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

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Summary

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

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

Introduction

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

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

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

Testing the FDE hypothesis requires consideration of "host receptivity", defined here as the differential compatibility of hosts with mycorrhizal symbionts. Accurate estimates of host receptivity are challenging to obtain, but to a first approximation (see Materials and Methods) host receptivity can be estimated as the total number of species of mycorrhizal fungi that a host has been observed to associate with. Although this broad definition undoubtedly includes specialist fungi that only associate with one specific host species or genus, it also consists of all fungi possessing one or more of the following ameliorating properties, which we consider to be the most pertinent to facilitating host distribution expansion: (i) association with multiple host genera (e.g. generalists; Ishida *et al.*, 2007; Peay *et al.*, 2015; Roy-Bolduc *et al.*, 2016), (ii) formation of long-lived resistant propagules (Pither and Pickles, 2017), (iii) rapid dispersal capabilities (Peay and Bruns, 2014). Given these considerations, the FDE hypothesis predicts that host receptivity towards mycorrhizal fungi, in general, will be positively associated with the rate of expansion at leading distribution boundaries (Fig. 1a). This prediction (henceforth represented by prediction FDE_1) is more readily tested for ectomycorrhizal (EM) than arbuscular mycorrhizal (AM) host tree genera, because associated fungal species richness estimates are presently attainable for EM host trees only (see Materials and Methods). A second prediction of the FDE, relevant to all host genera, rests on prior findings that, as a group, AM-associated hosts are more prone to generalism (i.e. are more receptive) on average than EM-associated hosts (Davison *et al.*, 2015; van der Heijden *et al.*, 2015) (but see Põlme *et al.*, 2017): hence, AM hosts are predicted to exhibit faster rates of leading-boundary distribution expansion than EM hosts (prediction FDE_2; Fig. 1b).

The EB hypothesis predicts that EM hosts should exhibit slower rates of trailing-boundary distribution contraction (prediction EB_1; Fig. 1b) because: (i) plant-soil feedbacks within established forests are generally more negative among AM host trees compared to EM hosts (Dickie *et al.*, 2014; Bennett *et al.*, 2017), with EM hosts appearing to benefit via facilitation of

seedling recruitment by adult trees and increased protection against belowground antagonists (Bennett *et al.*, 2017), and (ii) compared to AM trees, EM trees more consistently benefit from belowground common mycorrhizal networks (Horton & van der Heijden, 2008; Dickie *et al.*, 2014), which can buffer hosts against changing and stressful conditions through the transfer of nutrients, including nitrogen, sugars, and water (Selosse *et al.*, 2006; Simard *et al.*, 2012; van der Heijden *et al.*, 2015). A second prediction (EB_2), presently testable with EM hosts only, is that the more receptive the host, the slower the distribution contraction at trailing boundaries (Fig. 1a). This prediction assumes a positive association between taxonomic and functional diversity among EM fungal taxa, such that more receptive EM hosts are more likely to associate with EM fungi that provide benefits during high-stress scenarios such as drought (Gehring *et al.*, 2014, 2017).

To our knowledge, only FDE_2 and EB_1 have previously been tested at biogeographic scales. Using both contemporary Forest Inventory Assessment (FIA) data, and fossil pollen data from 12-10 thousand years before present (kaBP), Lankau and colleagues (2015) estimated the contemporary and geohistorical rates of distribution expansion and contraction of North American trees and found evidence consistent with EB_1 but not FDE_2: rates of distribution contraction (southern boundaries) were significantly slower among EM compared to AM hosts in both the contemporary (n = 97 tree species) and the geohistorical (n = 18 tree genera) data, whereas rates of distribution expansion (northern boundaries) did not differ among EM and AM hosts either within the contemporary (n = 84 tree species) or in the geohistorical (n = 18 tree genera) data. Furthermore, the effects of the two plant traits considered by Lankau *et al.* (2015), shade tolerance and seed mass, were either non-significant or inconsistent among southern and northern distribution margins, and among the geohistorical versus contemporary datasets.

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

(1) We derive estimates of receptivity for EM hosts, and use these to conduct the first tests of predictions FDE_1 and EB_2, i.e. that the rate of northward distribution expansion of EM host genera was positively associated with host receptivity, and the rate of southern distribution contraction of EM host genera was negatively associated with host receptivity (Fig 1.a).

(2) We test all four predictions (FDE_1, FDE_2, EB_1, EB_2; Fig. 1) using fossil pollen data from four time periods spanning 16 to 7kaBP. This approach takes account of the highly varied rates of distribution expansion and contraction exhibited by tree genera among time periods, including rates that were often greatest in time periods other than the 12-10kaBP period (Fig. S1).
(3) We test multivariate climate velocity as a predictor of distribution expansion and contraction rates alongside other predictors (see below). Here, climate velocity is broadly defined as a physical metric comprising the speed and direction of change in climate over time and across space measured in m/yr (and thus comparable to taxon distribution expansion and contraction). Specifically we use the latitudinal measure of regional-scale climatic velocity developed by Zhu et al. (2011) and Ordonez and Williams (2013), which integrates 12 climatic variables simultaneously, rather than the local-scale grid-square approach of Loarie et al (2009), which uses a single variable (mean annual temperature or mean annual precipitation).
(4) We used multi-model inference and model averaging for all four predictions to estimate the relative importance of abiotic and biotic variables for explaining expansion and contraction rates of taxa across multiple time periods. The selected variables were climate velocity, mycorrhizal traits (specifically mycorrhizal type, as defined by Moora (2014), and mycorrhizal receptivity, newly defined here), and four plant traits hypothesized to directly or indirectly moderate distribution dynamics (Aubin *et al.*, 2016): seed mass, maximum height, shade tolerance, and cold sensitivity (Table S1).

Materials and Methods

Pollen taxonomy

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

Estimation of distribution dynamics

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

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

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

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]'

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

Plant traits data

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

Statistical analyses

All analyses were conducted using "R" version 3.1.3 (R Core Team, 2015), and all R code and data associated with this study are available on the Open Science Framework (weblink). To explore the ability of different models and predictor variables to account for variation in our response variables, we used multi-model inference procedures (Burnham & Anderson, 2004) and implemented them using the *MuMIn* R package (Bartoń, 2015). The four plant traits were evaluated as potential predictors, as was either north or south boundary climate velocity. For analyses involving all 23 host genera (predictions FDE_2 and EB_1) we evaluated mycorrhizal type

(binary AM/EM) as our sixth and final potential predictor, and for analyses involving our 13 EM host genera (predictions FDE_1 and EB_2), we evaluated host receptivity as the final potential predictor. The analyses were conducted as follows. We evaluated pairwise rank correlations among predictors (Fig. S2), and with few exceptions (e.g. seed mass positively associated with cold sensitivity; rank correlation = 0.58; Fig. S2b), these revealed generally weak associations ($\leq |0.44|$). For each response variable, we fit a full model and used the *arm* package (Gelman & Su, 2015) to centre the response and explanatory variables on their means and standardized over two standard deviations to facilitate direct comparisons among regression coefficients in the presence of the binary predictor "mycorrhizal type" (Gelman, 2008). We then explored all possible combinations of predictor variables using the 'dredge' function within the *MuMIn* package (Bartoń, 2015). We did not consider interactions due to limited sample size. For each model we computed the Akaike's information criterion corrected for small samples (AIC_C), and ΔAIC_C, the difference between the given model's AIC_C and that of the "best" model, which exhibits the smallest value of AIC_C. Relative evidence weights (based on the AIC_C) were calculated and assigned to each model. We used a 95% confidence set of models to calculate model-averaged, standardized coefficient values, and did so using the "natural average" method, i.e. the average of the standardized coefficient values for all models in the candidate set in which the given predictor appeared, weighted by the models' relative evidence weights (Burnham & Anderson, 2004). We also calculated (i) the relative variable importance (RI) of each explanatory variable as the sum of the relative evidence weights of the candidate models in which the predictor appeared, (ii) the unconditional standard errors for the coefficient estimates, and (iii) the 95% confidence interval for the standardized coefficients. In the sensitivity analyses we additionally present 90% confidence intervals (see below). We conducted residual diagnostics on both the full regression models and the "AIC_C-best" models, and found that all models conformed to regression assumptions. Model averaging results are presented in Table 1 (see Results), and all model sets from the multi-model inference analyses are presented in Tables S4 and S5. Model averaging results corresponding to the 100^{th} percentile boundary definition are summarized in Table S6. We also conducted phylogenetically-informed regression analyses as described in Methods S1.

Sensitivity analyses

We conducted sensitivity analyses to evaluate the robustness of our results with respect to (i) alternative time periods (for all analyses), and (ii) alternative measures of receptivity (for analyses involving the EM host genera, i.e. predictions FDE_1 and EB_2). These sensitivity analyses were conducted using both the 95th and 100th percentile boundary definitions. Specifically, we conducted the following additional analyses:

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

Results

Overall distribution responses of host genera

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

Facilitated distribution expansion

We found strong support for FDE_1: among EM host genera, host receptivity emerged as a strong, positive predictor of leading-boundary expansion (Table 1), appearing in all candidate models (Table S4), and on its own accounting for 44% of the variation in rates of leading-boundary expansion (Fig. S3; Table S4). The AIC_C-best model included host receptivity, seed mass, and cold sensitivity (Table S4), and accounted for 75% of the variation in the rate of leading-boundary expansion. The most parsimonious model within 2 AIC_C units of the AIC_C-best model included host receptivity and seed mass, and accounted for 62% of the variation in the rate of leading-boundary expansion (Fig. 3; Table S4). Like host promiscuity, seed mass gained strong support as a predictor of leading boundary expansion rate: the 95% confidence interval for its model-averaged coefficient excluded zero, and its relative variable importance was 0.862 (Table 1).

We found no support for FDE_2: rates of leading boundary distribution expansion were not faster among AM hosts compared to EM hosts, and correspondingly, mycorrhizal type did not emerge as an important predictor in the multi-model inference analyses (Table 1). Rather, on average, EM hosts exhibited marginally faster rates of expansion than AM hosts, when considered in isolation from other factors (means ± SE: 76.2 ± 10.47m•yr^{-1} for EM plant genera and 46.7 ± 13.16m•yr^{-1} among AM plant genera; Fig. S4a). Indeed, mycorrhizal type was the sole predictor in the AIC_C-best model (Table S4), with an effect opposite to that predicted by the FDE. Mycorrhizal type also exhibited a modest effect size (0.34), though the 95% confidence interval for its coefficient overlapped zero (Table 1). The null (no predictor) model was within 2 AIC_C units of the AIC_C-best model, and should therefore be considered the most parsimonious, plausible model, given the data.

Environmental buffering

We found limited support for EB_1: mycorrhizal type was included in the AIC_C-best model along with climate velocity and cold sensitivity (Table S5), which together accounted for 33% of the variation in trailing boundary contraction rates among host genera. However, on average, AM and EM hosts exhibited similar rates of distribution contraction when considered in isolation from other factors (Fig. S4b). Furthermore, our model averaging analysis identified climate velocity as the sole strong predictor (Table 2). Nevertheless, mycorrhizal type and cold sensitivity gain some

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

We found no support for EB_2: host receptivity was not a predictor of the rates of distribution contraction at trailing boundaries for EM host genera (Table 2), nor was any other variable.

Sensitivity analyses

The results of all sensitivity analyses for tests of predictions associated with the FDE and EB hypotheses are presented in Tables S8-S11 and Figures S5-S8. The tables present the details of the model selection and model averaging results for each of the hypotheses, and the figures visually summarize the model averaging outcomes. Collectively, these reveal the following:

(i) Support for host receptivity as a predictor of distribution expansion rates among EM host genera (FDE_1) depends to some degree on the measure of host receptivity used. Specifically, support is strongest when using EM fungal richness per host and EM fungal richness as measures of receptivity, and weakest when using the number of EM fungal species shared with at least one other host genus in the present study (Fig. S5).

(ii) Support for host receptivity as a predictor of distribution expansion rates among EM host genera (FDE_1) is strongest when analysing time periods associated with maximum sample size (i.e. 13 EM host genera versus 11 genera; Fig. S5).

(iii) Seed mass has a consistently negative effect on distribution expansion rates among EM host genera (FDE_1) regardless of time period analysed, but its importance depends in part on the measure of host receptivity included in the models, and on the time period analysed (Fig. S5).

(iv) Among the analyses with the greatest sample size (N = 23) and thus greatest statistical power, mycorrhizal type exhibits the opposite effect to that predicted by FDE_2: model averaged coefficients indicate a positive effect of EM associations on the rates of leading boundary distribution expansion (Fig. S6), though most confidence intervals for coefficients encompassed zero.

(v) Support for climate velocity as a predictor of distribution contraction rates among EM and AM host genera (EB_1) is relatively consistent and strong among analyses (Fig. S7).

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

Discussion

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

Facilitated distribution expansion

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

Consistent with the findings of Lankau *et al.* (2015), we found no support for prediction FDE_2, i.e. that due to their more generalist habit overall, AM hosts should exhibit more rapid distribution expansion at leading boundaries compared to EM host genera. Rather, we found that rates of leading boundary distribution expansion were similar among AM and EM hosts (Fig. S4). Perhaps, as recently suggested (Põlme *et al.* 2017), receptivity is not as different among AM and EM hosts as traditionally thought. Alternatively, abiotic and biotic features of receiving landscapes may have diminished any advantage afforded to AM hosts by their generalist habit. Specifically, relative to AM host genera, EM host genera were prevalent in regions proximate to retreating ice sheets (Williams *et al.*, 2004) (Fig. 4), and we hypothesize that several features of recently deglaciated landscapes may have facilitated expansion among EM hosts relative to AM hosts. First, EM fungi are highly diverse in dwarf shrub-, herb-, and forb-dominated tundra ecosystems (Timling *et al.*, 2014) and associate with widely dispersed Arctic plants, including *Betula nana*, *Bistorta vivipara*, *Dryas integrifolia*, and *Salix arctica* (Timling *et al.*, 2012). These provide potential sources of fungal inoculum for EM hosts migrating beyond the present tree line (e.g. *Picea mariana*, black spruce; Reithmeier & Kernaghan, 2013), effectively "priming" the landscape for colonization by EM trees. In contrast, AM fungi display low diversity (Davison *et al.*, 2015) and lower root colonisation (Soudzilovskaia *et al.*, 2015) in such ecosystems. Second, nitrogen limitation increases with latitude (Gill & Finzi, 2016), being particularly acute in post-glacial environments (Lambers *et al.*, 2008), and whereas both EM and AM fungi can scavenge mineralizable forms of N (ammonium and nitrate) several species of EM fungi are also able to mine nitrogen from organic molecules (Read & Perez-Moreno, 2003; Lambers *et al.*, 2008). Third, CO_2 concentrations rose by 40% from approximately 190 to 265 ppmv between 18kaBP and 7kaBP (Shakun *et al.*, 2012), and relative to AM hosts, EM hosts are better able to take advantage of such increases, especially under nitrogen-limiting conditions (Terrer *et al.*, 2016). Collectively, these advantages will be accentuated once host populations are established, as forests dominated by EM trees tend to facilitate conspecific seedlings, at least over small spatial scales, whereas AM seedlings typically experience conspecific inhibition (Dickie *et al.*, 2014; Bennett *et al.*, 2017). In sum, although distribution expansion among AM hosts may have been facilitated by a generalist habit towards AM fungi, distribution expansion among EM hosts could have been facilitated by landscapes that were both biotically and abiotically favourable.

Environmental buffering

A wide variety of experimental work supports the importance of mutualists in providing hosts with resilience to changing climates, and for mycorrhizas there is evidence that EM fungi are more likely to provide such benefits to their hosts than AM fungi (e.g. van der Heijden and Horton, 2009; Lankau *et al.*, 2015). However, counter to Lankau *et al.* (2015), our tests of EB_1 did not support mycorrhizal type as an important factor in moderating postglacial distribution contraction among tree genera. We note that mycorrhizal type was included in the AIC_C-best model, with EM hosts contracting more slowly than AM hosts, and that model averaged coefficients consistently indicated more rapid contraction rates among AM than EM hosts. Nevertheless, only climate velocity gained strong support as a predictor of distribution contraction.

Much of the support for mycorrhizas being associated with environmental buffering comes from the literature on EM hosts and fungi (Selosse *et al.*, 2006; van der Heijden and Horton, 2009; Simard et al, 2012). Hence, in EB_2, we had predicted that host receptivity would be an important factor for EM host genera by enabling access to a wide array of fungi and hence a wider potential range of functions. We found no support for this prediction. Recent research suggests that individual fungal species may be associated with the provision of host drought resilience (Gehring *et al.*, 2017), hence the ability to associate with specific mutualist species, rather than a diverse community, may be more important in the south of the distribution during climate warming.

Plant traits

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

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

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

Climate velocity

In our analysis of all 23 plant taxa, climate velocity gained support as a predictor for trailing boundary distribution contraction (Table 2), but not as a predictor of leading boundary distribution expansion (Table 1). This was a surprising result, especially given the findings of Ordonez and Williams (2013), who, using the same data as we use here, found significantly positive model-2 regressions between biotic velocity and climate velocity (for AM and EM host taxa together) within each time period between 16 and 7kaBP (see their Figure 4). This can be attributed to methodological differences: Ordonez and Williams (2013) assumed that biotic velocity should be zero when climate velocity is negligible, and correspondingly, forced the model 2 regressions through the origin. We opted to relax this assumption (accommodating the possibility of migration lag, for example), and our analyses yielded very different outcomes: as shown in Figure S9, climate velocity is a significant predictor of biotic velocity in only one of the four time-periods: 12-10kaBP. Our sensitivity analyses are largely consistent with this finding (Figs. S5-S8): if we focus solely on the 12-10kaBP period, climate velocity emerges as the sole significant predictor of (i) leading boundary distribution expansion rates among AM and EM taxa (prediction FDE_2), (ii) trailing boundary distribution contraction among AM and EM taxa (prediction EB_1), and (iii) trailing boundary distribution contraction among EM taxa (EB_2). The only prediction for which climate velocity does not gain support is FDE_1.

In light of these developments, and for additional reasons outlined below, we suggest that analyses based on velocities from a pool of multiple time- periods have advantages relative to inferences 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 (Ordonez & 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, FDE_2, 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 FDE_2 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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Author contributions

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

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Supporting Information

Fig. S1. Most rapid distribution dynamics tallied among time periods.

Fig. S2. Scatterplot matrix of pairwise correlations among all variables in analyses.

Fig. S3. Regression of distribution expansion rate on host receptivity.

Fig. S4. Stripcharts of associations between distribution dynamics and mycorrhizal status.

Fig. S5. Sensitivity analyses for tests of the facilitated distribution expansion hypothesis (FDE1).

Fig. S6. Sensitivity analyses for tests of the facilitated distribution expansion hypothesis (FDE2).

Fig. S7. Sensitivity analyses for tests of the environmental buffering hypothesis (EB1).

Fig. S8. Sensitivity analyses for tests of the environmental buffering hypothesis (EB2).

Fig. S9. Scatterplots and model-2 regressions of biotic velocity versus climate velocity.

Table S1. Summary characteristics of host plant genera.

Table S2. Taxon- and time-specific biotic and climate velocities, 16-7KaBP.

Table S3. Trait values for 199 North America woody plant taxa, used to derive average trait values for 23 genera.

Table S4. Outcomes of the all-subsets multiple regression analysis for models testing the facilitated distribution expansion (FDE) hypothesis.

Table S5. Outcomes of the all-subsets multiple regression analysis for models testing the environmental buffering (EB) hypothesis.

Table S6. Model-averaging results associated with tests of the FDE predictions and the EB predictions, using the 100th percentile boundary definition.

Table S7. Results of analyses exploring phylogenetic signal and phylogenetic generalised least squares regression.

Table S8. Outcomes of the all-subsets multiple regression analysis for all 23 host genera.

Table S9. Sensitivity analyses of model averaging results for tests of predictions FDE2 and EB1.

Table S10. Outcomes of the all-subsets multiple regression analysis for 13 EM host genera.

Table S11. Sensitivity analyses of model averaging results for tests of predictions FDE1 and EB2.

Table S12. Partial correlation analysis for leading boundary distribution expansion (LBDE) among 13 ectomycorrhizal (EM) host genera.

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 ($N = 23$)	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 ($N = 13$)	Trailing boundary distribution contraction rate (m/yr)	Seed mass	-0.40 (-1.027, 0.237)	0.251
			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 (FDE_1 and EB_2), and **b.**
788 host mycorrhizal type (FDE_2 and EB_1), 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).

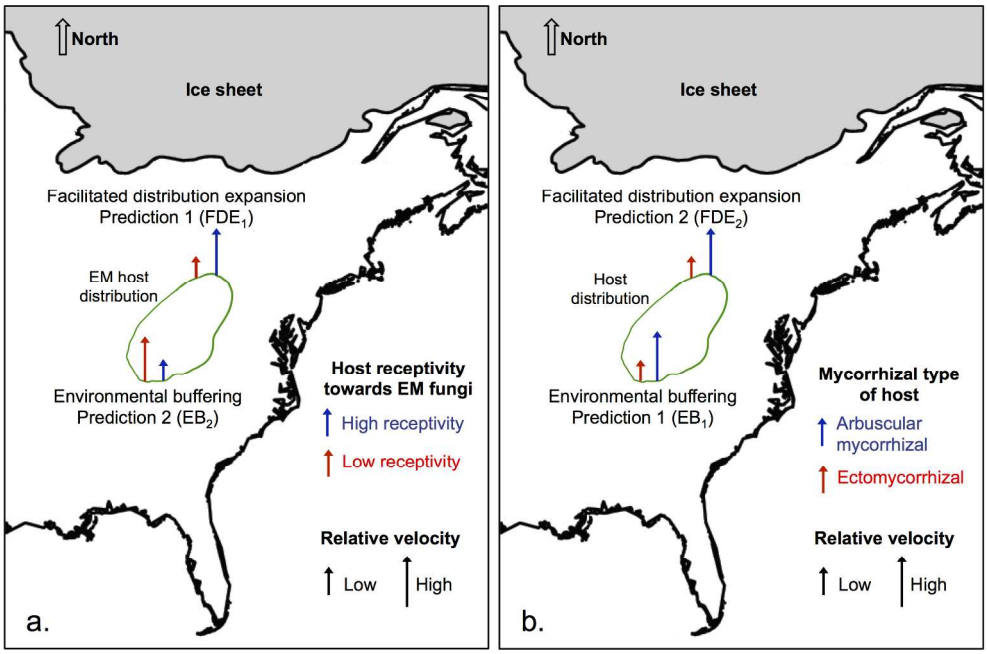

Figure 1. Predicted woody plant responses during the last deglaciation in North America (16 to 7 kaBP) at leading and trailing distribution boundaries according to the facilitated distribution expansion (FDE) and environmental buffering (EB) hypotheses. Panels display the predicted effects of a. host receptivity towards EM fungi (FDE_1 and EB_2), and b. host mycorrhizal type (FDE_2 and EB_1), on relative velocities of distribution expansion and contraction.

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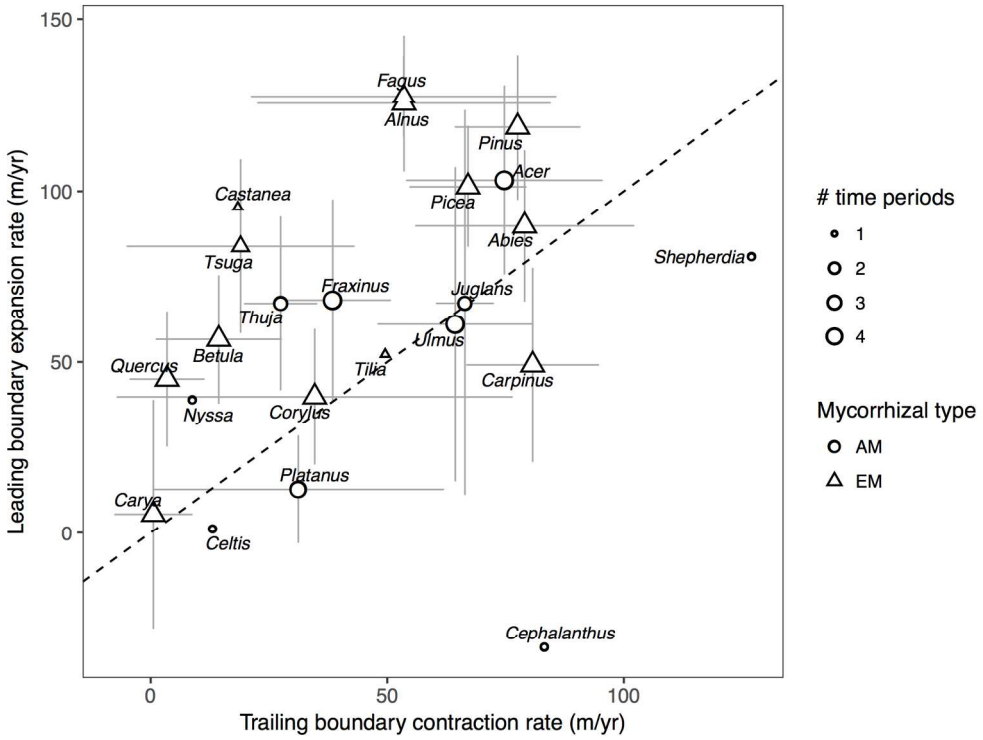

Figure 2. Average rates of poleward distribution expansion and contraction for 23 North American tree genera during the last deglaciation (16 to 7 kaBP). Rates of leading boundary expansion versus trailing boundary contraction for core distributions are presented. Points denote weighted averages calculated 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 +/- 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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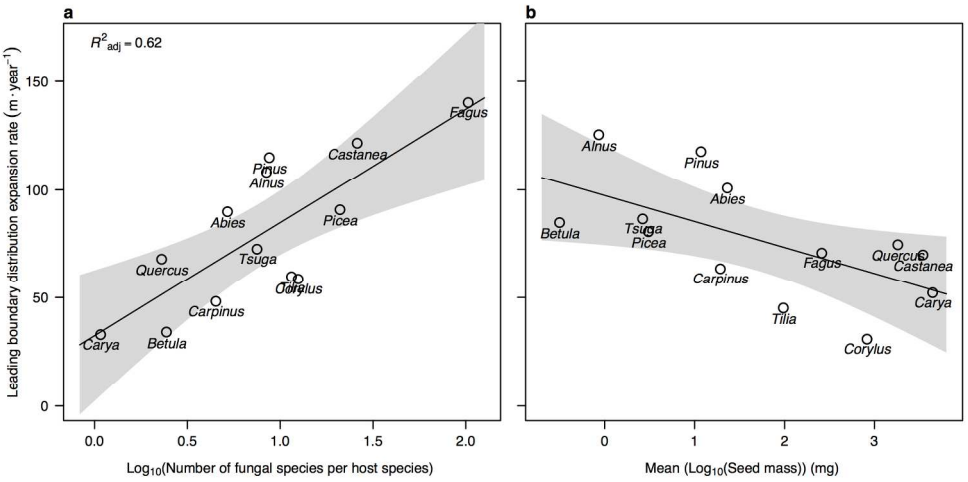

Figure 3. Predictors of leading boundary distribution expansion rates for 13 North American tree genera during the last deglaciation. Conditional partial regression plot of the most parsimonious, plausible model for leading boundary distribution expansion among 13 EM host genera. The model included host 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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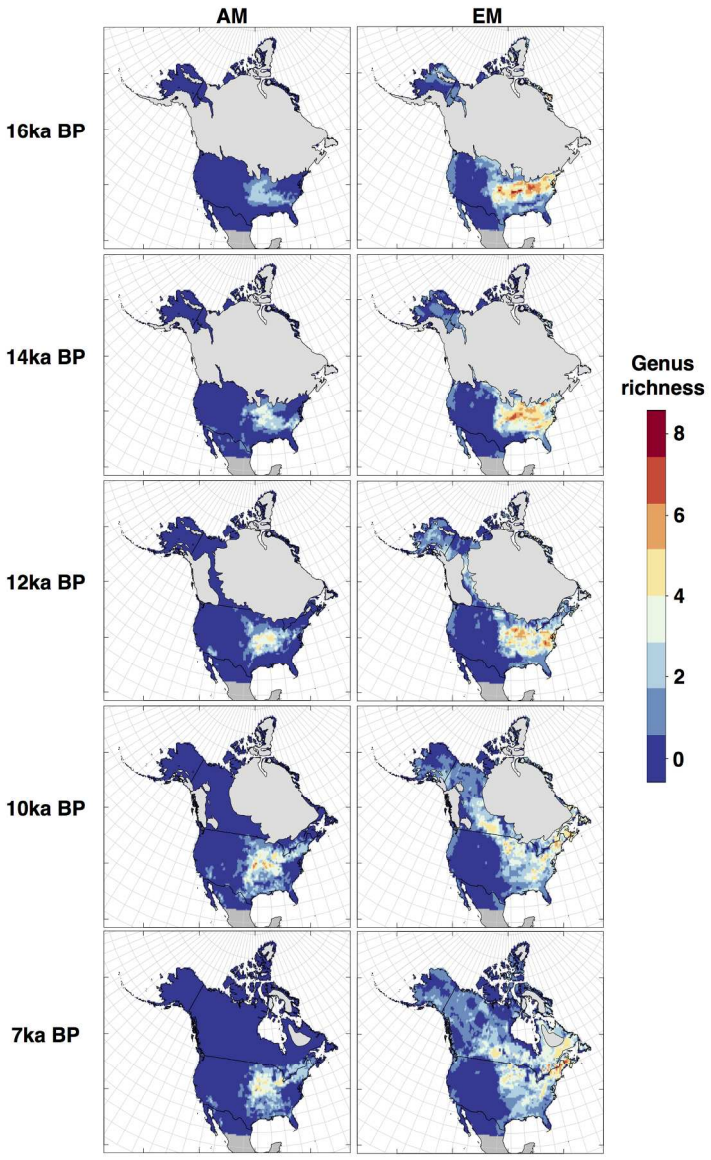

Figure 4. Spatial distribution of the richness of North American tree genera during the last deglaciation based on their mycorrhizal type. Genus richness patterns (colour scale) between 16 and 7 thousand years before present (ka BP) among tree genera, for 13 ectomycorrhizal (EM) (right column) and 10 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).

151x249mm (300 x 300 DPI)