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Research

The evolutionary assembly of forest communities along environmental gradients: recent diversification or sorting of pre-adapted clades?

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Summary

- Recent studies have demonstrated that ecological processes that shape community structure and dynamics change along environmental gradients. However, much less is known about how the emergence of the gradients themselves shape the evolution of species that underlie community assembly. In this study, we address how the creation of novel environments leads to community assembly via two nonmutually exclusive processes: immigration and ecological sorting of pre-adapted clades (ISPC), and recent adaptive diversification (RAD). We study these processes in the context of the elevational gradient created by the uplift of the Central Andes.
- We develop a novel approach and method based on the decomposition of species turnover into within- and among-clade components, where clades correspond to lineages that originated before mountain uplift. Effects of ISPC and RAD can be inferred from how components of turnover change with elevation. We test our approach using data from over 500 Andean forest plots.
- We found that species turnover between communities at different elevations is dominated by the replacement of clades that originated before the uplift of the Central Andes.
- Our results suggest that immigration and sorting of clades pre-adapted to montane habitats is the primary mechanism shaping tree communities across elevations.

Introduction

Large-scale biogeographic events – such as the emergence of novel environmental conditions, biotic interchanges or the evolution of key innovations – can have lasting consequences for biodiversity, community assembly and species distributions (Ricklefs, 2006; Fussmann *et al.*, 2007; Pelletier *et al.*, 2009; Claramunt & Cracraft, 2015; Givnish *et al.*, 2015; Uribe-Convers & Tank, 2015). Although theory and empirical evidence suggest that processes occurring in the deep past can contribute to the modern structure of local ecological communities, most research in community ecology during the last few decades has been dominated by a focus on mechanisms at small spatial and temporal scales (Ricklefs, 1987; Estes *et al.*, 2018). Studies have largely overlooked the broader biogeographic context in which communities of co-occurring species are embedded (Chesson, 2000; Adler *et al.*, 2007). Only recently have ecologists begun to bridge this gap by developing ecological theory and empirical tests that truly integrate community assembly across eco-evolutionary scales (Emerson & Gillespie, 2008; Thornhill *et al.*, 2017; Cavender-Bares *et al.*, 2018; McGill *et al.*, 2019; Bañares-de-Dios *et al.*, 2020; Segovia *et al.*, 2020). The extent to which community

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assembly is contingent upon regional context and biogeographic history has broad implications for ecological and evolutionary theory and for understanding how and why communities respond to environmental change (Chase, 2003; Fukami, 2015; Vellend, 2016; McPeek, 2017).

Recent studies provide important insights into how ongoing ecological processes change along environmental gradients (Bricca *et al.*, 2019; Bañares-de-Dios *et al.*, 2020; Neves *et al.*, 2020). However, much less is known about how the emergence of the gradients themselves shapes the evolution of species and phenotypes that underlie community assembly. Two nonmutually exclusive processes may explain how communities assemble along gradients following the emergence of novel environmental conditions (Fig. 1). First, the emergence of new environments (e.g. due to climate change, island formation or mountain orogeny) may create opportunities for immigration and ecological sorting of pre-adapted clades (ISPC hypothesis; Box 1; Fig. 1a; Donoghue, 2008).

According to this hypothesis, when environmental conditions change within a region and new gradients are created, community assembly across these new habitats is dominated by the immigration of species that are pre-adapted because they occupy similar habitats in a different region. This means that the combination of traits needed to colonize new habitats evolved before the origin of the environmental gradient. Diversification following colonization would not involve adaptation to novel environments (i.e. phylogenetic niche conservatism) owing, for example, to competition with species pre-adapted to other environments (Fukami, 2015; Tanentzap *et al.*, 2015). Thus, even though diversification might occur after the origin of the gradient, new species would occupy similar environments to which their ancestors were already pre-adapted. In this way, community assembly across environmental gradients would result in the ecological sorting of species within clades that pre-date the new environments in the region. This scenario of community assembly is consistent with the idea that 'it is easier to move than to evolve' (Donoghue, 2008).

Second, the emergence of new environments may create opportunities for recent adaptive diversification across environments (RAD hypothesis; Box 1; Fig. 1a). According to this hypothesis, when new environmental gradients are created, community assembly across habitats is dominated by adaptation in response to the emerging environmental conditions, resulting in the diversification of clades across the environmental gradient (Stroud & Losos, 2016; Menon *et al.*, 2018). Thus, the traits needed to colonize new habitats evolve after the origin of the

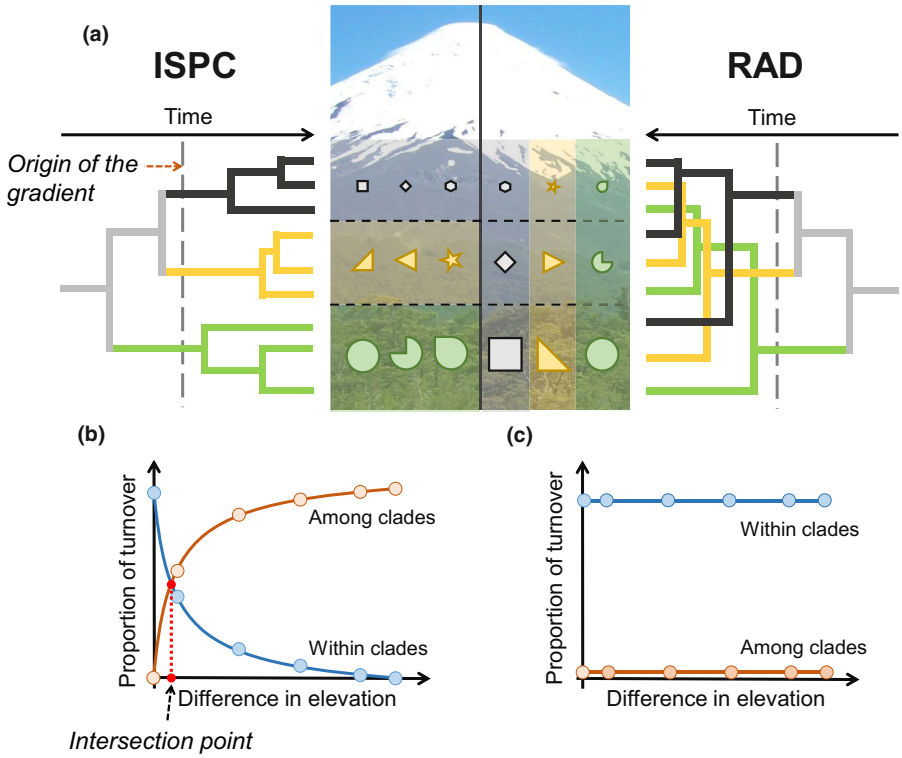

Fig. 1 Conceptual models to explain the assembly of regional biotas after the emergence of new environments. (a) The distributions of species (symbols), traits (sizes) and clades (colors) along an elevational gradient as expected by the immigration and ecological sorting of pre-adapted clades (ISPC; left) and recent adaptive diversification (RAD; right) hypotheses. The gray broken line marks the emergence of the novel environmental conditions due to mountain uplift. The phylogeny describes the evolutionary relationships among species in the target communities, and the colors indicate different clades of pre-Andean origin (clades that diverged before the uplift of the mountain). ISPC and RAD predict contrasting spatial patterns in how species turnover is partitioned into within- and among-clade components. (b) If ISPC is the dominant scenario of community assembly, the among-clade component will increase rapidly as differences in elevation between plots increase, while the within-clade component will decrease. (c) If RAD is the dominant scenario, the within-clade component will be greater than the among-clade component regardless of elevational distance.

Box 1 Glossary

Pre-Andean clade: A clade that diverged from others before the uplift of the Central Andes. Fig. 1 shows predicted elevational distributions of three pre-Andean clades (colors) based on our hypotheses.

Pre-adapted clade: A pre-Andean clade that had, before its immigration to the Central Andes, already evolved adaptations to the novel environmental conditions created by mountain uplift.

Turnover: Observed variation in species composition among forest communities. For example, in two communities [A, B] & [A, C], turnover is generated by the replacement of species B in the first community with species C in the second.

Within-clade turnover: Proportion of total turnover that corresponds to shifts in species composition within a pre-Andean clade. For example, in two communities [A, B] & [A, C], within-clade turnover would be high if species B and C belong to the same pre-Andean clade.

Among-clade turnover: Proportion of total turnover that corresponds to shifts in species composition among multiple pre-Andean clades. For example, in two communities [A, B] & [A, C], among-clade turnover would be high if species B and C belong to different pre-Andean clades.

environmental gradient. In this scenario, niche conservatism is minimal or nonexistent, and community assembly results from the diversification of clades that were originally adapted to a subset of environmental conditions but that diversified to occupy emerging novel environmental space. This scenario for community assembly following the emergence of environmental gradients is consistent with the classic ideas of biome shifts and adaptive radiation driven by ecological opportunity and competition (Givnish, 1997; Schluter, 2000; Losos, 2010; Donoghue & Edwards, 2014).

Here we present and test a novel community–phylogenetic framework and method to study the relative importance of ISPC and RAD in determining the assembly of communities along large-scale environmental gradients. These effects on community assembly can be inferred from unique patterns in the phylogenetic structure of compositional turnover. In particular, signatures of these two nonmutually exclusive processes can be traced when species turnover is decomposed into components that correspond to *within-* and *among-clade turnover*, where clades correspond to independent lineages that originated before the emergence of the gradient. These within- and among-clade turnover components, in turn, reflect the effects of diversification after and before the emergence of the gradient on community composition across environments. Here, we illustrate these patterns using a hypothetical elevational gradient created by mountain uplift (Fig. 1a). For clarity, we present opposing extremes of a continuum that involves the relative contribution of these two processes to community assembly. Most natural systems will probably occupy an intermediate space between these extremes. The ISPC hypothesis predicts that for communities *at the same elevation*, variation in community composition should be dominated by *within-clade turnover*, reflecting strong phylogenetic niche conservatism of clades that are pre-adapted to the environments at that specific elevation (Fig. 1b). As communities are *farther apart along the elevational (i.e. environmental) gradient*, variation in community composition should become increasingly dominated by *among-clade turnover*, reflecting the shift in dominance from species in one pre-adapted clade to another. On the other hand, the RAD hypothesis predicts that for communities at *similar or contrasting elevations*, variation in community composition should be dominated by turnover *within clades*, reflecting how multiple clades evolved niche differences in response to new environmental conditions that allow them to have broad elevational (i.e. environmental) distributions (Fig. 1c). Although we developed and tested this conceptual framework in the context of mountain uplift, our approach is applicable to study community assembly after the emergence of any type of environmental gradient at any spatial or temporal scale.

In the Neotropics, the geologically recent uplift of the Andean mountains created a striking elevational and environmental gradient that had profound consequences for global climate and biodiversity (Rahbek & Graves, 2001; Antonelli *et al.*, 2009; Ehlers & Poulsen, 2009; Graham, 2009; Jiménez *et al.*, 2009; Hoorn *et al.*, 2010). Indeed, the tropical Andes are considered the most species-rich biodiversity hotspot, containing 15% of all plant species (> 45 000 species) in only 1% of the world's land area (Myers *et al.*, 2000; Rahbek & Graves, 2001; Jiménez *et al.*, 2009; Ulloa *et al.*, 2017). However, our current understanding of the eco-evolutionary forces that shape community assembly across elevations in the hyperdiverse Andean biota is limited. First, many studies focus on the evolution and distribution of relatively small clades compared to entire communities; these studies have provided evidence for an important role of adaptive diversification in some cases (Antonelli *et al.*, 2009; Givnish *et al.*, 2014, 2015; Pérez-Escobar *et al.*, 2017) and immigration and colonization of pre-adapted clades in others (Hughes & Eastwood, 2006; Jin *et al.*, 2015; Lagomarsino *et al.*, 2016). Such studies demonstrate that both processes have occurred, but provide limited insights into how the evolutionary history of individual clades contribute to the assembly of entire ecological communities and regional biotas. Second, studies that focus on the phylogenetic structure of Andean communities are relatively few and often fail to differentiate the effects of diversification before and after the emergence of the gradient (Graham *et al.*, 2009; Parra *et al.*, 2011; Bacon *et al.*, 2018; Pouchon *et al.*, 2018; Montaño-Centellas *et al.*, 2019; Ramírez *et al.*, 2019). To date, no study has sought to disentangle the relative importance of immigration and sorting of pre-adapted clades vs post-Andean uplift adaptive radiation in shaping the enormous variation in plant community composition across elevational gradients.

In this study, we combined data on species distributions with phylogenetic information from two large networks of Andean forest plots to test how RAD and ISPC contribute to the assembly of Andean tree communities. We test these hypotheses in the context of the uplift of the Central Andes, which is associated with the formation of the Altiplano plateau during the last 30 million years (Myr) (Fig. 1). Moreover, we developed a novel method to decompose measures of species

turnover among plots distributed across the elevational gradient into among- and within-pre-Andean clade components (Fig. 1 and Box 1; Legendre & De Caceres, 2013). These components measure the relative contributions of ISPC and RAD, respectively. This work both provides a novel framework for examining phylogenetic community turnover and expands our current understanding of how historical processes contribute to community assembly.

Materials and Methods

Community composition data across elevations

We utilized data from two large-scale forest plot networks in the Central Andes of Bolivia (the Madidi Project; extent of 30 165 km^2) and Peru (the Andes Biodiversity and Ecosystem Research Group (ABERG); 1765 km^2). Both datasets contain information on tree community composition spanning the entire elevational range of forests in this region of the Andes from lowland Amazonia (175 m) to the tree line (3765 m; Supporting Information Fig. S1). Our datasets include information on species composition across 73 1-ha plots (large plots hereafter; 50 in Bolivia and 23 in Peru), as well as 454 0.1-ha plots (small plots hereafter; 418 in Bolivia and 36 in Peru; Fig. 2).

Within these plots, all woody plants with a diameter at breast height (DBH) ≥ 10 cm in large plots and DBH ≥ 2.5 cm in small plots were tagged, measured and identified to species or morphospecies. Large and small plots characterize different plant communities; while large plots consider only adults of large tree species, small plots include younger individuals and also species that do not reach 10 cm DBH, including many shrubs. The differences in body size and growth form included in the two plot types could reflect differences in evolutionary potential, as smaller trees and shrubs may have shorter generation times that could enable them to evolve at faster rates than larger trees (Verdui, 2002; Petit & Hampe, 2006), increasing the likelihood that they may show signs of adaptive diversification along the gradient (RAD). Because of this possibility we separated our data by plot size and conducted analyses independently. Additionally, we excluded high-elevation plots (> 3800 m) and plots with three or fewer species. Most of these plots represent *Polylepis*-dominated forest fragments within a matrix of páramo grasslands/shrublands. The ecology and composition of these páramo forests are clearly distinct from the continuous forest cover along the elevational gradient.

Within the Bolivian and Peruvian datasets, we conducted extensive taxonomic work to standardize species and morphospecies names across plots. Morphospecies, however, could not be standardized between the Bolivian and Peruvian data. To test the effect of morphospecies on results, analyses were repeated with and without morphospecies. Both analyses produced nearly identical results (Fig. S2); for simplicity, we present only analyses including morphospecies. Representative specimens at each site were collected and deposited in herbaria, mainly at the Herbario Nacional de La Paz (LPB), the Missouri Botanical Garden (MO) and Universidad Nacional de San Antonio Abad del Cusco (CUZ) in Peru. The small plots contained 2731 species, whereas the large plots contained 1904 species (Table 1).

Phylogenetic reconstruction and defining clades of pre-Andean origin

To test our hypotheses, we needed a phylogenetic framework that grouped species into clades that diverged from one another before the origin of the elevational gradient (i.e. clades that pre-date the uplift of the Central Andes). To do this, we used a combined megaphylogeny representing 74 531 vascular plant species based on Smith & Brown's (2018) global megaphylogeny of seed plants, results from the Open Tree of Life project (Hinchliff *et al.*, 2015) as well as Zanne *et al.*'s (2014) phylogeny that included pteridophytes. To incorporate species and morphospecies in our dataset that were not in the original phylogeny, we used the R package V.PHYLOMAKER (Jin & Qian, 2019). Using genus- and family-level taxonomic information, missing taxa not included in the megaphylogeny were joined to the halfway point of the family/genus branch (V.PHYLOMAKER scenario = 'S3"). For genera not represented in the megaphylogeny, we joined species to sister genera in the phylogeny based on support in the literature (when possible) using the 'bind.relative' option of V.PHYLOMAKER. Finally, we pruned from the phylogeny all species that were absent in our forest plots. The resulting phylogeny included 3143 species.

The formation of the Andean cordillera has been a complex and heterogeneous process. In the Central Andes, the history of mountain formation is closely tied to the development of the Altiplano plateau, currently located at nearly 3800 m elevation. While the traditional view of mountain uplift invokes a slow and gradual process, recent evidence suggests that the uplift of the Altiplano was dominated by spurts of rapid rise with intervening periods of stasis (Garzione *et al.*, 2008, 2017). Although the northern Andes is considered much younger, the best available evidence suggests that most of the uplift in the Central Andes occurred within the last 30 Myr (Hoorn *et al.*, 2010; Poulsen *et al.*, 2010; Boschman, 2021). Thus, our analyses used this age as a main reference for the origin of the elevational gradient and to delimit pre-Andean clades.

Pre-Andean clades in the time-calibrated regional phylogeny were defined as those whose stems intersect the 30 Myr reference. In this way, each pre-Andean clade in our study diverged from others before the uplift of the Central Andes, whereas all species within pre-Andean clades resulted from diversification that occurred after mountain uplift had started. We used the function treeSlice in the R package PHYTOOLS (Revell, 2012) to fragment the regional phylogeny into these clades. Species present in small plots formed 473 pre-Andean clades with an average of 5.77 species per clade, whereas species in the large plots formed 355 clades, averaging 5.36 species per clade (Table 1; Fig. S3). Finally, we sought to understand how our results varied by defining pre-Andean clades at different ages. Thus, in addition to creating a dataset with 30 Myr old pre-Andean clades, we made a second dataset classifying pre-Andean clades as those that intersect the 60 Myr reference. This represents a much more conservative estimate of the timing of Andean uplift (Hoorn *et al.*,

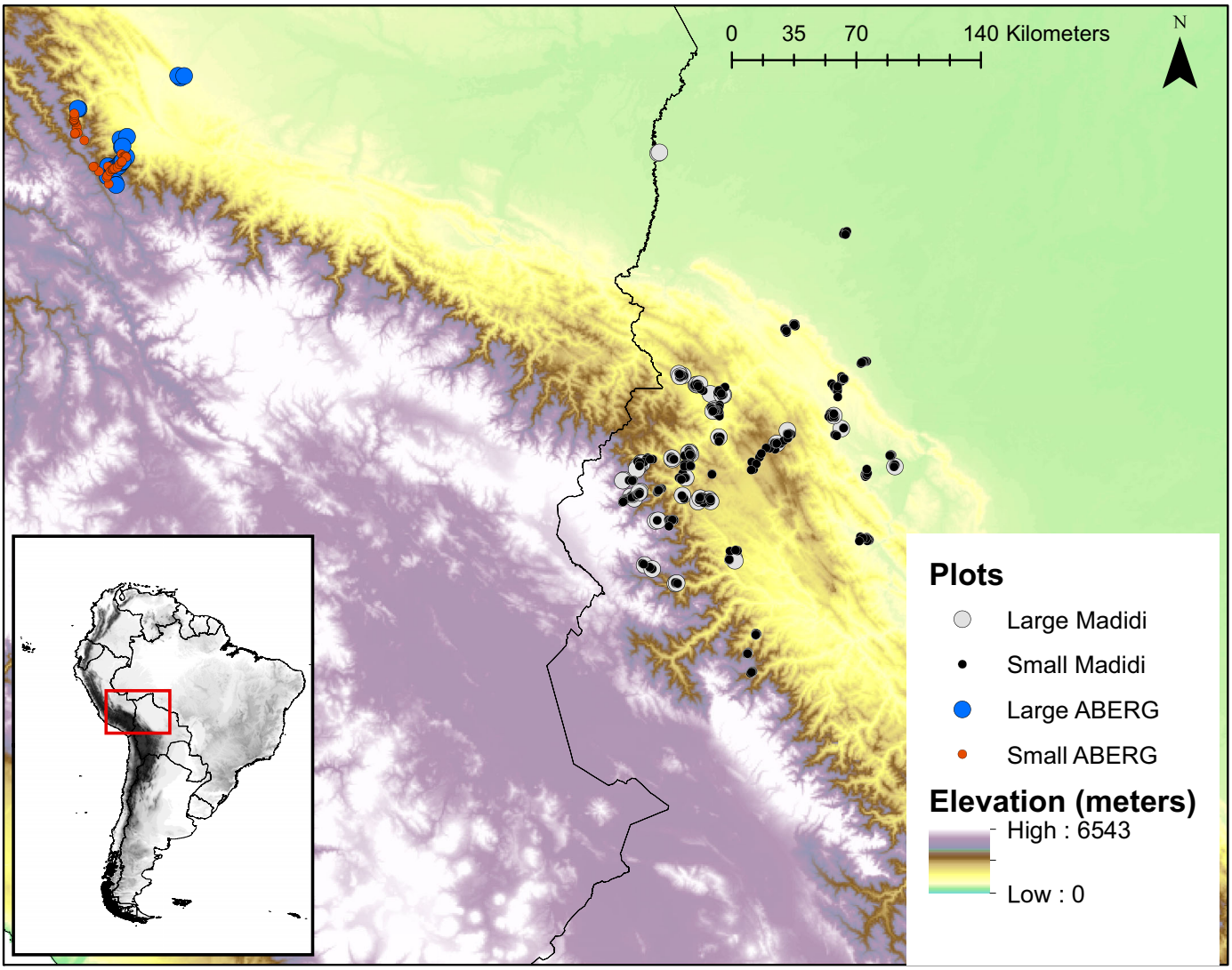

Fig. 2 Regional network of forest plots used in this study.

Table 1 Summary of datasets used for analyses and *P*-values assessing significance of observed gradients in among-clade and within-clade turnover across elevational (elev) and geographic (geo) distances. Datasets varied by plot size, inclusion of morphospecies and age of pre-Andean clades.

Inclusion of morphospecies	No. of species	Clade age (Myr)	No. of clades	No. of clades with one sp.	Mean species per clade	*P* (among-clade vs elev)	*P* (within-clade vs elev)	*P* (among-clade vs geo)	*P* (within-clade vs geo)
Large plots (73)									
Included	1904	30	355	203	5.36	0.001	0.001	0.553	0.553
Included	1904	60	141	34	13.50	0.001	0.001	0.424	0.424
Excluded	1354	30	310	168	4.37	0.001	0.001	0.223	0.223
Excluded	1354	60	138	34	9.81	0.001	0.001	0.87	0.87
Small plots (454)									
Included	2731	30	473	275	5.77	0.001	0.001	0.025	0.025
Included	2731	60	162	38	16.86	0.001	0.001	0.005	0.005
Excluded	1899	30	415	233	4.58	0.001	0.001	0.002	0.002
Excluded	1899	60	157	39	12.10	0.001	0.001	0.001	0.001

2010). The results from these alternative analyses were nearly identical, and thus are presented only in the Supporting Information (Fig. S4).

Decomposing total turnover into among- and within-clade turnover

To test hypotheses about the relative importance of ISPC and RAD, we developed a method to decompose species turnover into two additive components representing the contribution of turnover among groups and within groups (Legendre & De Caceres, 2013). For our analyses, groups are defined by clades of pre-Andean origin, but this decomposition method is broadly applicable to species groupings based on any criteria. Analyses were based on the Sørensen pairwise dissimilarity index (S; Sørensen 1948), which uses presence/absence data:

$$S = \frac{b + c}{2a + b + c}$$

Here, a represents the number of shared species between two communities, b is the number of species present only in the first community and c is the number of species present only in the second community. Since species are aggregated into clades, species in b can be further divided into two components: b_{WG} is the fraction of b that corresponds to species in groups present in both communities, while b_{AG} is the fraction of b corresponding to species in groups present only in the first community. The same process can be done for c, producing the corresponding components c_{WG} and c_{AG}. In this way, the additive within-group (S_{WG}) and among-group (S_{AG}) components of Sørensen dissimilarity are defined as:

$$S_{WG} = \frac{b_{WG} + c_{WG}}{2 \times a + b + c}$$

$$S_{AG} = \frac{b_{AG} + c_{AG}}{2 \times a + b + c}$$

Further details of the decomposition method can be found in the Supporting Information, where we also show that this approach could be applied to other turnover metrics, such as Bray–Curtis distances (Methods S1). The R code that performs this decomposition is available at https://github.com/Linan552/Madidi-project (function '*decompose.my.beta*'). When within- and among-clade dissimilarities are transformed into components of total turnover (S_{WG}/S and S_{AG}/S, respectively), these values correspond to the contribution of diversification after (S_{WG}/S) and before (S_{AG}/S) the uplift of the Central Andes to community species turnover (Figs 1, S5). Thus, a high among-clade component indicates that turnover is mainly dominated by species that diverged from one another before the uplift of the Central Andes (Fig. 1a, left). By contrast, a high within-clade component indicates that turnover is dominated by species that diverged from one another after the uplift of the Central Andes (Fig. 1a, right).

As described in the Introduction, the ISPC and the RAD hypotheses make predictions about how these components of turnover will be related to environmental (i.e. elevational) distances. Thus, we plotted the components of turnover for each pair of plots against their elevational distance. The ISPC hypothesis predicts that as communities are farther apart along the elevational gradient, variation in community composition should become increasingly dominated by among-clade turnover (Fig. 1b). Alternatively, the RAD hypothesis predicts that variation in community composition should be dominated by turnover within clades regardless of elevational distance (Fig. 1c).

Assessing significance of observed data using null models and ruling out effects of geographic distance

To test whether observed patterns are different from those expected by chance, we compared the components of turnover in the observed data with components produced by a null model that eliminated any phylogenetic structure in the distribution of species, but retained other important elements of the data that might shape turnover patters. We ran a 'tip-randomization null model' in which species were randomly reassigned to tips in the phylogeny, such that species were randomly reshuffled among pre-Andean clades. This randomization algorithm maintained the number of species per clade, the species richness gradient across elevations, the average range size in each community and, importantly, the turnover observed between pairs of plots. The only aspect of the data that was randomized was the membership of species in clades of pre-Andean origin. We randomized the data and recalculated components of turnover for each pair of plots 999 times. From these null expectations, we calculated standardized effect sizes as the observed value minus the mean of the null distribution divided by the standard deviation of the null distribution. These values represent the magnitude of the difference between the observed components of turnover and the components as expected by the null model, where there is no phylogenetic structure in species distributions. As for the observed components of turnover, we related standardized effect sizes against the difference in elevation for each pair of plots.

Additionally, we compared the rate of change in turnover components with the difference in elevation between observed data and null model expectations. To do this, we used slopes from a linear regression between components of turnover and elevational distance. Because these relationships are nonlinear, we used a logit transformation on species turnover prior to regression analyses (Cleveland, 1981). These transformations produced a reasonable linearization of the relationships in large- and small-plot datasets, allowing us to capture the rate of change in a single parameter (see Fig. S6). The observed slopes were then compared with the distribution of 999 slopes generated by the null model. If observed slopes were significantly greater or smaller ($P < 0.05$) than null slopes, we concluded that phylogenetic structure exists in the species turnover along the elevational gradient.

To tease apart the effects of geographic and elevational distance on components of turnover, our analyses used only a subset of all possible pairwise plot comparisons for each dataset. These

subsets minimized variation in geographic distances, but maximized the elevational range represented in the data (Fig. S7). For the large-plot dataset, we selected pairs of plots only between 50 and 90 km apart (8% of the total range in geographic distances), and for the small-plot dataset, we selected pairs of plots between 110 and 160 km apart (10% of the geographic range). In both subsets, however, the full extent of elevational distances is represented, ranging from 175 to 3765 m. Following plot subsetting, we saw no evidence of spatial autocorrelation in the residuals of our linear models between components of turnover and elevational distance.

Finally, we examined how turnover and its components change across space but within the same environmental conditions. To do this, we used pairs of plots spanning the entire geographic extent of the study (max. distance between plots: 495 km), but were at similar elevations (only pairs of plots with 0–200 m of elevational distance, Fig. S7). As for our analyses along the elevational gradient, we related components of turnover with geographic distances, and compared observed patterns against null model expectations. (results presented in the Supporting Information). Analyses were performed using the R packages VEGAN and GEOSPHERE (Hijmans *et al.*, 2019; Oksanen *et al.*, 2020).

Results

Species composition changed dramatically across elevations. Species turnover (Sørensen dissimilarity) among forest plots showed a saturating relationship with elevational distance, increasing rapidly as elevational distance increased and then reaching an asymptote at complete turnover (Fig. 3).

Indeed, plots separated by more than 2000–2500 m of elevation never shared species. We found a similar relationship between species composition and geographic distance (Fig. S8). However, Sørensen dissimilarity did not increase as dramatically with increasing geographic distance and it never reached complete turnover; for example, we found that geographically distant plots (i.e. 400 km away from one another, with one in Peru the other in Bolivia; Fig. S8) still shared species when they were in similar environments.

We also found strong elevational gradients in the within- and among-clade components of species turnover (Fig. 4a,d). For forest plots occurring at the same elevation (near 0 m in elevational difference), among- and within-clade components were equal in magnitude (Fig. 4a,d). This result indicates that communities in the same environment shared species in the same pre-Andean clades, but also that multiple different clades contributed to community composition among these plots. As elevational difference increased, among-clade turnover rose rapidly, while within-clade turnover decreased (Fig. 4a,d). Although the increase in the among-clade component was monotonic in the small-plots dataset, it saturated at around 2000 m of elevational difference for the large-plots dataset. In both datasets, however, when plots were separated by more than 1000–1500 m in elevation, turnover between at least some pairs of communities was completely associated with the among-clade component. This result means that some pairs of plots at opposite ends of the elevational gradient shared neither species nor clades 30 Myr old, which originated before the uplift of the Central Andes. These results support the ISPC hypothesis, whereby turnover along the elevational gradient largely consists of species belonging to different pre-Andean clades.

The predictions of the ISPC hypotheses were also supported using standardized effect sizes – as measured using our null model (Fig. 4c,f). Indeed, standardized effect sizes for within- and among-clade components were both close to zero for plots at the same elevation. As elevational differences increased, standardized effect sizes increased for among-clade turnover and decreased for within-clade turnover (Fig. 4c,f). Moreover, when plots were separated by > 1500 m in elevation, the observed values differed by more than two standard deviations from null expectations (i.e. standardized effect sizes greater than 2; Fig. 4c,d). Comparison of the observed and null regression slopes also showed that the change in the observed components was much more pronounced than the change expected by the null model (Fig. 5).

Finally, we found that geographic distance did not have the same effect on components of turnover as elevational difference. For large plots, among- and within-clade turnover remained constant and of similar magnitude with increasing geographic distance (Figs 4 vs S9). For small plots, on the other hand, the magnitude of the within-clade turnover component increased with geographic distance. This pattern remained when using standardized effect sizes (Figs 4 vs S9).

Discussion

Community assembly across contrasting elevations is dominated by the immigration and ecological sorting of clades that pre-date mountain uplift

Our results showed clearly that changes in species composition across elevations in the Central Andes were driven primarily by a replacement of clades of pre-Andean origin. These results were robust to analyses using different age estimates of pre-Andean clades (30 vs 60 Myr), inclusion or exclusion of morphospecies, or delimitations of forest communities (trees ≥ 10 cm DBH in large plots vs trees ≥ 2.5 cm DBH in small plots). While adaptive diversification is likely to have occurred in our study system, our results suggest that this process has had a reduced influence on patterns of community assembly. By contrast, we found strong evidence for a high relative importance of the ISPC hypothesis. The new environments created by the uplift of the Central Andes over the last 30 Myr were colonized primarily by species from clades that were pre-adapted to the emerging environmental conditions. Diversification within these clades resulted in new tree species that had elevational distributions similar to those occupied by the immigrating species. In this way, the ecological sorting of clades according to their pre-adaptations is the eco-evolutionary process that dominates the regional assembly of tree communities across the elevational gradient.

Our study focuses on the structure of species assemblages in the Central Andes, and how biogeographic processes shape

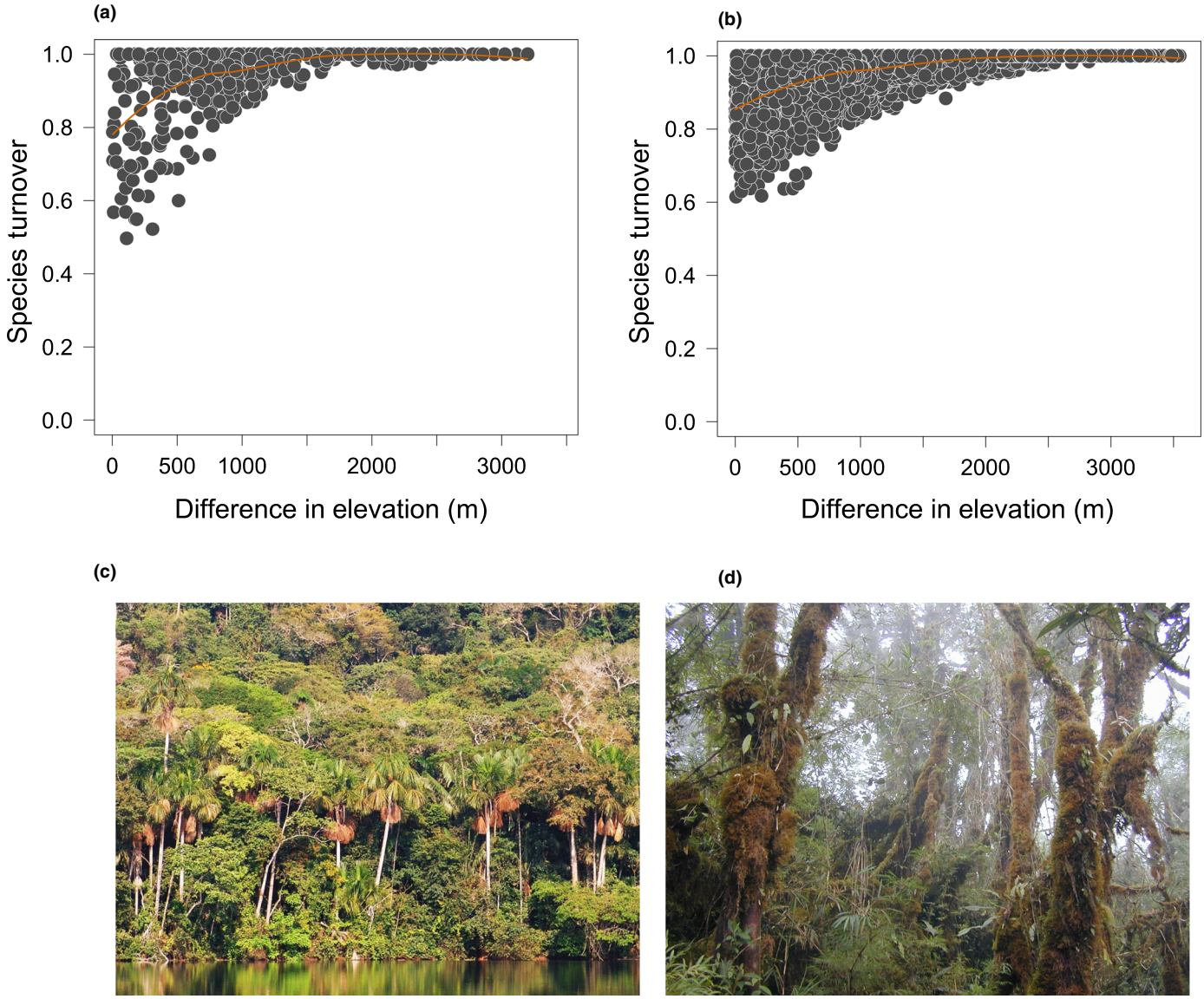

Fig. 3 Species turnover across elevations. Sørensen dissimilarity plotted against difference in elevation for each pair of plots in our two datasets. These patterns are presented separately for (a) large 1-ha plots and (b) small 0.1-ha plots. Photos highlight the species composition differences between lower elevation forests (c; Laguna Chalalan in Bolivia at 400 m elevation) and upper montane cloud forests (d; Trocha Union in Peru at 3260 m). Pictures by Christopher Davidson, Sharon Christoph and William Farfan-Ríos.

patterns of diversity. The assembly of communities, however, integrates the evolutionary history of multiple independent clades of species. Several previous studies have taken the approach of focusing on the evolution of clades in relation to Andean uplift. This research shows that groups of animals and plants across the Andes have diversified in ways that are consistent with our results, with related species occupying similar elevations (Bell & Donoghue, 2005; Hughes & Eastwood, 2006; Chaves *et al.*, 2011; Nürk *et al.*, 2013). One of the best studied biogeographic histories in the Andes is that of the plants in the genus *Lupinus*, which colonized the Andes from temperate North America (Hughes & Eastwood, 2006), and were probably pre-adapted to the cold conditions of alpine environments (Nevado *et al.*, 2016). This clade experienced an explosive diversification in the Andes, but most of the resulting species occupy only high-elevation habitats. Their diversification was probably fueled by the interaction between insularity of high-mountain habitats and climatic fluctuations during the Quaternary (Nevado *et al.*, 2018). Adaptive diversification also played an important role in the radiation of the Andean lupins (Nevado *et al.*, 2016). Indeed, species in the clade show a huge diversity of phenotypes, life forms and microhabitat use (Hughes & Eastwood, 2006). Their adaptive diversification, however, did not involve large numbers of species colonizing the new environments at different elevations created by mountain uplift. Several clades of plants distributed at the highest elevations in the Andes seem to show similar patterns of diversification (Madriñán *et al.*, 2013). A general pattern of conservatism in elevational distribution was also documented for several clades of trees by Griffiths *et al.* (2020). Clades with a biogeographic history similar to those of the Andean lupins would

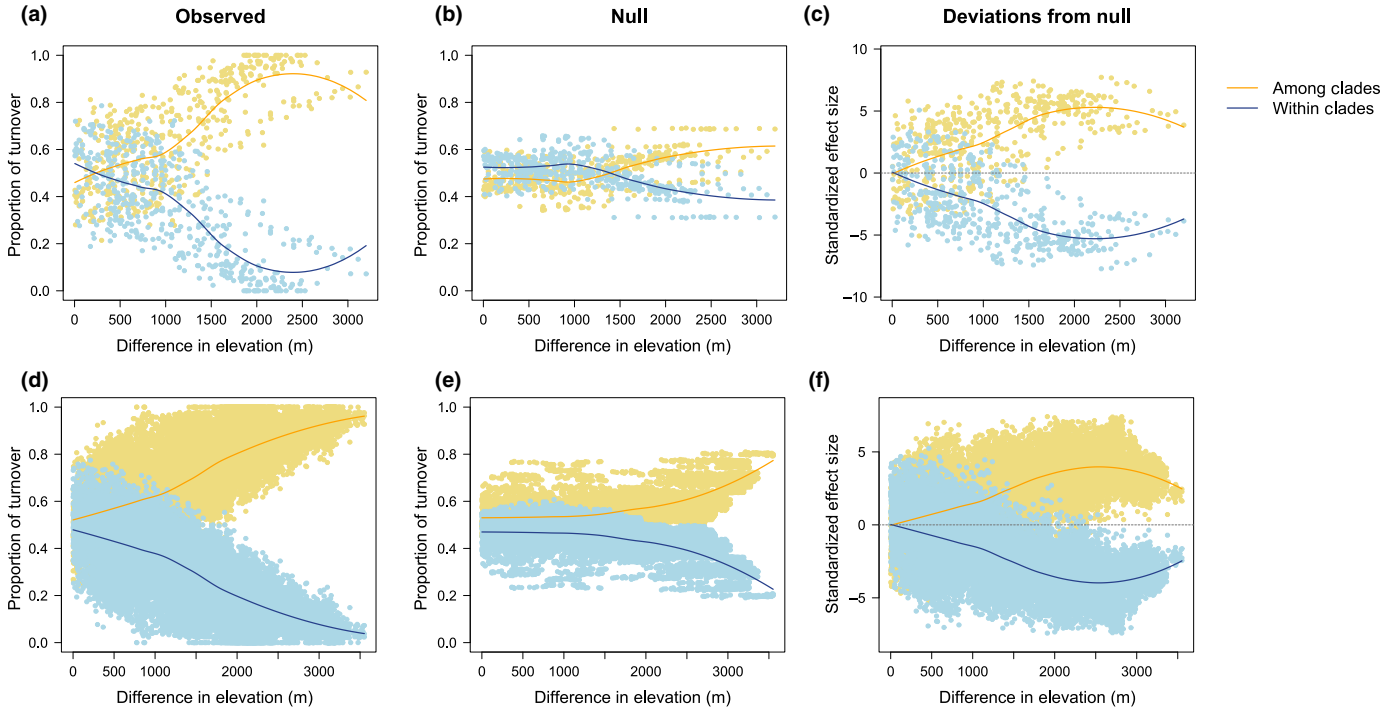

Fig. 4 Decomposition of species turnover across elevational gradients into among-clade and within-clade components – 30 Myr clades from small and large plots. Sørensen dissimilarities between each pair of plots were decomposed into within-clade (blue) and among-clade (yellow) components. We then plotted these components of turnover against difference in elevation in large plots (upper panels) and small plots (lower panels). Finally, we compared spatial patterns in variation of these components with a tip-randomization null model that removes any phylogenetic structure in the distribution of species across elevation. (a, d) Observed patterns; (b, e) patterns for the mean of the expectations in the null model; (c, f) patterns for standardized effect sizes showing the deviation of the observed values from null expectations.

contribute little to changes in species composition along the elevational gradient. Instead, this pattern of diversification, when experienced by numerous clades pre-adapted to different elevations, can lead to the observed patterns of clade turnover found in our study. Indeed, turnover among communities across the elevational gradient have an evolutionary origin that is rooted deep in the past, and that mostly pre-dates the emergence of the environmental gradient.

Although we found support for the ISPC hypothesis, an important question remains regarding how the ancestors of immigrating pre-adapted clades may have reached the Andes. If it is 'easier to move than to evolve' (Donoghue, 2008), how are lineages moving? While there is an increasing number of studies suggesting Neotropical lineages are not dispersal-limited (Hughes *et al.*, 2013; Segovia *et al.*, 2020), the ancestors of pre-adapted Andean clades may have dispersed great distances to reach the Andes. One way this may have occurred is through 'mountain-hopping' (Knox & Palmer, 1995, 1998; Sklenář *et al.*, 2014), whereby colonizers could have sequentially colonized adjacent mountains, leading to island-like diversification. Although evidence of this has been found in species occupying high-elevation páramo environments (Raven, 1963; Hughes & Eastwood, 2006; Moore & Donoghue, 2007; Bone *et al.*, 2011; Sklenář *et al.*, 2011; Luebert & Weigend, 2014), few studies have tested this hypothesis in lineages that occupy lower elevational bands in the Andes, which are presumably less insular (Kelly *et al.*, 1994).

Studies of particular clades, like those highlighted above, are insightful and have helped us advance our understanding of the patterns and mechanisms of diversification. However, this approach does not address directly the eco-evolutionary forces behind the assembly of diverse communities, which is the focus of our analyses. To the best of our knowledge, our study is the first effort to explicitly test the role that diversification before and after the origin of the environmental gradient (i.e. the uplift of the Central Andes) had on community structure across elevations. While previous studies have not tested the role of mountain uplift directly, our results are supported by previous research of Andean communities, which have suggested an important role for niche conservatism in community assembly across elevations (Graham *et al.*, 2009; Hardy *et al.*, 2012; Jin *et al.*, 2015; Ramírez *et al.*, 2019; Worthy *et al.*, 2019; Bañares-de-Dios *et al.*, 2020). A recent important study in this respect is that by Segovia *et al.* (2020), who demonstrated a clear link in the phylogenetic composition of Andean tree communities to temperate regions of North and South America. In particular, they highlight the role that freezing conditions at high elevations play in creating environments that are invaded by temperate clades. Similarly, phylogenetic niche conservatism has been implied in the eco-evolutionary assembly of seasonally dry forest communities, which occur in rain-shadowed valleys along the Andes (Pennington & Lavin, 2009). Our study, however, goes further than simply demonstrating phylogenetic niche conservatism or phylogenetic clustering of communities. By delineating clades

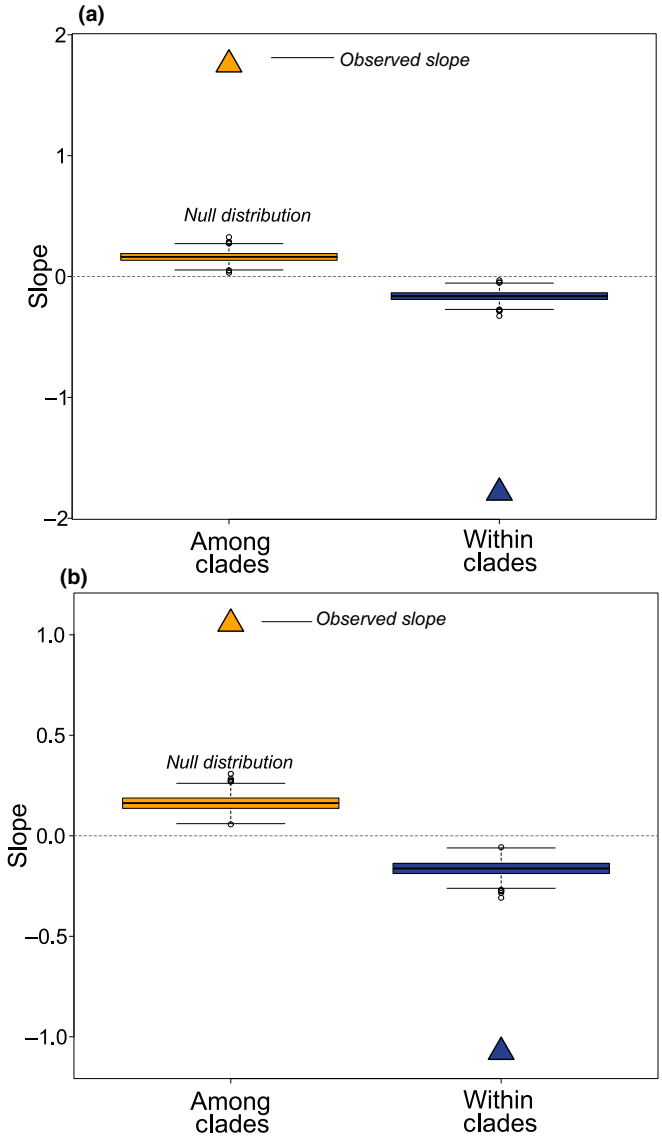

Fig. 5 Comparison of linear slopes. Observed slopes of logit-transformed proportional turnover across elevational distance (triangles) compared to the distribution of 999 slopes produced by the null model (boxplots) in (a) large plots and (b) small plots. The box depicts the interquartile range with the median denoted by the horizontal line. The whiskers represent 1.5 times the interquartile range with outliers denoted as circles.

based on the time of mountain uplift, we were able to directly test hypotheses of processes governing community assembly in the Central Andes and found evidence that the assembly of communities across elevations is driven primarily by the immigration and sorting of clades that evolved appropriate adaptations even before the emergence of the environmental gradient (Hardy *et al.*, 2012; Chi *et al.*, 2014; Kubota *et al.*, 2018).

Mountain uplift might create opportunities for adaptive diversification, but this process has a limited effect on community assembly along elevational gradients

Adaptive diversification has played a critical role in the formation of biodiversity, giving rise to an often stunning array of morphological and species diversity (Gillespie *et al.*, 2020). Newly formed and/or isolated habitats or regions (e.g. islands, mountains, lakes) probably drive adaptive radiation by providing ecological opportunity, and allowing competition among close relatives to fuel ecological divergence (Givnish, 1997; Stroud & Losos, 2016). The uplift of the Central Andes created environments that were previously unavailable in the region, probably opening up new unoccupied niche space for species. Moreover, as we discussed earlier, numerous rapid radiations of species have been documented in the Andes (Madriñán *et al.*, 2013); some of them, like that of *Lupinus* or *Espeletia* (Hughes & Eastwood, 2006; Pouchon *et al.*, 2018), are as dramatic as those in clades that epitomize adaptive diversification (e.g. stickleback fish or African Great Lake cichlids; Gillespie *et al.*, 2020). If ecological opportunity existed and rapid diversification in the mountains is well documented, then why did we not find a strong signal for RAD following montane uplift in the assembly of communities?

Several factors could explain our lack of evidence for adaptive diversification across the elevational gradient. First, recent and rapid radiations in the Andes may not involve adaptive diversification. Instead, high rates of species accumulation could be fueled solely by allopatric speciation resulting from repeated cycles of habitat isolation and reconnection driven by climatic oscillations (Nevado *et al.*, 2018; Flantua *et al.*, 2019). Topographically dissected montane regions provide many natural barriers (e.g. valleys, high-elevation ridges) to plant dispersal and gene flow, which alone could foster extensive geographic speciation (Givnish *et al.*, 2014, 2015). This process would produce a large number of species that replace one another across geography but within the same environment (Hughes & Eastwood, 2006; Chaves *et al.*, 2011). Second, adaptive diversification following montane uplift may have occurred along environmental dimensions other than those of the elevational gradient. Indeed, some of the classic examples of Andean diversification involve fast evolution of phenotypes, even if the elevational distribution of the clade is highly conserved (Hughes & Eastwood, 2006; Nürk *et al.*, 2018; Pouchon *et al.*, 2018). Third, some clades may have adaptively radiated across the elevational gradient, but these clades are rare and contribute little to overall assembly patterns. Indeed, biogeographic studies have documented significant shifts in elevational distribution during the evolutionary history of several groups of plants and animals (Elias *et al.*, 2009; Bacon *et al.*, 2018). Our results, however, show that only 35 of 473 pre-Andean (30 Myr) clades span large elevational ranges (> 2000 m); some examples include: *Aegiphila*, *Erythroxylum*, *Erythrina*, *Guatteria*, *Hieronyma*, *Meliosma*, *Piper*, *Prunus*, *Styrax* and *Symplocos*. Of these genera, *Stryax*, *Symplocos* and *Piper* are montane endemic genera, suggesting that they might have dispersed from outside the Andes and then diversified across elevations (Young *et al.*, 2002). Moreover, some shifts in elevational distribution might be accompanied by shifts in life form (as exemplified by *Espeletia*; Pouchon *et al.*, 2018; but see Zanne *et al.*, 2013) which do not contribute to the assembly of tree communities that are the focus of our study. While the role of adaptive diversification in community assembly deserves further study, our results suggest that Andean community assembly is mainly the result of different

pre-adapted clades that originated before Andean uplift, which colonized available niches before other clades could adaptively radiate to occupy a broad elevational gradient (Tanentzap *et al.*, 2015).

Conclusions: future directions and implications for conservation

In this study, we developed a novel conceptual framework (Fig. 1), as well as new methods of decomposing species turnover (Figs 1, S5), to investigate the biogeographic origins of community assembly along environmental gradients. We used this approach to study how the uplift of the Central Andes led to the variation in community composition along iconic elevational gradients. Our approach, however, can be applied to any system in which the timing of the emergence of an environmental gradient is known and time-calibrated phylogenies can be generated. We envision further development and use of this method beyond Central Andean forests at different geographical scales (including entire continents) and in a variety of environmental gradients such as precipitation gradients (Parolari *et al.*, 2020), across contrasting soil conditions (Capurucho *et al.*, 2020) or even under different disturbance regimes (Cavender-Bares & Reich, 2012). We also think that simulation studies to understand the properties of our methods in the context of eco-evolutionary hypotheses (including ISPC and RAD) will be particularly important. Methods such as these can be used to test hypotheses about specific processes of community assembly, going beyond documenting niche conservatism or phylogenetic aggregation. Our approach will facilitate deeper insights into how the emergence of environmental gradients shape modern natural ecosystems.

Our analyses demonstrate that species turnover across elevations in the Central Andes is driven primarily by the turnover of clades that are at least 30 Myr old. These results suggest a strong role for immigration and ecological sorting of pre-adapted clades to the novel environments across elevations created by the uplift of the Central Andes. Adaptive diversification following the emergence of the elevational gradient is probably restricted to a few clades or to narrow elevational bands, having little impact on the assembly of communities along such a large environmental gradient. Our results add to a growing body of evidence suggesting that present-day communities are strongly influenced by the ability of lineages to track environmental conditions through space and geological time (Donoghue, 2008; Emerson & Gillespie, 2008; Carvajal-Endara *et al.*, 2017; Griffiths *et al.*, 2020; Segovia *et al.*, 2020), which has important implications for the long-term persistence of communities facing the effects of human-mediated global change. Increases in atmospheric temperatures are predicted to cause elevational shifts in environmental conditions, such that climates that currently occur at specific elevations will occur at higher elevations in the future (Harsch *et al.*, 2009; Ruiz-Labourdette *et al.*, 2012; Freeman *et al.*, 2018; O'Sullivan *et al.*, 2020). Our work on historical patterns of community assembly suggests that ecosystems are more likely to track shifting habitats rather than adapt to novel conditions (Sheldon *et al.*, 2011; Ruiz-Labourdette *et al.*, 2012; Freeman *et al.*, 2018; Feeley *et al.*, 2020). Communities and species at the highest elevations might be especially threatened by climate change since their environments will disappear at the top of mountains and new pre-adapted competitors will move in from lower elevations (Colwell *et al.*, 2008). Thus, communities occupying the highest elevation sites in the Andes should be prioritized for monitoring and conservation efforts. Because their habitat may not persist over the long term, *ex situ* conservation (either through conservation seed banking or living collections) of the species endemic to the highest elevations should be a specific priority.

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Author contributions

JST, JAM, AEZ, SGC and CEE developed and designed the study. BNA, JST, LC, AFF, MIL, GA and MJM collected the Madidi Project dataset; MS, WFR, KGC, NSR and YM collected the ABERG dataset. SAS produced the phylogenetic data. AGL and JST performed data analyses. AGL and JST wrote the manuscript, and all authors contributed significantly to revisions.

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Data availability

The Madidi Project's dataset used in our analyses corresponds to version 4.1, which is deposited in Zenodo (https://doi.org/10.5281/zenodo.4276558). Additionally, raw data of the Madidi Project are stored and managed in Tropicos (https://tropicos.org/home), the botanical database of the Missouri Botanical Garden. These data can be viewed and accessed via the Madidi Project's module at http://legacy.tropicos.org/Project/MDI. The Andes Biodiversity and Ecosystem Research Group (ABERG) is a team of 38 researchers from 12 universities dedicated to understanding biodiversity distribution and ecosystem function in the Peruvian Andes. ABERG is committed to data exchange within the scientific community and promoting collaboration among other tropical ecosystem scientists. For more information and to request data contact Miles Silman or Yadvinder Malhi (http://www.andesconservation.org/). The R code created for analyses is available at https://github.com/Linan552/Madidi-project.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Frequency distribution of plots used in our study along an elevational gradient.

Fig. S2 Decomposed turnover across elevation excluding morphospecies.

Fig. S3 Number of species per clade across datasets.

Fig. S4 Decomposition of species turnover across elevational distance for 60 Myr clades.

Fig. S5 Decomposed turnover across elevation excluding morphospecies.

Fig. S6 Logit-transformed decomposition of turnover.

Fig. S7 Relationship between difference in elevation and geographic distance in our datasets.

Fig. S8 Species turnover across geographic distance.

Fig. S9 Decomposition of species turnover across geographic distance for 30 myr clades.

Methods S1 Additive decomposition of species turnover metrics.

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