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

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Summary

- Biogeographic events occurring in the deep past can contribute to the structure of modern ecological communities. However, little is known about how the emergence of environmental gradients shape the evolution of species that underlie community assembly. In this study, we address how the creation of novel environments lead to community assembly via two non-mutually exclusive processes: 1) the immigration and ecological sorting of pre-adapted clades (ISPC), and 2) 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 communities across elevations.

Keywords: Andes; community assembly; phylogenetics; turnover; neotropics; elevational gradient; adaptive diversification; dispersal

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; Uribe-Convers & Tank, 2015; Claramunt & Cracraft, 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). Studies largely overlook the broader biogeographic context in which communities of co-occurring species are embedded (Chesson, 2000; Adler *et al.*, 2007). Only recently have ecologists begun bridging this gap by developing ecological theory and empirical tests that truly integrate community assembly across eco-evolutionary scales (Emerson & Gillespie, 2008; McGill *et al.*, 2019; Bañares-de-Dios *et al.*, 2020; Segovia *et al.*, 2020). The extent to which community 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 shape the evolution of species and phenotypes that underlie community assembly. Two non-mutually 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. 1**a**; Donoghue 2008).

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.
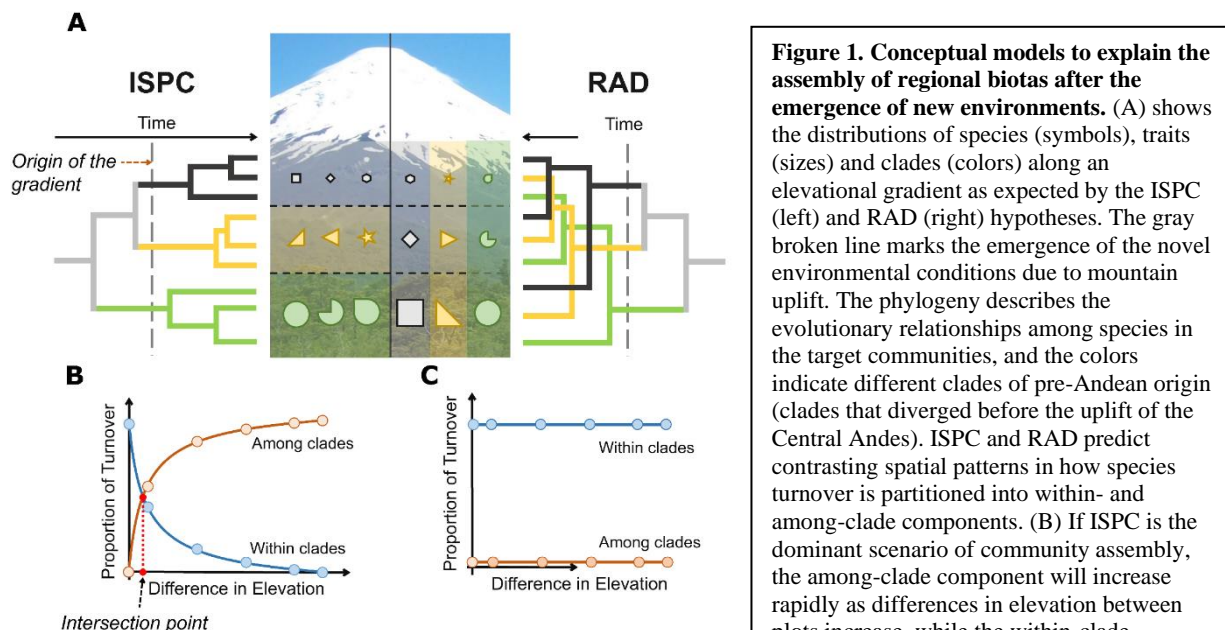*Pre-adapted clade:* A pre-Andean clade that had, before its immigration to the Central Andes, already evolved adaptations to the novel environmental conditions created by mountain uplift.
Turnover: Observed variation in species or functional-trait composition among forest plots or biogeographic regions. For example, in two species assemblages [A, B] & [A, C], turnover is generated by the replacement of species B in the first assemblage 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 assemblages [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 assemblages [A, B] & [A, C], among-clade turnover would be high if species B and C belong to different pre-Andean clades.

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Figure 1. Conceptual models to explain the assembly of regional biotas after the emergence of new environments. (A) shows the distributions of species (symbols), traits (sizes) and clades (colors) along an elevational gradient as expected by the ISPC (left) and 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 Central Andes). 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 dominate the turnover of species as geographic distances increase.

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

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

109   this scenario, niche conservatism is minimal or non-existent, and community assembly results
110   from the diversification of one or more clades that were originally adapted to a subset of
111   environmental conditions, but that diversify to occupy emerging novel environmental space. This
112   scenario for community assembly following the emergence of environmental gradients is
113   consistent with the classic ideas of biome shifts and adaptive radiation driven by ecological
114   opportunity (Schluter, 2000; Losos, 2010; Donoghue & Edwards, 2014).

115   Here we present and test a novel community-phylogenetic framework and method to
116   disentangle the relative importance of ISPC and RAD in determining the assembly of
117   communities along large-scale environmental gradients. These effects on community assembly
118   can be inferred from unique patterns in the phylogenetic structure of compositional turnover. In
119   particular, signatures of these two processes can be traced when species turnover is decomposed
120   into components that correspond to *within-* and *among-clade turnover*, where clades correspond
121   to independent lineages that originated before the emergence of the gradient. These within- and
122   among-clade turnover components, in turn, reflect the effects of diversification after and before
123   the emergence of the gradient on community composition across environments. Here, we
124   illustrate these patterns using a hypothetical elevational gradient of a mountain depicted in Fig.
125   1A. The ISPC hypothesis predicts that for communities *at the same elevation*, variation in
126   community composition should be dominated by *within-clade turnover*, reflecting strong niche
127   conservatism of a few clades that are pre-adapted to the environments at that specific elevation
128   (Fig. 1**b**). As communities are *farther apart along the elevational (i.e. environmental) gradient*,
129   variation in community composition should become increasingly dominated by *among-clade*
130   *turnover*, reflecting the shift in dominance from species in one pre-adapted clade to another.
131   Alternatively, the RAD hypothesis predicts that for communities at *similar or contrasting*
132   *elevations*, variation in community composition should be dominated by turnover *within clades,*
133   reflecting how multiple clades evolved niche differences in response to new environmental
134   conditions that allow them to have broad elevational (i.e., environmental) distributions (Fig. 1**c**).
135   Although we developed and tested this conceptual framework in the context of mountain uplift,
136   our approach is applicable to study community assembly after the emergence of any type of
137   environmental gradient at any spatial or temporal scale.

138   In the Neotropics, the geologically recent uplift of the Andean mountains created a striking
139   elevational and environmental gradient that had profound consequences for global climate and
140   biodiversity (Rahbek & Graves, 2001; Antonelli *et al.*, 2009; Ehlers & Poulsen, 2009; Jiménez *et*
141   *al.*, 2009; Graham, 2009; Hoorn *et al.*, 2010). Indeed, the tropical Andes are considered the most
142   species-rich biodiversity hotspot, containing 15% of all plant species (>45,000 species) in only
143   1% of the world's land area (Myers *et al.*, 2000; Rahbek & Graves, 2001; Jiménez *et al.*, 2009).
144   However, our current understanding of the eco-evolutionary forces that shape community
145   assembly across elevations in the hyper-diverse Andean biotas is limited. First, many studies

146   focus on the evolution and distribution of relatively small clades compared to entire
147   communities; these studies have provided evidence for an important role of adaptive
148   diversification (Antonelli *et al.*, 2009; Pérez-Escobar *et al.*, 2017) in some cases and immigration
149   and colonization of pre-adapted clades in others (Hughes & Eastwood, 2006; Jin *et al.*, 2015;
150   Lagomarsino *et al.*, 2016). Such studies demonstrate that both processes have occurred, but
151   provide limited insights into how evolutionary history of individual clades contribute to the
152   assembly of entire ecological communities and regional biotas. Second, studies that focus on the
153   phylogenetic structure of Andean communities are relatively few and often fail to differentiate
154   the effects of diversification before and after the emergence of the gradient (Graham *et al.*, 2009;
155   Parra *et al.*, 2011; Bacon *et al.*, 2018; Montaño-Centellas *et al.*, 2019; Ramírez *et al.*, 2019). To
156   date, no study has sought to disentangle the relative importance of immigration and sorting of
157   pre-adapted clades versus post-Andean uplift adaptive radiation in shaping the enormous
158   variation in plant community composition across elevational gradients.

159   In this study, we combined tree-species distribution data and phylogenetic information from
160   two large networks of Andean-forest plots to test how RAD and ISPC contribute to the assembly
161   of Andean tree communities. We test these hypotheses in the context of the uplift of the Central
162   Andes, which is associated with the formation of the Altiplano plateau during the last 30 my.
163   (Fig. 1). Moreover, we developed a novel method to decompose measures of species turnover
164   among plots distributed across the elevational gradient into among- and within- pre-Andean
165   clade components (Fig. 1 and Box 1; Legendre & Cáceres 2013). These components measure the
166   relative contributions of ISPC and RAD, respectively. This work provides both a novel
167   framework for examining phylogenetic community turnover and expands our current
168   understanding of how historical processes contribute to community assembly.

169

170   **Materials and Methods**

171   *Community composition data across elevations*

172   We utilized data from two large-scale forest plot networks in the Central Andes of Bolivia
173   (the Madidi Project; 30,165 km^2) and Peru (the Andes Biodiversity and Ecosystem Research
174   Group [ABERG]; 1,765 km^2). Both datasets contain information on tree community composition
175   spanning the entire elevational range of forests in this region of the Andes from lowland
176   Amazonia to the tree line. Our datasets include information on species composition across 73 1-
177   ha plots (large plots hereafter; 50 in Bolivia and 23 in Peru), as well as 494 0.1-ha plots (small

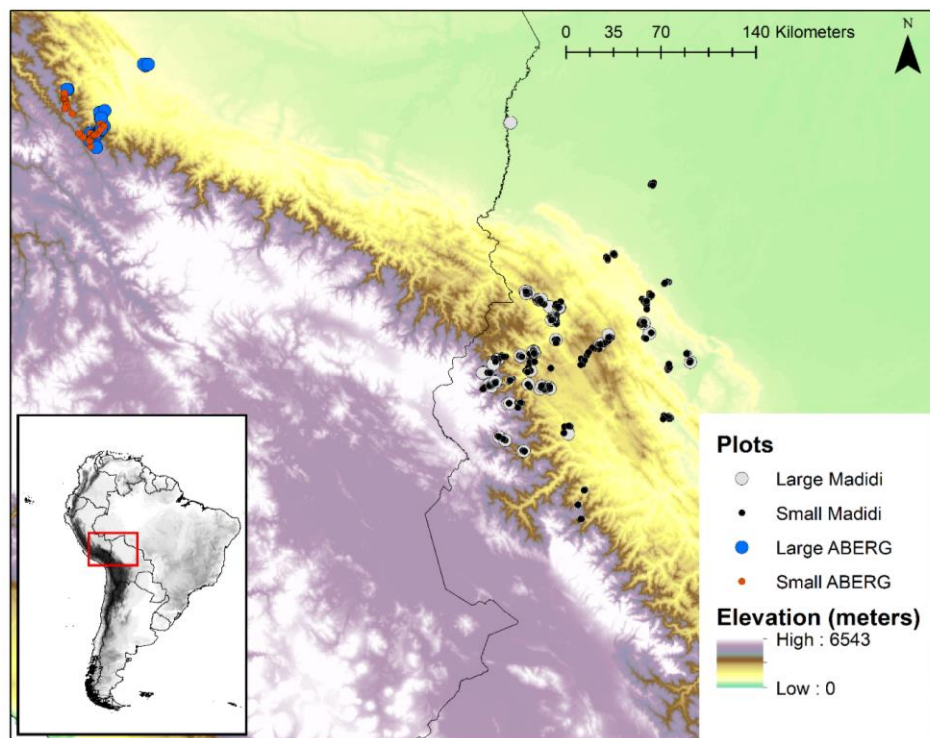178   plots hereafter; 458 in Bolivia and 36 in Peru; Fig. 2).

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

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 morpho-species. 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

198   do not reach 10 cm

199   DBH, including many shrubs. Thus, we separated out data by plot size and conducted analyses
200   independently. Additionally, we excluded high elevation plots (> 3,800 m) and plots with ≤ 3
201   species. Most of these plots represent *Polylepis*-dominated forests fragments within a matrix of
202   Paramo grasslands/shrublands. The ecology and composition of these Paramo forests is clearly
203   distinct from the continuous forest cover along the elevational gradient.

204   Within the Bolivian and Peruvian datasets, we conducted extensive taxonomic work to
205   standardize species and morpho-species names across plots. Morpho-species, however, could not
206   be standardized between the Bolivian and Peruvian data. To test the effect of morphospecies on
207   results, analyses were repeated with and without morphospecies. Both analyses produced nearly
208   identical results (Fig. S1); for simplicity, we present only analyses including morphospecies.
209   Representative specimens at each site were collected and deposited in herbaria, mainly at the
210   Herbario Nacional de La Paz (LPB), the Missouri Botanical Garden (MO) and Universidad
211   Nacional de San Antonio Abad del Cusco (CUZ) in Peru. The final dataset contains 494 small
212   plots and 73 large plots, distributed from 175 m to 4,365 m in elevation. The small plots
213   contained 2,731 species, whereas the large plots contained 1,904 species (Table 1).

214 **Table 1.** Summary of datasets used for analyses and p-values assessing significance of empirical
215 gradients in among-clade and within-clade turnover across elevational (elev) and geographic
216 (geo) distances.

Morpho-species status	No. species	Clade age	No. clades	No. 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	1889	30	352	202	5.37	0.001	0.001	0.553	0.553
Included	1889	60	142	34	13.30	0.001	0.001	0.424	0.424
Excluded	1349	30	309	168	4.37	0.001	0.001	0.223	0.223
Excluded	1349	60	139	34	9.71	0.001	0.001	0.87	0.87
Small plots (404)									
Included	2326	30	425	239	5.47	0.001	0.001	0.025	0.025
Included	2326	60	159	34	14.63	0.001	0.001	0.005	0.005
Excluded	1741	30	386	213	4.51	0.001	0.001	0.002	0.002
Excluded	1741	60	154	36	11.31	0.001	0.001	0.001	0.001

217

218 *Phylogenetic reconstruction and defining clades of pre-Andean origin*

219 To test our hypotheses, we needed a phylogenetic framework that grouped species into clades
220 that diverged from one-another before the origin of the elevational gradient (i.e. clades that pre-
221 date the uplift of the Central Andes). To do this, we based our analyses on Smith and Brown's (
222 2018) global mega-phylogeny of seed plants, which combined NCBI sequence data, results from
223 the Open Tree of Life project (Hinchliff *et al.*, 2015), and advances in bioinformatic methods
224 (PyPHLAWD; Smith & Walker 2019) to produce the most comprehensive time-calibrated
225 species-level phylogeny to date. To include species and morphospecies in our dataset that were
226 not in the original phylogeny, we used the R package V.PhyloMaker (Jin & Qian, 2019). Using
227 genus and family level taxonomic information, missing taxa not included in the mega-phylogeny
228 were joined to the halfway point of the family/genus branch (V.PhyloMaker scenario= "S3").
229 For genera not represented in the mega-phylogeny, we joined species to sister genera in the
230 phylogeny based on support in the literature (when possible) using the 'bind.relative' option of
231 V.PhyloMaker. Finally, we pruned from the phylogeny, all species that were absent in our forest
232 plots. The resulting phylogeny included 3,143 species.

233 The formation of the Andean cordillera has been a complex and heterogeneous process. In
234 the Central Andes, the history of mountain formation is closely tied to the development of the
235 Altiplano plateau, currently located at nearly 3,800 m in elevation. While the traditional view of
236 mountain uplift invokes a slow and gradual process, recent evidence suggests that the uplift of
237 the Altiplano was dominated by spurs of rapid rise with intervening periods of stasis (Garzione *et*
238 *al.*, 2008, 2017). Although the northern Andes is considered much younger, the best available

239   evidence suggests that most of the uplift in the Central Andes occurred within the last 30 million
240   years. Thus, our analyses used this age as a main reference for the origin of the elevational
241   gradient and to delimit pre-Andean clades.

242   Pre-Andean clades in the time-calibrated regional phylogeny were defined as those whose
243   stems intersect the 30 my reference. In this way, each pre-Andean clade in our study diverged
244   from others before the uplift of the central Andes, whereas all species within pre-Andean clades
245   resulted from diversification that occurred after mountain uplift had started. We used the
246   function treeSlice in the R package "Phytools" (Revell, 2012) to fragment the regional
247   phylogeny into these clades. Species present in small plots formed 473 pre-Andean clades with
248   an average of 5.77 species per clade, whereas species in the large plots formed 355 clades,
249   averaging 5.36 species per clade (Table 1 and Fig. S2). Finally, we sought see understand how
250   our results varied by defining different ages for pre-Andean clades. Thus, in addition to creating
251   a dataset with pre-Andean clades defined as 30 million years old, we made a second dataset
252   which defined clades as 60 million years old. This represents a much more conservative estimate
253   of the timing of Andean uplift (Hoorn *et al.*, 2010). The results from these alternative analyses
254   were nearly identical, and thus are presented only in the Supplementary Material (Fig. S3).

255

256   ***Decomposing total turnover into among- and within-clade turnover***

257   To test hypotheses about the relative importance of ISPC and RAD, we developed a method
258   to decompose variation in species turnover between two communities into additive components
259   representing the contribution of turnover among-groups and within-groups (Legendre & Cáceres,
260   2013). For our analyses, groups are defined by clades of pre-Andean origin, but this
261   decomposition method is broadly applicable to species groupings based on any criteria. Analyses
262   were based on the Sørensen pair-wise dissimilarity index (*S*; Sørensen 1948), which uses
263   presence/absence data:

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

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

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

274
$$S_{AG} = \frac{b_{AG} + c_{AG}}{2 \times a + b + c}$$

275   Further details of the decomposition method can be found in the Supplementary Material,
276 where we also show that this approach could be applied to other turnover metrics, such as Bray-
277 Curtis distances. The R code that performs this decomposition is available at
278 https://github.com/Linan552/Madidi-project. When within- and among-clade dissimilarities are
279 transformed into components of total turnover (S_{WG}/S and S_{AG}/S, respectively), these values
280 correspond to the contribution of diversification after (S_{WG}/S) and before (S_{AG}/S) the uplift of the
281 central Andes to community species turnover (Fig. 1, S4). Thus, a high among-clade component
282 indicates that turnover is mainly dominated by species that diverged from one another before the
283 uplift of the Central Andes (Fig. 1**a**, left). In contrast, high within-clade component indicates that
284 turnover is dominated by species that diverged from one another after the uplift of the Central
285 Andes (Fig. 1**a**, right).

286   As described in the introduction, the immigration and sorting of pre-adapted clades
287 (ISPC) and the recent adaptive diversification (RAD) hypotheses make predictions about how
288 these components of turnover will be related to environmental (i.e. elevational) distances. Thus,
289 we plotted the components of turnover for each pair of plots against their elevational distance.
290 The ISPC hypothesis predicts that as communities are farther apart along the elevational
291 gradient, variation in community composition should become increasingly dominated by among-
292 clade turnover (Fig. 1**b**). Alternatively, the RAD hypothesis predicts that variation in community
293 composition should be dominated by turnover within clades regardless of elevational distance
294 (Fig. 1**c**).

295

296 *Assessing significance of empirical data using null models and ruling out effects of*
297 *geographic distance*

298   To test whether observed patterns are different from those expected by chance, we compared
299 the components of turnover in the empirical data with components produced by a null model that
300 eliminated any phylogenetic structure in the distribution of species, but retained other important
301 elements of the data that might shape turnover patters. We ran a "tip-randomization null model"
302 in which species were randomly re-assigned to tips in the phylogeny, such that species were
303 randomly reshuffled among pre-Andean clades. This randomization algorithm maintained the
304 number of species per clade, the diversity gradient across elevations, the average range size in
305 each community, and importantly, the empirical turnover observed between pairs of plots. The
306 only aspect of the data that was randomized was the empirical membership of species in clades
307 of pre-Andean origin. We randomized the data and re-calculated components of turnover for
308 each pair of plots 999 times. From these null expectations, we calculated standardized effect
309 sizes as the empirical value minus the mean of null distribution divided by the standard deviation

310   of the null distribution. These values represent the magnitude of the difference between the
311   empirical components of turnover and the null expectation, where there is no phylogenetic
312   structure in species distributions. As was done for the empirical components of turnover, we
313   related these standardized effect values against the difference in elevation for each pair of plots.

314   Additionally, we compared the rate of change in turnover components with difference in
315   elevation between the empirical data and null model expectations. To do this, we used slopes
316   from a linear regression between components of turnover and elevational distance. Because these
317   relationships are non-linear, we used a logit transformation on species turnover prior to
318   regression analyses (Cleveland, 1981). These transformations produced a reasonable
319   linearization of the relationships in large and small plot datasets, allowing us to capture the rate
320   of change in a single parameter (see Fig. S5). The empirical slopes were then compared with the
321   distribution of 999 slopes generated by the null model. If empirical slopes were significantly
322   greater or smaller ($p<0.05$) than null slopes, we concluded that phylogenetic structure exists in
323   the community composition changes along the elevational gradient.

324   Finally, to control for the effects of geographic distance on the analysis of turnover across
325   elevations, only a subset of pair-wise plot comparisons for each dataset were used. This subset of
326   plot pairs minimized variation in geographic distances, but maximized the elevational range
327   represented in the data (Fig. S6). For the large-plot dataset, we selected plot pairs only between
328   50 and 90 km apart (8% of the total range in geographic distances), and for the small-plot
329   dataset, we selected plot pairs between 110 and 160 km apart (10% of geographic range). In both
330   datasets, the elevational distances between plots ranged from 175 to 3765 m.

331   Additionally, we analyzed how the within- and among-clade components of turnover changes
332   as a function of geographic distance. For these analyses, we used pairs of plots spanning the
333   entire geographic range of the study (max distance between plots; 495 km), but were at similar
334   elevations (0 to 200 m of elevational distance, Fig. S6). Like our analyses along elevational
335   distances, we compared patterns of variation in the within- and among-clade turnover against
336   null model expectations. These analyses show how turnover and its components change across
337   space but within the same environmental conditions (results presented in the Supplementary
338   Material).

339

340   **Results**

341   Species composition changed dramatically across elevations. Species turnover (Sørensen
342   dissimilarity) among forest plots showed a saturating relationship with elevational distance,
343   increasing rapidly as elevational distance increases and then reaching an asymptote at complete
344   turnover (Fig. 3).
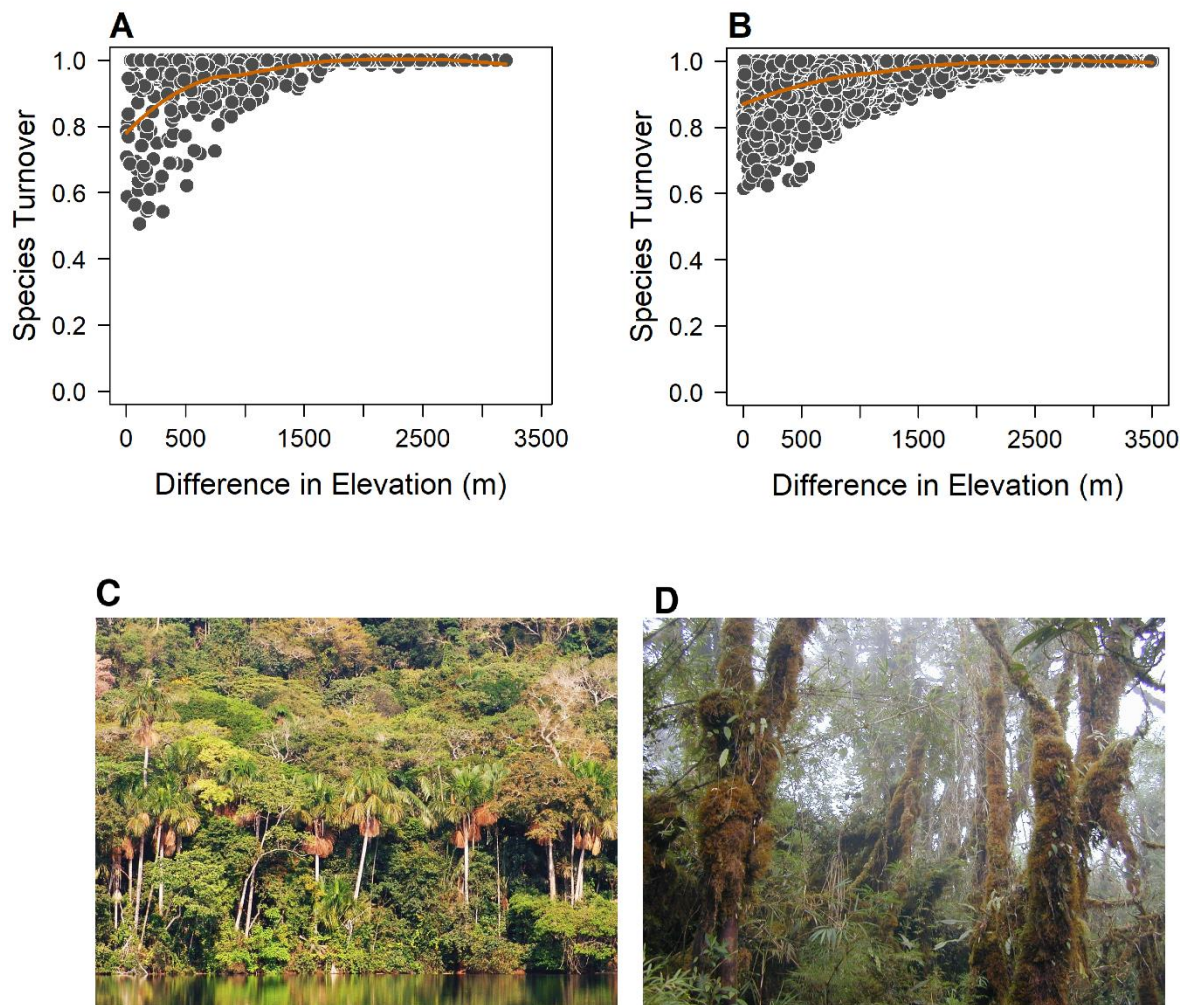
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Figure 3. Species turnover across elevations. Sørensen dissimilarity plotted against difference in elevation for each pair of plots in our two datasets. These patterns are presented separately for (A) large 1-ha plots and (B) small 0.1-ha plots. (C; Laguna Chalalan in Bolivia at 400 m elevation) and upper montane cloud forests (D; Trocha Union in Peru at 3,260 m). Pictures by Christopher Davidson, Sharon Christoph and William Farfan-Rios.

351   Indeed, plots separated by more than 2,000 to 2,500 m of elevation never shared species. We
352   found a similar relationship between species composition and geographic distance (Fig. S7).
353   However, Sørensen dissimilarity did not increase as dramatically with increasing geographic
354   distance and it never reached complete turnover; for example, we found that plots can still share
355   species when they are in similar environments even if plots are 400 km away from one another
356   (one in Peru the other in Bolivia; Fig. S7).

357   We also found strong elevational gradients in the within- and among-clade components of
358   species turnover (Fig. 4**a,d**). For forest plots occurring at the same elevation (zero meters in
359   elevational difference), among- and within-clade components were equal in magnitude (Fig.
360   4**a,d**). This result indicates that communities in the same environment shared species in the same
361   pre-Andean clades, but also that multiple different clades contributed to community composition
362   among these plots. As elevational difference increased, among-clade turnover rose rapidly, while
363   within-clade turnover decreased (Fig. 4**a,d**). Although the increase in the among-clade
364   component was monotonic in the small-plots dataset, it saturated at around 2,000 m of
365   elevational difference for the large-plots dataset. In both datasets, however, when plots were
366   separated by more than 1,000 to 1,500 m in elevation, pairs of communities were found where
367   100% of the turnover corresponded to the among-clade component. This result means that some
368   pairs of plots at opposite ends of the elevational gradient shared neither species nor clades 30 my
369   old, which originated before the uplift of the Central Andes. These results support the idea that
370   the immigration and ecological sorting of pre-Andean clades had a major effect in shaping
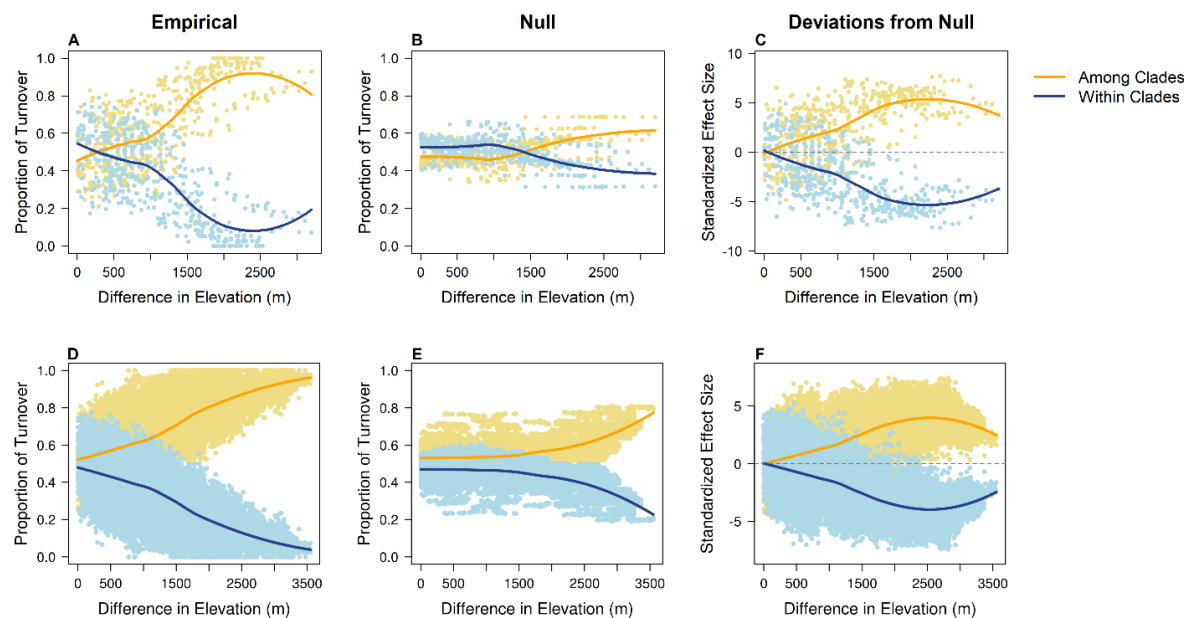371   community composition across elevations - the ISPC hypothesis.

Figure 4. Decomposition of species turnover across elevational gradients into among-clade and within-clade components – 30 MY clades from small and large plots. Sorensen dissimilarities between each pair of plots were decomposed into within-clades (blue lines) and among-clades (yellow lines) components. We then plotted these components of turnover against difference in elevation in large plots (first row) and small plots (second row). 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.) empirical 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 empirical values from null expectations.

373   The predictions of the ISPC hypotheses were also supported using standardized effect sizes –
374   as measured using our null model (Fig. 4 **c,f**). Indeed, standardized effect sizes for within- and
375   among-clade components were both close to zero for plots at the same elevation. As elevational
376   differences increased, standardized effect sizes increased for among-clade turnover and
377   decreased for within-clade turnover (Fig. 4 **c,f**). Moreover, when plots were separated by >1,500
378   m in elevation, the empirical values differed by more than two standard deviations from null
379   expectations (i.e. standardized effect sizes greater than 2; Fig. **c,d**). The comparison of the
380   empirical and null regression slopes also showed that the change in the empirical components
381   was much more pronounced than the change expected by the null model (Fig. 5).

382

Figure 5. Comparison of linear slopes. Empirical 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.

Finally, we found that geographic distance did not have the same effect on components of turnover as elevational difference. Among large plots, among- and within-clade turnover remained constant and of similar magnitude with increasing geographic distance (Fig. 4 vs. S8). For small plots, on the other hand, the magnitude of the within-clade turnover component increases with geographic distance. This pattern remained when using standardized effect sizes (Fig. 4 vs. S8).

Discussion

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

399   Our results showed clearly that changes in species composition across elevations were driven
400   primarily by a replacement of clades of pre-Andean origin. These results were robust to analyses
401   using different age estimates of pre-Andean clades (30 vs. 60 mya), inclusion or exclusion of
402   morpho-species, or delimitations of forest communities (trees ≥ 10 cm DBH in large plots vs.
403   trees ≥ 2.5 cm DBH in small plots). While adaptive diversification is likely to have occurred in

404   our study system, our results suggest that this process has had a reduced influence on patterns of
405   community assembly. In contrast, we found strong evidence for a high relative importance of the
406   ISPC hypothesis. The new environments created by the uplift of the Central Andes during the
407   last 30 my were colonized primarily by clades of species that were pre-adapted to the emerging
408   environmental conditions. Diversification within these clades resulted in new tree species that
409   had elevational distributions similar to those occupied by the immigrating species. In this way,
410   the ecological sorting of pre-Adapted clades according to their pre-adaptations is the eco-
411   evolutionary process that dominates the regional assembly of tree communities across the
412   elevational gradient.

413   Our study focuses on the structure of species assemblages, and how biogeographic processes
414   shape patterns of diversity. The assembly of communities, however, integrates the evolutionary
415   history of multiple independent clades of species. Several previous studies that have taken this
416   approach, focusing on the evolution of clades after the Andean uplift. This research shows that
417   groups of animals and plants across the Andes have diversified in ways that are consistent with
418   our results (Bell & Donoghue, 2005; Hughes & Eastwood, 2006; Chaves *et al.*, 2011; Nürk *et al.*,
419   2013). One of the best studied biogeographic histories in the Andes is that of the plants in the
420   genus *Lupinus*, which colonized the Andes from temperate North America (Hughes & Eastwood,
421   2006), and were likely pre-adapted to the cold conditions of alpine environments (Nevado *et al.*,
422   2016). This clade experienced an explosive diversification in the Andes, but most of the resulting
423   species occupy only high-elevation habitats. Their diversification was likely fueled by the
424   interaction between insularity of high-mountain habitats and climatic fluctuations during
425   Quaternary (Nevado *et al.*, 2018). Adaptive diversification also played an important role in the
426   radiation of the Andean lupins (Nevado *et al.*, 2016). Indeed, species in the clade show a huge
427   diversity of phenotypes, life forms and micro-habitat use (Hughes & Eastwood, 2006). Their
428   adaptive diversification, however, did not involve large numbers of species colonizing the new
429   environments at different elevations created by mountain uplift. Several clades of plants
430   distributed at the highest elevations in the Andes seem to show similar patterns of diversification
431   (Madriñán *et al.*, 2013). A general pattern of conservatism in elevational distribution was also
432   documented for several clades of trees by Griffiths et al. (2020). Clades with a biogeographic
433   history similar those of the Andean lupins would contribute little to changes in species
434   composition along the elevational gradient. Instead, this pattern of diversification, when
435   experienced by numerous clades pre-adapted to different elevations can lead to the observed
436   patterns of clade turnover found in our study. Indeed, turnover among communities across the
437   elevational gradient have an evolutionary origin that is rooted deep in the past, and that mostly
438   pre-dates the emergence of the environmental gradient.

439   Studies of particular clades, like those highlighted above, are insightful and have helped us
440   advance our understanding of the patterns and mechanisms of diversification. However, this
441   approach does not address directly the eco-evolutionary forces behind the assembly of diverse

442   communities, which is the focus of our analyses. To the best of our knowledge, our study is the
443   first effort to explicitly test the role that diversification before and after the origin of the
444   environmental gradient (i.e., the uplift of the Central Andes) had on community structure across
445   elevations. While previous studies have not tested the role of mountain uplift directly, our results
446   are supported by previous research of Andean communities, which have suggested an important
447   role for niche conservatism in community assembly across elevations (Graham *et al.*, 2009;
448   Hardy *et al.*, 2012; Jin *et al.*, 2015; Ramírez *et al.*, 2019; Worthy *et al.*, 2019; Bañares-de-Dios *et*
449   *al.*, 2020). A recent important study in this respect is that by Segovia *et al.* (2020), who
450   demonstrated a clear link in the phylogenetic composition of Andean tree communities to
451   temperate regions of North and South America. In particular, they highlight the role that freezing
452   conditions at high elevations play in creating environments that are invaded by temperate clades.
453   Similarly, niche conservatism has been implied in the eco-evolutionary assembly of seasonally
454   dry forest communities, which occur in rain-shadowed valleys along the Andes. Our study,
455   however, goes further than simply demonstrating niche conservatism or phylogenetic clustering
456   of communities. Instead, we provide evidence that the assembly of communities across
457   elevations is primarily driven by the immigration and sorting of clades that evolved appropriate
458   adaptations even before the emergence of the environmental gradient (Hardy *et al.*, 2012; Chi *et*
459   *al.*, 2014; Kubota *et al.*, 2018).

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

462   Adaptive radiations have played a critical role in the formation of biodiversity, giving rise to
463   an often-stunning array of morphological and species diversity (Gillespie *et al.*, 2020). Previous
464   studies have suggested that ecological opportunity is an important determinant, maybe a
465   prerequisite, of adaptive radiations (Stroud & Losos, 2016; Gillespie *et al.*, 2020), allowing
466   species to diversify rapidly to fill available niche space. The uplift of the Central Andes created
467   environments that were previously unavailable in the region, likely opening up new unoccupied
468   niche space for species. Moreover, as we discussed earlier, numerous rapid radiations have been
469   documented in the Andes (Madriñán *et al.*, 2013); some of them, like that of *Lupinus* or
470   *Espeletia* (Hughes & Eastwood, 2006; Pouchon *et al.*, 2018) are as dramatic as those in clades
471   that epitomize adaptive radiation (e.g. stickleback fish or African Great Lake cichlids; Gillespie
472   *et al.* 2020). If ecological opportunity existed and rapid diversification in the mountains is well
473   documented, then why did we not find a strong signal for recent adaptive radiation in the
474   assembly of communities across elevations?

475   There are several reasons that could explain our lack of evidence for recent adaptive
476   radiations across the elevational gradient. First, recent and rapid radiations in the Andes may not
477   involve adaptive diversification. Instead, high rates of species accumulation could be fueled
478   solely by allopatric speciation resulting from repeated cycles of habitat isolation and re-
479   connection driven by climatic oscillations (Nevado *et al.*, 2018; Flantua *et al.*, 2019). This

480   process would produce a large number of species that replace one another across geography but
481   within the same environment (Hughes & Eastwood, 2006; Chaves *et al.*, 2011). Furthermore,
482   nearly all cases of recent montane radiations occur in clades occupying the highest elevations
483   (Bell & Donoghue, 2005; Hughes & Eastwood, 2006; Nürk *et al.*, 2013; Hughes & Atchison,
484   2015), and more studies are needed to know if these patterns of diversification also occur at mid
485   or low elevations (but see Lagomarsino *et al.* 2016). Second, adaptive radiations may have
486   occurred along environmental dimensions other than those of the elevational gradient. Indeed,
487   some of the classic examples of Andean diversification involve fast evolution of phenotypes,
488   even if the elevational distribution of the clade is highly conserved (Hughes & Eastwood, 2006;
489   Nürk *et al.*, 2018; Pouchon *et al.*, 2018). Finally, some clades may have adaptively radiated
490   across the elevational gradient, but these clades are rare and contribute little to overall assembly
491   patterns. Indeed, biogeographic studies have documented significant shifts in elevational
492   distribution during the evolutionary history of several groups of plants and animals (Elias *et al.*,
493   2009; Bacon *et al.*, 2018). Some of these shift in elevational distribution might be accompanied
494   by shifts in life form (as exemplified by *Espeletia*; Pouchon *et al.* 2018; but see Zanne *et al.*
495   2013) which do not contribute to the assembly of tree communities that are the focus of our
496   study. The relative frequency of adaptive diversification across elevations versus niche
497   conservatism has not been evaluated; however, Griffith *et al.* (2020) found that in Peru, most
498   clades of trees have narrow elevational distributions, and only a few show wider elevational
499   distributions than expected by chance. The overall lack of clades that appear to have adaptively
500   radiated across elevations could be due to evolutionary priority effect, whereby different
501   elevational niches may have been preempted by immigrating pre-adapted clades (Fukami, 2015).
502   While the role of adaptive radiation in community assembly deserves further study, our results
503   suggest that Andean community assembly is mainly the result of different pre-adapted clades
504   that originated before Andean uplift, which colonized available niches before other clades could
505   adaptively radiate to occupy a broad elevational gradient (Tanentzap *et al.*, 2015).

506

Conclusions: future directions and implications for conservation

508   In this study, we developed a novel conceptual framework (Fig. 1), as well as new methods
509   of decomposing species turnover (Fig. 1, S4), to investigate the biogeographic origins of
510   community assembly along environmental gradients. We use this approach to study how the
511   uplift of the Central Andes led to the variation in community composition along iconic
512   elevational gradients. Our approach, however, can be applied to any system in which the timing
513   of the emergence of an environmental gradient is known and time-calibrated phylogenies can be
514   generated. We envision future studies using this method to understand the eco-evolutionary
515   assembly in systems beyond Andean forests such as along precipitation gradients (Parolari *et al.*,
516   2020), across contrasting soil conditions (Capurucho *et al.*, 2020), or even under different
517   disturbance regimes (Cavender-Bares & Reich, 2012). Methods such as these can be used to test

518   hypotheses about specific process of community assembly, going beyond documenting niche
519   conservatism or phylogenetic aggregation. Our approach will facilitate deeper insights into how
520   the emergence of environmental gradients shape modern natural ecosystems.

521   Our analyses demonstrate that species turnover across elevations in the Central Andes is
522   driven primarily by the turnover of clades that are at least 30 my old. These results suggest a
523   strong role for immigration and ecological sorting of pre-adapted clades to the novel
524   environments across elevations created by the uplift of the Central Andes. Adaptive
525   diversification following the emergence of the elevational gradient is likely restricted to a few
526   clades or to narrow elevational bands, having little impact on the assembly of communities along
527   such a large environmental gradient. Our results add to a growing body of evidence suggesting
528   that present day communities are strongly influenced by the ability of lineages to track
529   environmental conditions through space and geological time (Emerson & Gillespie, 2008;
530   Donoghue, 2008; Carvajal-Endara *et al.*, 2017; Griffiths *et al.*, 2020; Segovia *et al.*, 2020).

531   This finding has important implications for the long-term persistence of communities facing
532   the effects of human-mediated global change. Increases in atmospheric temperatures are
533   predicted to cause elevational shifts in environmental conditions, such that climates that
534   currently occur at specific elevations will occur at higher elevations in the future (Harsch *et al.*,
535   2009; Ruiz-Labourdette *et al.*, 2012; Freeman *et al.*, 2018; O'Sullivan *et al.*, 2020). Our work on
536   historical patterns of community assembly suggests that ecosystems are more likely to track
537   shifting habitats rather than adapt to novel conditions (Sheldon *et al.*, 2011; Ruiz-Labourdette *et
538   al.*, 2012; Freeman *et al.*, 2018; Feeley *et al.*, 2020). Communities and species at the highest
539   elevations might be specially threatened by climate change since their environments will
540   disappear at the top of mountains and new pre-adapted competitors will move in from lower
541   elevations (Colwell *et al.*, 2008). Thus, communities occupying the highest-elevation sites in the
542   Andes should be prioritized for monitoring and conservation efforts. Because their habitat may
543   not persist over the long term, ex situ conservation (either through conservation seed banking or
544   living collections) of the species endemic to the highest elevations should be a specific priority.

545

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560 **Author contribution***: JST, JAM, AEZ and CEE developed and designed the study. JST, CL,

561 AFF, MIL, GA and MJM collected the Madidi Project dataset; MS, WFR, KGC, NSR, and YM

562 collected the ABERG dataset. SAS produced the phylogenetic data. AGL and JST performed

563 data analyses. AGL and JST wrote the manuscript, and all authors contributed significantly to

564 revisions.

565 **Data availability:** The Madidi Project's dataset used in our analyses correspond to version 4.1,

566 which is deposited in Zenodo (https://doi.org/10.5281/zenodo.4276558). Additionally, raw data

567 of the Madidi Project are stored and managed in Tropicos (https://tropicos.org/home), the

568 botanical database of the Missouri Botanical Garden. These data can be viewed and accessed via

569 the Madidi Project's module at http://legacy.tropicos.org/Project/MDI. The Andes Biodiversity

570 and Ecosystem Research Group (ABERG) is a team of 38 researchers from 12 universities

571 dedicated to understanding biodiversity distribution and ecosystem function in the Peruvian

572 Andes. ABERG is committed to data exchange within the scientific community and promoting

573 collaboration among other tropical ecosystem scientists. For more information and to request

574 data contact Miles Silman or Yadvinder Malhi (http://www.andesconservation.org/). The R code

575 created for analyses is available at https://github.com/Linan552/Madidi-project.

576

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775 **Supporting Information legends**

Supplementary methods: Additive decomposition of species turnover metrics.

Figures S1: decomposed turnover across elevation excluding morphospecies.

Figures S2: number of species per clade across datasets.

Figure S3: decomposition of species turnover across elevational distance for 60my clades.

Figures S4: decomposed turnover across elevation excluding morphospecies.

Figure S5: logit transformed decomposition of turnover.

Figure S6: relationship between difference in elevation and geographic distance in our datasets.

Figure S7: Species turnover across geographic distance.

Figure S8: Decomposition of species turnover across geographic distance for 30my clades.

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