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Signals of recent tropical radiations in Cunoniaceae, an iconic family for understanding Southern Hemisphere biogeography

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Abstract

Extratropical angiosperm diversity is thought to have arisen from lineages that originated in the more diverse tropics, but studies of dispersal between tropical and extratropical environments and their consequences for diversification are rare. In order to understand the evolutionary effects of shifts between the tropics and extratropics, defined here as areas that *do* versus *do not* regularly experience freezing temperatures, we studied the biogeographic history and associated diversification patterns of Cunoniaceae. We mapped the distribution of all species in the family and combined this with a newly constructed phylogeny for the family. The family shows a long evolutionary association with both tropical and extratropical environments, the tropics house considerably greater species richness of Cunoniaceae. Indeed, both tropical and extratropical environments appear to have had a similar number of lineages until 12 Ma, after which time the number of lineages in tropical areas increased at a faster rate. In addition, community phylogenetic approaches show that tropical regions have markedly less phylogenetic diversity than expected given their species richness, which is further suggestive of recent species radiations in tropical areas. The Cunoniaceae show an atypical pattern for angiosperms of frequent shifts between tropical and extratropical environments, but despite this, shows a more conventional pattern of higher, although recent, diversification rates in the tropics. Our results support the idea that high angiosperm species richness in the tropics may result from the tropics acting as a cradle of recent angiosperm diversification.

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Introduction

The widely observed pattern of decreasing plant diversity from low to high latitudes is accompanied by conspicuous phylogenetic, taxonomic and functional turnover (*e. g.* [1, 2]). Within angiosperms, the evolutionary dispersal of tropical, low latitude lineages into extratropical, high latitudes is relatively rare [3, 4]. When such dispersal does occur, it is enabled by the evolution of functional traits conveying tolerance of freezing environments, such as herbaceous habit, deciduousness and hydraulic adjustments [5]. Similarly, the movement of temperate-adapted lineages back into truly tropical climates also seems rare [6]. As such, the modern distribution of angiosperm tree lineages across the Americas is strongly associated with the presence or absence of freezing temperatures [7]. Although the origin of extratropical plant diversity may be associated with the evolution of tolerance to freezing conditions [8], the persistent restriction of tropical lineages to tropical environments and extratropical lineages to extratropical environments [9] limits opportunities to study the evolutionary processes associated with shifts between tropical and extratropical environments (*e. g.* [10]). The angiosperm family Cunoniaceae offers one such rare opportunity to study the evolutionary history of a clade in the context of tropical-extratropical environmental shifts.

Cunoniaceae (Oxalidales) is an iconic Southern Hemisphere family, containing 28 genera and *c.* 300 species of trees and shrubs, inhabiting both tropical and extratropical environments [11]. The cross-continental distribution of genera such as *Cunonia, Weinmannia, Eucryphia* or *Caldcluvia* reflects a deep history in Southern Hemisphere landmasses. Indeed, the major diversification of the Cunoniaceae is thought to have occurred in the Gondwanan region [12]. However, whether tropical (*i. e.* frost-free environments)

and/or extratropical (*i. e.* freezing environments) environments are [31] associated with the initial and later diversification is currently unclear. [32] Similarly, a tropical or extratropical origin and diversification [33] of *Weinmannia*, the most speciose genus in the family (comprising [34] ~44% of species), has yet to be clarified [13]. [35]

Biogeographic studies on the distribution of the Southern [36] Hemisphere biota have traditionally centered on two main processes: [37] vicariance associated with the Gondwanan breakup [14, 15, 16, 17, [38] 18], and long-distance dispersal through wind and ocean currents [39] [19, 20, 21]. Yet, recently documented evidence for environmental [40] constraints on the evolution and dispersal of lineages [22, 23], underlines [41] the need to develop an alternative perspective in the study of [42] biogeography, based on the principle of phylogenetic niche or biome [43] conservatism. Moreover, Southern Hemisphere trends suggest that [44] the environmental divide between the tropics and extratropics may [45] be a key determinant of the distribution of modern-day diversity. For [46] example, phylogenetic analyses for lineages in the Southern Hemisphere [47] show that intercontinental dispersal events are more frequent [48] than environmental shifts, even between neighboring tropical and extratropical [49] biomes [24]. Furthermore, the fossil record shows a lower [50] than expected interchange of plant lineages between the Neotropics [51] and the extratropics of southern South America across the whole [52] Cenozoic [25]. [53]

Hypotheses regarding evolutionary biogeography can be [54] directly explored using phylogenetic approaches. For example, ancestral [55] state reconstructions can track the evolutionary history of [56] lineage characteristics, such as climatic niches, across a phylogenetic [57] tree [26, 27]. More recently, biogeographic insights have been provided [58] by analyzing variation in community phylogenetic structure [59] across biogeographic regions, biomes and environmental gradients [60] (*e. g.* [28, 29, 30, 31]). Standardized phylogenetic diversity (sPD), [61]

that is phylogenetic diversity (PD) given variation in species richness [62] (SR), can be used as a metric of community phylogenetic structure [63] [32]. Areas with significantly lower PD than expected, given SR, are [64] composed of closely related species. Such phylogenetic clustering of [65] related species in an assemblage can result from rapid speciation, se- [66] lective extinction of older lineages, or reduced interchange of lineages [67] among communities or geographic regions [33, 34]. In contrast, areas [68] with significantly greater PD than expected, given SR, are composed [69] of distantly related species. Such phylogenetic overdispersion can [70] result from lower diversification rates in recent time than deeper time, [71] higher recent extinction, or frequent interchange of distantly related [72] lineages among regions [33, 34]. [73]

In this study, we combine a newly derived phylogeny for [74] Cunoniaceae with global occurrence and climatic data to gain insight [75] into how dispersal events across the tropical-extratropical divide [76] shaped the evolutionary biogeography of the family. We firstly re- [77] construct the ancestral tropical or extratropical affiliation of all 28 [78] described genera within Cunoniaceae. In addition, we make a com- [79] parison of phylogenetic structure, phylogenetic signal, and variation [80] in lineage diversity through time between tropical, non-freezing envi- [81] ronments and extratropical, freezing environments. The evolutionary [82] origins of angiosperms in general is thought to have occurred in [83] tropical, non-freezing environments, with only a subset of lineages [84] evolving tolerance to freezing conditions and making the shift to [85] extratropical environments [8]. If the Cunoniaceae follow this gen- [86] eral tropical-origin trend, we anticipate a phylogenetically clustered [87] pattern in assemblages from extratropical environments and/or a [88] phylogenetic signal for extratropicality (*i. e.* extratropical species [89] will be more closely related than expected by chance). Alternatively, [90] if tropical distribution is an evolutionary novelty within the Cunon- [91] iaceae, with tropical lineages deriving from extratropical lineages, [92]

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we expect phylogenetic clustering in assemblages from tropical environments, and/or a phylogenetic signal for tropicality. Finally, we evaluate whether there is phylogenetic structure behind the variation in species richness of Cunoniaceae across climatic space. In environments where Cunoniaceae has experienced a recent and rapid species radiation, we expect assemblages to have both high species richness and display phylogenetic clustering (*i. e.* significantly low sPD values). In contrast, in environments where the diversification of Cunoniaceae has been comparatively slow, we expect random sPD values centred on zero, or a pattern of phylogenetic overdispersion (*i. e.* significantly high sPD values), if there are many old, yet undiversified lineages.

Material and Methods

Distribution dataset

Cunoniaceae occurrence data were downloaded from GBIF on August 28th, 2019 using the 'occ_search' function in the 'rgbif' package [35] for R [36]. First, we excluded duplicate and incomplete occurrences. Then, we used the function 'clean_coordinates' in the R package 'CoordinateCleaner' [37] to filter the occurrence data, excluding collections from capitals, centroids of countries, GBIF headquarters, natural history institutions, and collections occurring in the sea. We also identified records considered as outliers in the environmental space the given species occupies. Environmental outlier detection was performed by running a reverse-jackknife method on six climatic variables: mean annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, mean annual precipitation, precipitation of the wettest month, and precipitation of the driest month, extracted from WorldClim [38]. These

variables were selected to reflect the climatic averages and boundaries of species' ranges. The method, which has precedence (*e. g.* [39, 40], consists of identifying outlier samples (*i. e.* occurrences) for each climatic variable based on a critical threshold derived from the mean, standard deviation, and range of the whole set of samples for a given species (*i. e.* all occurrence points). Potential outlier occurrences were determined as those where values for at least 2 of the 6 ($> 20\%$) environmental variables were identified as statistical outliers. If there was not enough information to compute this analysis (here, less than 10 occurrences for a given species), then the environmental outlier analysis was not performed. The final GBIF distribution dataset contained 54,717 records, with an average of 181 records per species, a minimum of 1 record (for 19 spp) and a maximum of 26,432 records (for *Weinmannia racemosa*).

Ecological Classification

Given the climatic [41] and evolutionary [7] importance of freezing environments as a division between tropics and extratropics, we classified the species in our dataset as Tropical, Extratropical or Generalist based on the proportion of occurrences subject to regularly freezing temperatures. We defined the tropics as those environments not subject to freezing temperatures in a normal year. The extratropics were conversely defined as those environments subjected to regular freezing temperatures. Using a global climatic layer for cumulative frost days over 117 years between 1901 and 2018 (Climatic Research Unit (CRU), [42]), we defined 117 total days of freezing (*i. e.* one day of frost per year on average) as the threshold for 'regularly experiencing' freezing temperatures versus not. Some regions can sum 117 days with freezing temperatures in a non-regular way, such as areas subject to periodic polar outbreaks [43]. However, we consider our approach to provide an objective threshold for environments
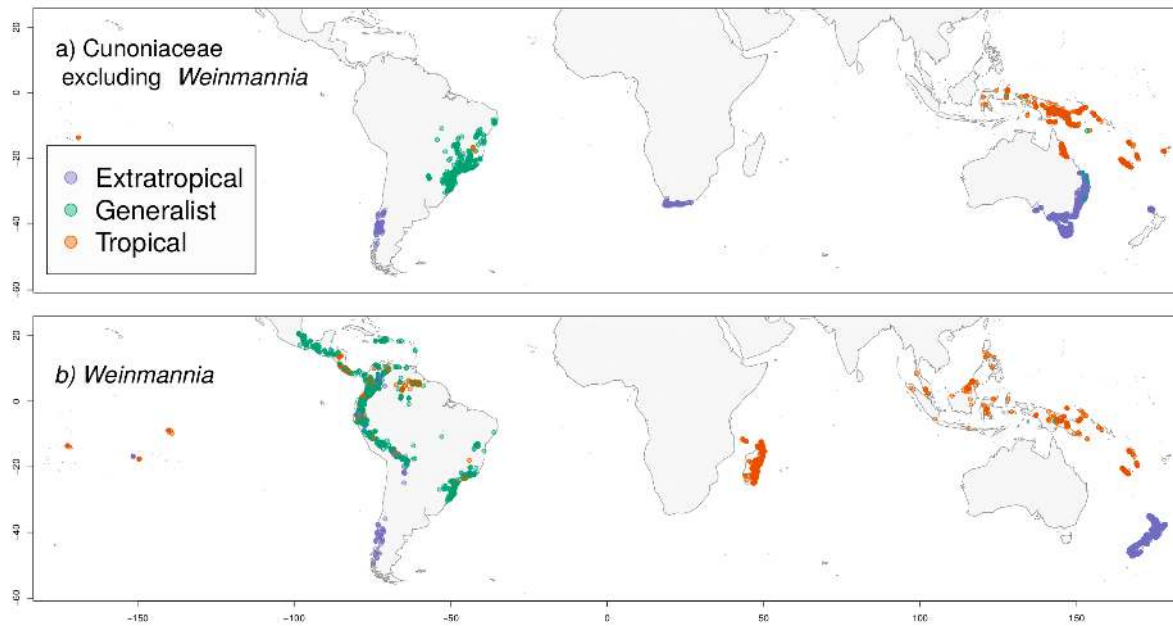
Figure 1. Distribution of the family Cunoniaceae. a) Distribution of the family Cunoniaceae excluding *Weinmannia* (169 non-Weinmannia spp) and b) Distribution of *Weinmannia* (133 spp). Purple dots represent occurrences of species classified as Extratropical. Orange dots represent occurrences of species classified as Tropical. Green dots represent occurrences of species classified as Generalist.

where freezing is relevant. Based on these freezing data we defined Extratropical species as those with more than 75% of their occurrences in regions with regular freezing temperatures and Tropical species as those with less than 25% of occurrences in regions with regular freezing. Those species with a percentage between 25% and 75% of occurrences in regions with regular freezing were classified as "Generalists" (Fig. 1).

Phylogeny Construction

In order to build the phylogeny, sequence data from NCBI were gathered using PyPHLAWD, with a clustering method [44]. The 6 best clusters (trnL (52 spp), phyC (45 spp), rbcL (42 spp), ncpGS (38 spp), GapC (20 spp), matK (15 spp)) were aligned individually in MAFFT [45]. The total matrix included 82 species from 22 genera,

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and 7,179 bps. A Maximum Likelihood tree was estimated using 170
RaxML v8.2.12 [46], with a separate GTR + Γ model for each 171
gene. This resulting phylogeny was then temporally calibrated using 172
treePL [47], with the crown age for the family taken from the its 173
first occurrence in the fossil record: Maastrichtian [48]. Thus, we set 174
crown age to a maximum of 70 Myr and a minimum of 66 Myr. 175

We manually added genera to the phylogeny for which no 176
DNA sequences were available. Exact placement of manual additions 177
was based on consultation of morphological and molecular phylogenies 178
for Cunoniaceae and sections thereof (Table 1). Added genera were 179
placed halfway along the branch leading to their sister genus or clade 180
in the phylogeny. Branch lengths leading to added genera were set 181
such that the tree remained ultrametric. Then, we randomly added 182
species without sequence data into their respective genus. 183

Table 1 Genera added to the molecular phylogeny in this study, because they were present in 184
the distributional dataset, but lacked DNA sequence data to be placed in molecular phylogeny we 185
generated. The position is represented in relation to the most closely related genera following the 186
cited reference. 187

Genus	Phylogenetic position	Reference
Ackama	(*Ackama, Spiraeopsis*)	[13]
Acrophyllum	(*Acrophyllum, Eucryphia*)	[49]
Acsmithia	(*Acsmithia, Spiraeanthemum*)	[13]
Aistopetalum	(*Aisotopetalum, Hooglandia*) *weakly supported	[49]
Bauera	(*Bauera, Ceratopetalum*)	[49]
Opocunonia	(*Opocunonia* (*Ackama, Spiraeopsis*))	[13]

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Analyses 189

To assess tropical or extratropical associations at deeper evolutionary 190
levels within our phylogeny, we reconstructed ancestral states accord- 191
ing to our ecological classification for species. These analyses were 192
conducted at the genus-level because the relationships of many species 193

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within genera are uncertain, particularly for un-sequenced species, [194] while we have greater confidence in the relationships amongst genera [195] (the majority of nodes in the phylogeny deeper than the genus-level [196] have maximum likelihood bootstrap support values ≥ 70). Genera [197] were classified as Tropical if all the species within a given genus [198] were classified as Tropical (10 genera). Those genera with all their [199] species classified as Extratropical were classified as Extratropical (7 [200] genera). Otherwise, genera were considered Generalist (11 genera). [201] Prior to ancestral state reconstruction, we evaluated support for an [202] equal or unequal transition rate model (for transitions among the [203] three states), with the equal transition rate model best supported. [204] Ancestral states were then estimated using a maximum likelihood [205] with an equal rates model [27]. In order to illustrate the distribution [206] of genera across environmental space, we show the frequency of classi- [207] fied species occurrences across gradients of mean annual temperature [208] (MAT) and mean annual precipitation (MAP). [209]

We estimated taxonomic and phylogenetic indices of diver- [210] sity for the groups of species classified as "Tropical", "Extratropical" [211] or "Generalists". For phylogenetic indices of diversity, we estimated [212] Phylogenetic Diversity (PD, [50]) and Time Integrated Lineage Diver- [213] sity (TILD, [51]). As the number of lineages monotonically increase [214] towards the present, PD is weighted heavily towards lineage diversity [215] in recent evolutionary time compared to deeper evolutionary time. [216] TILD is estimated from a log-transformed number of lineages at each [217] point in time, which down-weights the influence of recent lineage [218] diversity and gives greater weight to deep-time lineage diversity. The [219] indices therefore can be considered complementary when making com- [220] parisons of phylodiversity across groups of species or regions [51]. We [221] also compared values of standardized Phylogenetic Diversity (sPD) [222] to evaluate the phylogenetic structure of the tropical, extratropical [223] and generalist assemblages as a whole. We investigated phylogenetic [224]

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signal for tropical or extratropical affinity of species using the D index [52] for binary traits (with 1,000 permutations in each case to test for significance). Lastly, in order to illustrate variation in lineage diversity over time, we also constructed lineage through time (LTT) plots for a phylogeny comprising all species in tropical regions versus a phylogeny comprising all species occurring in extratropical regions.

In order to evaluate the relationship between species richness, phylogenetic structure and environmental conditions, we arrayed our distributional dataset across an environmental space defined by Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP). Each species occurrence was assigned to a 'bin' coordinated by evenly partitioned vectors of MAT and MAP (60 and 40 bins for each vector, respectively). Thus, we created 2,400 potential bins of species in the environmental space. Many combinations of MAP and MAT do not have any Cunoniaceae species, so not all bins are filled. For each of the bins with species, we estimated species richness and calculated standardized Phylogenetic Diversity (sPD). We efficiently derived the sPD index for so many bins by calculating the first two moments of the null expectation for Phylogenetic Diversity (PD), and then using the moments to calculate a standardized effect size of PD for each bin, which we equate with sPD [53]. Considering the preponderance of *Weinmannia* in the family (133 spp out of 302 spp in our dataset), we estimated these indices on datasets both including and excluding this genus.

We assessed the significance of phylogenetic clustering or overdispersion for species found in each environmental bin by comparing the observed sPD values to the distribution of these values under a null model scenario. We did this because of concerns around artefactual correlations between species richness and sPD values [54]. To develop the null expectation for sPD values, we maintained the total species richness of each bin while randomly

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assigning species identities by sampling without replacement from   256
the pool of species present in the community matrix. We created 1,000   257
null assemblages per environmental bin. This null model assumes   258
that all species present in our dataset are equally able to colonize   259
any environmental bin. Bins were considered to be significantly   260
phylogenetically overdispersed or clustered if they occurred in the   261
lowest or highest 2.5% of the distribution of values from the null   262
assemblages (*i. e.*, a two-tailed test with $\alpha = 0.05$).   263

All analyses were conducted in the R Statistical En-   264
vironment [36] using functions in the "geiger" [55], "ape" [56],   265
"caper" [57], "Picante" [58], "biogeo" [59] and "PhyloMeasures"   266
[53] packages. A repository with the codes can be found in   267
https://github.com/ricardosegovia/Cunoniaceae.   268

Results   269

Across taxa with enough data to classify, 47 species from   270
16 genera were classified as Extratropical, 215 species from 21 genera   271
were classified as Tropical and 40 species from five genera were clas-   272
sified as Generalists (Table 2). Eight genera included both Tropical   273
and Extratropical species, while an additional three also included   274
Generalist species. Thus eleven genera in total are classified as gen-   275
eralist. Most of the Generalist species are from the *Weinmannia*   276
genus (33 of 40) and are found in the Andes (Fig. 1), which repre-   277
sent a mosaic of regularly freezing and non-freezing environments.   278
The other genera containing generalist species are *Bauera* (1 sp),   279
Schizoemeria (1 sp), *Spiraeanthemum* (2 spp) and *Lamanonia* (3   280
spp). Tropical species are largely distributed in northern Australia,   281
the Malay Archipelago (plus New Guinea) and Madagascar (Fig.   282
1). In contrast, Extratropical species are associated with southern   283
Australia, New Zealand, South Africa and southern South America   284

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(Fig. 1). Interestingly, *Weinmannia* is absent in Australia and is the only representative of the family in Madagascar (Fig. 1).

Ancestral state reconstructions cannot resolve a tropical or extratropical origin for the oldest nodes in the Cunoniaceae family tree. For example, the sister clade to the remainder of the family, composed of *Spiraeanthemum* and *Acsmithia*, has a high association with tropical environments, while the next sister clade of the
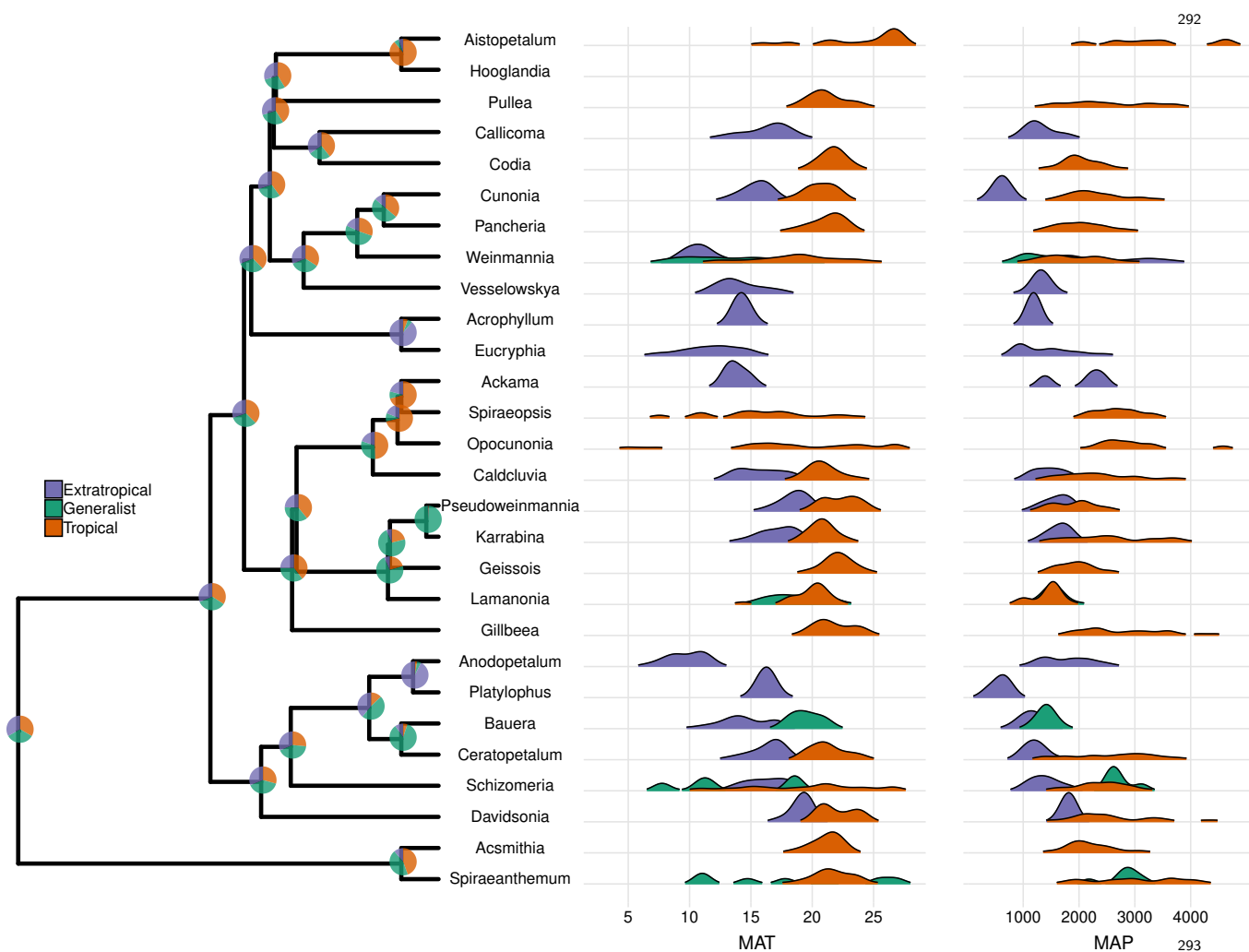

Figure 2. Genus-level phylogeny with ancestral state reconstruction for tropical or extratropical environments. The environmental distributions of Cunoniaceae genera across gradients of Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) are also shown. Colours in the right-hand panel illustrate the respective distributions for species within the genus classified as Tropical, Extratropical or Generalist.

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remainder of the family, composed by *Davidsonia*, *Schizoemeria*, 299
Ceratopetalum, *Bauera*, *Platylopus*, and *Anodopetalum*, tends more 300
towards an association with extratropical environments (Fig. 2). 301
In more recently derived clades, ancestral state probabilities show 302
environmental associations that have moved in both tropical-to- 303
extratropical, and extratropical-to-tropical directions (Fig. 2). The 304
high number of genera (11 of 28) with species in both the Tropics and 305
Extratropics further points to the high number of evolutionary shifts 306
between tropical and extratropical environments. Tropical species 307
tend to be distributed in areas with $\geq 20°C$ mean annual temperature 308
(MAT), although species from *Spiraeopsis* and *Opocunonia* can occur 309
at lower MAT (Fig. 2). On the other hand, Extratropical species are 310
distributed in environments with lower precipitation, especially the 311
African genera *Cunonia* and *Platylophus* (Fig. 2). 312

The lineage through time (LTT) plot shows that both 313
tropical and extratropical regions contain similar diversity in terms of 314
number of older lineages (~ 47 Ma) (Fig. 3). The tropical assemblage 315
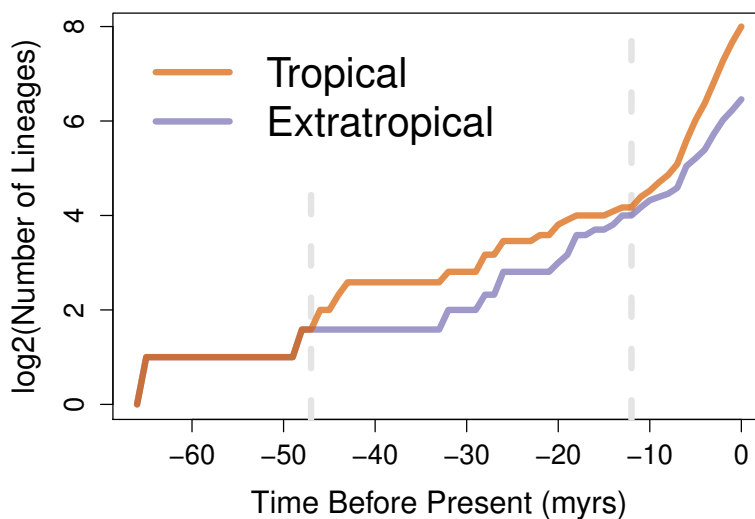
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Figure 3. Number of Lineages Through Time (LTT) for Tropical and Extratropical species 317
assemblages. Lineages from Generalist species have been included in both Tropical and Extratropical 318
assemblages. Vertical lines indicate evolutionary depths at which Extratropical and Tropical 319
Assemblages had a similar numbers of lineages. 320

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contains greater lineage diversity for intermediate evolutionary ages 321 (between ∼47 and ∼12 Myr old). Within the last 12 Myr, the 322 number of lineages in tropical regions has increased much faster than 323 in extratropical regions (note log-scale of y-axis in Fig. 3), which is 324 epitomized by the fact that at present, tropical regions have nearly 325 three times as many species as extratropical regions (245 versus 87 326 species, when including generalists in both). 327

Overall phylogenetic diversity (PD) is markedly higher for 328 the assemblage of species in tropical environments (non-freezing) 329 than in extratropical environments (freezing; Table 2). The TILD 330 measure of deeper-time lineage diversity is also higher in the tropics, 331 but the difference between tropics and extratropics for that measure 332 is less pronounced. In contrast, sPD is lower, or more negative, for 333 the tropical assemblage than the extratropical assemblage of species 334 (Table 2), indicating greater phylogenetic clustering in the tropics. 335 While the pattern of overall tropical clustering is stronger when 336 excluding *Weinmannia*, the trend of overdispersion in the Generalist 337 group disappears when *Weinmannia* is excluded (Table 2). As such, 338 the generalist distribution of the very speciose *Weinmannia* may be 339 strongly affecting phylodiversity indices and obscuring the patterns of 340 phylogenetic structure observed across the remainder of Cunoniaceae. 341 Complimentary to the above analyses, we find phylogenetic signal, 342 significantly different from random expectations (which would give 343 a D value of 1), for both tropical species ($D= 0.5$, $p < 0.001$) and 344 extratropical species (D= 0.64, $p < 0.001$). A lower D value in the 345 Tropics reinforces that tropical species are more closely related to 346 each other on average than extratropical species (as values closer to 347 zero indicate greater phylogenetic signal; Table 2). 348

The distribution of species richness (SR) in environmental 349 bins displays two distinguishable areas of high values (Fig. 4a, d). 350 One area of high species richness is distributed towards relatively 351

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Table 2 Taxonomic and phylogenetic diversity indices for Tropical, Extratropical and Generalists species assemblages. Some genera contain Tropical and/or Extratropical and/or Generalist species, and are included under more than one column for genus richness totals, as pertinent. The indices are estimated for the whole Cunoniaceae family and for Cunoniaceae excluding *Weinmannia*. For standardized phylogenetic diversity (sPD), asterisks represent the P-value (quantile) of observed PD vs. null communities produced by 1,000 randomizations. For *D*, asterisks represent the probability of estimated *D* resulting under no phylogenetic signal. * if p < 0.1, ** if p < 0.05, *** if p < 0.001.

	Extratropical	Generalists	Tropical
Cunoniaceae (all genera)			
Species Richness	47	40	215
Genera Richness	16	5	21
Phylogenetic Diversity (Myr)	509.48	364.21	1195.53
TILD (Myr)	88.09	90.07	135.05
Standardized Phylogenetic Diversity (sPD)	-0.72	-2.51**	-2.22**
D index	0.63***	0.68***	0.50***
Cunoniaceae excluding *Weinmannia*			
Species Richness	26	7	136
Genera Richness	15	4	20
Phylogenetic Diversity (Myr)	421.97	226.40	974.04
TILD (Myr)	85.11	76.89	132.75
Standardized Phylogenetic Diversity (sPD)	-0.70	0.46	-4.42***
D index	0.24***	0.55***	0.30***

high Mean Annual Temperature (MAT) and high Mean Annual Precipitation (Fig 4a, d), while a further area of high richness is distributed towards lower MAT and lower MAP (Fig 4a, d). When excluding *Weinmannia*, only the former peak of species richness (high MAT and MAP) remains (Fig. 4d).

A negative correlation (r = -0.313, p<0.0001) was found between SR and standardized Phylogenetic Diversity (sPD) when considering all Cunoniaceae species (Fig. 4a b) and when excluding *Weinmannia* (r = -0.401, p<0.001) (Fig. 4d e). The correlation between SR and sPD suggests that the most speciose assemblages are also the least phylogenetically diverse assemblages. Our null model analysis (Fig. 4c f) allows us to rule out a potentially artefactual relationship between SR and sPD, as cautioned by [54], at least for the extremes of species richness values. When considering the whole
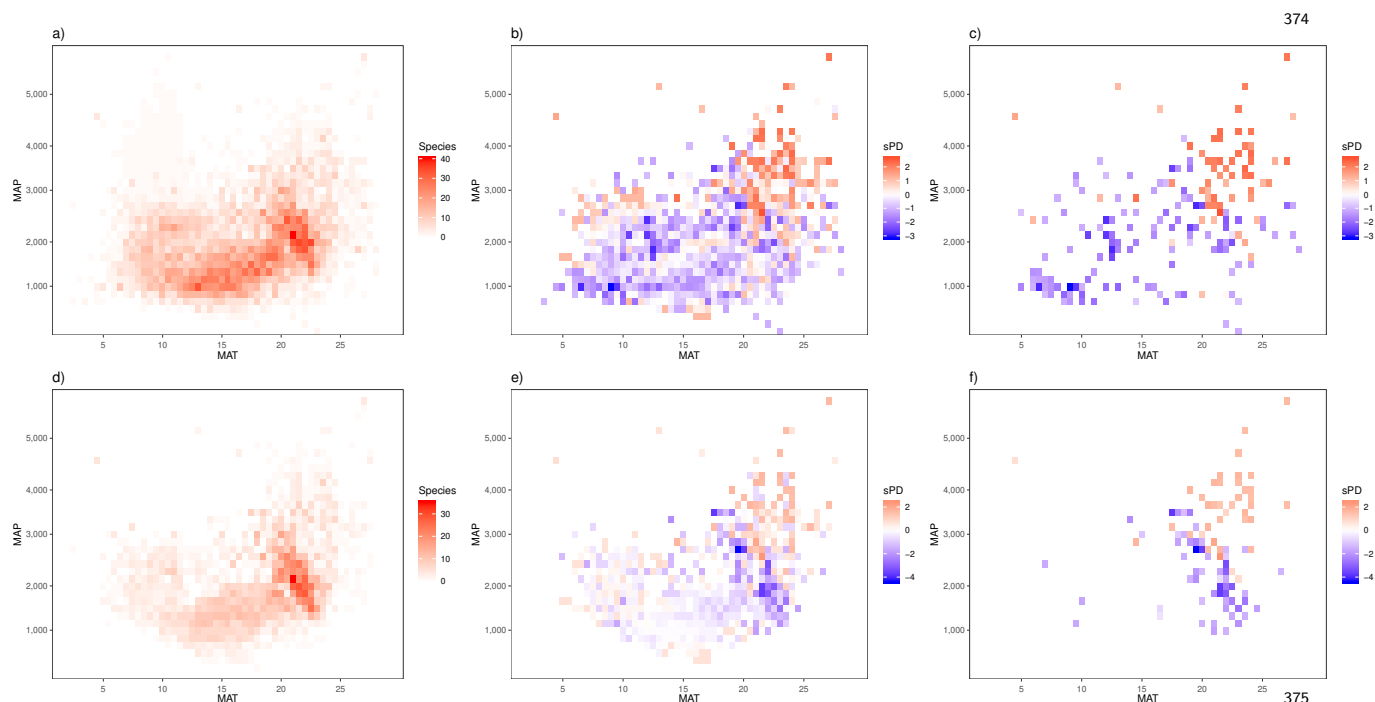
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Figure 4. Species Richness (SR) and Standardized Phylogenetic Diversity (sPD) across variation in Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP). Plots a), b) and c) consider the whole family Cunoniaceae, and d), e) and f) consider the Cunoniaceae family excluding *Weinmannia*. Panels c) and f) show the values of sPD that reflect significant phylogenetic clustering (negative values) or overdispersion (positive values), based on a null model analysis (see main text for details).

family (Fig 4a c), we see that the most phylogenetically overdispersed assemblages can be found within the hottest and wettest environments, while a number of phylogenetically clustered assemblages are found towards cooler and drier environments (in both tropical and extratropical portions of climatic space). When *Weinmannia* is excluded from analyses (Fig. 4e f), those environmental bins that show significant phylogenetic clustering are in relatively warm and wet (*i. e.* tropical) environments compared to the environmental range of the genus as a whole (Fig. 2). Meanwhile, there are few environmental bins that show significant phylogenetic overdispersion once *Weinmannia* is excluded from analyses. *Weinmannia* seems to constitute an independent pattern of diversification from the rest of the family with respect to environmental gradients and to have a

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strong influence on overall results (contrast Fig. 4a c versus d f).   395

Discussion   396

The angiosperm family Cunoniaceae has had strong associations   397
with both tropical and extratropical environments over its evolu-   398
tionary history (Fig. 2), yet tropical environments currently hold   399
many more species. Remarkably, this difference in diversity seems   400
to have arisen within the last 12 Myr (Fig. 3), suggesting higher   401
recent diversification in the tropics relative to the extratropics. We   402
also find significantly less phylogenetic diversity in tropical regions   403
than expected given their species richness (*i. e.* significant phyloge-   404
netic clustering; Fig. 4, Table 2), suggesting that recent radiations   405
have greatly increased the number of species in the tropics without   406
substantially increasing phylogenetic diversity.   407

The tropical radiations that comprise the majority of Cunon-   408
iaceae species may have arisen from extatropical ancestors. If so, this   409
would belie the general angiosperm pattern of species-poor extrat-   410
ropical lineages descending from tropical ancestors [9]. Rather, it   411
would suggest that that extratropics have been an important provider   412
of diversity in tropical regions. However, the frequent switching of   413
Cunoniaceae lineages between the extratropics and tropics limits   414
our ability to reconstruct ancestral environmental preferences of lin-   415
eages (Fig. 2), at least from distribution data for extant taxa. The   416
fossil record indicates that the family Cunoniaceae first appeared   417
during the Late Cretaceous in Antarctica (∼70 Ma, [60]. During this   418
time, Antarctica supported a highly diverse vegetation, dominated   419
by *Podocarpites* and *Nothofagus* [61], which is similar in taxonomic   420
composition to today's Valdivian rainforest in Chile ([48]; and refer-   421
ences therein). Although there are no climatic models which suggest   422
whether Antarctica experienced freezing or non-freezing conditions   423

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70 Ma, the compositional similarity with extant Valdivian forests, which do experience freezing, suggests that the ancestor of present-day Cunoniaceae lineages originated in an environment with freezing temperatures.

Based on distribution data from extant taxa, a tropical or extratropical origin for the most speciose genus in the family, *Weinmannia* is also not clear (Fig. 2). A morphological and molecular cladistic analysis shows that *Weinmannia* section Leiospermum, from extratropical New Zealand, tropical New Caledonia, and other islands from the South Pacific, is the sister taxon to the remainder of the genus [62]. These tropical and extratropical affiliations in the basal section of *Weinmannia* could indicate an origin of the clade associated with the interface between freezing and non-freezing environments. Meanwhile, in section Weinmannia, the most recently derived section of the genus, species from the tropical Mascarene islands are the sister clade of the American species [62]. The American species of section Weinmannia represent an impressive radiation that coincides with the Andean uplift (~60 species in the Andes from Argentina to Mexico). Following our ecological classification of species, the section Weinmannia is represented by only one extratropical species (in southern South America), yet those species distributed across the "Tropical Andes" are not inhabiting truly tropical environments (Fig. 1, Table 2). Rather, they occur at the interface between freezing and non-freezing temperatures in mid and high elevations, which is why so many of them are classified as generalists. Meanwhile, the fossil record shows a potential ancestor of section Weinmannia in the extratropical Tasmania [63]. Therefore, an extratropical origin is distinctly possible for the hyperdiverse genus *Weinmannia* as a whole and the recently radiated section Weinmannia.

Patterns of trait variation across species in different environments could also potentially give insights into the biogeographic

history of Cunoniaceae. For example, across angiosperms as a whole, [455] a pattern of decreasing hydraulic conduit diameter with increasing [456] latitude is thought to be an adaptive consequence of lineages moving into freezing environments [5, 64]. Evidence for this pattern in [458] *Weinmannia* [65] could be taken to suggest a tropical origin for this [459] genus, with a later dispersal into freezing environments. However, [460] phylogenetic evidence suggests an extratropical origin for *Weinmannia* [461] is as probable as a tropical origin (Fig. 2). We therefore suggest [462] that varying conduit diameter among species may just as likely represent either a plastic response to the presence or absence of freezing [464] conditions or an adaptive trend of increasing conduit diameter when [465] lineages move into tropical environments from extratropical ones. [466] The latter pattern in vessel diameter is evident in *Nothofagus*, a [467] genus whose extratropical origin is more certain. *Nothofagus* species [468] inhabiting tropical environments are only found in New Guinea and [469] have larger vessel diameters than the remaining species of the genus, [470] which inhabit extratropical environments [66]. These patterns in [471] Cunoniaceae and *Nothofagus* suggest that extratropical biota can [472] potentially change their hydraulic architecture when dispersing into [473] tropical, non-freezing environments. [474]

Beyond the origin of Cunoniaceae and its most species-rich [475] genus, the diversification history of the family shows two time periods [476] during which tropical lineages became more numerous than extratropical lineages, beginning ∼47 and ∼12 Ma (Fig. 3). The start of [478] the first time period is synchronous with the early Eocene Climatic [479] Optimum [67], which is the warmest period of the Cenozoic and may [480] have spurred lineage diversification in the tropics. This warm period [481] ended ∼30 Myr before present, corresponding with the inception of [482] Antarctic freezing around the Eocene–Oligocene boundary [67]. This [483] freezing is linked with the extinction of the Antarctic flora, including [484] Cunoniaceae present there [68, 69]. The second time period during [485]

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ing which tropical lineages gained predominance started in the late 486
Miocene (after 12 Myr). During this later time period, global temper- 487
atures continued to cool, culminating in the Pleistocene glaciations. 488
At this time the southern extratropical regions of the world would 489
have been subject to important environmental changes, including 490
increased seasonality and dryness in southern mid-latitudes, which 491
may have caused a large number of extinctions [70]. Such extinctions 492
could explain the discrepancy in diversification rate between the 493
tropics and extratropics over the last 12 Myr. It is important to keep 494
in mind however, that these differences in lineage diversity over the 495
evolutionary history of Cunoniaceae are inferred from phylogenetic 496
data on extant lineages. The actual lineage diversity of Cunoniaceae 497
in extratropical or tropical regions of the world during past geological 498
epochs may well have been higher, with some lineages not surviving 499
until the present day. 500

The negative relationship between species richness (SR) and 501
standardized phylogenetic diversity (sPD) observed across environ- 502
mental bins (Fig. 4) suggests that the environmental peak of SR 503
in the Cunoniaceae family is explained by radiation of a subset of 504
lineages into new environments. Similar reasoning has been applied 505
to other systems. On one hand, phylogenetic clustering (*i. e.* low 506
sPD) in Floridan plant communities has been interpreted as a conse- 507
quence of habitat filtering for a subset of lineages containing specific, 508
phylogenetically conserved ecological traits [71]. On the other hand, 509
evidence for phylogenetic clustering in the western Cape flora of 510
South Africa has been discussed as a function of multiple, rapid 511
radiations [72, 73]. Indeed, differences in the mean number of species 512
per genus for genera inhabiting the tropics versus the extratropics 513
in Cunoniaceae reinforce the hypothesis of restricted radiation for 514
a largely tropical subset of lineages. While the tropics house 215 515
species from 21 genera (10.2 spp per genus on average), the extrat- 516

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ropics house 47 species from 16 genera (2.9 spp per genus on average) [517] (Table 2). In other words, the relatively few species inhabiting the [518] extratropics come from a roughly similar number of genera as the [519] many species in the tropics. [520]

Higher species richness in the tropics can arise from multiple, [521] non-mutually exclusive mechanisms, such as area effects, time for [522] speciation, stronger biotic interactions or increased mutation rates [523] (reviewed by [74]). In the case of Cunoniaceae, area effects do not [524] seem a feasible explanation because its truly tropical distribution is [525] restricted to Australasia and Madagascar, a much narrower distri- [526] bution than the combined generalist and extratropical distribution [527] of the family (Fig. 1). An explanation based on time for speciation [528] also seems unlikely, because this would imply a later dispersion of [529] Cunoniaceae into freezing environments and, as we have shown here, [530] an extratropical origin for the family seems as likely (Fig. 2), or per- [531] haps more likely considering the fossil record, than a tropical origin. [532] Furthermore, tropical species are more phylogenetically clustered [533] than extratropical species, which suggests that a tropical distribution [534] may be novel for the family compared to an extratropical distribution. [535] Instead, high tropical species richness in Cunoniaceae may be due [536] to high recent diversification rates in tropical Cunoniaceae lineages, [537] which could in turn be due to a multiplicity of processes including [538] stronger biotic interactions within tropical lineages (*e. g.* [75]) or in- [539] creased mutation rates linked to higher temperature [76]. Regardless, [540] future studies are clearly needed to address the mechanisms behind [541] the radiation of Cunoniaceae into non-freezing environments. [542]

The prominent radiation of *Weinmannia* in the Andean [543] mountains is not easily reconciled with environmental factors gener- [544] ally considered to increase speciation rate. An historical perspective [545] may work better. The Andes are not older than the South American [546] extratropics, yet they are much more diverse (∼60 vs. 1 spp of [547]

Weinmannia) [77]. Making time for speciation explanations unlikely.   548

Higher mutation rates due to increased temperatures and/or solar   549
radiation are also not feasible, because *Weinmannia* prefers relatively   550
colder and cloudy environments in the Andes [78]. An explanation   551
for the radiation based on competition does not represent a strong   552
hypothesis either, since *Weinmannia* is a pioneer genus and a weak   553
competitor [79]. In contrast, the high taxonomic diversity in low   554
latitudes of the Andes may be associated mainly with topographic   555
dynamism during the relatively recent Andean uplift [80, 81].   556

Our findings present an explanation for Southern Hemi-   557
sphere biogeographic trends which goes beyond the traditional   558
dispersal-vicariance dichotomy by explicitly focusing on the   559
environmental context under which lineages evolved. The family   560
Cunoniaceae is of clear importance, in terms of diversity and abun-   561
dance, in both tropical and extratropical regions. As such it serves   562
as a model family for understanding the nature of shifts between   563
tropical and extratropical environments, and their consequence for   564
diversification. In contrast to the general pattern in angiosperm   565
biogeography [9, 5], we find that Cunoniaceae lineages have made   566
frequent shifts between tropical and extratropical environments.   567
Further, while the general narrative for biogeography in angiosperms   568
is one of tropical-origin lineages spreading into the extratropics [8],   569
the New Caledonian and Indonesian radiation of Cunoniaceae and   570
the radiation of *Weinmannia* in the tropical Andes, may represent   571
exceptions to this rule. These radiations seem to have extratropical   572
origins or at least to come from lineages that have continually existed   573
at the extratropical-tropical interface. Therefore, the dispersal of   574
Cunoniaceae lineages into tropical biomes represents a striking   575
case of non-tropical biota contributing taxonomic and evolutionary   576
diversity to tropical biodiversity hotspots.   577

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Acknowledgements

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