

Below-ground biotic interactions moderated the postglacial range dynamics of trees

Article

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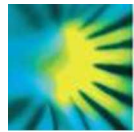
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1 **Belowground biotic interactions moderated the post-glacial range dynamics of trees**

2

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27

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29 Summary

- 30 • Tree range shifts during geohistorical global change events provide a useful real-world
31 model for how future changes in forest biomes may proceed. In North America, during the
32 last deglaciation, the distributions of tree taxa varied significantly in the rate and direction
33 of their responses for reasons that remain unclear. Local-scale processes such as
34 establishment, growth, and resilience to environmental stress ultimately influence range
35 dynamics. Despite the fact that interactions between trees and soil biota are known to
36 influence local-scale processes profoundly, evidence linking belowground interactions to
37 distribution dynamics remains scarce.
- 38 • We evaluated climate velocity and plant traits related to dispersal, environmental tolerance,
39 and belowground symbioses, as potential predictors of the geohistorical rates of expansion
40 and contraction of the core distributions of tree genera between 16-7kaBP.
- 41 • The receptivity of host genera towards ectomycorrhizal fungi was strongly supported as a
42 positive predictor of poleward rates of distribution expansion, and seed mass was
43 supported as a negative predictor. Climate velocity gained support as a positive predictor of
44 rates of distribution contraction, but not expansion.
- 45 • Our findings indicate that understanding how tree distributions, and thus forest ecosystems,
46 respond to climate change requires the simultaneous consideration of traits, biotic
47 interactions, and abiotic forcing.

48
49 **Key words:** climate velocity, facilitation, mycorrhizal fungi, plant migration, range expansion.

50

51 **Introduction**

52 Understanding how forests will respond to rapid climate change is challenging, but crucial for
53 devising effective strategies and policies for adaptation, management, and mitigation (Millar *et al.*,
54 2007; Bonan, 2008; Corlett & Westcott, 2013; Aitken & Bemmels, 2016). Central to this
55 challenge is identifying the factors that moderate the responses of species' geographic ranges to
56 climate change, yet the causes of observed variation in species range dynamics have proven
57 elusive (Williams *et al.*, 2004; Zhu *et al.*, 2012; Ordonez & Williams, 2013). This uncertainty has
58 prolonged debates about the primary factors underlying rapid migrations in response to
59 geohistorical climate change (e.g. post-glacial range dynamics; Davis, 1986; Prentice *et al.*, 1991;
60 McLachlan *et al.*, 2005; Feurdean *et al.*, 2013), and underscores questions about the adaptive
61 capacity of forest ecosystems given current rates of climate change (Millar *et al.*, 2007; Williams
62 & Jackson, 2007). Although plant traits related to dispersal, life-history, and physiology are clearly
63 relevant in determining climate change responses (Corlett & Westcott, 2013; Aubin *et al.*, 2016),
64 evidence of their effects – in either geohistorical or contemporary distribution data – remains
65 mixed (Zhu *et al.*, 2012; Nogués-Bravo *et al.*, 2014; Lankau *et al.*, 2015). In addition, biotic
66 interactions both above and below ground can strongly influence plant demographic processes and
67 range limits (Afkhami *et al.*, 2014; Klock *et al.*, 2015), implying key roles in the moderation of
68 responses to climate change (Perry *et al.*, 1990; van der Putten, 2012). However, the influences of
69 these interactions at biogeographic scales are often difficult to detect (Blois *et al.*, 2013; Urban *et al.*,
70 2013; Svenning *et al.*, 2014). This is exemplified by the mycorrhizal symbiosis: a major biotic
71 interaction that occurs below ground between plants and fungi.

72
73 Mycorrhizal fungi form symbioses with most vascular plant species (Brundrett, 2009), exchanging
74 nutrients from the soil for photosynthate (van der Heijden *et al.*, 2015). It has long been
75 recognized that plant range responses to climate change could be mediated by mycorrhizal fungi
76 (Perry *et al.*, 1990), and in recent years two hypotheses have emerged for how mycorrhizal
77 associations could affect changes in the leading boundary and trailing boundary of host plant
78 ranges (Corlett & Westcott, 2013; Lankau *et al.*, 2015). The “facilitated distribution expansion
79 hypothesis” (henceforth “FDE”) is derived from the invasion literature and posits that the
80 establishment success of plant colonists during range expansions will be greater when those plants
81 are more likely to encounter compatible symbionts (Horton & van der Heijden, 2008; Nuñez *et al.*,

82 2009; Pringle *et al.*, 2009; Nuñez & Dickie, 2014; Hayward *et al.*, 2015). The “environmental
83 buffering hypothesis” (henceforth “EB”) proposes that some types of symbiosis are better at
84 buffering hosts against rapidly changing and potentially deteriorating conditions at trailing
85 distribution boundaries, and correspondingly, predicts that hosts engaged in such symbioses
86 should exhibit slower rates of trailing-boundary distribution contraction (Lankau *et al.*, 2015).

87

88 Testing the FDE hypothesis requires consideration of “host receptivity”, defined here as the
89 differential compatibility of hosts with mycorrhizal symbionts. Accurate estimates of host
90 receptivity are challenging to obtain, but to a first approximation (see Materials and Methods) host
91 receptivity can be estimated as the total number of species of mycorrhizal fungi that a host has
92 been observed to associate with. Although this broad definition undoubtedly includes specialist
93 fungi that only associate with one specific host species or genus, it also consists of all fungi
94 possessing one or more of the following ameliorating properties, which we consider to be the most
95 pertinent to facilitating host distribution expansion: (i) association with multiple host genera (e.g.
96 generalists; Ishida *et al.*, 2007; Peay *et al.*, 2015; Roy-Bolduc *et al.*, 2016), (ii) formation of long-
97 lived resistant propagules (Pither and Pickles, 2017), (iii) rapid dispersal capabilities (Peay and
98 Bruns, 2014). Given these considerations, the FDE hypothesis predicts that host receptivity
99 towards mycorrhizal fungi, in general, will be positively associated with the rate of expansion at
100 leading distribution boundaries (Fig. 1a). This prediction (henceforth represented by prediction
101 FDE₁) is more readily tested for ectomycorrhizal (EM) than arbuscular mycorrhizal (AM) host tree
102 genera, because associated fungal species richness estimates are presently attainable for EM host
103 trees only (see Materials and Methods). A second prediction of the FDE, relevant to all host
104 genera, rests on prior findings that, as a group, AM-associated hosts are more prone to generalism
105 (i.e. are more receptive) on average than EM-associated hosts (Davison *et al.*, 2015; van der
106 Heijden *et al.*, 2015) (but see Pöhlme *et al.*, 2017): hence, AM hosts are predicted to exhibit faster
107 rates of leading-boundary distribution expansion than EM hosts (prediction FDE₂; Fig. 1b).

108

109 The EB hypothesis predicts that EM hosts should exhibit slower rates of trailing-boundary
110 distribution contraction (prediction EB₁; Fig. 1b) because: (i) plant-soil feedbacks within
111 established forests are generally more negative among AM host trees compared to EM hosts
112 (Dickie *et al.*, 2014; Bennett *et al.*, 2017), with EM hosts appearing to benefit via facilitation of

113 seedling recruitment by adult trees and increased protection against belowground antagonists
114 (Bennett *et al.*, 2017), and (ii) compared to AM trees, EM trees more consistently benefit from
115 belowground common mycorrhizal networks (Horton & van der Heijden, 2008; Dickie *et al.*,
116 2014), which can buffer hosts against changing and stressful conditions through the transfer of
117 nutrients, including nitrogen, sugars, and water (Selosse *et al.*, 2006; Simard *et al.*, 2012; van der
118 Heijden *et al.*, 2015). A second prediction (EB₂), presently testable with EM hosts only, is that the
119 more receptive the host, the slower the distribution contraction at trailing boundaries (Fig. 1a).
120 This prediction assumes a positive association between taxonomic and functional diversity among
121 EM fungal taxa, such that more receptive EM hosts are more likely to associate with EM fungi that
122 provide benefits during high-stress scenarios such as drought (Gehring *et al.*, 2014, 2017).

123
124 To our knowledge, only FDE₂ and EB₁ have previously been tested at biogeographic scales.
125 Using both contemporary Forest Inventory Assessment (FIA) data, and fossil pollen data from 12-
126 10 thousand years before present (kaBP), Lankau and colleagues (2015) estimated the
127 contemporary and geohistorical rates of distribution expansion and contraction of North American
128 trees and found evidence consistent with EB₁ but not FDE₂: rates of distribution contraction
129 (southern boundaries) were significantly slower among EM compared to AM hosts in both the
130 contemporary ($n = 97$ tree species) and the geohistorical ($n = 18$ tree genera) data, whereas rates of
131 distribution expansion (northern boundaries) did not differ among EM and AM hosts either within
132 the contemporary ($n = 84$ tree species) or in the geohistorical ($n = 18$ tree genera) data.
133 Furthermore, the effects of the two plant traits considered by Lankau *et al.* (2015), shade tolerance
134 and seed mass, were either non-significant or inconsistent among southern and northern
135 distribution margins, and among the geohistorical versus contemporary datasets.

136
137 Here we examine the geohistorical, post-glacial distribution dynamics of North American trees,
138 building on previous work by focusing on four novel approaches to the study of past plant
139 migrations:

140 (1) We derive estimates of receptivity for EM hosts, and use these to conduct the first tests of
141 predictions FDE₁ and EB₂, i.e. that the rate of northward distribution expansion of EM host genera
142 was positively associated with host receptivity, and the rate of southern distribution contraction of
143 EM host genera was negatively associated with host receptivity (Fig 1.a).

144 (2) We test all four predictions (FDE₁, FDE₂, EB₁, EB₂; Fig. 1) using fossil pollen data from four
145 time periods spanning 16 to 7kaBP. This approach takes account of the highly varied rates of
146 distribution expansion and contraction exhibited by tree genera among time periods, including
147 rates that were often greatest in time periods other than the 12-10kaBP period (Fig. S1).

148 (3) We test multivariate climate velocity as a predictor of distribution expansion and contraction
149 rates alongside other predictors (see below). Here, climate velocity is broadly defined as a physical
150 metric comprising the speed and direction of change in climate over time and across space
151 measured in m/yr (and thus comparable to taxon distribution expansion and contraction).
152 Specifically we use the latitudinal measure of regional-scale climatic velocity developed by Zhu et
153 al. (2011) and Ordonez and Williams (2013), which integrates 12 climatic variables
154 simultaneously, rather than the local-scale grid-square approach of Loarie et al (2009), which uses
155 a single variable (mean annual temperature or mean annual precipitation).

156 (4) We used multi-model inference and model averaging for all four predictions to estimate the
157 relative importance of abiotic and biotic variables for explaining expansion and contraction rates
158 of taxa across multiple time periods. The selected variables were climate velocity, mycorrhizal
159 traits (specifically mycorrhizal type, as defined by Moora (2014), and mycorrhizal receptivity,
160 newly defined here), and four plant traits hypothesized to directly or indirectly moderate
161 distribution dynamics (Aubin *et al.*, 2016): seed mass, maximum height, shade tolerance, and cold
162 sensitivity (Table S1).

163

164 **Materials and Methods**

165 *Pollen taxonomy*

166 Details regarding the pollen taxonomy are presented in Methods S1. In brief, an initial data set of
167 30 pollen taxa was reduced to a final set of 10 AM and 13 EM host genera following the removal
168 of genera with insufficient records, unreliable velocity estimates, or uncertain mycorrhizal status.
169 Collectively, these 23 genera account for 43% of the tree genera in North America (Little 1971,
170 1976, 1977), and most of the aboveground biomass in North American temperate and boreal
171 forests, including >80% of the total aboveground biomass and volume of forested lands within
172 Canada (Canada's National Forest Inventory, <http://nfi.nfis.org>; accessed July 2016).

173

174 *Estimation of distribution dynamics*

175 Methodological details are presented in Methods S1. In brief, the response variables of interest are
176 (i) the rate of leading (northern) boundary distribution expansion (LBDE), and (ii) the rate of
177 trailing (southern) boundary distribution contraction (TBDC; each expressed in metres per year)
178 for each taxon. These were calculated using the pollen-derived estimates of the geohistorical core
179 distributions of taxa presented in Ordonez & Williams (2013). The authors estimated velocities of
180 the northern and southern boundaries of core distributions for each of the following time periods:
181 16-14 kaBP, 14-12 kaBP, 12-10 kaBP, 10-7 kaBP, 7-4 kaBP, 4-1 kaBP. Here we focus on the four
182 periods spanning 16 to 7 kaBP, which encompasses the timeframe of almost complete retreat of
183 the Laurentide Ice Sheet (Dyke, 2004), the onset and end of rapid Bølling-Allerød warming
184 (14.7kaBP) and Younger Dryas cooling (12.9kaBP) events, and end of Younger Dryas warming
185 (11.7kaBP) marking the start of the Holocene interglacial. Correspondingly, by 7 kaBP most tree
186 genera had completed their broad-scale distribution expansions (Williams *et al.*, 2004).

187 For each genus, we calculated an overall measure of LBDE and TBDC as follows. For
188 each range-boundary, we first calculated the mean and standard error of biotic velocity for each
189 time period, based on the observations across 0.5° longitudinal-bands. We then estimated an
190 overall per-genus average velocity by calculating the weighed mean biotic velocity across time
191 periods (using between 1 and 4 time-specific mean velocity values). Weights were defined as
192 $1/SEb_t^2$, where SEb_t represents the standard error of species specific biotic velocities for time
193 interval “t”.

194 “Climate velocities” were estimated for each location within the leading and trailing edge
195 as the climatic space latitudinal displacement (location of the most similar climate) within a 0.5°
196 longitudinal band between time periods (see Ordonez & Williams (2013) for details). Briefly,
197 climatic space was characterized using the dissimilarity of 12 temperature and precipitation
198 variables for both annual and seasonal climates. Hence, climate velocity as described here is the
199 rate of latitudinal displacement of individual climate cells over time (m/yr), which allows for
200 comparison with the movement rate of taxon distribution boundaries over the same spatial and
201 temporal scales. As with our estimates of distribution expansion and contraction rates, for each
202 genus, we calculated a measure of overall climate velocity, at northern and southern boundaries
203 separately, as the mean of the time-specific climate velocities, weighted by $1/SEC_t^2$, where SEC_t
204 represents the standard error of climate velocities for time interval “t”.

205

206 *Estimating receptivity of EM host genera*

207 We calculated host receptivity as the number of different named EM fungal species that have been
208 documented to associate with a host genus (regardless of geographic location), normalized by the
209 richness of the host genus (see Methods S1), and \log_{10} -transformed for analyses. We obtained
210 these estimates using the search function provided by the UNITE sequence database (Kõljalg *et*
211 *al.*, 2013). UNITE is a fungi-specific database that is curated and updated by expert mycologists,
212 thus it benefits from increased accuracy of sequence assignment to species. We conducted our
213 search between 11.08.15 and 15.08.15 using the ‘Search Pages’ section of the UNITE website,
214 which enables sequence searches through the International Nucleotide Sequence Database
215 Collaboration (Chochrane *et al.*, 2016; www.insdc.org). The INSDC databases are open to all
216 sequence submissions and thus populated with a large number of sequences, though the quality of
217 their assignment is expected to be variable. Our search employed the following protocol: (i) each
218 EM host genus in OW was examined separately by placing [EM host genus] in the Host box, (ii)
219 for each EM host in (i) the Organism box was filled with [EM fungal genus] for each of the fungal
220 genera currently known to form EM associations (see DataS2 in Tedersoo *et al.* 2014); the name
221 of each distinct species was recorded, with UNITE expert annotations used preferentially where
222 available, (iii) for each EM host in (i) the Taxon name (‘by annotated data in UNITE database’)
223 box was filled with [EM fungal genus] and results recorded as in (ii) above. We further ensured
224 that: i) host genus information was reliable (e.g. *Abies* not *Picea abies*; *Fagus* not *Nothofagus*;
225 *Pinus* not *Carpinus*; *Tsuga* not *Pseudotsuga*; a single host identity for any given sequence), ii)
226 only fungal species that have previously been identified as being ectomycorrhizal, or jointly
227 ectomycorrhizal and ericoid mycorrhizal, were counted (see DataS2 in Tedersoo *et al.* (2014), iii)
228 named species were never counted twice for a given host species, iv) ‘uncultured [species name]’
229 was only counted if [species name] had not already been counted, and was only counted once for a
230 given host species.

231
232 We considered the resulting number of distinct EM fungal species names per host genus (referred
233 to as “EM fungal species richness” throughout; Table S1) as a conservative estimate of host
234 receptivity due to (i) the large number of EM fungal sequences that lack metadata on the
235 associated host species [a common issue with sequence submissions to databases in general
236 (Lindahl *et al.*, 2013)], and (ii) the fact that, within sequence databases, the ‘uncultured [name]’

237 category can include a large number of unidentified species. Further analysis of the species
238 richness represented by these ‘uncultured’ fungi may be possible through phylogenetic analyses,
239 but this was not considered necessary or desirable for the present study. We assume that the
240 associations between EM host trees and EM fungi documented within the UNITE database were
241 also viable during the 25 kaBP up to and including the LGM, which appears reasonable based on
242 current estimates of the timescale for rapid speciation events in EM fungi (e.g. 1.453 Myr^{-1} in
243 North American *Amanita*; Sánchez-Ramírez *et al.*, 2015). As described in Methods S1, we
244 calculated several alternative measures of host receptivity, and our sensitivity analyses include
245 results based on these.

246

247 *Plant traits data*

248 For species within each host genus we obtained data about the following traits: maximum height,
249 seed mass, shade tolerance, and cold sensitivity. Genus-level averages were necessary due to the
250 taxonomic resolution of the pollen data, and were calculated based on a list of 199 species for
251 which height, seed mass, and /or shade tolerance data existed (Table S3). Details on this procedure
252 are provided in Methods S1. Table S3 also shows, for each trait, the percent of the variation in trait
253 values that resides at the among-genus and within-genus (among species) levels. For cold
254 sensitivity and maximum height the majority of the trait variation resides at the within-genus level
255 (84 and 54% respectively), whereas for shade tolerance and especially seed mass, the majority
256 resides at the among-genus level (68 and 93%, respectively). Thus, all else being equal, our ability
257 to detect effects of traits using genus-level averages is strongest for seed mass, and weakest for
258 cold sensitivity.

259

260 *Statistical analyses*

261 All analyses were conducted using “R” version 3.1.3 (R Core Team, 2015), and all R code and
262 data associated with this study are available on the Open Science Framework (weblink). To
263 explore the ability of different models and predictor variables to account for variation in our
264 response variables, we used multi-model inference procedures (Burnham & Anderson, 2004) and
265 implemented them using the *MuMIn* R package (Bartoń, 2015). The four plant traits were
266 evaluated as potential predictors, as was either north or south boundary climate velocity. For
267 analyses involving all 23 host genera (predictions FDE₂ and EB₁) we evaluated mycorrhizal type

268 (binary AM/EM) as our sixth and final potential predictor, and for analyses involving our 13 EM
269 host genera (predictions FDE₁ and EB₂), we evaluated host receptivity as the final potential
270 predictor. The analyses were conducted as follows. We evaluated pairwise rank correlations
271 among predictors (Fig. S2), and with few exceptions (e.g. seed mass positively associated with
272 cold sensitivity; rank correlation = 0.58; Fig. S2b), these revealed generally weak associations (\leq
273 |0.44|). For each response variable, we fit a full model and used the *arm* package (Gelman & Su,
274 2015) to centre the response and explanatory variables on their means and standardized over two
275 standard deviations to facilitate direct comparisons among regression coefficients in the presence
276 of the binary predictor “mycorrhizal type” (Gelman, 2008). We then explored all possible
277 combinations of predictor variables using the ‘dredge’ function within the *MuMIn* package
278 (Bartoń, 2015). We did not consider interactions due to limited sample size. For each model we
279 computed the Akaike’s information criterion corrected for small samples (AIC_C), and Δ AIC_C, the
280 difference between the given model’s AIC_C and that of the “best” model, which exhibits the
281 smallest value of AIC_C. Relative evidence weights (based on the AIC_C) were calculated and
282 assigned to each model. We used a 95% confidence set of models to calculate model-averaged,
283 standardized coefficient values, and did so using the “natural average” method, i.e. the average of
284 the standardized coefficient values for all models in the candidate set in which the given predictor
285 appeared, weighted by the models’ relative evidence weights (Burnham & Anderson, 2004). We
286 also calculated (i) the relative variable importance (RI) of each explanatory variable as the sum of
287 the relative evidence weights of the candidate models in which the predictor appeared, (ii) the
288 unconditional standard errors for the coefficient estimates, and (iii) the 95% confidence interval
289 for the standardized coefficients. In the sensitivity analyses we additionally present 90%
290 confidence intervals (see below). We conducted residual diagnostics on both the full regression
291 models and the “AIC_C-best” models, and found that all models conformed to regression
292 assumptions. Model averaging results are presented in Table 1 (see Results), and all model sets
293 from the multi-model inference analyses are presented in Tables S4 and S5. Model averaging
294 results corresponding to the 100th percentile boundary definition are summarized in Table S6. We
295 also conducted phylogenetically-informed regression analyses as described in Methods S1.

296

297 *Sensitivity analyses*

298 We conducted sensitivity analyses to evaluate the robustness of our results with respect to (i)
299 alternative time periods (for all analyses), and (ii) alternative measures of receptivity (for analyses
300 involving the EM host genera, i.e. predictions FDE₁ and EB₂). These sensitivity analyses were
301 conducted using both the 95th and 100th percentile boundary definitions. Specifically, we
302 conducted the following additional analyses:

- 303 1. We repeated all our multi-model inference analyses using velocity estimates derived from the
304 following periods individually: (i) 14-7kaBP; (ii) 12-7kaBP; (iii) 12-10kaBP (the period of fastest
305 overall climate and biotic velocities); (iv) 16-10kaBP; (v) for each host genus, the single period in
306 which climate velocity was most rapid; and (vi) for each host genus, the single period in which
307 biotic velocity was most rapid. Sample size necessarily varied among analyses due to varied
308 availability of data.
- 309 2. In addition to our main measure of host receptivity (EM fungal richness per host), we repeated
310 all our multi-model inference analyses using two additional measures of host receptivity: (i) The
311 total number of EM fungal species documented to have associated with the host genus (“EMF
312 rich”, log₁₀ transformed for analyses), and (ii) The total number of EM fungal species shared with
313 at least one other host genus in the present study (“EMF shared”, log₁₀ transformed).
- 314 3. Lastly, owing to our limited sample sizes and thus statistical power, we calculate 90%
315 confidence intervals in addition to 95% confidence intervals for model-averaged, standardized
316 coefficients.

317

318 **Results**

319 *Overall distribution responses of host genera*

320 Our time-averaged estimates of distribution expansion and contraction rates show patterns
321 consistent with those reported in previous studies that focused on individual time periods (Ordóñez
322 & Williams, 2013; Lankau *et al.* 2015). For instance, between 16-7kaBP, rates of leading
323 boundary expansion are positively associated with rates of trailing boundary contraction (Fig. 2),
324 and the latitudinal extents of core distributions expanded for the vast majority of the genera (Fig.
325 2). *Fagus* and *Alnus* exhibited the greatest time-averaged rates of distribution expansion, near
326 125m•yr⁻¹, while a similar rate of distribution contraction was observed for *Shepherdia* during the
327 single time period for which pollen data were available (12-10kaBP).

328

329 *Facilitated distribution expansion*

330 We found strong support for FDE₁: among EM host genera, host receptivity emerged as a strong,
 331 positive predictor of leading-boundary expansion (Table 1), appearing in all candidate models
 332 (Table S4), and on its own accounting for 44% of the variation in rates of leading-boundary
 333 expansion (Fig. S3; Table S4). The AIC_C-best model included host receptivity, seed mass, and
 334 cold sensitivity (Table S4), and accounted for 75% of the variation in the rate of leading-boundary
 335 expansion. The most parsimonious model within 2 AIC_C units of the AIC_C-best model included
 336 host receptivity and seed mass, and accounted for 62% of the variation in the rate of leading-
 337 boundary expansion (Fig. 3; Table S4). Like host promiscuity, seed mass gained strong support as
 338 a predictor of leading boundary expansion rate: the 95% confidence interval for its model-
 339 averaged coefficient excluded zero, and its relative variable importance was 0.862 (Table 1).

340
 341 We found no support for FDE₂: rates of leading boundary distribution expansion were not faster
 342 among AM hosts compared to EM hosts, and correspondingly, mycorrhizal type did not emerge as
 343 an important predictor in the multi-model inference analyses (Table 1). Rather, on average, EM
 344 hosts exhibited marginally faster rates of expansion than AM hosts, when considered in isolation
 345 from other factors (means \pm SE: $76.2 \pm 10.47\text{m}\cdot\text{yr}^{-1}$ for EM plant genera and $46.7 \pm 13.16\text{m}\cdot\text{yr}^{-1}$
 346 among AM plant genera; Fig. S4a). Indeed, mycorrhizal type was the sole predictor in the AIC_C-
 347 best model (Table S4), with an effect opposite to that predicted by the FDE. Mycorrhizal type also
 348 exhibited a modest effect size (0.34), though the 95% confidence interval for its coefficient
 349 overlapped zero (Table 1). The null (no predictor) model was within 2 AIC_C units of the AIC_C-
 350 best model, and should therefore be considered the most parsimonious, plausible model, given the
 351 data.

352
 353 *Environmental buffering*

354 We found limited support for EB₁: mycorrhizal type was included in the AIC_C-best model along
 355 with climate velocity and cold sensitivity (Table S5), which together accounted for 33% of the
 356 variation in trailing boundary contraction rates among host genera. However, on average, AM and
 357 EM hosts exhibited similar rates of distribution contraction when considered in isolation from
 358 other factors (Fig. S4b). Furthermore, our model averaging analysis identified climate velocity as
 359 the sole strong predictor (Table 2). Nevertheless, mycorrhizal type and cold sensitivity gain some

360 support as potential predictors, as their 95% confidence intervals for their standardized coefficients
361 only slightly overlapped zero, and their relative variable importance values were greater than 0.4
362 (Table 2).

363
364 We found no support for EB₂: host receptivity was not a predictor of the rates of distribution
365 contraction at trailing boundaries for EM host genera (Table 2), nor was any other variable.

367 *Sensitivity analyses*

368 The results of all sensitivity analyses for tests of predictions associated with the FDE and EB
369 hypotheses are presented in Tables S8-S11 and Figures S5-S8. The tables present the details of
370 the model selection and model averaging results for each of the hypotheses, and the figures
371 visually summarize the model averaging outcomes. Collectively, these reveal the following:
372 (i) Support for host receptivity as a predictor of distribution expansion rates among EM host
373 genera (FDE₁) depends to some degree on the measure of host receptivity used. Specifically,
374 support is strongest when using EM fungal richness per host and EM fungal richness as measures
375 of receptivity, and weakest when using the number of EM fungal species shared with at least one
376 other host genus in the present study (Fig. S5).

377 (ii) Support for host receptivity as a predictor of distribution expansion rates among EM host
378 genera (FDE₁) is strongest when analysing time periods associated with maximum sample size
379 (i.e. 13 EM host genera versus 11 genera; Fig. S5).

380 (iii) Seed mass has a consistently negative effect on distribution expansion rates among EM host
381 genera (FDE₁) regardless of time period analysed, but its importance depends in part on the
382 measure of host receptivity included in the models, and on the time period analysed (Fig. S5).

383 (iv) Among the analyses with the greatest sample size (N = 23) and thus greatest statistical power,
384 mycorrhizal type exhibits the opposite effect to that predicted by FDE₂: model averaged
385 coefficients indicate a positive effect of EM associations on the rates of leading boundary
386 distribution expansion (Fig. S6), though most confidence intervals for coefficients encompassed
387 zero.

388 (v) Support for climate velocity as a predictor of distribution contraction rates among EM and AM
389 host genera (EB₁) is relatively consistent and strong among analyses (Fig. S7).

390 (vi) Mycorrhizal type has a consistently negative effect on distribution contraction rates among
391 EM and AM host genera (EB_1), which reflects slower contraction rates among EM hosts compared
392 to AM hosts, but the strength of effect varies among time period analysed (Fig. S7).

393

394 **Discussion**

395 A long-standing challenge in ecology and biogeography is to identify the traits and processes that
396 moderate the responses of taxon distributions to environmental changes. We addressed this
397 challenge here using estimates of post-glacial (16-7kaBP) distribution expansion and contraction
398 rates among woody North American plant genera. We tested hypotheses that propose roles for
399 biotic interactions, specifically belowground interactions with mycorrhizal fungi, as determinants
400 of range responses. We also simultaneously evaluated the influences of mycorrhizal fungi, climate
401 velocity and key traits including seed size, maximum height, cold sensitivity, and shade tolerance.
402 Despite unavoidable constraints of limited sample size and data resolution (e.g. pollen and trait
403 data resolved only to genus), we found compelling evidence that (i) interactions with mycorrhizal
404 fungi and seed mass moderated leading boundary distribution responses to geohistorical climate
405 change, and (ii) climate velocity had a detectable influence on trailing boundary contraction rates
406 only, when analysing all 23 tree genera.

407

408 *Facilitated distribution expansion*

409 Using multi-model inference and model averaging, we found support for the facilitated
410 distribution expansion hypothesis (prediction FDE_1). This support was expressed by a positive
411 effect of increasing receptivity towards EM fungi on the distribution expansion rates of EM host
412 genera at leading (northward) boundaries. In other words, tree genera that can form associations
413 with a greater richness of EM fungal taxa tended to expand their distributions poleward more
414 rapidly than more specialized EM host genera. To our knowledge, this is a novel finding that is
415 consistent with positive plant-soil feedbacks in EM associations (Bennett *et al.* 2017), the
416 tendency for EM fungal mycelial networks to generate positive outcomes for hosts (van der
417 Heijden and Horton, 2009), and the potential for EM fungi to assist in plant establishment and
418 survival outside of their current range (e.g. Reithmeyer and Kernaghan, 2013; Nuñez and Dickie,
419 2014).

420

421 Consistent with the findings of Lankau *et al.* (2015), we found no support for prediction FDE₂, i.e.
422 that due to their more generalist habit overall, AM hosts should exhibit more rapid distribution
423 expansion at leading boundaries compared to EM host genera. Rather, we found that rates of
424 leading boundary distribution expansion were similar among AM and EM hosts (Fig. S4).
425 Perhaps, as recently suggested (Pöhlme *et al.* 2017), receptivity is not as different among AM and
426 EM hosts as traditionally thought. Alternatively, abiotic and biotic features of receiving
427 landscapes may have diminished any advantage afforded to AM hosts by their generalist habit.
428 Specifically, relative to AM host genera, EM host genera were prevalent in regions proximate to
429 retreating ice sheets (Williams *et al.*, 2004) (Fig. 4), and we hypothesize that several features of
430 recently deglaciated landscapes may have facilitated expansion among EM hosts relative to AM
431 hosts. First, EM fungi are highly diverse in dwarf shrub-, herb-, and forb-dominated tundra
432 ecosystems (Timling *et al.*, 2014) and associate with widely dispersed Arctic plants, including
433 *Betula nana*, *Bistorta vivipara*, *Dryas integrifolia*, and *Salix arctica* (Timling *et al.*, 2012). These
434 provide potential sources of fungal inoculum for EM hosts migrating beyond the present tree line
435 (e.g. *Picea mariana*, black spruce; Reithmeier & Kernaghan, 2013), effectively “priming” the
436 landscape for colonization by EM trees. In contrast, AM fungi display low diversity (Davison *et*
437 *al.*, 2015) and lower root colonisation (Soudzilovskaia *et al.*, 2015) in such ecosystems. Second,
438 nitrogen limitation increases with latitude (Gill & Finzi, 2016), being particularly acute in post-
439 glacial environments (Lambers *et al.*, 2008), and whereas both EM and AM fungi can scavenge
440 mineralizable forms of N (ammonium and nitrate) several species of EM fungi are also able to
441 mine nitrogen from organic molecules (Read & Perez-Moreno, 2003; Lambers *et al.*, 2008). Third,
442 CO₂ concentrations rose by 40% from approximately 190 to 265 ppmv between 18kaBP and
443 7kaBP (Shakun *et al.*, 2012), and relative to AM hosts, EM hosts are better able to take advantage
444 of such increases, especially under nitrogen-limiting conditions (Terrer *et al.*, 2016). Collectively,
445 these advantages will be accentuated once host populations are established, as forests dominated
446 by EM trees tend to facilitate conspecific seedlings, at least over small spatial scales, whereas AM
447 seedlings typically experience conspecific inhibition (Dickie *et al.*, 2014; Bennett *et al.*, 2017). In
448 sum, although distribution expansion among AM hosts may have been facilitated by a generalist
449 habit towards AM fungi, distribution expansion among EM hosts could have been facilitated by
450 landscapes that were both biotically and abiotically favourable.
451

452 *Environmental buffering*

453 A wide variety of experimental work supports the importance of mutualists in providing hosts with
454 resilience to changing climates, and for mycorrhizas there is evidence that EM fungi are more
455 likely to provide such benefits to their hosts than AM fungi (e.g. van der Heijden and Horton,
456 2009; Lankau *et al.*, 2015). However, counter to Lankau *et al.* (2015), our tests of EB₁ did not
457 support mycorrhizal type as an important factor in moderating postglacial distribution contraction
458 among tree genera. We note that mycorrhizal type was included in the AIC_C-best model, with EM
459 hosts contracting more slowly than AM hosts, and that model averaged coefficients consistently
460 indicated more rapid contraction rates among AM than EM hosts. Nevertheless, only climate
461 velocity gained strong support as a predictor of distribution contraction.

462
463 Much of the support for mycorrhizas being associated with environmental buffering comes from
464 the literature on EM hosts and fungi (Selosse *et al.*, 2006; van der Heijden and Horton, 2009;
465 Simard *et al.*, 2012). Hence, in EB₂, we had predicted that host receptivity would be an important
466 factor for EM host genera by enabling access to a wide array of fungi and hence a wider potential
467 range of functions. We found no support for this prediction. Recent research suggests that
468 individual fungal species may be associated with the provision of host drought resilience (Gehring
469 *et al.*, 2017), hence the ability to associate with specific mutualist species, rather than a diverse
470 community, may be more important in the south of the distribution during climate warming.

471

472 *Plant traits*

473 Due to pollen data being limited in taxonomic resolution to the level of genera, we were required
474 to average species-level trait data across all species in each genus. This clearly has the potential to
475 reduce statistical power, particularly for the cold sensitivity and maximum height, for which most
476 of the trait variation resided at the species level (Table S3). This was less of a limitation for seed
477 mass, and indeed, we found strong evidence in support of a negative effect of seed mass on rates
478 of leading boundary distribution expansion among EM hosts. This is consistent with long-
479 standing views that dispersal limitation moderates rates of expansion of plant distributions (Clark
480 *et al.*, 1998; Svenning *et al.*, 2014), but contrasts with recent findings that seed size does not
481 predict climate-tracking ability among taxa, given 20th-century climate trends (Zhu *et al.*, 2012)
482 and earlier hypotheses that animal dispersal of nuts could weaken dispersal limitations associated

483 with seed size (Johnson & Webb III, 1989). Notably, post-hoc partial correlation analyses
484 revealed that the influence of seed mass only becomes evident once host receptivity is accounted
485 for (Table S12). This could explain why the effects of seed mass have hitherto been elusive
486 (Urban *et al.* 2013).

487
488 With respect to the remaining plant traits, we found no compelling evidence in support of their
489 effects. The genus-wide averaging of plant trait data, combined with limited sample sizes, may
490 have precluded the detection of all but the strongest of effects (e.g. seed mass).

491

492 *Climate velocity*

493 In our analysis of all 23 plant taxa, climate velocity gained support as a predictor for trailing
494 boundary distribution contraction (Table 2), but not as a predictor of leading boundary distribution
495 expansion (Table 1). This was a surprising result, especially given the findings of Ordonez and
496 Williams (2013), who, using the same data as we use here, found significantly positive model-2
497 regressions between biotic velocity and climate velocity (for AM and EM host taxa together)
498 within each time period between 16 and 7kaBP (see their Figure 4). This can be attributed to
499 methodological differences: Ordonez and Williams (2013) assumed that biotic velocity should be
500 zero when climate velocity is negligible, and correspondingly, forced the model 2 regressions
501 through the origin. We opted to relax this assumption (accommodating the possibility of
502 migration lag, for example), and our analyses yielded very different outcomes: as shown in Figure
503 S9, climate velocity is a significant predictor of biotic velocity in only one of the four time-
504 periods: 12-10kaBP. Our sensitivity analyses are largely consistent with this finding (Figs. S5-
505 S8): if we focus solely on the 12-10kaBP period, climate velocity emerges as the sole significant
506 predictor of (i) leading boundary distribution expansion rates among AM and EM taxa (prediction
507 FDE₂), (ii) trailing boundary distribution contraction among AM and EM taxa (prediction EB₁),
508 and (iii) trailing boundary distribution contraction among EM taxa (EB₂). The only prediction for
509 which climate velocity does not gain support is FDE₁.

510

511 In light of these developments, and for additional reasons outlined below, we suggest that analyses
512 based on velocities from a pool of multiple time- periods have advantages relative to inferences
513 based on velocities from a single time period (cf. Lankau *et al.* 2015). Firstly, maximum rates of

514 distribution expansion and contraction occurred in different time periods for different plant genera
515 (Fig. S1). For instance, nine of 23 plant genera exhibited maximum rates of distribution expansion
516 outside of the 12-10kaBP period, and maximum rates of distribution contraction were distributed
517 across all four time-periods (Fig. S1). Secondly, despite the 12-10kaBP period exhibiting the most
518 rapid overall change in climate (Ordóñez & Williams, 2013), maximum rates of climate velocity
519 occurred in different time periods for different genera (Fig. S1). For example, 6 of 23 plant genera
520 exhibited maximum rates of leading-boundary climate velocity outside of the 12-10kaBP period,
521 and 10 of 23 genera exhibited maximum rates of trailing-boundary climate velocity outside of the
522 12-10kaBP period (Fig. S1). Lastly, the number of time periods for which velocity estimates
523 could be calculated varied among plant genera (Table S2). By calculating for each genus a
524 weighted average of velocities across all time periods, we maximized data use and thus statistical
525 power, while simultaneously accounting for the varied precision of estimates among genera (see
526 above). For example, focusing solely on the 12-10kaBP period would reduce the number of tree
527 genera from 23 to 18. In our sensitivity analyses we explored alternative combinations of time
528 periods, but we place greatest credence in our main analyses for the reasons outlined above.

529
530 The second aspect of post-glacial distribution expansion, FDE₂, had previously been considered by
531 Lankau *et al.* (2015) using likelihood ratio based tests and a response variable that assumed a
532 climatic contribution to distribution expansion (climatic and biotic velocity data were combined to
533 derive a single response variable akin to climate pacing). In our analysis we decoupled climate
534 velocity from biotic velocity, and found that, across all host genera, climate velocity was not
535 supported as an important factor in northward distribution expansion. This was true when
536 considering all time periods together, and when examining each time period individually.
537 However, climate velocity was supported as an important predictor of distribution expansion when
538 the model in which expansion data for each genus was taken from the time period of fastest biotic
539 velocity. In support of Lankau *et al.* (2015) we did not find a significant effect of mycorrhizal
540 type on distribution expansion, although contrary to the FDE₂ hypothesis there was weak evidence
541 of faster expansion of EM host genera compared to AM host genera.

542
543 For decades, ecologists have debated the relative importance of climatic and biotic controls on
544 species distributions and the timescales at which plant distributions are in dynamic equilibrium

545 with climate (Davis, 1986; Prentice *et al.*, 1991). By analysing the roles of climate and biotic
546 factors simultaneously, we found that the importance of climate as a driver of distributional
547 changes was context-dependent among North American tree genera. Climate velocity was the
548 primary determinant of post-glacial distribution contraction rates at trailing boundaries, whereas
549 biotic interactions, specifically mycorrhizal associations, and seed mass were the primary
550 determinant of distribution expansion rates at leading boundaries. Thus, our findings indicate that
551 inter-taxon variation in climatic sensitivity, dispersal-related plant traits, and biotic interactions –
552 particularly mycorrhizal symbioses – acted together to modulate plant responses to the rapid
553 climate changes accompanying the last deglaciation.

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564 **Author contributions**

565 J.P. conceived the study with B.J.P.; J.P. refined the range dynamics analyses originally developed
 566 by A.O. and J.W.W. from the Neotoma Paleocology Database; B.J.P. analysed and extracted
 567 fungal species richness data from the INSD and UNITE databases, and data on species richness
 568 from the USDA PLANTS database; J.P. conducted the spatial analyses to estimate cold sensitivity,
 569 and developed and implemented all statistical analyses; A.O. produced Figure 4; B.J.P. and J.P. co-
 570 led the writing of the manuscript, with substantial input from S.W.S., A.O., and J.W.W.

572 **References**

- 573 **Afkhami ME, McIntyre PJ, Strauss SY. 2014.** Mutualist-mediated effects on species' range
 574 limits across large geographic scales. *Ecology letters* **17**: 1265–73.
- 575 **Aitken SN, Bemmels JB. 2016.** Time to get moving: Assisted gene flow of forest trees.
 576 *Evolutionary Applications* **9**: 271–290.
- 577 **Aubin I, Munson AD, Cardou F, Burton PJJ, Isabel N, Pedlar JHH, Paquette A, Taylor**
 578 **ARR, Delagrance S, Kebli H, et al. 2016.** Traits to stay, traits to move: a review of functional
 579 traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change.
 580 *Environmental Reviews* **23**: 1–23.
- 581 **Bartoń K. 2015.** MuMIn: Multi-Model Inference. [WWW document] URL
 582 <http://cran.rproject.org/package=MuMIn>
- 583 **Bennett JA, Maherali H, Reinhart KO, Lekberg Y, Hart MM, Klironomos J. 2017.** Plant-soil
 584 feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* **355**:

- 585 181–184.
- 586 **Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S. 2013.** Climate change and the past,
587 present, and future of biotic interactions. *Science* **341**: 499–504.
- 588 **Bonan GB. 2008.** Forests and climate change: forcings, feedbacks, and the climate benefits of
589 forests. *Science* **320**: 1444–1449.
- 590 **Brundrett MC. 2009.** Mycorrhizal associations and other means of nutrition of vascular plants:
591 understanding the global diversity of host plants by resolving conflicting information and
592 developing reliable means of diagnosis. *Plant and Soil* **320**: 37–77.
- 593 **Burnham KP, Anderson DR. 2004.** *Model Selection and Multimodel Inference*. New York, NY:
594 Springer New York.
- 595 **Clark JS, Fastie C, Hurtt G, Jackson ST, Johnson C, King GA, Lewis M, Lynch J, Pacala S,
596 Prentice C, et al. 1998.** Reid’s paradox of rapid dispersal theory and interpretation of
597 paleoecological records. *Bioscience*: 13–24.
- 598 **Cochrane G, Karsch-Mizrachi I, Takagi T, International Nucleotide Sequence Database
599 Collaboration. 2016.** The International Nucleotide Sequence Database Collaboration. *Nucleic
600 Acids Research* **44**: D48–D50.
- 601 **Corlett RT, Westcott DA. 2013.** Will plant movements keep up with climate change? *Trends in
602 Ecology and Evolution* **28**: 482–488.
- 603 **Davis MB. 1986.** Climatic instability, time lags, and community disequilibrium. In: Diamond J,
604 Case TJ, eds. *Community Ecology*. New York, USA: Harper & Row, 269–284.
- 605 **Davison J, Moora M, Öpik M, Adholeya A, Ainsaar L, Bâ A, Burla S, Diedhiou AG, Hiiesalu
606 I, Jairus T, et al. 2015.** Global assessment of arbuscular mycorrhizal fungus diversity reveals very
607 low endemism. *Science* **127**: 970–973.
- 608 **Dickie IA, Koele N, Blum JD, Gleason JD, McGlone MS. 2014.** Mycorrhizas in changing
609 ecosystems. *Botany* **92**: 149–160.
- 610 **Dyke AS. 2004.** An outline of North American deglaciation with emphasis on central and northern
611 Canada. *Developments in Quaternary Sciences* **2**: 373–424.
- 612 **Feurdean A, Bhagwat SA, Willis KJ, Birks HJB, Lischke H, Hickler T. 2013.** Tree migration-
613 rates: narrowing the gap between inferred post-glacial rates and projected rates. *PloS one* **8**:
614 e71797.
- 615 **Gehring CA, Mueller RC, Haskins KE, Rubow TK, Whitham TG. 2014.** Convergence in

- 616 mycorrhizal fungal communities due to drought, plant competition, parasitism, and susceptibility
 617 to herbivory: Consequences for fungi and host plants. *Frontiers in Microbiology* **5**: 1–9.
- 618 **Gehring CA, Sthultz CM, Flores-Rentería L, Whipple AV. 2017.** Tree genetics defines fungal
 619 partner communities that may confer drought tolerance. *Proceedings of the National Academy of*
 620 *Sciences* **114**: 11169–11174.
- 621 **Gelman A. 2008.** Scaling regression inputs by dividing by two standard deviations. *Statistics in*
 622 *medicine* **27**: 2865–2873.
- 623 **Gelman A, Su YS. 2015.** arm: Data Analysis Using Regression and Multilevel/Hierarchical
 624 Models. [WWW document] URL <http://cran.rproject.org/package=arm>
- 625 **Gill AL, Finzi AC. 2016.** Belowground carbon flux links biogeochemical cycles and resource-use
 626 efficiency at the global scale. *Ecology Letters* **19**: 1419–1428.
- 627 **Hayward J, Horton TR, Pauchard A, Nuñez MA, Hoeksema JD. 2015.** A single
 628 ectomycorrhizal fungal species can enable a Pinus invasion. *Ecology* **96**: 1438–1444.
- 629 **van der Heijden MGA, Martin FM, Selosse M-A, Sanders IR. 2015.** Mycorrhizal ecology and
 630 evolution: the past, the present, and the future. *New Phytologist* **205**: 1406–1423.
- 631 **Horton TR, Van Der Heijden MGA. 2008.** The role of symbioses in seedling establishment and
 632 survival. In: Leck MA, Parker VT, Simpson RL, eds. *Seedling Ecology and Evolution*. Cambridge,
 633 UK: Cambridge University Press, 189–214.
- 634 **Ishida T, Nara K, Hogetsu T. 2007.** Host effects on ectomycorrhizal fungal communities: insight
 635 from eight host species in mixed conifer–broadleaf forests. *New Phytologist* **174**: 430–440.
- 636 **Johnson WC, Webb III T. 1989.** The role of blue jays (*Cyanocitta cristata* L.) in the postglacial
 637 dispersal of fagaceous trees in eastern North America. *Journal of Biogeography* **16**: 561–571.
- 638 **Klock MM, Barrett LG, Thrall PH, Harms KE. 2015.** Host promiscuity in symbiont
 639 associations can influence exotic legume establishment and colonization of novel ranges. *Diversity*
 640 *and Distributions* **21**: 1193–1203.
- 641 **Kõljalg U, Nilsson R, Abarenkov K, Tedersoo L, Taylor AFS, Bahram M, Bates ST, Bruns**
 642 **T, Bengtsson-Palme J, Callaghan TM, et al. 2013.** Towards a unified paradigm for sequence-
 643 based identification of fungi. *Molecular Ecology* **22**: 5271–5277.
- 644 **Lambers H, Raven JA, Shaver GR, Smith SE. 2008.** Plant nutrient-acquisition strategies change
 645 with soil age. *Trends in Ecology and Evolution* **23**: 95–103.
- 646 **Lankau RA, Zhu K, Ordóñez A. 2015.** Mycorrhizal strategies of tree species correlate with

- 647 trailing range edge responses to current and past climate change. *Ecology* **96**: 1451–1458.
- 648 **Lindahl B, Nilsson RH, Tedersoo L, Abarenkov K, Carlsen T, Kjoller R, Kõljalg U,**
649 **Pennanen T, Rosendahl S, Stenlid J, et al. 2013.** Fungal community analysis by high-throughput
650 sequencing of amplified markers--a user's guide. *New Phytologist* **199**: 288–299.
- 651 **Little ELJ. 1971.** *Atlas of United States trees, volume 1, conifers and important hardwoods,*
652 *miscellaneous publication 1146.* Washington: U.S. Department of Agriculture.
- 653 **Little ELJ. 1976.** *Atlas of United States trees, volume 3, minor Western hardwoods,*
654 *miscellaneous publication 1314.* Washington, DC: U.S. Department of Agriculture.
- 655 **Little ELJ. 1977.** *Atlas of United States trees, volume 4, minor Eastern hardwoods, miscellaneous*
656 *publication 1146.* Washington, DC: U.S. Department of Agriculture.
- 657 **McLachlan JS, Clark JS, Manos PS. 2005.** Molecular indicators of tree migration capacity
658 under rapid climate change. *Ecology* **86**: 2088–2098.
- 659 **Millar CI, Stephenson NL, Stephens SL. 2007.** Climate change and forests of the future:
660 Managing in the face of uncertainty. *Ecological Applications* **17**: 2145–2151.
- 661 **Moora M. 2014.** Mycorrhizal traits and plant communities: perspectives for integration. *Journal*
662 *of Vegetation Science* **25**: 1126-1132.
- 663 **Nogués-Bravo D, Pulido F, Araújo MB, Diniz-Filho JAF, García-Valdés R, Kollmann J,**
664 **Svenning JC, Valladares F, Zavala MA. 2014.** Phenotypic correlates of potential range size and
665 range filling in European trees. *Perspectives in Plant Ecology, Evolution and Systematics* **16**: 219–
666 227.
- 667 **Nuñez MA, Dickie IA. 2014.** Invasive belowground mutualists of woody plants. *Biological*
668 *Invasions* **16**: 645–661.
- 669 **Nuñez MA, Horton TR, Simberloff D. 2009.** Lack of belowground mutualisms hinders Pinaceae
670 invasions. *Ecology* **90**: 2352–2359.
- 671 **Ordóñez A, Williams JW. 2013.** Climatic and biotic velocities for woody taxa distributions over
672 the last 16 000 years in eastern North America. *Ecology letters* **16**: 773–81.
- 673 **Peay KG, Bruns TD. 2014.** Spore dispersal of basidiomycete fungi at the landscape scale is
674 driven by stochastic and deterministic processes and generates variability in plant–fungal
675 interactions. *New Phytologist* **204**: 180-191.
- 676 **Peay KG, Russo SE, McGuire KL, Lim Z, Chan JP, Tan S, Davies SJ. 2015.** Lack of host
677 specificity leads to independent assortment of dipterocarps and ectomycorrhizal fungi across a soil

- 678 fertility gradient. *Ecology Letters* **18**: 807-816.
- 679 **Perry DA, Borchers JG, Borchers SL, Amaranthus MP. 1990.** Species migrations and
 680 ecosystem stability during climate change: the belowground connection. *Conservation Biology* **4**:
 681 266–274.
- 682 **Pither J, Pickles BJ. 2017.** The paleosymbiosis hypothesis: host plants can be colonised by root
 683 symbionts that have been inactive for centuries to millenia. *FEMS Microbiology Ecology* **93**:
 684 fix061.
- 685 **Pölme S, Bahram M, Jacquemyn H, Kennedy P, Kohout P, Moora M, Oja J, Öpik M,**
 686 **Pecoraro L, Tedersoo L. 2017.** Host preference and network properties in biotrophic plant-fungal
 687 associations. *New Phytologist* **217**: 1230-1239.
- 688 **Prentice IC, Bartlein PJ, Webb T. 1991.** Vegetation and climate change in eastern North
 689 America since the last glacial maximum. *Ecology* **72**: 2038–2056.
- 690 **Pringle A, Bever JD, Gardes M, Parrent JL, Rillig MC, Klironomos JN. 2009.** Mycorrhizal
 691 Symbioses and Plant Invasions. *Annual Review of Ecology, Evolution, and Systematics* **40**: 699–
 692 715.
- 693 **van der Putten WH. 2012.** Climate change, aboveground-belowground interactions, and species'
 694 range shifts. *Annual Review of Ecology, Evolution, and Systematics* **43**: 365–383.
- 695 **R Core Team. 2015.** *R Project* (H Fehske, R Schneider, and A Weiße, Eds.). Berlin, Heidelberg:
 696 Springer Berlin Heidelberg.
- 697 **Read DJ, Perez-Moreno J. 2003.** Mycorrhizas and Nutrient Cycling in Ecosystems : A Journey
 698 towards Relevance? *New Phytologist* **157**: 475–492.
- 699 **Reithmeier L, Kernaghan G. 2013.** Availability of ectomycorrhizal fungi to black spruce above
 700 the present treeline in Eastern Labrador. *PloS one* **8**: e77527.
- 701 **Roy-Bolduc A, Laliberté E, Hijri M. 2016.** High richness of ectomycorrhizal fungi and low host
 702 specificity in a coastal sand dune ecosystem revealed by network analysis. *Ecology and evolution*
 703 **6**: 349–362.
- 704 **Sánchez-Ramírez S, Tulloss RE, Amalfi M, Moncalvo J-M. 2015.** Palaeotropical origins,
 705 boreotropical distribution and increased rates of diversification in a clade of edible
 706 ectomycorrhizal mushrooms (Amanita section Caesareae). *Journal of Biogeography* **42**: 351–363.
- 707 **Selosse M-A, Richard F, He X, Simard SW. 2006.** Mycorrhizal networks: des liaisons
 708 dangereuses? *Trends in Ecology & Evolution* **21**: 621–628.

- 709 **Shakun JD, Clark PU, He F, Marcott SA, Mix AC, Liu Z, Otto-Bliesner B, Schmittner A,**
710 **Bard E. 2012.** Global warming preceded by increasing carbon dioxide concentrations during the
711 last deglaciation. *Nature* **484**: 49–54.
- 712 **Simard SW, Beiler KJ, Bingham MA, Deslippe JR, Philip LJ, Teste FP. 2012.** Mycorrhizal
713 networks: mechanisms, ecology and modelling. *Fungal Biology Reviews* **26**: 39–60.
- 714 **Soudzilovskaia NA, Douma JC, Akhmetzhanova AA, van Bodegom PM, Cornwell WK,**
715 **Moens EJ, Treseder KK, Tibbett M, Wang Y-P, Cornelissen JHC. 2015.** Global patterns of
716 plant root colonization intensity by mycorrhizal fungi explained by climate and soil chemistry.
717 *Global Ecology and Biogeography* **24**: 371–382.
- 718 **Svenning J-C, Gravel D, Holt RD, Schurr FM, Thuiller W, Münkemüller T, Schiffers KH,**
719 **Dullinger S, Edwards TC, Hickler T, et al. 2014.** The influence of interspecific interactions on
720 species range expansion rates. *Ecography* **37**: 1198–1209.
- 721 **Tedersoo L, Bahram M, Pöhlme S, Kõljalg U, Yorou NS, Wijesundera R, Ruiz LV, Vasco-**
722 **Palacios AM, Thu PQ, Suija A, et al. 2014.** Global diversity and geography of soil fungi. *Science*
723 **346**: 1256688.
- 724 **Terrer C, Vicca S, Hungate BA, Phillips RP, Prentice IC. 2016.** Mycorrhizal association as a
725 primary control of the CO₂ fertilization effect. *Science* **353**: 72–74.
- 726 **Timling I, Dahlberg A, Walker D, Imling IT, Ahlberg AD, Alker DAW, Ardes MG,**
727 **Harcosset JYC, Elker JMW. 2012.** Distribution and drivers of ectomycorrhizal fungal
728 communities across the North American Arctic. *Ecosphere* **3**: 1–25.
- 729 **Timling I, Walker DA, Nusbaum C, Lennon NJ, Taylor DL. 2014.** Rich and cold: diversity,
730 distribution and drivers of fungal communities in patterned-ground ecosystems of the North
731 American Arctic. *Molecular ecology* **23**: 3258–3272.
- 732 **Urban MC, Zarnetske PL, Skelly DK. 2013.** Moving forward: Dispersal and species interactions
733 determine biotic responses to climate change. *Annals of the New York Academy of Sciences* **1297**:
734 44–60.
- 735 **Williams JW, Jackson ST. 2007.** Novel climates, no-analog communities, and ecological
736 surprises. *Frontiers in Ecology and the Environment* **5**: 475–482.
- 737 **Williams JW, Shuman BN, Webb T, Bartlein PJ, Leduc PL. 2004.** Late-Quaternary vegetation
738 dynamics in North America: scaling from taxa to biomes. *Ecological Monographs* **74**: 309–334.
- 739 **Zhu K, Woodall CW, Clark JS. 2012.** Failure to migrate: Lack of tree range expansion in

740 response to climate change. *Global Change Biology* **18**: 1042–1052.

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742 **Supporting Information**743 **Fig. S1.** Most rapid distribution dynamics tallied among time periods.744 **Fig. S2.** Scatterplot matrix of pairwise correlations among all variables in analyses.745 **Fig. S3.** Regression of distribution expansion rate on host receptivity.746 **Fig. S4.** Stripcharts of associations between distribution dynamics and mycorrhizal status.747 **Fig. S5.** Sensitivity analyses for tests of the facilitated distribution expansion hypothesis (FDE1).748 **Fig. S6.** Sensitivity analyses for tests of the facilitated distribution expansion hypothesis (FDE2).749 **Fig. S7.** Sensitivity analyses for tests of the environmental buffering hypothesis (EB1).750 **Fig. S8.** Sensitivity analyses for tests of the environmental buffering hypothesis (EB2).751 **Fig. S9.** Scatterplots and model-2 regressions of biotic velocity versus climate velocity.752 **Table S1.** Summary characteristics of host plant genera.753 **Table S2.** Taxon- and time-specific biotic and climate velocities, 16-7KaBP.754 **Table S3.** Trait values for 199 North America woody plant taxa, used to derive average trait
755 values for 23 genera.756 **Table S4.** Outcomes of the all-subsets multiple regression analysis for models testing the
757 facilitated distribution expansion (FDE) hypothesis.758 **Table S5.** Outcomes of the all-subsets multiple regression analysis for models testing the
759 environmental buffering (EB) hypothesis.760 **Table S6.** Model-averaging results associated with tests of the FDE predictions and the EB
761 predictions, using the 100th percentile boundary definition.762 **Table S7.** Results of analyses exploring phylogenetic signal and phylogenetic generalised least
763 squares regression.764 **Table S8.** Outcomes of the all-subsets multiple regression analysis for all 23 host genera.765 **Table S9.** Sensitivity analyses of model averaging results for tests of predictions FDE2 and EB1.766 **Table S10.** Outcomes of the all-subsets multiple regression analysis for 13 EM host genera.767 **Table S11.** Sensitivity analyses of model averaging results for tests of predictions FDE1 and
768 EB2.769 **Table S12.** Partial correlation analysis for leading boundary distribution expansion (LBDE)
770 among 13 ectomycorrhizal (EM) host genera.771 **Methods S1.** Expanded details of specific methodological approaches.

772 **Table 1:** Model-averaging results from tests of predictions associated with the facilitated distribution expansion hypothesis (FDE).
 773

Prediction	Dataset	Response variable	*Predictor	Standardized coefficient (95% confidence limits)	†RI
FDE ₁	13 ectomycorrhizal (EM) host genera ($N = 13$)	Leading boundary distribution expansion rate (m/yr)	Host receptivity	0.78 (0.378, 1.185)	1.000
			Seed mass	-0.59 (-1.070, -0.117)	0.862
			Cold sensitivity	0.45 (0.036, 0.859)	0.487
			Shade tolerance	-0.33 (-0.774, 0.119)	0.226
			Max height	0.31 (-0.163, 0.774)	0.099
			Climate velocity	-0.18 (-0.555, 0.195)	0.055
FDE ₂	13 EM & 10 arbuscular mycorrhizal (AM) host genera ($N = 23$)	Leading boundary distribution expansion rate (m/yr)	Mycorrhizal type	0.34 (-0.101, 0.780)	0.473
			Maximum height	0.26 (-0.221, 0.736)	0.285
			Cold sensitivity	-0.13 (-0.618, 0.349)	0.192
			Climate velocity	0.11 (-0.364, 0.584)	0.173
			Seed mass	-0.11 (-0.568, 0.346)	0.172
			Shade tolerance	0.04 (-0.452, 0.525)	0.166

774 * Bold text indicates predictor variables whose confidence intervals for parameter estimates exclude zero, and $RI > 0.60$.

775 † Relative variable importance

776

777

778 **Table 2:** Model-averaging results from tests of predictions associated with the environmental buffering hypothesis (EB).
 779

Prediction	Dataset	Response variable	*Predictor	Standardized coefficient (95% confidence limits)	†RI
EB ₁	13 EM & 10 arbuscular mycorrhizal (AM) host genera (<i>N</i> = 23)	Trailing boundary distribution contraction rate (m/yr)	Climate velocity	0.46 (0.027, 0.893)	0.753
			Cold sensitivity	-0.37 (-0.803, 0.060)	0.524
			Mycorrhizal type	-0.33 (-0.747, 0.094)	0.448
			Maximum height	-0.27 (-0.745, 0.201)	0.293
			Seed mass	-0.15 (-0.653, 0.348)	0.185
			Shade tolerance	0.07 (-0.394, 0.525)	0.137
			EB ₂	13 ectomycorrhizal (EM) host genera (<i>N</i> = 13)	Trailing boundary distribution contraction rate (m/yr)
Host receptivity	0.38 (-0.234, 0.996)	0.249			
Climate velocity	0.37 (-0.263, 1.005)	0.225			
Shade tolerance	0.27 (-0.370, 0.918)	0.144			
Cold sensitivity	-0.09 (-0.793, 0.623)	0.097			
Maximum height	0.09 (-0.591, 0.776)	0.086			

780 * Bold text indicates predictor variables whose confidence intervals for parameter estimates exclude zero, and RI > 0.60.

781 † Relative variable importance

782 **Figure legends**

783

784 **Figure 1. Predicted woody plant responses during the last deglaciation in North America**
 785 **(16 to 7 kaBP) at leading and trailing distribution boundaries according to the facilitated**
 786 **distribution expansion (FDE) and environmental buffering (EB) hypotheses.** Panels
 787 display the predicted effects of **a.** host receptivity towards EM fungi (FDE₁ and EB₂), and **b.**
 788 host mycorrhizal type (FDE₂ and EB₁), on relative velocities of distribution expansion and
 789 contraction.

790

791 **Figure 2. Average rates of poleward distribution expansion and contraction for 23 North**
 792 **American tree genera during the last deglaciation (16 to 7 kaBP).** Rates of leading
 793 boundary expansion versus trailing boundary contraction for core distributions are presented.
 794 Points denote weighted averages calculated using one to four time periods (indicated by
 795 relative size of symbols), weighted by $1/SE^2$ from each contributing time period (see Methods).
 796 Error bars denote +/- one standard error. Genera falling above the dashed 1:1 line exhibited
 797 overall expansion of latitudinal extent between 16 and 7 kaBP. The overall association
 798 between the leading- and trailing-boundary rates is positive (Spearman $r = 0.38$, $P = 0.07$) and
 799 strong if the outlier genus *Cephalanthus* is excluded ($r = 0.57$, $P = 0.007$).

800

801 **Figure 3. Predictors of leading boundary distribution expansion rates for 13 North**
 802 **American tree genera during the last deglaciation.** Conditional partial regression plot of the
 803 most parsimonious, plausible model for leading boundary distribution expansion among 13 EM
 804 host genera. The model included host receptivity (a) and seed mass (b) as predictors. Hollow
 805 black circles denote individual genus observations, solid black lines indicate partial regression
 806 lines, and grey shading encompasses the 95% confidence bands.

807

808 **Figure 4. Spatial distribution of the richness of North American tree genera during the**
 809 **last deglaciation based on their mycorrhizal type.** Genus richness patterns (colour scale)
 810 between 16 and 7 thousand years before present (ka BP) among tree genera, for 13
 811 ectomycorrhizal (EM) (right column) and 10 arbuscular mycorrhizal (AM) (left column) host
 812 genera. Genus richness in each grid cell was calculated by summing the number of
 813 overlapping core distributions. Ice sheet extents (grey) from Williams *et al.* (2004); modern
 814 coastlines are shown for all time periods. Distributions could not be estimated for areas west
 815 of the Rockies in the United States (see Materials & Methods).

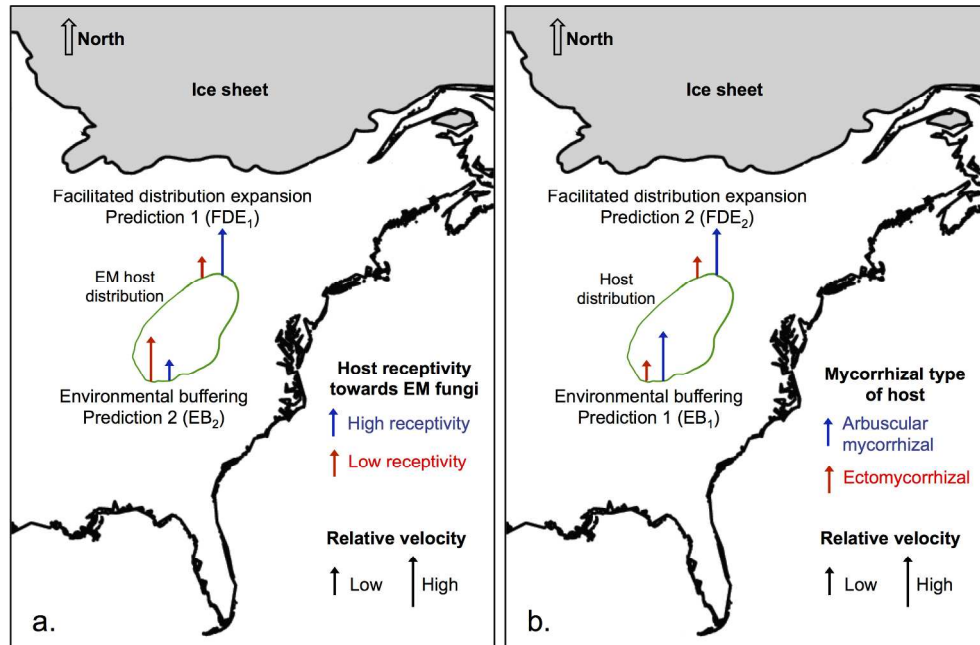


Figure 1. Predicted woody plant responses during the last deglaciation in North America (16 to 7 kaBP) at leading and trailing distribution boundaries according to the facilitated distribution expansion (FDE) and environmental buffering (EB) hypotheses. Panels display the predicted effects of a. host receptivity towards EM fungi (FDE₁ and EB₂), and b. host mycorrhizal type (FDE₂ and EB₁), on relative velocities of distribution expansion and contraction.

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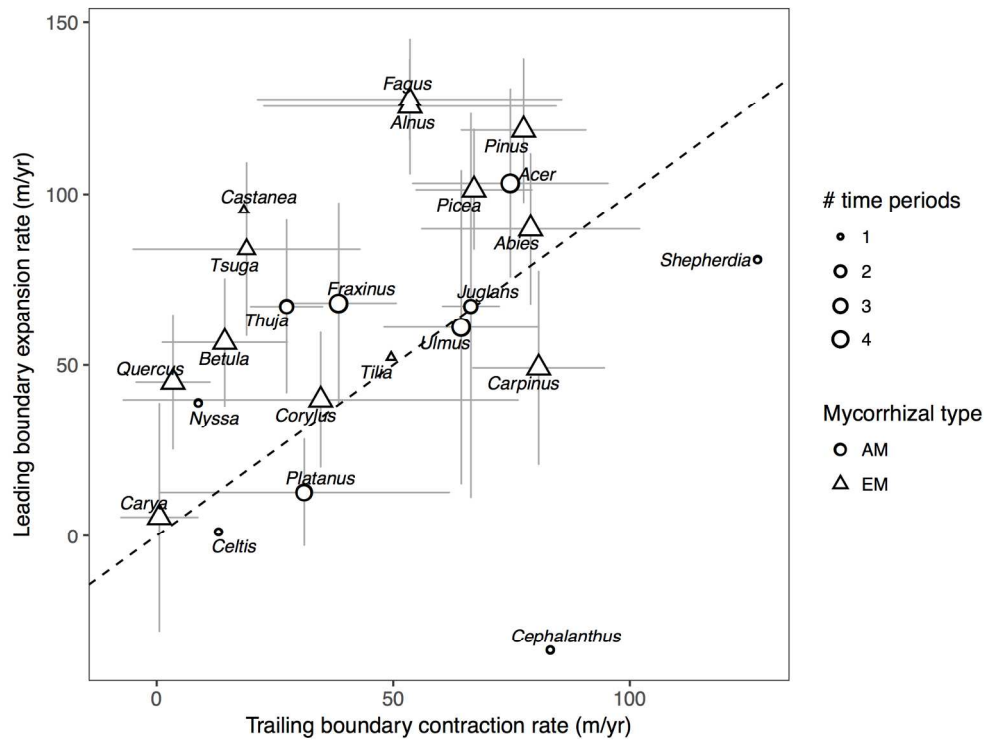


Figure 2. Average rates of poleward distribution expansion and contraction for 23 North American tree genera during the last deglaciation (16 to 7 kaBP). Rates of leading boundary expansion versus trailing boundary contraction for core distributions are presented. Points denote weighted averages calculated using one to four time periods (indicated by relative size of symbols), weighted by $1/SE^2$ from each contributing time period (see Methods). Error bars denote \pm one standard error. Genera falling above the dashed 1:1 line exhibited overall expansion of latitudinal extent between 16 and 7 kaBP. The overall association between the leading- and trailing-boundary rates is positive (Spearman $r = 0.38$, $P = 0.07$) and strong if the outlier genus *Cephalanthus* is excluded ($r = 0.57$, $P = 0.007$).

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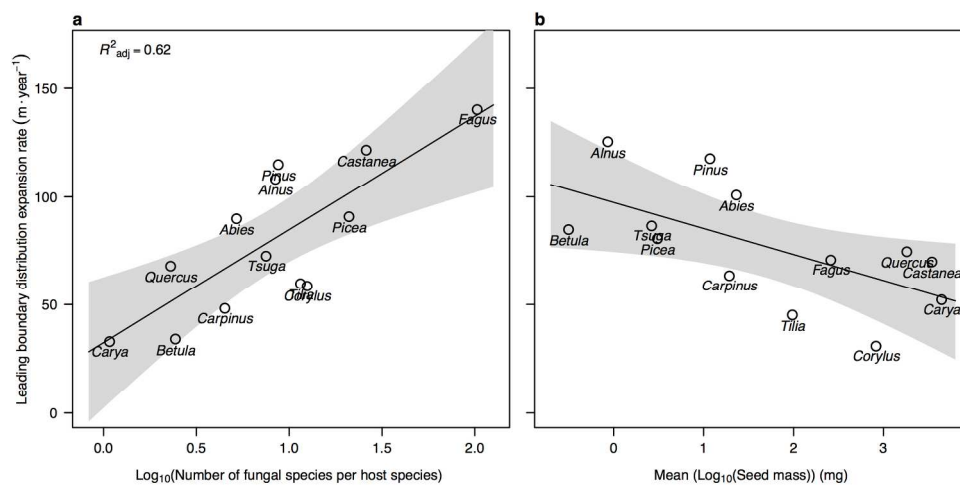


Figure 3. Predictors of leading boundary distribution expansion rates for 13 North American tree genera during the last deglaciation. Conditional partial regression plot of the most parsimonious, plausible model for leading boundary distribution expansion among 13 EM host genera. The model included host receptivity (a) and seed mass (b) as predictors. Hollow black circles denote individual genus observations, solid black lines indicate partial regression lines, and grey shading encompasses the 95% confidence bands.

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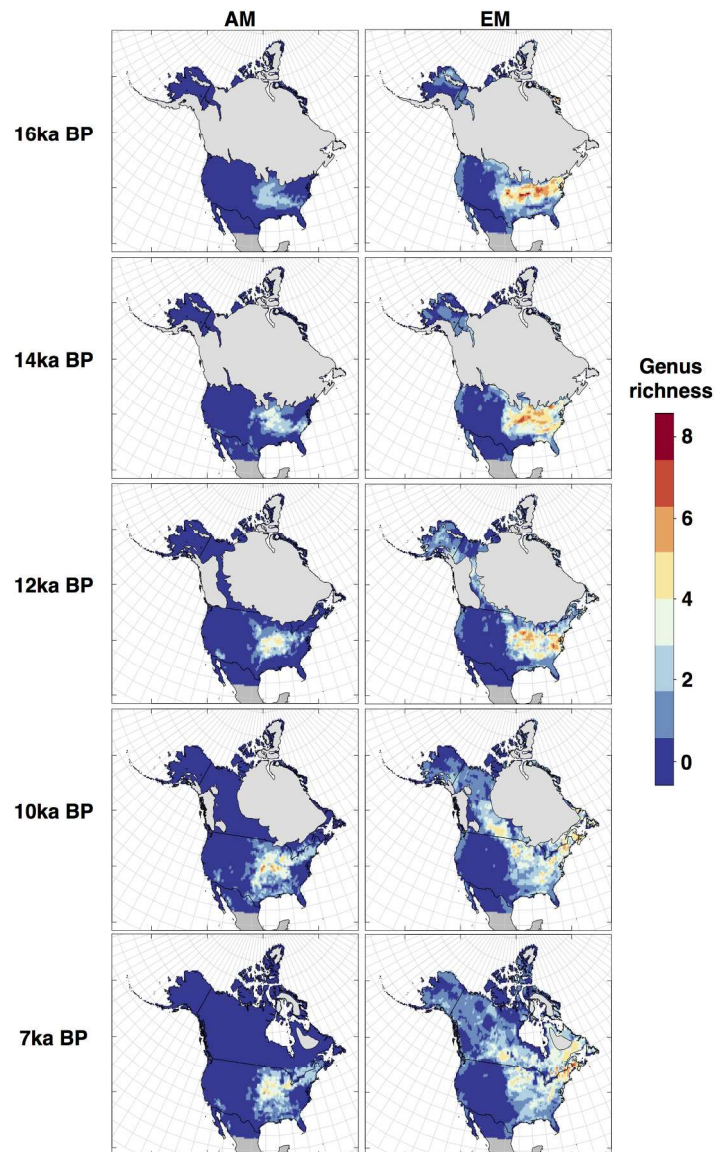


Figure 4. Spatial distribution of the richness of North American tree genera during the last deglaciation based on their mycorrhizal type. Genus richness patterns (colour scale) between 16 and 7 thousand years before present (ka BP) among tree genera, for 13 ectomycorrhizal (EM) (right column) and 10 arbuscular mycorrhizal (AM) (left column) host genera. Genus richness in each grid cell was calculated by summing the number of overlapping core distributions. Ice sheet extents (grey) from Williams et al. (2004); modern coastlines are shown for all time periods. Distributions could not be estimated for areas west of the Rockies in the United States (see Materials & Methods).

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