

COMPARING THE EFFECT OF DISPERSAL LIMITATION AND
ENVIRONMENTAL FILTERING ON BETA DIVERSITY
PATTERNS ALONG ALTITUDINAL RANGES AT TWO FOREST
OF CONTRASTING SPECIES POOL



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Picture front page: Muniellos forest



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Abstract

Latitude and altitude are considered two of the most important ecological gradients shaping diversity patterns across the globe. It is expected that similar ecological processes shape species distributions along these gradients due to the similar decrease in species number from low to high elevations and from low to high latitudes but this is subjected to debate. Traditionally two main mechanisms have been considered to influence the spatial distribution of species, the effect of environment (environmental filtering) and the effect of dispersal limitation. Therefore, unrevealing the mechanisms that maintain diversity at different latitudes and elevations is a central topic in ecology. This study aims to compare the community assembly mechanisms generating beta diversity patterns of woody plants at lowland and mountainous temperate and tropical forests. We studied four regions of contrasting elevations (lowland and mountainous) and latitudes (tropical and temperate) with a total of 236 plots of 0.1 ha, in which all the woody plants with a DBH > 2.5 cm were inventoried. Beta diversity was calculated as Bray Curtis dissimilarity between pair of plots in each forest sampled. We compared beta diversity variation between regions at different latitudes and altitudinal ranges. The large difference in the regional species pool between each forest makes it necessary the use of a null model in order to compare beta diversity patterns. Beta diversity variation was partitioned using a dbRDA analysis, in which a set of environmental variables and spatial predictors was used as explanatory variables in each region. We found that beta diversity was greater at the tropical and mountainous sampled. After controlling for the effect of the species pool, beta diversity patterns were similar at both tropical and temperate forest studied. Despite the similarity of beta diversity patterns across latitudes, the mechanisms generating these patterns differed between tropical and temperate forests. In both tropical forests spatial variables and spatially structured environmental variables were responsible for explaining the majority of the beta diversity variation, while in both temperate forests only environmental variables explained the beta diversity variation. Although in both mountainous forests beta diversity values were greater than in the lowland ones, the main ecological processes shaping this beta diversity patterns remained similar at the different elevations considered. This study shows for the first time that community assembly mechanism do not change substantially across the elevations selected, at the tropical and temperate forests sampled.

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Introduction

Studying the spatial arrangement of species communities and the processes that determine them is a central topic in ecology (Austin, 2002). Traditionally beta diversity has been defined as the variation of species composition between sites, representing a direct link between alpha diversity (species diversity in each site) and gamma diversity (total diversity of a group of sites) (Whittaker 1960, 1972). Due to the aforementioned characteristic, the importance of beta diversity for community ecologists resides in the fact that it reflects the processes that generate and maintain biodiversity in ecosystems at large scales (Condit et al. 2002; Legendre and Cáceres, 2013). Following the revision of beta diversity concept in Anderson et al. (2011), this study will address beta diversity as the variation of woody plant species (= floristic dissimilarity) among a set of sampling units in a given spatial extent.

Two main mechanisms are expected to have an effect over the spatial distribution of species. Environmental determinism, which is the sorting of species according to environmental factors that vary in the space (Schoener, 1974; Levine and HilleRisLambers, 2009). In this case community composition dissimilarities will be the consequence of the change of environmental variables with distance. These processes would be based by the different evolutionary adaptations of species to different environmental conditions (e.g: Tuomisto et al., 2003). According to Vellend (2010) environmental species sorting is analogous to niche selection, where deterministic interactions between environmental factors and species traits shape which species occur at a given site. Dispersal limitation, which is caused by the limited dispersal ability of species regardless the environmental conditions involved (Tilman, 1994; Hubell, 2001, Jhonson et al., 2012). This second mechanism predicts species similarity to decay with distance due to limited dispersal ability of species without the intervention of any environmental force, which represents one of the explanations of the neutral theory of biodiversity (Hubell, 2001). In this sense, dispersal limitation would represent a completely stochastic event (Clarck, 2009).

The role of environmental filtering and dispersal limitation on species variation through space has been long debated (Hubell, 2001; Condit et al., 2002; Tuomisto, 2003; Chase, 2010). Distinguishing the importance of both processes is hard in natural systems because of the generally strong correlation between space and environment (Gilbert and Lechowicz, 2004; Smith and Lundholm, 2010). Recently, there seems to be more agreement on the combined effect of both non-exclusive mechanisms (Tilman,

2004; Gravel et al., 2006; Wang et al., 2013), both having different importance across scales (Arellano et al. In Press), regions (Myers et al. 2013) and among different organisms (Legendre et al., 2009).

Added to these two mechanisms that tend to operate at regional to landscape level scale and ecological time scales, large scale processes like speciation, extinction or ecological drift (Hubbell, 2001) also affect the species composition of local communities, blurring the effects of the two abovementioned mechanisms (Zobel, 1992; Chisholm & Pacala, 2011). For this reason, when the size of the regional species pool (gamma diversity) increases (e.g. from high to low latitudes), beta diversity will also increase if the local diversity (alpha diversity) does not increase at the same rate as the regional species pool (Kraft et al., 2011; Myers et al., 2013).. Moreover, an increase in beta diversity can be expected in regions with larger species pools, because a smaller proportion of individuals or species can potentially form part of any given local community (Chase et al, 2011). For that reason, stochastic processes could be higher just because sampling effects in regions with large regional species pool, while the effect of deterministic processes (niche related processes) can be hidden by such stochasticity (Chase and Myers, 2011).

Therefore, to understand the importance of niche or neutral processes over beta diversity (landscape-scale processes within ecological time frames) it is important to account the amount of beta diversity that changes as a result of the biogeographical or historical scale processes affecting the gamma diversity across different biogeographical regions (e.g. tropical vs temperate forests).

The direct influence of local and regional species pool over beta diversity patterns (Chase et al., 2011; Kraft et al., 2011) makes the use of a null model that can control for this random variation of the species pool necessary to compare beta diversity patterns among ecosystems. Controlling for this variation is even more important when the ecosystems being compared have significant differences on the total number of species as is the case of the present study (Chase et al. 2011; De Cáceres et al., 2012; Myers et al., 2013). The null model approach will be focused in controlling variation in regional species pool (gamma diversity) while letting beta diversity fluctuate randomly, before comparing community assembly mechanisms between biogeographical regions. It will be fundamental for predicting to which extent observed beta diversity differs from a random expectation under the assumption of no habitat specialization and no dispersal limitation. These differences, called beta deviations, reflect the level of

aggregation of species due to dispersal limitation and/or environmental filtering happening at more localized landscape spatial scales and ecological time frames.

Although research about the processes responsible of generating diversity in forests across latitudes has been done before (Kraft et al., 2011; Myers et al., 2013), there is still uncertainty about how stochastic/deterministic processes interact to shape communities when an altitudinal range is included (Rahbek, 2005). Altitude, together with latitude, is considered one of the most important ecological gradients shaping diversity patterns (Janzen, 1967). The increase of species diversity from the poles to the tropics and the decrease from low to high altitude seems to be based on comparable environmental processes, creating similar community assembly patterns (Stevens, 1992). Despite the fact that species richness decreases with altitude, the increase of environmental and topographical variation along the altitudinal gradient could generate greater species aggregation, and consequently greater beta diversity values (De Cáceres et al., 2012). In general it has been shown that the importance of deterministic processes like environmental filtering increases with altitude in both tropical (Hernandez-Calderón et al., 2014) and temperate (Mori et al., 2013) ecosystems. The limited ability of tropical species to adapt to temperature changes make tropical forest more prone to be affected by environmental filtering processes along altitudinal ranges than temperate forests (Ghalambor et al. 2006).

In temperate ecosystem, deterministic processes (environmental filtering) explain a greater amount of the spatial structure of species than stochastic (Gazol and Ibañez, 2010; Yuan et al., 2011). Contrary, previous studies in tropical ecosystems suggest that species variation here is more affected by stochastic processes (Condit et al., 2002; Myers et al., 2013). Chase (2010) suggested that this difference in the processes that generate diversity (stochastic/deterministic) is related with the productivity of the ecosystem. Also this relation between productivity and community assembly processes could be responsible of diversity patterns along altitudinal gradients, as showed by Mori et. al (2013). These authors found along an altitudinal range in a Japanese temperate forest that environmental filtering explains greater parts of the variation of species at high elevations (normally with lower productivity), whereas at low elevations (high productivity) priority effects are more important.

Nevertheless, caution is needed in order to explain and compare the processes that generate differences in beta diversity across latitudes and altitudes. For example Kraft et al. (2011) stated that the linear decrease of beta diversity with increasing altitude/latitude is a function of the species pool (gamma diversity). However it has

been shown how deterministic and stochastic mechanisms play an important role shaping beta diversity at different levels of productivity (Chase, 2010), different rates of speciation (Chisolm and Pacala, 2011), between high/low diversity ecosystems (Myers et al., 2013) and at different altitudes in temperate forests (Mori et al., 2013) and in tropical forests (Tello et al., 2015).

Climate and soil factors are one of the main environmental forces influencing vegetation composition around the globe. Generally, vegetation-environment relationships are scale dependent, having edaphic factors a greater influence at local scales (<2000 km²) while climatic factors are prevalent at larger scales (Siefert et al., 2012). In tropical forest, the local and regional effect of soils, and the broad effect of climatic variables on the vegetation composition has been shown by authors like Tuomisto et al. (2003), John et al. (2007), Toledo et al. (2011) and Arellano et al. (In press). Similar local effects of soil have been shown in temperate forests to explain their vegetation composition (Gilbert and Lechowicz, 2004; Gazol and Ibañez, 2010).

Understanding how these mechanisms interact to shape diversity across latitudinal and altitudinal ranges is the main objective of this study. This is relevant to predict how environmental change will affect biodiversity and how to implement better management strategies, depending on the level of spatial aggregation of species. For example, most species are expected to be forced to shift their distributions to higher altitudes and/or higher latitudes in the warmer future (Sheldon et al., 2011) and thus could potentially reflect a shift in the processes that generate diversity at different regions.

With this goal we addressed three main questions: 1) Do forest placed at different latitudes/ elevational ranges have similar beta diversity patterns? 2) What is the contribution of environment and dispersal limitation to beta diversity variation in each studied region? 3) What is the contribution of soil and climatic variables to beta diversity in each studied region?

Materials and Methods

Study area

We studied four regions that differed in latitudinal and altitudinal ranges, covering low diversity ecosystems (lowland oak temperate forest at Ozark Mountains, Missouri, USA and mountainous oak forest situated at Northeast Spain) and high diversity ecosystem (lowland and mountainous tropical forest at Madidi National Park, Bolivia) (Table 1, Figure 1). In each region, 22 to 147 0.1-ha plots (20x50m) were established using similar methodologies, making a total of 236 plots (Table 2). Due to logistical constraints, plots were distributed in different localities, with 6 to 8 plots per locality. In each plot, all woody plants rooting within the plot limits with a diameter at breast height (130 cm above ground) \geq 2.5 cm were inventoried. All individuals were identified to species or morphospecies.

Table 1. Location, climatic conditions and altitudinal range of the study regions. BL : Tropical lowland, BH: Tropical mountainous, USA: Temperate lowland, SP: Temperate mountainous

| Region | No. of plots | Latitude | Longitude | Climate | Precipitation (mm) ⁺ | Temperature (°C) * | Altitudinal range (m) |
|--------|--------------|----------|-----------|-----------|---------------------------------|--------------------|-----------------------|
| BL | 49 | 14.636 S | 67.839 E | Tropical | 1868 | 16.5 to 31.8 | 254 to 456 |
| BH | 147 | 14.489 S | 68.62 E | Tropical | 1725 | 14.6 to 27.7 | 503 to 1593 |
| USA | 28 | 38.251 N | 91.038 E | Temperate | 1019 | (-7.9) to 31.8 | 175 to 295 |
| SP | 22 | 42.001 N | 6.588 E | Temperate | 920 | (-0.8) to 23.3 | 342 to 1439 |

⁺ Mean Annual Precipitation

* Minimum Temperature of the Coldest Month - Maximum Temperature of the Warmest Month

To capture the maximum effect size of regional species pool, a higher number of plots were used for the analyses in regions with greater species pool (Table 2) (Chase and Knight, 2013). This decision was taken after checking the species accumulation curves (Appendix 2) and environmental heterogeneity of each site (Appendix 3). The use of a similar number of plots per region is conditioned by the limited amount of plots at temperate forests (22 – 28) and would leave out of the analyses more than half of the species at tropical regions. Even though, we carried out also the analyses using 22 plots per region in order to compare if the results show big differences between the approaches of using all plots available in each region (Appendices 4 and 5).

Plots were located with at least 250 m of distance between each other, avoiding gaps or recent human disturbances, covering in total a distance between 0,25 and 80 km. When establishing plots on slopes, plot centre line was established perpendicular to slopes to minimize elevational gradients within plots. In addition, regions categorized as lowland have an altitude ranging from 200 to 300 m.a.s.l), while the altitude of the highland forests varies from 400 to 1600 m.a.s.l). This similar spatial distribution between plots will make possible the comparison of the effect of dispersal limitation and environmental filtering across regions.

In each study plot the following measures were done: geographical coordinates, elevation, aspect, slope and topographic position (ridge top, hillside and bottom land). Additionally a compound superficial (0-30 cm) soil sample was taken at each plot. Samples were air dried and sieved through a 2mm sieve. Soil pH was determined in a water and 1M KCl solution, both 1:2.5 Soil:Solution proportion. The granulometric analysis was performed with the sedimentation and Bouyoucos' densimeter technique. The concentration of macro (Ca, Mg, K) was determined with a Mehlich-3 extraction (Mehlich, 1984). Total content of N were determined via total combustion technique (Appendix 1)

A total of 19 bioclimatic variables were used from WorldClim (Hijmans et al. 2005; www.worldclim.org/). These variables were extracted from a raster layer with a resolution of 1 arcseg and represent annual trends, seasonality and extreme environmental factors (Appendix 1, Appendix 2)

We expect that the spatial patterns of diversity arisen by dispersal are similar to in order to estimate how much of the beta deviation is caused by dispersal limitation, geographical coordinates (latitude and longitude) were used in addition with the eigenfunctions obtained performing a Principal Components of Neighbour Matrices (PCNM)(Borcard and Legendre, 2002). PCNM eigenfunction describe all spatial scales that can be fitted in the sampling design. They are obtained by a principal coordinate analysis (PCoA) of a truncated geographic distance matrix of the plots sampled (Borcard et al. 2004; Dray et al. 2006). The advantage of this analysis in comparison with the use of trend surface polynomes or the use of only latitude and longitude values is that these methods can only describe accurately the space when the sampling area is homogeneous, there is a big sample and the spatial structure to be modeled is simple, like a gradient (Dray et al., 2006). The calculation of PCoA was done with the function *pcnm* of *vegan* package in R (Oksanen, 2013).

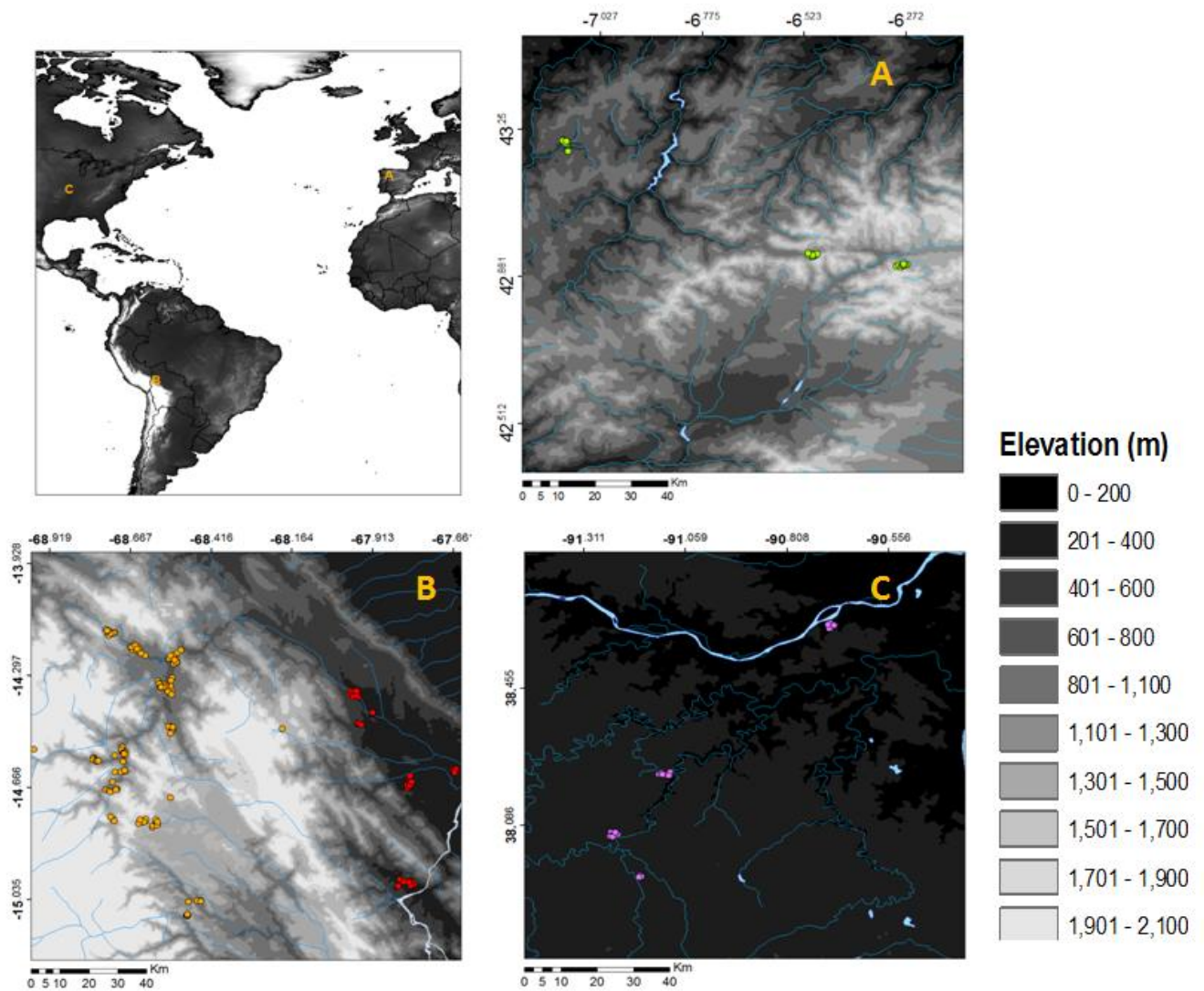


Figure 1. Geographical location and spatial distribution of the four regions studied. A: Temperate mountainous forest situated in the north east region of Spain (SP), B: Tropical lowland (red, BL) and mountainous (yellow, BH) forests both placed at Madidi National Park in Bolivia, C: Temperate lowland forest in the Missouri Ozarks (USA).

In each region the following analysis were performed:

Null model

The observed beta diversity was calculated as floristic dissimilarity between each pair of plots in a region using abundance based (Bray-Curtis) index (Anderson et al., 2011). This resulted in a dissimilarity matrix per region, with the advantage of being able. In order to estimate how much of the observed beta diversity deviates from an expected value under the assumption of complete random assembly, a null model will be used.

The null model will randomize the location of species among plots, while keeping the total number of individuals per plot and the total number of species in the region constant (Kraft et al., 2011; De Cáceres et al., 2012 and Mori et al., 2013). The null distribution was calculated after at least 1000 iterations, which average represented the matrix of null dissimilarities for each of the regions. The deviation of beta diversity from expected values was calculated as the standardized effect size of beta diversity: (Observed beta diversity – Expected beta diversity)/ Standard Deviation of Expected beta diversity (Myers et al. 2013). This difference indicates variations in Beta diversity after controlling for the species pool (De Cáceres et al. 2012).

Variation partitioning analysis

To disentangle the processes generating beta diversity patterns in each region, we did a variation partitioning analysis. Firstly, both observed beta diversity and beta deviations variability was partitioned by spatial, soil and climatic variables (Figure 2). To understand the variation explained by the environment, soils and climate variables were clustered together in a matrix, used in the same analysis of partition of the variation before mentioned. Total variation explained by environmental variables and space were based on a distance based redundancy analysis (dbRDA). This analysis is similar to a common RDA but uses instead of a compositional matrix, a set of PCo vectors obtained from the dissimilarity matrices (observed beta diversity and beta deviations, separately). Collinearity between variables were accounted by performing Principal Component Analysis (PCA) over each set of variables (soil, climate and spatial) using the first four orthogonal PCA axes as explanatory variables in the dbRDA analysis.

According to Blanchet et al. (2008), before the partition of the variance, in order to control for Type I error and the overestimation of variance explained by the model (R^2_{adj}), a global test with all variables (spatial, soil, climate) was done.. This analysis was followed by the forward selection of the variables with p-value (< 0.05) and the total explained variation (R^2_{adj}) of the global model as criterion to stop the selection. The forward selection was performed using the function *ordR2step* in the R package *vegan* (Oksanen et al. 2013). The variables selected by the forward selection were used to partition the observed beta diversity and the beta deviations with the function *varpart*, also from *vegan* package (Legendre and Anderson, 1999).

Fractions a, b and c represent the percentage of variance explained by space, soils and climate alone, respectively. Rest of the fractions represents the variance explained by the joint action of each of the set of variables. Fraction h is the variation not explained by any of the variables used. (Legendre et al., 2009; De Cáceres et al., 2012)(Figure 2)

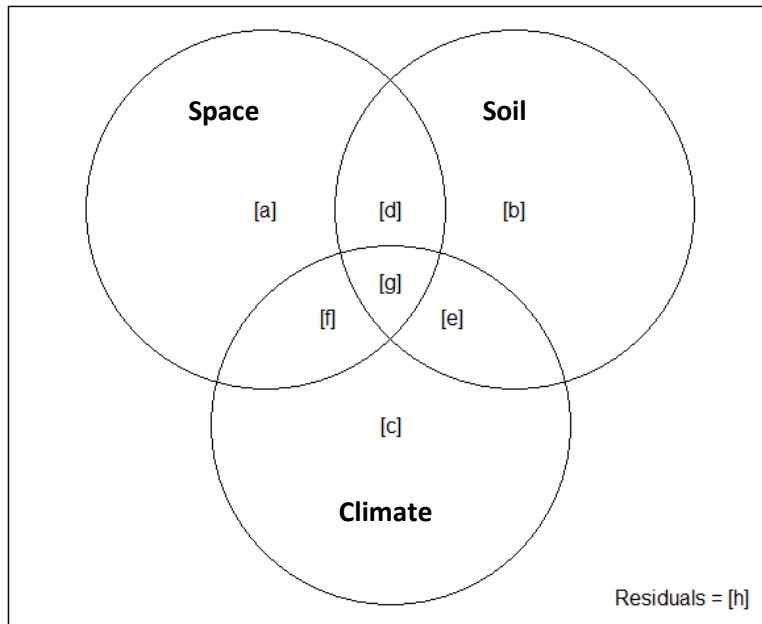


Figure 2. Venn diagram showing all the fractions resulting from the second level variation partitioning analysis. Fractions: a = variation explained by the space alone, b = variation explained by the soil alone, c = variation explained by the climate alone, d = variation explained by spatially structured soils, e = variation explained by soils and climate together, f = variation by spatially structured climate, g = variation explained by space, soils and climate together, h = variation not explained by any variable.

Comparisons between regions

Differences of beta diversity and beta deviations between regions were tested with a multivariate homogeneity of group dispersions test. Function *betadisper* (Anderson, 2006) of *vegan* package performs this analysis, a multivariate equivalent of Levene's test for homogeneity of variances. For a group of samples it calculates the average distance of group members to the group centroid. After, to test if dispersions are different between each group, the distances are subject of an ANOVA. This approach was also used to compare the environmental and the spatial heterogeneity among regions.

Result

Diversity patterns

Regional species pool ranged between 34 and 1131 species at the temperate and tropical mountainous forest sampled (Table 2). Both tropical forests (BL and BH) have the highest rates of diversity and species richness (Table 2). Although tropical mountainous forest (BH) has lower alpha diversity compared with tropical lowland forest (BL), it has higher beta diversity values. Similar effect occurs in temperate forest, where mountainous forest (SP) show a lower alpha diversity and species pool but great beta diversity, compared with temperate lowland forest (USA) (Table 2). The mountainous forest at tropical and temperate locations (BH and SP) accumulate the highest beta diversity values, where between 40 and 70 % of the plots does not share almost any specie (Table 2).

Table 2. Species diversity patterns of each study region. All woody plants with a DBH > 2.5 cm rooted in the 0.1 ha plot were inventoried. BL : Tropical lowland, BH: Tropical mountainous, USA: Temperate lowland, SP: Temperate mountainous

| Region | Individuals/plot | Total no. of species | Alpha Diversity ⁺ | Observed Beta Div.* | Beta Div. > 0.9 (%)‡ | Beta Div = 1 (%)‡ |
|--------|------------------|----------------------|------------------------------|---------------------|----------------------|-------------------|
| BL | 210 ± 40 | 647 | 73.36 ± 15.7 | 0.81 ± 0.09 | 16 | 0 |
| BH | 310 ± 92 | 1131 | 51.71 ± 20.1 | 0.92 ± 0.12 | 71 | 26 |
| USA | 126 ± 49 | 43 | 13.82 ± 3.6 | 0.71 ± 0.15 | 7 | 0 |
| SP | 120 ± 49 | 34 | 8.32 ± 4.0 | 0.79 ± 0.20 | 40 | 5 |

⁺ Average number of species per plot ± Standard Deviation. Values close to 1 mean high dissimilarity.

* Average Bray-Curtis distance ± Standard Deviation.

‡ Percentage of pairs of plots with a beta diversity (Bray-Curtis dissimilarity) greater than 0.9

Null Model and Comparisons between regions:

Observed beta diversity significantly higher in the tropical regions studied (BH and BL), than the temperate region evaluated (SP and USA). It was also significantly higher in both mountainous forest (BH and SP) when compared with lowland forests (BL and USA) at the same latitude (Figure 3, Table 3).

Beta diversity generated under the null expectation of random sampling from the regional species pool was in all cases lower than the observed beta diversity. Expected beta diversity was greater in both tropical forests than in temperate forests studied

(Figure 3, Table 3), given the difference in each regional specie pool (1131 – 647 in both tropical forest vs. 43 -34 in their temperate counterparts).

Table 3. Homogeneity of multivariate dispersion test. Beta diversity variances comparison between each region sampled.

| | Observed Beta Div. | | Expected Beta Div. | | Beta deviation | |
|------------|--------------------|-----------|--------------------|-----------|----------------|-----------|
| | F | p - value | F | p - value | F | p - value |
| BL vs. BH | 89.21 | *** | 2.17 | 0.14 | 112.01 | *** |
| BL vs. USA | 20.53 | *** | 243.85 | *** | 10.85 | ** |
| BH vs. SP | 41.05 | *** | 279.59 | *** | 0.1 | 0.71 |
| SP vs. USA | 3.67 | 0.061 | 1.27 | 0.26 | 1.89 | 0.17 |

BL : Tropical lowland, BH: Tropical mountainous, USA: Temperate lowland, SP: Temperate mountainous.

*** (> 0.001), ** (> 0.01), * (> 0.05)

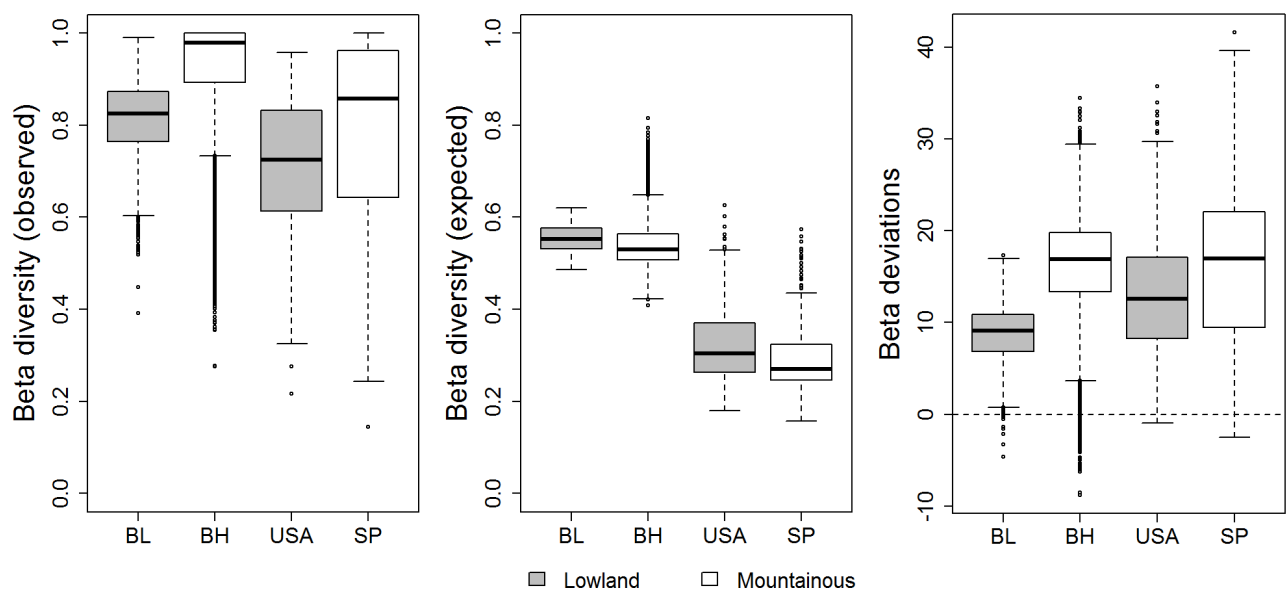


Figure 3. Beta diversity comparisons between regions. BL: Tropical Lowland, BH: Tropical Mountainous, USA: Temperate Lowland, SP: Temperate Mountainous.

As a result, beta deviations in each region were generally positive (Figure 3), showing a level of species turnover higher than the one expected by random community assembly processes. Beta deviations were not significantly different between mountainous forest across latitudes (Bolivia high vs. Spain) and significantly higher in temperate lowlands (USA), compared with tropical lowland forest (Bolivia low), (Figure 3, Table 3). Beta deviations at tropical mountainous forest sampled (Bolivia high) were significantly higher than beta deviations of tropical lowland forest (Bolivia low), (Table 3). However, Beta deviation differences between temperate

mountainous and temperate lowland forest (Spain and USA respectively) were not significant (Table 3).

Beta diversity variation partition:

In total, the variation of beta diversity explained when all selected axes of the environmental and spatial PCA were included in the db-RDA, ranged between R^2_{adj} of 0.22 in temperate lowlands (USA) and 0.4 in temperate mountainous forest (Spain) (Figure 4, Table 4). For beta deviations the variation explained by the selected variables was lower, ranging between R^2_{adj} of 0.15 in temperate lowlands (USA) and 0.3 in tropical lowlands (Bolivia low)(Table 4). This decrease in explained variation from beta diversity to beta deviations was particularly stronger in mountainous forests (Bolivia high and Spain). For both beta diversity and beta deviations, most of the variation remained unexplained (Figure 4, Table 4).

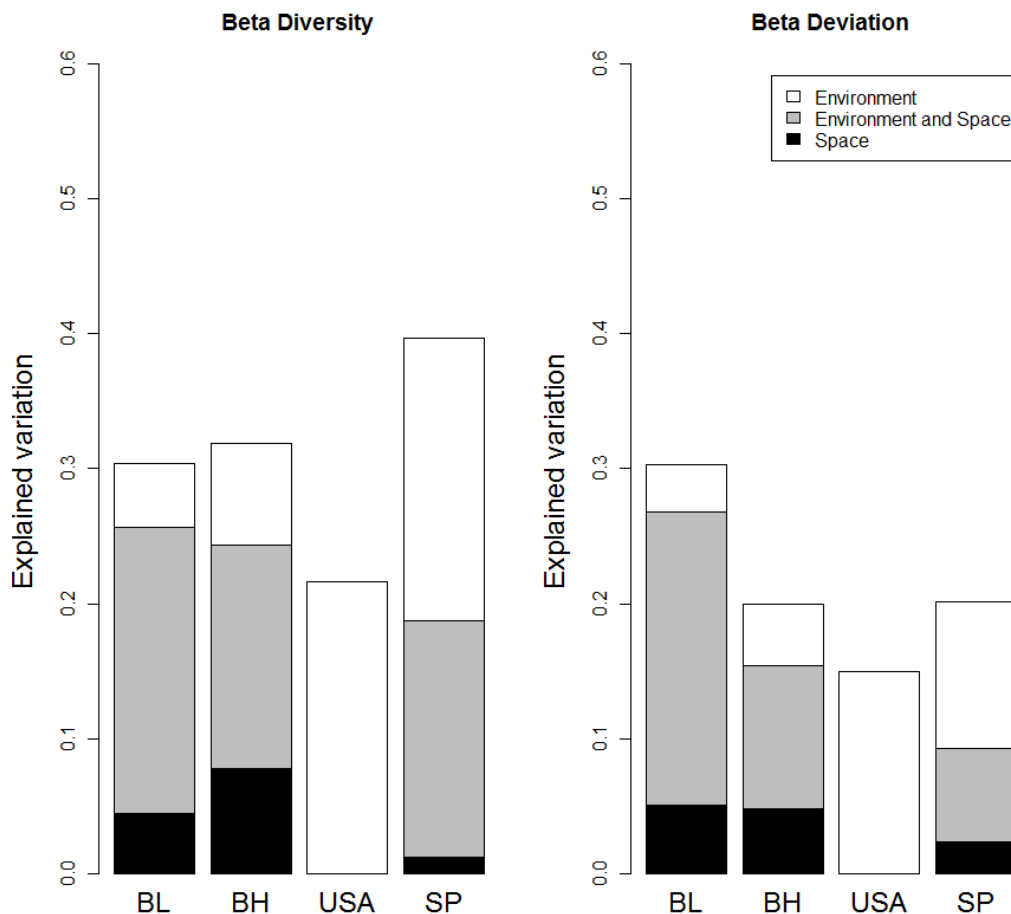


Figure 4. Partition of observed Beta diversity and Beta deviations. BL Tropical Lowlands, BH: Tropical Mountainous, USA: Temperate Lowland, SP: Temperate Mountainous.

The greatest difference between the ecological processes that generate beta diversity patterns at the sampled forest is the higher variation explained by spatial variables alone at both tropical forest (Figure 4, Table 4). Spatial variables explained a similar amount of variation at both mountainous and lowland tropical forests (Bolivia high and Bolivia Low, respectively) (Figure 4, Figure 5, Table 4) compared with the variation explained by environmental variables alone. Environmental variables alone explain more variation in both temperate forests (Spain and Ozarks) (Figure 4, Figure 5, and Table 4).

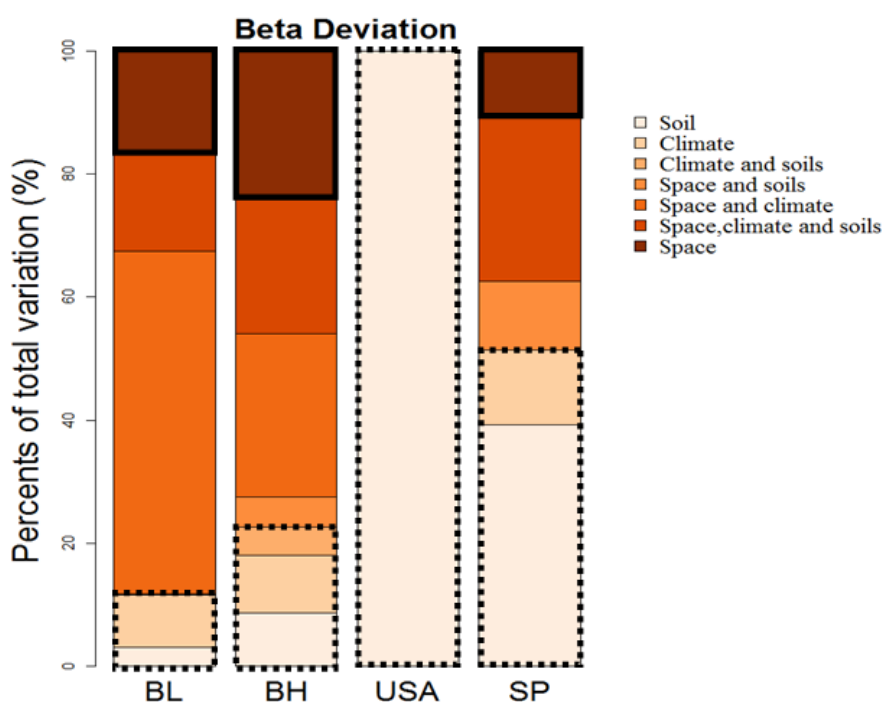


Figure 5. Proportion of the total variation explained by each spatial and environmental fraction. Dashed line encloses variation explained by environmental variables alone. Continuous line encloses the variation explained by spatial variables alone. BL: Tropical Lowlands, BH: Tropical Mountainous, USA: Temperate Lowland, SP: Temperate Mountainous.

In all the forests, except temperate lowland (USA), spatially structured environmental variables (fractions d + f + g) explained more (BH and BL) or at least similar (SP) variation than spatial (fraction a) or environmental variables alone (fractions b + c + e) (Figure 3, Table 4).

The importance of different environmental variables was also different between forests. In the temperate forest regions (SP and USA) soils alone represented the main environmental force (Figures 4 and 5). In tropical lowlands and mountains (BL and BH)

sampled, climatic variables explained a higher amount of variation than soil variables. Especially the variation explained by the spatially structured climatic gradients in the tropical forest sample (R^2_{adj} of 0.17) was important.

Table 4. Variation partitioning results for the four different regions.

| Region | space [a+d+f+g] | soil [b+d+e+g] | climate [c+e+f+g] | a | b | c | d | e | f | g | h |
|-------------------------------|--------------------|-------------------|----------------------|------|------|------|------|------|------|------|------|
| <i><u>Beta diversity</u></i> | | | | | | | | | | | |
| BL | 0.26 | 0.06 | 0.25 | 0.04 | 0.01 | 0.04 | 0.00 | 0.00 | 0.17 | 0.05 | 0.69 |
| BH | 0.24 | 0.12 | 0.20 | 0.08 | 0.03 | 0.03 | 0.02 | 0.01 | 0.09 | 0.06 | 0.68 |
| SP | 0.19 | 0.31 | 0.21 | 0.01 | 0.12 | 0.04 | 0.06 | 0.05 | 0.03 | 0.09 | 0.60 |
| USA | 0.00 | 0.16 | 0.03 | 0.00 | 0.16 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.81 |
| <i><u>Beta deviations</u></i> | | | | | | | | | | | |
| BL | 0.27 | 0.06 | 0.24 | 0.05 | 0.01 | 0.03 | 0.00 | 0.00 | 0.17 | 0.05 | 0.70 |
| BH | 0.15 | 0.08 | 0.12 | 0.05 | 0.02 | 0.02 | 0.01 | 0.01 | 0.05 | 0.04 | 0.80 |
| SP | 0.11 | 0.17 | 0.08 | 0.02 | 0.09 | 0.03 | 0.02 | 0.00 | 0.00 | 0.06 | 0.78 |
| USA | 0.00 | 0.15 | 0.00 | 0.00 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.85 |

Notes: Fractions a - h (adjusted R2 statistics): a = variation explained by the space alone, b = variation explained by the soil alone, c = variation explained by the climate alone, d = variation explained by spatially structured soils, e = variation explained by soils and climate together, f = variation by spatially structured climate, g = variation explained by space, soils and climate together, h = variation not explained by any variable.

Discussion

This study has compared directly for the first time the drivers involved in generating diversity patterns at a lowland and mountainous forest placed at contrasting latitudes. Showing for the first time that elevational patterns in beta deviations do not reflect shifts in the relative importance of different ecological processes at least for the latitudes and elevational range considered. The results found in this study support the idea of different processes given rise to similar beta diversity patterns in the studied tropical and temperate forests (Figures 3 and 4). Several studies have previously showed that different ecological processes generate similar species turnover rates in a tropical and temperate lowland forest (De Cáceres et al., 2012; Myers et al., 2013); but this is the first one to show the aforementioned trend in a tropical and temperate mountainous forest. Although large scale processes, like ecological drift or speciation, determine the size of species pool and generate the latitudinal gradient of beta diversity (Kraft et al., 2011), this study indicates that local ecological processes determining beta diversity vary especially across forests placed at different latitudes, but not at different elevations at the same latitude. Therefore, this study highlights the importance of taking in account the effect of species pool when comparing the processes generating diversity at forests placed at different latitudes.

The effect of latitude and elevation on beta diversity patterns

Observed beta diversity was greater at both tropical forests, but once taken in to account the effect of the species pool, this difference between latitudes disappears (Figure 3, Table 3). The effect of species pool over beta diversity has been shown before in different studies (Kraft et al. 2011, De Cáceres et al. 2012; Myers et al. 2013), although we show the same effect in mountainous forest at different latitudes. This means that the latitudinal effect of species pool determines beta diversity patterns, not only at lowland forest sampled, but also at the mountainous ones.

When comparing forest at different elevations, both observed beta diversity and beta diversity after controlling for the different species pool (beta deviations) were higher at mountainous forest in tropical latitudes (Figure 3, Table 3). The lack of significant differences in species turnover (beta deviation) between temperate lowland (USA) and temperate mountainous forest (Spain) could be due to the huge variation of beta deviations in the latter. In this case the variation in the species pool between lowland

and mountainous forests at the same latitude does not reflect the higher beta diversity values found at higher elevations. This means that the higher beta diversity at high elevations is not explained by a greater species pool. At a similar spatial scale than this study, other authors also found higher levels of observed beta diversity and beta deviations at higher altitudes in temperate (Mori et al. 2013) and tropical (Tello et al. 2015) forests. According to their findings, these patterns result from the variation of ecological processes between altitudes and not from an effect of the species pool, which are reflected also in our study. Contrary to Janzen's (1967) and Stevens (1992) predictions of a larger altitudinal turnover at low latitudes (specially at tropical regions) due to the narrower climatic tolerance of the species, the turnover of species in this study appears to be constant across latitudes at similar altitudinal ranges (Lowland vs. lowland and mountainous vs. mountainous).

Partition of Beta diversity variation between spatial and environmental variables

Different ecological processes generate similar species turnover rates at different latitudes, independently of the elevation range, once the effect of the species pool is removed. On the other hand, the processes generating these different beta diversity patterns at different altitudinal ranges do not change in such a clear extent when comparing the lowland and mountainous forest placed at the same latitude. In both studied temperate forests environmental variables alone, specially differences in soil composition, had a greater importance than spatial variables (Figures 4 and 5). These findings are in accordance with previous studies done in temperate forest (Gilbert and Lechovitz 2004; Laliberté et al. 2009 or Qiao et al. 2015). At tropical lowland and mountainous forests, spatial variables alone had a bigger impact than environmental variables, although spatially structured variables have also a large influence on beta diversity. When considering the effect of environmental variables in more detail, climatic variables have a greater impact over beta diversity than soils in the studied tropical forests. The importance of environmental variables in tropical forests at regional scales has been shown previously (Tuomisto et al. 2002; Shipley et al. 2012); especially the effect of climate (Toledo et al. 2012; Siefert et al. 2012; Arellano et al. In press) like is the case in our study.

The greater influence of spatial variables at both studied mountainous and lowland tropical forest than on the temperate forests sampled, could reflect a greater impact of dispersal limitation in these specific forest types (Condit et al. 2002; De Cáceres et al.

2012; Myers et al. 2013). The mechanism of dispersal limitation is based on the tradeoff between dispersal and competitive ability of plants (Tillman, 1994; Hurt and Paccala, 1995), what means that the resources invested in dispersal mechanism cannot be invested in survival and growth mechanism. Dispersal limitation could be more common in species- rich forests due to several reasons (Myers and Hams, 2011). Firstly, in high diverse regions, many species could form part of the local community, increasing the influence of immigration and colonization history (Chase, 2003) and therefore dispersal limitation. Secondly, in these systems rare species are more abundant and normally suffer from dispersal limitation. When a gap is opened species with a lower competitive ability but better dispersed establish. Then, this limited recruitment of rare species delay competitive exclusion and favors coexistence (Hurt and Paccala, 1995), what maintains or increases diversity. Short dispersal distances is also related with stablishing processes like Jazen- Connell hypothesis, that also contribute to the maintenance of diversity (Barot, 2004) Finally, rare species may not interact often, making interespecific competition low (Myers and Hams, 2011). The spatial variables used in this study could reflect other processes than dispersal limitation, such as unmeasured spatially structured environmental gradients (Legendre et al. 2009). Also this spatial fraction could be the result of fragmentation processes that limits species dispersal (Wang et al. 2013). It is also remarkable the great variation (10 – 22%, Table 4) explained by spatially structured environmental variables, particularly at both tropical forests sampled. This fraction could represent environmental variables that change gradually along the space (Legendre et al. 2009). Furthermore, the effect of environmental and dispersal processes may be confounded by the fact that spatial patterns created by dispersal limitation often correlate with the spatial composition of environment (Anderson et al., 2011). This study reflects the importance of both spatial and environmental predictors in order to explain the maintenance of diversity at the two tropical communities sampled (Gazol and Ibañez 2010, Wang et al. 2013). Also the presence of this spatially structured environmental variables at the temperate mountainous forest studied could as result of strong gradients related with elevation like temperature.

At the scale of this study, the different beta diversity patterns found between lowlands and mountainous forests are probably due to differences in processes not measured in this study. The definitive causes of these patterns remain not clear at all (after including a total of 35 spatial, climatic, edaphic and topographic variables), even so, this study manage to show the relative importance of pure spatial, pure environmental variables and spatially structured environmental variables.

Although the explained variation in this study was not very high at any of the forests (between 15% and 40% of the total variation, Table 4), it is similar to other studies covering the same spatial extent (Myers et al. 2013, Wang et al. 2013). Unexplained beta diversity could be interpreted as the result of local stochastic processes arising from forest dynamics (mortality and recruitment; De Cáceres et al. 2013) and from unmeasured environmental variables like light availability (e.g., gap disturbance; Legendre et al. 2009). Potential stochastic factors could be historical random events (i.e., historical contingency; Fukami and Nakajima, 2011) at different localities that condition the arrival of different species (priority effects; Chase, 2010) and therefore the community assembly processes. Also disturbance regime could change local diversity (alpha diversity) patterns in a stochastic way altering the probability of recruitment from the species pool after the event occurs. If the alpha diversity decreases and the regional species pool is not altered by the disturbance, beta diversity will increase (Chase and Myers, 2011). Even if the used null model randomizes the local diversity (alpha) reproducing aleatory community assembly processes, this effect of perturbations along the history of the region could persist, representing the fractions of unexplained variation. The increase of unexplained variation at these mountainous forests highlights their complexity and the need of further research to disentangle the drivers that rule species turnover.

Beta diversity (represented as the decrease of similarity between plots with increasing distance) provides a simple descriptor of how species diversity is distributed in a given area, and therefore, can provide information for developing strategies to follow for its management. The maintenance of beta diversity requires a spatial network of reserves with the rate of distance decay determining the number and distance between protected areas (Nekola and White, 2002). The questions formulated in this study cannot suggest the number or size of conservation areas needed to preserve the diversity of these forests. Even though, it highlights the importance of taking into account the effect of environmental heterogeneity (climatic or edaphic depending on the latitude) and dispersal limitation in the management of these areas. Therefore, areas with a higher species turnover, like mountainous forest studied, would require a large number of areas (Baselaga, 2010) to ensure the protection of dispersal limited species or species that appear only under determined environmental conditions. Consequently, in areas with lower species turnover the size and number of conservation areas could be lower than in high turnover regions (Wiersma and Urban, 2005). Further research could include distance decay rates, in order to contribute more specifically to the SLOSS (Single Large Or Several Small) debate. The greater

influence of climatic variables at the tropical forest studied should be considered in order to manage future diversity shifts at these forests due to the future global warming.

The great amount of variance not explained by any variable suggests that further research should include variables to take in account disturbance effects, environmental variables like light availability, species functional traits or better measurements of dispersal limitation. The effect of climate at any of the studied forests could be under represented because of the low resolution (1 km²) of the variables used. Particularly, at mountainous forests, where topographical changes occur at very small spatial scales. Even though all the spatial arrangement and sampling methods were exactly the same in all the plots, the use of different methods for some of the soil variables like P or C, made impossible their inclusion in the comparison. Therefore, a complete standardization of soil analysis would help to better understand the effect of soils in tropical forest.

Conclusions

Our study contributes to a better understanding on the processes that generate diversity at contrasting elevations and latitudes. The latitudinal differences in species turnover found in this study, seem to be affected by the size of the species pool. Once the effect of species pool is controlled, different mechanisms interact at each latitude to shape woody plants species diversity. Spatial variables have a greater influence on species turnover at the two tropical forest sampled than at the temperate ones. This study suggests also a shift in importance of different environmental variables between latitudes. Climatic variables explain greater parts of species turnover at tropical forests studied, meanwhile soil variables represent the main environmental force shaping diversity at the temperate ones.

We found that elevational differences in species turnover at each latitude sampled seemed to be generated mainly through community assembly processes and not through the effect of species pool. Even if this study has its limitations, it manages to give some light on the mechanism generating diversity at the four forests analyzed, particularly when comparing forest at different elevation ranges.

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APPENDIX 1. List of soil, topographic and climatic variables used in the analyses.

Appendix 1. Average values \pm Standard deviations of soil and topographical variables used in each region. BL: Tropical Lowland; BH: Tropical Highland; USA: Temperate Lowland; SP: Temperate Mountainous

| Region | Sand (%) | Silt (%) | Clay (%) | K (mg/kg) | Ca (mg/kg) | Mg (mg/kg) | Na(mg/kg) | N(%) | pH | Northness | Eastness | Slope (%) | Elevation(m) |
|--------|-------------------|-------------------|-------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------|-------------------|----------------------|
| BL | 38.12 \pm 19.53 | 50.08 \pm 15.2 | 11.79 \pm 8.97 | 0.18 \pm 0.12 | 3.76 \pm 3.73 | 1.31 \pm 1.02 | 0.05 \pm 0.04 | 0.17 \pm 0.15 | 5.08 \pm 0.62 | 0.15 \pm 0.73 | -0.05 \pm 0.67 | 16.26 \pm 11.53 | 340.57 \pm 44.19 |
| BH | 32.19 \pm 17.99 | 31.65 \pm 15.25 | 36.22 \pm 14.21 | 0.41 \pm 0.3 | 6.42 \pm 8.74 | 2.5 \pm 2.48 | 0.24 \pm 0.67 | 0.4 \pm 0.23 | 5.31 \pm 1.12 | 0 \pm 0.7 | 0.11 \pm 0.7 | 29.68 \pm 17.65 | 1109.97 \pm 259.97 |
| USA | 22.41 \pm 10.03 | 67.41 \pm 9.91 | 10.17 \pm 2.62 | 0.21 \pm 0.04 | 4.5 \pm 2.87 | 0.89 \pm 0.49 | 0.07 \pm 0.03 | 0.13 \pm 0.04 | 4.86 \pm 0.73 | 0.02 \pm 0.61 | 0.24 \pm 0.76 | 13.99 \pm 11.18 | 247.25 \pm 34.65 |
| SP | 65.25 \pm 5.33 | 21.85 \pm 4.96 | 12.89 \pm 2.88 | 2.11 \pm 2.72 | 1.41 \pm 1.43 | 0.66 \pm 0.46 | 0.22 \pm 0.12 | 0.77 \pm 0.3 | 4.11 \pm 0.65 | 0.21 \pm 0.72 | -0.18 \pm 0.65 | 61.84 \pm 12.24 | 1048.68 \pm 402.16 |

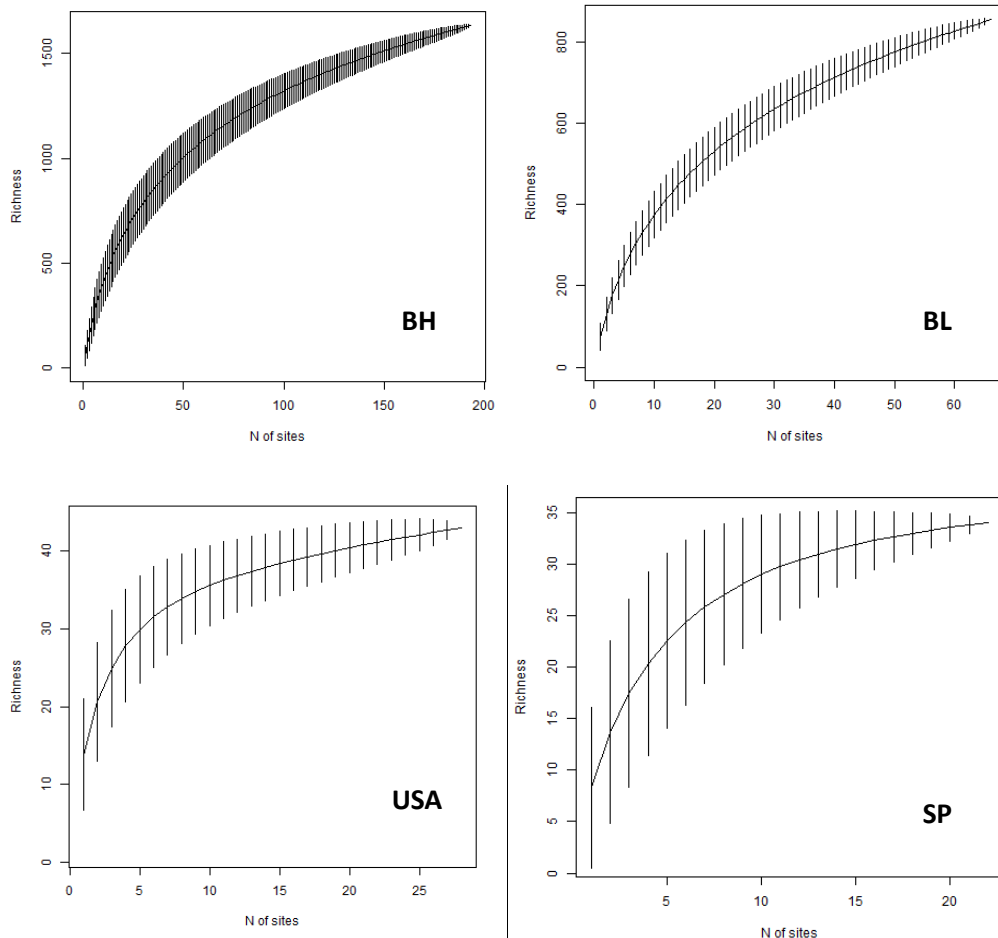
Appendix 1. Average values \pm Standard deviations of Climatic variables used in each region. BL: Tropical Lowland; BH: Tropical Highland; USA: Temperate Lowland; SP: Temperate Mountainous. Units Bio_1 to Bio_ 11 (°C); Bio_12 to Bio_19 (mm)

| Region | bio_1 | bio_2 | bio_3 | bio_4 | bio_5 | bio_6 | bio_7 | bio_8 | bio_9 | bio_10 |
|--------|--------------------|----------------------|--------------------|----------------------|--------------------|--------------------|--------------------|----------------------|---------------------|--------------------|
| BL | 24.71 \pm 0.137 | 10.614 \pm 0.188 | 6.906 \pm 0.077 | 145.687 \pm 5.765 | 31.787 \pm 0.228 | 16.489 \pm 0.155 | 15.297 \pm 0.347 | 25.934 \pm 0.2 | 23.206 \pm 0.369 | 25.959 \pm 0.203 |
| BH | 21.437 \pm 1.091 | 9.414 \pm 0.287 | 7.149 \pm 0.069 | 124.436 \pm 4.453 | 27.675 \pm 1.179 | 14.597 \pm 0.973 | 13.077 \pm 0.405 | 22.345 \pm 1.156 | 19.65 \pm 1.016 | 22.576 \pm 1.097 |
| USA | 12.371 \pm 0.089 | 13.714 \pm 0.676 | 3.396 \pm 0.14 | 910.164 \pm 15.266 | 31.835 \pm 0.257 | -7.989 \pm 0.166 | 39.825 \pm 0.378 | 18.05 \pm 2.919 | -0.078 \pm 0.265 | 23.603 \pm 0.152 |
| SP | 9.404 \pm 1.783 | 9.818 \pm 0.581 | 4.009 \pm 0.061 | 498.427 \pm 35.011 | 23.381 \pm 0.795 | -0.836 \pm 2.164 | 24.218 \pm 1.576 | 4.9 \pm 2.042 | 15.981 \pm 1.299 | 16.027 \pm 1.356 |
| Region | bio_11 | bio_12 | bio_13 | bio_14 | bio_15 | bio_16 | bio_17 | bio_18 | bio_19 | |
| BL | 22.512 \pm 0.107 | 1867.63 \pm 48.86 | 274.75 \pm 11.26 | 67.48 \pm 4.49 | 48.26 \pm 0.63 | 782.12 \pm 18.11 | 221.55 \pm 5.545 | 697.71 \pm 100.524 | 241.71 \pm 18.205 | |
| BH | 19.512 \pm 1.051 | 1725.34 \pm 210.78 | 257.95 \pm 29.5 | 46.42 \pm 13.39 | 53.05 \pm 2.46 | 736.29 \pm 80.55 | 163.91 \pm 36.38 | 553.7 \pm 57.595 | 176.59 \pm 39.325 | |
| USA | -0.078 \pm 0.265 | 1019.21 \pm 26.02 | 113.32 \pm 3.59 | 50 \pm 1.01 | 19.89 \pm 0.31 | 305.75 \pm 6.43 | 181.35 \pm 4.209 | 276.64 \pm 5.005 | 181.35 \pm 4.209 | |
| SP | 3.422 \pm 2.158 | 957.18 \pm 53.84 | 122.5 \pm 5.8 | 37.04 \pm 3.84 | 31.77 \pm 1.63 | 337.5 \pm 18.88 | 138.22 \pm 11.62 | 142.27 \pm 8.276 | 304.72 \pm 20.967 | |

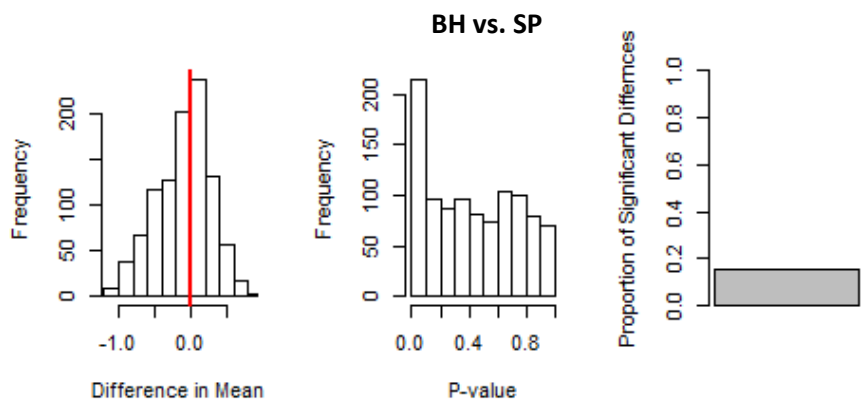
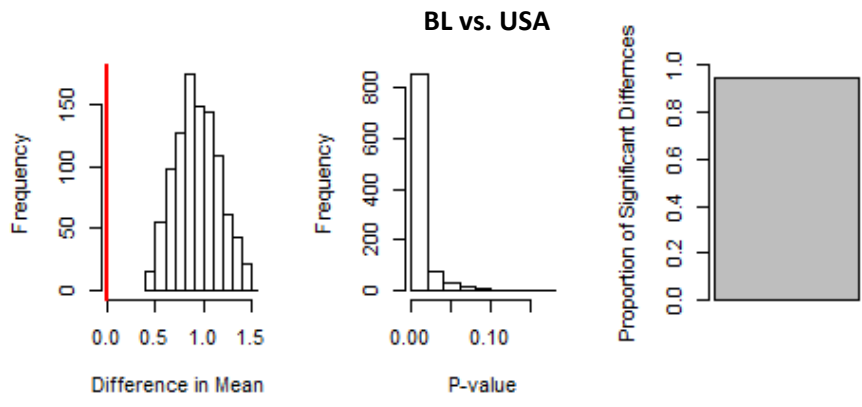
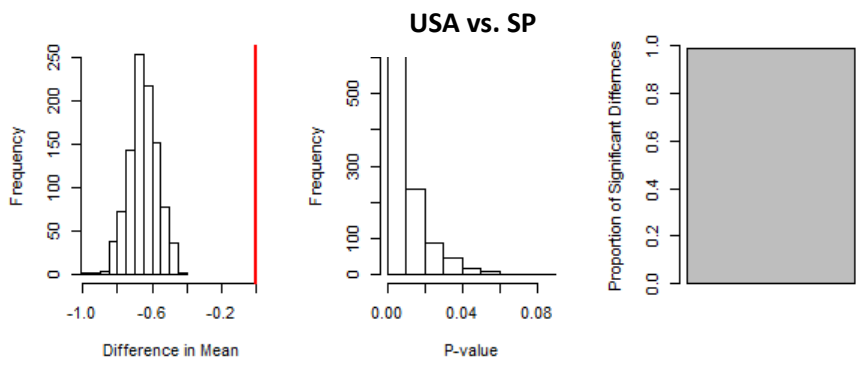
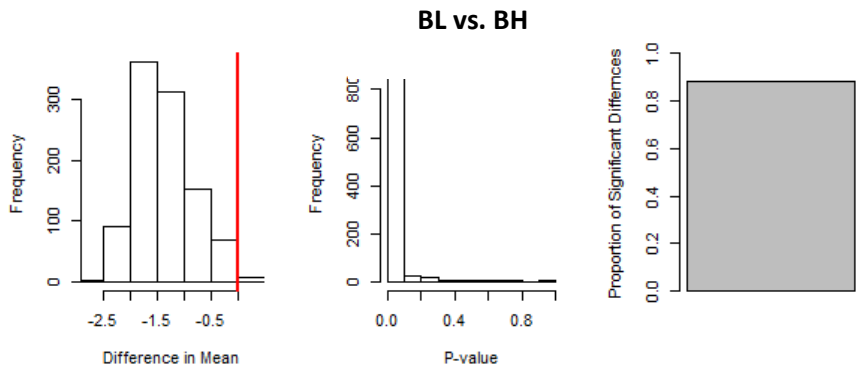
APPENDIX 2. List of climatic variables used in the analyses.

| Climatic variables used in the analyses. Obtained from a raster layer of 0.1 arcseg. | |
|--|--|
| BIO1 | Annual Mean Temperature |
| BIO2 | Mean Diurnal Range (Mean of monthly (max temp - min temp)) |
| BIO3 | Isothermality (BIO2/BIO7) (* 100) |
| BIO4 | Temperature Seasonality (standard deviation *100) |
| BIO5 | Max Temperature of Warmest Month |
| BIO6 | Min Temperature of Coldest Month |
| BIO7 | Temperature Annual Range (BIO5-BIO6) |
| BIO8 | Mean Temperature of Wettest Quarter |
| BIO9 | Mean Temperature of Driest Quarter |
| BIO10 | Mean Temperature of Warmest Quarter |
| BIO11 | Mean Temperature of Coldest Quarter |
| BIO12 | Annual Precipitation |
| BIO13 | Precipitation of Wettest Month |
| BIO14 | Precipitation of Driest Month |
| BIO15 | Precipitation Seasonality (Coefficient of Variation) |
| BIO16 | Precipitation of Wettest Quarter |
| BIO17 | Precipitation of Driest Quarter |
| BIO18 | Precipitation of Warmest Quarter |
| BIO19 | Precipitation of Coldest Quarter |
| Aspect | Orientation of the plots in radians |

APPENDIX 3. Species/plot accumulation curve per sampled forest. BH: Tropical Mountainous, BL: Tropical Lowland, USA: Temperate Lowland, SP: Temperate Mountainous.

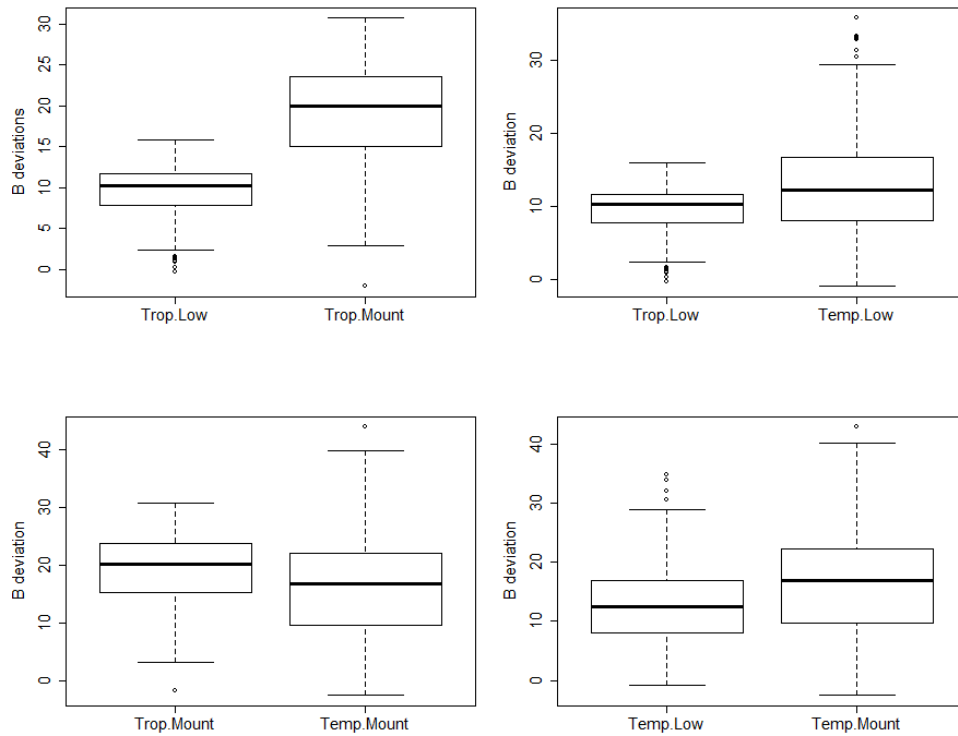


APPENDIX 4. Bootstrap estimation of multivariate homogeneity of dispersions.

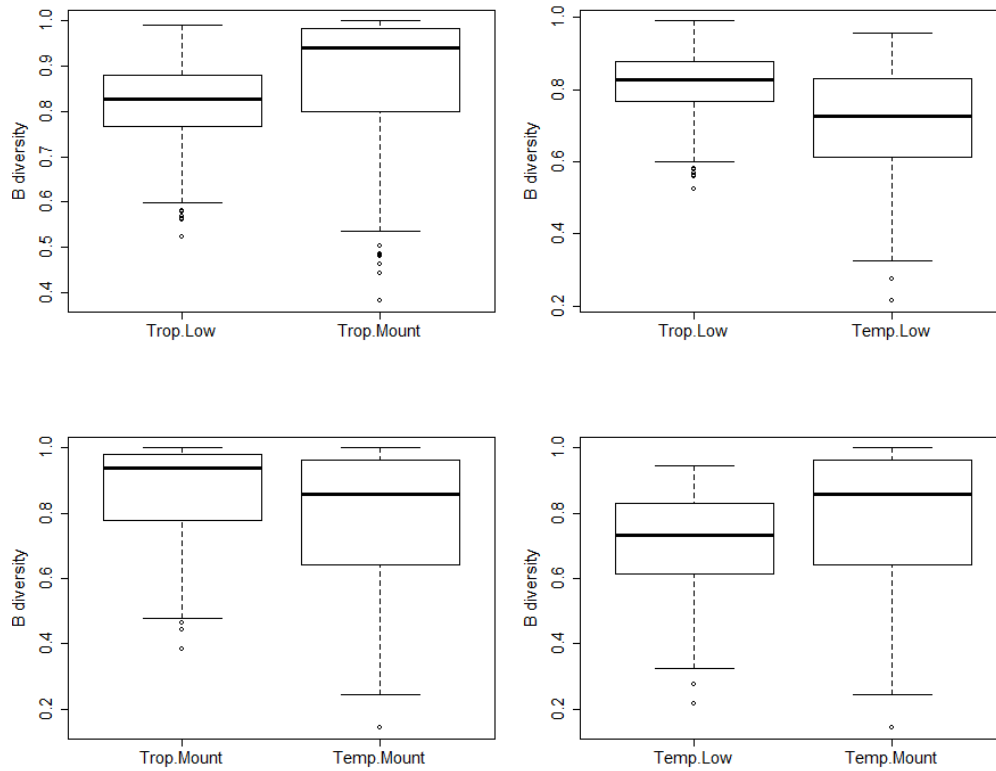


APPENDIX 5. Results obtained from the analyses performed using only 22 plots per forest sampled. Beta diversity patterns.

Beta deviations



Beta diversity



APPENDIX 6. Results obtained from the analyses performed using only 22 plots per forest sampled. Variation portioning results. A: Spatial variables, B: Spatially structured environmental variables, C: Environmental variables.

