11-26-2018

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Recommended Citation

Aparicio-Chavez, Claudia Andrea, "Temporal Changes in the Diversity and Composition of Tropical Andean Forest Communities" (2018). *Theses*. 342.
https://irl.umsl.edu/thesis/342

Temporal Changes in the Diversity and Composition of Tropical Andean Forest Communities

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A Thesis Submitted to the Graduate School at the University of Missouri
St. Louis in partial fulfillment of the requirements for the degree
Master of Science in Biology

December 2018

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ABSTRACT

During the last few thousand years, human population growth and resource use has been reshaping the planet's nutrient cycles, climate and biodiversity and might be causing significant changes to spatial and temporal patterns in the distribution of species, and a general erosion of biodiversity at global scales. Many studies have been looking to model and predict how species could respond to actual rates of change on environmental conditions, with a high interest in terms of species distribution and richness with potential extinctions. However, how global change impact local communities still remains unclear. Moreover, previous research suffers from a significant bias against Tropical montane regions. In this study, we evaluate whether diversity and composition of communities in an Andean Tropical forest are changing, potentially in response to changes in environmental conditions. We analyze the dynamics in 26 forest plots that are part of a larger network of nearly 490 plots located on the eastern slopes of the Bolivian Andes. We quantify mortality and recruitment rates, document changes in diversity and compare changes in species composition to null model expectations. We have that mortality and recruitment rates occur at about 1.6% per year, and that richness seems to be increasing in regions of cold climates, but decreasing in warm regions. Finally, we find evidence that community composition is shifting across all environmental conditions. Our analyses support the idea that communities in the Tropical Andes are going through changes consistent with an effect of global change. However, the final causes for the changes we observe are yet unknown. Understanding the responses of forest communities is urgently needed to advance theory in community ecology, but also to understand and manage natural ecosystems in a changing World.

KEYWORDS

Andes, Bolivia, community composition, global change, null model, species richness, tropical forest.

INTRODUCTION

During the last few hundred years, human population growth and resource use has been reshaping the planet's nutrient cycles, climate and biodiversity. Massive deforestation, habitat fragmentation, pollution, nitrogen deposition, climate change, and ocean acidification are some examples of how human activities might be degrading environmental conditions. We are just beginning to understand the consequences that these global changes have for the functioning of ecosystems, human health and economies around the globe (Parmesan et al. 2003, Lyons et al. 2016).

Large-scale human activity represent a significant challenge to biodiversity conservation because it might be causing significant changes in spatial and temporal patterns in the distribution of species, and there is good evidence of a general erosion of biodiversity at global scales (Williams et al. 2007, Nolan et al. 2018). At smaller spatial scales, however, there is still much uncertainty about how species and communities might be responding to global changes. Many studies have been using models to and predict how species could respond in particular to change on environmental conditions, with a high interest in terms of species distributions and richness (Clark 2001, Thomas et al. 2004, Báez et al. 2016). In terms of species distribution, some researchers have examined how elevational and latitudinal ranges of species might be changing due to responses to temperature increases based on species-specific thermal tolerances (Sheldon 2011; Colwell et al. 2008). For example, a recent meta-analysis (Freeman et al. 2018) concluded that species' geographic distributions in mountains are shrinking as they shift up slope. This meta-analysis agrees with results from specific mountain chains around the world that have measured an upward migration in species distributions of 1.1 to 3.5 m/year (Lenoir et al. 2008, Chen et al. 2011, Feeley et al. 2011a, Feeley et al. 2013, Duque et al. 2015). However, most estimates of changes in species distributions still are biased towards temperate regions, with fewer examples in the tropics (Freeman et al. 2018).

To complement this species-level perspective, researchers have also been studying how local assemblages are responding to changes in environmental conditions through time (Iverson and Prasad 1988, Feeley et al. 2011). For example, Vellend et al. (2017) recently reviewed studies that quantify temporal changes in local plant diversity during the Anthropocene. Their study found no evidence of systematic loss of species in communities. Dornelas et al. (2014) reported similar results in another global meta-analysis. Authors of these studies use their results to suggest that the environmental shifts owing to human impacts might not be causing losses of diversity in local communities around the world, which contradicts the widespread expectation that global change is eroding diversity from global to local scales. However, as Chaideftou et al. (2012) have suggested, most studies of temporal change in local communities focus on richness, emphasizing loss or accumulation of species, with less attention to patterns of species composition. Changes in species composition of local communities, although rarer, have also been documented. Importantly, Dornelas et al. (2014) suggest that, although species richness in local communities is not changing, community composition is becoming less variable (that is, beta-diversity is decreasing). This implies a pattern of biotic homogenization, and a shift in species composition for local communities. A number of studies have also found shifts in the functional composition of communities (Swenson et al. 2012, Pescador et al. 2015, Moor et al. 2015), and a pattern of "thermophilization" whereby species characteristic of warmer environments are increasing in abundance across communities, particularly in regions of low temperature (Gottfried et al. 2012, Duque et al. 2015, Osazuwa-Peters et al. 2015).

However, analyses and meta-analyses of responses of local communities to global change suffer from significant biases, particularly because of an underrepresentation of tropical communities, Gonzalez et al. 2015). Therefore, the debate continues regarding how global changes of the Anthropocene are reshaping the diversity of local communities. Gonzales et al. (2015) document this bias in Vellend et al. and Dornelas et al. studies, and use it as a critical piece of evidence against their conclusions. This bias is also evident in a recently published data base of biological time series: BioTime (Dornelas et al. 2018), which shows that the vast majority of datasets of this kind are located in temperate regions for both aquatic and terrestrial communities. Tropical systems are important because of their high biodiversity, but also because many people live in these regions. For example, within the Tropics, the Tropical Andes are considered one of the major global hotspots of biodiversity (Báez et al. 2016), where millions of people depend on the ecosystem services that natural communities provide such as water capture, pollution removal and food production. Understanding the dynamics of communities of the Tropical Andes over time is therefore of particular importance in order to elaborate conservation and management plans of tropical forests.

In this study, we evaluated whether the diversity and composition of species in Andean tropical forest local communities are changing, potentially in response to changes in environmental conditions. Additionally, we are also interested in understanding if shifts in those communities vary across climatic gradients. For this, we present an analysis of forest change across a large network of forest plots in Northwestern Bolivia. We studied the changes in species richness, and the shifts in composition compared to a null model. We found no significant change in the total diversity across these communities. However, our analysis suggests that variation in richness change is related with temperature, whereby communities are losing species in warm elevation belts while communities are gaining species in cold elevation belts. Regarding shifts in composition, we found evidence of greater change than expected purely by stochastic demographic processes. These composition changes are not related to environmental conditions.

MATERIAL AND METHODS

a. Study site and data

In this study, we evaluated temporal changes in richness and species composition in local communities of tropical woody plants. For our analyses, we used data of the Madidi Project (www.mobot.org/madidi), a collaborative research effort by the Missouri Botanical Garden (MBG), the Herbario Nacional de Bolivia (LPB), the Universidad Autónoma de Madrid and other associate researchers and institutions. The dataset consists of a large network of forest plots distributed along a broad elevational gradient (~250 to 4,000 m elevation) in the Madidi Region of Northwestern Bolivia (Figure 1). The network of forest plots contains 442 small temporary plots (0.1-ha in area), where all woody plants with a diameter at breast height (dbh) >= 2.5 cm have been measured and identified (Tello et al. 2015; Arellano et al. 2016). The network also includes 48 large permanent plots (1-ha), where all woody plants with a dbh >= 10 cm have been surveyed. Of these 48 permanent plots, a subset of 26 has been re-surveyed on average seven years after their establishment (range 4 to 11 years, media 7) (Figure 2b). These 26 plots contain information on mortality, recruitment, and temporal changes in richness and composition, and are the focus of our study. In each small or large plot, we collected plant samples to document each species at each site. Herbarium specimens are available at LPB and MO These specimens were used to identify species and morpho-species with standardized criteria across the full network of forest plots. The Madidi Project's plot dataset used in these analyses correspond to version 2.0. The plot data are permanently stored and can be found online in Tropicos®, the botanical database of the Missouri Botanical Garden, at http://tropicos.org/Project/MDI/.

b. Testing for temporal changes in species richness.

We calculated the observed temporal change in richness and composition for each permanent plot. The absolute change in richness (RC_r) was measured as the difference in the number of species present in the plot at the second census minus those in the first census: $RC_r = (R_2 - R_1)$. To account for variation in species richness and the length of the interval between censuses, we also calculated a standardized measure of richness change (RC) by dividing this difference by the richness of the first census and then by the corresponding census interval length (IL) in years ($RC = \frac{R_2 - R_1}{R_1 \times IL}$). All further analyses in this manuscript use this standardized measure of richness change. If forest communities have been losing species over time consistently across our forest plots, the mean value of richness change should be significantly less than zero. To test this prediction, we performed a one-sample *t*-test.

c. Testing for temporal changes in species composition

Changes in species composition (CC_r) were measured using the Bray-Curtis and Jaccard distances between censuses. Both measures led to identical conclusions, so here we present results based only on Bray-Curtis distances. Like for richness change, we also standardized change in composition by dividing this measure by the length of the census interval: $CC = \frac{CC_r}{IL}$. All analyses in our manuscript use this standardized measure.

If species composition in these forest communities were shifting (owing to climate change or disturbance, for example), we predict that our standardized values of CC should be greater than expected by non-directional random changes in composition driven by stochastic demographic processes, but constrained by the observed rates of mortality and recruitment. To test whether species composition changed significantly, we compared our empirical values of composition change with values expected by a null model where random mortality, recruitment, and immigration from a narrow species pool are the only factors at play, and where species in communities are not being driven to lower and higher abundances by any specific process.

c. 1) Null model rationale

Null models are based on randomization algorithms that produce data as expected by a null hypothesis, and where a specific effect of interest has been removed. In this way, when empirical data are compared to null model data, any difference might suggest a significant effect of the mechanisms intentionally excluded from the algorithm generating null expectations. In our study, the effect of interest is any directional change in species composition. This is manifested by any force that changes the abundances of species by making mortality and recruitment rates unequal between species. Species with elevated recruitment rates would increase in abundance, while species with elevated mortality would decrease in abundance. Thus, our null hypothesis states that per-species mortality and recruitment rates are equal across species, leading to a non-directional change in species composition through time. According to this null hypothesis, temporal changes in the composition are solely those expected by stochasticity in mortality and recruitment, but where underlying rates are equal for each species.

In the specific null hypothesis implemented in our analyses, dynamics are neutral, meaning that all individuals, irrespective of species identity, have the same probability to die or to be recruited. Algorithms are detailed below. A positive deviation of the empirical data from null values indicates more change in species composition than expected by the null model; a negative deviation indicates a more stable community than expected.

c. 2) Description of null model algorithm

Our null model algorithm constructs null matrices of species abundances across censuses 1 and 2 for each of the 26 plots that are the focus of our study. The algorithm starts with an empirical composition matrix, where columns represent species, rows are censuses, and the values that fill this matrix are abundances (number of individuals). To obtain a null matrix:

1. We copy the abundances in census 1 (first row) from the empirical matrix to the null matrix.
2. For census 2 (second row), we copy the abundances in census 1. Thus, initially, census 1 and 2 in the null matrix are identical.
3. Random mortality: We randomly select a set of M individuals from the second census. This number M is equal to the number of individuals found dead in the empirical plot re-surveys. In our null model, all individuals have the same probability of being chosen, independent of their species identity.
4. These M individuals are then removed from the second census.
5. Random recruitment: We randomly select a set of R individuals from the species pool (we defined the species pool in several ways to identify the most appropriate approach; details are described in the next section). This number R is equal to the number of recruits found in the empirical plot re-surveys.
6. Finally, these R individuals are added to the second census.

The final product is a null matrix where the first census is identical to the empirical matrix, but the second census results from random mortality and recruitment across species. This process was repeated 1,000 times resulting in 1,000 null matrices for each of the 26 local plots. The final step of the null model analysis is to calculate the composition change (standardized Bray-Curtis distances) between censuses in the empirical matrix, and in each of the null matrices. This produces a distribution of null values of composition change against which the empirical values can be compared.

In order to interpret the results from the null model, we use a standardized effect size (SES). This value quantifies the difference between the observed value of the metric and the mean of the null values; and is given by the formula: $SES = [CC_{emp} - mean(CC_{null})] / sd(CC_{null})$. The standardized effect sizes are positive for communities that experience more temporal turnover than expected, and it is negative for those that are more stable. If forest communities have been shifting in species composition over time consistently across our forest plots, the mean of SES values should be significantly greater than zero. To test this prediction, we performed a one-sample *t*-test.

c. 3) Definition of species pools and recruitment probabilities

Our null model uses a species pool to define the potential set of species that can contribute to the recruitment of new individuals during randomizations for the second census. Defining the species pool only as the species found in the focal plot is too narrow and can lead to an underestimation of the potential change in composition that can happen by simple random dispersal from adjacent areas. Defining the pool as all the species found in the regions is too broad and can lead to an overestimation of the potential turnover owing to null recruitment of species that cannot possibly disperse to or tolerate the conditions in a particular local community. Thus, we built species pools that represent a balance by using the total abundances of each species found in a specific region surrounding each focal plot.

The region around each focal plot was delimited using elevational distances (as a proxy for environmental conditions). For each plot, we constructed three species pools, which include species data for all plots in elevational bands of 100 m, 200 m and 300 m centered on the focal plot. For building these species pools, we considered species present in the 26 re-measured plots, but also species found in the other 22 large 1-ha plots and the 442 small plots. In the small plots, we considered only data from trees with a dbh ≥ 10 cm to match the diameter cut-off in the large focal plots. As expected, the number of species in the species pool increased with the width of the elevational band (Figure S1). We did not use elevational bands larger than 300 m because our null hypothesis implies that the recruitment occurs only from species that can tolerate the conditions in the focal plot, thus maintaining the same species composition from census 1 to census 2.

Additionally, the probability of contributing to recruitment in the local plot was not equal across the entire species pool. Instead, we modeled the recruitment so that the species in plots geographically near the focal plot are more likely to be recruited, than species in plots far away. To do this, we used an exponential function to describe the decay in recruitment probability with increasing distance. This function is based on an exponential dispersal kernel as described by Nathan et al. (2012): $P_{\text{disp}} = \frac{1}{2\pi a^2} \exp\left(-\frac{r}{a}\right)$, where *r* is the distance to the focal plot, and a is half the mean dispersal distance. The function is parameterized by one value that corresponds to the "mean dispersal distance". To evaluate how "dispersal distance" modifies our results, we varied this parameter from 0.01 km to a maximum of 22.16 km (half of the median of the distances among plots). Small values of dispersal distance cause individual arrival probabilities to fall quickly with geographic distance; larger values increase the chances that individuals in plots far away can contribute to dispersal. Figure 2 shows how the recruitment probability for individuals in the species pool changes with geographic distance, and how the shape of this curve is influenced by the "mean dispersal distance" parameter.

Null model analyses were run for each plot (26 plots), and for each combination of species pool size (3 elevational bands) and dispersal distance (50 values). In total, we run 3,900 null model analyses. We use these to document the variation in results and find the most appropriate combination of species pool size and dispersal distance used to interpret our results (detail in results). All functions for null model analyses were written in *R* and are available in the Supplementary Material.

d. Changes in richness and composition across climatic gradients

To evaluate the relationship between richness and composition changes with climate, we performed a series of multiple linear regressions. In these analyses, empirical values of richness change and change in composition were used as dependent variables, while mean annual temperature and annual precipitation were used as predictors. Climate data was extracted from WorldClim version 2.0 using plot coordinates.

We also conducted similar analyses to evaluate the relationship between climate and standardized effect sizes (SES) of change in species composition. These analyses look to explain the change in species composition after null model expectations are taken into account. We conducted separate analyses for the subset of null models defined by using the different band widths and the maximum mean dispersal distance where the richness change is not significant in each species pool (d_R values in Figure 4). These values represent the dispersal distances that maintain the observed local richness between census

1 and 2, and are consistent with the null hypothesis in the null model of no change in community structure. The values used were 0.60 km for mean dispersal distance in the 100 m elevational band, and 0.32 km for the 200 m and 30 m elevational bands (Figure 4).

RESULTS

There was significant turnover of individuals between censuses in our data: we found that on average both mortality and recruitment happens at a 1.6% per year rate (both community-wide rates are not significantly different from one another; Figure 2c). This translates into an average of about 75 deaths and 78 recruitments between censuses across plots. We later describe how these rates are enough to create temporal shifts in diversity and composition.

Species diversity

During the first census, species richness in the 26 focal plots varies broadly from 20 to 100 species (Figure 2a). When comparing species richness between censuses 1 and 2, we found losses of one to three species for some plots, gains of not more than three species for others and 5 plots did not show any change in richness at all (Figure 3a). I fact, a one-sample *t*-test showed that the mean standardized change in species richness between censuses did not differ significantly from zero (Figure 3b), indicating that there was not a consistent gain or loss of species across local communities.

Importantly, however, regression analyses did find that temperature was a significant predictor of variation in richness change (p = 0.034; Table 1; Figure 4). Most of the plots with a positive change occur below 13 ^{o}C temperature (3 out of 5), while all the plots with a negative change in richness occur in sites above 14 ^{o}C (16 out of 16). This analysis suggests that communities experiencing warm temperatures tended to lose species, while communities in colder environments might be gaining species (Table 1, Figure 4). The same analysis failed to find an effect of precipitation (p = 0.192; Table 1), or an interaction between temperature and precipitation (not shown).

Species composition

Species composition for these communities changed to some degree between censuses, with an average standardized Bray-Curtis distance of 0.0089 (Figure 3c and 3d). However, unlike for richness, we cannot know if these values are more than expected by chance with a simple statistical test. To understand if community composition in these communities is changing directionally, we compared empirical values to values expected by a null model.

First, we compared the observed change in species richness (RC) to null model expectations. This analysis helped us find the values of dispersal distance for each species pool (i.e., elevational band) that result in no change in species richness in the null communities (Figure 5; first row). This was important because our null model assumes no changes in the number of species in the community. Dramatic changes in species richness by unrealistic recruitment of new species in the null model could confound results in community composition. Our results corroborate that the larger the species pool and dispersal distances are, the larger the increase in null species richness (Figure 5). We found that dispersal distances of more than about 0.6 km lead to increases in species richness that are significantly greater than zero (Figure 5a). These null increases are also inconsistent with the empirical change in richness across plots, which is slightly negative (but not significantly so; Figures 3 & 5). Thus, if we use dispersal distances greater than 0.6 km, null composition will change owing to increases in richness, not directional changes in abundance that are our factor of interest.

We then compared the observed change in species composition (CC) to null model expectations. Specifically, we calculated standardized effect sizes, which represent the difference between empirical and null values of composition change (Figure 6). We found that SES of composition change varies with species pool size and mean dispersal distances used during null model analyses (Figure 6). At small to intermediate dispersal distances, mean SES of composition change is significantly higher than zero. This indicates a consistent change in community composition that is greater than expected by the null model. Beyond a certain dispersal distance (d_C; Figure 6), however, mean SES does not differ significantly from zero (Figure 6). Also, with a wider species pool, the maximum mean dispersal distance for which communities show a significant compositional change is smaller. Importantly, the dispersal distances in our null model that produce zero change in richness (d_R; Figure 5) always lead to the conclusion that community composition is changing more than expected purely by stochastic demographic processes (compare Figures 5 and 6; Figure 7).

Finally, despite evidence for significant changes in species composition across communities, community compositional change did not show environmental gradients, suggesting that all the communities are changing along that gradient. Neither empirical values of composition change (Bray-Curtis distances) nor SES values have significant relationship with temperature or precipitation (Table 1).

DISCUSSION

Our analysis of how tropical Andean communities change over time provide insights into biodiversity trends during the Anthropocene. First, we find that although trees are long-lived, rates of mortality and recruitment reach around 1.6% individuals per year. We also show that these rates are enough to detect temporal trends of community change over the 4 to 11 years between censuses in our data. We find that there is not a consistent change in richness in local communities, but that this is the result of a balance between communities losing species, and others gaining species which translates in no change in a more regional scale. Specifically, we find that communities in cold climates might be increasing in richness, while communities in warm climates might be decreasing. This pattern is probably also linked to our finding that communities are shifting significantly in species composition across all elevations and climates.

No consistent change in species richness, but change is related to temperature

Whether local species richness is changing during the Anthropocene has been the subject of recent debate (Cardinale et al. 2018). The common belief is that biodiversity is declining (McGill et al. 2015). However, even though there is evidence that this is so at the global scale, patterns within local communities are less clear. While recent meta-analyses claim that communities are not gaining or losing species (Vellend et al. 2013, Dornelas et al. 2014, Vellend et al. 2017), others point towards problems with analyses and data to suggest that human impacts are decreasing diversity at all spatial scales

(Cardinale et al. 2018). Our study helps to fill an important gap in previous meta-analyses, where tropical communities have been dramatically under-represented.

Our analysis showed that the general change in richness is not significantly different from zero across local communities for this region (Figure 3b). This initial result supports the conclusions of Vellend, et al. and Dornelas, et al. suggesting no change in local diversity. One potential explanation for our result is that time between censuses is not enough to detect any changes if they are happening. However, when we ran our null model randomizations and estimated the number of species lost or gained, many scenarios led to significant changes in richness. Particularly, null communities lost species when recruitment considered only individuals near the focal plot, while null communities gained many species when recruitment considered individuals also from far away (Figure 4). This demonstrates that our analyses have enough statistical power to detect species losses and species gains, as well as changes in community composition.

Despite no consistent change in richness, we found that among-community variation in richness change showed a significant relationship with annual mean temperature (Table 1; Figure 7). This suggest contrasting patterns for communities at opposing ends of the elevational gradient. While communities in warmer temperatures are losing species, communities in colder environments are gaining species (above the expected by random demography). Although we do not know what processes are responsible for this pattern of richness change, its significant relationship with temperature suggests that one plausible explanation is global warming. Species elevational ranges can respond in multiple ways to changes in temperature: they can migrate to higher elevations to track their preferred environmental conditions, some species can be subject to lags and encounter new conditions and/or competitors, or they can adapt and retain their distributions (Alexander et al. 2016, Colwell et al. 2008). Our results are consistent with this first simple model of species responses to climate change, whereby upslope shifts in species distributions might be causing attrition of biodiversity of lowland communities, and an initial enrichment of higher elevation communities. Our results are also consistent with a pattern showed in other empirical studies that show an upward migration of species tracking their thermal preferences (Feeley et al. 2013, Duque et al. 2015, Lamprecht et al. 2018), however we cannot conclude about the directionality just from our results. According to Feeley (2011b), Andean species need to migrate at a rate of 5.5-7.5 m/year in order to remain in equilibrium following the observed increase of temperature over the past four decades. As a result, tropical lowlands could suffer species richness reduction due to a lack of species adapted to higher temperature which can cause a range retraction for some species (Duque et al. 2015), while species sift upwards enriching communities at higher elevations (Colwell et al. 2008**,** Feeley and Silman 2010). This enrichment, however, could potentially be temporary, with an extinction debt at higher elevations that will reduce diversity as new competitors and climate change drive some species extinct as consequence of a reduction of suitable habitats for species from those elevations (Alexander et al. 2016, Freeman et al. 2018).

Local community composition is changing across a broad elevational gradient

Our analyses showed also that there was a significant shift in species composition. When we used the null models for which change in richness was zero, our communities showed higher temporal turnover than expected by chance. In fact, significant changes occurred, even for much larger “dispersal” distances in our analyses (Figure 5). Additionally, these changes in composition were significant for most individual sites (Figure 7), but showed no relationship with temperature or precipitation, suggesting that communities are changing irrespective of their climatic conditions. These results are consistent with the pattern observed in previous studies, which have found evidence of species migration in the tropics in response to climate change. For example, Feely et al. documented upward shifts in species distributions in the order of 1.18 m/year in Costa Rica (Feeley et al. 2013), and of 2.5-3.5 m/year in in Peru (Feeley et al. 2011b), while Duque et al. documented a shift of 2.2 m/year in Colombia (Duque et al. 2015). However, solely based on our analysis, we cannot infer the directionality or mechanisms behind these changes. Although climate change is an important potential explanation, other forces that might be driving community change include recovery from past human or natural disturbances, nitrogen deposition, or ongoing disturbance by human activity. Direct impact of human activity, however, is unlikely, as most of these sites are remote, and nearby towns are relatively small. Regardless of the causes, the observed consistency of changes in community composition are important. Shifts in the structure of natural communities can cause concomitant changes to the functioning of ecosystem (Williams et al. 2007, Garcia et al. 2014, Nolan et al. 2018). The relationship between ecosystem functions and species composition, however, is poorly understood.

Few communities showed non-significant changes in species composition, and some have less change than expected by chance. So, although there is no significant relationship with temperature or climate, some communities might be less affected by processes driving community change, and some might also be regulated to remain constant through time. This regulation in community structure was documented as widespread for natural communities by Gotelli et al.(2010). What makes some communities stable through time, and others shifting is unclear and deserve further analysis. The relative frequency of regulated vs. changing communities itself is unclear, but it might vary across regions. Mountainous regions seem to be more strongly impacted by climate change (Rixen et al. 2018), and in particular high elevations in the Andes seem to be changing in climate more rapidly than other regions (Feeley et al. 2012, Báez et al. 2016). So Andean communities might be prone to shifts in community composition more than the global average. This explanation requires further study, however, it is consistent with the findings of Fadrique et al. (2018) who also document that most Andean tree communities are suffering from widespread but heterogeneous shifts in mean community temperature (i.e. thermophilization) across all elevations.

Limitations of our analyses and data

As mentioned before, one of the most frequent criticisms to datasets like ours is the short time interval between censuses, particularly considering that trees can be long lived. However, our null model analyses prove that there is enough mortality and recruitment in our datasets to detect changes in species richness and composition. Additionally, previous studies with similar systems and intervals length between censuses also found that distribution of species showed evidence of upward migration (Feeley et al. 2011b, Feeley et al. 2013). Thus, we are confident that our analyses reflect real patterns in ecological communities, and not a lack of statistical power.

Another aspect to consider is that, even though null models are easy to implement, and have been used for many ecological studies trying to understand how communities are assembled in time and space (Gotelli 2001), we need to be cautious when applying them. Previous studies show that results of null model analyses can vary significantly depending on how randomizations are constructed. This is part of the reasons why we varied the size of the species pool and the “mean dispersal distance” in our null models, creating 150 different scenarios (3 species pools times 50 dispersal distances). We then focus our conclusions on the values of dispersal distance that lead to zero change in richness, which is consistent with our null model.

Additionally, we re-ran our analysis with two alternative null models to compare our results and interpretations. We used a very basic null model described by Gotelli et al. (2010), which has been used in previous ecological studies. Unlike our null model, Gotelli et al.’s algorithm assumes 100% mortality and recruitment: to create null matrices all individuals are removed and matrices are randomly filled again. With this null model, SES for change in community composition is significantly lower than zero, which would lead to the conclusion that communities are more stable than expected by chance where they are created from scratch from the species pool (Figure S3). The null model described by Gotelli et al., however, is not appropriate for dataset like ours, where many individuals survive between censuses. The null model algorithm used for our analysis improves upon Gotelli et al.’s by considering the empirical rates of mortality, recruitment and survival, while also uses data from an external species pool for recruitments.

Nevertheless, our conclusions are contingent on using the correct null model, and null models are always coarse tools that only allow us to make first steps toward understanding mechanisms (Gotelli et al. 2010, de Bello 2012, Götzenberger et al. 2016). Future analyses should consider shifts in the functional structure of communities that will allow us to test more specific predictions about hypothesized mechanisms behind the community changes we observe (Ackerly and Cornwell 2007). At the moment, however, complete functional data for species in our communities are not yet available. Complementarily, experimental studies are needed to test for mechanisms of community change operating in these Andean communities. Such experiments, however, are expensive and can be accomplished solely at smaller spatial and temporal scales. Though, a better understanding of temporal changes in community composition can be gained by large-scale observational studies like ours, complemented with functional data and experimental tests.

Conclusions

In conclusion, our analysis supports the idea that communities in the Tropical Andes are going through changes in their diversity and composition. Richness seems to be increasing in communities in cold climates, and decreasing in communities in warm climates. Species composition is shifting in most communities and across climate gradients. The patterns we find are consistent with an effect of global change, and particularly climate change, matching previous studies in other regions of the Andes; but more other analysis are necessary to test hypothesis regarding possible responsible mechanisms. Our study and previous work suggests that human impacts might be reaching biodiversity even in remote places away from evident human activity. However, as mentioned the final causes for the changes we observe are yet unknown, and to better understand them we would need to expand on our analyses to consider other forms of diversity, like functional community composition, and other approaches, like experimental manipulation. This type of research is urgently needed to advance theory in community ecology, but also to understand and manage natural communities in a changing world.

AKNOWLEGEMENTS

First, I would like to thank my committee, Dr. Robert Ricklefs, Dr. Robert Marquis and Dr. J. Sebastián Tello for their support and feedback at every stage of this study. I would like to thank also the Madidi Project and all the people involved in the collection of data used in this study. I am particularly thankful to Dr. Alfredo Fuentes and Leslie Cayola, who have led the data collection in the field and herbarium, and to Ana Antezana and Tatiana Miranda, who have done much of the organizational and curatorial work in the herbarium. Dr. Gabriel Arellano and Dr. Manuel Macía also contributed key pieces of data for this study. Many additional people helped during fieldwork, and assisted in the identification of specimens. I thank Dr. Mónica Moraes and Dr. Carla Maldonado for their personal and institutional support through the Herbario Nacional de Bolivia. Thanks also to the Dirección General de Biodiversidad, the Bolivian Park Service (SER-NAP), the Madidi National Park and local communities for permits, access and collaboration in Bolivia. The Madidi Project and this study has been supported by the National Science Foundation (DEB-0743457, DEB-1836353), National Geographic Society (NGS-03052, NGS 8047-06), I-CARES at Washington University in St. Louis, the Missouri Botanical Garden, the Consejería de Educación (Comunidad de Madrid, Spain) and Universidad Autónoma de Madrid – Banco Santander, and other funding agencies. Finally, a special thanks to Christopher Davidson and Sharon Christoph, who generously funded the fellowship that allowed me to complete this work.

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TABLES

***Table 1.* Relationships between changes in species richness and composition with climate.** Regression analyses show the association between changes in species richness and temperature (in italics; Figure 6), but fail to find other significant relationships. These analyses were conducted for the observed standardized values of richness change (RC) and composition change (CC; measured as Bray-Curtis distances). Analyses were also conducted using standardized effect sizes of composition change (SES_{CC}) from null model analyses. For SES of composition, we present three different results, which correspond to varying elevational band widths used to define species pool. Moreover, we used the maximum mean dispersal distance where the richness change is not significant in each elevational band (d_R values in Figure 4). These values represent the dispersal distances that maintain the observed local richness between census 1 and 2, and are consistent with the null hypothesis in our null model of no change in community structure. The values used for band 1 were 100 m of elevation width and 10.09 km for mean dispersal distance; for band 2 were 200 m and 3.93 km; for band 3 were 300 m and 2.45 km.

Response	**Intercept**	**Temperature**		**Precipitation**		**Adjusted R^2**
		Coefficient	P	Coefficient	P	
Standardized RC	-0.0014	***-0.0017***	***0.034***	-0.0010	0.192	***0.224***
Standardized CC	0.0089	-0.0002	0.742	0.0008	0.202	-0.011
SES_{CC} band 1	3.0835	-0.5866	0.306	0.0549	0.923	-0.036
SES_{CC} band 2	3.1887	-0.5291	0.335	0.0117	0.983	-0.040
SES_{CC} band 3	3.1451	-0.5542	0.312	0.0408	0.940	-0.037

FIGURES

***Figure 1*. Location of the study region and plot network.** (a) The Madidi Region, where this study was conducted, is located in eastern slopes of the Bolivian Andes in the areas inside and around the Madidi National Park. (b) The plot network used in our study includes 48 large (1-ha) permanent plots (circles), and 442 small (0.1-ha) temporary plots (white squares). Twenty-six of the large plots have been re-surveyed and are the focus of our study (orange circles). The plot network covers a broad elevational range from lowland Amazon forests (~ 250 m) to the tree line (~ 4,250 m). For details, see methods or visit www.mobot.org/madidi.

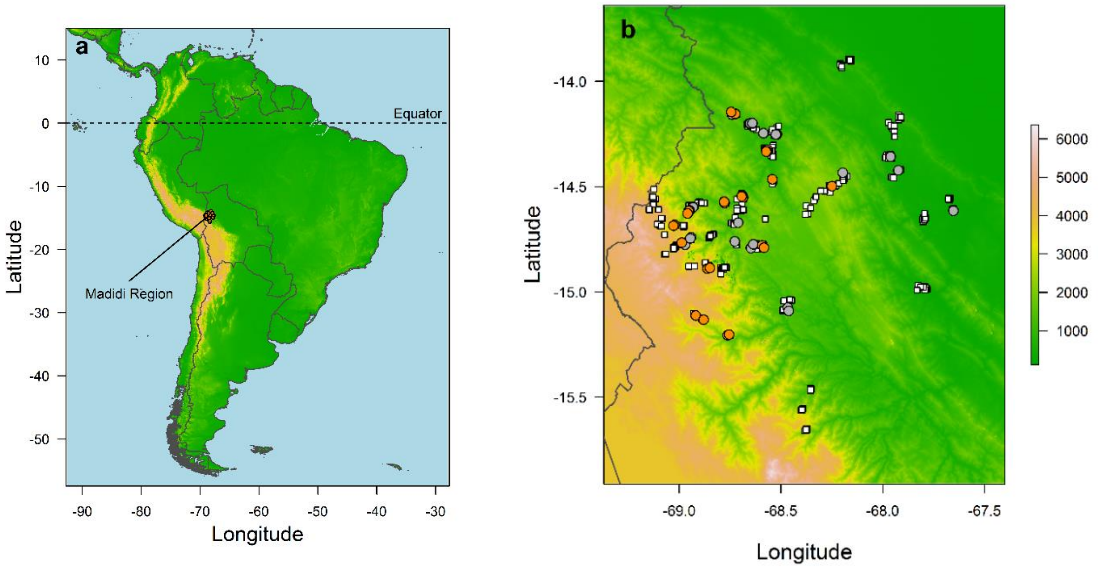


Figure 2. **Fundamental data in the twenty-six permanent plots with re-survey data.** (a) Variation in species richness in each plot at the time of the initial survey (i.e., census 1). (b) Interval length in years between census 1 and census 2 for each plot. (c) Variation in mortality and recruitment rates (measured as a proportion of individuals per year). A paired two-sample t-test found no significant differences between mean mortality and recruitment across the 26 plots.

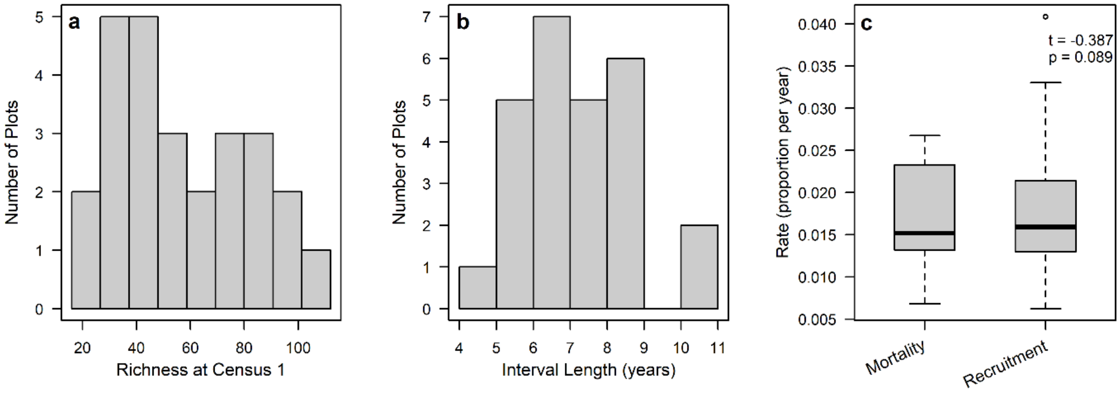


***Figure 3*. Observed temporal changes in richness and community composition.** (a) Temporal change in richness between first and second censuses measured as difference in numbers of species. (b) Same as in (a), but change in richness has been standardized to consider variation in initial richness and interval length between censuses in each plot (see Methods). Here, a one-sample *t*-test shows no significant difference from zero in average richness change per year. (c) Temporal change in species composition between censuses measured as Bray-Curtis distances. (d) Same as in (c), but composition change has been standardized to account for variation in interval length.

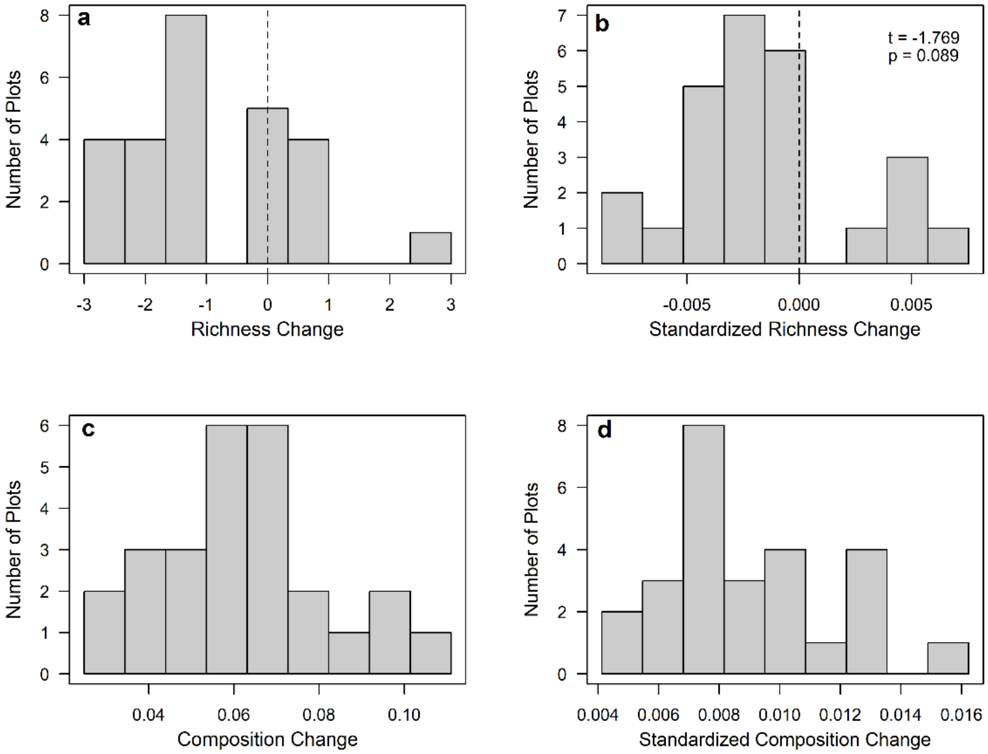


Figure 4. **Relationship between changes in richness and temperature.** The figure shows results form a linear regression where mean annual temperature (in °C) is used to predict variation in standardized richness change. This was the only significant relationship with climate found in our regression analyses ($R^2 = 0.224$; see Table 1), suggesting that plots in cold climates might be gaining species, while plots in warm climates might be losing species. Each circle represents one plot (*n* = 26). The black line is the univariate regression line, and the grey dashed line is the tendency curve. The horizontal line indicates the richness change of zero. Regression statistics can be found in Table 1.

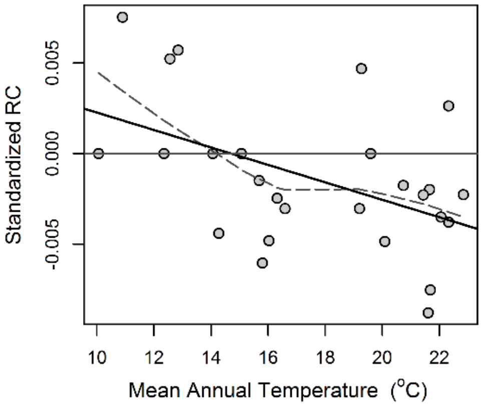


***Figure 5*. Patterns in null richness change as expected by the varying conditions of the null model algorithm.** This figure shows how the null values of standardized change in richness (i.e., produced by the null model) vary when using different elevational bands (panels) and dispersal distances (x-axes) to define recruitments during randomizations of the null model analyses (see Methods). The horizontal solid line represents the absence of change in richness with time (RC = 0). The horizontal dashed line represents the average change in richness observed in the empirical data across all 26 plots (Figure 3b). Tringles represent the average of null model expectations across 26 plots for each combination of elevational band and mean dispersal distance. Grey areas around triangles indicate 95% confidence intervals around those null averages. Green triangles represent average null richness change statistically different from zero based on one-sample t-tests, while black triangles represent null richness change values not different from zero. The vertical dashed line and the number next to it indicates the maximum distance where null richness change is not significantly different from zero. This indicates the maximum dispersal distance that the null model can use and that does not lead to a null increase in species richness by recruitment from outside the plot.

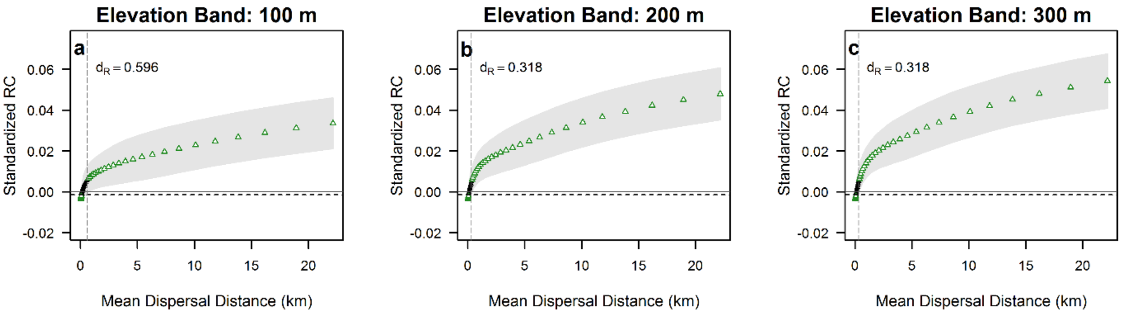


Figure 6. **Patterns in standardized effect size of temporal change in composition with varying size of species pools and mean dispersal distance.** This figure shows how the empirical change in species composition differs from the values expected by the null model (standardized effect sizes: SES) under different conditions for the random recruitment of individuals: different elevational bands (panels) and dispersal distances (x-axes; see Methods). Composition change in the empirical and null data was calculated using standardized Bray-Curtis distances. Circles represent the average standardized effect size (SES) across 26 plots for each combination of elevational band and mean dispersal distance. Grey areas indicate 95% confidence intervals around those averages. Positive SES indicate changes in composition that are greater than expected, while negative SES represent changes smaller than expected. Red circles represent average SES statistically different from zero based on a one-sample t-test. Black circles represent SES values not different from zero. The solid horizontal line indicates the SES of zero. The vertical dashed line and the number next to it indicates the maximum distance where the SES is significantly greater than expected by the null model (d_C). For reference, we also include d_R, or the maximum distance that does not lead to an increase in null richness due to immigration during recruitment (see Figure 4).

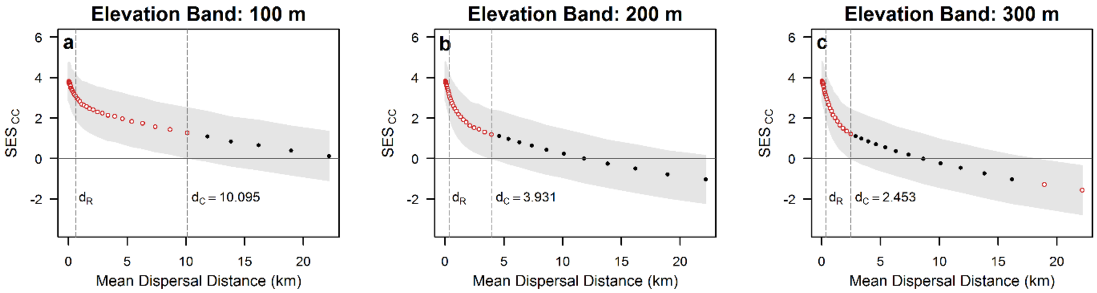
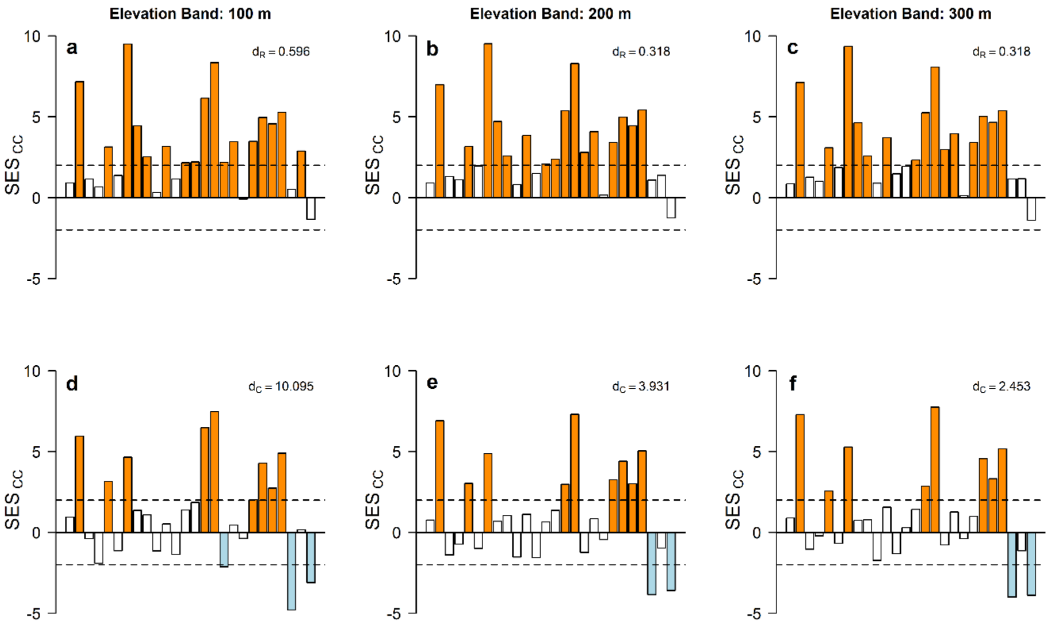


Figure 7. **Variation in the standardized effect size of temporal change in composition for each of the 26 large plots.** Each panel shows the SES of composition change under a different combination of elevational band and dispersal distance. The first row correspond to the three elevational bands, each using the maximum dispersal mean distance where our null model produces a zero change in null richness (d_R values from Figure 4). The second row corresponds also to the three elevational bands, each using the maximum dispersal distance where mean SES_{CC} is significantly greater than expected by the null model (d_C values from Figure 5). Orange bars are higher than 2 and indicate individual communities that are changing more than expected by the null model. Light-blue bars are less than -2, and indicate communities that are changing less than expected. White bars indicate commununites that show no evidence of significant change in composition.



SUPPLEMENTARY MATERIAL

Figure S1. **Variation in size of species pools across elevational band widths.** The size of the species pool was defined as the number of species found across all plots within an elevational band centered at a specific plot. The boxes show the variation in size of species pools for each for the 26 focal plots. All species in the species pool could potentially contribute to recruitments (see Methods).

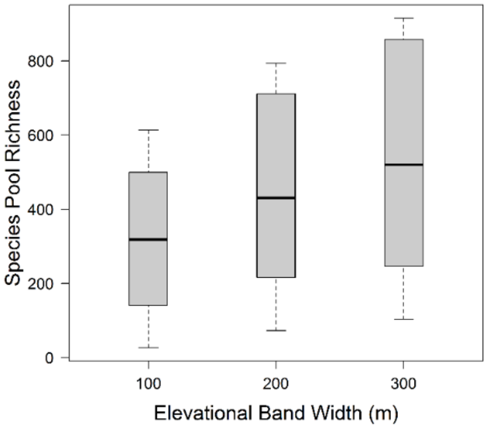


***Figure S2: Shapes of the relationship between recruitment probability and distance from focal plot for varying values of mean* dispersal distance.** Each curve describes the distribution of relative probabilities of contributing to recruitment in the local plot as a function of distance from the focal plot. We obtained these curves by using an exponential dispersal kernel parameterized by the mean dispersal distance (Nathan et al., 2012). In this way, individuals in plots near the focal plot are more likely to “contribute” to the recruitment, while individuals in plots far away are less likely to do so. However, the relative probabilities change with mean dispersal distance. If dispersal distance is small (green line), the probabilities decline very rapidly. If the dispersal distance is large (red line), the probabilities decline less abruptly. All the individuals in plots within the species pool (defined by an elevational band centered in the focal plot) are considered.

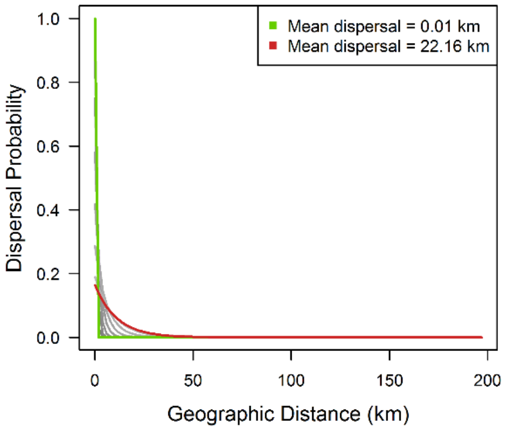
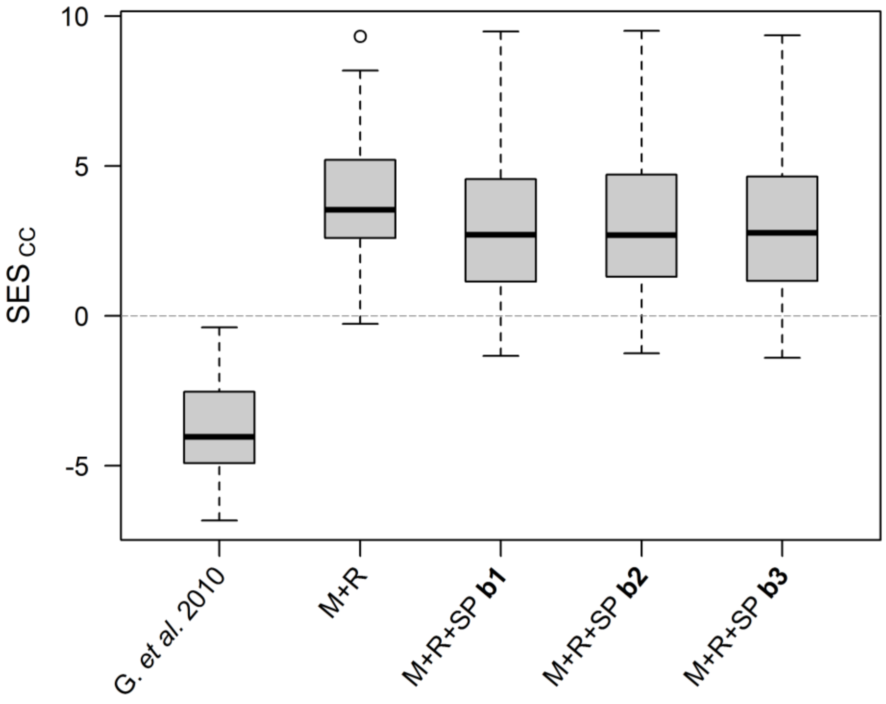


Figure S3. **Standardized effect size of temporal change in composition using three different null models.** Each box shows the variation in standardized effect size across the 26 plots analyzed for each null model. G.2010 refers to the null model described by Gotelli et al. 2010, where there is a complete turnover of individuals (i.e. 100% of deaths and recruits). M+R is a null model that considers empirical data on mortality, recruitment and survival rates, but where random recruitment considers only data from the focal plot. For the M+R+SP null model, we present three different results, which correspond to varying elevational band widths. For each band, we used the maximum mean dispersal distance where the richness change is not significant (d_R values in Figure 4). This represent the dispersal distances that maintain the observed local richness between census 1 and 2, and are consistent with the null hypotheses of no change in community structure. The values used for band 1 were 100 m of elevation width and 10.09 km for mean dispersal distance; for band 2 were 200 m and 3.93 km; for band 3 were 300 m and 2.45 km. Further null models details are given in the text.



```
## Supplementary code for the thesis:
## Title: Temporal changes in the diversity and composition Tropical Andean
##        Forest communities
## Author: Claudia A. Aparicio-Chavez

#################################################################
########## NULL MODELS
#################################################################

## DESCRIPTION ##
# MatrixRandom creates random matrices based on a composition
# matrix.

## ARGUMENTS ##
# compo : a composition data matrix. Columns are species and rows
# are censuses.
# n.rand : number of randomizations.
# rand.type : null model type analysis; rand.type = 1 applies the
# null model described by Gotelli et al. 2010; rand.type = 2
# applies the null model based on the empirical data for
# mortality and recruitment during the re:survey.
# pool.probs : Matrix with recruitment probabilities for the
# species conforming the pool. If missing, the probabilities are
# calculated based on the composition matrix.
# N.mort : Number of individuals dead
# N.recruit : Number of individuals recruited

## VALUE ##
## empirical : the empirical matrix of composition
## null : list containing all the randomized matrices

## REFERENCES ##
# Gotelli, N. J. et al. 2010. Detecting temporal trends in
# species assemblages with bootstrapping procedures and
# hierarchical models. - Philos. Trans. R. Soc. B Biol. Sci.
# 365: 3621-3631.

MatrixRandom <- function(compo, n.rand, rand.type = 1,
pool.probs, N.mort, N.recruit){
    if (missing(pool.probs)) {
    pool.probs <- colSums(compo)
    pool.probs <- pool.probs / sum(pool.probs)
  }

  if(sum(pool.probs) != 1)
    warning("Pool probabilities do not sum to 1")

  if(!all(colnames(compo) %in% names(pool.probs)))
     stop("Not all species in the local community are in the
     meta-community vector")
```

```
## Probability of belonging to a given species
s <- pool.probs

## Total abundances of individual per census, for each species
Abund.t <- rowSums(compo)

## Total number of individuals in the plot from all the species
# and censuses
N <- sum(Abund.t)

## Probability of being present in a given census
q <- Abund.t / N

compo <- compo[, match(names(pool.probs), colnames(compo))]
colnames(compo) <- names(pool.probs)
compo[is.na(compo)] <- 0

Matrix.r <- sapply(rep(NA, n.rand), list)
Richness.M <- rep(NA, n.rand)

  for(i in 1:n.rand) {
    if(rand.type == 1) {

## Assign N individual to a census with probability q
Census.new <- sample(rownames(compo), N, prob = q, replace =
TRUE)

## Assign N individual to a species with probability s
Sp.new <- sample(colnames(compo), N, prob = s, replace = TRUE)

## Matrix of new values for census and species for the new
# individuals
compo.rand <- table(Census.new, Sp.new)
    }

if(rand.type == 2) {

### Matrix with new values
## Census 1 is fixed
compo.rand <- compo
compo.rand [2, ] <- NA

# Matrix with individuals selected randomly for mortality
M <- rep(colnames(compo), compo[1, ])
sp.mort <- sample(M, N.mort)
compo.mort <- table(sp.mort)
compo.mort <- compo.mort[match(colnames(compo),
names(compo.mort))]
names(compo.mort) <- colnames(compo)
compo.mort[is.na(compo.mort)] <- 0
```

```
## New matrix after mortality
compo.rand[2, ] <- compo[1, ]-compo.mort

# Matrix with individuals selected randomly for recruitment
sp.recruit <- sample(colnames(compo), replace = TRUE,
                           size = N.recruit, prob = s)

compo.recruit <- table(sp.recruit)

compo.recruit <- compo.recruit[match(colnames(compo),
names(compo.recruit))]
names(compo.recruit) <- colnames(compo)
compo.recruit[is.na(compo.recruit)] <- 0

## New matrix after recruitment
compo.rand[2, ] <- compo.rand[2, ] + compo.recruit
      }

compo.rand <- compo.rand[,match(colnames(compo),
colnames(compo.rand))]
colnames(compo.rand) <- colnames(compo)
compo.rand[is.na(compo.rand)] <- 0

compo.rand <- compo.rand[match(rownames(compo),
rownames(compo.rand)),]

Matrix.r[[i]] <- as.matrix(compo.rand)
      }

output <- list(compo, Matrix.r)
names(output) <- c("empirical", "null")
output
}

#################################################################
### 2. DISSIMILARITY MEASURES
#################################################################

## DESCRIPTION ##
# DistanceComposition Calculates similarity indices based on the
# vegdist function for the empirical and null composition
# matrices.

## ARGUMENTS ##
# compo : An empirical composition data matrix. Columns are
# species and rows are censuses.
# Matrix.r : List of null matrices. Its format is the same as
# compo
# method : Dissimilarity index, as used by the vegdist{vegan}
# function
# IL : Interval length in years between censuses.
```

```
## VALUE ##
# compo.dist.Emp.raw : Empirical composition change value
# diffR.Emp.raw : Empirical richness change value
# diffR.ES.Emp : Standardized empirical change in richness by
# year
# compo.dist : Standardized change in composition by year
# ses : Satndardized effect size for the change in composition
# p.value : P value for the change in composition as a
# proportion of null values greater than the empirical value
# p.value2 : P value for the change in composition as a
# proportion of null values lower than the empirical value
# diffR : Richness difference for the null matrices
# ses.diffR : Standrdized effect size for the richness
# difference for each null matrix
# p.value.diffR : P value for the change in richness as a
# proportion of null values greater than the empirical value.
# p.value2.diffR : P value for the change in richness as a
# proportion of null values lower than the empirical value

## Similarity distance of compo between censuses
DistanceComposition <- function(compo, Matrix.r, method, IL) {

# Required packages
require(vegan)
require(gtools)

# Distance for the empirical matrix
compo.dist.Emp.raw <- vegdist(compo, method = method)
compo.dist.Emp <- compo.dist.Emp.raw / IL

CensusR <- rowSums(compo > 0)
diffR.Emp.raw <- CensusR[2] - CensusR[1]
diffR.Emp <- (diffR.Emp.raw / CensusR[1]) / IL
diffR.ES.Emp <- ln((CensusR[2]/CensusR[1]) / IL*0.1)

# Distance for the randomized matrices
n.rand <- length(Matrix.r)
compo.dist <- sapply(rep(NA, n.rand), array)
diffR <- rep(NA, n.rand)

  for(k in 1:n.rand) {
    compo.dist[k] <- as.vector(vegdist(Matrix.r[[k]], method =
method))

CensusR.rand <- rowSums(Matrix.r[[k]] > 0)
diffR[k] <-  (CensusR.rand[2] - CensusR.rand[1]) /
CensusR.rand[1]
  }

compo.dist <- compo.dist / IL
diffR <- diffR / IL
```

```
# Composition and richness changes
compo.dist <- c(compo.dist.Emp, compo.dist)
diffR <- c(diffR.Emp, diffR)

## Standard Effect Size (SES): composition
ses <- (compo.dist.Emp - mean(compo.dist)) / sd(compo.dist)
## P VALUES
p.value <- sum(compo.dist.Emp <= compo.dist) / n.rand
p.value2 <- sum(compo.dist.Emp >= compo.dist) / n.rand

## Standard Effect Size (SES): richness
#ses.diffR <- (diffR.Emp - mean(diffR))/sd(diffR)
ses.diffR <- (0 - mean(diffR)) / sd(diffR)

## P VALUES
p.value.diffR <- sum(diffR.Emp <= diffR) / n.rand
p.value2.diffR <- sum(diffR.Emp >= diffR) / n.rand

output <- list(compo.dist.Emp.raw, diffR.Emp.raw, diffR.ES.Emp,
compo.dist, ses, p.value, p.value2, diffR, ses.diffR,
p.value.diffR, p.value2.diffR)
names(output) <- c("compo.dist.Emp.raw", "diffR.Emp.raw",
"diffR.ES.Emp", "compo.dist", "ses", "p.value", "p.value2",
"diffR", "ses.diffR", "p.value.diffR", "p.value2.diffR")
output
}
```