

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.

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 associated with the initial and later diversification is currently unclear. Similarly, a tropical or extratropical origin and diversification of *Weinmannia*, the most speciose genus in the family (comprising ~44% of species), has yet to be clarified [13].

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

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

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

In this study, we combine a newly derived phylogeny for Cunoniaceae with global occurrence and climatic data to gain insight into how dispersal events across the tropical-extratropical divide shaped the evolutionary biogeography of the family. We firstly reconstruct the ancestral tropical or extratropical affiliation of all 28 described genera within Cunoniaceae. In addition, we make a comparison of phylogenetic structure, phylogenetic signal, and variation in lineage diversity through time between tropical, non-freezing environments and extratropical, freezing environments. The evolutionary origins of angiosperms in general is thought to have occurred in tropical, non-freezing environments, with only a subset of lineages evolving tolerance to freezing conditions and making the shift to extratropical environments [8]. If the Cunoniaceae follow this general tropical-origin trend, we anticipate a phylogenetically clustered pattern in assemblages from extratropical environments and/or a phylogenetic signal for extratropicality (*i. e.* extratropical species will be more closely related than expected by chance). Alternatively, if tropical distribution is an evolutionary novelty within the Cunoniaceae, with tropical lineages deriving from extratropical lineages,

we expect phylogenetic clustering in assemblages from tropical environments, and/or a phylogenetic signal for tropicity. 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

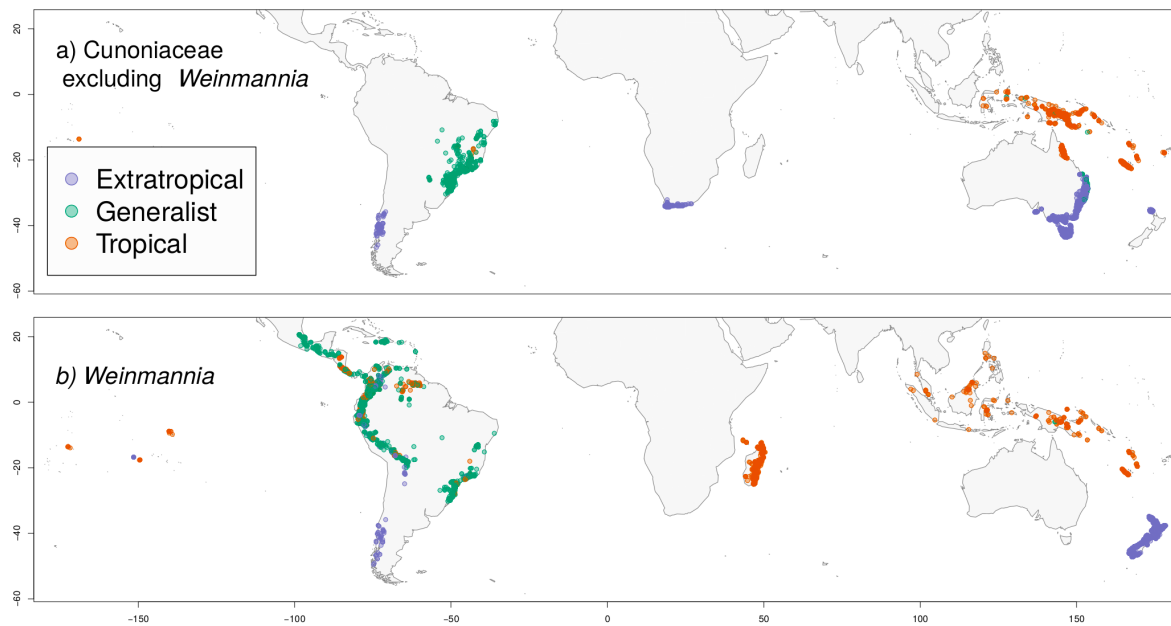


Figure 1. Distribution of the family Cunoniaceae. a) Distribution of the family Cunoniaceae excluding *Weinmannia* (169 non-*Weinmannia* spp) and b) Distribution of *Weinmannia* (133 spp). Purple dots represent occurrences of species classified as Extratropical. Orange dots represent occurrences of species 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,

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

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

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

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

Analyses

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

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

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

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

All analyses were conducted in the R Statistical Environment [36] using functions in the “geiger” [55], “ape” [56], “caper” [57], “Picante” [58], “biogeo” [59] and “PhyloMeasures” [53] packages. A repository with the codes can be found in <https://github.com/ricardosegovia/Cunoniaceae>.

Results

Across taxa with enough data to classify, 47 species from 16 genera were classified as Extratropical, 215 species from 21 genera were classified as Tropical and 40 species from five genera were classified as Generalists (Table 2). Eight genera included both Tropical and Extratropical species, while an additional three also included Generalist species. Thus eleven genera in total are classified as generalist. Most of the Generalist species are from the *Weinmannia* genus (33 of 40) and are found in the Andes (Fig. 1), which represent a mosaic of regularly freezing and non-freezing environments. The other genera containing generalist species are *Bauera* (1 sp), *Schizoemia* (1 sp), *Spiraeanthemum* (2 spp) and *Lamanonia* (3 spp). Tropical species are largely distributed in northern Australia, the Malay Archipelago (plus New Guinea) and Madagascar (Fig. 1). In contrast, Extratropical species are associated with southern Australia, New Zealand, South Africa and southern South America

(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

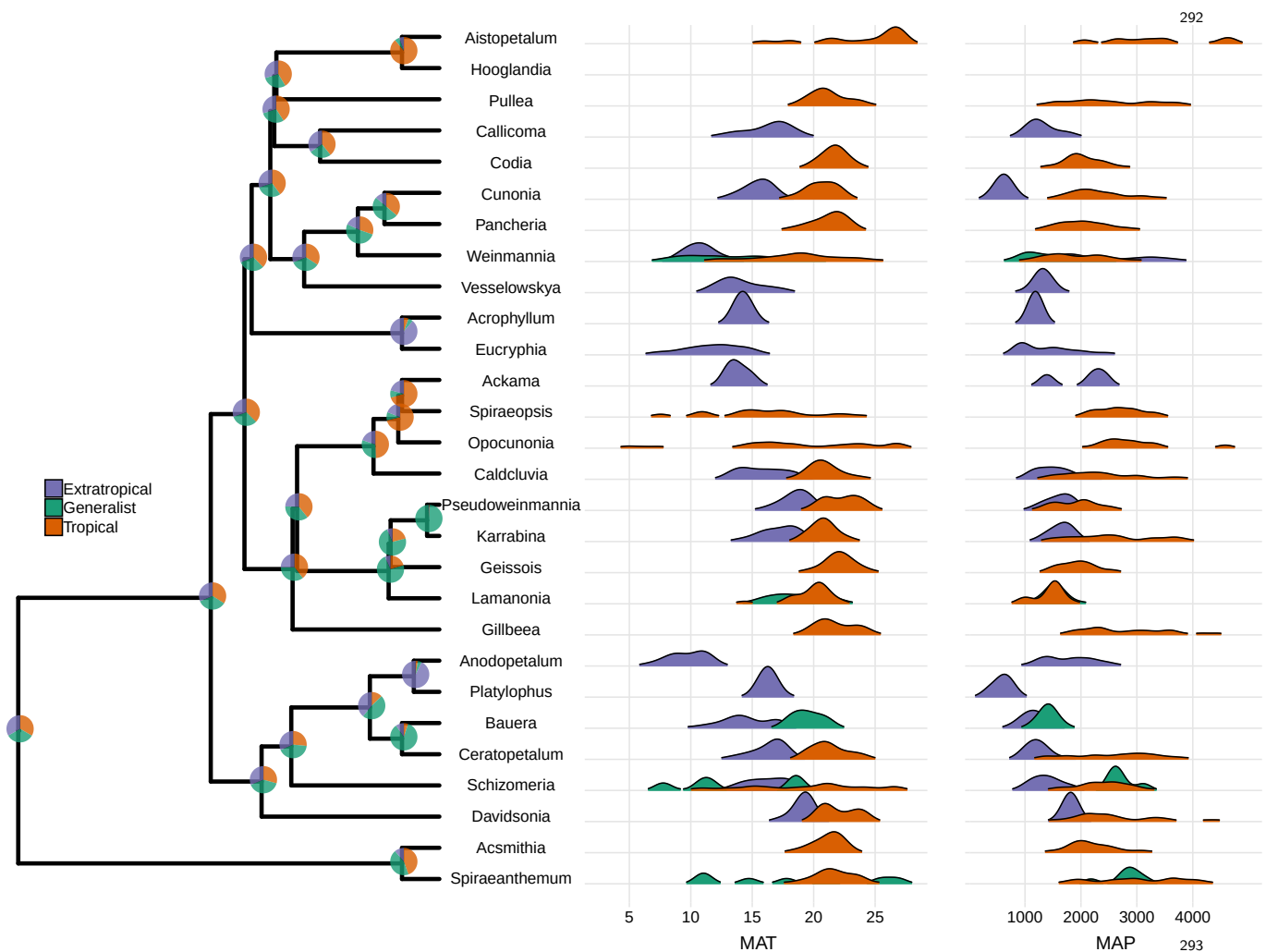


Figure 2. Genus-level phylogeny with ancestral state reconstruction for tropical or extratropical environments. The environmental distributions of Cunoniaceae genera across gradients of Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) are also shown. Colours in the right-hand panel illustrate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

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

The lineage through time (LTT) plot shows that both
tropical and extratropical regions contain similar diversity in terms of
number of older lineages (~ 47 Ma) (Fig. 3). The tropical assemblage

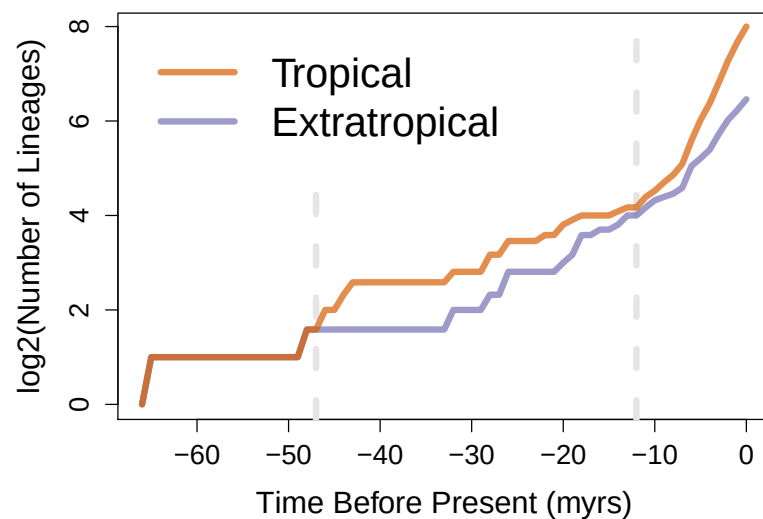


Figure 3. Number of Lineages Through Time (LTT) for Tropical and Extratropical species assemblages. Lineages from Generalist species have been included in both Tropical and Extratropical assemblages. Vertical lines indicate evolutionary depths at which Extratropical and Tropical Assemblages had a similar numbers of lineages.

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

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

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

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**
<i>D</i> index	0.63***	0.68***	0.50***
Cunoniaceae excluding <i>Weinmannia</i>			
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***
<i>D</i> 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

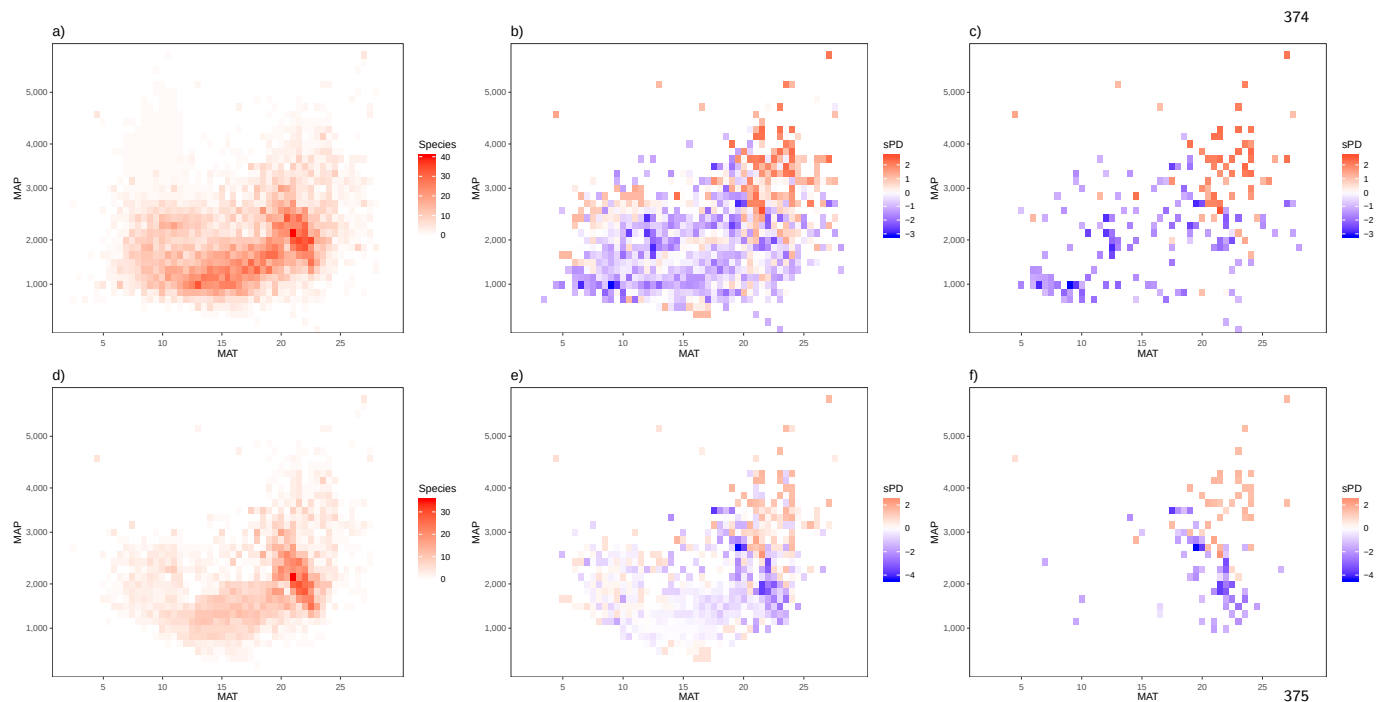


Figure 4. Species Richness (SR) and Standardized Phylogenetic Diversity (sPD) across variation in Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP). Plots a), b) and c) consider the whole family Cunoniaceae, and d), e) and f) consider the Cunoniaceae family excluding *Weinmannia*. Panels 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

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

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

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

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

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

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

The prominent radiation of *Weinmannia* in the Andean mountains is not easily reconciled with environmental factors generally considered to increase speciation rate. An historical perspective may work better. The Andes are not older than the South American extratropics, yet they are much more diverse (~60 vs. 1 spp of

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

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

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References

- [1] Robert F Thorne. Classification and geography of the flowering plants. *The botanical review*, 58(3):225–327, 1992.
- [2] Elgene O Box. Plant functional types and climate at the global scale. *Journal of Vegetation Science*, 7(3):309–320, 1996.
- [3] Walter S Judd, Roger W Sanders, and Michael J Donoghue. Angiosperm family pairs: preliminary phylogenetic analyses. *Harvard papers in Botany*, pages 1–51, 1994.
- [4] Robert E Ricklefs and Susanne S Renner. Species richness within families of flowering plants. *Evolution*, 48(5):1619–1636, 1994.
- [5] Amy E Zanne, David C Tank, William K Cornwell, Jonathan M Eastman, Stephen A Smith, Richard G FitzJohn, Daniel J McGlinn, Brian C O’Meara, Angela T Moles, Peter B Reich, et al. Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506(7486):89, 2014.
- [6] Michael J Donoghue. A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences*, 105(Supplement 1):11549–11555, 2008.
- [7] Ricardo A Segovia, Toby Pennington, Tim Baker, Fernanda Coelho De Souza, Danilo Neves, Charles C Davis, Juan J Armesto, Ary Olivera-Filho, and Kyle Dexter. Freezing and water availability structure the evolutionary diversity of trees across the americas. *BioRxiv*, page 728717, 2019.
- [8] John J Wiens and Michael J Donoghue. Historical biogeography, ecology and species richness. *Trends in ecology & evolution*, 19(12):639–644, 2004.
- [9] Andrew J Kerkhoff, Pamela E Moriarty, and Michael D Weiser. The latitudinal species richness gradient in new world woody angiosperms is consistent with the tropical conservatism hypothesis. *Proceedings of the National Academy of Sciences*, 111(22):8125–8130, 2014.
- [10] Elizabeth L Spriggs, Wendy L Clement, Patrick W Sweeney, Santiago Madriñán, Erika J Edwards, and Michael J Donoghue. Temperate radiations and dying embers of a tropical past: the diversification of *viburnum*. *New Phytologist*, 207:340–354, 2015.
- [11] Richard W Barnes, Robert S Hill, and Jason C Bradford. The history of cunoniaceae in australia from macrofossil evidence. *Australian Journal of Botany*, 49(3):301–320, 2001.

- [12] Jörg Schönenberger, Eric M. Lavett, and Peter C. Hochberg. On the origin of the Cretaceous of Europe: Evidence from fossil flowers. *Annals of Botany*, 88(3):423 – 437, 2001.
- [13] Jason C Bradford and Richard W. Barnes. Phylogenetics and classification of Cunoniaceae (Oxalidales) using chloroplast DNA sequences and morphology. *Systematic Botany*, 26(2):354 – 385 – 32, 2001.
- [14] Peter H Raven and Daniel I Axelrod. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden*, 61(3):539–673, 1974.
- [15] GE Wilford and PJ Brown. Maps of late mesozoic-cenozoic Gondwana break-up: some palaeogeographical implications. *History of the Australian vegetation: Cretaceous to Recent*, pages 5–13, 1994.
- [16] Peter H Weston and Robert S Hill. Southern (austral) ecosystems. 2013.
- [17] Peter Wilf, N Rubén Cúneo, Ignacio H Escapa, Diego Pol, and Michael O Woodburne. Splendid and seldom isolated: the paleobiogeography of Patagonia. *Annual Review of Earth and Planetary Sciences*, 41, 2013.
- [18] Vanessa C Bowman, Jane E Francis, Rosemary A Askin, James B Riding, and Graeme T Swindles. Latest Cretaceous–earliest Paleogene vegetation and climate change at the high southern latitudes: palynological evidence from Seymour Island, Antarctic Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 408:26–47, 2014.
- [19] Richard C. Winkworth, Steven J. Wagstaff, David Glenney, and Peter J. Lockhart. Plant dispersal n.e.w.s from New Zealand. *Trends in Ecology & Evolution*, 17(11):514 – 520, 2002.
- [20] Jesus Munoz, Angel M Felicísimo, Francisco Cabezas, Ana R Burgaz, and Isabel Martinez. Wind as a long-distance dispersal vehicle in the southern hemisphere. *Science*, 304(5674):1144–1147, 2004.
- [21] Isabel Sanmartín, Livia Wanntorp, and Richard C Winkworth. West wind drift revisited: testing for directional dispersal in the southern hemisphere using event-based tree fitting. *Journal of Biogeography*, 34(3):398–416, 2007.
- [22] Michael D Crisp, Mary TK Arroyo, Lyn G Cook, Maria A Gandolfo, Gregory J Jordan, Matt S McGlone, Peter H Weston, Mark Westoby, Peter Wilf, and H Peter Linder. Phylogenetic biome conservatism on a global scale. *Nature*, 458(7239):754, 2009.
- [23] Edeline Gagnon, Jens J Ringelberg, Anne Bruneau, Gwilym P Lewis, and Colin E Hughes. Global succulent biome phylogenetic conservatism across the pantropical Caesalpinia group (Leguminosae). *New Phytologist*, 222(4):1994–2008, 2019.
- [24] Isabel SanMartín and Fredrik Ronquist. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic biology*, 53(2), 2004.
- [25] Carlos Jaramillo and Andrés Cárdenas. Global warming and neotropical rainforests: a historical perspective. *Annu. Rev. Earth Planet. Sci.*, 41:741–766, 2013.
- [26] Dolph Schluter, Trevor Price, Arne Ø Mooers, and Donald Ludwig. Likelihood of ancestor states in adaptive radiation. *Evolution*, 51(6):1699–1711, 1997.
- [27] Mark Pagel. The Maximum Likelihood Approach to Reconstructing Ancestral Character States of Discrete Characters on Phylogenies. *Systematic Biology*, 48(3):612–622, 07 1999.

- [28] Kevin J. Gaston. Environmental predictors of global parrot (aves: Psittaciformes) species richness and phylogenetic diversity. *Global Ecology and Biogeography*, 16(2):220–233, 2007.
- [29] W Daniel Kissling, Wolf L Eiserhardt, William J Baker, Finn Borchsenius, Thomas LP Couvreur, Henrik Balslev, and Jens-Christian Svenning. Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences*, 109(19):7379–7384, 2012.
- [30] Euridice N Honorio Coronado, Kyle G Dexter, R Toby Pennington, Jérôme Chave, Simon L Lewis, Miguel N Alexiades, Esteban Alvarez, Atila Alves de Oliveira, Iêda L Amaral, Alejandro Araujo-Murakami, et al. Phylogenetic diversity of amazonian tree communities. *Diversity and Distributions*, 21(11):1295–1307, 2015.
- [31] Vanessa L Rezende, Kyle G Dexter, R Toby Pennington, and Ary T Oliveira-Filho. Geographical variation in the evolutionary diversity of tree communities across southern south america. *Journal of biogeography*, 44(10):2365–2375, 2017.
- [32] Marten Winter, Vincent Devictor, and Oliver Schweiger. Phylogenetic diversity and nature conservation: where are we? *Trends in ecology & evolution*, 28(4):199–204, 2013.
- [33] Marcel Cardillo. Phylogenetic structure of mammal assemblages at large geographical scales: linking phylogenetic community ecology with macroecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1577):2545–2553, 2011.
- [34] Caroline M. Tucker and Marc W. Cadotte. Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. *Diversity and Distributions*, 19(7):845–854, 2013.
- [35] Scott A Chamberlain and Carl Boettiger. R python, and ruby clients for gbif species occurrence data. Technical report, PeerJ Preprints, 2017.
- [36] R Core Team et al. R: A language and environment for statistical computing. 2013.
- [37] Alexander Zizka, Daniele Silvestro, Tobias Andermann, Josué Azevedo, Camila Duarte Ritter, Daniel Edler, Harith Farooq, Andrei Herdean, María Ariza, Ruud Scharn, et al. Coordinatecleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, 10(5):744–751, 2019.
- [38] Robert J Hijmans, Susan E Cameron, Juan L Parra, Peter G Jones, and Andy Jarvis. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, 25(15):1965–1978, 2005.
- [39] Arthur D Chapman. *Principles of data quality*. GBIF, 2005.
- [40] Josep M Serra-Diaz, Brian J Enquist, Brian Maitner, Cory Merow, and Jens-C Svenning. Big data of tree species distributions: how big and how good? *Forest Ecosystems*, 4(1):30, 2017.
- [41] Kenneth J Feeley and James T Stroud. Where on earth are the “tropics”? *Frontiers in Biogeography*, 10(1-2), 2018.
- [42] IPDJ Harris, Philip D Jones, Timothy J Osborn, and David H Lister. Updated high-resolution grids of monthly climatic observations—the cru ts3. 10 dataset. *International journal of climatology*, 34(3):623–642, 2014.

- [43] J. A. Marín and J. C. Martínez. Assessing the impact of climate change during modern and past climates. In *Interhemispheric climate linkages*, pages 31–51. Elsevier, 2001.
- [44] Stephen A Smith and Joseph F Walker. Py phlawd: A python tool for phylogenetic dataset construction. *Methods in Ecology and Evolution*, 10(1):104–108, 2019.
- [45] Kazutaka Katoh and Daron M Standley. Mafft multiple sequence alignment software version 7: improvements in performance and usability. *Molecular biology and evolution*, 30(4):772–780, 2013.
- [46] Alexandros Stamatakis. Raxml version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30(9):1312–1313, 2014.
- [47] Stephen A Smith and Brian C O’Meara. treepl: divergence time estimation using penalized likelihood for large phylogenies. *Bioinformatics*, 28(20):2689–2690, 2012.
- [48] Imogen Poole, Alberta MW Mennega, and David J Cantrill. Valdivian ecosystems in the late cretaceous and early tertiary of antarctica: further evidence from myrtaceous and eucryphiaceous fossil wood. *Review of Palaeobotany and Palynology*, 124(1-2):9–27, 2003.
- [49] Patrick W Sweeney, Jason C Bradford, and Porter P Lowry. Phylogenetic position of the new caledonian endemic genus *hooglandia* (cunoniaceae) as determined by maximum parsimony analysis of chloroplast dna. *Annals of the Missouri Botanical Garden*, pages 266–274, 2004.
- [50] Daniel P Faith. Conservation evaluation and phylogenetic diversity. *Biological conservation*, 61(1):1–10, 1992.
- [51] Kyle G Dexter, Ricardo A Segovia, and Andy R Griffiths. Exploring the concept of lineage diversity across north american forests. *Forests*, 10(6):520, 2019.
- [52] Susanne A Fritz and Andy Purvis. Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, 24(4):1042–1051, 2010.
- [53] Constantinos Tsirogiannis and Brody Sandel. Phylomeasures: a package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography*, 39(7):709–714, 2016.
- [54] Brody Sandel. Richness-dependence of phylogenetic diversity indices. *Ecography*, 41(5):837–844, 2018.
- [55] LJ Harmon, JT Weir, CD Brock, RE Glor, and W Challenger. Geiger: investigating evolutionary radiations. *Bioinformatics*, 24:129–131, 2008.
- [56] E. Paradis and K. Schliep. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35:526–528, 2018.
- [57] David Orme, Rob Freckleton, Gavin Thomas, Thomas Petzoldt, Susanne Fritz, Nick Isaac, and Will Pearse. *caper: Comparative Analyses of Phylogenetics and Evolution in R*, 2018. R package version 1.0.1.
- [58] Steven W Kembel, Peter D Cowan, Matthew R Helmus, William K Cornwell, Helene Morlon, David D Ackerly, Simon P Blomberg, and Campbell O Webb. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26(11):1463–1464, 2010.
- [59] Mark P. Robertson, Vernon Visser, and Cang Hui. Biogeo: an r package for assessing and improving data quality of occurrence record datasets. *Ecography*, 39(4):394–401, 2016.

- [60] Imogen Poole, David Cantrill, and Torsten Utescher. A multi-proxy approach to determine antarctic terrestrial palaeoclimate during the late cretaceous and early tertiary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 222(1-2):95–121, 2005.
- [61] Jason C Bradford. A cladistic analysis of species groups in weinmannia (cunoniaceae) based on morphology and inflorescence architecture. *Annals of the Missouri Botanical Garden*, pages 565–593, 1998.
- [62] RJ Carpenter and AM Buchanan. Oligocene leaves, fruit and flowers of the cunoniaceae from cethana, tasmania. *Australian Systematic Botany*, 6(2):91–109, 1993.
- [63] Amy E Zanne, William D Pearse, William K Cornwell, Daniel J McGlinn, Ian J Wright, and Josef C Uyeda. Functional biogeography of angiosperms: life at the extremes. *New Phytol.*, 218(4):1697–1709, 2018.
- [64] William C Dickison. Wood anatomy of weinmannia (cunoniaceae). *Bulletin of the Torrey Botanical Club*, pages 12–23, 1977.
- [65] HE Dadswell and HD Ingle. The wood anatomy of new guinea nothofagus b1. *Australian journal of botany*, 2(2):141–153, 1954.
- [66] James Zachos, Mark Pagani, Lisa Sloan, Ellen Thomas, and Katharina Billups. Trends, rhythms, and aberrations in global climate 65 ma to present. *Science*, 292(5517):686–693, 2001.
- [67] JE Francis. *Antarctic palaeobotany: clues to climate change*. 1996.
- [68] EM Truswell and MK Macphail. Polar forests on the edge of extinction: what does the fossil spore and pollen evidence from east antarctica say? *Australian Systematic Botany*, 22(2):57–106, 2009.
- [69] Dallas C Mildenhall. New zealand late cretaceous and cenozoic plant biogeography: a contribution. *Palaeogeography, palaeoclimatology, palaeoecology*, 31:197–233, 1980.
- [70] Jeannine Cavender-Bares, Adrienne Keen, and Brianna Miles. Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology*, 87(sp7):S109–S122, 2006.
- [71] Félix Forest, Richard Grenyer, Mathieu Rouget, T Jonathan Davies, Richard M Cowling, Daniel P Faith, Andrew Balmford, John C Manning, Șerban Procheș, Michelle van der Bank, et al. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, 445(7129):757, 2007.
- [72] G Anthony Verboom, Jenny K Archibald, Freek T Bakker, Dirk U Bellstedt, Ferozah Conrad, Leanne L Dreyer, Félix Forest, Chloé Galley, Peter Goldblatt, Jack F Henning, et al. Origin and diversification of the greater cape flora: ancient species repository, hot-bed of recent radiation, or both? *Molecular Phylogenetics and Evolution*, 51(1):44–53, 2009.
- [73] Gary G. Mittelbach, Douglas W. Schemske, Howard V. Cornell, Andrew P. Allen, Jonathan M. Brown, Mark B. Bush, Susan P. Harrison, Allen H. Hurlbert, Nancy Knowlton, Harilaos A. Lessios, Christy M. McCain, Amy R. McCune, Lucinda A. McDade, Mark A. McPeck, Thomas J. Near, Trevor D. Price, Robert E. Ricklefs, Kaustuv Roy, Dov F. Sax, Dolph Schluter, James M. Sobel, and Michael Turelli. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10(4):315–331, 2007.

- [75] Douglas W. Schemske. *Ecological speciation: the origins of tropical diversity*. *Foundations of tropical forest biology*, pages 163–173, 2002.
- [76] Andrew P Allen, James F Gillooly, Van M Savage, and James H Brown. Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences*, 103(24):9130–9135, 2006.
- [77] KM Gregory-Wodzicki. Uplift history of the Central and Northern Andes: A review. *Geological society of america bulletin*, 112(7):1091–1105, JUL 2000.
- [78] J Homeier, FA Werner, SR Gradstein, S Breckle, and M Richter. Potential vegetation and floristic composition of andean forests in south ecuador, with a focus on the rbsf. *Ecological Studies*, 198:87, 2008.
- [79] Christopher H Lusk. Long-lived light-demanding emergents in southern temperate forests: the case of *weinmannia trichosperma* (cunoniaceae) in chile. *Plant Ecology*, 140(1):111–115, 1999.
- [80] Alexandre Antonelli, Johan AA Nylander, Claes Persson, and Isabel Sanmartin. Tracing the impact of the andean uplift on neotropical plant evolution. *Proceedings of the National Academy of Sciences*, 106(24):9749–9754, 2009.
- [81] Thiago F Rangel, Neil R Edwards, Philip B Holden, José Alexandre F Diniz-Filho, William D Gosling, Marco Túlio P Coelho, Fernanda AS Cassemiro, Carsten Rahbek, and Robert K Colwell. Modeling the ecology and evolution of biodiversity: biogeographical cradles, museums, and graves. *Science*, 361(6399):eaar5452, 2018.