

A peer-reviewed version of this preprint was published in PeerJ on 16 March 2018.

[View the peer-reviewed version](https://doi.org/10.7717/peerj.4388) (peerj.com/articles/4388), which is the preferred citable publication unless you specifically need to cite this preprint.

Bacon CD, Velásquez-Puentes FJ, Hinojosa LF, Schwartz T, Oxelman B, Pfeil B, Arroyo MTK, Wanntorp L, Antonelli A. 2018. Evolutionary persistence in *Gunnera* and the contribution of southern plant groups to the tropical Andes biodiversity hotspot. PeerJ 6:e4388
<https://doi.org/10.7717/peerj.4388>

Evolutionary persistence in *Gunnera* and the contribution of southern plant groups to the tropical Andes biodiversity hotspot

Christine D. Bacon^{Corresp., 1,2,3}, Francisco Velásquez-Puentes^{3,4}, Luis Felipe Hinojosa⁵, Thomas Schwartz², Bengt Oxelman², Bernard Pfeil², Mary T. K. Arroyo⁵, Livia Wanntorp⁶, Alexandre Antonelli^{1,2,7}

¹ Gothenburg Global Biodiversity Centre, Gothenburg, Sweden

² Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

³ Laboratorio de Biología Molecular (CINBIN), Universidad Industrial de Santander, Bucaramanga, Colombia

⁴ Departamento de Química y Biología, Universidad del Norte, Barranquilla, Colombia

⁵ Institute of Ecology and Biodiversity, Facultad de Ciencias, Universidad de Chile, Santiago, Chile

⁶ Department of Phanerogamic Botany, Swedish Museum for Natural History, Stockholm, Sweden

⁷ Gothenburg Botanical Garden, Gothenburg, Sweden

Corresponding Author: Christine D. Bacon

Email address: christinedbacon@gmail.com

Several studies have demonstrated the contribution of northern immigrants to the flora of the tropical Andes – the world’s “hottest” biodiversity hotspot. However, much less is known about the biogeographic history and diversification of Andean groups with southern origins, although it has been suggested that northern and southern groups have contributed roughly equally to the high Andean (i.e. páramo) flora. Here we infer the evolutionary history of the southern hemisphere plant genus *Gunnera*, a lineage with a rich fossil history and an important ecological role as an early colonising species characteristic of wet, montane environments. Our results show striking contrasts in species diversification, where some species may have persisted for some 90 million years, whereas others date to less than 2 Ma since origination. The outstanding longevity of the group is likely linked to a high degree of niche conservatism across its highly disjunct range, whereby *Gunnera* tracks damp and boggy soils in cool habitats. Colonisation of the northern Andes is related to Quaternary climate change, with subsequent rapid diversification appearing to be driven by their ability to take advantage of environmental opportunities. This study demonstrates the composite origin of a mega-diverse biota.

1 **Title**

2 Evolutionary persistence in *Gunnera* and the contribution of southern plant groups to the tropical
3 Andes biodiversity hotspot

4

5 **Authors**

6 Christine D. Bacon^{a,b*}, Francisco J. Velásquez-Puentes^{c,d}, Luis F. Hinojosa^e, Thomas Schwartz^a,
7 Bengt Oxelman^{a,b}, Bernard Pfeil^{a,b}, Mary T. K. Arroyo^e, Livia Wanntorp^f, Alexandre
8 Antonelli^{a,b,g}

9

10 **Author institutions**

11 ^aDepartment of Biological and Environmental Sciences, University of Gothenburg, Carl

12 Skottsbergs gata 22B, SE - 413 19 Göteborg, Sweden

13 ^bGothenburg Global Biodiversity Centre, Box 461, SE-405 30 Gothenburg, Sweden

14 ^cLaboratório de Biología Molecular (CINBIN), Department of Biology, Universidad Industrial
15 de Santander, Bucaramanga, Colombia

16 ^dDepartamento de Química y Biología, Universidad del Norte, Barranquilla, Colombia

17 ^eInstitute of Ecology and Biodiversity, Facultad de Ciencias, Universidad de Chile, Casilla 653,
18 Santiago, Chile

19 ^fDepartment of Phanerogamic Botany, Swedish Museum of Natural History, Box 50007, SE -
20 104 05 Stockholm, Sweden

21 ^gGothenburg Botanical Garden, Carl Skottsbergs gata 22A, SE - 413 19 Göteborg, Sweden

22

23

24 **Corresponding authors (*)**

25 christinedbacon@gmail.com

26

27 **Running title**

28 *Gunnera*: diversification and persistence

29 **Abstract**

30 Several studies have demonstrated the contribution of northern immigrants to the flora of the
31 tropical Andes – the world’s “hottest” biodiversity hotspot. However, much less is known about
32 the biogeographic history and diversification of Andean groups with southern origins, although it
33 has been suggested that northern and southern groups have contributed roughly equally to the
34 high Andean (i.e. páramo) flora. Here we infer the evolutionary history of the southern
35 hemisphere plant genus *Gunnera*, a lineage with a rich fossil history and an important ecological
36 role as an early colonising species characteristic of wet, montane environments. Our results show
37 striking contrasts in species diversification, where some species may have persisted for some 90
38 million years, whereas others date to less than 2 Ma since origination. The outstanding longevity
39 of the group is likely linked to a high degree of niche conservatism across its highly disjunct
40 range, whereby *Gunnera* tracks damp and boggy soils in cool habitats. Colonisation of the
41 northern Andes is related to Quaternary climate change, with subsequent rapid diversification
42 appearing to be driven by their ability to take advantage of environmental opportunities. This
43 study demonstrates the composite origin of a mega-diverse biota.

44

45 **Key words**

46 Biogeography, climate change, diversification, Gondwana, Neotropics, species longevity

47 1. Introduction

48

49 Among the 34 biodiversity hotspots currently recognized, the tropical Andes is the richest and
50 most diverse, comprising some 30,000 plant species [1]. This equates to nearly a tenth of the
51 world's flora contained in less than one per cent of its land area. The tropical Andean hotspot,
52 which stretches from western Venezuela to northern Chile and Argentina, constitutes an ideal
53 arena for investigating the role of historical migrations in generating the exceptional plant
54 species diversity found in the American tropics (the Neotropics).

55 Most evolutionary models proposed to explain Neotropical diversity [2, 3] postulate a
56 major role for *in situ* diversification, e.g. in Amazonia [e.g. 4, 5, but see 6] and the Andes [7, 8].
57 The relative contribution of immigrant lineages to modern Neotropical diversity is less
58 understood, but has certainly played an important role [9]. For example, northern immigrants
59 contributed more to the species diversity of the high elevation Andean páramo than southern
60 immigrants [e.g. 10]. The contribution of immigrant taxa to modern Neotropical diversity may be
61 primarily explained by either continuous range expansions from neighboring regions or long-
62 distance dispersal, both from what today are temperate lineages into tropical latitudes (often
63 facilitated by climatic change and mountain building), and from other trans-oceanic tropical
64 regions [11]. Modern distributions reflect ancestral ecological requirements [niche conservatism;
65 12], but they also are affected by biome shifts, such as adaptation of cool temperate immigrants
66 into cold tropical areas [13]. More rarely, migration events can also be directly associated with
67 physiological adaptations into new environments [14, 15].

68 One of the characteristic elements of the Andes is the plant genus *Gunnera* (Gunneraceae;
69 Fig. S1). Although eleven *Gunnera* species are reported in the páramo [16], most of these are

70 found in montane forests and only one is a strict páramo species, *G. magellanica* – which is also
71 found in the southern temperate Andes in wet habitats both below and above treeline [10].
72 *Gunnera* has been present in montane forests since at least the Middle Pliocene in Colombia
73 [17]. Unlike the numerous examples of páramo species from the southern regions of the Andes
74 colonising the northern Andes, fewer montane forest dwellers, such as *Gunnera*, have
75 successfully dispersed to the region [18].

76 *Gunnera* includes 58 species primarily of the Southern Hemisphere (Africa, New Zealand,
77 South America, and Tasmania), but also reaches Hawaii, Mexico, and Southeast Asia [Fig. 1; 19,
78 20]. Despite this wide geographical distribution encompassing all southern continents apart from
79 Antarctica, the majority of extant species of *Gunnera* (41 spp., subgenus *Panke*) are distributed
80 in Central and South America [20], most of them within the northern Andean biodiversity
81 hotspot. However, *Gunnera* had an even wider geographic distribution during the Cretaceous, as
82 demonstrated by numerous fossil pollen records from the Antarctic Peninsula, Australia, the
83 Kerguelen Plateau, as well as in both North and South America [21]. The oldest of these dates to
84 the Turonian (ca. 90 Ma) of Peru [22] and ten million years later *Gunnera* became widespread
85 across all landmasses that previously formed Gondwana [21]. Initial evidence suggested that
86 biogeographic patterns in *Gunnera* are in agreement with the sequence of Gondwanan break-up,
87 prompting Wanntorp and Wanntorp (2003) to suggest a Gondwanan origin for the genus and
88 vicariance by continental drift as a plausible hypothesis to explain the present-day distribution of
89 most species in the genus. However, these conclusions involved neither formal ancestral area
90 analyses nor molecular dating. The study also did not explicitly investigate the biogeographical
91 history of the Andean species comprising subgenus *Panke*.

92 The current widespread distribution of *Gunnera*, its rich fossil record and the many still
93 unanswered questions regarding its biogeographic history all make *Gunnera* an ideal target for
94 investigating the role of southern immigrants in the assembly of the flora of the Andean
95 biodiversity hotspot. Here we infer the biogeographic, climatic, and evolutionary history of
96 *Gunnera* to explicitly address the following questions: Where did *Gunnera* most likely originate?
97 How and when did it attain its current distribution? When did it colonise the northern Andes
98 where it is most diverse? Are areas of high diversity in the genus associated with higher rates of
99 net diversification, or is diversity instead due to gradual accumulation of species? To what extent
100 have species of *Gunnera* tracked the ancestral climatic niche? We also discuss why so few
101 southern hemisphere montane forest dwellers have entered the northern Andes and what makes
102 *Gunnera* different. Our study sheds further light on the geographical and temporal origins and
103 composition of the highly diverse Andean flora.

104

105 **2. Material and methods**

106

107 **(a) Phylogeny and divergence time estimation**

108 Taxon sampling was complete at the species level for five of six subgenera of *Gunnera*. Within
109 subgenus *Panke* we could only obtain material for 14 of the 40 species, because many species
110 are only known from few collections or localities [20]. DNA sequence data was generated
111 following the respective author protocols for the chloroplast regions *rps16* [23], *rpoC1* and *ycf5*
112 from the Plant Working Group (www.kew.org/barcoding), *psbA-trnH* [24], as well as the nuclear
113 genes ITS [25] and SEX4 [26]. All new sequences generated in this study have been deposited
114 in GenBank (Appendix 1). Nucleotide alignments were obtained independently for each of the

115 loci using default parameters for MUSCLE in Geneious (Biomatters, New Zealand). Due to poor
116 alignability, the ITS sequences of *G. herteri* and *G. perpensa* were removed. We used the Akaike
117 Information Criterion implemented in MrModelTest 2.2 [27] to select the best-fitting nucleotide
118 substitution model(s) and incorporated it in the inference of the species tree.

119 We used STACEY 1.04 (see <http://www.indriid.com/software.html>) in BEAST 2.3.0 and the
120 DISSECT method [28] to infer a multispecies coalescent tree. The method uses a version of the
121 birth/death branching model for the species tree, which assigns high probabilities for branching
122 events close to time zero; how close is defined by the “collapse height” parameter, which should
123 be set as small as possible [see 28]. The approach thus enables simultaneous exploration of
124 species tree and species delimitation space. Individuals or groups of individuals known to belong
125 to the same single species are operationally defined as minimal species. Clusters below the
126 collapse height are considered to belong to the same species, as defined by the multispecies
127 coalescent model. Here we defined all sequences from the same individual as minimal species. A
128 lognormal (mean 4.6, standard deviation 2) growth rate prior distribution was used for the
129 species tree. The growth rate is roughly 1 divided by the branch length, so that 95% of the
130 distribution falls within the interval [2, 5000] with median $e^{4.6} \approx 100$. Beta priors with shape
131 parameters 1, 1 (resulting in uniform distributions) were used on collapse weight and relative
132 death rates. A lognormal (-7, 2) prior was used for popPriorScale, which should approximate the
133 average time to coalescence between two gene copies. In order to scale branch lengths in
134 substitutions per site, the ITS rate was set to 1 and lognormal (0, 1) priors for the relative rates of
135 the cpDNA and SEX4 trees were used. Collapse height was set to 0.0001. Ploidy was set to 1 for
136 cpDNA and 2 for the two nuclear genes. The substitution model was GTR with a gamma prior
137 distribution (0.05, 10) on each substitution type, with rate variation among sites was modeled

138 with a gamma distribution (four rate categories) for all three loci. Each locus also had branch
139 rates constrained to an uncorrelated lognormal clock. The MCMC was run for 100 million
140 generations and all parameters had effective sample sizes > 180 after removing the first 10
141 million generations as burn-in. The maximum clade credibility species tree was generated by
142 sampling trees every 50,000th generation in the stationary phase (the last 90 million generations),
143 where the heights are common ancestor heights, scaled in substitutions/site.

144 A fossil *Gunnera* pollen grain was used to calibrate the phylogeny. *Tricolpites reticulatus*
145 from the Turonian of Peru [22] represents the first unambiguous appearance of the genus. Based
146 on this calibration point, the Turonian/Coniacian boundary (Late Cretaceous) was used to
147 provide a crown age of *Gunnera* by scaling the root of the STACEY tree (see above) using a
148 mean age of 90 Ma. Its placement on the crown of *Gunnera* is based on a morphological review
149 of extant and fossil pollen of *Gunnera* species, as assessed with scanning electron microscopy to
150 define morphological characters of the exine and its structure to support its placement on the
151 topology [29].

152

153 **(b) Biogeographic analyses**

154 Distribution data were compiled from Mora-Osejo et al. [20] and Wanntorp and Wanntorp [18]
155 together with records from the Global Biodiversity Information Facility (www.gbif.org) and
156 regional herbaria (CONC and MEL) that were vetted by the authors. Using the extant
157 distribution of *Gunnera* we defined nine operational areas for ancestral area estimation (Fig. 2):
158 (A) northern Andes, from Venezuela and Colombia to northernmost Peru, corresponding to the
159 páramos north of the Huancabamba Depression; (B) central Andes, from northern Peru (south of
160 the Huancabamba Depression) south to the Tropic of Capricorn and including the Altiplano,

161 Jalca, and Puna; (C) southern Andes, from northern Chile south to Patagonia, including the
162 islands off the coasts of Chile and Argentina; (D) southeastern South America, including the
163 lowlands of southeastern Brazil and the Rio Paraná drainage; (E) Mesoamerica, from southern
164 Mexico to southernmost Panama; (F) the Hawaiian islands; (G) Africa, including Madagascar;
165 (H) the Malay archipelago, including New Guinea; (I) Tasmania and New Zealand.

166 We inferred ancestral biogeographic ranges using the package BioGeoBEARS 0.2.1 [30]
167 in the R platform [R Core 31]. BioGeoBEARS implements widely used models of range
168 evolution [e.g. 32], but it includes an additional parameter of cladogenetic speciation mediated
169 by founder events: the jump parameter “j”. This parameter allows daughter species to
170 instantaneously “jump” outside the geographical range of parental species. We considered this
171 model appropriate since several *Gunnera* species occur on oceanic islands (e.g., the Hawaiian
172 and Juan Fernandez Islands). We inferred ancestral ranges across the *Gunnera* phylogeny using
173 the Dispersal Extinction Cladogenesis (DEC) model with the J parameter (+j). The among-area
174 connectivity was constrained in the following time slices as follows: northern and central
175 Andean co-distributions were not permitted before 40 Ma [33, 34], Hawaiian distributions were
176 not permitted before 30 Ma [35], lower connectivity (0.1 rate of dispersal) was set between
177 Africa and South America throughout the last 90 Ma, as well as between South America and
178 New Zealand plus Tasmania throughout the last 30 Ma [36].

179

180 (c) Diversification rate analysis

181 To test for diversification rate shifts we used the software BAMM 2.0 [Bayesian Analysis of
182 Macroevolutionary Mixtures; 37]. BAMM implements a Bayesian framework to estimate
183 evolutionary rate parameters and explore candidate models of lineage diversification to quantify
184 and detect heterogeneity in evolutionary rates. We ran BAMM for 1,000,000 generations

185 sampling every 20 steps and accounting for incomplete taxon sampling. We analysed the output
186 in R using the BAMMtools package 2.0.2 [37]. We discarded the first 25% estimates as burn-in
187 based on the convergence of our data (effective sampling size of parameters greater than 200).
188 We generated plots of net diversification and speciation rates through time and inferred the
189 occurrence and position of rate shifts accounting for the 95% HPD of BAMM-inferred rate shifts
190 based on a Bayes factor cut-off of 5.

191

192 **(d) Climatic niche evolution**

193 We performed ecological niche modeling for all 27 species of *Gunnera* included in the
194 phylogenetic analysis using Maxent [38] with 8 WorldClim bioclimatic variables at a resolution
195 of approximately 1 km² [39], following the methodology of Evans *et al.* [40]. The bioclimatic
196 variables associated with temperature are: Mean annual temperature (MAT), minimum
197 temperature of coldest month (MTCM), mean temperature of warmest quarter (MTWQ), and
198 mean temperature of coldest quarter (MTCQ). Bioclimatic variables associated with precipitation
199 are: Mean annual precipitation (MAP), precipitation of wettest quarter (PWETQ), precipitation
200 of driest quarter (PDQ), and precipitation of warmest quarter (PWARMQ). We choosing these
201 climatic variables because their biological meaning and by removal of the other 11 correlated
202 WorldClim variables after a principal components analysis. We used a total of 882 vetted species
203 occurrence points [see (b) above]. For the niche models we obtained the mean value for each of
204 the 8 bioclimatic variables weighted by the cumulative probability of each value (weighted
205 mean; w_{mean}) using the R package phylolclim [41].

206 Climatic history was assessed using the projection of our phylogenetic tree in environmental
207 (bioclimatic variable) and temporal space assuming Brownian motion evolution [BM; 40, 42].
208 For this we used the R package phytools [43].

209 Phylogenetic niche conservatism (PNC), defined as the retention of ecological traits over
210 time among related species [12], was estimated using Pagel's lambda [44] in the R package
211 GEIGER [42]. Lambda ranges from one when trait evolution is strongly influenced by
212 phylogeny, and a species niche-to-phylogeny correlation is equal to the Brownian model
213 expectation, to zero when trait evolution is independent of phylogeny [45]. We used a likelihood
214 ratio test [46] to determine whether the observed values differed significantly from zero and one.
215 In general, phylogenetic signal indicates a statistical non-independence among species trait
216 values due to relatedness, consistent with PNC [12]. To examine PNC explicitly we used the
217 Akaike Information Criterion ($wAIC$) to compare the relative fit of three models of evolution to
218 each bioclimatic variable (w_{mean} values). The models include i) a Brownian motion (BM)
219 model of gradual and continuous drift, ii) a stabilizing selection Ornstein–Uhlenbeck (OU)
220 model with one optimum; and iii) a white noise (WN) model of random variation, in which the
221 similarity of species is independent of their phylogenetic relationships [47]. We performed this
222 comparison using GEIGER. The phylogenetic dependence of the realized climatic variation
223 between related species, combined with the comparison of BM and OU models, provides an
224 assessment for testing PNC (Losos, 2008; Wiens et al., 2010) and was thus suitable for our study.
225

226

227 **3. Results**

228

229 **(a) Multispecies coalescent tree**

230 The multispecies coalescent tree reconstructed here is consistent with the topology of the
231 maximum parsimony tree based on molecular and morphological data of Wanntorp and
232 Wanntorp (2003). All major clades were resolved with moderate to high support (> 0.80
233 posterior probabilities; Fig. 2), but some recent species-level relationships received poor branch
234 support.

235 Wide time intervals (95% highest posterior density, HPD, values) were inferred for early
236 nodes on the phylogeny (Nodes I and III, Fig. 2) but more recent nodes had little variation
237 around the mean inferred age (e.g. Nodes VI and VII, Fig. 2). Overall the crown node of
238 *Gunnera* was inferred at a mean age of 90 Ma (95% HPD 165 – 40 Ma). Following the origin
239 and diversification of the genus in the Late Cretaceous, the two major clades of *Gunnera*
240 originated between 31 (46 – 17 Ma, Node III, Fig. 2) and 10 Ma (15 – 5 Ma, Node II, Fig. 2).
241 Contrasting results were resolved with regard to the time of origin of species, where *Gunnera*
242 *herteri* had a mean age of 90 Ma and many others, particularly the Andean species, are younger
243 than 2 Ma (Fig. 2)

244

245 **(b) Biogeographic and diversification history**

246 The BioGeoBEARS analysis resulted in broadly distributed ancestral nodes at the backbone of
247 the tree, reflected in the uncertainty in ancestral range (distributions with $> 5\%$ probability of
248 occurrence, white sections in pie charts; Fig. 2). Despite this, internal nodes ca. 12 Ma and

249 younger were inferred with less ambiguity in ancestral area. These results reveal an ancient
250 lineage that began extending its distribution significantly as of the Oligocene (ca. 30 Ma; node
251 III; Fig. 2). BioGeoBEARS results show ambiguity in the biogeographic origin of the genus
252 (node I; Fig. 2), but early lineages were distributed in the Southern Hemisphere (areas C, G, I).

253 Results from the BAMM diversification rate through time analysis shows that diversification
254 in *Gunnera* generally increased over the last ca. 20 Ma (Fig. 3). However, this increase is almost
255 exclusively due to the Pliocene diversification of the *Panke* clade, when the genus colonized the
256 Andes. This is shown by a significant increase in net diversification rate in the *Panke* clade,
257 either at its crown (Node VI, probability of 25%) or at its stem (Node V, probability of 22%).
258 The highest rates of diversification were found during the Pleistocene in the *Panke* clade for the
259 lineage distributed in the northern Andes.

260

261 (c) Climatic niches and history

262 Extant species of *Gunnera* are inferred to occupy cool (microthermal) and moderate
263 (mesothermal) climatic conditions according to the classification of Nix [48], with a w_{mean} for
264 mean annual temperature (MAT) ranging from 6.4° - 20.3°C and a w_{mean} mean annual
265 precipitation (MAP) ranging from 813 - 3588 mm (Fig. S2; Tables S1 and S2). Microthermal
266 species are distributed mainly in temperate latitudes of the Southern Hemisphere, with the
267 exception of *G. talamancana*, which is found at high altitudes (1900-3400 m) in Central America
268 [20]. Mesothermal species are distributed in tropical latitudes in South and Central America,
269 Hawaii, New Guinea, and Africa, with the exception of *G. arenaria* that occurs in temperate
270 areas in New Zealand.

271 According to the estimation of ancestral climatic variables, the most recent common
272 ancestor (MRCA) of *Gunnera* lived under a mesothermal climate *sensu* Nix (1992), with a MAT
273 of 15.3°C and MAP of 1577 mm. Phylogenetic signal using Pagel λ was detected for MAT ($\lambda =$
274 0.93) and MTCQ ($\lambda = 0.92$) between temperature variables and PWETQ ($\lambda = 1$) and PWARMQ (λ
275 $= 0.93$) between precipitation variables (Table S1). *w*AIC analyses showed that the evolution of
276 the climatic niche is best described by the OU model, suggesting that selection pulls the climatic
277 values toward an optimum. Minimum temperature of coldest month (Bio 6) and mean annual
278 precipitation (Bio 12) showed no difference from a white noise model of evolution, indicating
279 that these variables are independent of phylogenetic relationships in *Gunnera* species (Table S1).

280

281 4. Discussion

282

283 Based on the divergence times and relationships of the *Gunnera* multispecies coalescent tree, we
284 examined the contribution of a southern hemisphere taxon to the mega-diverse tropical Andean
285 flora of South America. Our results show the tempo of range expansion and lineage
286 diversification.

287

288 (a) Biogeographic history of *Gunnera*

289 A question that has long intrigued biogeographers about widespread southern hemisphere
290 lineages such as *Gunnera* is whether present-day disjunctions are the result of vicariance or
291 dispersal events. Given the geographically extensive fossil record dating to the Cretaceous [21,
292 29] and the current distribution in all southern continents except Antarctica [19], *Gunnera* has
293 long been considered a typical Gondwanan element [20, 49], with vicariance proposed as the

294 main driver of its current geographic distribution [18]. Here we do not find support for
295 unequivocal vicariance events in the biogeographical history of *Gunnera*, but instead interpret a
296 general pattern of long distance dispersal from our results.

297 The mean crown age of 90 Ma for *Gunnera* is consistent with previous findings and the
298 variation around the mean age (95% HPD 165 – 40 Ma) reflects what has been found in earlier
299 work [50-52]. *Gunnera* is inferred to have been widespread in the former Gondwanan territories
300 including the southern Andes (area C), southeastern South America (area D), and Africa (area G
301 at Node I in Fig. 2) during the Cretaceous. A Gondwanan distribution is also supported by
302 several fossils from southernmost South America, southwest Africa, the Antarctic Peninsula,
303 Australia, and Tasmania [53]. *Gunnera herteri* from South America is sister to the remaining
304 *Gunnera* species, in agreement with previous studies [18, 20, 49], which supports a long history
305 in the southern portions of the continent.

306 A vicariance event could be interpreted at the node where the Australasian lineages (Node II)
307 diverge from the South American and African lineages (Node III), based on the phylogenetic
308 pattern. However, the divergence time for that event dates to the Late Eocene (ca. 40 Ma) and
309 geological evidence does not support division of these continents at that time [54]. Suitable areas
310 for *Gunnera* in the tropical latitudes of New Guinea were available when this region emerged
311 above sea level and Australia reached its current latitudinal position, both of which occurred at
312 the end of the Cenozoic [12 Ma; 49]. In agreement with and according to our estimations the
313 tropical lineage *G. macrophylla*, distributed from the Philippines and Sumatra east to New
314 Guinea and the Solomon Islands, split from the southern Australia and Tasmania lineages at ca.
315 10 Ma. This result suggests that the arrival of extant *Gunnera* in tropical regions (e.g. area H)

316 occurred via long distance dispersal, as has been inferred for other Gondwanan taxa such as
317 *Nothofagus* [e.g. 55].

318 Another long distance dispersal is inferred at Node III where the African lineage *G. perpensa*
319 split from rest of the genus at ca. 30 Ma, at the time when Africa and South America were
320 completely separated [54]. Node IV joins the Andean species (areas A, B, C) with subgenus
321 *Panke* (areas A, B, C, D, E, F). Node V infers a colonisation event to Hawaii (area F) and Node
322 VI shows a division between southern South American species (areas B, C, and D) and those
323 from the north of South America and Central America (areas A and E respectively).

324

325 **(b) Range expansion in the Andes**

326 *Gunnera* is inferred to have been present in southern South America for its entire evolutionary
327 history (Fig. 2). By the Mid-Miocene the stem node of the *Panke* clade (15 Ma; Node IV) was
328 distributed in the Andes and began to diversify, expanding north into Central America and south
329 again into the southern Andes (Fig. 2). The estimated mean age overlaps with that proposed for
330 the formation of the Isthmus of Panama [56], a primarily terrestrial lowland region that has
331 connected North and South America since ca. 15 Ma. Bacon *et al.* [57] proposed that closure of
332 the isthmus enabled taxa to expand their distributions both north and southwards during pulses of
333 migration (ca. 23, 8, and 5 Ma). Range expansion at Node IV occurred after a long stasis (ca. 15
334 Ma) where there was a dearth of speciation or substantial extinction – two alternative
335 explanations that are generally difficult to distinguish [58].

336 The colonisation of the northern Andes (area A at Node VII, Fig. 2) is inferred to have likely
337 taken place from Central American ancestors, sometime in the Early Pleistocene (ca. 2.27 Ma).
338 Although the Andes began to rise as early as the Early Paleogene [33], it is often difficult to

339 disentangle the roles of Andean uplift and climate change on Neotropical diversification [but see
340 59] because they occurred contemporaneously [7]. *Gunnera* is primarily a wet montane, rather
341 than páramo, lineage, and does not require high elevations for successful dispersal.

342

343 **(C) North American fossils: crown or stem relatives of *Panke*?**

344 A sister relationship between the northernmost species of *Gunnera* (*G. mexicana*) and all other
345 species in subgenus *Panke*, combined with the fact that there are several North American fossil
346 localities from the Late Cretaceous to the Eocene [80–50 Ma; 21], led Wanntorp and Wanntorp
347 (2003) to suggest that the South American species of *Panke* represented a recolonisation of
348 South America from the north. This result is further supported by morphological similarities of
349 leaf impressions and pollen size between the Late Cretaceous fossils and modern *Panke* species
350 [21, 60], and the placement of the Hawaiian species *G. petaloidea* and *G. kauaiensis* as the next
351 branching lineage after *G. mexicana*.

352 This scenario implies that the North American fossils belong to the crown or stem group of
353 *Panke*, i.e. they would have been derived either from the branch connecting *Misandra* (*G. lobata*
354 and *G. magellanica*) to *Panke* (Node IV, Fig. 2) or from the branch leading to *G. mexicana*.
355 Although this is a possible conclusion based on the topology of our *Gunnera* phylogeny, the
356 divergence times estimated here suggest otherwise. The splits connecting *Misandra* to the
357 MRCA of *Panke* (where the dispersal to North America would have taken place) are estimated at
358 ca. 15 Ma, which is almost 65 Ma later than the first documented North American fossils.
359 Whereas determining the exact position of these fossils would require a well-sampled
360 micromorphological dataset of both living and fossil *Gunnera* relatives, our results suggest that
361 the North American fossils do not belong to the crown group of *Panke*. Instead, we suggest they

362 likely represent a lineage that reached North America during the Cretaceous, but did not leave
363 any living descendants. A similar scenario was found in the inconsistency between DNA-based
364 divergence times and pollen fossils of *Nothofagus*, where ‘incongruent’ fossils might have been
365 erroneously assigned to crown *Nothofagus*, whereas they in fact represented extinct stem
366 relatives [55, 61].

367

368 **(d) Stasis vs. rapid speciation**

369 A remarkable aspect of our results is the striking difference in the stem ages of *Gunnera* species.
370 *Gunnera herteri* is inferred to have originated 90 Ma during the Late Cretaceous (Node I),
371 whereas 18 species in the phylogeny are inferred to be younger than 2 Ma (Fig. 2). The contrast
372 between stasis and rapid speciation is also seen in the BAMM results (Fig. 3), where low net
373 diversification rates are shown at ancestral branches and a shift in diversification rate detected in
374 the Andean *Panke* clade is followed by a steady rate increase (Fig. 3C).

375 It is puzzling why some lineages have experienced long evolutionary stasis, whereas others
376 underwent rapid speciation – all within the genetic constraints of a single clade. This result could
377 be an artefact of extinction, if the lineages leading to the ancient species in fact diversified but all
378 lineages except one went extinct [58, 62]. However, there is palaeontological support for these
379 exceptionally old stem ages. Fossil pollen on the Vega Peninsula of Antarctica dated from the
380 Campanian/Late Maastrichtian have a distinctive exine that is nearly indistinguishable from that
381 found in pollen grains of extant species of Australia, New Zealand, and Southeast Asia
382 (Wanntorp et al. 2004). This pollen evidence suggests a lack of extinction bias and hints to PNC
383 as an important mechanism behind evolutionary stasis.

384 The persistence of *Gunnera* for a much longer time (up to 165 Ma) than most other
385 angiosperm genera is remarkable. We interpret our results with caution, but consider them as
386 indicative of strong niche conservatism across the highly disjunct range of *Gunnera* for wet,
387 montane forest environments. Indeed, our climatic reconstruction shows a mesothermal niche
388 preference for the crown node of *Gunnera* (Fig. S2), similar to that identified in other Cretaceous
389 lineages [63]. Further, our estimate of phylogenetic signal shows high values (Table S1),
390 particularly those associated with both mean annual and coldest quarter temperature variables,
391 and an Ornstein-Uhlenbeck model, which together indicate that the climatic history of *Gunnera*
392 underwent selection pressure (e.g. stabilizing selection) that favoured the ancestral niche over
393 time [12]. Recently, Hinojosa *et al.* [55] suggested that lineages of Gondwanan origin expanded
394 into the tropics by tracking mesothermal climates. Dispersal towards current tropical zones has
395 been possible because species have tracked ancestral climatic niches from high or mid-latitudes
396 into lower latitudes, sometimes facilitated by climatic and geological changes.

397 It is interesting that *Gunnera*, a montane forest clade of Gondwanan origin, successfully
398 dispersed to the northern tropical Andes, where few other similar plant clades could. A key
399 element to this may be due to its colonising nature. *Gunnera* comprises species of forest edges
400 and marginal habitats [64], appear after landslides in wet forests [Fig. 3C; 65], underwent long
401 distance dispersal events to Hawaiian and the Juan Fernandez Islands, and is persistent in the
402 seed bank [66, 67]. *Gunnera* species also quickly colonise glacial forelands [68] and their pollen
403 is commonly found in glacial and post-glacial sediments in both southern South America and in
404 Tasmania [69, 70]. Lastly and potentially most convincingly, the fact that some *Gunnera* species
405 are invasive [71, 72] clearly shows their aggressive colonising abilities that likely differentiate
406 them from other montane plant groups.

407

408 **(e) Comparison with other Andean groups**

409 There are multiple examples of plant clades that have colonised the Andes from the north, as we
410 suggest for the Panke clade of *Gunnera*. Some are ‘boreotropical’ elements that probably
411 reached South America around the Palaeocene-Eocene Thermal Maximum [~55 Ma; 73], when a
412 large belt of tropical forest covered much of southern Laurasia, thus functioning as a biotic
413 corridor for Palaeotropical lineages [e.g. 74, 75]. Later, dispersals southwards from North to
414 South America may have been facilitated by the Greater Antilles and the Aves Ridge around the
415 Eocene/Oligocene boundary [76], and finally through the Panama Isthmus after its uplift ca. 15
416 Ma [56]. Examples of northern taxa colonising the Andes with local radiations include
417 *Hedyosmum* [62, 77] and *Lupinus* [78]. Many of these northern lineages have undergone
418 significant radiation in the páramo.

419 In contrast, there is relatively little evidence of Andean plant clades that are derived from
420 the south, as our results show more generally for *Gunnera*. Some well-known southern
421 Hemisphere (“Gondwana”) groups, such as *Nothofagus* and *Araucaria*, simply do not enter the
422 Andean tropical zone, but reach tropical areas in Australasia [76]. *Fuchsia*, which is considered
423 to have a southern origin based on a rich Antarctic Cenozoic fossil record, does not show a clear
424 biogeographic pattern from molecular phylogenies [79]. Nevertheless, there are several taxa that
425 are similar to *Gunnera* and appear to represent southern groups that reached the northern Andes
426 at some point, where they then diversified significantly [e.g. *Ceroxylon*, see 80 for a review of
427 the pattern].

428

429 **5. Conclusions**

430 For many decades *Gunnera* has attracted the attention of botanists and biogeographers concerned
431 with southern hemisphere disjunctions and the break-up of Gondwana. Here we have shown that
432 it also constitutes a model taxon to study biogeography in general, as well as the colonisation and
433 diversification of southern elements in the tropical Andes in particular. The extraordinary species
434 longevity inferred here for species in Southeast Asia, Africa and eastern Brazil – up to ca. 165
435 Ma according to our results – is most likely due to morphological and climatic conservatism
436 despite the massive geotectonic and climatic changes that took place during its history. In
437 contrast, the recent and rapid diversification of Andean lineages are best explained by the
438 massive increase in the area of suitable habitats and opportunities for allopatric speciation, as a
439 consequence of the Andean uplift and late Neogene climatic changes. Understanding the
440 evolution of Andean mega-diversity thus requires identifying and tracing the diversification of
441 southern, northern and locally derived taxa.

442

443 **Authors' contributions**

444 AA and CDB conceived, designed, and coordinated the study and led the writing of the
445 manuscript; AA, TS, and LW carried out the molecular lab work, participated in data analysis,
446 carried out sequence alignments, participated in the design of the study and drafted the
447 manuscript; CDB, FJVP, LFH, BO, BP, and AA carried out the statistical analyses. All authors
448 contributed to the text and gave final approval for publication.

449

450 **Funding statement**

451 Financial support was provided by the Swedish Research Council (B0569601), the European
452 Research Council under the European Union's Seventh Framework Programme (FP/2007-2013,

453 ERC Grant Agreement n. 331024), the Swedish Foundation for Strategic Research and the Knut
454 and Alice Wallenberg Foundation (through a Wallenberg Academy Fellowship) to A.A. LFH
455 was funded by FONDECYT 1150690, Millennium Institute of Ecology and Biodiversity (IEB)
456 Grant P05-002 from MIDEPLAN (Chile), PFB-023 from CONICYT (Chile).

457

458 **Acknowledgments**

459 We would like to thank C. Hughes and U. Swenson for reading and commenting on early
460 versions of the manuscript and S. Razafimandimbison for attempts to sequence ITS for
461 *Myrothamnus*. We are also thankful to Herbarium GB for allowing us to extract samples for
462 DNA analyses. Vivian Aldén provided laboratory assistance. The analyses were performed on
463 the bioinformatics computer cluster Albiorix at the Department of Biological and Environmental
464 Sciences, University of Gothenburg.

465

466 **References**

- 467 1. Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B., Kent J. 2000
468 Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-858.
- 469 2. Antonelli A., Sanmartín I. 2011 Why are there so many plant species in the Neotropics?
470 *Taxon* **60**, 403-414.
- 471 3. Rull V. 2011 Neotropical biodiversity: Timing and potential drivers. *Trends in Ecology*
472 *and Evolution* **26**(10), 508-513. (doi:10.1016/j.tree.2011.05.011).
- 473 4. Haffer J. 1969 Speciation in Amazon forest birds. *Science* **165**, 131-137.

- 474 5. Smith B.T., McCormack J.E., Cuervo A.M., Hickerson M.J., Aleixo A., Cadena C.D.,
475 Perez-Eman J., Burney C.W., Xie X., Harvey M.G., et al. 2014 The drivers of tropical
476 speciation. *Nature* **515**(7527), 406-409. (doi:10.1038/nature13687
477 <http://www.nature.com/nature/journal/v515/n7527/abs/nature13687.html> - supplementary-
478 information).
- 479 6. Dexter K.G., Lavin M., Torke B.M., Twyford A.D., Kursar T.A., Coley P.D., Drake C.,
480 Hollands R., Pennington R.T. 2017 Dispersal assembly of rain forest tree communities across the
481 Amazon basin. *Proceedings of the National Academy of Sciences* **114**(10), 2645-2650.
- 482 7. Gentry A.H. 1982 Neotropical floristic diversity: phytogeographical connections between
483 Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean
484 orogeny? *Annals of the Missouri Botanical Garden* **69**(3), 557-593.
- 485 8. Luebert F., Weigend M. 2014 Phylogenetic insights into Andean plant diversification.
486 *Frontiers in Ecology and Evolution* **2**. (doi:10.3389/fevo.2014.00027).
- 487 9. Villagrán C., Hinojosa L.F. 1997 Historia de los bosques del sur de Sudamérica, II:
488 Análisis fitogeográfico. *Revista Chilena de Historia Natural* **70**(2), 1-267.
- 489 10. Sklenář P., Dušková E., Balslev H. 2011 Tropical and Temperate: Evolutionary History
490 of Páramo Flora. *The Botanical Review* **77**, 71-108. (doi:10.1007/s12229-010-9061-9).
- 491 11. Antonelli A., Zizka A., Silvestro D., Scharn R., Cascales-Miñana B., Bacon C.D. 2015
492 An engine for global plant diversity: highest evolutionary turnover and emigration in the
493 American tropics. *Frontiers in Genetics* **6**, e130.
- 494 12. Wiens J.J., Ackerly D.D., Allen A.P., Anacker B.L., Buckley L.B., Cornell H.V.,
495 Damschen E.I., Davies T.J., Grytnes J.A., Harrison S.P., et al. 2010 Niche conservatism as an

- 496 emerging principle in ecology and conservation biology. *Ecol Lett* **13**(10), 1310-1324. (doi:Doi
497 10.1111/J.1461-0248.2010.01515.X).
- 498 13. Donoghue M.J., Edwards E.J. 2014 Biome shifts and niche evolution in plants. *Annual*
499 *Review of Ecology, Evolution, and Systematics* **45**, 547-572.
- 500 14. Crisp M.D., Arroyo M.T., Cook L.G., Gandolfo M.A., Jordan G.J., McGlone M.S.,
501 Weston P.H., Westoby M., Wilf P., Linder H.P. 2009 Phylogenetic biome conservatism on a
502 global scale. *Nature* **458**, 754-756.
- 503 15. Simon M.F., Grether R., de Querioz L.P., Skema C., Pennington R.T., Hughes C.E. 2009
504 Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of
505 adaptations to fire. *Proceedings of the National Academy of Sciences, USA* **106**(48), 20359-
506 20364.
- 507 16. Luteyn J.L. 1999 Páramos: A checklist of plant diversity, geographical distribution, and
508 botanical literature. *Memoirs of the New York Botanical Garden* **84**, 1-278.
- 509 17. Hooghiemstra H., Wijninga V.M., Cleef A.M. 2006 The paleobotanical record of
510 Colombia: implications for biogeography and biodiversity. *Annals of the Missouri Botanical*
511 *Garden* **93**, 297-324.
- 512 18. Wanntorp L., Wanntorp H.E. 2003 The biogeography of *Gunnera* L.: Vicariance and
513 dispersal. *Journal of Biogeography* **30**(7), 979-987.
- 514 19. Bader F.W.J. 1961 Das Areal der Gattung *Gunnera* L. *Botanische Jahrbücher für*
515 *Systematik, Pflanzengeschichte und Pflanzengeographie* **80**(3), 281-293.
- 516 20. Mora-Osejo L.E., Pabón-Mora N., González F. 2011 *Gunneraceae*. New York, The New
517 York Botanical Garden; 166 p.

- 518 21. Jarzen D.M. 1980 The occurrence of *Gunnera* pollen in the fossil record. *Biotropica*
519 **12**(2), 117-123.
- 520 22. Brenner G.J. 1968 Middle Cretaceous spores and pollen from northeastern Peru. *Pollen et*
521 *Spores* **10**(2), 341–383.
- 522 23. Oxelman B., Liden M., Berglund D. 1997 Chloroplast *rps16* intron phylogeny of the tribe
523 Sileanae (Caryophyllaceae). *Plant Systematics and Evolution* **206**(1), 393-410.
- 524 24. Pang X., Liu C., Shi L., Liu R., Liang D., Li H., Chemy S.S., Chen S. 2012 Utility of the
525 *trnH-psbA* intergenic spacer region and its combinations as plant DNA barcodes: a meta-
526 analysis. *PLoS ONE* **7**, e48833. (doi:DOI: 10.1371/journal.pone.0048833).
- 527 25. Blattner F.R. 1999 Direct amplification of the entire ITS region from poorly preserved
528 plant material using recombinant PCR. *BioTechniques* **27**, 1180-1186.
- 529 26. Kotting O., Santella D., Edner C., Eicke S., Marthaler T., Gentry M.S., Comparot-Moss
530 S., Chen J., Smith A.M., Steup M., et al. 2009 STARCH-EXCESS4 is a laforin-like
531 phosphoglucan phosphatase required for starch degradation in *Arabidopsis thaliana*. *The Plant*
532 *Cell* **21**(1), 334-346.
- 533 27. Nylander J.A.A. 2004 MrModeltest v2. Program distributed by the author. *Evolutionary*
534 *Biology Centre, Uppsala University*.
- 535 28. Jones G., Aydin Z., Oxelman B. 2014 DISSECT: an assignment-free Bayesian discovery
536 method for species delimitation under the multispecies coalecent. *Bioinformatics* **31**(7), 991-998.
- 537 29. Wanntorp L., Dettmann M.E., Jarzen D.M. 2004 Tracking the Mesozoic distribution of
538 *Gunnera*: Comparison with the fossil pollen species *Tricolpites reticulatus* Cookson. *Review of*
539 *Palaeobotany and Palynology* **132**(3-4), 163-174.

- 540 30. Matzke N.J. 2014 Model selection in historical biogeography reveals that founder-event
541 speciation is a crucial process in island clades. *Systematic Biology* **63**(6), 951-970.
- 542 31. Team R.C. 2012 R: A Language and Environment for Statistical Computing. (Vienna,
543 Austria, R Foundation for Statistical Computing.
- 544 32. Ree R.H., Smith S.A. 2008 Maximum likelihood inference of geographic range evolution
545 by dispersal, local extinction, and cladogenesis. *Systematic Biology* **57**(1), 4-14.
- 546 33. Garzzone C.N., Hoke G.D., Libarkin J.C., Withers S., MacFadden B., Eiler J., Ghosh P.,
547 Mulch A. 2008 Rise of the Andes. *Science* **320**(5881), 1304-1307.
- 548 34. Hoorn C., Wesseling F.P., ter Steege H., Bermudez M.A., Mora A., Sevink J., Sanmartín
549 I., Sanchez-Meseguer A., Anderson C.L., Figuieredo J., et al. 2010 Amazonia through time:
550 Andean uplift, climate change, landscape evolution and biodiversity. *Science* **330**(6006), 927-
551 931.
- 552 35. Clague D.A., Braga J.C., Bassi D., Fullagar P.D., Renema W., Webster J.M. 2010 The
553 maximum age of Hawaiian terrestrial lineages: geological constraints from the Koko Seamount.
554 *Journal of Biogeography* **37**(6), 1022-1033.
- 555 36. McLoughlin S. 2001 The breakup history of Gondwana and its impact on pre-Cenozoic
556 floristic provincialism. *Australian Journal of Botany* **49**(3), 271-300.
- 557 37. Rabosky D.L. 2014 Automatic detection of key innovations, rate shifts, and diversity-
558 dependence on phylogenetic trees. *PLoS ONE* **9**(2), e89543.
- 559 38. Phillips S.J., Anderson R.P., Schapire R.E. 2006 Maximum entropy modeling of species
560 geographic distributions. *Ecological Modeling* **190**, 231-259.

- 561 39. Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A. 2005 Very high resolution
562 interpolated climate surfaces for global land areas. *Int J Climatol* **25**(15), 1965-1978. (doi:Doi
563 10.1002/Joc.1276).
- 564 40. Evans M.E.K., Smith S.A., Flynn R.S., Donoghue M.J. 2009 Climate, niche evolution,
565 and diversification of the "Bird-Cage" evening primroses (*Oenothera*, sections *Anogra* and
566 *Kleinia*). *The American Naturalist* **173**(2), 225-240.
- 567 41. Heibl C. 2011 PHYLOCLIM: Integrating phylogenetics and climatic niche modelling. (
- 568 42. Schluter D., Price T., Mooers A.O., Ludwig D. 1997 Likelihood of ancestor states in
569 adaptive radiation. *Evolution* **51**(6), 1699-1711.
- 570 43. Revell L.J. 2012 Phytools: an R package for phylogenetic comparative biology (and other
571 things). *Methods in Ecology and Evolution* **3**(2), 217-223.
- 572 44. Pagel M. 1994 Detecting correlated evolution on phylogenies: A general method for the
573 comparative analysis of discrete characters. *Proceedings of the Royal Society B: Biological*
574 *Sciences* **255**(1342), 37-45.
- 575 45. Pagel M. 1999 The maximum likelihood approach to reconstructing ancestral character
576 states of discrete characters on phylogenies. *Systematic Biology* **48**(3), 612-622.
- 577 46. Neyman J., Pearson E.S. 1928 On the use and interpretation of certain test criteria for
578 purposes of statistical inference: Part 1. *Biometrika* **20A**, 175-240.
- 579 47. Hansen T.F., Pienaar J., Orzack S.H. 2008 A comparative method for studying adaptation
580 to a randomly evolving environment. *Evolution* **62**(8), 1965-1977. (doi:Doi 10.1111/J.1558-
581 5646.2008.00412.X).

- 582 48. Nix H. 1991 An environmental analysis of Australian rainforests. In *The rainforest*
583 *legacy, Australian National Rainforest Study Vol 2* (eds. Warren G., Kershaw P.), pp. 1-26.
584 Canberra, Australian Government Publishing Service.
- 585 49. Fuller D.Q., Hickey L.J. 2005 Systematics and leaf architecture of the Gunneraceae. *The*
586 *Botanical Review* **71**(3), 295-353.
- 587 50. Bell C.D., Soltis D.E., Soltis P.S. 2010 The age and diversification of the angiosperms re-
588 revised. *American Journal of Botany* **97**(8), 1296-1303.
- 589 51. Magallón S., Gómez-Acevedo S., Sánchez-Reyes L.L., Hernández-Hernández T. 2015 A
590 metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New*
591 *Phytologist* **207**(2), 437-453.
- 592 52. Tank D.C., Eastman J.M., Pennel M.W., Soltis P.S., Soltis D.E., Hinchliff C.E., Brown
593 J.W., Sessa E.B., Harmon L.J. 2015 Nested radiation and the pulse of angiosperm
594 diversification: increased diversification rates often follow whole genome duplications. *New*
595 *Phytologist* **207**, 454-467.
- 596 53. Macphail K. 2007 Australian palaeoclimates: Cretaceous to Tertiary: a review of
597 palaeobotanical and related evidence to the year 2000. (Brently, Western Australia, CRC
598 LEME.
- 599 54. Sanmartín I., Ronquist F. 2004 Southern hemisphere biogeography inferred by event-
600 based models: plant versus animal patterns. *Systematic Biology* **53**(2), 216-243.
- 601 55. Hinojosa L.F., Gaxiola A., Perez M.F., Carvajal F., Campano M.F., Quattrocchio M.,
602 Nichida H., Uemura K., Yabe A., Bustamante R., et al. 2016 Non-congruent fossil and
603 phylogenetic evidence on the evolution of climatic niche in the Gondwana genus *Nothofagus*.
604 *Journal of Biogeography* **43**, 555-567.

- 605 56. Montes C., Cardona A., Jaramillo C.A., Pardo A., Silva J.C., Valencia V., Ayala C.,
606 Perez-Angel L.C., Rodriguez-Parra L.A., Ramirez V., et al. 2015 Middle Miocene closure of the
607 Central American Seaway. *Science* **348**(6231), 226-229.
- 608 57. Bacon C.D., Silvestro D., Jaramillo C.A., Tilston Smith B., Chakrabarty P., Antonelli A.
609 2015 Biological evidence supports an early and complex emergence of the Isthmus of Panama.
610 *Proceedings of the National Academy of Sciences, USA* **112**(19), 6110-6115.
- 611 58. Crisp M.D., Cook L.G. 2009 Explosive radiation or cryptic mass extinction? Interpreting
612 signatures in molecular phylogenies. *Evolution* **63**(9), 2257-2265. (doi:10.1111/j.1558-
613 5646.2009.00728.x).
- 614 59. Lagomarsino L.P., Condamine F.L., Antonelli A., Mulch A., Davis C.C. 2016 The abiotic
615 and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). *New*
616 *Phytologist* **210**(4), 1430-1442.
- 617 60. Wilkinson H.P. 2000 A revision of the anatomy of Gunneraceae. *Botanical Journal of the*
618 *Linnean Society* **134**(1-2), 233-266.
- 619 61. Cook L.G., Crisp M.D. 2005 Not so ancient: The extant crown group of *Nothofagus*
620 represents a post-Gondwanan radiation. *Proceedings of the Royal Society B: Biological Sciences*
621 **272**(1580), 2535-2544.
- 622 62. Antonelli A., Sanmartín I. 2011 Mass extinction, gradual cooling, or rapid radiation?
623 Reconstructing the spatiotemporal evolution of the ancient angiosperm genus *Hedyosmum*
624 (Chloranthaceae) using empirical and simulated approaches. *Systematic Biology* **60**(5), 596-615.
625 (doi:10.1093/sysbio/syr062).

- 626 63. DeConto R.M., Hay W.W., Thompson S.L., Bergengren J. 1999 Late Cretaceous climate
627 and vegetation interactions: cold continental interior paradox. *Geological Society of America*
628 **Special Paper 332**, 391-406.
- 629 64. Greimler J., Lopez-Sepulveda K., Reiter K., Baeza C., Penailillo P., Ruíz E., Navoa P.,
630 Gatica A., Stuessy T.F. 2013 Vegetation of Alejandro Selkirk Islands (Isla Masafuera), Juan
631 Fernandez Archipelago, Chile. *Pacific Science* **67**, 267-282.
- 632 65. Vanacker V., Vanderschaeghe M., Govers G., Willems E., Poesen J., Deckers J., De
633 Bievre B. 2003 Linking hydrological, infinite slope stability and land-use change models through
634 GIS for assessing the impact of deforestation on slope stability in high Andean watersheds.
635 *Geomorphology* **52**, 299-315.
- 636 66. Arroyo M.T.K., Cavieres L.A., Humana A.M. 2004 Experimental evidence of potential
637 for persistent seed bank formation at a subantarctic alpine site in Tierra del Fuego, Chile. *Annals*
638 *of the Missouri Botanical Garden* **91**, 357-365.
- 639 67. Fesq-Martin M., Friedman A., Peters M., Behrmann J., Kilian R. 2004 Late-glacial and
640 Holocene vegetation history of the Magellanic rain forest in southwestern Patagonia, Chile.
641 *Vegetation History and Archaeobotany* **13**, 249-255.
- 642 68. Perez C.A., Aravena J.C., Silva W.A., Enriquez K.M., Farina J.M., Armesto J.J. 2014
643 Ecosystem development in short-term postglacial chronosequences: N and P limitation in glacier
644 forelands from Santa Ines Island, Magellan Strait. *Austral Ecology* **39**, 288-303.
- 645 69. Heusser C.J., Heusser L.E., Hauser A. 1992 Paleoecology of late Quaternary deposits in
646 Chiloe Continental, Chile. *Revista Chilena de Historia Natural* **65**, 235-245.
- 647 70. McKensie G.M., Kershaw A.P. 2000 The last glacial cycle from Wyelangta, the Otway
648 region of Victoria, Australia. *Palaeogeography Palaeoclimatology Palaeoecology* **155**, 177-193.

- 649 71. Fennell M., Murphy J.E., Gallagher T., Osborne B. 2013 Simulating the effects of
650 climate change on the distribution of an invasive plant, using a high resolution, local scale,
651 mechanistic approach: challenges and insights. *Global Change Biology* **19**, 1262-1274.
- 652 72. Skeffington M.S., Hall K. 2011 The ecology, distribution and invasiveness of *Gunnera* L.
653 species in Connemara, Western Ireland. *Proceedings of the Royal Irish Academy* **111B**, 157-175.
- 654 73. Zachos J.C., Dickens G.R., Zeebe R.E. 2008 An early Cenozoic perspective on
655 greenhouse warming and carbon-cycle dynamics. *Nature* **451**(7176), 279-283.
- 656 74. Bacon C.D., Baker W.J., Simmons M.P. 2012 Miocene dispersal drives island radiations
657 in the palm tribe Trachycarpeae (Arecaceae). *Systematic Biology* **61**(3), 426-442.
- 658 75. Antonelli A., Nylander J.A.A., Persson C., Sanmartín I. 2009 Tracing the impact of the
659 Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences*
660 **106**(24), 9749-9754. (doi:10.1073/pnas.0811421106).
- 661 76. Iturralde-Vinent M.A., MacPhee R.D.E. 1999 Paleogeography of the Caribbean region:
662 implication for Cenozoic paleogeography. *Bulletin of the American Museum of Natural History*
663 **238**, 1-95.
- 664 77. Zhang Q., Feild T.S., Antonelli A. 2015 Assessing the impact of phylogenetic
665 incongruence on taxonomy, floral evolution, biogeographical history, and phylogenetic diversity.
666 *American Journal of Botany* **102**(4), 566-580. (doi:10.3732/ajb.1400527).
- 667 78. Hughes C., Eastwood R. 2006 Island radiation on a continental scale: Exceptional rates of
668 plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences*
669 *of the United States of America* **103**(27), 10334-10339.

670 79. Berry P.E., Hahn W.J., Sytsma K.J., Hall J.C., Mast A. 2004 Phylogenetic relationships
671 and biogeography of *Fuchsia* (Onagraceae) based on noncoding nuclear and chloroplast DNA
672 data. *Am J Bot* **91**(4), 601-614.

673 80. Sanín M.J., Kissling W.D., Bacon C.D., Borchsenius F., Galeano G., Svenning J.-C.,
674 Olivera J., Ramírez R., Ternel P., Pintaud J.-C. 2016 The Neogene rise of the tropical Andes
675 facilitated diversification of wax palms (Ceroxylon: Arecaceae) through geographical
676 colonization and climatic niche separation. *Botanical Journal of the Linnean Society* **182**, 303-
677 317.

678

679 **Figures**

680 Figure 1. Map of the extant distribution of *Gunnera*, where high numbers of georeferences are
681 reflected by darker blue colour. The *Tricolpites reticulatus* pollen fossil was used to calibrate the
682 *Gunnera* phylogeny in absolute time for this study and is also mapped through major geological
683 time periods. Elevation is shown in grey scale where the lowest and highest global elevations are
684 found in white and black, respectively.

685

686 Figure 2. Biogeographic history based on the BioGeoBEARS optimization of the *Gunnera*
687 topology calibrated in absolute time using *Tricolpites reticulatus* pollen (light microscopy image
688 from Wikicommons). All nodes over 0.8 PP are marked and node bars representing the 95%
689 HPD time interval are shown for nodes of interest. Clades discussed in the text are marked with
690 numerals I-VII. **Inset:** Operational areas used: (A) northern Andes; (B) Central Andes; (C)
691 southern Andes; (D) southeastern South America; (E) Central America; (F) Hawaii; (G) Africa;

692 (H) the Malay Archipelago; (I) Tasmania and New Zealand; and other biogeographic areas based
693 on combinations of those defined a priori.

694

695 Figure 3. Diversification rate through time analysis using BAMM for all species sampled within
696 *Gunnera*. (A) The results show a single, positive diversification rate shift, either at the stem (with
697 0.22 PP) or the crown (with 0.25 PP) node of the Andean Panke clade. (B) Results also support
698 an increase in net diversification rate through time. (C) Some *Gunnera* species are aggressive
699 colonisers, here showing successful colonisation and persistence in the margins of a landslide in
700 Costa Rica (image from Wikicommons).

701

702 Figure S1. Morphological diversity of *Gunnera*: **A.** *G. manicata* (subgenus *Panke*), **B.** *G.*
703 *insignis* (subgenus *Panke*), **C.** *G. perpensa* (subgenus *Gunnera*), **D.** *G. magellanica* (subgenus
704 *Misandra*), **E.** *G. dentata* (subgenus *Milligania*), **F.** *G. herteri* (subgenus *Ostenigunnera*).

705 Photos: A–B: A. Antonelli; C, E: I. Trift; D: I. Kärnefeldt, F: J.-T. Johansson.

706

707 Figure S2. Traitgram of ancestral states of *Gunnera* climatic niche. Black lines correspond to a
708 projection of the phylogenetic tree in a space defined by the bioclimatic variable mean annual
709 temperature and annual precipitation.

710

Figure 1(on next page)

Flg. 1

Figure 1. Map of the extant distribution of *Gunnera*, where high numbers of georeferences are reflected by darker blue colour. The *Tricolpites reticulatus* pollen fossil was used to calibrate the *Gunnera* phylogeny in absolute time for this study and is also mapped through major geological time periods. Elevation is shown in grey scale where the lowest and highest global elevations are found in white and black, respectively.

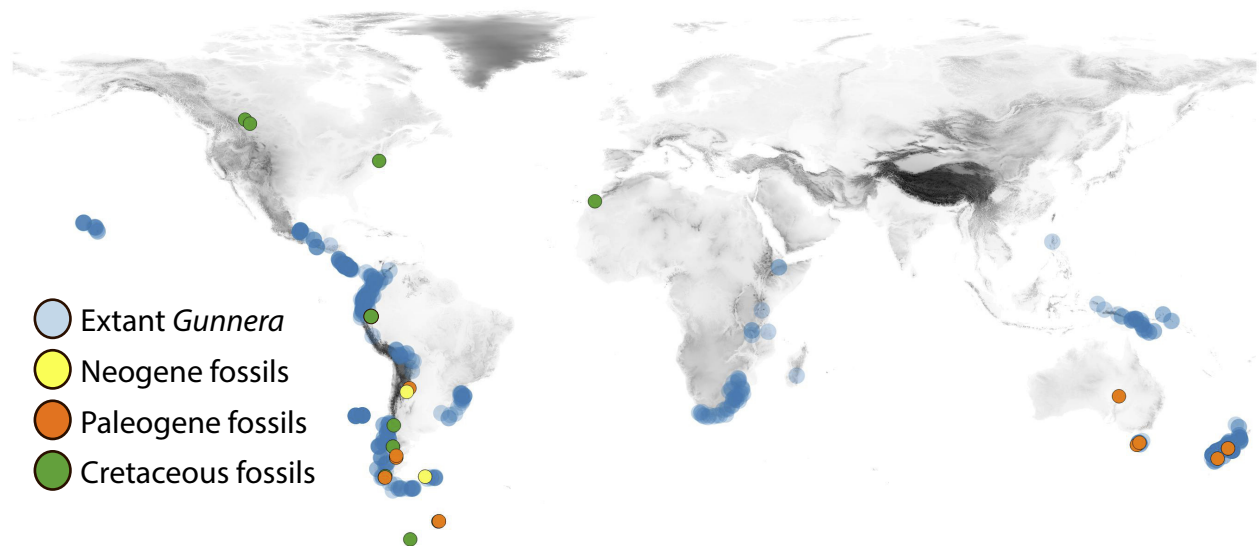


Figure 2 (on next page)

Fig. 2

Figure 2. Biogeographic history based on the BioGeoBEARS optimization of the *Gunnera* topology calibrated in absolute time using *Tricolpites reticulatus* pollen (light microscopy image from Wikicommons). All nodes over 0.8 PP are marked and node bars representing the 95% HPD time interval are shown for nodes of interest. Clades discussed in the text are marked with numerals I-VII. **Inset:** Operational areas used: (A) northern Andes; (B) Central Andes; (C) southern Andes; (D) southeastern South America; (E) Central America; (F) Hawaii; (G) Africa; (H) the Malay Archipelago; (I) Tasmania and New Zealand; and other biogeographic areas based on combinations of those defined a priori.

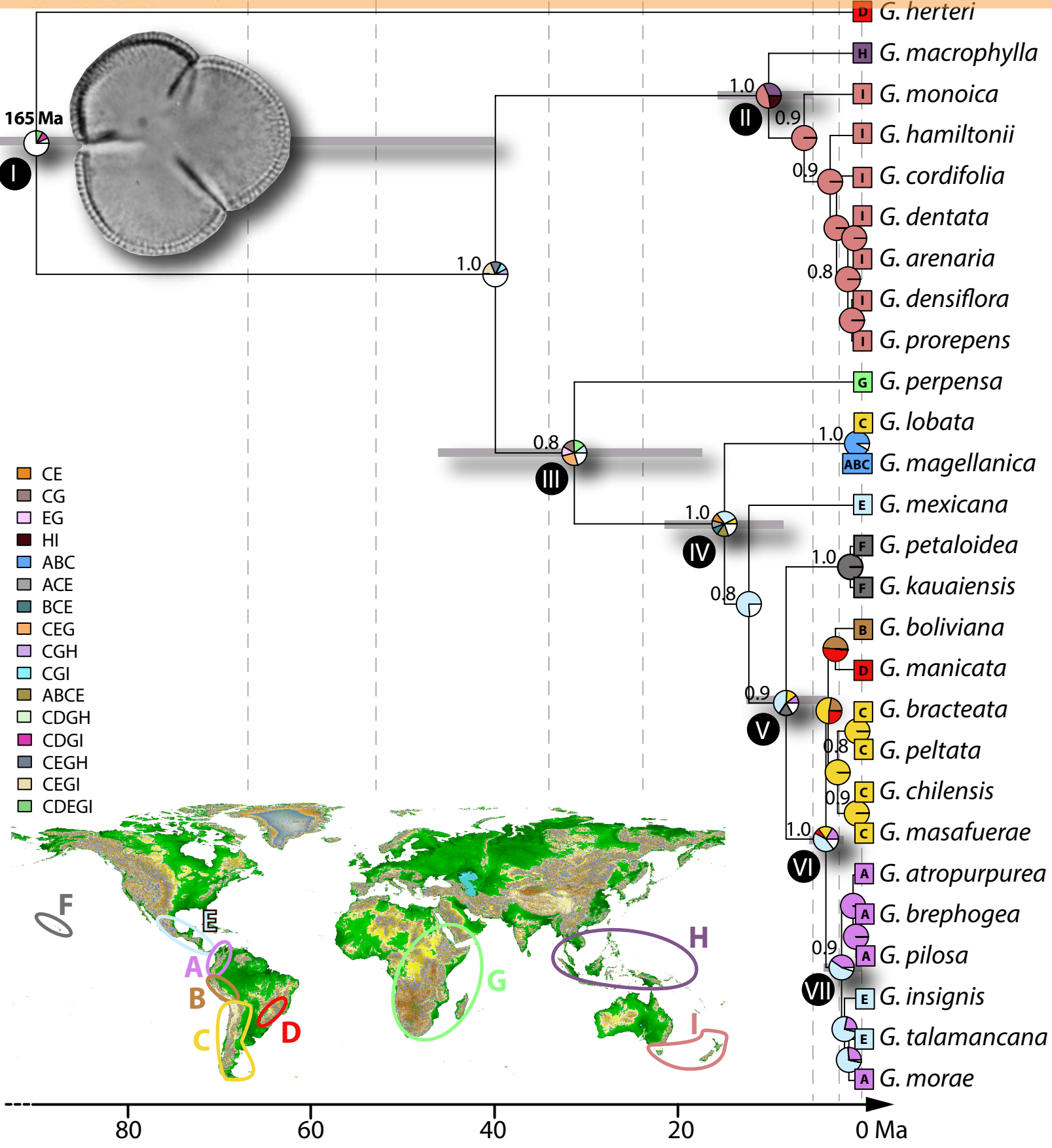


Figure 3(on next page)

Fig. 3

Figure 3. Diversification rate through time analysis using BAMM for all species sampled within *Gunnera*. (A) The results show a single, positive diversification rate shift, either at the stem (with 0.22 PP) or the crown (with 0.25 PP) node of the Andean Panke clade. (B) Results also support an increase in net diversification rate through time. (C) Some *Gunnera* species are aggressive colonisers, here showing successful colonisation and persistence in the margins of a landslide in Costa Rica (image from Wikicommons).

