

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

3 Alexander G. Linan<sup>1\*†</sup> [0000-0002-8281-1346](#), Jonathan A. Myers<sup>2</sup> [0000-0002-2058-8468](#),  
4 Christine E. Edwards<sup>1</sup> [0000-0001-8837-4872](#), Amy E. Zanne<sup>3</sup> [0000-0001-6379-9452](#), Stephen A.  
5 Smith<sup>4</sup> [0000-0003-2035-9531](#), Gabriel Arellano<sup>4</sup> [0000-0003-3990-5344](#), Leslie Cayola<sup>1,5</sup>,  
6 William Farfan-Ríos<sup>1,2</sup> [0000-0002-3196-0317](#), Alfredo F. Fuentes<sup>1,5</sup> [0000-0003-4848-4182](#),  
7 Karina Garcia-Cabrera<sup>6</sup> [0000-0001-8535-5086](#), Sebastián Gonzales-Caro<sup>7</sup> [0000-0002-2287-](#)  
8 [7431](#), M. Isabel Loza<sup>1,5,8</sup>, Manuel J. Macía<sup>9,10</sup> [0000-0002-4676-612X](#), Yadvinder Malhi<sup>11</sup> [0000-](#)  
9 [0002-3503-4783](#), Beatriz Nieto-Ariza<sup>12</sup>, Norma Salinas<sup>13</sup> [0000-0001-9941-2109](#), Miles Silman<sup>14</sup>,  
10 and J. Sebastián Tello<sup>1†</sup> [0000-0003-2539-6796](#)

- 11
- 12 1. Center for Conservation and Sustainable Development, Missouri Botanical Garden, St.  
13 Louis, Missouri, 63110 USA
  - 14 2. Department of Biology, Washington University in St. Louis, St. Louis, Missouri, 63130 USA
  - 15 3. Department of Biological Sciences, The George Washington University, Washington DC,  
16 20052 USA
  - 17 4. Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor,  
18 Michigan, 48109 USA
  - 19 5. Herbario Nacional de Bolivia, Universidad Mayor de San Andrés, La Paz, Bolivia
  - 20 6. Escuela Profesional de Biología, Universidad Nacional de San Antonio Abad del Cusco,  
21 Cusco, Peru
  - 22 7. Departamento de Ciencias Forestales, Universidad Nacional de Colombia Sede Medellín,  
23 Universidad Nacional de Colombia, Medellín, Colombia
  - 24 8. Department of Biology, University of Missouri-St Louis, St. Louis, Missouri, 63121 USA
  - 25 9. Departamento de Biología, Área de Botánica, Universidad Autónoma de Madrid, Madrid,  
26 Spain
  - 27 10. Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad  
28 Autónoma de Madrid, Madrid, Spain.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/NPH.17674](#)

29 11. Environmental Change Institute, School of Geography and the Environment, University of  
30 Oxford, Oxford, England, United Kingdom

31 12. Hospital Central de Ivirgarzama, Puerto Villarroel, Bolivia

32 13. Institute for Nature Earth and Energy, Pontificia Universidad Catolica del Peru, Lima, Peru

33 14. Center for Energy, Environment and Sustainability, Winston-Salem, North Carolina, 27109  
34 USA

35 † These authors contributed equally to this study

36 \*corresponding/contact author; E-mail: [alanan@mobot.org](mailto:alanan@mobot.org); phone: 1(314)-577-9473 ext.77264

37

38 Received: 11 January 2021

39 Accepted: 3 August 2021

40

#### 41 **Summary**

- 42 • Recent studies have demonstrated that ecological processes that shape community  
43 structure and dynamics change along environmental gradients. However, much less is  
44 known about how the emergence of the gradients themselves shape the evolution of  
45 species that underlie community assembly. In this study, we address how the creation of  
46 novel environments lead to community assembly via two non-mutually exclusive  
47 processes: 1) immigration and ecological sorting of pre-adapted clades (ISPC), and 2)  
48 recent adaptive diversification (RAD). We study these processes in the context of the  
49 elevational gradient created by the uplift of the Central Andes.
- 50 • We develop a novel approach and method based on the decomposition of species  
51 turnover into within- and among-clade components, where clades correspond to lineages  
52 that originated before mountain uplift. Effects of ISPC and RAD can be inferred from  
53 how components of turnover change with elevation. We test our approach using data  
54 from over 500 Andean forest plots.
- 55 • We found that species turnover between communities at different elevations is dominated  
56 by the replacement of clades that originated before the uplift of the Central Andes.

- 57 • Our results suggest that immigration and sorting of clades pre-adapted to montane  
58 habitats is the primary mechanism shaping tree communities across elevations.

59

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

62

63

## 64 **Introduction**

65 Large-scale biogeographic events—such as the emergence of novel environmental  
66 conditions, biotic interchanges, or the evolution of key innovations—can have lasting  
67 consequences for biodiversity, community assembly, and species distributions (Ricklefs, 2006;  
68 Fussmann *et al.*, 2007; Pelletier *et al.*, 2009; Givnish *et al.*, 2015; Uribe-Convers & Tank, 2015;  
69 Claramunt & Cracraft, 2015). Although theory and empirical evidence suggest that processes  
70 occurring in the deep past can contribute to the modern structure of local ecological  
71 communities, most research in community ecology during the last few decades has been  
72 dominated by a focus on mechanisms at small spatial and temporal scales (Ricklefs, 1987; Estes  
73 *et al.*, 2018). Studies largely overlook the broader biogeographic context in which communities  
74 of co-occurring species are embedded (Chesson, 2000; Adler *et al.*, 2007). Only recently have  
75 ecologists begun bridging this gap by developing ecological theory and empirical tests that truly  
76 integrate community assembly across eco-evolutionary scales (Emerson & Gillespie, 2008;  
77 Thornhill *et al.*, 2017; Cavender-Bares *et al.*, 2018; McGill *et al.*, 2019; Bañares-de-Dios *et al.*,  
78 2020; Segovia *et al.*, 2020). The extent to which community assembly is contingent upon  
79 regional context and biogeographic history has broad implications for ecological and  
80 evolutionary theory and for understanding how and why communities respond to environmental  
81 change (Chase, 2003; Fukami, 2015; Vellend, 2016; McPeck, 2017).

82 Recent studies provide important insights into how ongoing ecological processes change  
83 along environmental gradients (Bricca *et al.*, 2019; Bañares-de-Dios *et al.*, 2020; Neves *et al.*,  
84 2020). However, much less is known about how the emergence of the gradients themselves

85 shape the evolution of species and phenotypes that underlie community assembly. Two non-  
86 mutually exclusive processes may explain how communities assemble along gradients following  
87 the emergence of novel environmental conditions (Fig. 1). First, the emergence of new  
88 environments—e.g., due to climate change, island formation, or mountain orogeny— may create  
89 opportunities for immigration and ecological sorting of pre-adapted clades (ISPC hypothesis;  
90 Box 1; Fig. 1a; Donoghue 2008).

91

#### **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.

92

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

104 scenario of community assembly is consistent with the idea that “it is easier to move than to  
105 evolve” (Donoghue, 2008).

106 Second, the emergence of new environments may create opportunities for recent adaptive  
107 diversification across environments (RAD hypothesis; Box 1; Fig. 1a). According to this  
108 hypothesis, when new environmental gradients are created, community assembly across habitats  
109 is dominated by adaptation in response to the emerging environmental conditions, resulting in  
110 the diversification of clades across the environmental gradient (Stroud & Losos, 2016; Menon *et*  
111 *al.*, 2018). Thus, the traits needed to colonize new habitats evolve after the origin of the  
112 environmental gradient. In this scenario, niche conservatism is minimal or non-existent, and  
113 community assembly results from the diversification of clades that were originally adapted to a  
114 subset of environmental conditions, but that diversify to occupy emerging novel environmental  
115 space. This scenario for community assembly following the emergence of environmental  
116 gradients is consistent with the classic ideas of biome shifts and adaptive radiation driven by  
117 ecological opportunity and competition (Givnish, 1997; Schluter, 2000; Losos, 2010; Donoghue  
118 & Edwards, 2014).

119 Here we present and test a novel community-phylogenetic framework and method to study  
120 the relative importance of ISPC and RAD in determining the assembly of communities along  
121 large-scale environmental gradients. These effects on community assembly can be inferred from  
122 unique patterns in the phylogenetic structure of compositional turnover. In particular, signatures  
123 of these two non-mutually exclusive processes can be traced when species turnover is  
124 decomposed into components that correspond to *within-* and *among-clade turnover*, where clades  
125 correspond to independent lineages that originated before the emergence of the gradient. These  
126 within- and among-clade turnover components, in turn, reflect the effects of diversification after  
127 and before the emergence of the gradient on community composition across environments. Here,  
128 we illustrate these patterns using a hypothetical elevational gradient created by mountain uplift(  
129 Fig. 1A). For clarity, we present opposing extremes of a continuum that involves the relative  
130 contribution of these two processes to community assembly. Most natural systems will likely  
131 occupy an intermediate space between these extremes. The ISPC hypothesis predicts that for

132 communities *at the same elevation*, variation in community composition should be dominated by  
133 *within-clade turnover*, reflecting strong phylogenetic niche conservatism of clades that are pre-  
134 adapted to the environments at that specific elevation (Fig. 1b). As communities are *farther*  
135 *apart along the elevational (i.e. environmental) gradient*, variation in community composition  
136 should become increasingly dominated by *among-clade turnover*, reflecting the shift in  
137 dominance from species in one pre-adapted clade to another. On the other hand, the RAD  
138 hypothesis predicts that for communities at *similar or contrasting elevations*, variation in  
139 community composition should be dominated by turnover *within clades*, reflecting how multiple  
140 clades evolved niche differences in response to new environmental conditions that allow them to  
141 have broad elevational (i.e., environmental) distributions (Fig. 1c). Although we developed and  
142 tested this conceptual framework in the context of mountain uplift, our approach is applicable to  
143 study community assembly after the emergence of any type of environmental gradient at any  
144 spatial or temporal scale.

145 In the Neotropics, the geologically recent uplift of the Andean mountains created a striking  
146 elevational and environmental gradient that had profound consequences for global climate and  
147 biodiversity (Rahbek & Graves, 2001; Antonelli *et al.*, 2009; Ehlers & Poulsen, 2009; Jiménez *et*  
148 *al.*, 2009; Graham, 2009; Hoorn *et al.*, 2010). Indeed, the tropical Andes are considered the most  
149 species-rich biodiversity hotspot, containing 15% of all plant species (>45,000 species) in only  
150 1% of the world's land area (Myers *et al.*, 2000; Rahbek & Graves, 2001; Jiménez *et al.*, 2009;  
151 Ulloa *et al.*, 2017). However, our current understanding of the eco-evolutionary forces that shape  
152 community assembly across elevations in the hyper-diverse Andean biotas is limited. First, many  
153 studies focus on the evolution and distribution of relatively small clades compared to entire  
154 communities; these studies have provided evidence for an important role of adaptive  
155 diversification (Antonelli *et al.*, 2009; Givnish *et al.*, 2014, 2015; Pérez-Escobar *et al.*, 2017) in  
156 some cases and immigration and colonization of pre-adapted clades in others (Hughes &  
157 Eastwood, 2006; Jin *et al.*, 2015; Lagomarsino *et al.*, 2016). Such studies demonstrate that both  
158 processes have occurred, but provide limited insights into how evolutionary history of individual  
159 clades contribute to the assembly of entire ecological communities and regional biotas. Second,  
160 studies that focus on the phylogenetic structure of Andean communities are relatively few and

161 often fail to differentiate the effects of diversification before and after the emergence of the  
162 gradient (Graham *et al.*, 2009; Parra *et al.*, 2011; Bacon *et al.*, 2018; Pouchon *et al.*, 2018;  
163 Montaña-Centellas *et al.*, 2019; Ramírez *et al.*, 2019). To date, no study has sought to  
164 disentangle the relative importance of immigration and sorting of pre-adapted clades versus post-  
165 Andean uplift adaptive radiation in shaping the enormous variation in plant community  
166 composition across elevational gradients.

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

177

## 178 **Materials and Methods**

### 179 *Community composition data across elevations*

180 We utilized data from two large-scale forest plot networks in the Central Andes of Bolivia  
181 (the Madidi Project; extent of 30,165 km<sup>2</sup>) and Peru (the Andes Biodiversity and Ecosystem  
182 Research Group [ABERG]; 1,765 km<sup>2</sup>). Both datasets contain information on tree community  
183 composition spanning the entire elevational range of forests in this region of the Andes from  
184 lowland Amazonia (175 m) to the tree line (3,765 m; Fig. S1). Our datasets include information  
185 on species composition across 73 1-ha plots (large plots hereafter; 50 in Bolivia and 23 in Peru),  
186 as well as 454 0.1-ha plots (small plots hereafter; 418 in Bolivia and 36 in Peru; Fig. 2).

187

188

189 Within these plots, all woody plants with a diameter at breast height (DBH)  $\geq$  10 cm in large  
190 plots and DBH  $\geq$  2.5 cm in small plots were tagged, measured and identified to species or  
191 morphospecies. Large and small plots characterize different plant communities; while large plots  
192 consider only adults of large tree species, small plots include younger individuals and also  
193 species that do not reach 10 cm DBH, including many shrubs. The differences in body size and  
194 growth form included in the two plot types could reflect differences in evolutionary potential, as  
195 smaller trees and shrubs may have shorter generation times that could enable them to evolve at  
196 faster rates than larger trees (Verdui, 2002; Petit & Hampe, 2006), increasing the likelihood that  
197 they may show signs of adaptive diversification along the gradient (RAD). Because of this  
198 possibility we separated out data by plot size and conducted analyses independently.  
199 Additionally, we excluded high elevation plots ( $>$  3,800 m) and plots with  $\leq$  3 species. Most of  
200 these plots represent *Polylepis*-dominated forests fragments within a matrix of páramo  
201 grasslands/shrublands. The ecology and composition of these páramo forests is clearly distinct  
202 from the continuous forest cover along the elevational gradient.

203 Within the Bolivian and Peruvian datasets, we conducted extensive taxonomic work to  
204 standardize species and morphospecies names across plots. Morphospecies, however, could not  
205 be standardized between the Bolivian and Peruvian data. To test the effect of morphospecies on  
206 results, analyses were repeated with and without morphospecies. Both analyses produced nearly  
207 identical results (Fig. S2); for simplicity, we present only analyses including morphospecies.  
208 Representative specimens at each site were collected and deposited in herbaria, mainly at the  
209 Herbario Nacional de La Paz (LPB), the Missouri Botanical Garden (MO) and Universidad  
210 Nacional de San Antonio Abad del Cusco (CUZ) in Peru. The small plots contained 2,731  
211 species, whereas the large plots contained 1,904 species (Table 1).

### 212 213 ***Phylogenetic reconstruction and defining clades of pre-Andean origin***

214 To test our hypotheses, we needed a phylogenetic framework that grouped species into clades  
215 that diverged from one-another before the origin of the elevational gradient (i.e. clades that pre-  
216 date the uplift of the Central Andes). To do this, we used a combined mega-phylogeny  
217 representing 74,531 vascular plant species based on Smith and Brown's (2018) global mega-



218 phylogeny of seed plants, results from the Open Tree of Life project (Hinchliff *et al.*, 2015), as  
219 well as Zanne *et al.*'s (2014) phylogeny that included pteridophytes. To incorporate species and  
220 morphospecies in our dataset that were not in the original phylogeny, we used the R package  
221 'V.PhyloMaker' (Jin & Qian, 2019). Using genus and family level taxonomic information,  
222 missing taxa not included in the mega-phylogeny were joined to the halfway point of the  
223 family/genus branch (V.PhyloMaker scenario= "S3"). For genera not represented in the mega-  
224 phylogeny, we joined species to sister genera in the phylogeny based on support in the literature  
225 (when possible) using the 'bind.relative' option of V.PhyloMaker. Finally, we pruned from the  
226 phylogeny all species that were absent in our forest plots. The resulting phylogeny included  
227 3,143 species.

228 The formation of the Andean cordillera has been a complex and heterogeneous process. In  
229 the Central Andes, the history of mountain formation is closely tied to the development of the  
230 Altiplano plateau, currently located at nearly 3,800 m in elevation. While the traditional view of  
231 mountain uplift invokes a slow and gradual process, recent evidence suggests that the uplift of  
232 the Altiplano was dominated by spurs of rapid rise with intervening periods of stasis (Garziona *et*  
233 *al.*, 2008, 2017). Although the northern Andes is considered much younger, the best available  
234 evidence suggests that most of the uplift in the Central Andes occurred within the last 30 million  
235 years (Poulsen *et al.*, 2010; Hoorn *et al.*, 2010; Boschman, 2021). Thus, our analyses used this  
236 age as a main reference for the origin of the elevational gradient and to delimit pre-Andean  
237 clades.

238 Pre-Andean clades in the time-calibrated regional phylogeny were defined as those whose  
239 stems intersect the 30 my reference. In this way, each pre-Andean clade in our study diverged  
240 from others before the uplift of the central Andes, whereas all species within pre-Andean clades  
241 resulted from diversification that occurred after mountain uplift had started. We used the  
242 function treeSlice in the R package 'Phytools' (Revell, 2012) to fragment the regional phylogeny  
243 into these clades. Species present in small plots formed 473 pre-Andean clades with an average  
244 of 5.77 species per clade, whereas species in the large plots formed 355 clades, averaging 5.36  
245 species per clade (Table 1 and Fig. S3). Finally, we sought to understand how our results varied  
246 by defining pre-Andean clades at different ages. Thus, in addition to creating a dataset with 30

247 million years old pre-Andean clades , we made a second dataset classifying pre-Andean clades as  
248 those that intersect the 60 my reference. This represents a much more conservative estimate of  
249 the timing of Andean uplift (Hoorn *et al.*, 2010). The results from these alternative analyses were  
250 nearly identical, and thus are presented only in the Supporting Information (Fig. S4).

251

### 252 ***Decomposing total turnover into among- and within-clade turnover***

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

$$259 \quad S = \frac{b + c}{2a + b + c}$$

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

$$268 \quad S_{WG} = \frac{b_{WG} + c_{WG}}{2 \times a + b + c}$$

$$269 \quad S_{AG} = \frac{b_{AG} + c_{AG}}{2 \times a + b + c}$$

270 Further details of the decomposition method can be found in the Supporting Information,  
271 where we also show that this approach could be applied to other turnover metrics, such as Bray-  
272 Curtis distances (Methods S1). The R code that performs this decomposition is available at

273 <https://github.com/Linan552/Madidi-project> (function “*decompose.my.beta*”). When within- and  
274 among-clade dissimilarities are transformed into components of total turnover ( $S_{WG}/S$  and  $S_{AG}/S$ ,  
275 respectively), these values correspond to the contribution of diversification after ( $S_{WG}/S$ ) and  
276 before ( $S_{AG}/S$ ) the uplift of the central Andes to community species turnover (Fig. 1, S5). Thus, a  
277 high among-clade component indicates that turnover is mainly dominated by species that  
278 diverged from one another before the uplift of the Central Andes (Fig. 1a, left). In contrast, high  
279 within-clade component indicates that turnover is dominated by species that diverged from one  
280 another after the uplift of the Central Andes (Fig. 1a, right).

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

290

### 291 *Assessing significance of observed data using null models and ruling out effects of geographic* 292 *distance*

293 To test whether observed patterns are different from those expected by chance, we compared  
294 the components of turnover in the observed data with components produced by a null model that  
295 eliminated any phylogenetic structure in the distribution of species, but retained other important  
296 elements of the data that might shape turnover patterns. We ran a “tip-randomization null model”  
297 in which species were randomly re-assigned to tips in the phylogeny, such that species were  
298 randomly reshuffled among pre-Andean clades. This randomization algorithm maintained the  
299 number of species per clade, the species richness gradient across elevations, the average range  
300 size in each community, and importantly, the turnover observed between pairs of plots. The only  
301 aspect of the data that was randomized was the membership of species in clades of pre-Andean

302 origin. We randomized the data and re-calculated components of turnover for each pair of plots  
303 999 times. From these null expectations, we calculated standardized effect sizes as the observed  
304 value minus the mean of null distribution divided by the standard deviation of the null  
305 distribution. These values represent the magnitude of the difference between the observed  
306 components of turnover and the components as expected by the null model, where there is no  
307 phylogenetic structure in species distributions. As for the observed components of turnover, we  
308 related standardized effect sizes against the difference in elevation for each pair of plots.

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

319 Finally, in order to tease apart the effects geographic and elevational distance on components  
320 of turnover, our analyses used only a subset of all possible pair-wise plot comparisons for each  
321 dataset. These subsets minimized variation in geographic distances, but maximized the  
322 elevational range represented in the data (Fig. S7). For the large-plot dataset, we selected pairs of  
323 plots only between 50 and 90 km apart (8% of the total range in geographic distances), and for  
324 the small-plot dataset, we selected pairs of plots between 110 and 160 km apart (10% of  
325 geographic range). In both subsets however, the full extent of elevational distances is  
326 represented, ranging from 175 to 3765 m. Following plot subsetting, we saw no evidence of  
327 spatial autocorrelation in the residuals of our linear models between components of turnover and  
328 elevational distance.

329 Additionally, we examined how turnover and its components change across space but within  
330 the same environmental conditions. To do this, we used pairs of plots spanning the entire

331 geographic extent of the study (max. distance between plots: 495 km), but were at similar  
332 elevations (only pairs of plots with 0 to 200 m of elevational distance, Fig. S7). Like for our  
333 analyses along the elevational gradient, we related components of turnover with geographic  
334 distances, and compared observed patterns against null model expectations. (results presented in  
335 the Supporting Information). Analyses were performed using R packages ‘vegan’ and  
336 ‘geosphere’ (Hijmans *et al.*, 2019; Oksanen *et al.*, 2020).

337

## 338 **Results**

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

343 Indeed, plots separated by more than 2,000 to 2,500 m of elevation never shared species. We  
344 found a similar relationship between species composition and geographic distance (Fig. S8).  
345 However, Sørensen dissimilarity did not increase as dramatically with increasing geographic  
346 distance and it never reached complete turnover; for example, we found that geographically  
347 distant plots (i.e., 400 km away from one another, with one in Peru the other in Bolivia; Fig. S8)  
348 still shared species when they were in similar environments.

349 We also found strong elevational gradients in the within- and among-clade components of  
350 species turnover (Fig. 4A&D). For forest plots occurring at the same elevation (near zero meters  
351 in elevational difference), among- and within-clade components were equal in magnitude (Fig.  
352 4A&D). This result indicates that communities in the same environment shared species in the  
353 same pre-Andean clades, but also that multiple different clades contributed to community  
354 composition among these plots. As elevational difference increased, among-clade turnover rose  
355 rapidly, while within-clade turnover decreased (Fig. 4A&D). Although the increase in the  
356 among-clade component was monotonic in the small-plots dataset, it saturated at around 2,000 m  
357 of elevational difference for the large-plots dataset. In both datasets, however, when plots were  
358 separated by more than 1,000 to 1,500 m in elevation, turnover between at least some pairs of  
359 communities was completely associated with the among-clade component. This result means that

360 some pairs of plots at opposite ends of the elevational gradient shared neither species nor clades  
361 30 my old, which originated before the uplift of the Central Andes. These results support the  
362 ISPC hypothesis, whereby turnover along the elevational gradient largely consists of species  
363 belonging to different pre-Andean clades.

364 The predictions of the ISPC hypotheses were also supported using standardized effect sizes –  
365 as measured using our null model (Fig. 4 C&F). Indeed, standardized effect sizes for within- and  
366 among-clade components were both close to zero for plots at the same elevation. As elevational  
367 differences increased, standardized effect sizes increased for among-clade turnover and  
368 decreased for within-clade turnover (Fig. 4 C&F). Moreover, when plots were separated by  
369 >1,500 m in elevation, the observed values differed by more than two standard deviations from  
370 null expectations (i.e. standardized effect sizes greater than 2; Fig. C&D). The comparison of the  
371 observed and null regression slopes also showed that the change in the observed components was  
372 much more pronounced than the change expected by the null model (Fig. 5).

373

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

379

## 380 **Discussion**

### 381 *Community assembly across contrasting elevations is dominated by the immigration and* 382 *ecological sorting of clades that pre-date mountain uplift*

383 Our results showed clearly that changes in species composition across elevations in the  
384 Central Andes were driven primarily by a replacement of clades of pre-Andean origin. These  
385 results were robust to analyses using different age estimates of pre-Andean clades (30 vs. 60  
386 my), inclusion or exclusion of morphospecies, or delimitations of forest communities (trees  $\geq$  10  
387 cm DBH in large plots vs. trees  $\geq$  2.5 cm DBH in small plots). While adaptive diversification is

388 likely to have occurred in our study system, our results suggest that this process has had a  
389 reduced influence on patterns of community assembly. In contrast, we found strong evidence for  
390 a high relative importance of the ISPC hypothesis. The new environments created by the uplift of  
391 the Central Andes during the last 30 my were colonized primarily by species from clades that  
392 were pre-adapted to the emerging environmental conditions. Diversification within these clades  
393 resulted in new tree species that had elevational distributions similar to those occupied by the  
394 immigrating species. In this way, the ecological sorting of pre-adapted clades according to their  
395 pre-adaptations is the eco-evolutionary process that dominates the regional assembly of tree  
396 communities across the elevational gradient.

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

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

424 Although we found support for the ISPC hypothesis, an important question remains  
425 regarding how the ancestors of immigrating pre-adapted clades may have reached the Andes. If it  
426 is “easier to move than to evolve” (Donoghue, 2008), how are lineages moving? While there is  
427 an increasing number of studies suggesting Neotropical lineages are not dispersal-limited  
428 (Hughes *et al.*, 2013; Segovia *et al.*, 2020), the ancestors of pre-adapted Andean clades may have  
429 dispersed great distances to reach the Andes. One way this may have occurred is through  
430 “mountain-hopping” (Knox & Palmer, 1995, 1998; Sklenář *et al.*, 2014), whereby colonizers  
431 could have sequentially colonized adjacent mountains, leading to island-like diversification.  
432 Although evidence of this has been found in species occupying high-elevation páramo  
433 environments (Raven, 1963; Hughes & Eastwood, 2006; Moore & Donoghue, 2007; Bone *et al.*,  
434 2011; Sklenář *et al.*, 2011; Luebert & Weigend, 2014), few studies have tested this hypothesis in  
435 lineages that occupy lower elevational bands in the Andes, which are presumably less insular  
436 (Kelly *et al.*, 1994).

437 Studies of particular clades, like those highlighted above, are insightful and have helped us  
438 advance our understanding of the patterns and mechanisms of diversification. However, this  
439 approach does not address directly the eco-evolutionary forces behind the assembly of diverse  
440 communities, which is the focus of our analyses. To the best of our knowledge, our study is the  
441 first effort to explicitly test the role that diversification before and after the origin of the  
442 environmental gradient (i.e., the uplift of the Central Andes) had on community structure across  
443 elevations. While previous studies have not tested the role of mountain uplift directly, our results  
444 are supported by previous research of Andean communities, which have suggested an important  
445 role for niche conservatism in community assembly across elevations (Graham *et al.*, 2009;  
446 Hardy *et al.*, 2012; Jin *et al.*, 2015; Ramírez *et al.*, 2019; Worthy *et al.*, 2019; Bañares-de-Dios *et*



447 *al.*, 2020). A recent important study in this respect is that by Segovia *et al.* (2020), who  
448 demonstrated a clear link in the phylogenetic composition of Andean tree communities to  
449 temperate regions of North and South America. In particular, they highlight the role that freezing  
450 conditions at high elevations play in creating environments that are invaded by temperate clades.  
451 Similarly, phylogenetic niche conservatism has been implied in the eco-evolutionary assembly of  
452 seasonally dry forest communities, which occur in rain-shadowed valleys along the Andes  
453 (Pennington & Lavin, 2009). Our study, however, goes further than simply demonstrating  
454 phylogenetic niche conservatism or phylogenetic clustering of communities. By delineating  
455 clades based on the time of mountain uplift, we were able to directly test hypotheses of processes  
456 governing community assembly in the central Andes and found evidence that the assembly of  
457 communities across elevations is primarily driven by the immigration and sorting of clades that  
458 evolved appropriate adaptations even before the emergence of the environmental gradient (Hardy  
459 *et al.*, 2012; Chi *et al.*, 2014; Kubota *et al.*, 2018).

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

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

475 Several factors could explain our lack of evidence for adaptive diversification across the  
476 elevational gradient. First, recent and rapid radiations in the Andes may not involve adaptive  
477 diversification. Instead, high rates of species accumulation could be fueled solely by allopatric  
478 speciation resulting from repeated cycles of habitat isolation and re-connection driven by  
479 climatic oscillations (Nevado *et al.*, 2018; Flantua *et al.*, 2019). Topographically dissected  
480 montane regions provide many natural barriers (e.g., valleys, high-elevation ridges) to plant  
481 dispersal and gene flow, which alone could foster extensive geographic speciation (Givnish *et*  
482 *al.*, 2014, 2015). This process would produce a large number of species that replace one another  
483 across geography but within the same environment (Hughes & Eastwood, 2006; Chaves *et al.*,  
484 2011). Second, adaptive diversification following montane uplift may have occurred along  
485 environmental dimensions other than those of the elevational gradient. Indeed, some of the  
486 classic examples of Andean diversification involve fast evolution of phenotypes, even if the  
487 elevational distribution of the clade is highly conserved (Hughes & Eastwood, 2006; Nürk *et al.*,  
488 2018; Pouchon *et al.*, 2018). Third, some clades may have adaptively radiated across the  
489 elevational gradient, but these clades are rare and contribute little to overall assembly patterns.  
490 Indeed, biogeographic studies have documented significant shifts in elevational distribution  
491 during the evolutionary history of several groups of plants and animals (Elias *et al.*, 2009; Bacon  
492 *et al.*, 2018). Our results however, show that only 35 of 473 pre-Andean (30my) clades span  
493 large elevational ranges (>2000 m); some examples include: *Aegiphila*, *Erythroxyllum*, *Erythrina*,  
494 *Gutteria*, *Hieronyma*, *Meliosma*, *Piper*, *Prunus*, *Styrax*, and *Symplocos*. Of these genera,  
495 *Stryax*, *Symplocos*, and *Piper* are montane endemic genera, suggesting that they might have  
496 dispersed from outside the Andes and then diversified across elevations (Young *et al.*, 2002).  
497 Moreover, some shifts in elevational distribution might be accompanied by shifts in life form (as  
498 exemplified by *Espeletia*; Pouchon *et al.* 2018; but see Zanne *et al.* 2013) which do not  
499 contribute to the assembly of tree communities that are the focus of our study. While the role of  
500 adaptive diversification in community assembly deserves further study, our results suggest that  
501 Andean community assembly is mainly the result of different pre-adapted clades that originated  
502 before Andean uplift, which colonized available niches before other clades could adaptively  
503 radiate to occupy a broad elevational gradient (Tanentzap *et al.*, 2015).

504

505 ***Conclusions: future directions and implications for conservation***

506 In this study, we developed a novel conceptual framework (Fig. 1), as well as new methods  
507 of decomposing species turnover (Fig. 1, S5), to investigate the biogeographic origins of  
508 community assembly along environmental gradients. We used this approach to study how the  
509 uplift of the Central Andes led to the variation in community composition along iconic  
510 elevational gradients. Our approach, however, can be applied to any system in which the timing  
511 of the emergence of an environmental gradient is known and time-calibrated phylogenies can be  
512 generated. We envision further development and use of this method beyond Central Andean  
513 forests, at larger geographic scales including entire continents, in a variety of environmental  
514 gradients such as precipitation gradients (Parolari *et al.*, 2020), across contrasting soil conditions  
515 (Capurucho *et al.*, 2020), or even under different disturbance regimes (Cavender-Bares & Reich,  
516 2012). We also think that simulation studies to understand the properties of our methods in the  
517 context of eco-evolutionary hypotheses (including ISPC and RAD) will be particularly  
518 important. Methods such as these can be used to test hypotheses about specific process of  
519 community assembly, going beyond documenting niche conservatism or phylogenetic  
520 aggregation. Our approach will facilitate deeper insights into how the emergence of  
521 environmental gradients shape modern natural ecosystems.

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

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

546

#### 547 **Acknowledgements**

548 We thank the Dirección General de Biodiversidad, the Bolivian Park Service (SERNAP),  
549 the Madidi National Park and local communities for permits, access, and collaboration in  
550 Bolivia, where fieldwork was supported by the National Science Foundation (DEB 0101775,  
551 DEB 0743457, DEB 1836353). Additional financial support to the Madidi Project has been  
552 provided by the Missouri Botanical Garden, the National Geographic Society (NGS 7754-04 and  
553 NGS 8047-06), International Center for Advanced Renewable Energy and Sustainability (I-  
554 CARES) at Washington University in St. Louis, the Comunidad de Madrid (Spain), Consejo  
555 Superior de Investigaciones Científicas (Spain), Centro de Estudios de América Latina (Banco  
556 Santander and Universidad Autónoma de Madrid, Spain), and the Taylor and Davidson families.  
557 Fieldwork in the ABERG transect was supported by NSF, the Gordon and Betty Moore  
558 Foundation and the UK Natural Environment Research Council. This work was developed in  
559 part during the working group "A Synthesis of Patterns and Mechanisms of Diversity and Forest  
560 Change in the Andes" funded by the Living Earth Collaborative at Washington University in St.  
561 Louis. We thank all the researchers, students and local guides that were involved in the  
562 collection of the data, particularly Carla Maldonado, Maritza Cornejo, Alejandro Araujo, Javier

563 Quisbert, Narel Paniagua and Peter Jørgenson. Finally, we thank Iván Jiménez for helpful  
564 discussions, ideas and comments.

565 **Author contribution:** JST, JAM, AEZ, SGC and CEE developed and designed the study. BNA,  
566 JST, LC, AFF, MIL, GA and MJM collected the Madidi Project dataset; MS, WFR, KGC, NSR,  
567 and YM collected the ABERG dataset. SAS produced the phylogenetic data. AGL and JST  
568 performed data analyses. AGL and JST wrote the manuscript, and all authors contributed  
569 significantly to revisions. AGL and JST contributed equally to this work.

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

581

## 582 References

583 **Adler PB, HilleRisLambers J, Levine JM. 2007.** A niche for neutrality. *Ecology Letters* **10**: 95–  
584 104.

585 **Antonelli A, Nylander JAA, Persson C, Sanmartin I. 2009.** Tracing the impact of the Andean  
586 uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences* **106**:  
587 9749–9754.

588 **Bacon CD, Velásquez-Puentes FJ, Hoorn C, Antonelli A. 2018.** Iriarteeae palms tracked the  
589 uplift of Andean Cordilleras. *Journal of Biogeography* **45**: 1653–1663.

- 590 **Bañares-de-Dios G, Macía MJ, Granzow-de la Cerda Í, Arnelas I, Martins de Carvalho G,**  
591 **Espinosa CI, Salinas N, Swenson NG, Cayuela L, et al. 2020.** Linking patterns and processes  
592 of tree community assembly across spatial scales in tropical montane forests. *Ecology* **101**: 1–13.
- 593 **Bell C, Donoghue MJ. 2005.** Phylogeny and biogeography of Valerianaceae (Dipsacales) with  
594 special reference to the South American valerians. *Organisms Diversity & Evolution* **5**: 147–159.
- 595 **Bone TS, Downie SR, Affolter JM, Spalik K. 2011.** A Phylogenetic and Biogeographic Study  
596 of the Genus *Lilaeopsis* (Apiaceae tribe Oenantheae). *Systematic Botany* **36**: 789–805.
- 597 **Boschman LM. 2021.** Andean mountain building since the Late Cretaceous: A paleoelevation  
598 reconstruction. *Earth-Science Reviews* **220**: 1–40.
- 599 **Bricca A, Conti L, Tardella MF, Catorci A, Iocchi M, Theurillat JP, Cutini M. 2019.**  
600 Community assembly processes along a sub-Mediterranean elevation gradient: analyzing the  
601 interdependence of trait community weighted mean and functional diversity. *Plant Ecology* **220**:  
602 1139–1151.
- 603 **Capurcho JMG, Borges SH, Cornelius C, Vicentini A, Prata EMB, Costa FM, Campos P,**  
604 **Sawakuchi AO, Rodrigues F, Zular A, et al. 2020.** Patterns and Processes of Diversification in  
605 Amazonian White Sand Ecosystems: Insights from Birds and Plants. In: Rull V, Carnaval AC,  
606 eds. Neotropical diversification: patterns and processes. Cham, Switzerland: Springer Nature,  
607 245–270.
- 608 **Carvajal-Endara S, Hendry AP, Emery NC, Davies TJ. 2017.** Habitat filtering not dispersal  
609 limitation shapes oceanic island floras: species assembly of the Galápagos archipelago. *Ecology*  
610 *Letters* **20**: 495–504.
- 611 **Cavender-Bares J, Kothari S, Meireles JE, Kaproth MA, Manos PS, Hipp AL. 2018.** The  
612 role of diversification in community assembly of the oaks (*Quercus* L.) across the continental  
613 U.S. *American Journal of Botany* **105**: 565–586.
- 614 **Cavender-Bares J, Reich PB. 2012.** Shocks to the system: community assembly of the oak  
615 savanna in a 40-year fire frequency experiment. *Ecology* **93**: 52–69.
- 616 **Chase JM. 2003.** Community assembly: when should history matter? *Oecologia* **136**: 489–498.

- 617 **Chaves JA, Weir JT, Smith TB. 2011.** Diversification in *Adelomyia* hummingbirds follows  
618 Andean uplift. *Molecular Ecology* **20**: 4564–4576.
- 619 **Chesson P. 2000.** Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology*  
620 *and Systematics* **31**: 343–366.
- 621 **Chi X, Tang Z, Fang J. 2014.** Patterns of phylogenetic beta diversity in China’s grasslands in  
622 relation to geographical and environmental distance. *Basic and Applied Ecology* **15**: 416–425.
- 623 **Claramunt S, Cracraft J. 2015.** A new time tree reveals Earth history’s imprint on the  
624 evolution of modern birds. *Science Advances* **1**: 1–13.
- 625 **Cleveland WS. 1981.** LOWESS: A program for smoothing scatterplots by robust locally  
626 weighted regression. *American Statistician* **35**: 54.
- 627 **Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT, Cardelus CL, Gilman AC,**  
628 **Longino JT. 2008.** Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in  
629 the Wet Tropics. *Science* **322**: 258–261.
- 630 **Donoghue MJ. 2008.** A phylogenetic perspective on the distribution of plant diversity.  
631 *Proceedings of the National Academy of Sciences* **105**: 11549–11555.
- 632 **Donoghue MJ, Edwards EJ. 2014.** Biome shifts and niche evolution in plants. *Annual Review*  
633 *of Ecology, Evolution, and Systematics* **45**: 547–572.
- 634 **Ehlers TA, Poulsen CJ. 2009.** Influence of Andean uplift on climate and paleoaltimetry  
635 estimates. *Earth and Planetary Science Letters* **281**: 238–248.
- 636 **Elias M, Joron M, Willmott K, Silvia-Brandao KL, Kaiser V, Arias CF, Gomez Pinerez**  
637 **LM, Uribe S, Brower AVZ, Freitas AVL, et al. 2009.** Out of the Andes: patterns of  
638 diversification in clearwing butterflies. *Molecular Ecology* **18**: 1716–1729.
- 639 **Emerson BC, Gillespie RG. 2008.** Phylogenetic analysis of community assembly and structure  
640 over space and time. *Trends in Ecology and Evolution* **23**: 619–630.
- 641 **Estes L, Elsen PR, Treuer T, Ahmed L, Caylor K, Chang J, Choi JJ, Ellis EC. 2018.** The  
642 spatial and temporal domains of modern ecology. *Nature Ecology and Evolution* **2**: 819–826.

643 **Feeley KJ, Bravo-Avila C, Fadrique B, Perez TM, Zuleta D. 2020.** Climate-driven changes in  
644 the composition of New World plant communities. *Nature Climate Change* **10**: 965–970.

645 **Flantua SGA, O’Dea A, Onstein RE, Giraldo C, Hooghiemstra H. 2019.** The flickering  
646 connectivity system of the north Andean páramos. *Journal of Biogeography* **46**: 1808–1825.

647 **Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW. 2018.** Climate change causes  
648 upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the*  
649 *National Academy of Sciences of the United States of America* **115**: 11982–11987.

650 **Fukami T. 2015.** Historical Contingency in Community Assembly: Integrating Niches, Species  
651 Pools, and Priority Effects. *Annual Review of Ecology, Evolution, and Systematics* **46**: 1–23.

652 **Fussmann GF, Loreau M, Abrams PA. 2007.** Eco-evolutionary dynamics of communities and  
653 ecosystems. *Functional Ecology* **21**: 465–477.

654 **Garzzone CN, Hoke GD, Libarkin JC, Withers S, MacFadden B, Eiler J, Ghosh P, Mulch**  
655 **A. 2008.** Rise of the Andes. *Science* **320**: 1304–1307.

656 **Garzzone CN, McQuarrie N, Perez ND, Ehlers TA, Beck SL, Kar N, Eichelberger N,**  
657 **Chapman AD, Ward KM, Ducea MN, et al. 2017.** Tectonic Evolution of the Central Andean  
658 Plateau and Implications for the Growth of Plateaus. *Annual Review of Earth and Planetary*  
659 *Sciences* **45**: 529–559.

660 **Gillespie RG, Bennett GM, Meester L De, Feder JL, Fleischer RC, Harmon LJ, Andrew P,**  
661 **Knope ML, Mallet J, Martin C, et al. 2020.** Comparing Adaptive Radiations Across Space,  
662 Time, and Taxa. *Journal of Heredity*: 1–20.

663 **Givnish T. 1997.** Adaptive radiations and molecular systematics: issues and approaches. In:  
664 Givnish T., Systma KJ, eds. *Molecular Evolution and Adaptive Radiation*. Cambridge:  
665 Cambridge University Press, 1–54.

666 **Givnish TJ, Barfuss MHJ, Ee B Van, Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily**  
667 **RS, Crayn DM, Smith JAC, et al. 2014.** Adaptive radiation, correlated and contingent  
668 evolution, and net species diversification in Bromeliaceae. *Molecular Phylogenetics and*  
669 *Evolution* **71**: 55–78.



670 **Givnish TJ, Spalink D, Ames M, Lyon SP, Hunter SJ, Zuluaga A, Iles WJD, Clements MA,**  
671 **Arroyo MTK, Leebens-Mack J, et al. 2015.** Orchid phylogenomics and multiple drivers of  
672 their extraordinary diversification. *Proceedings of the Royal Society B: Biological Sciences* **282**:  
673 1–13.

674 **Graham A. 2009.** The Andes: A geological overview from a biological perspective. *Annals of*  
675 *the Missouri Botanical Garden* **96**: 371–385.

676 **Graham CH, Parra JL, Rahbek C, McGuire J. 2009.** Phylogenetic structure in tropical  
677 hummingbird communities. *Proceedings of the National Academy of Sciences* **106**: 19673–  
678 19678.

679 **Griffiths AR, Silman MR, Farfán Rios W, Feeley KJ, Cabrera G, Meir P, Salinas N, Dexter**  
680 **KG, Vargas H. 2020.** Evolutionary heritage shapes tree distributions along an Amazon-to-  
681 Andes elevation gradient. *Biotropica* **53**: 38–50.

682 **Hardy OJ, Coutron P, Munoz F, Ramesh BR, Pélissier R. 2012.** Phylogenetic turnover in  
683 tropical tree communities: Impact of environmental filtering, biogeography and mesoclimatic  
684 niche conservatism. *Global Ecology and Biogeography* **21**: 1007–1016.

685 **Harsch MA, Hulme PE, McGlone MS, Duncan RP. 2009.** Are treelines advancing? A global  
686 meta-analysis of treeline response to climate warming. *Ecology Letters* **12**: 1040–1049.

687 **Hijmans RJ, Williams E, Vennes C. 2019.** Package ‘geosphere’. *spherical trigonometry*  
688 *package, version 1.5-10*, <https://CRAN.R-project.org/package=geosphere>.  
689

690 **Hinchliff CE, Smith SA, Allman JF, Burleigh JG, Chaudhary R, Coghill LM, Crandall**  
691 **KA, Deng J, Drew BT, Gazis R, et al. 2015.** Synthesis of phylogeny and taxonomy into a  
692 comprehensive tree of life. *Proceedings of the National Academy of Sciences* **112**: 12764–12769.

693 **Hoorn W, Steeg H, Bermudez MA, Mora A, Sevink J, Sanmartin I, Sanchez-Meseguer A,**  
694 **Anderson CL, Figueiredo JP, Jaramillo C, et al. 2010.** Amazonia Through Time: Andean  
695 Uplift, Climate Change, Landscape Evolution, and Biodiversity. *Science* **330**: 927–931.

696 **Hughes C, Eastwood R. 2006.** Island radiation on a continental scale: Exceptional rates of plant

697 diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences* **103**:  
698 10334–10339.

699 **Hughes CE, Pennington RT, Antonelli A. 2013.** Neotropical Plant Evolution: Assembling the  
700 Big Picture. *Botanical Journal of the Linnean Society* **171**: 1–18.

701 **Jiménez I, Distler T, Jørgensen PM. 2009.** Estimated plant richness pattern across northwest  
702 South America provides similar support for the species-energy and spatial heterogeneity  
703 hypotheses. *Ecography* **32**: 433–448.

704 **Jin LS, Cadotte MW, Fortin MJ. 2015.** Phylogenetic turnover patterns consistent with niche  
705 conservatism in montane plant species. *Journal of Ecology* **103**: 742–749.

706 **Jin Y, Qian H. 2019.** V.PhylMaker: an R package that can generate very large phylogenies for  
707 vascular plants. *Ecography* **42**: 1353–1359.

708 **Kelly DL, Tanner EVJ, Lughadha EMN, Kapos V. 1994.** Floristics and Biogeography of a  
709 Rain Forest in the Venezuelan Andes. *Journal of Biogeography* **21**: 421–440.

710 **Knox EB, Palmer JD. 1995.** Chloroplast DNA evidence on the origin and radiation of the giant  
711 lobelias in eastern Africa. *Systematic Botany* **23**: 109–149.

712 **Knox EB, Palmer JD. 1998.** Chloroplast DNA Evidence on the Origin and Radiation of the  
713 Giant Lobelias in Eastern Africa. *Systematic Botany* **23**: 109–149.

714 **Kubota Y, Kusumoto B, Shiono T, Ulrich W. 2018.** Environmental filters shaping angiosperm  
715 tree assembly along climatic and geographic gradients. *Journal of Vegetation Science* **29**: 607–  
716 618.

717 **Lagomarsino LP, Condamine FL, Antonelli A, Mulch A, Davis CC. 2016.** The abiotic and  
718 biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). *New Phytologist*  
719 **210**: 1430–1442.

720 **Legendre P, Cáceres M De. 2013.** Beta diversity as the variance of community data:  
721 dissimilarity coefficients and partitioning (H Morlon, Ed.). *Ecology Letters* **16**: 951–963.

722 **Losos JB. 2010.** Adaptive radiation, ecological opportunity, and evolutionary determinism. *The*

- 723 *American naturalist* **175**: 623–39.
- 724 **Luebert F, Weigend M. 2014.** Phylogenetic insights into Andean plant diversification.  
725 *Frontiers in Ecology and Evolution* **2**: 1–17.
- 726 **Madriñán S, Cortés AJ, Richardson JE. 2013.** Páramo is the world's fastest evolving and  
727 coolest biodiversity hotspot. *Frontiers in Genetics* **4**: 1–7.
- 728 **McGill BJ, Chase JM, Hortal J, Overcast I, Rominger AJ, Rosindell J, Borges PAV,**  
729 **Emerson BC, Etienne R, Hickerson MJ, et al. 2019.** Unifying macroecology and  
730 macroevolution to answer fundamental questions about biodiversity. *Global Ecology and*  
731 *Biogeography* **28**: 1925–1936.
- 732 **McPeck MA. 2017.** *Evolutionary Community Ecology*. Princeton: Princeton University Press.
- 733 **Menon M, Bagley JC, Friedline CJ, Whipple A V., Schoettle AW, Leal-Sàenz A, Wehenkel**  
734 **C, Molina-Freaner F, Flores-Rentería L, Gonzalez-Elizondo MS, et al. 2018.** The role of  
735 hybridization during ecological divergence of southwestern white pine (*Pinus strobiformis*) and  
736 limber pine (*P. flexilis*). *Molecular Ecology* **27**: 1245–1260.
- 737 **Montaño-Centellas FA, McCain C, Loiselle BA. 2019.** Using functional and phylogenetic  
738 diversity to infer avian community assembly along elevational gradients. *Global Ecology and*  
739 *Biogeography* **29**: 232–245.
- 740 **Moore BR, Donoghue MJ. 2007.** Correlates of Diversification in the Plant Clade Dipsacales :  
741 Geographic Movement and Evolutionary Innovations. *The American Naturalist* **170**: 28–55.
- 742 **Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000.** Biodiversity  
743 hotspots for conservation priorities. *Nature* **403**: 853–858.
- 744 **Nevado B, Atchison GW, Hughes CE, Filatov DA. 2016.** Widespread adaptive evolution  
745 during repeated evolutionary radiations in New World lupins. *Nature Communications* **7**: 1–9.
- 746 **Nevado B, Contreras-Ortiz N, Hughes C, Filatov DA. 2018.** Pleistocene glacial cycles drive  
747 isolation, gene flow and speciation in the high-elevation Andes. *New Phytologist* **219**: 779–793.
- 748 **Neves DM, Dexter KG, Baker TR, Coelho de Souza F, Oliveira-Filho AT, Queiroz LP,**

- 749 **Lima HC, Simon MF, Lewis GP, Segovia RA, et al. 2020.** Evolutionary diversity in tropical  
750 tree communities peaks at intermediate precipitation. *Scientific Reports* **10**: 1–7.
- 751 **Nürk NM, Michling F, Linder HP. 2018.** Are the radiations of temperate lineages in tropical  
752 alpine ecosystems pre-adapted? *Global Ecology and Biogeography* **27**: 334–345.
- 753 **Nürk NM, Scheriau C, Madriñán S. 2013.** Explosive radiation in high Andean *Hypericum*-  
754 rates of diversification among New World lineages. *Frontiers in Genetics* **4**: 1–14.
- 755 **O’Sullivan KSW, Ruiz-Benito P, Chen JC, Jump AS. 2020.** Onward but not always upward:  
756 individualistic elevational shifts of tree species in subtropical montane forests. *Ecography* **44**:  
757 112–123.
- 758 **Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’hara RB, Simpson GL,  
759 Solymos P, Stevens MHH, Wagner H, et al. 2020.** Package ‘vegan’. *Community ecology*  
760 *package, version 2.5-6*, <https://cran.r-project.org/package=vegan>.
- 761 **Parolari AJ, Paul K, Griffing A, Condit R, Perez R, Aguilar S, Schnitzer SA. 2020.** Liana  
762 abundance and diversity increase with rainfall seasonality along a precipitation gradient in  
763 Panama. *Ecography* **43**: 25–33.
- 764 **Parra JL, Rahbek C, McGuire JA, Graham CH. 2011.** Contrasting patterns of phylogenetic  
765 assemblage structure along the elevational gradient for major hummingbird clades. *Journal of*  
766 *Biogeography* **38**: 2350–2361.
- 767 **Pelletier F, Garant D, Hendry AP. 2009.** Eco-evolutionary dynamics. *Philosophical*  
768 *Transactions of the Royal Society B: Biological Sciences* **364**: 1483–1489.
- 769 **Pennington RT, Lavin M. 2009.** Woody plant diversity, evolution, and ecology in the tropics:  
770 perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution, and*  
771 *Systematics* **40**: 437–457.
- 772 **Pérez-Escobar OA, Chomicki G, Condamine FL, Karremans AP, Bogarín D, Matzke NJ,  
773 Silvestro D, Antonelli A. 2017.** Recent origin and rapid speciation of Neotropical orchids in the  
774 world’s richest plant biodiversity hotspot. *New Phytologist* **215**: 891–905.

- 775 **Petit RJ, Hampe A. 2006.** Some Evolutionary Consequences of Being a Tree. *Annual Review of*  
776 *Ecology, Evolution, and Systematics* **37**: 187–214.
- 777 **Pouchon C, Fernández A, Nassar JM, Boyer F, Aubert S, Lavergne S, Mavárez J. 2018.**  
778 Phylogenomic analysis of the explosive adaptive radiation of the *Espeletia* complex (Asteraceae)  
779 in the tropical Andes. *Systematic Biology* **67**: 1041–1060.
- 780 **Poulsen CJ, Ehlers TA, Insel N. 2010.** Onset of convective rainfall during gradual late miocene  
781 rise of the central Andes. *Science* **328**: 490–493.
- 782 **Rahbek C, Graves GR. 2001.** Multiscale assessment of patterns of avian species richness.  
783 *Proceedings of the National Academy of Sciences* **98**: 4534–4539.
- 784 **Ramírez S, González-Caro S, Phillips J, Cabrera E, Feeley KJ, Duque Á. 2019.** The  
785 influence of historical dispersal on the phylogenetic structure of tree communities in the tropical  
786 Andes. *Biotropica* **51**: 500–508.
- 787 **Raven PH. 1963.** Amphitropical Relationships in the Floras of North and South America. *The*  
788 *Quarterly Review of Biology* **38**: 151–177.
- 789 **Revell LJ. 2012.** phytools: an R package for phylogenetic comparative biology (and other  
790 things). *Methods in ecology and evolution* **3**: 217–223.
- 791 **Ricklefs RE. 1987.** Community Diversity: Relative Roles of Local and Regional Processes.  
792 *Science* **235**: 167–171.
- 793 **Ricklefs RE. 2006.** Evolutionary diversification and the origin of the diversity-environment  
794 relationship. *Ecology* **87**: 3–13.
- 795 **Ruiz-Labourdette D, Nogués-Bravo D, Ollero HS, Schmitz MF, Pineda FD. 2012.** Forest  
796 composition in Mediterranean mountains is projected to shift along the entire elevational  
797 gradient under climate change. *Journal of Biogeography* **39**: 162–176.
- 798 **Schluter D. 2000.** *The ecology of adaptive radiation*. Oxford, U.K.: Oxford University Press.
- 799 **Segovia RA, Pennington RT, Baker TR, de Souza FC, Neves DM, Davis CC, Armesto JJ,**  
800 **Olivera-Filho AT, Dexter KG. 2020.** Freezing and water availability structure the evolutionary

801 diversity of trees across the Americas. *Science Advances* **6**: 1–9.

802 **Sheldon KS, Yang S, Tewksbury JJ. 2011.** Climate change and community disassembly:  
803 Impacts of warming on tropical and temperate montane community structure. *Ecology Letters*  
804 **14**: 1191–1200.

805 **Sklenář P, Dušková E, Balslev H. 2011.** Tropical and Temperate: Evolutionary History of  
806 Páramo Flora. *Botanical Review* **77**: 71–108.

807 **Sklenář P, Hedberg I, Cleef AM. 2014.** Island biogeography of tropical alpine floras. *Journal*  
808 *of Biogeography* **41**: 287–297.

809 **Smith SA, Brown JW. 2018.** Constructing a broadly inclusive seed plant phylogeny. *American*  
810 *Journal of Botany* **105**: 302–314.

811 **Sorensen TA. 1948.** A method of establishing groups of equal amplitude in plant sociology  
812 based on similarity of species content and its application to analyses of the vegetation on Danish  
813 commons. *Biol. Skar.* **5**: 1–34.

814 **Stroud JT, Losos JB. 2016.** Ecological Opportunity and Adaptive Radiation. *Annual Review of*  
815 *Ecology, Evolution, and Systematics* **47**: 507–532.

816 **Tanentzap AJ, Brandt AJ, Smissen RD, Heenan PB, Fukami T, Lee WG. 2015.** When do  
817 plant radiations influence community assembly? The importance of historical contingency in the  
818 race for niche space. *New Phytologist* **207**: 468–479.

819 **Thornhill AH, Baldwin BG, Freyman WA, Nosratinia S, Kling MM, Morueta-Holme N,**  
820 **Madsen TP, Ackerly DD, Mishler BD. 2017.** Spatial phylogenetics of the native California  
821 flora. *BMC Biology* **15**: 1–18.

822 **Ulloa CU, Acevedo-rodríguez P, Beck S, Belgrano MJ, Bernal R, Berry PE, Brako L, Celis**  
823 **M, Davidse G, León-yáñez S, et al. 2017.** An integrated assessment of the vascular plant  
824 species of the Americas. *Science*: 1–5.

825 **Uribe-Convers S, Tank DC. 2015.** Shifts in diversification rates linked to biogeographic  
826 movement into new areas: An example of a recent radiation in the Andes. *American Journal of*

827 *Botany* **102**: 1854–1869.

828 **Vellend M. 2016.** *The Theory of Ecological Communities*. Princeton: Princeton University Press.

829 **Verdui M. 2002.** Age at Maturity and Diversification in Woody Angiosperms. *Evolution* **56**:

830 1352–1361.

831 **Worthy SJ, Jiménez Paz RA, Pérez ÁJ, Reynolds A, Cruse-Sanders J, Valencia R, Barone**

832 **JA, Burgess KS. 2019.** Distribution and community assembly of trees along an Andean

833 elevational gradient. *Plants* **8**: 7–10.

834 **Young KR, Ulloa CU, Luteyn JL, Knapp S. 2002.** Plant evolution and endemism in Andean

835 South America: An introduction. *Botanical Review* **68**: 4–21.

836 **Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, Fitzjohn RG, McGlenn DJ,**

837 **O’Meara BC, Moles AT, Reich PB, et al. 2014.** Three keys to the radiation of angiosperms into

838 freezing environments. *Nature* **506**: 89–92.

839 **Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, FitzJohn RG, McGlenn DJ,**

840 **O’Meara BC, Moles AT, Reich PB, et al. 2013.** Three keys to the radiation of angiosperms into

841 freezing environments. *Nature* **506**: 89–92.

842

843 **Supporting Information legends**

**Methods S1: Additive decomposition of species turnover metrics.**

**Figure S1: Frequency distribution of plots used in our study along elevational gradient.**

**Figure S2: decomposed turnover across elevation excluding morphospecies.**

**Figure S3: number of species per clade across datasets.**

**Figure S4: decomposition of species turnover across elevational distance for 60my clades.**

**Figure S5: decomposed turnover across elevation excluding morphospecies.**

**Figure S6: logit transformed decomposition of turnover.**

**Figure S7: relationship between difference in elevation and geographic distance in our datasets.**

**Figure S8: Species turnover across geographic distance.**

**Figure S9: Decomposition of species turnover across geographic distance for 30my clades.**

844

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

858

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

860

861 **Figure 3. Species turnover across elevations.** Sørensen dissimilarity plotted against difference  
862 in elevation for each pair of plots in our two datasets. These patterns are presented separately for  
863 (A) large 1-ha plots and (B) small 0.1-ha plots. (C; Laguna Chalalan in Bolivia at 400 m  
864 elevation) and upper montane cloud forests (D; Trocha Union in Peru at 3,260 m). Pictures by  
865 Christopher Davidson, Sharon Christoph and William Farfan-Ríos.

866



867 **Figure 4. Decomposition of species turnover across elevational gradients into among-clade**  
868 **and within-clade components – 30 my clades from small and large plots.** Sorensen  
869 dissimilarities between each pair of plots were decomposed into within-clades (blue lines) and  
870 among-clades (yellow lines) components. We then plotted these components of turnover against  
871 difference in elevation in large plots (upper panels) and small plots (lower panels). Finally, we  
872 compared spatial patterns in variation of these components with a tip-randomization null model  
873 that removes any phylogenetic structure in the distribution of species across elevation. (A. & D.)  
874 observed patterns; (B. & E.) patterns for the mean of the expectations in the null model; (C & F)  
875 patterns for standardized effect sizes showing the deviation of the observed values from null  
876 expectations.

877  
878 **Figure 5. Comparison of linear slopes.** Observed slopes of logit transformed proportional  
879 turnover across elevational distance (triangles) compared to the distribution of 999 slopes  
880 produced by the null model (boxplots) in (A) large plots and (B) small plots. The box depicts the  
881 inter-quartile range with the median denoted by the horizontal line. The whiskers represent 1.5  
882 times the inter-quartile range with outliers denoted as circles.

883  
884  
885  
886  
887 **Table 1.** Summary of datasets used for analyses and p-values assessing significance of observed  
888 gradients in among-clade and within-clade turnover across elevational (elev) and geographic  
889 (geo) distances. Datasets varied by plot size, inclusion of morphospecies, and age of clades.

Inclusion of Morpho-species.	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)
<b>Large plots (73)</b>									
Included	1889	30	355	203	5.36	0.001	0.001	0.553	0.553
Included	1889	60	141	34	13.50	0.001	0.001	0.424	0.424
Excluded	1349	30	310	168	4.37	0.001	0.001	0.223	0.223
Excluded	1349	60	138	34	9.81	0.001	0.001	0.87	0.87

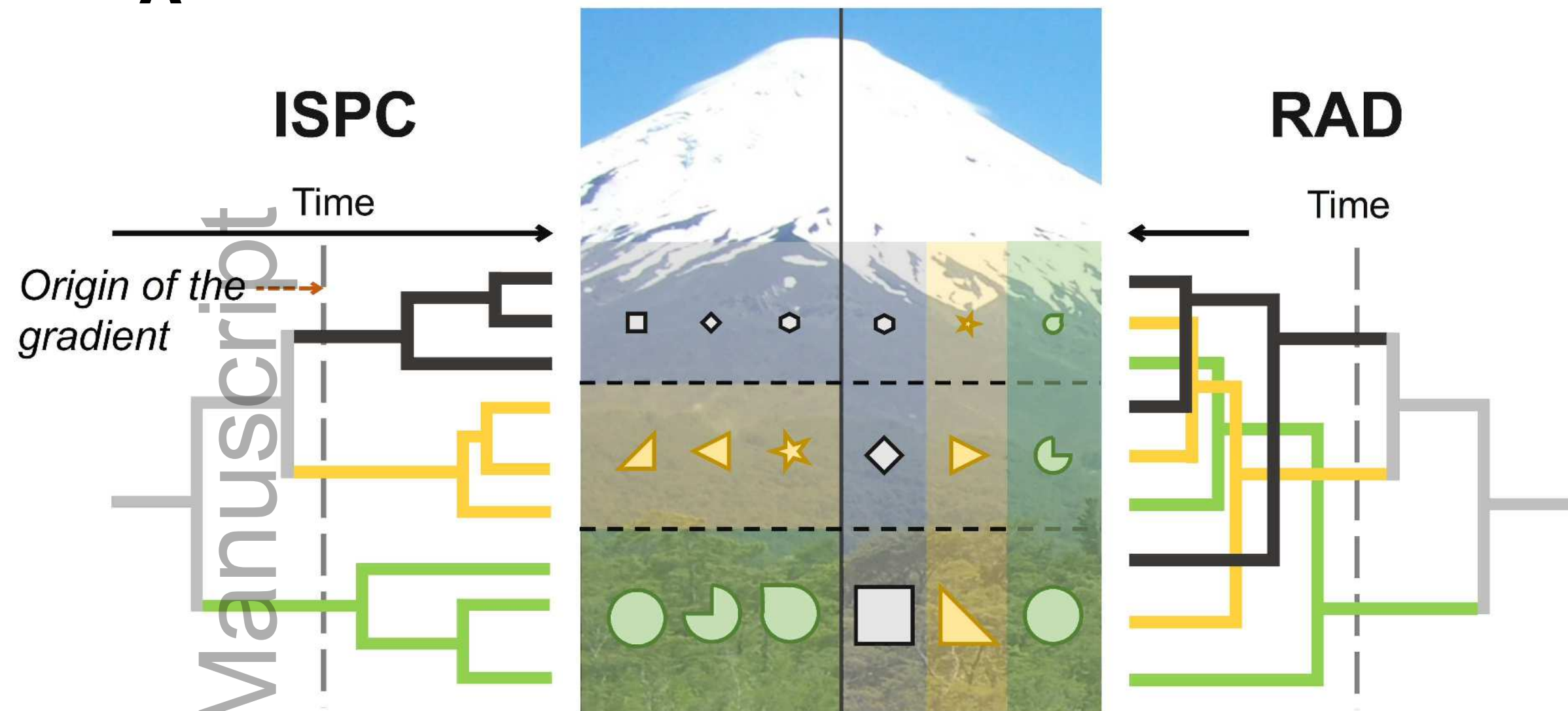
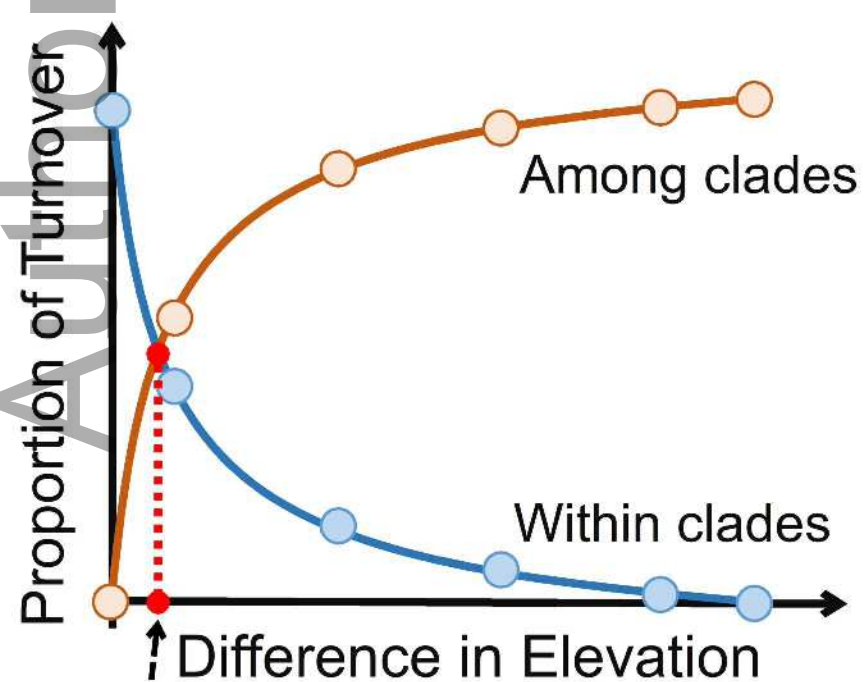
**Small plots (454)**

Included	2326	30	473	275	5.77	0.001	0.001	0.025	0.025
Included	2326	60	162	38	16.86	0.001	0.001	0.005	0.005
Excluded	1741	30	415	233	4.58	0.001	0.001	0.002	0.002
Excluded	1741	60	157	39	12.10	0.001	0.001	0.001	0.001

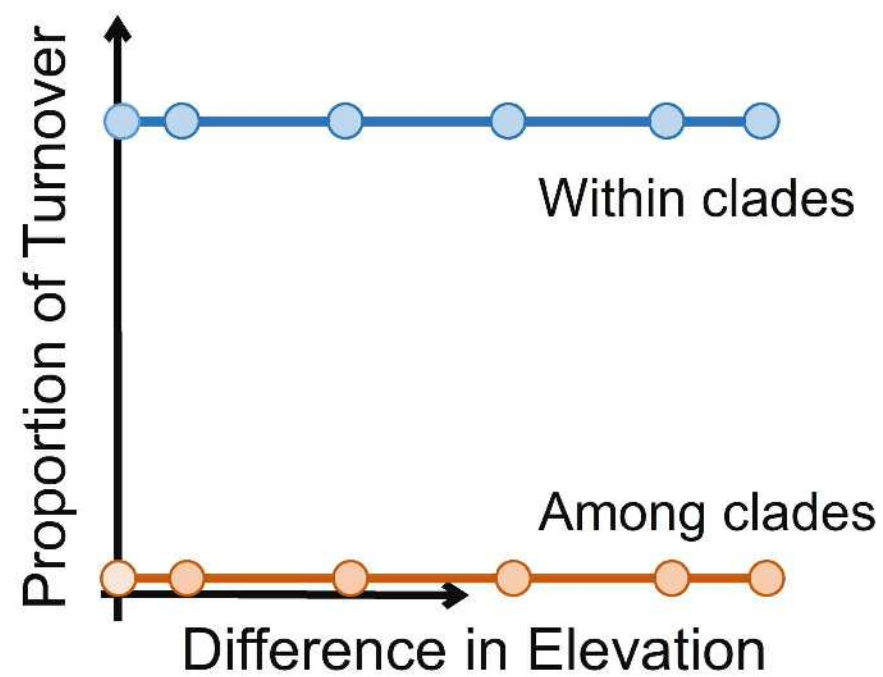
---

890

Author Manuscript

**A****B**

This article is protected by copyright. All rights reserved

*Intersection point***C**

Author Manuscript

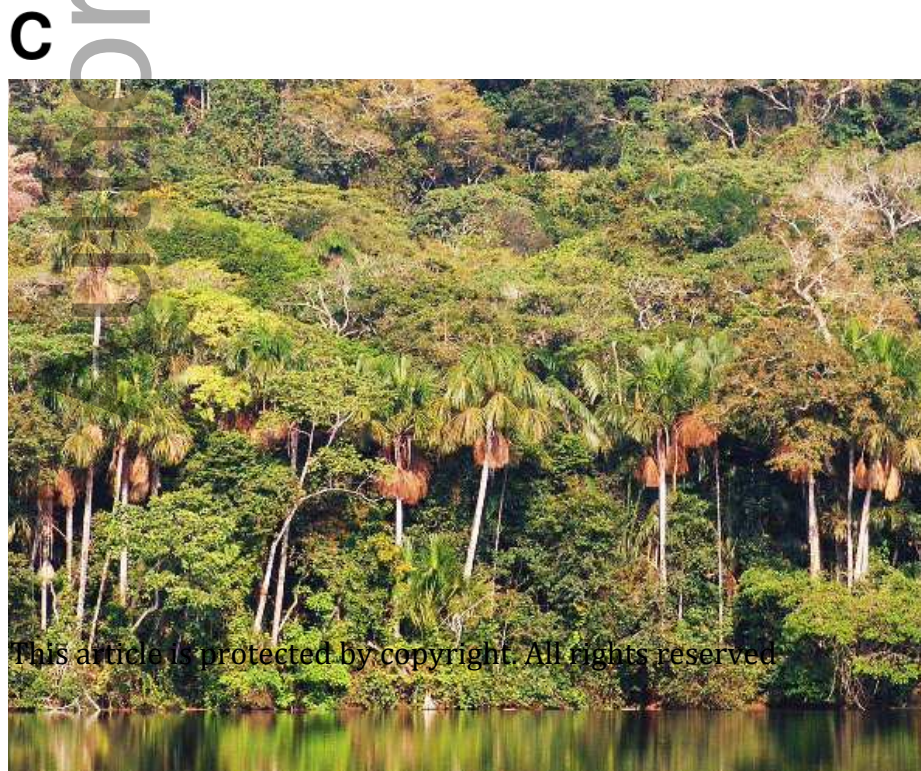
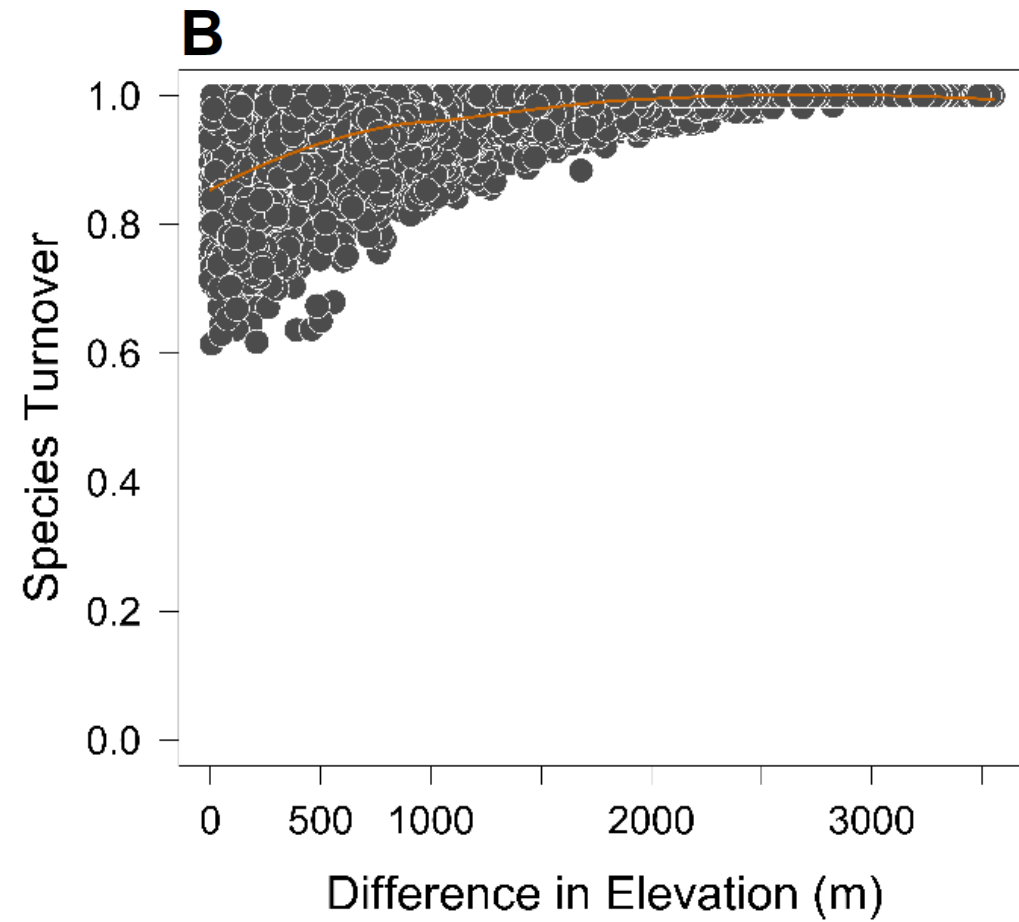
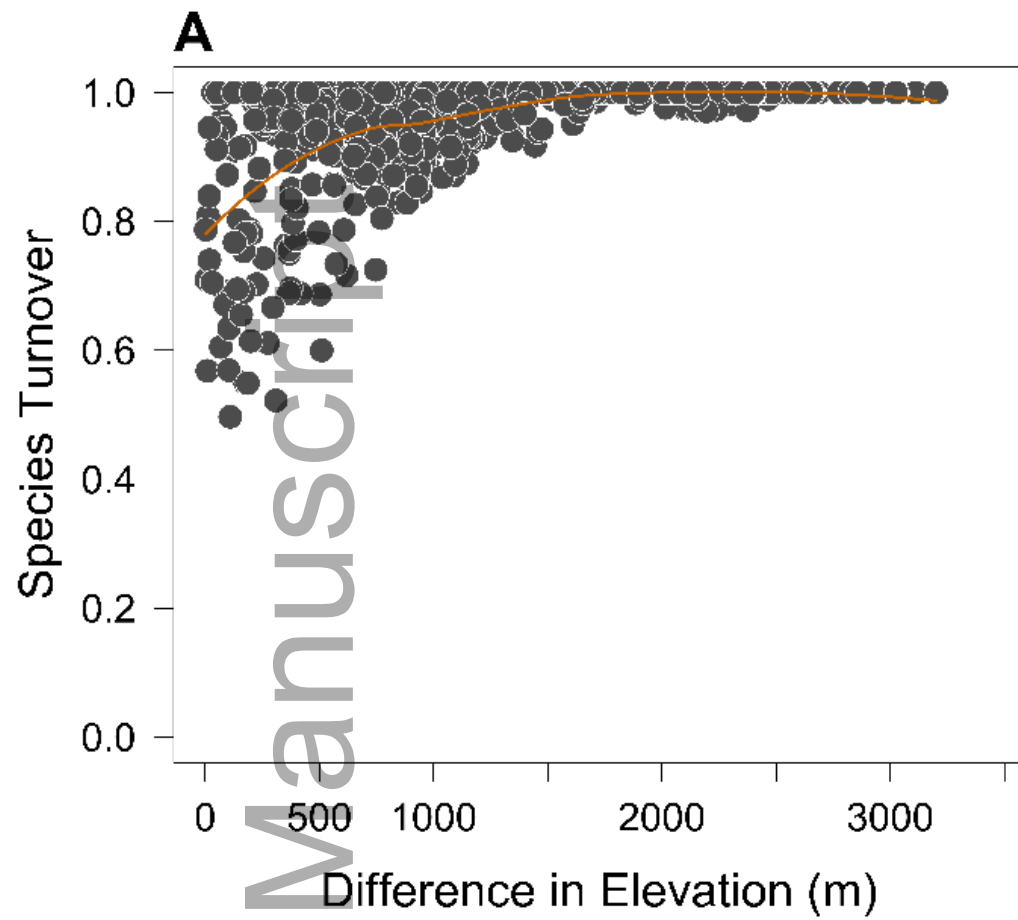
**Plots**

- Large Madidi
- Small Madidi
- Large ABERG
- Small ABERG

**Elevation (meters)**

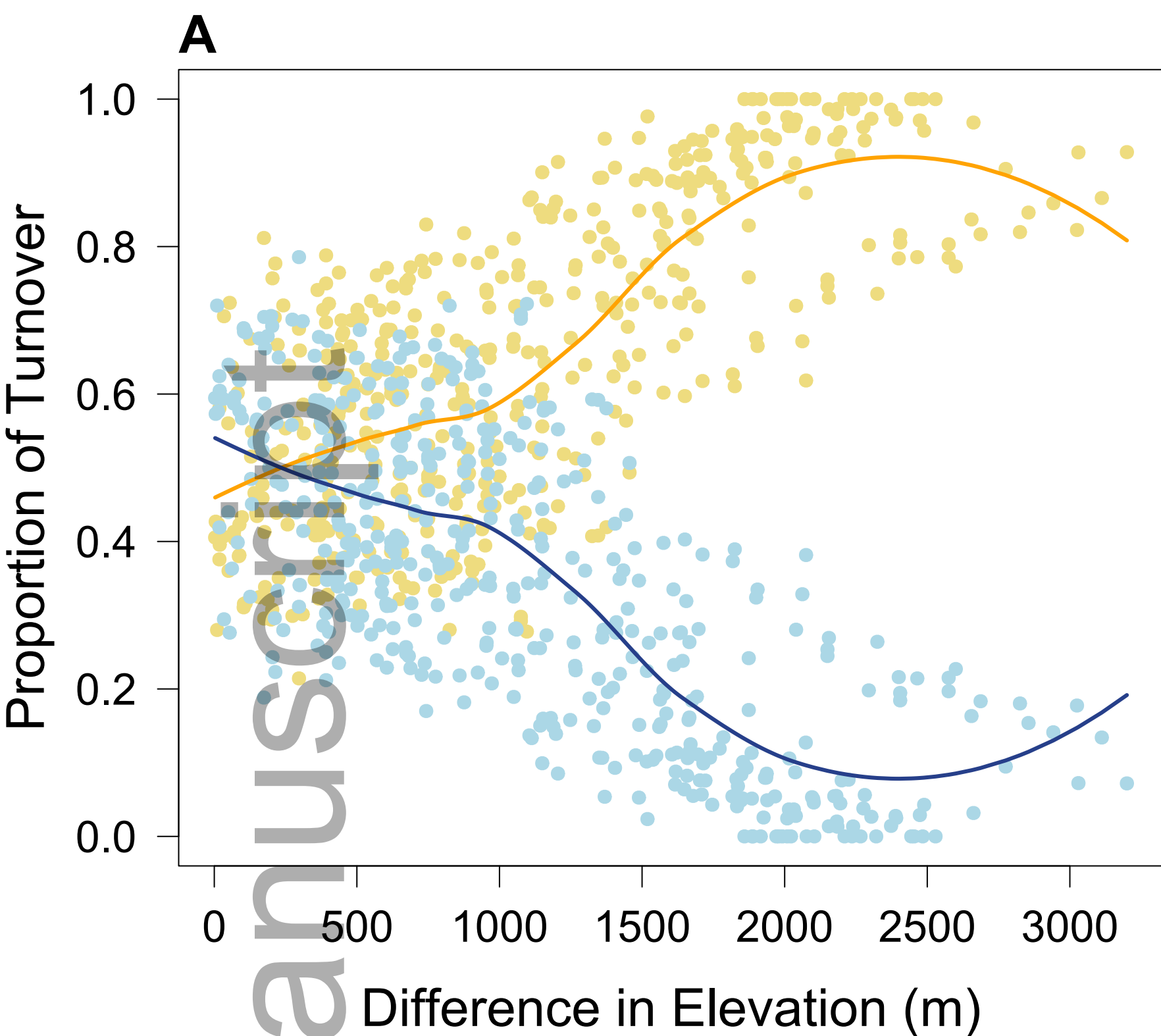
- High : 6543
- Low : 0





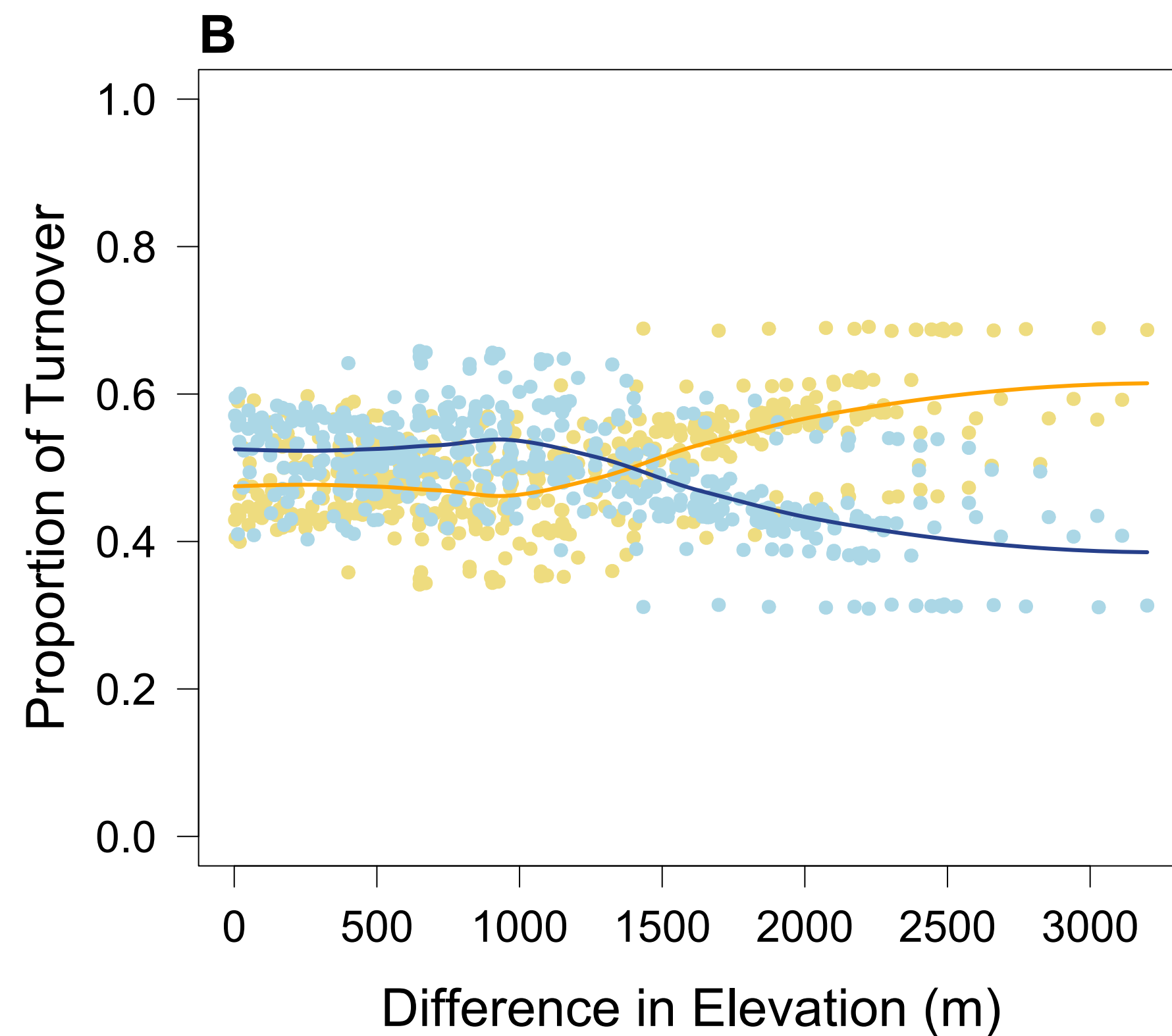


# Observed

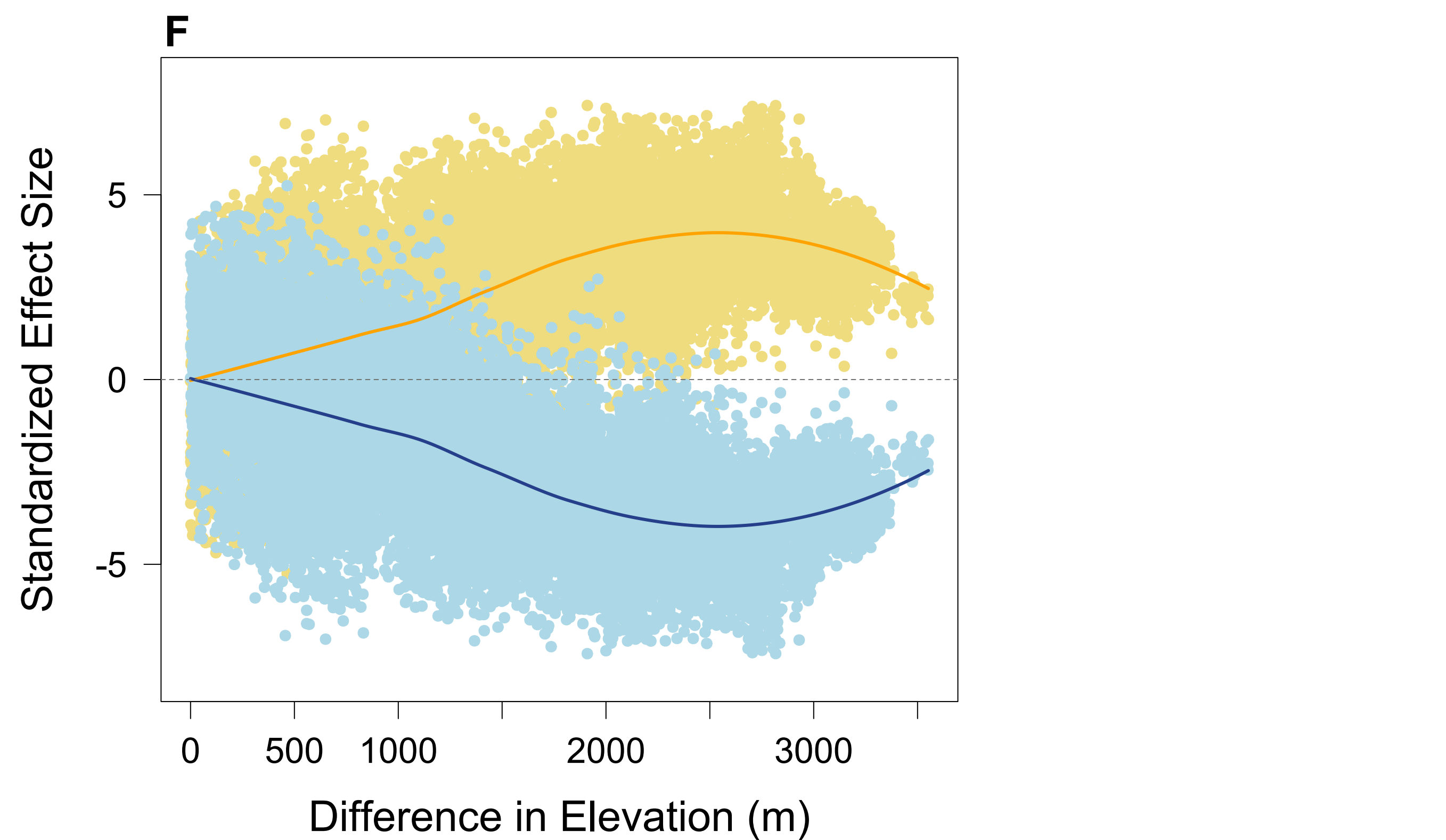
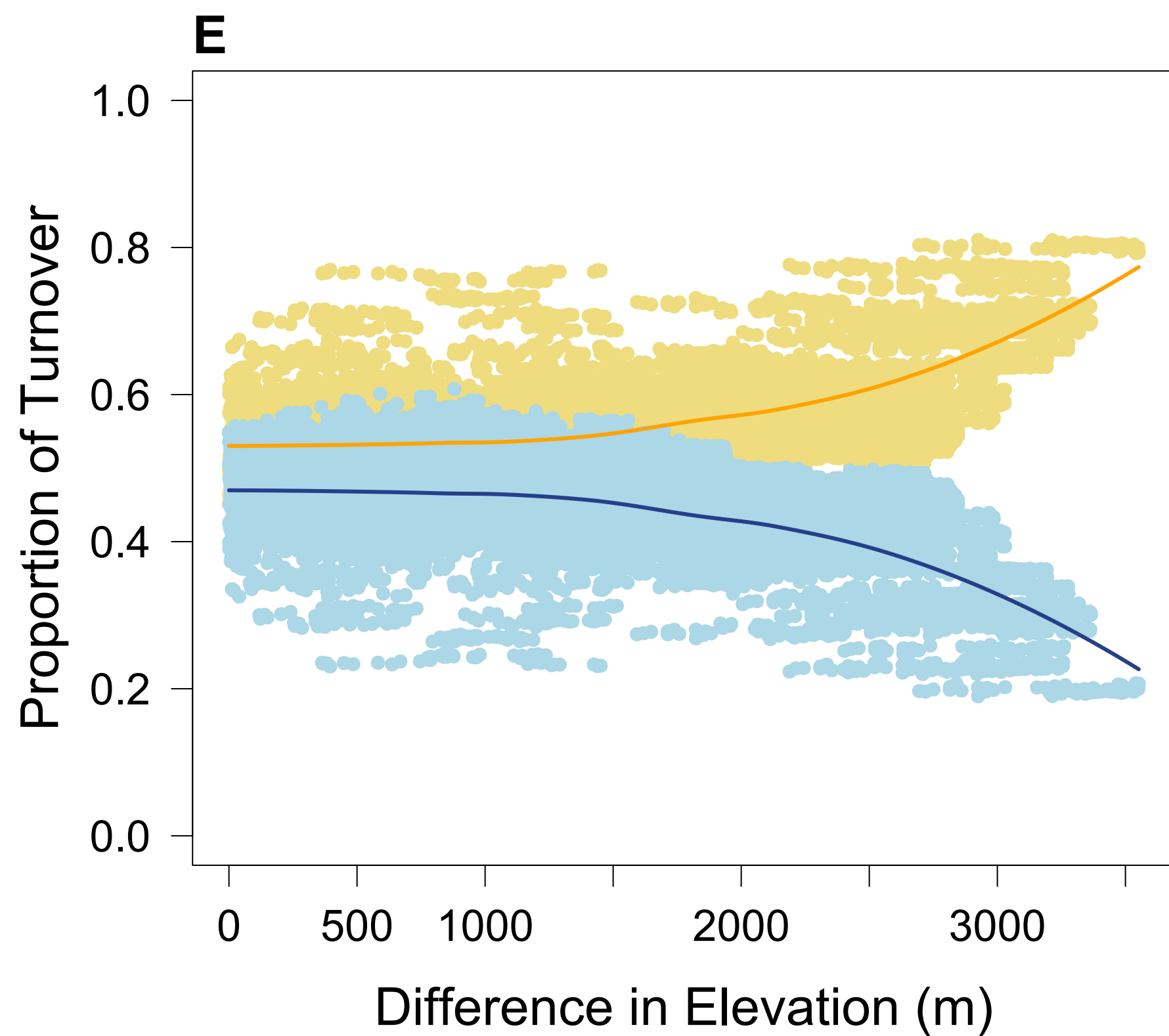
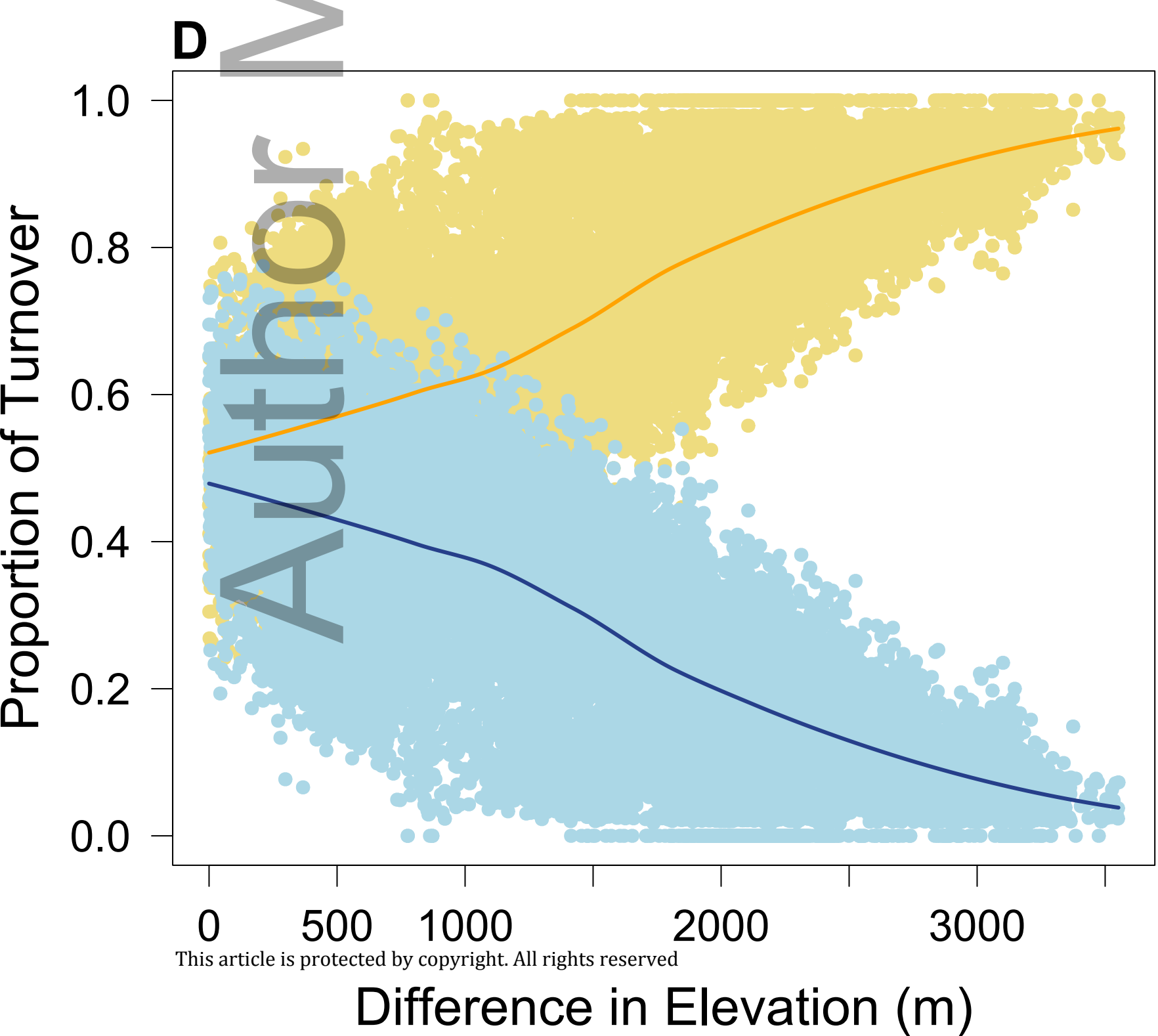
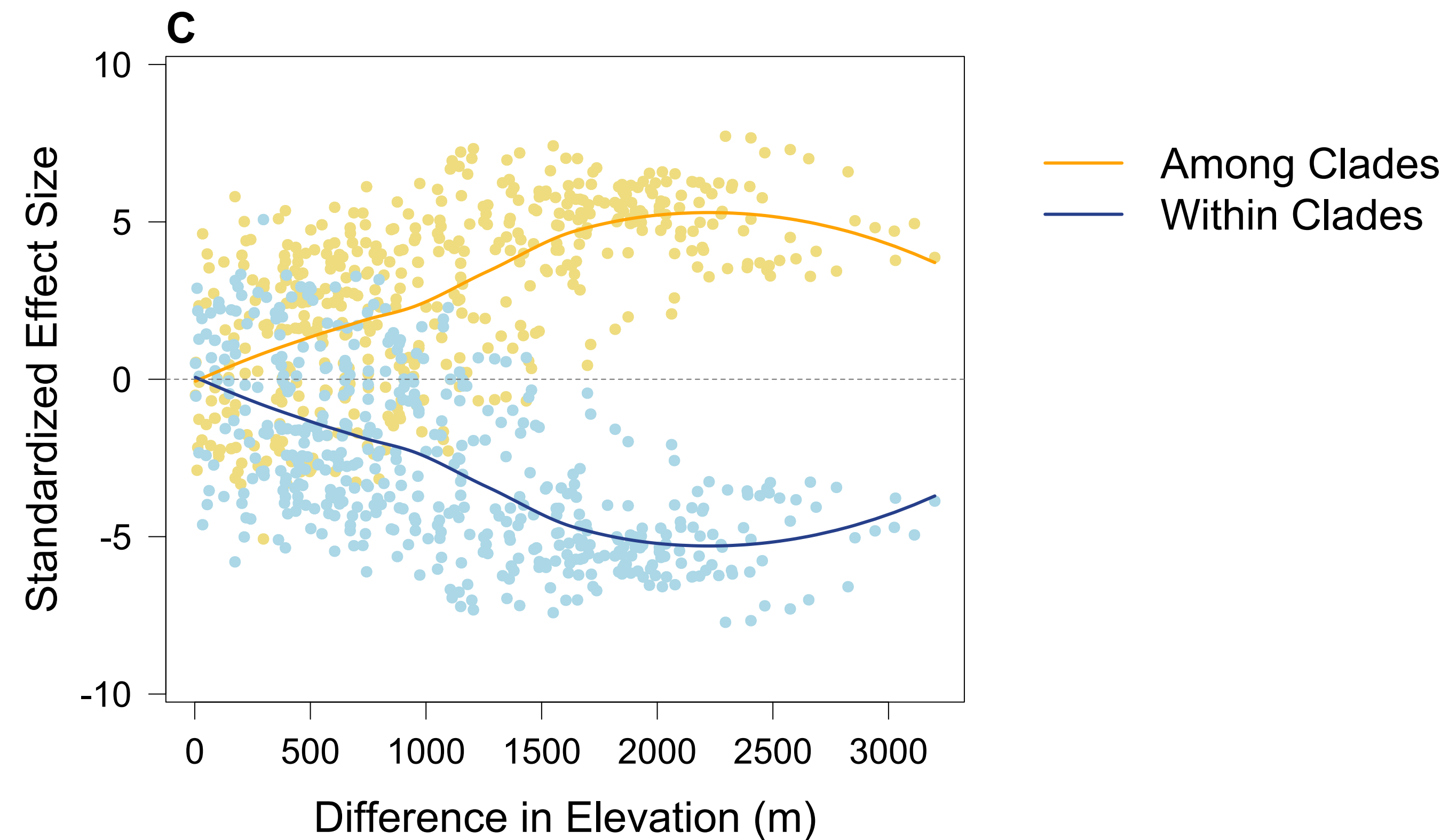


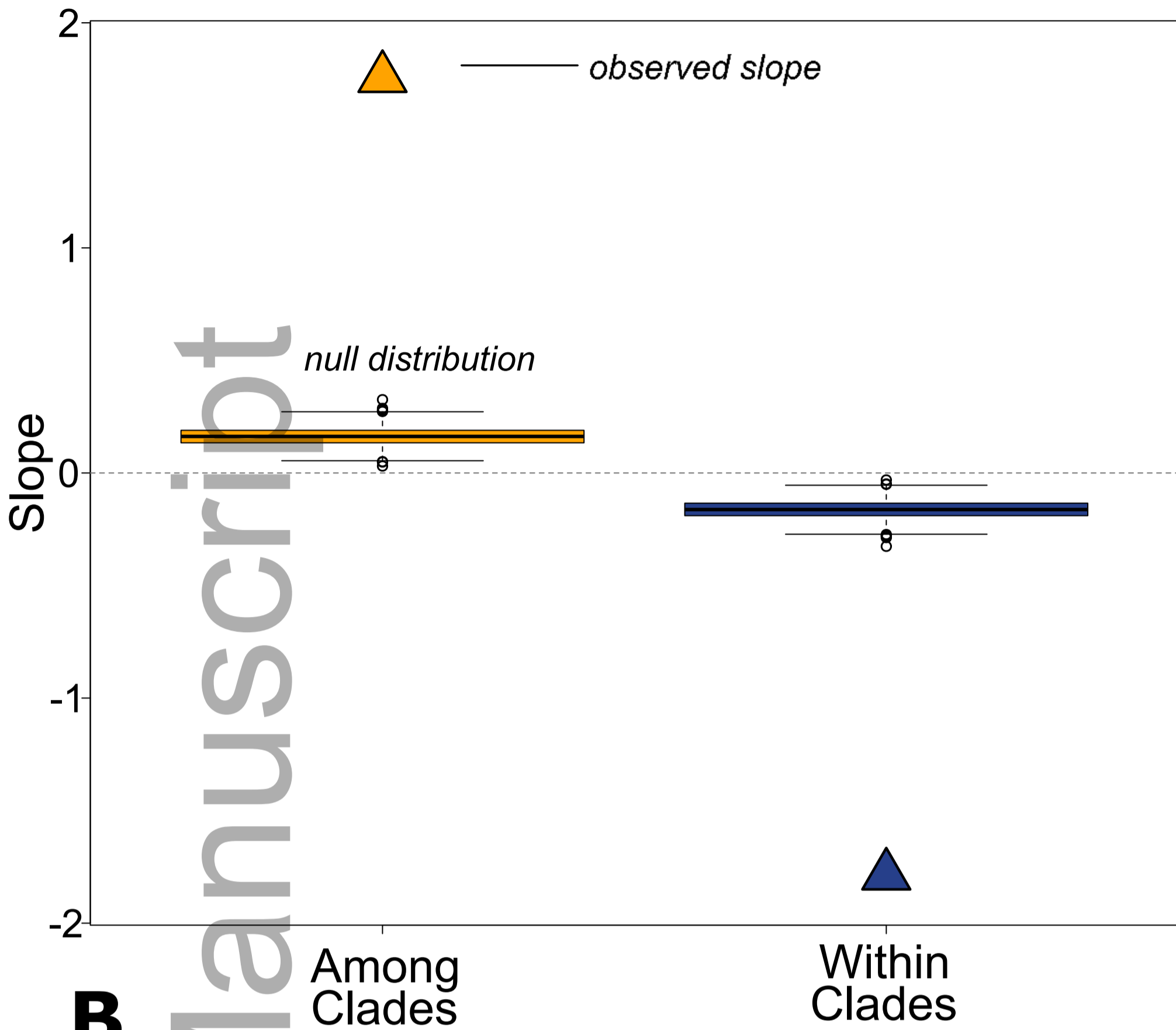
# Null

nph\_17674\_f4.pdf



# Deviations from Null



**A****B**