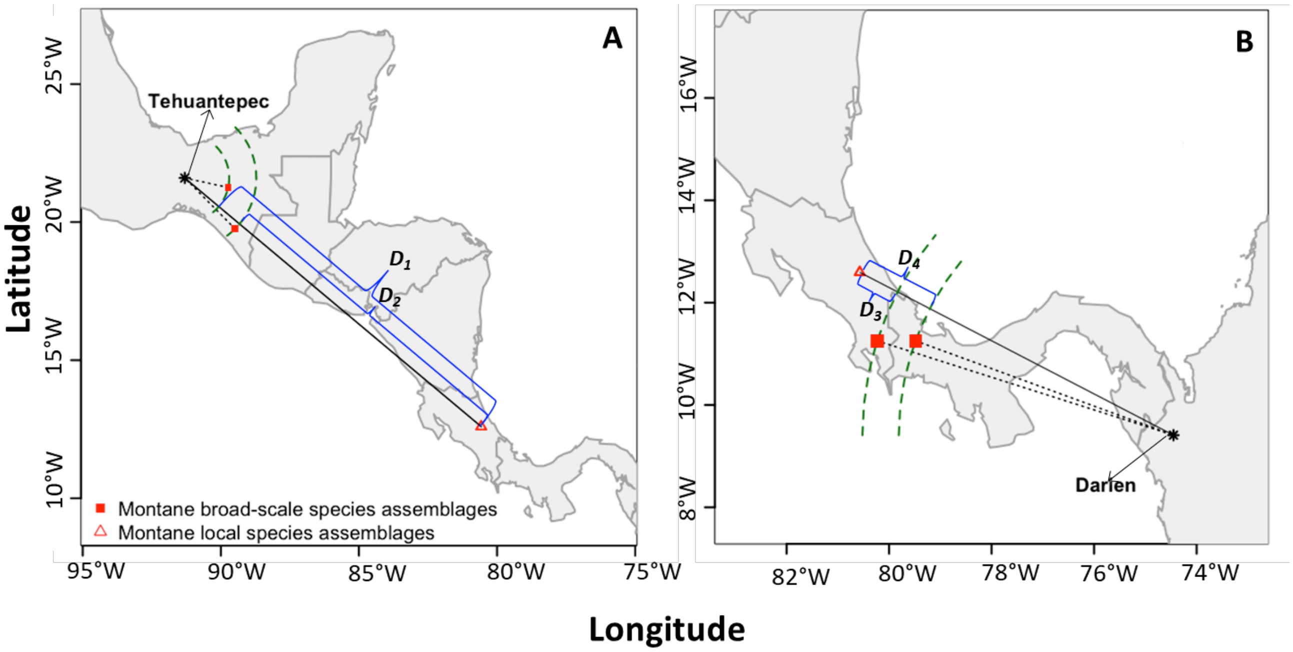
A
Tehuantepec
D1
D2
25°W
20°W
15°W
10°W
■ Montane broad-scale species assemblages
△ Montane local species assemblages
95°W
90°W
85°W
80°W
75°W
B
D4
D3
Darien
16°W
14°W
12°W
10°W
8°W
82°W
80°W
78°W
76°W
74°W
Latitude
Longitude

Figure 4

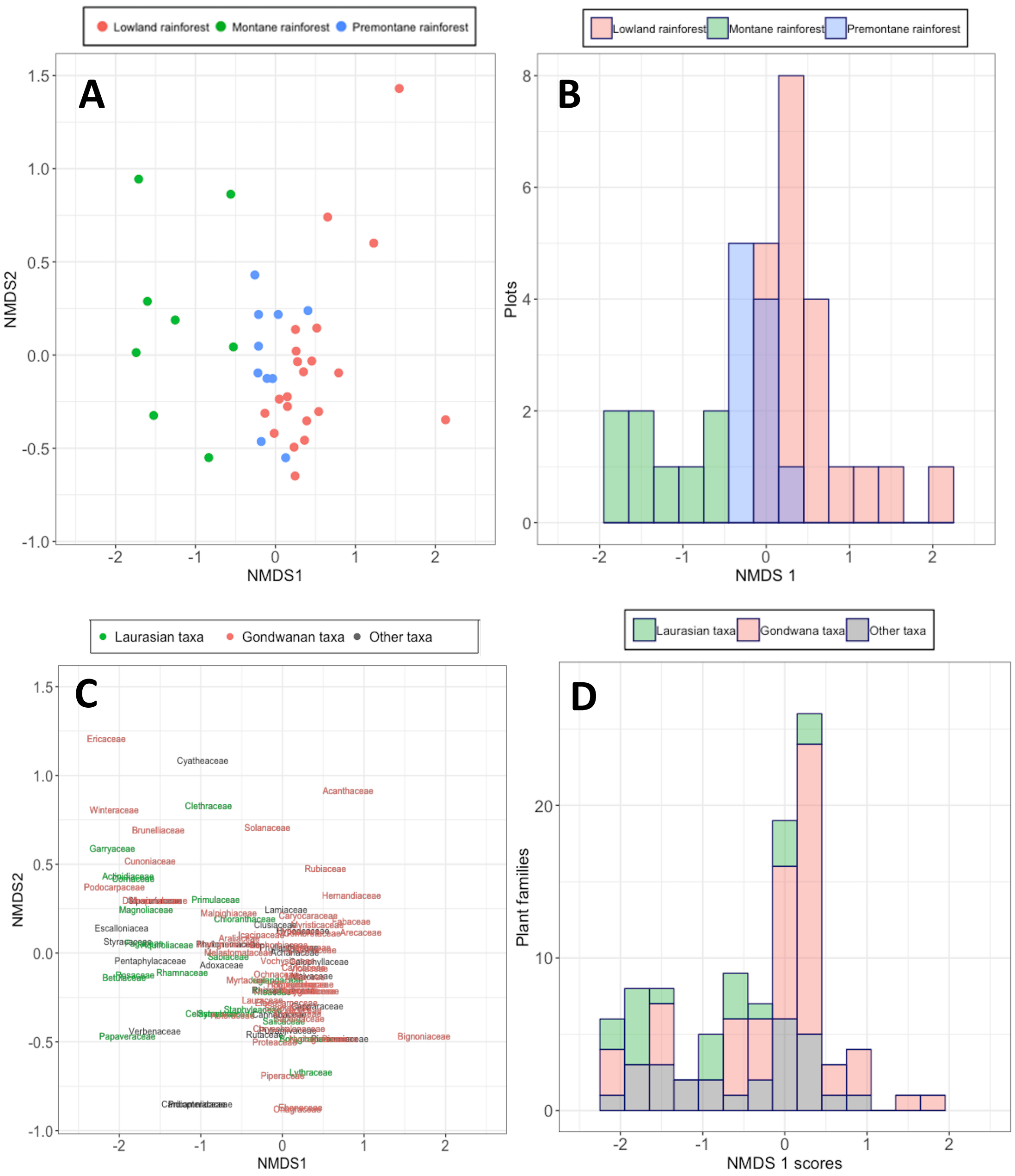
● Lowland rainforest ● Montane rainforest ● Premontane rainforest
A
NMDS2
NMDS1
1.5
1.0
0.5
0.0
-0.5
-1.0
-2
-1
0
1
2
🟥 Lowland rainforest 🟩 Montane rainforest 🟦 Premontane rainforest
B
Plots
NMDS 1
8
6
4
2
0
-2
-1
0
1
2
● Laurasian taxa ● Gondwanan taxa ● Other taxa
C
NMDS2
NMDS1
Ericaceae
Cyatheaceae
Acanthaceae
Winteraceae
Clethraceae
Brunelliaceae
Solanaceae
Garryaceae
Cunoniaceae
Rubiaceae
Actinidiaceae
Cornaceae
Podocarpaceae
Primulaceae
Hernandiaceae
Magnoliaceae
Malpighiaceae
Lamiaceae
Chloranthaceae
Caryocaraceae
Escalloniacea
Clusiaceae
Myristicaceae
Fabaceae
Hypericaceae
Arecaceae
Araliaceae
Icacinaceae
Styracaceae
Aquifoliaceae
Melastomataceae
Achariaceae
Sabiaceae
Pentaphylacaceae
Adoxaceae
Calophyllaceae
Betulaceae
Rosaceae
Rhamnaceae
Malvaceae
Lauraceae
Capparaceae
Staphyleaceae
Cannabaceae
Salicaceae
Verbenaceae
Papaveraceae
Rutaceae
Proteaceae
Bignoniaceae
Piperaceae
Lythraceae
Onagraceae
1.5
1.0
0.5
0.0
-0.5
-1.0
-2
-1
0
1
2
🟩 Laurasian taxa 🟥 Gondwana taxa ⬜ Other taxa
D
Plant families
NMDS 1 scores
20
10
0
-2
-1
0
1
2

Figure 5

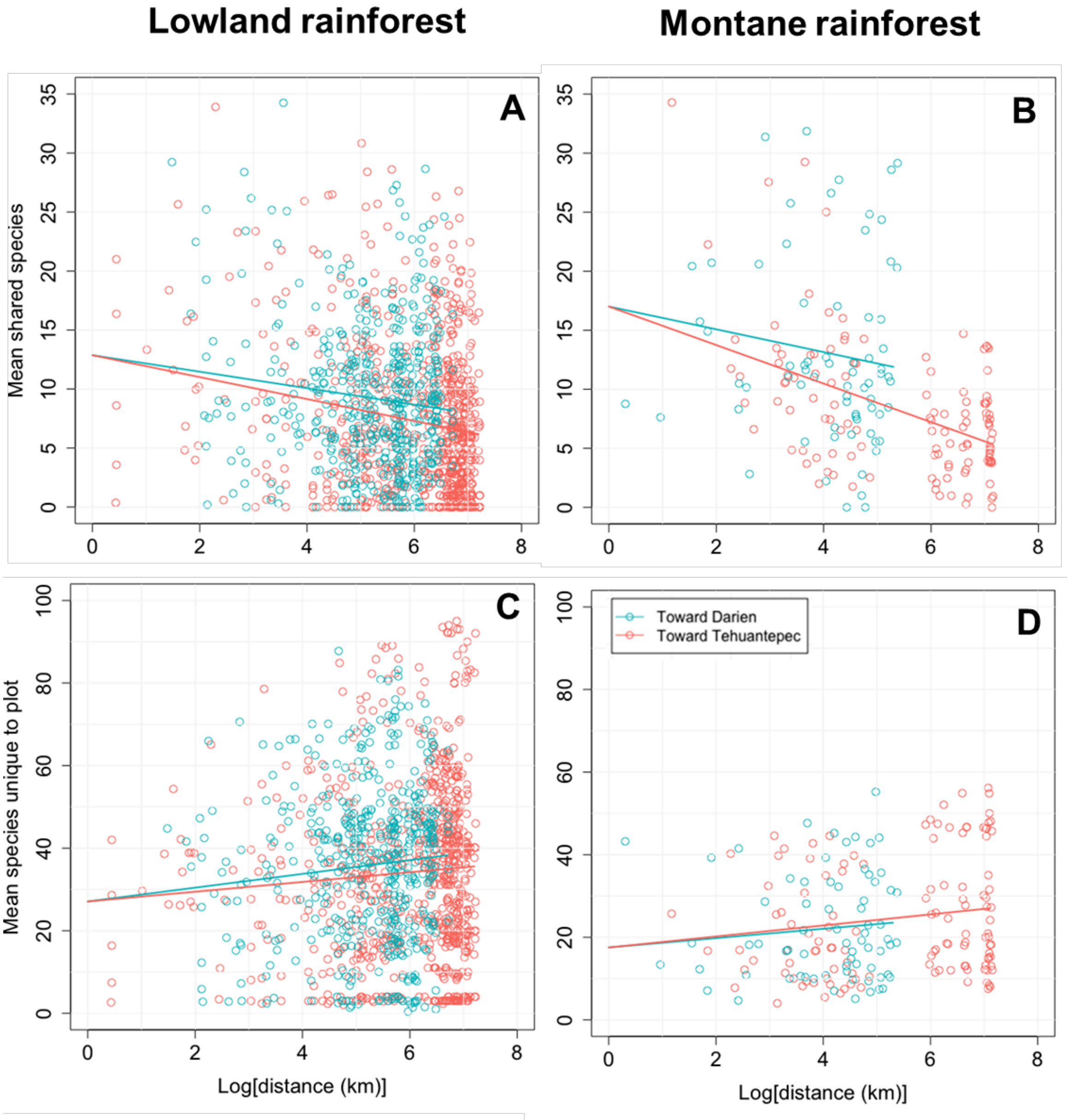
Lowland rainforest
Montane rainforest
A
B
C
D
Mean shared species
Mean species unique to plot
0
5
10
15
20
25
30
35
0
20
40
60
80
100
0
2
4
6
8
Log[distance (km)]
Toward Darien
Toward Tehuantepec

Table 1. Regression coefficients describing the relationship between geographic distance and the number of shared species and the number of species unique to a local assemblage (tree plot). These results come from pairwise comparisons between local (tree plots) and broad-scale assemblages (25 × 25 km sampling units) across lowland and montane rainforest in Central America. Statistical significance, as determined by p-values, is shown in parentheses.

	Shared species		**Species unique to the plot**	
	Lowland rainforest	**Montane rainforest**	**Lowland rainforest**	**Montane rainforest**
Intercept	12.86 (0.001)	17 (0.001)	27.09 (0.001)	17.53 (0.005)
Slope toward Darien	-0.69 (0.01)	-0.96 (0.06)	1.67 (0.005)	1.13 (0.07)
Difference in slope between Darien and Tehuantepec	-0.22 (0.08)	-0.67 (0.04)	-0.49 (0.1)	0.2 (0.3)

SUPLEMENTARY MATERIAL

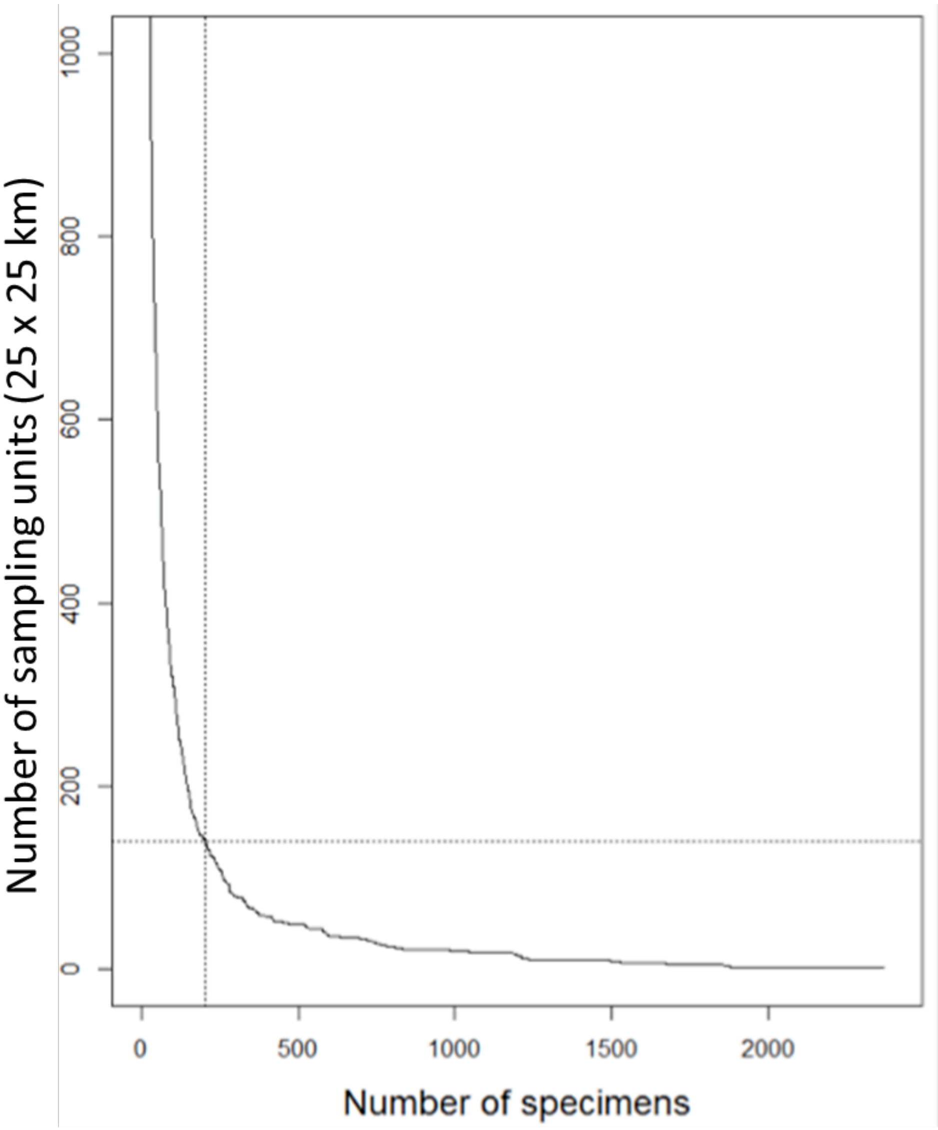

Figure S1. Frequency of sampling units (25 X 25 Km) as a function of the number of specimen's records. Many sampling units have few specimen records and few sampling units contain a high number of specimen records. We used for the analysis only sampling units with at least 200 specimen records (vertical dotted line). Using a higher cut-off value would imply a large reduction of the number of sampling units entering the analysis (below the horizontal dotted line).

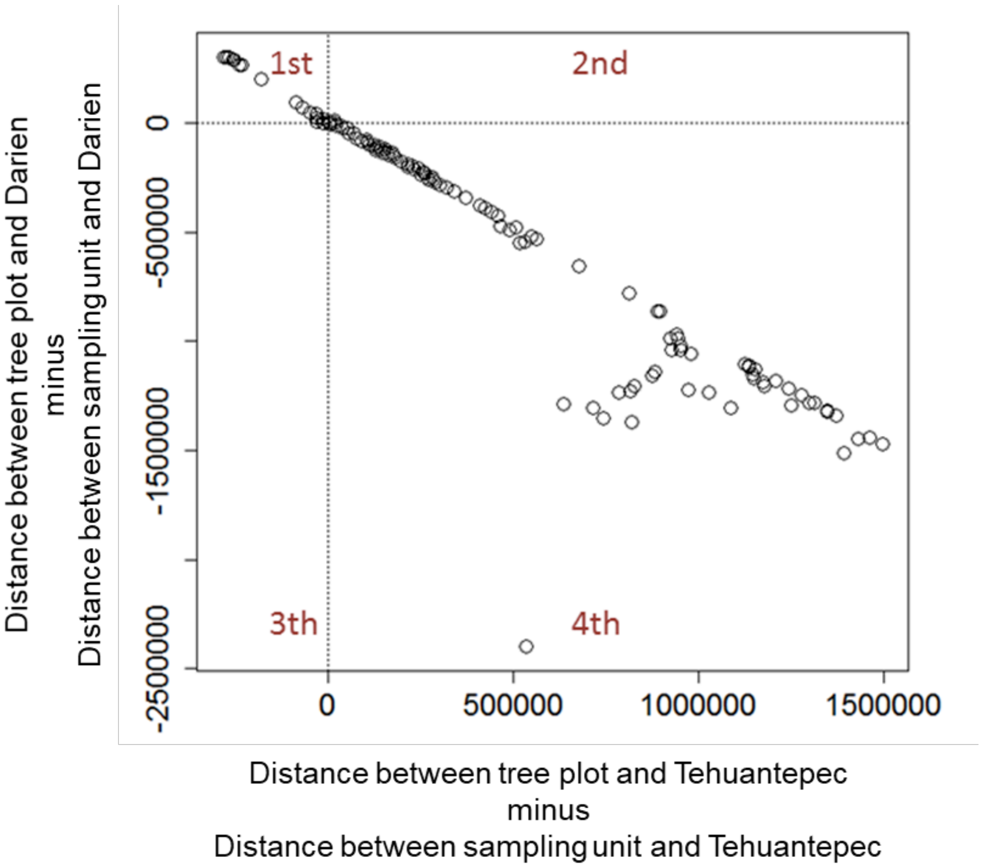

Figure S2. Position of sampling units of 25 x 25 km (open circles) across Central America, between the Isthmus of Tehuantepec and the Darien region, in relation to a specific tree plot. Sampling units in the first quadrant (labeled “1st”) are closer to the Darien region than to the Isthmus of Tehuantepec. Sampling units in the fourth quadrant (labeled “4th") are closer to the Isthmus of Tehuantepec than to the Darien region. Sampling units found in the second and third quadrants were not included in the analysis.

Table S1. Central American families used in the analysis with Gentry's (1982) classification according to biogeographic origin. Numbers indicate species present in each of three rainforest types.

Families	**Origin (Gentry 1982)**	**Lowland rainforest**	**Premontane rainforest**	**Montane rainforest**
Acanthaceae	Gondwana	1	0	0
Achariaceae	NA	2	1	0
Actinidiaceae	Laurasia	0	0	1
Adoxaceae	NA	2	0	2
Anacardiaceae	Gondwana	5	5	1
Annonaceae	Gondwana	10	4	2
Apocynaceae	Gondwana	5	2	1
Aquifoliaceae	Laurasia	0	1	3
Araliaceae	Gondwana	3	3	9
Arecaceae	Gondwana	14	6	1
Asteraceae	Gondwana	2	1	1
Betulaceae	Laurasia	0	0	1
Bignoniaceae	Gondwana	7	6	0
Bixaceae	Gondwana	2	0	0
Boraginaceae	Laurasia	3	2	1
Brunelliaceae	Gondwana	0	0	1
Burseraceae	Gondwana	5	3	0
Calophyllaceae	NA	1	1	2
Cannabaceae	NA	1	1	1
Capparaceae	NA	3	0	0
Cardiopteridaceae	NA	0	0	1
Caricaceae	Gondwana	2	1	0
Caryocaraceae	Gondwana	1	0	0
Celastraceae	Laurasia	2	1	3
Chloranthaceae	Laurasia	1	1	1
Chrysobalanaceae	Gondwana	4	1	0
Clethraceae	Laurasia	0	1	2
Clusiaceae	NA	4	5	4
Combretaceae	Gondwana	3	2	0
Cornaceae	Laurasia	0	0	1
Cunoniaceae	Gondwana	0	1	2
Cyatheaceae	NA	0	2	3
Dichapetalaceae	Gondwana	0	0	1
Ebenaceae	Gondwana	1	0	0
Elaeocarpaceae	Gondwana	4	4	1
Ericaceae	Gondwana	0	0	2
Escalloniacea	NA	0	0	1
Euphorbiaceae	Gondwana	8	9	5
Fabaceae	Gondwana	44	15	2

Table S1. Continued

Fagaceae	Laurasia	0	0	4
Garryaceae	Laurasia	0	0	1
Hernandiaceae	Gondwana	3	2	0
Humiriaceae	Gondwana	2	1	0
Hypericaceae	NA	1	2	0
Icacinaceae	Gondwana	1	1	1
Juglandaceae	Laurasia	1	2	1
Lacistemataceae	Gondwana	1	1	1
Lamiaceae	NA	1	0	1
Lauraceae	Gondwana	13	12	10
Lecythidaceae	Gondwana	5	1	1
Lythraceae	Laurasia	1	0	0
Magnoliaceae	Laurasia	0	0	2
Malpighiaceae	Gondwana	1	3	1
Malvaceae	NA	28	16	2
Marcgraviaceae	Gondwana	0	0	1
Melastomataceae	Gondwana	4	16	15
Meliaceae	Gondwana	8	8	3
Monimiaceae	Gondwana	0	0	1
Moraceae	Gondwana	22	12	3
Myristicaceae	Gondwana	6	5	0
Myrtaceae	Gondwana	2	2	2
Nyctaginaceae	Gondwana	3	0	0
Ochnaceae	Gondwana	3	3	1
Olacaceae	Gondwana	4	1	0
Onagraceae	Gondwana	0	1	0
Papaveraceae	Laurasia	0	0	1
Pentaphylacaceae	NA	0	0	3
Phyllanthaceae	NA	1	1	1
Phyllonomaceae	NA	0	0	1
Picramniaceae	NA	1	0	0
Piperaceae	Gondwana	1	0	0
Podocarpaceae	Gondwana	0	0	2
Polygonaceae	Gondwana	6	1	0
Pricamniaceae	NA	0	0	1
Primulaceae	Laurasia	2	4	6
Proteaceae	Gondwana	1	1	1
Putranjivaceae	NA	1	0	0
Rhamnaceae	Laurasia	1	1	2
Rhizophoraceae	Gondwana	1	1	0
Rosaceae	Laurasia	0	0	3
Rubiaceae	Gondwana	21	16	13

Table S1. Continued

Rutaceae	NA	7	2	2
Sabiaceae	Laurasia	1	2	3
Salicaceae	Laurasia	11	6	3
Sapindaceae	Gondwana	11	8	2
Sapotaceae	Gondwana	8	10	3
Simaroubaceae	Gondwana	3	1	0
Siparunaceae	NA	0	0	1
Solanaceae	Gondwana	1	0	1
Staphyleaceae	Laurasia	1	1	1
Styracaceae	Gondwana	0	0	1
Symplocaceae	Laurasia	1	1	1
Theaceae	Laurasia	0	1	0
Urticaceae	Gondwana	5	4	2
Verbenaceae	NA	0	0	3
Violaceae	Gondwana	3	0	0
Vochysiaceae	Gondwana	3	3	1
Winteraceae	Gondwana	0	0	1

CHAPTER 3.

Postglacial migration lags in Neotropical palms since the Last Glacial Maximum

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ABSTRACT

Migration lags due to the Last Glacial Maximum (LGM) are still controversial, especially in tropical areas. Lowland tropical regions are considered to be climatically more stable than temperate regions because they have not experienced directly the displacements experienced in temperate regions during the LGM. However tropical climates during the LGM are generally thought to have been colder and drier than current climates, and may have caused the contraction of the geographic distribution of species characteristic of warm and wet environments such as lowland humid-to-superhumid forest. As a consequence, species in these forests might be in disequilibrium with the current climate, if they have yet to expand their distributions to match climate change since the LGM. Here, we used the palm (Arecaceae) clade as a study system to investigate three questions: i) Are there palm species restricted to climates suitable for tropical lowland humid-to-superhumid forest? ii) Did climate suitable for these forests expand to new areas since the LGM? And, iii) Do palm species occur more frequently in areas with stable climates, suitable for tropical lowland humid-to-superhumid forest, than in areas where climate became suitable for these forest after the LGM? We used an extensive palm occurrence database for the Neotropics in conjunction with climate data for the LGM and the present. We found that i) out of 501 palm species occurring in climates suitable for lowland humid-to-superhumid forest, only 196 are restricted to such climates, many species (200) are also found in dry climates and a few (27) in cold climates and combinations of dry and cold climates (78); ii) only a few areas have become climatically suitable for lowland humid-to-superhumid forest since the LGM; and iii) out of 196 palm species restricted to climates suitable for lowland humid-to-superhumid forest, few (ca. 39 %) do occur in areas that have become climatically suitable for lowland humid-to-superhumid forest since the LGM. The first two results indicate that the LGM may not have had a strong impact on the current distribution of many palm species, because they occur in dry areas. Besides, because we found few areas with climate that became suitable for lowland humid-to-superhumid forest after the LGM, there seems to be little opportunity for species to experience postglacial migration lags following the LGM. However, our last result indicates that palm species seem to experience some degree of postglacial migration lag as a consequence of the LGM. In conclusion, it seems that the LGM has had only a minor effect on the present distribution of palm species.

KEYWORDS: leading edge disequilibrium, Arecaceae, LGM, migration lags, lowland humid-to-superhumid forest.

INTRODUCTION

Climate has been recognized as one of the most important influences on the distributions of plant species globally (MacArthur 1972, Woodward 1987, Woodward 1990, Gaston 2003, Ricklefs 2004, Lomolino et al., 2006 Svenning and Sandel 2013, Svenning et al., 2015). Particular arrangements of climatic conditions usually are associated with species distribution limits and changes in environmental conditions often cause the distributions of species to shift in response (Gaston 2003). The Quaternary record provides many examples of species distributions moving in response to climate change (Hewitt 2000). Indeed, climates of the past sometimes are reconstructed or estimated from historical distributions of species assemblages (e.g., Coope and Lemdahl 1996), often based on current relationships between the distributions of vegetation types and climate (e.g., Holdridge et al., 1971). However, species respond individualistically to climate change (Lawton 2000, Jackson and Overpeck 2000) and, therefore, whether species maintain equilibria with climate following major climatic changes (e.g., Quaternary glaciation-interglaciation shifts) remains an important point for discussion (Araújo and Pearson 2005). For a species to maintain a distribution in equilibrium with climate, it has to respond rapidly to major climate shifts (Pretince et al., 1991, Webb 1986) and occur in all climatically suitable areas (Hutchinson 1957).

Species may often exist out of equilibrium with climate following major climate events (Svenning and Skov 2004, Araújo and Pearson 2005, Normand et al., 2010). By example, species that contract their geographic ranges in response to climate change can be in disequilibrium with climate when individuals persist in sites after climate conditions have worsened, resulting in *trailing-edge disequilibrium* (Svenning and Sandel 2013). Conversely, *leading-edge disequilibrium* occurs when species are delayed in reaching newly suitable areas owing to migration lags (Svenning and Sandel 2013). Migration lags result from slow species migration rates relative to the velocity of climate change (Loarie et al., 2009), and can be determined by complex interactions between environmental characteristics (e.g., dispersal barriers, habitat continuity), species characteristics (e.g., plant height, seed morphology) and biotic interactions.

One type of migration lag discussed extensively in the literature is *postglacial migration lag,* which implies that some species have not reached areas suitable to them due to the effects of past glaciations. Support for this idea comes from studies in Europe and North America. In Europe, temperate and Mediterranean species were primarily restricted to southern parts of the continent at the LGM, although some evidence points to the presence of several tree species in central and eastern Europe (Willis and Van Andel 2004). European plant species restricted to southern regions experienced postglacial migration lags, as shown by their geographic ranges not having fully expanded in response to postglacial warming (Dullinger et al., 2012, Normand et al., 2011, Svenning and Skov 2004). In North America, mesic-adapted species, which likely occurred in coastal, unglaciated areas at the LGM, expanded their ranges fully within these moist areas but expanded little within previously glaciated areas that currently have suitable climates (Gavin 2009). Examples of species that appear to have experienced postglacial migration lags include *Tsuga canadensis*, *Acer saccharum* and *Fagus americana* (Gavin 2009, Svenning et al., 2015).

Lowland tropical regions are considered to be climatically more stable than temperate regions because they did not experience directly Quaternary glaciations (Rudidiman 2001). However, climate fluctuations between glacial and interglacial periods during the Quaternary, particularly with respect to precipitation and temperature, still influenced the distribution of vegetation in lowland tropical regions (Anhuf et al., 2006). Changes from cold to warm temperatures, low to high precipitation, and low to high CO_2 levels might have caused the retraction and expansion, respectively, of the lowland rainforest in tropical areas (Harrison and Prentice 2003). In this context, *leading-edge disequilibrium* has been considered an important outcome of climate change, especially since the LGM, in tropical ecosystems (Svenning and Sandel 2013). A handful of studies of lowland tropical forest have reported that fewer species-rich areas are associated with unstable paleoclimates. For example, areas in Africa, where temperatures changed dramatically between the LGM (21,000 years ago, Bennet et al., 1991) and the present, have fewer species than climatically more stable areas (Kissling et al., 2012). Similarly, areas in the southeastern Amazon Basin with unstable paleoclimates have fewer genera than in the western Amazon Basin, which is thought to have been more stable (ter Steege et al., 2010). Thus, even as climate suitable for lowland tropical forest was becoming available after the LGM, species may have not expanded their geographic distributions to newly suitable areas (Svenning and Skov 2004, Svenning et al., 2008). In this regard, one study reports that some palm species remain restricted to former glacial refugia despite the wider availability of areas with suitable climate (Blach-Overgaard et al., 2010). Although these studies suggest leading-edge disequilibrium due to the LGM as a possible explanation, few studies have examined this idea formally.

Here, we ask whether palm species experienced postglacial migration lags following the LGM by examining their present distributions within the Neotropics in relation to current and past climatic conditions. Palm species are associated with warm and humid climates (Corner 1966, Condit et al., 1996), and are very diverse and abundant in tropical lowland humid-to-superhumid forest (moist forest, wet forest and rainforest), especially in lowlands (Pitman et al., 2001, Dransfield et al., 2008). This forest is thought to have been restricted and fragmented at the Last GIacial Maximum due to low regional temperatures and precipitation, before suitable environments expanded after the LGM (Anhuf et al., 2006). Thus, a palm species restricted to climate suitable for lowland humid-to-superhumid forest at the LGM (Figure 1A), would be considered to exhibit postglacial migration lag if it has not yet expanded its geographic range into areas with newly available suitable climate (Figure 1B). In this context, we ask here: i) Are there palm species restricted to climates suitable for tropical lowland humid-to-superhumid forest? ii) Did climate suitable for these forests expand to new areas since the LGM? And, iii) Do palm species occur more frequently in areas with stable climates, suitable for lowland humid-to-superhumid forest, than in areas where climate became suitable for these forest after the LGM? To answer these questions we used an extensive palm database from the BIEN working group (Botanical Information and Ecology Network; http://bien.nceas.ucsb.edu/bien/) in conjunction with climate data (annual precipitation and annual mean temperature) for the LGM and for the present from Worldclim (http://www.worldclim.org/). We found that more than half of palm species currently occurring in climates suitable for lowland humid-to-superhumid forest are not restricted to those climates; instead, many (200 out of 501) palm species also occur in dry climates. Surprisingly, we found few areas where climate suitable for the lowland humid-to-superhumid forest has expanded since the LGM; instead, the geographic distribution of this lowland forest seems to have been relatively stable across the Neotropics. We also found that palm species restricted to climates suitable for lowland humid-to-superhumid forest exhibited postglacial migration lags because they tend not to occur in climatically suitable areas that were available after the LGM.

METHODS

Study taxa

Palms (Arecaceae) are a keystone clade of plants in tropical and subtropical areas (Dransfield et al 2008). They provide food for pollinator and frugivore communities (Henderson 2002), and are also an important resource of food, construction materials, fabrics, fuel, medicine, and ornamentals for humans (Sosnowska and Balslev 2009). Palms probably originated in the early Cretaceous (Dransfield et al., 2008) and the pantropical clade currently includes more than 5 subfamilies, 183 genera, and 2400 species worldwide (Dransfield et al., 2008). They appear to have diversified at high rates in lower latitudes, especially in warm-humid habitats (Svenning et al 2008b), and are most abundant and species-rich in tropical and subtropical areas (Pitman et al., 2001, Dransfield et al., 2008, Eiserhardt et al., 2011), with only a handful of species occurring in warm temperate areas (Dransfield et al., 2008). Palms lack physiological and morphological adaptations for tolerating freezing temperatures (Larcher and Winter 1981) and therefore are susceptible to climate cooling (Tomlinson 2006). Thus, temperature shapes the distributions of palm species at regional and global scales, although topography and water availability figure more prominently at local scales (Svenning et al., 2008, Eiserhardt et al., 2011). Also, most palm species are associated with warm-humid climates (Corner 1966, Condit et al., 1996), although some species inhabit areas with low precipitation (Blach-Overgaard et al., 2010). Additionally, palm abundance and species richness decrease with elevation (Eischardt et al., 2011). Because palm distributions are strongly influenced by climate, especially temperature and precipitation (Corner 1966, Bjorholm et al., 2005, 2006) palm fossils have been used as indicators for the paleodistribution of rainforest (Morley 2000, Walther et al., 2007). Because of these characteristics, palms are an excellent system for studying postglacial migration lags in tropical lowland humid-to-superhumid forest as a consequence of climate change since the LGM.

Study region and suitable climate for Neotropical lowland humid-to-superhumid forest

Here, we consider the New World tropics, extending between the Tropic of Cancer (23° 26' N) and the Tropic of Capricorn (23° 26' S). This region comprises different types of forests and other vegetation; we focus our analyses on Neotropical climates suitable for lowland humid-to-superhumid forest, which includes moist forest, wet forest and rainforests (Figure 1A). We define the suitable climate these vegetation following Holdridge et al. (1971), based on a combination of elevation, annual mean temperature, and annual precipitation. Accordingly, Neotropical lowland humid-to-superhumid forest occur at elevations from 0 to 500 meters above sea level, where annual precipitation exceeds 1000 mm and the annual mean temperature lies between 17 and 24 °C, or where precipitation exceeds 2000 mm/yr. and temperature is above 24 °C (Figure 3B, Figure 1 in Holdridge et al., 1971).

Geographic extent of suitable climate for Neotropical lowland humid-to-superhumid forest: current.

To delineate the current geographic extent of suitable climate for Neotropical lowland humid-to-superhumid forest, based on Holdridge et al.'s (1971) definition (above), we obtained current climate layers (annual precipitation and annual mean temperature) from the Worldclim dataset (version 2.0; http://www.worldclim.org), with a spatial resolution of 25 km^2 (grid cells of 5 x 5 km). The elevation layer was acquired from CGIAR-SRTM (version 4.1; http://srtm.csi.cgiar.org/), also with a spatial resolution of 25 km^2. We then identified grid-cells of 5 x 5 km that had the combination of values of elevation, annual precipitation, and annual mean temperature within the ranges that define the currently suitable climate conditions for Neotropical lowland humid-to-superhumid forest (see definition in the last section, Figure 2).

Geographic extent of suitable climate for Neotropical lowland humid-to-superhumid forest: Last Glacial Maximum.

We also used Holdridge et al.'s (1971) definition to delineate the extent of suitable climate for Neotropical lowland humid-to-superhumid forest at the LGM (LGM). Reconstructions of past climates under different general circulation models can render contrasting hydrological patterns, and may be strongly influenced by assumptions about geographic scale and orography (Buytaert et al., 2010). For example, these models tend to underestimate the strong effect of the Andes Mountains on South American climate, which results in a bias towards drier reconstructed environments (Sepulchre et al., 2010). To account for some of this uncertainty, we used climatic reconstructions based on three circulation models: the Community Climate

System Model Version 4 (CCSM4, Gent et al., 2011), the Model for Interdisciplinary Research on Climate-Earth System Model (MIROC-ESM, Watanabe et al., 2011), and the new Max-Planck-Institute Earth System Model (MPI-ESM-P, Stevens et al., 2013). The three climatic reconstructions were obtained from WorldClim and provided by the Coupled Model Intercomparison Project Phase 5 (CMIP5; https://www.wcrp-climate.org/wgcm-cmip/wgcm-cmip5). For each of these circulation models, we assembled annual precipitation and annual mean temperature layers from the Worldclim data set (version 1.4; http://www.worldclim.org). As we did in delineating the current extent of suitable climate for Neotropical lowland humid-to-superhumid forest, we identified the grid-cells of 5 x 5 km with combinations of elevation and climate at the LGM that where within the ranges defining this forest according to Holdridge et al., (1971). Note that we produced three versions of this analysis, based on the three circulation models mentioned above.

Palm species in climates suitable for lowland humid-to-superhumid forest

To identify palm species occurring in climates suitable for lowland humid-to-superhumid forest, we used specimen records from the BIEN database (version 4.0, http://bien.nceas.ucsb.edu). This database 1) amalgamates records from several sources, including herbaria, vegetation inventories, and regional checklists; 2) standardizes the recorded species names using the Taxonomic Name Resolution Service (TNRS); and 3) validates the records geographically (Enquist et al., 2016). We first downloaded all the specimen records for New World. We considered only specimen records that represented a physical herbarium specimen, that were identified to species level, and that had associated geographic coordinates. Even though these data were validated geographically, we removed records with poor specific geospatial data. We also removed species that are not native to the region or that are cultivated. Second, for each specimen record, we acquired the elevation, current annual precipitation, and annual mean temperature using the geographic coordinates of the collection locality as well as the elevation, annual precipitation, and annual mean temperature layers obtained from Worldclim. Third, we used this environmental and topographic information to obtain the pool of species represented by at least one specimen in climates suitable for Neotropical lowland humid-to-superhumid forest as defined by Holdridge et al., (1971).

Gauging the potential for postglacial migration lags in lowland humid-to-superhumid forest palms since the Last Glacial Maximum

We addressed three questions to determine the extent to which palm species currently occurring in climates suitable for lowland humid-to-superhumid forest experience postglacial migration lags following the LGM: i) Are there palm species restricted to climates suitable for tropical lowland humid-to-superhumid forest? ii) Did climate suitable for tropical lowland humid-to-superhumid forest expand to new areas since the LGM? And, iii) Do palm species occur more frequently in areas with stable climate, suitable for lowland humid-to-superhumid forest, than in areas where climate became suitable for this forest after the LGM? Next, we describe the methods used to address each of these three questions.

A. *Are there palm species restricted to climates suitable for tropical lowland humid-to-superhumid forest?*

To quantify the correspondence of palm species distributions with climates suitable for lowland tropical lowland humid-to-superhumid forest, we used current annual precipitation and annual mean temperature at the collection localities of the specimens representing each species with at least one occurrence in climates suitable for this forest (see section above on “Palm species in lowland humid-to-superhumid forest”). We determine if each collection locality had a combination of values of annual precipitation and annual mean temperature within the ranges that define the climate suitable for Neotropical lowland humid-to-superhumid forest according to Holdridge et al., (1971, see section above on “Study region and suitable climate for Neotropical lowland humid-to-superhumid forest**”**): annual mean temperature between 17 and 24 °C and ≥ 1000 mm of annual precipitation, or annual mean temperature > 24 °C and ≥ 2000 mm of annual precipitation (Figure 3B). Specimens falling outside these ranges were classified according to whether the respective collection locality was characterized by climates that are too dry (annual mean temperature above 24°C and annual precipitation below 2000 mm, or annual mean temperature above 17°C and annual precipitation below 1000 mm), too cold (annual mean temperature below 17°C and annual precipitation above 1000 mm), or too dry and too cold (annual mean temperature below 17°C and annual precipitation below 1000 mm, Fig. 3B) for lowland humid-to-superhumid forest. The criterion to regard a palm species as restricted to climates suitable for tropical lowland humid-to-superhumid forest was that all specimen records came from localities with such a climate.

B. *Did climate suitable for tropical lowland humid-to-superhumid forest expand to new areas since the Last Glacial Maximum?*

We calculated areas of expansion of suitable climate for Neotropical lowland humid-to-superhumid forest using maps developed for current and past (LGM) suitable climates for this forest. The maps were drawn based on elevation, annual precipitation, and annual mean temperature, according to the definition by Holdridge et al. (1971) of climates suitable for lowland humid-to-superhumid forest (see definition above). Using the raster package (Hijmans et al., 2017) in R 3.6.1software (R Development Core Team 2019), we identified areas of expansion by determining in which grid-cells (of 5 x5 km) climate was not suitable for lowland humid-to-superhumid forest during the LGM but became suitable towards the present. We classified these areas of expansion of suitable climate for Neotropical lowland humid-to-superhumid forest (grid cells of 5 x 5 km) according to whether, at the LGM, they were too dry (annual mean temperature above 24°C and annual precipitation below 2000 mm, or annual mean temperature above 17°C and annual precipitation below 1000 mm), too cold (annual mean temperature below 17°C and annual precipitation above 1000 mm), or too dry and too cold (annual mean temperature below 17°C and annual precipitation below 1000 mm) for lowland humid-to-superhumid forest. We conducted these analyses based on climate maps for the LGM generated by three circulation models (CCSM4, MIROC-ESM, and MPI-ESM-P; see the previous section on "Geographic extent of suitable climate for Neotropical lowland rainforest: Last Glacial Maximum").

C. *Do palm species occur more frequently in areas with stable climate, suitable for lowland humid-to-superhumid forest, than in areas where climate became suitable for these forest after the Last Glacial Maximum?*

If palms species currently restricted to climates suitable for tropical lowland humid-to-superhumid forest experience postglacial migration lags following the LGM, then these palm species should occur more frequently in areas where climate was suitable for this forest during the LGM than in areas where climate became suitable after the LGM. To test this prediction we quantified the area of the current geographic distribution of species in terms of extent of occurrence (EOO), by drawing a minimum convex polygon around specimen records representing any given species (Gaston 2009). This procedure was used for species represented by at least 4 specimen records. For species represented by fewer records, we measured the sum of the areas of the grid-cells (5 X 5 km) where the species occurred. For each species, we calculated how much of the area of the current geographic distribution corresponded to areas (grid cells of 5 x 5 km) with climate that was not suitable for the lowland humid-to-superhumid forest during the LGM but became suitable towards the present (i.e., areas identified as described above, in the section on “Did climate suitable for tropical lowland humid-to-superhumid forest expand to new areas since the Last Glacial Maximum?”). We contrasted these values with those generated by a null model in which the geographic distribution of species was randomly placed across areas that became climatically suitable for lowland humid-to-superhumid forest since the LGM and those that were climatically suitable for this forest at the LGM. This null model only considered areas in which current climate is suitable for lowland humid-to-superhumid forest, and preserved the area of the current distribution of each species (measured as describe above). The comparison of observed values against the distributions generated by 1,000 iterations of the null model was carried out separately for each of the three circulation models (CCSM4, MIROC-ESM, and MPI-ESM-P).

RESULTS

A. Are there palm species restricted to climates suitable for tropical lowland humid-to-superhumid forest?

Our dataset included 501 palm species represented by 38,724 occurrence records. Each of these species had at least one occurrence within climate suitable for Neotropical lowland humid-to-superhumid forest. Only 196 of these species were restricted to climates suitable for lowland humid-to-superhumid forest. *Attalea amygdalina* (155 records), *Syagrus orinocensis* (148 records), and *Bactris fissifrons* (115 records) had the highest number of records among these species. Of all the palm species with at least one occurrence in climates suitable for lowland humid-to-superhumid forest, 200 were also found in climates that were too dry for this forest. *Geonoma stricta* (620 records in total, 28 in dry climates), *Bactris maraja* (549 records, 70 in dry climates) and *Iriartella setigera* (373 records, 17 in dry climates) had the highest number of specimen records among them. In addition, 27 species also occurred in climates that were too cold for lowland humid-to-superhumid forest. *Geonoma orbignyana* (469 records, 125 in cold climates), *Wettinia praemorsa* (152 records, 23 in cold climates) and *Geonoma edulis* (126 records, 30 in cold climates) had the highest number of specimen records among the species in this third category. The rest of the species (78 altogether) occurred in different combinations of climates that were too dry, too cold or too dry and cold for lowland humid-to-superhumid forest (Table S1, Figure 3A). Most of the palm specimen records occurred in climates suitable for lowland humid-to-superhumid forest, followed by occurrences in climates that were too dry, too cold, and too dry and too cold for this forest (Figure 3B).

B. Did climate suitable for tropical lowland humid-to-superhumid forest expand to new areas since the Last Glacial Maximum?

According to all three-circulation models, the climate suitable for tropical lowland humid-to-superhumid forest did expand to new areas since the LGM. According to two circulation models, CCSM4 and MPI-ESM-P, these areas covered 122,617 and 21,577 km^2, respectively, which represent a relatively small portion of the land currently covered by climate suitable for lowland humid-to-superhumid forest (0.4% and 2.2%, respectively, Figure 4). However, estimates based on MIROC-ESM circulation model suggest that the areas of expansion cover 654,452 km^2, which is 12.9% of the current extension of climate suitable for lowland humid-to-superhumid forest (Figure 4C). The spatial distribution of the areas of expansion varied substantially between circulation models. In the MPI-ESM-P circulation model these areas where around Los Llanos in Colombia and Venezuela, as well near the Andes in northern Colombia and in a few scattered places in Central America (Figure 4D). In the CCSM4 circulation model the areas of expansion also included inter-Andean valleys in northern Colombia, southern Venezuela, Western Amazonia in Peru and Bolivia, parts of the Atlantic forest and a concentration of areas in northeastern Honduras. In the MIROC-ESM circulation model the areas of expansion were mainly in four large clusters (Figure 4C). The largest cluster is located in northern Brazil, in the States of Roraima and Amazonia, another is in Los Llanos of Colombia and Venezuela, and two are in northeastern Brazil, in the State of Amapá and around city of Belém. Additionally, there are some areas of expansion in the Guyanas, around the northern Andes in Colombia and Venezuela as well as in several places in Central America.

C. Do palm species occur more frequently in areas with stable climate, suitable for lowland humid-to-superhumid forest, than in areas where climate became suitable for these forest after the Last Glacial Maximum?

As stated in the first section of the results, we found that 196 palm species were restricted to climates suitable for lowland humid-to-superhumid forest. The geographic range of the majority of these species did not include areas having suitable climates for the lowland humid-to-superhumid forest that became available since the LGM, regardless of which circulation model was used. This result was more extreme than expected by the null model (Figure 6A). Moreover, we found, also, that the median (across species) of the observed area of distribution in new climatically suitable areas was lower than expected by the null model, according to estimates based on the CCSM4 and MIROC-ESM circulation models. For the MPI-

ESM-P model, the observed median was not significantly different from the null distribution (Figure 6B). Based on these results, palm species restricted to climates suitable for lowland humid-to-superhumid forest seem to exhibit postglacial migration lags as a consequence of the LGM. However, there were 22, 76 and 16 palm species that occur in new suitable climates according to analyses based on CCSM4, MIROC-ESM, and MPI-ESM-P circulation models, respectively.

DISCUSSION

The geographic distributions of many species are thought to be in disequilibrium with respect to climate due to postglacial migration lags since the LGM. However, most well-established examples of postglacial migration lags come from temperate regions that were directly impacted by massive ice sheets. There seem to be few, if any, well-documented examples from tropical lowlands, where climates during the LGM are generally thought to have been colder and drier than current climates, but not cold enough for the formation of significant ice sheets. Here we studied palm species occurring in lowland Neotropical humid-to-superhumid forest to test for migration lags following the LGM. We found that about half of the palm species occurring in climates suitable for lowland humid-to-superhumid forest are restricted to these climates. Many species also occur in dry habitats, and a few of them in cold habitats (Figure 3A and B). This implies that palms, as a group, are also generally adapted to dry climates, in which case decreased precipitation during the LGM may not have had a strong impact on their current distributions. We also found that, since the LGM, suitable climates for lowland humid-to-superhumid forest expanded to new areas that may account for less than 2.5% and up to 12% of the current extent of climate suitable for these lowland forests (Figure 4). These results imply that relatively few new areas exist where species of palms could have expanded their geographic ranges; accordingly, there seems to have been little opportunity for postglacial migration lags. Yet, we found that species restricted to climates suitable for lowland humid-to-superhumid forest tend not to occur within the few new suitable areas for this lowland forest that appeared after the LGM. This result is consistent with the idea that species are in disequilibrium with climate due to postglacial migration lags as a consequence of the LGM. Below we will discuss the implications of our findings and possible caveats.

Most palm species are distributed in warm-humid climates, but some are associated with areas of low precipitation (Eiserhardt et al., 2011). This pattern is reflected in our findings: 501 palm species occurred in lowland humid-to-superhumid forest of the Neotropics (represented by at least one specimen record in these forests), among which only 196 species were restricted to climates suitable for lowland humid-to-superhumid forest, and 200 species were also found in drier climates (with lower precipitation). Although it has been reported that water availability influences the species richness of palms (Svenning et al 2008a, Blach-Overgaard et al., 2010), relatively low water availability does not appear to constrain the distribution of some species. For example, the species richness of the subfamilies Coryphoideae and Ceroxyloideae is not strongly related to water availability (Bjorholm et al., 2006). Our analyses show that genera in the Coryphoideae subfamily (e.g., *Aceolorraphe*, *Copernicia*, *Sabal*, and *Thrinax*) had more occurrences in dry than humid-to-superhumid climates (Table S1). One explanation for this pattern is that palm trunks or stems can store considerable quantities of water (Holbrook and Sinclair 1992), which could help to maintain leaf turgor under sparse rainfall (Renninger and Phillips 2015). Many studies report temperature also to be a strong factor determining the distribution and richness of palms (Tomlinson 2006, Gatti et al., 2008, Svenning 2008, Sesnie et al., 2009). This is in agreement with our results, for which only 27 species occurred in cold habitats (Figure 3A and 3B). Palm species tolerate freezing temperatures poorly (Larcher and Winter 1981, Tomlinson 2006, Walther et al., 2007, Gatti et al., 2008) because they lack suitable anatomical and physiological adaptations. Palm species exposed to freezing temperatures (e.g., *Trachycarpus* spp., *Euterpe edulis*) exhibit tissue damage, especially in fronds and spears (Walther et al., 2007), which is always followed by non-reversible tissue injury (Gatti et al., 2008). Therefore, while many palm species seem to move freely between lowland humid-to-superhumid forest and drier climates, they cannot move easily to cold climates.

Our results indicate that no matter which circulation model was used in the analysis, the suitable climate for Neotropical lowland humid-to-superhumid forest expanded to relatively few geographic areas since the LGM (Figure 4B to 4D). These areas were mostly dry and cold at the LGM (Figure 5A to 5D). This results imply that opportunities for postglacial migration lags are limited for palms due to the scarcity of new, climatically suitable areas for lowland humid-to-superhumid forest towards the present. This also implies that most areas that currently have climates suitable for lowland humid-to-superhumid forest also had climates suitable for those forests at the LGM (Figure 4A to 4D). Studies based on paleoecological evidence (e.g., Colinavux and De Oliveira 2000) suggest continuous lowland rainforest through the LGM, which is largely consistent with our results. However, this view differs from the Pleistocene refuge hypothesis

(Haffer 1987), which suggests lowland aridity in many areas of the Amazon basin leading to fragmentation of the lowland humid-to-superhumid forest at the LGM (e.g., van der Hammen and Hooghiemstra 2000). We know that, at the LGM the Amazon Basin experienced lower temperature; for the New World tropics as a whole, the minimum annual temperature was ~ 4.5 to 7.5 C lower than at present (Bush and Colinvaux 1990, Webb et al., 1997 Figure S1A, S1C, S1E). Nonetheless, whether precipitation in the Amazon basin was lower or higher at the LGM than today is still debated. One view based on isotope records supports the idea that the Amazon basin was drier than today (Thompson et al., 1995). Another view based on reconstructions of Altiplano lake levels supports the idea that the Amazon basin was wetter than today (Baker et al., 2001). Our results support the latter view that many areas exhibited high levels of precipitation (Figure S1B, S1D, S1F). Thus, the question should be, were changes in temperature and precipitation at the LGM sufficient to make parts of the Amazon Basin an arid habitat unsupportive of moist forest, wet forest and lowland rainforest, or were the changes not so pronounced as to change the distribution of these forests within the region? Following this last idea, some studies argue that climate at the LGM was not sufficiently cold and dry to disrupt the geographic extension of the lowland Neotropical forests (Colinvaux 2001).

One unexpected result from our analysis was that the climate of many geographical areas shifted from being suitable for lowland humid-to-superhumid forest at the LGM, to being currently unsuitable for those forests. Areas having a climate suitable for lowland rainforest that does not exist in the present, depending on the climate model, were for CCSM4 = 3,592,165 km^2 (62.6 % of the total area at the present), for MIROC-ESM = 3,086,343 km^2 (53.8 %), and for MPI-ESM-P = 3,799,425 km^2 (66.2 %). This kind of climatic shift was obvious in analysis based on all three circulation models (Figure 4), and occurred mostly around the border of the Amazon Basin, but also in sections of Central America such as the Yucatan Peninsula in the analysis based on the MPI-ESM-P circulation model (Figure 4A to 4D). We attribute this retraction to the relatively high levels of precipitation at the LGM (Figure S1A, S1C, S1E), which may have maintained lowland rainforest at that time. This does not support the prediction of the refugee hypothesis (Haffer 1969), but it is consistent with studies that have found high levels of precipitation at the LGM in tropical regions (e.g., Rakotoarinivo et al 2012, Leite et al., 2016, Arruda et al., 2017), and less fragmented forest area at the LGM than at present for the Atlantic forest of Brazil (Leite et al., 2016). Also, pollen records from the Amazon basin center and margin suggest that the basin remained largely forested (Mayle et al., 2009). Thus, forest refuges may have had little impact on the distribution of species in Neotropical lowland forests.

Of 196 palm species restricted to climates suitable for lowland humid-to-superhumid forest, more than fifty percent have geographic distributions that do not include areas acquiring suitable climate since the LGM (Figure 6A). Thus, these species could be experiencing postglacial migration lags (leading-edge disequilibrium, Figure 1) as suitable climates expanded since the LGM. We developed a null model in which we randomly assigned species geographic ranges across geographic areas that either became climatically suitable for lowland humid-to-superhumid forest since the LGM or that were climatically suitable for these forests at the LGM as well as the present. This analysis revealed that more palm species than expected by chance do not occur within geographic areas with newly suitable climate, which reinforce the idea that palm species experienced postglacial migration lags following the LGM. These results were consistent among the three circulation models (Figure 6A).

We considered uncertainty in the paleoclimatic data by using three circulation models (CCSM4, MIROC-ESM, and MPI-ESM-P). Our results regarding the increment in precipitation at the LGM and the percentage of new area of suitable climate for lowland humid-to-superhumid forest were similar among the three circulation models (Figure 4B to 4D, and Figure S1B, S1D, S1F), although the MIROC-ESM circulation model presented a particularly strong pattern (Figure 4B and SD1). Thus, our results appear to be robust. Global circulation models are susceptible to the orography (topographic relief) of the Earth surface, showing a bias towards drier reconstructed past climates (Sepulcre et al., 2010). Thus, if biases favor drier reconstructed past climates, our results would be particularly robust because, despite such bias, they show fairly high precipitation levels at the LGM. Therefore, if biases favor drier reconstructed past climates, our findings would constitute particularly strong evidence against studies that report a reduction in precipitation across the Amazon basin and the possibility of a large areas of savanna vegetation at the LGM (van der Hammen and Hooghiemstra 2000). Our results would also support recent studies report an increase in precipitation within tropical regions at the LGM (Arruda et al., 2017, Rakotoarinivo et al., 2013), which suggest that instead of widespread savanna within the Amazon basin at the LGM, other types of forest could have been established (Arruda et al., 2017).

One of the difficulties in studying historical and present species distribution patterns is that we know little about the current geographic distributions of most species (Wallacean shortfall, Lomolino 2004), and nearly nothing about their past distributions. Many initiatives are attempting to close this gap (e.g., GBIF, BIEN datasets), but more effort is needed. In this regard, our results are influenced by specimen collecting effort within the Neotropics (Figure 2) in three main ways. First, some palm species restricted to lowland humid-to-superhumid forest may have never been collected (and thus discovered and described) because they have relatively small geographic ranges (Sheth et al. 2012); in addition, collecting effort within the Amazon basin has been low across many areas and spatially highly aggregated in comparison with surrounding regions (e.g., the Andes region, Central America, Figure 2A). Second, among the species included in the analysis, the relative frequency of palm species restricted to climates suitable for lowland humid-to-superhumid forest (Figure 3A) could decrease with further collecting effort in drier climates. Still, the frequency of species in colder habitats may be unlikely to increase much because collection effort in the Andean region is relatively high, although certainly not ideal. Third, further collecting effort might reveal a higher frequency of palm species occurrences in areas where climate for the lowland humid-to-superhumid forest that became available only after the LGM, which would suggest less support for the idea of postglacial migration lags following the LGM.

Understanding the role of historical climatic conditions on species distributions is important for predicting the consequences of future climate change (Skov and Svenning 2004). Here, we provided an assessment of postglacial migration lags for palm species from Neotropical lowland humid-to-superhumid forest. We have shown that most of the palm species occurring in climates suitable for this forest also occur in other climates and, therefore, are unlikely to have experienced postglacial migration lags. Among the 501 palm species that occurred in climates suitable for lowland humid-to-superhumid forest, defined here by precipitation, temperature, and elevation (*sensu* Holdridge et al., 1971), only 39 % were restricted to climates suitable for this forest; the remainders were distributed largely within drier and very few in colder habitats. Palm species distributions appear to be constrained more by cold temperature (Kissling et al., 2012) than low precipitation. If this were true then climate warming, as we are experiencing in the present, could be beneficial for palms. This trend was observed in Europe for *Trachycarpus sp.,* which is moving into new areas where winters are shorter and temperatures are warmer (Walther et al., 2007). Moreover, we also have shown that most of the species presently restricted to climates suitable for humid-to-superhumid forest (39%) seem to be experiencing postglacial migration lags following the expansion of suitable habitat after the LGM. However, we should interpret this result with caution. Identifying paleoclimatic legacies is challenging owing to difficulties in reconstructing past climate conditions and also, in this particular study, due to limited specimen collection effort (the Wallacean shortfall). Finally, we have shown, in contrast to previous studies (e.g., van der Hammen and Hooghiemstra 2000), that suitable climate for lowland humid-to-superhumid forest at the LGM occurred over a large area, and so forest refuges may have played a minor role in the Neotropics. This pattern was also found for the Atlantic Forest, where forest habitat seems to be more fragmented at present than at the LGM (Leite et al., 2016). In addition, precipitation levels were higher at the LGM than at the present, which contrasts with drivers identified in previous analyses of forest change in Europe (e.g. Svenning and Skov 2007, Sandel et al., 2011). Our results agree, however, with other studies of tropical regions (e.g., Rakotoarinivo et al., 2013, Leite et al., 2016). This reinforces the idea that biomes within the tropics experienced the effects of the LGM differently than did temperate biomes.

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FIGURES

Figure 1. Conceptual diagram of postglacial migration lag (leading-edge disequilibrium). **A.** Geographic range of a species at the Last Glacial Maximum (LGM), occupying climatically suitable habitat. **B.** Suitable climate for the species becomes available in many areas only after the LGM, but the species does not occupy these areas. Gray points represent species occurrences and light brown area represents climatically suitable conditions for that particular species.

Figure 2. **A.** Distribution of specimen records of palms across the New World tropics. The area highlighted in green represents the current distribution of climate suitable for lowland humid-to-superhumid forest (LHSF), based on annual mean temperature, annual precipitation, and elevation following Holdridge et al., (1971). **B**. Frequency distribution of herbarium specimen records across 5 X 5 km grid cells within the New World tropics (gray bars) and within climates suitable for LHSF (green bars).

Figure 3. Distribution of palm species occurring in climates suitable for lowland humid-to-superhumid forest (LHSF) across climates suitable (green) and unsuitable (other colors) for this forest. **A.** Frequency of species restricted (green bar) and not restricted (bars of other colors) to climates suitable for LHSF. Species not restricted to climates suitable for LHSF are classified according to whether occurrence records come from climates that are too dry (red bar), too cold (blue bar), too dry and too cold (brown bar), or combinations of these three categories (gray bars). Species where considered to be restricted to climates suitable for LHSF if all occurrences came from that climate. **B.** Climatic distribution of the specimen records of palm species occurring in climates suitable for LHSF. Records are classified according to whether they come from climates that are suitable for LHSF (green), or not. Records in climates unsuitable for this forest are classified according to whether the respective climate is too dry (red), too cold (blue) or too dry and too cold (brown) for LHSF.

Figure 4. Spatial distribution of the climates suitable for lowland humid-to-superhumid forest (LHSF) in the New World tropics, as measured by annual precipitation, annual mean temperature and elevation (Holdridge et al., 1971). **A.** Current distribution of climate suitable for LHSF. Changes in the distribution of climates suitable for LHSF since the Last Glacial Maximum (LGM) were estimated based on the circulation models CCSM4 (**B**) MIROC-ESM (**C**) and MPI-ESM-P (**D**). Light blue areas represent climates that were suitable for LHSF at the LGM (~21,000 years BP) but not currently, light green areas represent climates that were suitable for LHSF

during the LGM and are also currently suitable for LHSF, and dark green areas represent climates that became suitable for LHSF after the LGM.

Figure 5. Current and past climates of the areas (grid cells of 5 x 5 km) that currently have climates suitable for lowland humid-to-superhumid forest (LHSF). Climates are described in terms of annual precipitation and annual mean temperature, based on the CCSM4 (**A**) MIROC-ESM (**B**) and MPI-ESM-P (**C**) circulation models. In **A**-**C** green points show current climates, red points represent areas that were too dry for LHSF at the Last Glacial Maximum (LGM); blue dots represent the areas that were too cold for LHSF at the LGM, and brown points represent areas that were too dry and too cold for LHSF at the LGM. **D.** Cumulative area of grid cells of 5 x 5 km that currently have climates suitable for LHSF, but that were too dry, too cold, and too dry and too cold for this forest at the LGM. Estimates for the three circulation models are provided.

Figure 6. A. Number of palm species that are restricted to climates suitable for lowland humid-to-superhumid forest (LHSF) but did not occur in areas with climates that became suitable for this forest after the Last Glacial Maximum (LGM). Gray bars represent the observed number of species and red intervals represent the 2.5 and 97.5 percentiles of the null model distribution. **B.** Area of the geographic range of palm species in areas with climates that became suitable for LHSF after the LGM. Only palm species restricted to climates suitable for LHSF are considered. Gray bars represent the observed values and red lines represent the 2.5 and 97.5 percentiles of the medians obtained in 1,000 iterations of the null model. The results are shown for the three circulation models CCSM4, MIROC-ESM and MPI-ESM-P.

Figure 1

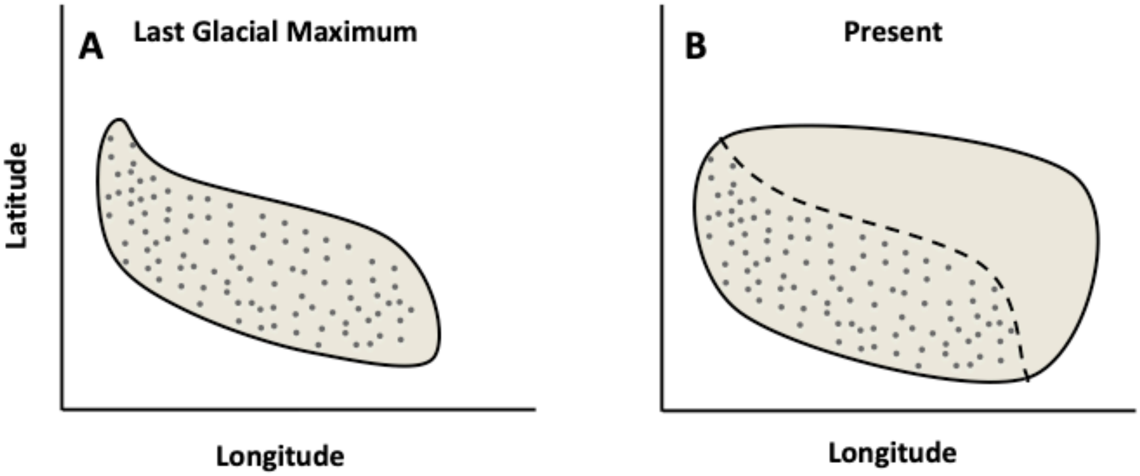

A
Last Glacial Maximum
Latitude
Longitude
B
Present
Longitude

Figure 2

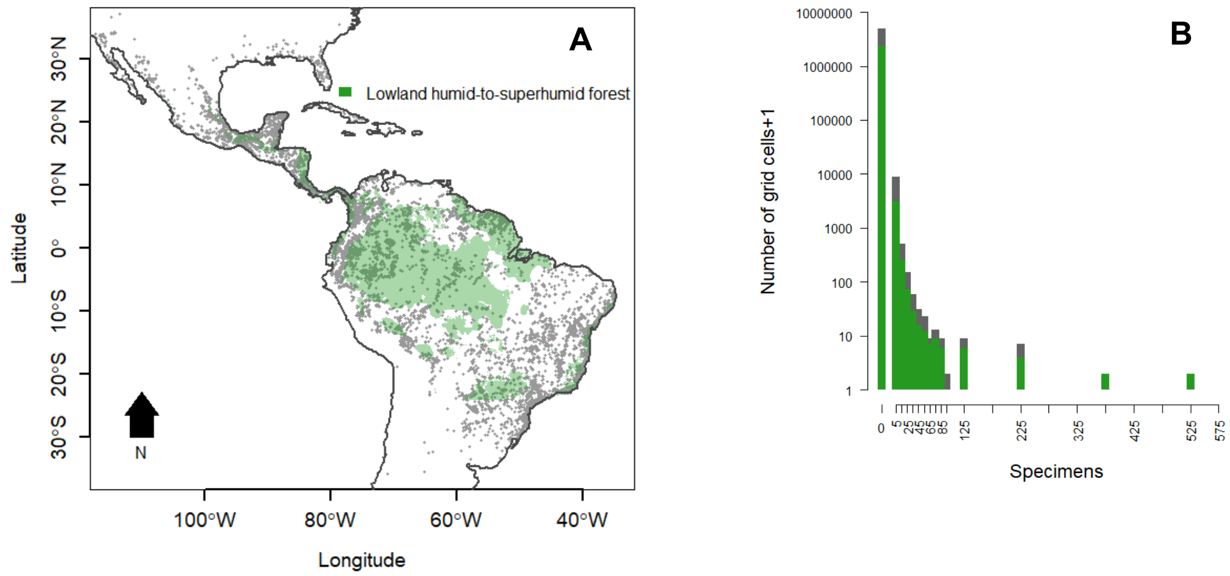

A
🟩 Lowland humid-to-superhumid forest
30°N
20°N
10°N
0°
10°S
20°S
30°S
Latitude
N
100°W
80°W
60°W
40°W
Longitude
B
10000000
1000000
100000
10000
1000
100
10
1
Number of grid cells+1
0
5
25
45
65
85
125
225
325
425
525
575
Specimens

Figure 3

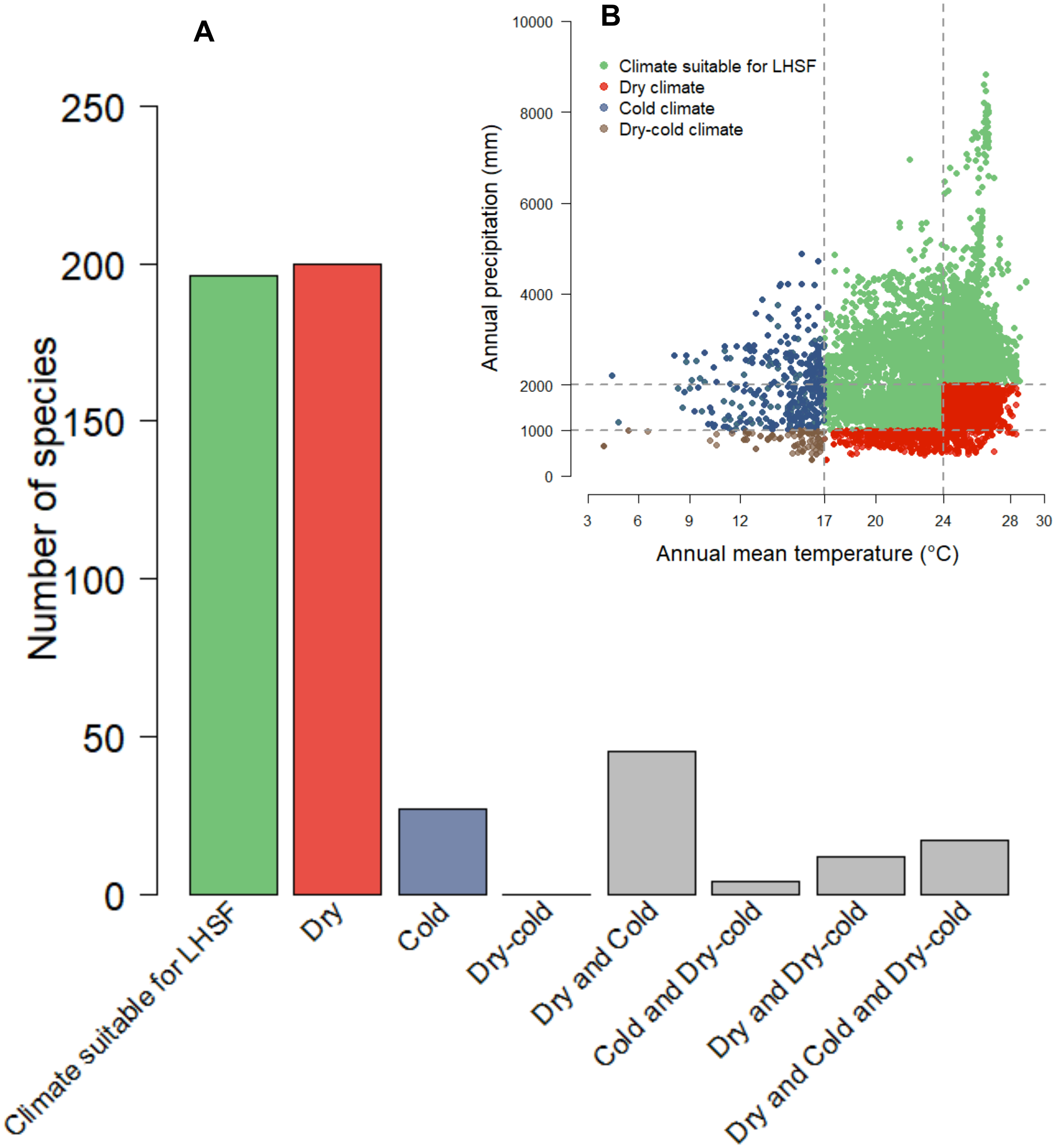

A
Number of species
250
200
150
100
50
0
Climate suitable for LHSF
Dry
Cold
Dry-cold
Dry and Cold
Cold and Dry-cold
Dry and Dry-cold
Dry and Cold and Dry-cold
B
Climate suitable for LHSF
Dry climate
Cold climate
Dry-cold climate
Annual precipitation (mm)
10000
8000
6000
4000
2000
1000
0
Annual mean temperature (°C)
3
6
9
12
17
20
24
28
30

Figure 4

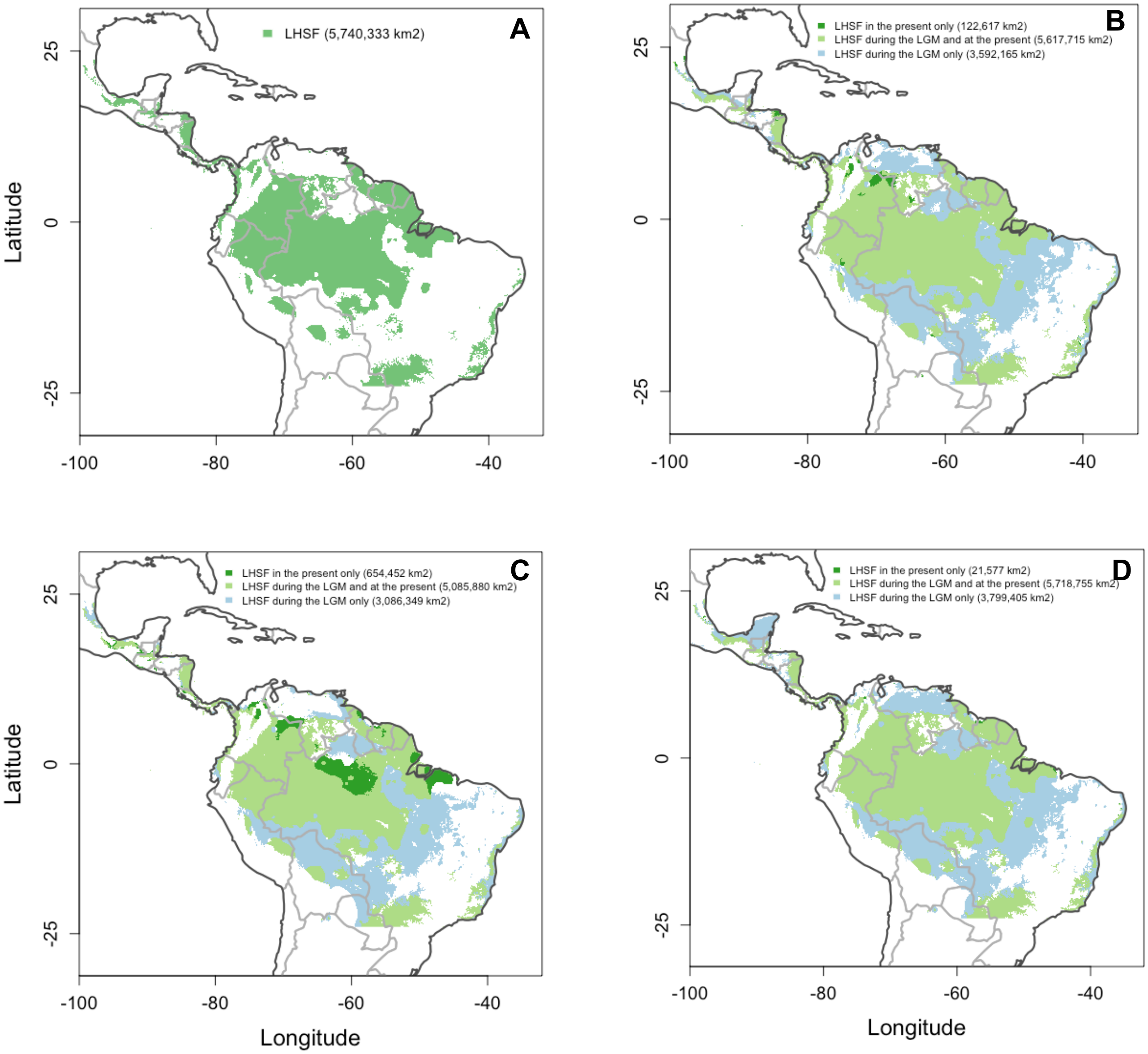

A
LHSF (5,740,333 km2)
B
LHSF in the present only (122,617 km2)
LHSF during the LGM and at the present (5,617,715 km2)
LHSF during the LGM only (3,592,165 km2)
C
LHSF in the present only (654,452 km2)
LHSF during the LGM and at the present (5,085,880 km2)
LHSF during the LGM only (3,086,349 km2)
D
LHSF in the present only (21,577 km2)
LHSF during the LGM and at the present (5,718,755 km2)
LHSF during the LGM only (3,799,405 km2)
Latitude
25
0
-25
Longitude
-100
-80
-60
-40

Figure 5

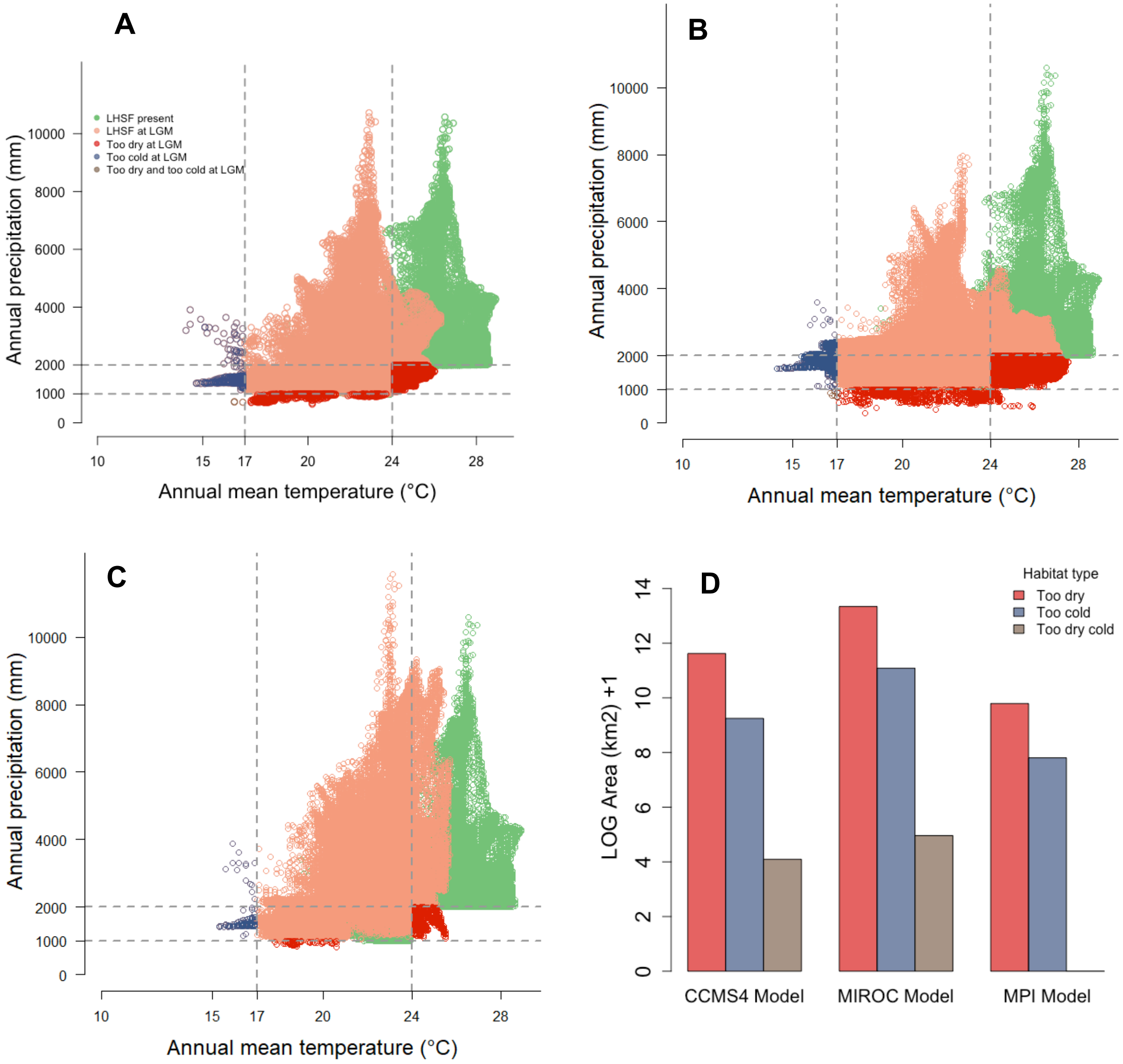
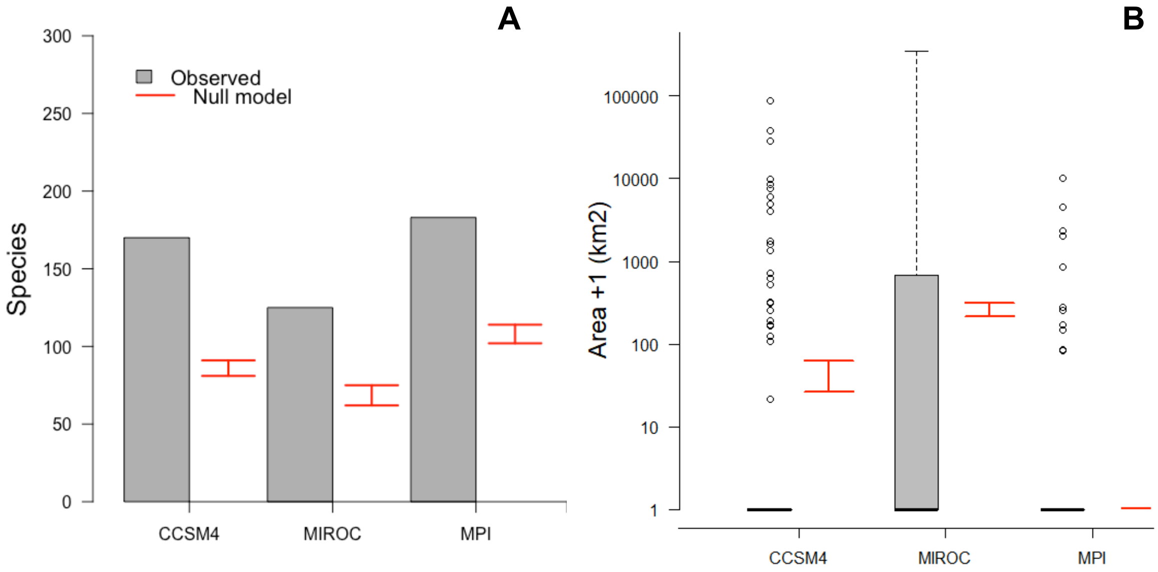
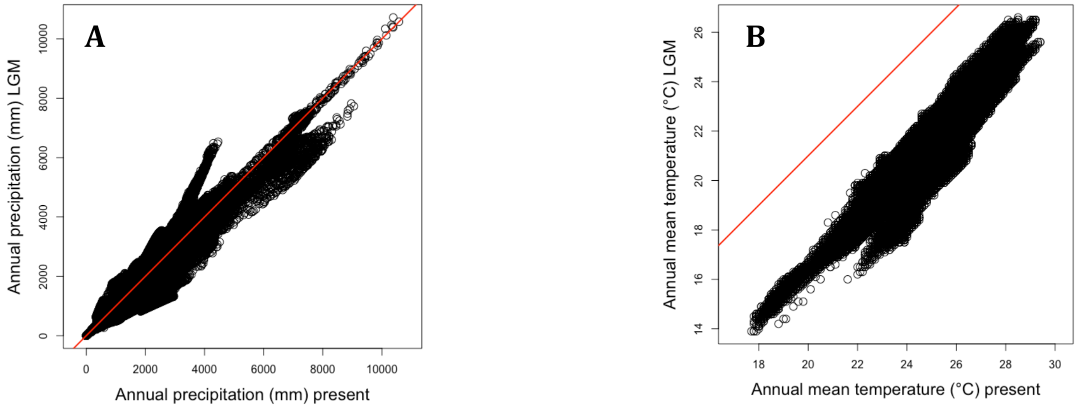

A
LHSF present
LHSF at LGM
Too dry at LGM
Too cold at LGM
Too dry and too cold at LGM
Annual precipitation (mm)
0
1000
2000
4000
6000
8000
10000
10
15
17
20
24
28
Annual mean temperature (°C)
B
Annual precipitation (mm)
0
1000
2000
4000
6000
8000
10000
10
15
17
20
24
28
Annual mean temperature (°C)
C
Annual precipitation (mm)
0
1000
2000
4000
6000
8000
10000
10
15
17
20
24
28
Annual mean temperature (°C)
D
Habitat type
Too dry
Too cold
Too dry cold
LOG Area (km2) +1
0
2
4
6
8
10
12
14
CCMS4 Model
MIROC Model
MPI Model

Figure 6

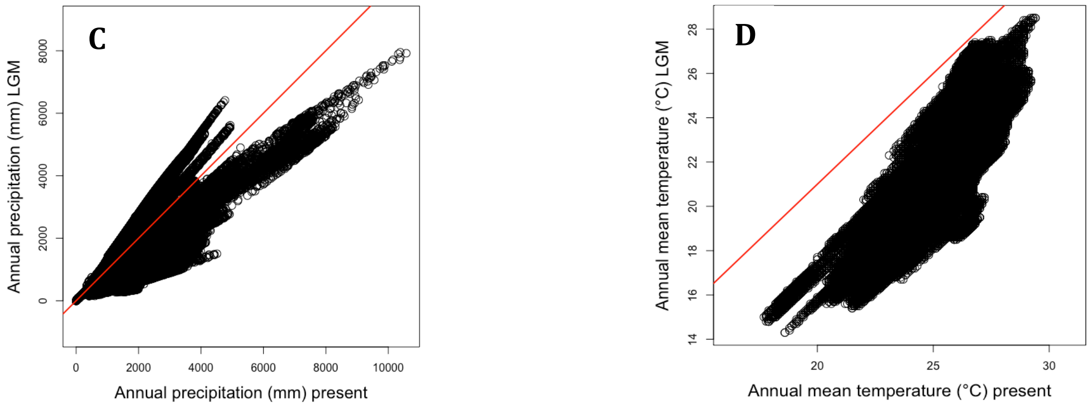

A
300
250
200
150
100
50
0
Species
Observed
Null model
CCSM4
MIROC
MPI
B
100000
10000
1000
100
10
1
Area +1 (km2)
CCSM4
MIROC
MPI

SUPLEMENTARY MATERIAL

CCSM4 Circulation



MIROC-ESM Circulation



MPI-ESM-P Circulation model

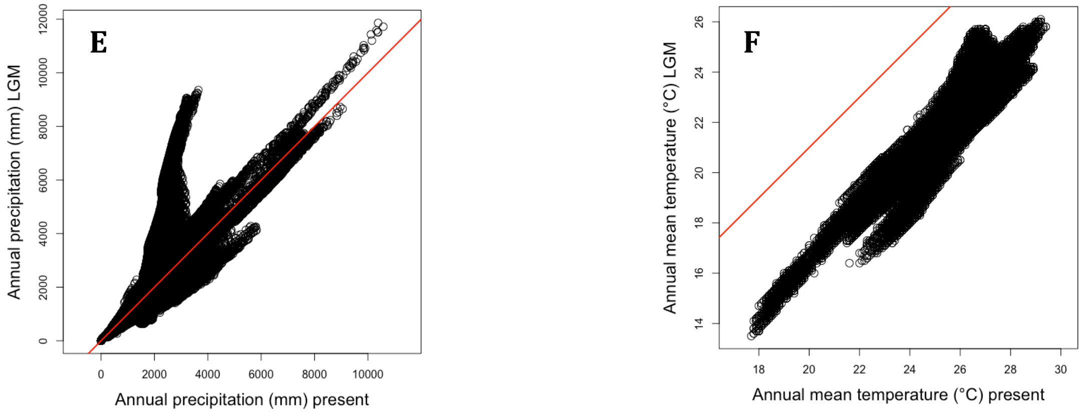


Figure S1. Relationship between current annual precipitation and estimated annual precipitation at the Last Glacial Maximum (LGM) across New World tropical lowland areas (0-500 meters above sea level) (**A**, **C**, and **D**). Also shown is the relationship between current annual mean temperature and annual mean temperature at the LGM (**B**, **D** and **F**). Points represent grid-cells of 5 X 5 km. The red line represents the 1:1 relationship, thus points below the line represent areas where annual precipitation or annual mean temperature increased, and points above the line areas were annual precipitation or annual mean temperature were higher during the LGM than now.

Table S1. Distribution of palm specimen records of different species among climates suitable for lowland humid-to-superhumid forest and those that are too dry, too cold and too dry and too cold for this forest, defined based on annual precipitation, annual mean temperature, and elevation, following Holdridge et al., (1971).

Species	Number of specimens	Humid-to-superhumid forest	Too dry	Too cold	Too dry and - too cold
Chamaedorea pinnatifrons	2015	1640	97	269	9
Geonoma macrostachys	898	800	96	2	0
Geonoma deversa	810	722	84	3	1
Euterpe precatoria	783	643	129	10	1
Geonoma maxima	644	568	72	4	0
Geonoma undata	636	433	5	171	27
Geonoma stricta	620	592	28	0	0
Geonoma cuneata	601	583	8	10	0
Hyospathe elegans	590	547	38	4	1
Bactris maraja	549	479	70	0	0
Chamaedorea tepejilote	540	506	26	8	0
Bactris simplicifrons	535	489	44	2	0
Socratea exorrhiza	497	440	55	1	1
Geonoma orbignyana	469	337	0	125	7
Geonoma interrupta	462	425	26	11	0
Chamaedorea linearis	459	309	24	116	10
Chamaedorea costaricana	435	343	28	64	0
Geonoma pohliana	430	326	89	15	0
Prestoea acuminata	425	300	8	114	3
Geonoma schottiana	417	353	23	41	0
Iriartella setigera	373	356	17	0	0
Oenocarpus bataua	369	312	43	14	0
Desmoncus polyacanthos	368	278	90	0	0
Asterogyne martiana	367	349	18	0	0
Reinhardtia gracilis	361	347	14	0	0
Bactris hirta	342	283	59	0	0
Synechanthus warscewiczianus	319	309	8	2	0
Acrocomia aculeata	303	151	152	0	0
Allagoptera campestris	289	176	113	0	0
Iriartea deltoidea	278	257	19	2	0
Desmoncus orthacanthos	270	119	150	1	0
Syagrus flexuosa	270	176	93	1	0
Syagrus romanzoffiana	268	238	6	24	0
Chamaedorea pauciflora	261	240	21	0	0
Chamaedorea oblongata	259	215	42	2	0
Euterpe edulis	255	204	48	3	0

Table S1. Continued

Chamaedorea ernesti-augusti	249	229	20	0	0
Bactris acanthocarpa	246	169	77	0	0
Geonoma congesta	245	234	10	1	0
Bactris major	244	119	125	0	0
Astrocaryum gynacanthum	242	192	50	0	0
Geonoma ferruginea	240	231	7	2	0
Chamaedorea dammeriana	236	235	1	0	0
Oenocarpus mapora	232	204	26	0	2
Acoelorraphe wrightii	222	59	163	0	0
Lepidocaryum tenue	218	216	2	0	0
Bactris hondurensis	217	212	5	0	0
Mauritia flexuosa	214	172	42	0	0
Syagrus comosa	195	82	113	0	0
Calyptrogyne ghiesbreghtiana	189	186	1	2	0
Euterpe catinga	177	175	1	1	0
Attalea butyracea	175	126	47	1	1
Geonoma brongniartii	175	138	36	1	0
Chamaedorea elegans	172	141	24	5	2
Desmoncus mitis	172	149	23	0	0
Brahea dulcis	168	50	73	1	44
Chamaedorea deckeriana	168	167	0	1	0
Geonoma occidentalis	166	83	83	0	0
Thrinax radiata	166	2	163	0	1
Chamaedorea macrospadix	164	158	0	6	0
Attalea amygdalina	155	155	0	0	0
Pholidostachys synanthera	155	150	5	0	0
Syagrus harleyi	155	30	125	0	0
Syagrus coronata	154	21	133	0	0
Oenocarpus bacaba	153	134	19	0	0
Wettinia praemorsa	152	123	0	23	6
Syagrus orinocensis	148	148	0	0	0
Chamaedorea elatior	147	121	20	4	2
Attalea maripa	145	115	30	0	0
Euterpe oleracea	145	103	42	0	0
Geonoma elegans	145	117	25	3	0
Prestoea schultzeana	144	140	3	0	1
Chamaedorea seifrizii	143	5	137	1	0
Bactris corossilla	141	137	4	0	0
Attalea insignis	140	136	4	0	0
Geonoma leptospadix	139	117	22	0	0
Bactris setosa	137	100	27	10	0

Table S1 Continued

Geonoma camana	137	128	9	0	0
Chamaedorea pumila	136	135	0	1	0
Chamaedorea palmeriana	132	121	0	11	0
Chamaedorea scheryi	131	106	0	25	0
Cryosophila stauracantha	131	39	92	0	0
Prestoea decurrens	130	126	4	0	0
Bactris gasipaes	129	116	13	0	0
Geonoma baculifera	128	94	34	0	0
Geonoma edulis	126	96	0	30	0
Prestoea longepetiolata	126	105	0	21	0
Wettinia maynensis	125	124	0	1	0
Allagoptera arenaria	123	31	92	0	0
Synechanthus fibrosus	123	121	1	1	0
Bactris concinna	120	94	26	0	0
Geonoma oxycarpa	120	114	6	0	0
Aiphanes ulei	119	117	2	0	0
Mauritiella armata	118	77	41	0	0
Bactris elegans	117	79	38	0	0
Bactris mexicana	116	95	21	0	0
Bactris fissifrons	115	115	0	0	0
Chamaedorea warscewiczii	114	111	0	3	0
Sabal mexicana	114	15	99	0	0
Elaeis oleifera	111	98	13	0	0
Chamaedorea pygmaea	110	70	2	38	0
Astrocaryum campestre	108	28	80	0	0
Oenocarpus minor	108	100	8	0	0
Calyptrogyne costatifrons	106	105	1	0	0
Geonoma pauciflora	106	68	38	0	0
Bactris gracilior	105	105	0	0	0
Cryosophila warscewiczii	105	102	3	0	0
Mauritiella aculeata	104	81	23	0	0
Butia paraguayensis	102	96	6	0	0
Chamaedorea neurochlamys	102	90	12	0	0
Attalea humilis	101	58	43	0	0
Wettinia kalbreyeri	101	88	0	12	1
Bactris setulosa	100	85	9	6	0
Geonoma pinnatifrons	100	93	4	3	0
Pholidostachys pulchra	100	99	0	1	0
Chamaedorea lucidifrons	99	99	0	0	0
Allagoptera leucocalyx	96	42	53	0	1
Attalea speciosa	95	43	52	0	0
Aiphanes horrida	93	70	19	4	0

Table S1. Continued

Attalea eichleri	93	19	74	0	0
Attalea racemosa	92	90	2	0	0
Geonoma longevaginata	92	92	0	0	0
Astrocaryum mexicanum	91	85	6	0	0
Manicaria saccifera	91	91	0	0	0
Syagrus inajai	91	72	19	0	0
Geonoma poeppigiana	88	84	4	0	0
Attalea geraensis	85	65	20	0	0
Bactris coloradonis	84	81	1	2	0
Bactris vulgaris	84	50	34	0	0
Bactris balanophora	83	83	0	0	0
Astrocaryum chambira	82	80	2	0	0
Astrocaryum jauari	81	65	16	0	0
Bactris campestris	81	72	9	0	0
Syagrus oleracea	81	47	34	0	0
Astrocaryum acaule	80	68	12	0	0
Geonoma procumbens	80	77	3	0	0
Bactris dianeura	79	79	0	0	0
Sabal yapa	79	1	78	0	0
Aiphanes hirsuta	77	76	0	1	0
Dictyocaryum lamarckianum	76	70	0	5	1
Chamaedorea tuerckheimii	75	75	0	0	0
Leopoldinia pulchra	75	73	2	0	0
Prestoea ensiformis	75	68	5	2	0
Wettinia quinaria	75	72	0	3	0
Syagrus pseudococos	72	64	8	0	0
Syagrus graminifolia	71	55	16	0	0
Attalea microcarpa	70	65	5	0	0
Attalea phalerata	70	29	41	0	0
Neonicholsonia watsonii	70	68	2	0	0
Pholidostachys dactyloides	70	66	2	2	0
Chamaedorea pittieri	69	38	0	31	0
Syagrus schizophylla	69	9	60	0	0
Astrocaryum aculeatissimum	67	54	13	0	0
Bactris acanthocarpoides	66	56	10	0	0
Bactris riparia	66	56	10	0	0
Calyptrogyne trichostachys	66	66	0	0	0
Phytelephas macrocarpa	66	43	23	0	0
Sabal mauritiiformis	66	18	47	0	1
Bactris pilosa	65	54	11	0	0
Bactris brongniartii	64	49	15	0	0
Chamaedorea sartorii	64	54	7	3	0

Table S1. Continued

Iriartella stenocarpa	64	59	5	0	0
Chamaedorea schiedeana	62	50	2	9	1
Welfia regia	62	61	1	0	0
Chamaedorea nubium	61	54	1	6	0
Chamaedorea undulatifolia	61	57	0	4	0
Copernicia alba	61	13	48	0	0
Bactris killipii	60	59	1	0	0
Chamaedorea allenii	60	56	2	2	0
Chamaedorea angustisecta	58	35	23	0	0
Astrocaryum vulgare	57	22	35	0	0
Geonoma aspidiifolia	57	55	2	0	0
Bactris pickelii	56	38	18	0	0
Geonoma gamiova	55	50	0	5	0
Chamaedorea amabilis	54	54	0	0	0
Astrocaryum alatum	53	53	0	0	0
Geonoma triglochin	53	51	1	0	1
Wendlandiella gracilis	53	35	18	0	0
Butia capitata	51	24	27	0	0
Chelyocarpus ulei	51	35	16	0	0
Syagrus vagans	51	1	50	0	0
Astrocaryum aculeatum	50	38	12	0	0
Astrocaryum sciophilum	50	45	5	0	0
Chamaedorea pochutlensis	50	43	6	0	1
Geonoma epetiolata	50	50	0	0	0
Wettinia augusta	50	42	8	0	0
Bactris bahiensis	49	19	30	0	0
Syagrus petraea	49	47	2	0	0
Astrocaryum standleyanum	48	45	2	0	1
Bactris bifida	48	41	7	0	0
Gaussia maya	48	5	43	0	0
Bactris gastoniana	47	43	4	0	0
Bactris glandulosa	47	47	0	0	0
Calyptrogyne allenii	47	45	2	0	0
Wettinia drudei	47	47	0	0	0
Calyptrogyne panamensis	46	46	0	0	0
Chamaedorea robertii	46	46	0	0	0
Mauritia carana	46	46	0	0	0
Aiphanes weberbaueri	45	36	6	2	1
Bactris glaucescens	45	10	35	0	0
Calyptrogyne brachystachys	45	43	0	2	0
Syagrus cocoides	45	16	29	0	0
Chamaedorea graminifolia	44	31	8	5	0

Table S1. Continued

Chamaedorea liebmannii	44	30	2	12	0
Chamaedorea tenella	44	43	1	0	0
Geonoma laxiflora	44	40	4	0	0
Reinhardtia koschnyana	44	42	2	0	0
Syagrus ruschiana	44	39	5	0	0
Bactris guineensis	43	5	38	0	0
Desmoncus schippii	43	42	1	0	0
Chamaedorea woodsoniana	42	39	3	0	0
Cryosophila nana	42	21	20	0	1
Attalea barreirensis	41	12	29	0	0
Oenocarpus distichus	41	4	37	0	0
Phytelephas tenuicaulis	41	40	1	0	0
Attalea funifera	40	16	24	0	0
Bactris caryotifolia	40	34	6	0	0
Oenocarpus balickii	40	36	4	0	0
Reinhardtia latisecta	40	39	1	0	0
Syagrus botryophora	40	14	26	0	0
Syagrus sancona	40	24	15	0	1
Bactris bidentula	39	35	4	0	0
Bactris aubletiana	38	38	0	0	0
Bactris oligocarpa	38	36	2	0	0
Itaya amicorum	38	38	0	0	0
Astrocaryum murumuru	37	34	3	0	0
Aiphanes linearis	36	26	1	9	0
Attalea allenii	36	35	1	0	0
Bactris coloniata	36	33	3	0	0
Bactris grayumii	36	36	0	0	0
Allagoptera brevicalyx	35	9	26	0	0
Bactris barronis	35	35	0	0	0
Bactris ferruginea	35	20	15	0	0
Bactris oligoclada	35	31	4	0	0
Attalea dubia	34	34	0	0	0
Chamaedorea brachyclada	34	34	0	0	0
Attalea nucifera	33	27	6	0	0
Desmoncus giganteus	33	33	0	0	0
Attalea burretiana	32	16	16	0	0
Bactris macroacantha	32	25	7	0	0
Socratea salazarii	32	26	6	0	0
Syagrus loefgrenii	32	32	0	0	0
Aiphanes chiribogensis	31	19	0	12	0
Elaeis guineensis	31	22	8	1	0
Geonoma longepedunculata	31	30	0	1	0

Table S1. Continued

Astrocaryum ciliatum	30	30	0	0	0
Chamaedorea rossteniorum	30	30	0	0	0
Bactris glassmanii	29	19	10	0	0
Bactris polystachya	29	29	0	0	0
Chamaedorea correae	29	29	0	0	0
Desmoncus horridus	29	20	9	0	0
Attalea tessmannii	28	14	14	0	0
Bactris schultesii	28	28	0	0	0
Chamaedorea arenbergiana	28	19	5	2	2
Socratea rostrata	28	27	0	1	0
Trithrinax schizophylla	28	7	21	0	0
Astrocaryum urostachys	27	27	0	0	0
Attalea compta	27	27	0	0	0
Bactris tomentosa	27	26	1	0	0
Manicaria martiana	27	27	0	0	0
Raphia taedigera	27	26	0	1	0
Attalea attaleoides	26	25	1	0	0
Attalea rostrata	26	17	6	3	0
Barcella odora	26	19	7	0	0
Chamaedorea geonomiformis	26	24	2	0	0
Geonoma euspatha	26	24	2	0	0
Geonoma scoparia	26	26	0	0	0
Wettinia radiata	26	26	0	0	0
Astrocaryum malybo	25	18	7	0	0
Bactris ptariana	25	17	8	0	0
Chamaedorea metallica	25	25	0	0	0
Chamaedorea zamorae	25	22	0	3	0
Desmoncus chinantlensis	25	16	9	0	0
Prestoea simplicifolia	25	25	0	0	0
Astrocaryum paramaca	24	24	0	0	0
Attalea oleifera	23	9	14	0	0
Bactris horridispatha	23	10	13	0	0
Colpothrinax cookii	23	23	0	0	0
Acrocomia hassleri	22	18	4	0	0
Bactris constanciae	22	22	0	0	0
Calyptrogyne anomala	22	22	0	0	0
Geonoma concinnoidea	22	22	0	0	0
Leopoldinia piassaba	22	22	0	0	0
Phytelephas seemannii	22	21	0	1	0
Aiphanes tricuspidata	21	13	8	0	0
Aphandra natalia	21	20	0	1	0
Astrocaryum huaimi	21	7	14	0	0

Tables S1. Continued

Attalea cohune	21	8	13	0	0
Bactris baileyana	21	21	0	0	0
Bactris caudata	21	21	0	0	0
Geonoma diversa	21	21	0	0	0
Roystonea regia	21	10	7	3	1
Chamaedorea radicalis	20	3	16	0	1
Dypsis lutescens	20	16	3	1	0
Geonoma mooreana	20	20	0	0	0
Attalea spectabilis	19	16	3	0	0
Attalea vitrivir	19	6	13	0	0
Chamaedorea alternans	19	18	1	0	0
Chamaedorea microspadix	19	13	3	3	0
Desmoncus leptoclonos	19	7	12	0	0
Desmoncus myriacanthos	19	11	8	0	0
Geonoma hugonis	19	19	0	0	0
Attalea iguadummat	18	18	0	0	0
Chamaedorea sullivaniorum	18	18	0	0	0
Cryosophila guagara	18	18	0	0	0
Wettinia aequalis	18	17	1	0	0
Attalea luetzelburgii	17	17	0	0	0
Bactris rhaphidacantha	17	17	0	0	0
Calyptrogyne condensata	17	17	0	0	0
Calyptrogyne deneversii	17	17	0	0	0
Chamaedorea subjectifolia	17	17	0	0	0
Desmoncus cirrhifer	17	17	0	0	0
Desmoncus costaricensis	17	17	0	0	0
Hyospathe frontinensis	17	17	0	0	0
Aiphanes macroloba	16	16	0	0	0
Ammandra dasyneura	16	16	0	0	0
Attalea colenda	16	11	5	0	0
Bactris sphaerocarpa	16	15	1	0	0
Brahea salvadorensis	16	15	1	0	0
Copernicia tectorum	16	5	10	1	0
Cryosophila kalbreyeri	16	8	8	0	0
Desmoncus vacivus	16	16	0	0	0
Dictyocaryum ptarianum	16	16	0	0	0
Geonoma concinna	16	16	0	0	0
Mauritiella pumila	16	16	0	0	0
Phytelephas aequatorialis	16	12	2	1	1
Bactris cuspidata	15	12	3	0	0
Bactris militaris	15	15	0	0	0
Bactris panamensis	15	15	0	0	0

Table S1. Continued

Chamaedorea cataractarum	15	12	2	0	1
Colpothrinax aphanopetala	15	15	0	0	0
Desmoncus intermedius	15	15	0	0	0
Geonoma rodeiensis	15	6	9	0	0
Geonoma umbraculiformis	15	14	1	0	0
Leopoldinia major	15	15	0	0	0
Syagrus picrophylla	15	9	6	0	0
Syagrus smithii	15	15	0	0	0
Allagoptera caudescens	14	6	8	0	0
Bactris chaveziae	14	4	10	0	0
Bactris hatschbachii	14	14	0	0	0
Calyptrogyne osensis	14	14	0	0	0
Geonoma oligoclona	14	14	0	0	0
Oenocarpus circumtextus	14	14	0	0	0
Acrocomia intumescens	13	5	8	0	0
Attalea exigua	13	8	5	0	0
Bactris pliniana	13	13	0	0	0
Butia campicola	13	12	1	0	0
Chamaedorea schippii	13	13	0	0	0
Geonoma monospatha	13	13	0	0	0
Geonoma poiteauana	13	9	4	0	0
Prestoea pubens	13	13	0	0	0
Wettinia longipetala	13	12	1	0	0
Aiphanes deltoidea	12	10	2	0	0
Astrocaryum rodriguesii	12	11	1	0	0
Astrocaryum sociale	12	12	0	0	0
Attalea brejinhoensis	12	1	11	0	0
Chamaedorea rojasiana	12	10	1	1	0
Desmoncus isthmius	12	12	0	0	0
Geonoma oldemanii	12	12	0	0	0
Orbignya cohune	12	9	3	0	0
Pholidostachys panamensis	12	12	0	0	0
Chamaedorea anemophila	11	11	0	0	0
Chamaedorea ricardoi	11	11	0	0	0
Desmoncus setosus	11	11	0	0	0
Geonoma triandra	11	10	1	0	0
Scheelea butyracea	11	5	6	0	0
Astrocaryum confertum	10	10	0	0	0
Bactris syagroides	10	7	3	0	0
Chamaedorea matae	10	10	0	0	0
Chelyocarpus dianeurus	10	10	0	0	0
Geonoma chococola	10	10	0	0	0

Table S1. Continued

Syagrus campylospatha	10	6	4	0	0
Syagrus evansiana	10	10	0	0	0
Chelyocarpus repens	9	9	0	0	0
Roystonea oleracea	9	9	0	0	0
Syagrus stratincola	9	9	0	0	0
Acrocomia totai	8	6	2	0	0
Aiphanes parvifolia	8	8	0	0	0
Ammandra decasperma	8	8	0	0	0
Archontophoenix alexandrae	8	7	0	1	0
Attalea septuagenata	8	8	0	0	0
Bactris charnleyae	8	8	0	0	0
Bactris herrerana	8	8	0	0	0
Calyptrogyne sanblasensis	8	8	0	0	0
Geonoma calyptrogynoidea	8	8	0	0	0
Reinhardtia elegans	8	6	2	0	0
Syagrus weddelliana	8	6	0	2	0
Astrocaryum macrocalyx	7	7	0	0	0
Attalea dahlgreniana	7	5	2	0	0
Attalea plowmanii	7	7	0	0	0
Bactris turbinocarpa	7	7	0	0	0
Butia exospadix	7	7	0	0	0
Chamaedorea ponderosa	7	6	1	0	0
Chamaedorea pringlei	7	1	6	0	0
Geonoma paradoxa	7	7	0	0	0
Socratea hecatonandra	7	7	0	0	0
Attalea amylacea	6	6	0	0	0
Attalea brasiliensis	6	6	0	0	0
Bactris kunorum	6	6	0	0	0
Bactris soeiroana	6	2	4	0	0
Chamaedorea selvae	6	6	0	0	0
Chamaedorea stenocarpa	6	6	0	0	0
Desmoncus moorei	6	6	0	0	0
Desmoncus phoenicocarpus	6	6	0	0	0
Geonoma simplicifrons	6	1	5	0	0
Oenocarpus simplex	6	6	0	0	0
Syagrus lorenzoniorum	6	4	2	0	0
Aiphanes acaulis	5	5	0	0	0
Asterogyne guianensis	5	5	0	0	0
Attalea cuatrecasana	5	5	0	0	0
Bactris halmoorei	5	5	0	0	0
Bactris longiseta	5	5	0	0	0
Bactris tefensis	5	5	0	0	0

Table S1. Continued

Caryota urens	5	4	1	0	0
Chamaedorea serpens	5	5	0	0	0
Desmoncus obovoideus	5	5	0	0	0
Desmoncus parvulus	5	5	0	0	0
Desmoncus stans	5	5	0	0	0
Geonoma frontinensis	5	5	0	0	0
Geonoma multisecta	5	5	0	0	0
Iriartea deltoides	5	5	0	0	0
Mauritiella macroclada	5	5	0	0	0
Ptychosperma macarthurii	5	2	3	0	0
Aiphanes buenaventurae	4	4	0	0	0
Astrocaryum faranae	4	4	0	0	0
Astrocaryum ferrugineum	4	4	0	0	0
Astrocaryum javarense	4	4	0	0	0
Bactris faucium	4	2	2	0	0
Cryosophila bartletii	4	4	0	0	0
Geonoma galeanoae	4	4	0	0	0
Geonoma spinescens	4	1	3	0	0
Licuala grandis	4	4	0	0	0
Reinhardtia simplex	4	4	0	0	0
Acrocomia sclerocarpa	3	2	1	0	0
Aiphanes truncata	3	2	1	0	0
Astrocaryum farinosum	3	1	2	0	0
Attalea anisitsiana	3	1	2	0	0
Attalea apoda	3	3	0	0	0
Bactris neomilitaris	3	3	0	0	0
Desmoncus interjectus	3	3	0	0	0
Euterpe longibracteata	3	2	1	0	0
Gaussia gomez-pompae	3	2	1	0	0
Geonoma divisa	3	3	0	0	0
Nypa fruticans	3	3	0	0	0
Reinhardtia rostrata	3	2	0	1	0
Scheelea lundellii	3	2	1	0	0
Synechanthus cuatrecasanus	3	3	0	0	0
Trithrinax brasiliensis	3	3	0	0	0
Welfia georgii	3	2	0	1	0
Aiphanes monostachys	2	2	0	0	0
Areca catechu	2	2	0	0	0
Astrocaryum gratum	2	1	1	0	0
Astrocaryum perangustatum	2	2	0	0	0
Attalea magdalenica	2	2	0	0	0
Attalea maripensis	2	2	0	0	0

Table S1. Continued

Butia eriospatha	2	2	0	0	0
Calyptrogyne pubescens	2	2	0	0	0
Chamaedorea falcifera	2	2	0	0	0
Chamaedorea hooperiana	2	2	0	0	0
Desmoncus kunarius	2	2	0	0	0
Desmoncus pumilus	2	2	0	0	0
Geonoma calostachys	2	2	0	0	0
Lobia erosa	2	2	0	0	0
Trithrinax acanthocoma	2	2	0	0	0
Wettinia panamensis	2	1	1	0	0
Arenga pinnata	1	1	0	0	0
Astrocaryum scopatum	1	1	0	0	0
Attalea camopiensis	1	1	0	0	0
Attalea degranvillei	1	1	0	0	0
Attalea guianensis	1	1	0	0	0
Bactris acida	1	1	0	0	0
Bactris martiana	1	1	0	0	0
Bactris obovata	1	1	0	0	0
Butia microspadix	1	1	0	0	0
Calyptrogyne baudensis	1	1	0	0	0
Calyptrogyne kunorum	1	1	0	0	0
Caryota mitis	1	1	0	0	0
Catoblastus radiatus	1	1	0	0	0
Chamaedorea brachypoda	1	1	0	0	0
Chamaedorea coralliana	1	1	0	0	0
Chamaedorea pachecoana	1	1	0	0	0
Chamaedorea skutchii	1	1	0	0	0
Daemonorops angustifolia	1	1	0	0	0
Daemonorops jenkinsiana	1	1	0	0	0
Daemonorops melanochaetes	1	1	0	0	0
Desmoncus osensis	1	1	0	0	0
Desmoncus prunifer	1	1	0	0	0
Dictyocaryum fuscum	1	1	0	0	0
Geonoma dindoensis	1	1	0	0	0
Geonoma granditrijuga	1	1	0	0	0
Geonoma metensis	1	1	0	0	0
Geonoma platyphylla	1	1	0	0	0
Geonoma poiteana	1	1	0	0	0
Lepidocaryum gujanense	1	1	0	0	0
Oenocarpus altissima	1	1	0	0	0
Oenocarpus makeru	1	1	0	0	0

Table S1. Continued

Pholidostachys kalbreyeri	1	1	0	0	0
Pholidostachys mooreana	1	1	0	0	0
Rhapis excelsa	1	1	0	0	0
Sabinaria magnifica	1	1	0	0	0
Syagrus x teixeiriana	1	1	0	0	0

Table S2. Area of the geographic distribution of palm species restricted to climate suitable for lowland humid-to-superhumid forest within areas where climate became suitable for this forests after the Last Glacial Maximum. Area of the geographic distribution was measured as the extent of occurrence. The areas were calculated using three circulation models: CCSM4, MIROC-ESM and MPI-ESM-P.

	Circulation Model		
Species	**CCSM4 (Km^2)**	**MIROC-ESM (Km^2)**	**MPI-ESM-P (Km^2)**
Aiphanes acaulis	0.0	0.0	0.0
Aiphanes macroloba	0.0	0.0	0.0
Aiphanes parvifolia	0.0	0.0	0.0
Ammandra dasyneura	0.0	0.0	0.0
Ammandra decasperma	0.0	0.0	0.0
Astrocaryum alatum	724.1	7717.9	0.0
Astrocaryum ciliatum	0.0	0.0	0.0
Astrocaryum confertum	0.0	0.0	0.0
Astrocaryum macrocalyx	0.0	0.0	0.0
Astrocaryum paramaca	0.0	101161.6	0.0
Astrocaryum sociale	0.0	64.0	0.0
Astrocaryum urostachys	0.0	0.0	0.0
Attalea amygdalina	0.0	0.0	0.0
Attalea compta	0.0	0.0	0.0
Attalea cuatrecasana	0.0	0.0	0.0
Attalea dubia	1336.8	962.9	273.9
Attalea iguadummat	0.0	0.0	0.0
Attalea luetzelburgii	256.0	0.0	0.0
Bactris aubletiana	0.0	0.0	0.0
Bactris baileyana	0.0	1075.6	0.0
Bactris balanophora	4994.2	330584.6	0.0
Bactris barronis	0.0	1670.8	0.0
Bactris caudata	0.0	2624.5	0.0
Bactris charnleyae	0.0	0.0	0.0
Bactris constanciae	0.0	130885.8	0.0
Bactris dianeura	312.9	5349.5	0.0
Bactris fissifrons	4076.0	104511.1	0.0
Bactris glandulosa	0.0	4412.4	0.0
Bactris gracilior	0.0	5674.7	0.0
Bactris grayumii	0.0	4008.4	0.0
Bactris halmoorei	0.0	0.0	0.0
Bactris hatschbachii	528.8	176.0	254.3
Bactris herrerana	0.0	590.4	0.0
Bactris kunorum	0.0	0.0	0.0
Bactris longiseta	0.0	903.2	0.0

Table S2 Continued

Bactris militaris	0.0	737.2	0.0
Bactris panamensis	0.0	0.0	0.0
Bactris pliniana	0.0	2705.8	0.0
Bactris polystachya	0.0	1869.0	0.0
Bactris rhaphidacantha	0.0	0.0	0.0
Bactris schultesii	0.0	0.0	0.0
Bactris turbinocarpa	0.0	121557.4	0.0
Butia eriospatha	9959.4	22030.2	2313.5
Butia exospadix	0.0	11937.7	0.0
Butia microspadix	6101.1	8198.6	2039.6
Calyptrogyne anomala	0.0	0.0	0.0
Calyptrogyne condensata	0.0	526.9	0.0
Calyptrogyne deneversii	0.0	0.0	0.0
Calyptrogyne osensis	0.0	253.2	0.0
Calyptrogyne panamensis	0.0	21.1	0.0
Calyptrogyne sanblasensis	0.0	0.0	0.0
Calyptrogyne trichostachys	0.0	840.4	0.0
Chamaedorea amabilis	0.0	1896.7	0.0
Chamaedorea anemophila	0.0	211.2	0.0
Chamaedorea brachyclada	0.0	379.8	0.0
Chamaedorea correae	0.0	42.2	0.0
Chamaedorea lucidifrons	0.0	2611.3	0.0
Chamaedorea matae	0.0	1287.0	0.0
Chamaedorea metallica	0.0	2603.2	0.0
Chamaedorea ricardoi	0.0	0.0	0.0
Chamaedorea robertii	0.0	1559.4	0.0
Chamaedorea rossteniorum	0.0	421.5	0.0
Chamaedorea schippii	0.0	0.0	0.0
Chamaedorea selvae	0.0	0.0	0.0
Chamaedorea serpens	0.0	0.0	0.0
Chamaedorea stenocarpa	166.5	7052.5	145.1
Chamaedorea subjectifolia	0.0	0.0	0.0
Chamaedorea sullivaniorum	0.0	1517.7	0.0
Chamaedorea tuerckheimii	20.5	1878.3	82.3
Chelyocarpus dianeurus	0.0	0.0	0.0
Chelyocarpus repens	0.0	0.0	0.0
Colpothrinax aphanopetala	0.0	1664.5	0.0
Colpothrinax cookii	624.5	2811.8	0.0
Cryosophila guagara	0.0	632.9	0.0
Desmoncus cirrhifer	0.0	0.0	0.0
Desmoncus costaricensis	0.0	716.1	0.0
Desmoncus giganteus	0.0	0.0	0.0

Table S2. Continued

Desmoncus intermedius	0.0	0.0	0.0
Desmoncus isthmius	0.0	0.0	0.0
Desmoncus moorei	0.0	1238.6	0.0
Desmoncus obovoideus	0.0	21.1	0.0
Desmoncus parvulus	1771.0	71364.2	0.0
Desmoncus phoenicocarpus	4034.1	73543.4	4574.2
Desmoncus stans	0.0	0.0	0.0
Desmoncus vacivus	0.0	0.0	0.0
Dictyocaryum ptarianum	4994.2	14847.9	0.0
Geonoma calyptrogynoidea	0.0	0.0	0.0
Geonoma chococola	168.2	1308.0	84.8
Geonoma concinna	0.0	42.2	0.0
Geonoma concinnoidea	0.0	21.1	0.0
Geonoma diversa	0.0	11303.2	0.0
Geonoma epetiolata	0.0	1749.2	0.0
Geonoma frontinensis	0.0	0.0	0.0
Geonoma galeanoae	0.0	0.0	0.0
Geonoma hugonis	0.0	0.0	0.0
Geonoma longevaginata	0.0	5889.3	0.0
Geonoma monospatha	0.0	126.7	0.0
Geonoma mooreana	0.0	211.2	0.0
Geonoma oldemanii	0.0	0.0	0.0
Geonoma oligoclona	0.0	0.0	0.0
Geonoma paradoxa	0.0	0.0	0.0
Geonoma scoparia	0.0	0.0	0.0
Hyospathe frontinensis	0.0	0.0	0.0
Iriartea deltoides	106.0	4497.8	84.8
Itaya amicorum	0.0	0.0	0.0
Leopoldinia major	7544.3	148483.1	0.0
Leopoldinia piassaba	1599.5	80823.9	0.0
Manicaria martiana	0.0	0.0	0.0
Manicaria saccifera	86788.8	346009.0	10193.6
Mauritia carana	0.0	89242.7	0.0
Mauritiella macroclada	0.0	0.0	0.0
Mauritiella pumila	0.0	0.0	0.0
Pholidostachys panamensis	0.0	42.2	0.0
Prestoea pubens	0.0	21.1	0.0
Prestoea simplicifolia	0.0	0.0	0.0
Reinhardtia simplex	0.0	205.2	0.0
Roystonea oleracea	28740.2	46174.0	169.2
Syagrus evansiana	123.9	0.0	0.0
Syagrus loefgrenii	317.2	178.4	0.0

Table S2. Continued

Syagrus orinocensis	38057.7	46999.2	850.1
Syagrus smithii	191.3	0.0	0.0
Syagrus stratincola	0.0	596.9	0.0
Trithrinax brasiliensis	8563.8	22379.9	2039.6
Wettinia drudei	0.0	0.0	0.0
Wettinia radiata	0.0	0.0	0.0
Aiphanes buenaventurae	0.0	0.0	0.0
Aiphanes monostachys	0.0	0.0	0.0
Areca catechu	0.0	0.0	0.0
Arenga pinnata	0.0	0.0	0.0
Asterogyne guianensis	0.0	0.0	0.0
Astrocaryum faranae	0.0	0.0	0.0
Astrocaryum ferrugineum	0.0	0.0	0.0
Astrocaryum javarense	0.0	0.0	0.0
Astrocaryum perangustatum	0.0	0.0	0.0
Astrocaryum scopatum	0.0	0.0	0.0
Attalea amylacea	0.0	0.0	0.0
Attalea apoda	0.0	0.0	0.0
Attalea brasiliensis	0.0	0.0	0.0
Attalea camopiensis	0.0	0.0	0.0
Attalea degranvillei	0.0	0.0	0.0
Attalea guianensis	0.0	0.0	0.0
Attalea magdalenica	0.0	0.0	0.0
Attalea maripensis	0.0	0.0	0.0
Attalea plowmanii	0.0	0.0	0.0
Attalea septuagenata	0.0	0.0	0.0
Bactris acida	0.0	0.0	0.0
Bactris martiana	0.0	0.0	0.0
Bactris neomilitaris	0.0	0.0	0.0
Bactris obovata	0.0	0.0	0.0
Bactris tefensis	0.0	0.0	0.0
Calyptrogyne baudensis	0.0	0.0	0.0
Calyptrogyne kunorum	0.0	0.0	0.0
Calyptrogyne pubescens	0.0	0.0	0.0
Caryota mitis	0.0	0.0	0.0
Catoblastus radiatus	0.0	0.0	0.0
Chamaedorea brachypoda	0.0	0.0	0.0
Chamaedorea coralliana	0.0	0.0	0.0
Chamaedorea falcifera	0.0	0.0	0.0
Chamaedorea hooperiana	0.0	0.0	0.0
Chamaedorea pachecoana	0.0	0.0	0.0
Chamaedorea skutchii	0.0	0.0	0.0

Table S2. Continued

Cryosophila bartletii	0.0	0.0	0.0
Daemonorops angustifolia	0.0	0.0	0.0
Daemonorops jenkinsiana	0.0	0.0	0.0
Daemonorops melanochaetes	0.0	0.0	0.0
Desmoncus interjectus	0.0	0.0	0.0
Desmoncus kunarius	0.0	0.0	0.0
Desmoncus osensis	0.0	0.0	0.0
Desmoncus prunifer	0.0	0.0	0.0
Desmoncus pumilus	0.0	0.0	0.0
Desmoncus setosus	0.0	0.0	0.0
Dictyocaryum fuscum	0.0	0.0	0.0
Geonoma calostachys	0.0	0.0	0.0
Geonoma dindoensis	0.0	0.0	0.0
Geonoma divisa	0.0	0.0	0.0
Geonoma granditrijuga	0.0	0.0	0.0
Geonoma metensis	0.0	0.0	0.0
Geonoma multisecta	0.0	0.0	0.0
Geonoma platyphylla	0.0	0.0	0.0
Geonoma poiteana	0.0	0.0	0.0
Lepidocaryum gujanense	0.0	0.0	0.0
Licuala grandis	0.0	0.0	0.0
Lobia erosa	0.0	0.0	0.0
Nypa fruticans	0.0	0.0	0.0
Oenocarpus altissima	0.0	0.0	0.0
Oenocarpus circumtextus	0.0	0.0	0.0
Oenocarpus makeru	0.0	0.0	0.0
Oenocarpus simplex	0.0	0.0	0.0
Pholidostachys kalbreyeri	0.0	0.0	0.0
Pholidostachys mooreana	0.0	21.1	0.0
Rhapis excelsa	0.0	0.0	0.0
Sabinaria magnifica	0.0	0.0	0.0
Socratea hecatonandra	0.0	0.0	0.0
Syagrus x teixeiriana	0.0	0.0	0.0
Synechanthus cuatrecasanus	0.0	0.0	0.0
Trithrinax acanthocoma	0.0	0.0	0.0