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Published on: 26 Aug 2018 - bioRxiv (Cold Spring Harbor Laboratory)

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The dimensions of species diversity

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ABSTRACT

1 Diversification processes underpin the patterns of species diversity that fascinate biologists.
2 Two competing hypotheses disagree about the effect of competition on these processes.
3 The bounded hypothesis suggests that species diversity is limited (bounded) by competition
4 between species for finite niche space, while the unbounded hypothesis proposes that evolution
5 and ecological opportunity associated with speciation, render competition unimportant. We
6 use phylogenetically structured niche modelling, to show that processes consistent with both
7 these diversification models have driven species accumulation in conifers. In agreement with
8 the bounded hypothesis, niche competition constrained diversification, and in line with the
9 unbounded hypothesis, niche evolution and partitioning promoted diversification. We then
10 analyse niche traits to show that these diversification enhancing and inhibiting processes
11 can occur simultaneously on different niche dimensions. Together these results suggests a
12 new hypothesis for lineage diversification based on the multi-dimensional nature of ecological
13 niches that accommodates both bounded and unbounded diversification processes.

14 Species diversity has changed dramatically over geological time¹. Although diversity has
15 clearly increased since life began, reconstructions using the fossil record are ambiguous about
16 the causes of, and constraints on, this increase²⁻⁴. One important open question is whether
17 the rate of species accumulation slows as diversity increases, or is independent of diversity⁴⁻⁶.
18 The latter *unbounded hypothesis* implies that time, and the rate of evolution within clades
19 (monophyletic branches of phylogenies) control diversification and that there is essentially
20 no limit on total diversity³. Alternatively, the former *bounded hypothesis* suggests that
21 competitive ecological processes result in a diversity-dependent ceiling on species richness⁷.
22 Resolving this debate is essential for understanding limits to biodiversity, and why diversity
23 is unevenly distributed in space and time and between clades.

24 Previous attempts to discriminate between bounded and unbounded diversification have
25 focused on modelling species accumulation inferred from phylogenies^{8,9} and fossil assem-
26 blages^{5,6,10}, and to a lesser extent testing how ecological niche evolution impacts diversi-
27 fication^{11,12}. The results to date have been inconclusive and often contradictory^{2-4,13,14},
28 suggesting that a more nuanced explanation may be required^{4,14}. Here we quantify the
29 extent to which both bounded and unbounded processes influence species accumulation in

30 the conifers. Our analysis exploits methodological advances that allow us to infer multi-
31 dimensional physiological-niche properties for large suites of species^{15,16}. We use this data
32 to discriminate between the distinctive niche-characteristics predicted by the bounded and
33 unbounded hypotheses. Specifically we test support for the bounded hypothesis' prediction
34 that diversification should slow as niche overlap increases within clades^{2,17} and the unbounded
35 hypothesis' prediction that niche evolution accommodates increasing diversity by allowing
36 the partitioning or expansion of niche space^{3,18,19}.

37 Conifers are an ecologically important, globally distributed division of plants (Fig. 1)
38 that are ideal for this analyses. This large, well-studied lineage has well-defined clades,
39 excellent distribution data²⁰, and is ancient enough (> 300 myo;²¹) to assess how species
40 accumulate through time. We use distribution data and a process-based species distribution
41 model (SDM) to infer physiological niche parameters for each of 455 conifer species (75
42 % of extant conifers). The niche parameters are combined with a robust fossil calibrated
43 phylogeny²¹, and interpreted statistically using an *a-priori* conceptual model of how niche
44 and phylogenetic parameters relate to species richness (Fig. 2). The model postulates that
45 species richness can be impacted both directly and/or indirectly by clade age (CA), the
46 multivariate niche evolution rate (NER), as well as two novel metrics: clade niche size (CNS)
47 and phylogenetic competition index (PCI). Clade niche size is the projected potential niche
48 size (number of grid cells occupied by all species in the clade) corrected for clade species
49 number (see Methods). The phylogenetic competition index is the product of niche overlap
50 and geographic overlap between species within clades. The parameters of this model are
51 estimated using phylogenetically constrained Bayesian path analysis. We conduct the analysis
52 at two phylogenetic levels, using 10 large clades and 42 smaller clades.

53 Results

54 We found that diversification in conifers was influenced in almost equal measure by bounded
55 and unbounded processes (Fig. 3a). In line with the bounded hypothesis, competition
56 with relatives (PCI) had a strong negative effect on species richness, which suggests that
57 available niche space can limit species accumulation. This effect was strong in both the 10
58 (-1.02) and 42 (-0.88) clade analyses. Support for the unbounded hypothesis was evidenced
59 by our finding that niche evolution rate (NER) contributed positively to species richness,
60 suggesting that higher niche evolution rates within clades allow more species to accumulate.
61 This effect was stronger in the 42 clade analysis (0.56) than in the 10 clade analysis (0.31).
62 Furthermore we found that CNS had neutral or negative influence on SR, suggesting that
63 niche partitioning constitutes the main mode of niche evolution in conifers. The negative
64 effect of clade niche size in the 10 clade analysis is somewhat counter-intuitive since it suggests
65 that clades with smaller niche volumes accommodate more species. However, this pattern
66 is consistent with niche partitioning accompanied by allee effects and/or competition^{17,22}
67 driving random extinction processes that lead to a reduction in clade-niche-size as postulated
68 in Fig. 3b. In fact the significant direct effect of competition (PCI, -0.37) and relatively
69 strong effect of clade age (CA, -0.26) on clade nice size (Fig. 3a), are consistent with such
70 competition driven extinction processes unfolding through time¹⁷. The absence of this effect

71 in the 42 clade analysis probably reflects the much younger average clade age (17my compared
72 112my), and smaller clade sizes, which mean that partitioning/extinction processes (Fig. 3b)
73 will be less frequent and therefore more difficult to detect. This is also in line with previous
74 work²³ suggesting extinction played a pivotal role in the diversification of older conifer clades.

75 Although most previous work has favoured either bounded^{2,8,12,24} or unbounded^{3,25,26}
76 processes driving diversification, our results are consistent with previous observational^{10,18},
77 theoretical¹⁴ and modelling^{4,10} work, which suggests that both bounded and unbounded
78 processes influence diversification. For example, much of the empirical evidence is consistent
79 with diversification slowing, rather than reaching an asymptote^{14,18}. This led to the "damped
80 increase" hypothesis, which in line with our results, suggests that competition induced by
81 niche filling reduces diversification rate, while specialisation or new ecological opportunities
82 counteract this effect¹⁴. Others have extended these ideas to show that the incongruity
83 between strict bounded and unbounded views could be overcome by allowing diversity-
84 accumulation-models to vary between periods of either bounded or unbounded diversification⁴.
85 These studies do not however provide a population/species level mechanism that could drive
86 shifts in diversification processes⁴.

87 To address this mechanistic basis, we examined whether niche dimensionality can drive
88 variation in diversification processes^{4,27}. To explore this possibility we examined evidence for
89 conservatism in the evolution of the traits that define the physiological niche of species in our
90 dataset (see Methods). We found substantial variation in the level of conservatism within and
91 between traits (Supplementary Materials Table S1), suggesting that some niche dimensions
92 may be more evolutionarily labile than others. Indeed, a comparison of trait disparity and
93 trait evolution rates for each trait and clade combination (10 clade classification), showed high
94 levels of variation in evolution rate between traits within clades (Fig. 3c). The deviations
95 from the trend line in Figure 3c highlights this variation. For example in Clade 4, traits
96 a and d (highlighted with solid circles) are more labile than predicted by the degree of trait
97 disparity, whereas traits b and c (highlighted with dashed circles) are more conservative
98 than expected. Such variation in evolutionary flexibility between traits within clades may
99 accommodate the operation of both bounded and unbounded processes. This can be seen
100 more clearly by focussing attention on single clades. For example, in Clade 7 (*Pinus*, Fig. 4),
101 the effect of soil moisture on growth (panel f) is highly conserved in the sub-clades highlighted
102 with solid ellipses, suggesting that interspecific competition is likely to be high along this
103 niche dimension in these sub-clades. However, these same sub-clades are labile in terms of
104 their temperature requirements for growth (traits b and c, highlighted with dashed ellipses in
105 Fig. 4b and Fig. 4c), indicating that evolution and specialisation are possible along these
106 niche dimensions (Fig. 4). Analogous patterns can be seen in the other *Pinus* sub-clades
107 (Fig. 4) and the other clades (Supplementary Materials Fig. S1-S9).

108 Thus, by considering the multi-dimensional nature of niche evolution, we have shown how
109 bounded and un-bounded diversification processes may simultaneously control diversification
110 rates. Niche dimensionality has long been thought to promote diversity by partitioning
111 resources and facilitating coexistence²⁸, and there is considerable empirical support for
112 this hypothesis²⁷. Most previous assessments of how niche characteristics impact macro-

113 diversification have used low dimensional proxies of the niche such as body size¹² or climatic
114 range¹¹. In contrast, our assessment of multiple, physiological niche traits, reveals that both
115 diversity-limiting competition, and diversity-promoting evolution may operate concurrently.
116 At the population level these processes are likely to be separated in space and/or time - in line
117 with models by McPeck²⁹ and Marshall and Quental⁴ respectively. For example, populations
118 along environmental gradients could experience variation in the opportunity for specialisation
119 or niche expansion along some niche dimensions but experience competition along other
120 niche dimensions²⁹. Similarly, changes in the environment could induce temporal variation in
121 selection pressure that affects the interplay between conservative and labile niche traits⁴.

122 In summary, we have identified how processes that define the niche geometry of conifer
123 clades can jointly promote and constrain diversification. Our results confirm that the con-
124 trasting processes that underpin bounded and unbounded diversification have both operated
125 during the evolution of a major lineage. Our study thereby provides an analysis frame-
126 work for a new multi-dimensional-niche hypothesis that unifies the bounded and unbounded
127 hypotheses^{4,10,14,18}. The study also highlights a potential anthropogenic obstruction to
128 future diversification. Habitat loss and fragmentation threaten existing global biodiversity
129 by (among other things) increasing extinction rates³⁰. Our results suggest that habitat
130 loss and fragmentation could also have a compounding negative effect on future diversity
131 accumulation. Communities that are "crowded" into smaller areas of remnant habitat are
132 likely to experience increased competition³⁰, thereby increasing the likelihood that bounded
133 processes will constrain diversification.

134 **Methods**

135 **Data acquisition and preparation**

136 Geo-referenced collection data for all conifer species were extracted from the Global Biodiver-
137 sity Information Facility (www.gbif.org). These data were supplemented by published species
138 records not in GBIF from:³¹⁻³⁶. Climate estimates were made for each point record, using
139 Worldclim (37). Data was cleaned manually by firstly eliminating duplicate records, then
140 for consistency with species distribution descriptions³¹, and then by comparing Worldclim
141 estimates of altitude, with the altitudes provided with each site record. Where Worldclim
142 altitudes were inconsistent with the altitude in species descriptions by more than 300 m, we
143 replaced these records with estimates from nearby sites with altitudes consistent with the
144 descriptions.

145 **Estimating physiological niche traits**

146 We estimated the physiological niche traits of the study species using a physiologically-based
147 approach to species distribution modelling¹⁵. This method uses the Thornley Transport
148 Resistance (TTR) model of plant growth³⁷ to estimate the niche traits that match the
149 observed distribution of species. The TTR model³⁷, is an ordinary differential equation
150 model that considers how plant growth is influenced by carbon uptake, nitrogen uptake, and
151 the allocation of carbon and nitrogen between roots and shoots. It explicitly separates the
152 physiological processes of resource uptake from biomass growth. The implementation by¹⁵

153 relates the uptake and growth processes to environmental forcing variables. Specifically, the
154 model considers how carbon uptake might be limited by temperature, soil moisture, solar
155 radiation, and shoot nitrogen; nitrogen uptake might be limited by temperature, soil moisture,
156 and soil nitrogen; and growth and respiration loss might be influenced by temperature.
157 The model runs on a monthly time step, which allows it to explicitly consider how seasonal
158 fluctuations in the forcing variables interactively influence plant resource uptake and growth.¹⁵
159 provides a full description of the model and its assumptions.

160 We use the cleaned presence dataset described above to identify locations where the
161 species occur. A variety of methods for simulating absence points (often called pseudoabsence
162 points) are available, but the method adopted is regarded as a relatively small source of
163 error³⁸. Our method balances the number of presence and absence points and stratifies by
164 environment type the selection of absence points. To define environment types we use a
165 partitioning algorithm *clara*³⁹ to classify the TTR input variables into 25 environmental
166 zones. We further restricted the selection of absence points to the zoological realm(s) where
167 the species occurs and to distances >0.25 km from the presence points.

168 The model predicts the potential biomass of an individual plant as a function of the
169 environmental forcing variables at a site. Following the work of¹⁵, we assume that p_i , the
170 probability of a species occurring at site i , is described by the complementary log-log of the
171 modelled plant biomass at site i and that the likelihood of observing the presence absence data
172 (y_i) at site i is described by the Bernoulli distribution. To estimate the parameters, we used the
173 differential evolution optimization algorithm⁴⁰ to find the set of parameters that maximizes
174 this likelihood over all sites. The model fits were evaluated by examining the confusion matrix
175 (a matrix comparing the number of true positives, true negative, false positives and false
176 negatives), with particular weight given to the false negative rate, i.e. instances where the
177 model predicts the species to be absent, but it is actually present (Supplementary Materials
178 Table S2).

179 We restrict projection of potential species ranges to the subset of environmental zones (see
180 above) present in each species' occurrence data; this prevents predictions beyond the data
181 domain used for estimating the model parameters. We calculated the niche size of species
182 in two ways: 1) projecting species ranges for the world, and 2) using a resampled dataset
183 that assumes that the world's environmental zones are equally common. This second method
184 corrects for any bias in projected range size introduced by variation in the extent of different
185 environmental zones, but maintains the covariance structure of the environmental data⁴¹. To
186 create a dataset where each environmental zone is equally common, we created a resampled
187 dataset of the environmental data. We again use *clara* to classify the global TTR input
188 data into 50 environmental zones. We then sampled a finite number (1,000 in our case) of
189 locations from each of 50 environmental zones, which produces an environmental dataset
190 where each environment zone is equally represented. We then project the range sizes of species
191 in this resampled environmental space. Analyses conducted using geographic locations and
192 resampled locations yielded very similar results. The analysis based on resampled locations is
193 presented in the main manuscript while the analysis based on geographic locations is available
194 in Supplementary Materials Fig. S10.

195 **Phylogenetic methods**

196 We used the fossil calibrated conifer phylogeny of Leslie et al.²¹, which is based on two
197 chloroplast genes and two nuclear genes. We pruned this 487 species tree to match the 455
198 species for which we had good distributional data. Although a clade is any monophyletic
199 group in a phylogeny, the ability to detect effects in clade-wise analysis will be in part reliant
200 on having enough variation in clade size⁴². Therefore we developed two clade classifications.
201 The first inclusive division is based on tree topology at deeper well supported nodes, and
202 it aimed to retain major taxonomic groups such as *Pinus*, resulting in 10 clades (supple-
203 mentary Information 3). The second lower division is based on a time-slice approach at
204 Eocene/Oligocene boundary (33.9ma) because using tree topology closer to the tips becomes
205 more difficult. This second approach produced 68 clades, 28 of which included a single
206 species. These single species were dropped from the analysis, leaving 42 clades and 429 species
207 in the second analysis (Supplementary Materials Table S2). We recognize that removing
208 single species clades might bias rate estimates because these are the clades with the lowest
209 diversification. However, the dataset still covers a wide range of clade species richness (2 - 45
210 species), and meaningful estimates for single species cannot be calculated for most subsequent
211 metrics used in our analysis (e.g. niche evolution rate, clade niche overlap, clade geographic
212 overlap etc.). Furthermore, this potential bias only affects the 42 clade analysis and the
213 general agreement between the 10 and 42 clade analyses (see main text) suggests that any
214 effect is inconsequential.

215 **Clade level data**

216 For each clade we calculate the following metrics: age, niche size corrected for species number,
217 niche evolution rate, and phylogenetic competition index. The crown age of the clade was
218 calculated directly from the tree using the branching time function in APE^{43,44}. Because
219 clades with more species could have larger clade niche sizes by chance, we used the mean of
220 10,000 bootstrap resamples to obtain corrected estimates of the clade niche size relative to
221 the smallest clade (12 and 2 for the 10 and 42 clade datasets respectively).

222 The calculation of niche evolution rate involves using a multi-variate model. The TTR
223 species distribution model estimates 24 parameters associated with plant growth (see above).
224 For this reason we first extracted the most informative of the 24 niche parameters for the
225 analysis. Specifically we used phylogenetically corrected principal components analysis (PCA)
226 to identify which model parameters had the most influence on shaping niche space in our
227 dataset. PC 1 to 8 explained over 94 percent of the variation in the data set. The most
228 influential parameters were identified based on the eigen vector loadings > 0.3, and vector
229 plots were used to exclude correlated parameters. This procedure identified 11 parameters
230 (Fig. 3 and 4) which were ranked in order of importance by summing the effect of each trait
231 on each PC weighted by the proportion of the variance explained by that PC. For each clade
232 these 11 parameters were fit together in a multivariate Brownian Motion (BM) of evolution in
233 OUCH⁴⁵. In the 42 clade analysis, clades with fewer than 12 species had insufficient degrees
234 of freedom to fit the model, and parameters were dropped, (starting with the lowest ranked),
235 until a model could be fitted. Following¹¹, the trait evolution model was used to calculate
236 the variance-covariance matrix for each clade. The diagonal elements of this matrix represent

237 the phylogenetic rate of character evolution which were summed to provide a multivariate
238 rate parameter for each clade - the NER¹¹.

239 The bounded hypothesis proposes that competition plays a key role in limiting diversi-
240 fication. Competition is likely to be most intense between close relatives due to similar
241 physiological requirements (or niches) wherever species co-occur¹⁷. To estimate competition,
242 we produce a metric which summarises the degree of expected niche overlap and observed
243 geographic overlap between species within clades. Geographic overlap between each species
244 pair was estimated by producing a matrix of pairwise distance between all geo-referenced
245 occurrence records. The average of this matrix was taken for each pair to produce a pairwise
246 matrix of geographic distances between all species. This distance matrix was transformed to
247 scale between 0 and 1, and the inverse was taken to provide an index of observed geographic
248 similarity (overlap). Schoener's index⁴⁶ of niche overlap was estimated for each pair of species
249 from the projected species distributions (i.e. the potential niche of the species) in SPAA⁴⁷,
250 and the subsequent matrix was also rescaled between 0 and 1. We then took the product
251 of these overlap estimates to produce the phylogenetic competition index, thus the index
252 has a potential range from 0 to 1, so that species pairs with high niche overlap and high
253 geographic overlap have a high competition score, and those with low overlaps for one or
254 both metrics have a low competition index. The mean was taken from clade level subsets
255 of this matrix to produce the phylogenetic competition index for each clade. It should
256 be noted that this index is a minimum estimate, because competition with more distantly
257 related species is also possible^{24,48,49} (p. 77). Incorporating community wide competition
258 is theoretically possible using our approach (geographic overlap*niche overlap), although it
259 would be very data intensive and is outside the scope of this work. Additionally, despite
260 the possible underestimate of competition, our model structure(see below) means that the
261 calculation of un-associated dependencies (i.e. CA on SR; NER on SR; NER on CNS; CNS
262 on SR, see Fig. 2) are not affected.

263 **Regression modelling**

264 We developed an a-priori conceptual model (Fig. 2) to estimate the relationships between
265 SR, CNS, NER, CA and the PCI. The unbounded model predicts that specific evolutionary
266 characteristics, controlled by phylogenetic niche conservatism, lead to clade specific diversifi-
267 cation rates. This has two consequences, 1) when the effect of diversification rate is factored
268 out older clades will have more species than younger clades; and 2) positive diversification
269 will involve niche evolution that manifests as either the expansion or partitioning of clade
270 niche space as species accumulate. In line with these predictions our model allows: 1) CA
271 to directly influence SR; and 2) NER to influence SR both directly, and indirectly, via its
272 effect on CNS, with the direct relationship between CNS and SR indicating the mode of niche
273 evolution (expansion or partitioning). Conversely, the bounded diversity model predicts that
274 competition for limited resources places a limit on species number. It has long been recognised
275 that competition is likely to be most intense between close relatives, because the ecological
276 requirements of relatives are likely to be similar due to phylogenetic niche conservatism. Our
277 estimate of PCI quantifies expected competition between species within clades. Therefore we
278 allow PCI to directly effect SR, however, because PCI quantifies interactions between niches,

279 it is also allowed to indirectly influence SR via NER, and CNS.

280 We used Bayesian path analysis to calculate the effects in the path diagram (Fig. 2),
281 while accounting for non-independence associated with phylogenetic relationships⁵⁰. The
282 total effect of each model parameter on the response variable (SR) was calculated from the
283 direct and indirect effects following⁵¹. All model parameters were normalised and centred to
284 a mean of zero and constant standard deviation. Following⁵², we use relative log-transformed
285 species richness. For each analysis (10 and 42 clade), the full phylogenetic tree was collapsed
286 to the clade level, and the inverse of the variance covariance matrix from this clade-tree was
287 used to explicitly correct for the phylogenetic dependencies between clades. Modelling was
288 undertaken using JAGS⁵³ running three chains for 15,000 iterations, after a burnin of 25,000,
289 and thinning the chains to every fifth sample. Normal uniformed priors we used for the path
290 effects and convergence was assessed using a range of diagnostics in coda⁵⁴.

291 **Niche trait analysis**

292 We investigated the role of niche dimensionality in promoting both bounded and unbounded
293 process, by using a trait like analysis to quantify the evolution of individual niche dimensions
294 at the level of the full phylogeny and within clades. This analysis focused on the 11 niche
295 dimensions identified above. Phylogenetic signal across the full phylogeny was estimated
296 using Pagel's λ ⁵⁵ with significance assessed using likelihood ratio tests in PHYTOOLS⁵⁶.
297 The PHYTOOLS function "contMap" was used to produce ancestral state reconstructions
298 for each of the 11 most important niche traits. A second round of niche evolution modelling
299 focused on estimating the evolution rate of the 11 primary niche dimensions independently
300 for each clade in the 10 clade analysis. This was done as above except single variate BM
301 models were fitted in OUCH rather than multi variate models. the subsequent trait evolution
302 rate's for each clade were rescaled between zero and one to allow comparisons across clades.
303 In order to produce a corresponding estimate of trait disparity (the magnitude of variation in
304 actual trait values) average pairwise distance between species in each clade was calculated
305 from raw trait data, and rescaled between 0 and 1. These two metrics were plotted in xy
306 space to allow visualisation of clade level variation in evolutionary flexibility (Fig. 3c). We
307 also made clade level ancestral reconstructions of the 11 main niche dimensions for the 10
308 large clades to assess variation in the conservation of niche dimensions within clades (Fig. 4;
309 Supplementary Material Fig. S1-S9).

310 **Data availability**

311 The data and computer code that support the findings of this study are available from the
312 corresponding author upon request.

313 **Author contributions**

314 All authors were involved in developing the ideas. GJJ provided the distribution data
315 and phylogeny. MJL and SIH undertook the analysis. MJL lead the writing. All authors
316 contributed to the text. SIH and DB secured funding for the research.

317 **Acknowledgements**

318 We thank Bill Lee, Richard Gill, Esther Dale and members of the Eucalypt Genetics Research
319 Group (University of Tasmania) for key discussion about the ideas. The work was funded by
320 Te Aparangi Marsden Fund grant UOO1411.

321 **Author Information**

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323 declare no competing financial interests. Correspondence and requests for materials should be
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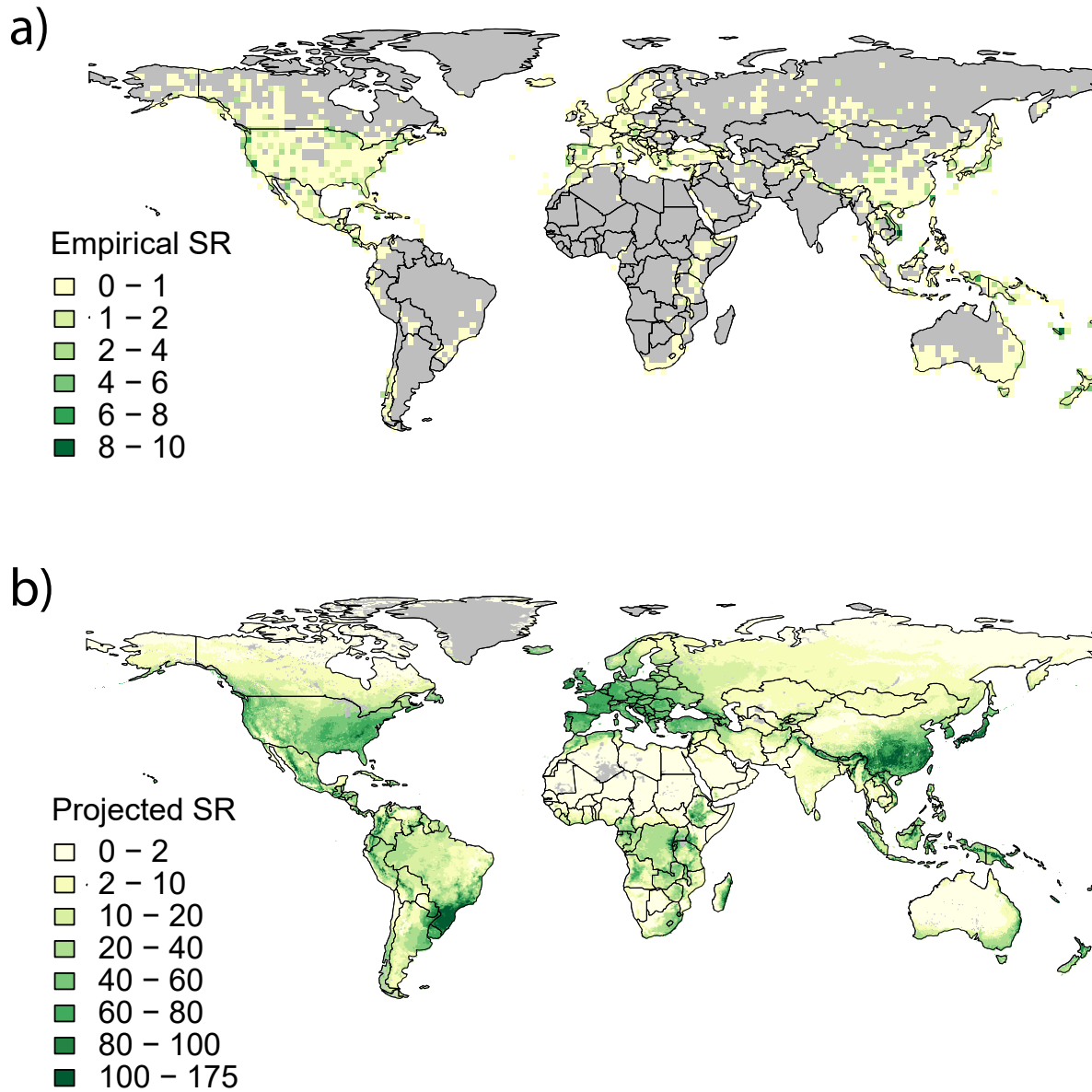


Figure 1. Global species richness (SR) for 455 conifer species based on: a) the cleaned empirical distribution data; and b) projections from process based species distribution models.

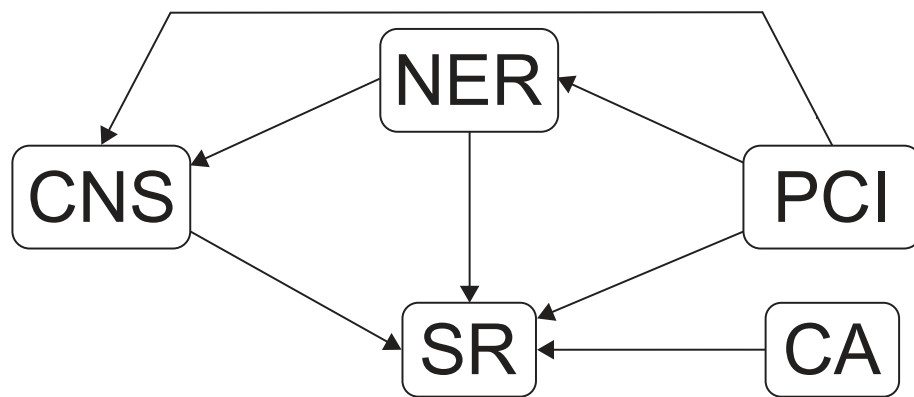


Figure 2. *A-priori* conceptual model of direct and indirect effects of niche and phylogenetic parameters on clade species richness (SR). Bounded diversification predicts a negative effect of PCI, and unbounded diversification a positive effect of NER in combination with variation in CNS, indicating niche partitioning and/or expansion. SR = species richness; CA = clade age; PCI = phylogenetic competition index; NER = multivariate niche evolution rate; CNS = clade niche size.

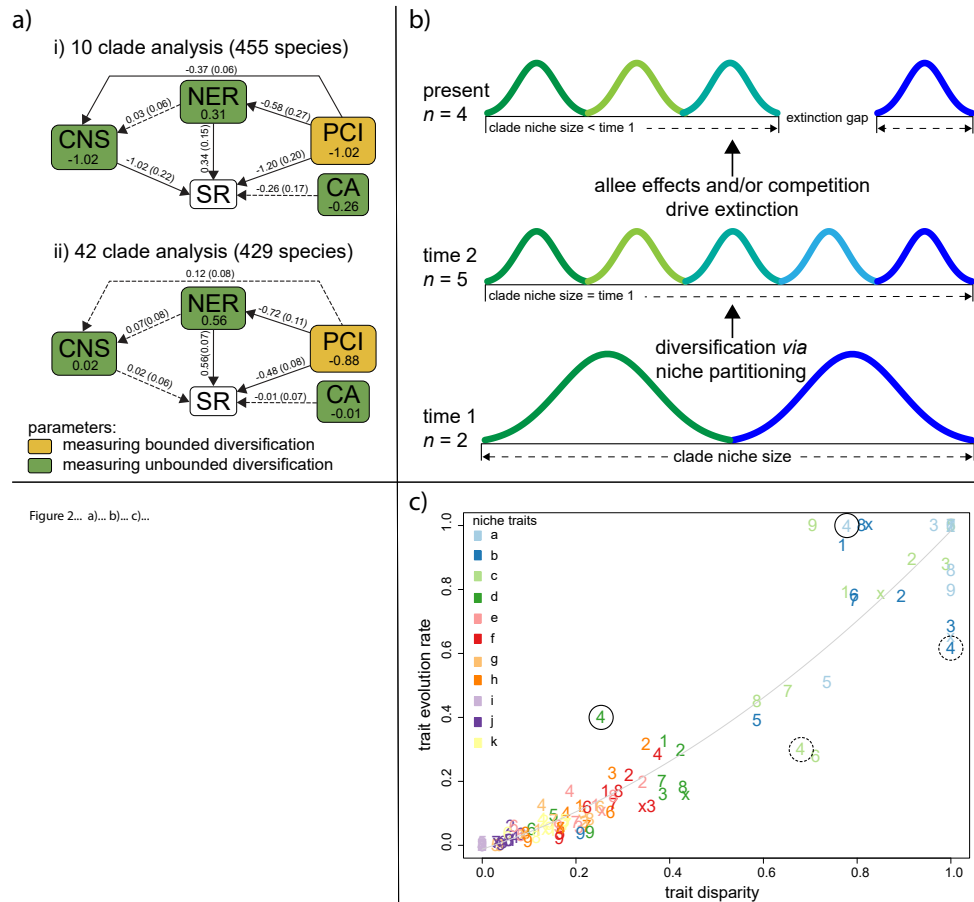


Figure 2... a)... b)... c)...

Figure 3. a) Bayesian path analysis showing the relative effects of niche and phylogenetic parameters on clad species richness for 455 conifer species in i) 10 large clades, and ii) 42 smaller clades. Total effect size is shown with the parameters, while direct effects and their standard deviation are shown along the vertices. Solid lines are significantly different from zero (95% credible intervals not including zero). SR = species richness; CA = clade age; PCI = phylogenetic competition index; NER = multivariate niche evolution rate; CNS = clade niche size. b) example of how niche partitioning combined with extinction associated with allee effects and/or competition, can result in a negative relationship between clade niche size and species richness. Different coloured curves represent species. c) within clade variation in the flexibility of niche traits. Coloured numbers refer to clades 1-10 (with $x=10$), and different colours refer to different niche dimensions. The order and definition of niche dimensions (a-k) are as Fig 3. The best fit line (grey) is to allow visualisation of residual deviance (see text). Niche traits in solid and dashed circles are discussed in the text.

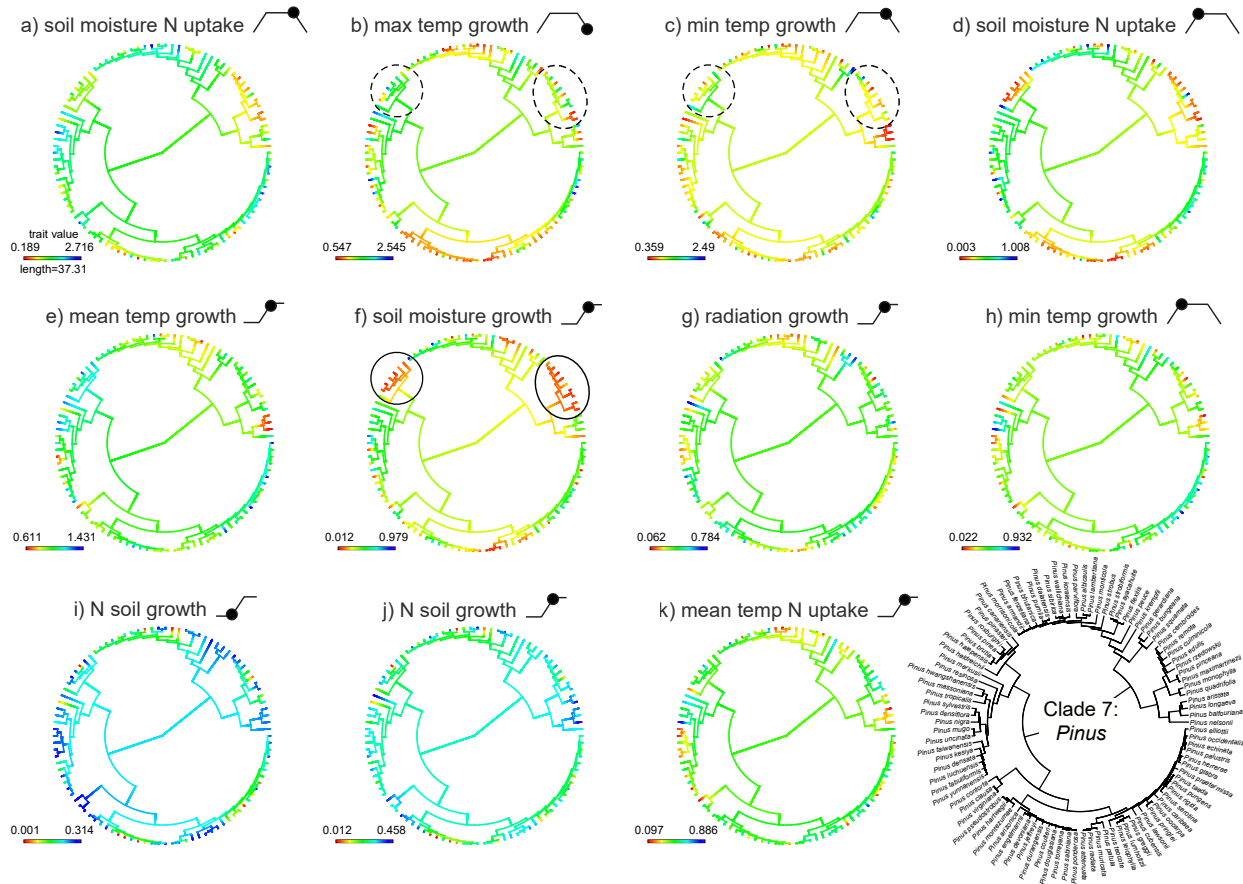


Figure 4. Phylogenies of Clade 7 (*Pinus*) showing ancestral state reconstructions of the 11 most important niche dimensions in order of importance (a-k). The bottom right panel shows the same phylogeny with species names. Sub clades within *Pinus* with conservative (solid ellipse) and labile (dashed ellipse) niche dimensions are highlighted and discussed in the text. The filled circle on trapezoid and logistic diagrams beside the trait names, show how the trait relates to the modelled growth or resource acquisition function. For example, (a) is the point at which soil moisture causes a reduction in N uptake, that is, when waterlogging reduces N uptake.