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

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Article type: Full paper
Total word count: **6315**; Introduction: 1392; Methods 1898; Results 897; Discussion: 2021;
Acknowledgements: 107.
Number of Tables: 2
Number of Figures: 3 [Colour figures: 1]
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 as regards 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 below-ground interactions to distribution dynamics remains scarce.

- We evaluated climate velocity and plant traits related to dispersal, environmental tolerance and below-ground symbioses, as potential predictors of the geohistorical rates of expansion and contraction of the core distributions of tree genera between 16 and 7 ka bp.

- 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.
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. postglacial range dynamics; Davis, 1986; Prentice et al., 1991; McLachlan et al., 2005; Feurdean et al., 2013), and underlines 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;
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 the Materials and Methods section) host receptivity can be estimated as the total number of species of mycorrhizal fungi with which a host has been observed to associate. 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: (1) association with multiple host genera (e.g. generalists; Ishida et al., 2007; Peay et al., 2015; Roy-Bolduc et al., 2016), (2) formation of long-lived resistant propagules (Pither & Pickles, 2017) and (3) rapid dispersal capabilities (Peay & 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 FDE₁) 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 FDE₂; Fig. 1b).
Figure 1 Predicted woody plant responses during the last deglaciation in North America (16 000–7000 years before present) 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 ectomycorrhizal (EM) fungi (FDE and EB), and (b) host mycorrhizal type (FDE and EB), on relative velocities of distribution expansion and contraction.

The EB hypothesis predicts that EM hosts should exhibit slower rates of trailing-boundary distribution contraction (prediction EB; Fig. 1b) because: (1) plant–soil feedbacks within established forests are generally more negative among AM host trees than among 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 below-ground antagonists (Bennett et al., 2017), and (2) compared to AM trees, EM trees more consistently benefit from below-ground 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), 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 12 000 to 10 000 years before present (ka bp), Lankau et al. (2015) estimated the contemporary and geohistorical rates of distribution expansion and contraction of North American trees and found evidence consistent with EB, 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 within either the contemporary ($n = 84$ tree species) or 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 nonsignificant or inconsistent among southern and northern distribution margins, and among the geohistorical vs contemporary datasets.

Here we examine the geohistorical, postglacial 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$_2$, that is 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. 1a).
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 16–7 ka bp. 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 12–10 ka bp period (Supporting Information Fig. S1).
3. We test multivariate climate velocity as a predictor of distribution expansion and contraction rates alongside other predictors (see point 4 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$^{-1}$ (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. (2012) and Ordonez & 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 above-ground biomass in North American temperate and boreal forests, including > 80% of the total above-ground 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 (1) the rate of leading (northern) boundary distribution expansion (LBDE) and (2) the rate of trailing (southern) boundary distribution contraction (TBDC; each expressed in m yr⁻¹) for each taxon. These were calculated using the pollen-derived estimates of the geohistorical core distributions of taxa presented by 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, 14–12, 12–10, 10–7, 7–4 and 4–1 ka bp. Here we focus on the four periods spanning 16–7 ka bp, which encompasses the timeframe of almost complete retreat of the Laurentide Ice Sheet (Dyke, 2004), the onset and end of rapid Bølling–Allerød warming (14.7 ka bp) and Younger Dryas cooling (12.9 ka bp) events, and the end of Younger Dryas warming (11.7 ka bp) marking the start of the Holocene interglacial.

Correspondingly, by 7 ka bp 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° longitudinal-bands. We then estimated an overall per-genus average velocity by calculating the weighed mean biotic velocity across time periods, using between one and four time-specific mean velocity values (Table S2). Weights were defined as $1/\text{SE}^2_b t$, where SE_b 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° 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$^{-1}$), 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 $1/\text{SE}^2_c t$, where SE_c represents the standard error of climate velocities for time interval $t$ (Table S2).

Estimating receptivity of EM host genera

We calculated host receptivity as the number of different named EM fungal species that have been documented to associate with a host genus (regardless of geographic location), normalized by the richness of the host genus (see Methods S1), and log$_{10}$-transformed for analyses. We obtained these estimates using the search function provided by the UNITE sequence database (Kõljalg et al., 2013). UNITE is a fungi-specific database that is curated and updated by expert mycologists, and thus it benefits from increased accuracy of sequence assignment to species. We conducted our search between 11 and 15 August 2015 using the ‘Search Pages’ section of the UNITE website, which enables sequence searches through the International Nucleotide Sequence Database Collaboration (Cochrane et al., 2016; www.insdc.org). The INSDC databases are open to all sequence submissions and thus populated with a large number of sequences, although the quality of their assignment is expected to be variable. Our search employed the following protocol: (1) each EM host genus in
Ordonez & Williams (2013) was examined separately by placing [EM host genus] in the Host box, (2) for each EM host in (1) the Organism box was filled with [EM fungal genus] for each of the fungal genera currently known to form EM associations (see data S2 in Tedersoo et al., 2014); the name of each distinct species was recorded, with UNITE expert annotations used preferentially where available, (3) for each EM host in (1) the Taxon name (‘by annotated data in UNITE database’) box was filled with [EM fungal genus] and results recorded as in (2) above. We further ensured that: (1) host genus information was reliable (e.g. Abies not Picea abies; Fagus not Nothofagus; Pinus not Carpinus; Tsuga not Pseudotsuga; a single host identity for any given sequence), (2) only fungal species that have previously been identified as being ectomycorrhizal, or jointly ectomycorrhizal and ericoid mycorrhizal, were counted (see data S2 in Tedersoo et al. (2014), (3) named species were never counted twice for a given host species, (4) ‘uncultured [species name]’ was only counted if [species name] had not already been counted, and was only counted once for a given host species.

We considered the resulting number of distinct EM fungal species names per host genus (referred to as ‘EM fungal species richness’ throughout; Table S1) as a conservative estimate of host receptivity due to (1) the large number of EM fungal sequences that lack metadata on the associated host species (a common issue with sequence submissions to databases in general; Lindahl et al., 2013), and (2) 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 ka bp up to and including the Last Glacial Maximum (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 percentage 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 v.3.1.3 (R Core Team, 2015), and all R code and data associated with this study are available on the Open Science Framework (https://osf.io/vuhe8/). 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 FDE₂ and EB₁) we evaluated mycorrhizal type (binary AM/EM) as our sixth and final potential predictor, and for analyses involving our 13 EM host genera (predictions FDE₁ and EB₂), 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 (≤ |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 (AICc), and ΔAICc, the difference between the given model’s AICc and that of the ‘best’ model, which exhibits the smallest value of AICc. Relative evidence weights (based on
The AICc 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, which is 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 (1) 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, (2) the unconditional standard errors for the coefficient estimates and (3) the 95% confidence interval for the standardized coefficients. In the sensitivity analyses we additionally present 90% confidence intervals (see later). We conducted residual diagnostics on both the full regression models and the ‘AICc-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 100th percentile boundary definition are summarized in Table S6. We also conducted phylogenetically informed regression analyses as described in Methods S1, the results for which are presented in Table S7.

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

<table>
<thead>
<tr>
<th>Prediction</th>
<th>Dataset</th>
<th>Response variable</th>
<th>Predictor</th>
<th>Standardized coefficient (95% confidence limits)</th>
<th>RI</th>
</tr>
</thead>
<tbody>
<tr>
<td>FDE</td>
<td>13 ectomycorrhizal (EM) host genera ($n = 13$)</td>
<td>Leading-boundary distribution expansion rate (m yr⁻¹)</td>
<td>Host receptivity</td>
<td>0.78 (0.378, 1.185)</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed mass</td>
<td>−0.59 (−1.070, −0.117)</td>
<td>0.862</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Cold sensitivity</td>
<td>0.45 (0.036, 0.859)</td>
<td>0.487</td>
</tr>
<tr>
<td>Prediction</td>
<td>Dataset</td>
<td>Response variable</td>
<td>Predictor</td>
<td>Standardized coefficient (95% confidence limits)</td>
<td>RIb</td>
</tr>
<tr>
<td>------------</td>
<td>---------</td>
<td>-------------------</td>
<td>-----------</td>
<td>-----------------------------------------------</td>
<td>-----</td>
</tr>
<tr>
<td>FDE$_2$</td>
<td>13 EM &amp; 10 arbuscular mycorrhizal (AM) host genera ($n = 23$)</td>
<td>Leading-boundary distribution expansion rate (m yr$^{-1}$)</td>
<td>Shade tolerance</td>
<td>$-0.33 (-0.774, 0.119)$</td>
<td>0.226</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Maximum height</td>
<td>$0.31 (-0.163, 0.774)$</td>
<td>0.099</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Climate velocity</td>
<td>$-0.18 (-0.555, 0.195)$</td>
<td>0.055</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mycorrhizal type</td>
<td>Mycorrhizal type</td>
<td>$0.34 (-0.101, 0.780)$</td>
<td>0.473</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Maximum height</td>
<td>$0.26 (-0.221, 0.736)$</td>
<td>0.285</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Cold sensitivity</td>
<td>$-0.13 (-0.618, 0.349)$</td>
<td>0.192</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Climate velocity</td>
<td>$0.11 (-0.364, 0.584)$</td>
<td>0.173</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed mass</td>
<td>$-0.11 (-0.568, 0.346)$</td>
<td>0.172</td>
</tr>
<tr>
<td>Prediction</td>
<td>Dataset</td>
<td>Response variable</td>
<td>Predictor</td>
<td>Standardized coefficient (95% confidence limits)</td>
<td>RIb</td>
</tr>
<tr>
<td>------------</td>
<td>---------</td>
<td>-------------------</td>
<td>-----------</td>
<td>-----------------------------------------------</td>
<td>-----</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Shade tolerance</td>
<td></td>
<td>0.04 (−0.452, 0.525)</td>
<td>0.166</td>
</tr>
</tbody>
</table>

- **a** Bold text indicates predictor variables whose confidence intervals for parameter estimates exclude zero, and RI > 0.60.
- **b** Relative variable importance.

**Sensitivity analyses**

We conducted sensitivity analyses to evaluate the robustness of our results with respect to (1) alternative time periods (for all analyses) and (2) alternative measures of receptivity (for analyses involving the EM host genera, i.e. predictions FDE and EB₂). 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: (1) 14–7 ka bp, (2) 12–7 ka bp, (3) 12–10 ka bp (the period of fastest overall climate and biotic velocities), (4) 16–10 ka bp, (5) for each host genus, the single period in which climate velocity was most rapid; and (6) 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: (1) the total number of EM fungal species documented to have associated with the host genus (‘EMF rich’, log₁₀ transformed for analyses) and (2) 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 and 7 ka bp, 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 125 m yr$^{-1}$, while a similar rate of distribution contraction was observed for *Shepherdia* during the single time period for which pollen data were available (12–10 ka bp).

Figure 2. Average rates of poleward distribution expansion and contraction for 23 North American tree genera during the last deglaciation (16 000–7000 years before present (ka bp)). Rates of leading-boundary expansion vs 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/SE² from each contributing time period (see the Materials and Methods section). Error bars denote ± 1 SE. Genera falling above the dashed 1 : 1 line exhibited overall expansion of latitudinal extent between 16 and 7 ka bp. 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). AM, arbuscular mycorrhizal; EM, ectomycorrhizal.

Facilitated distribution expansion

We found strong support for FDE₁: 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 AICc-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 AICc-units of the AICc-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).

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 ectomycorrhizal (EM) host genera. The model included host receptivity (a) and seed mass (b) as predictors. Open black circles denote individual genus observations, solid black lines indicate partial regression lines and grey shading encompasses the 95% confidence bands.
We found no support for FDE: 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 ± 10.47 m yr⁻¹ for EM plant genera and 46.7 ± 13.16 m yr⁻¹ for AM plant genera; Fig. S4a). Indeed, mycorrhizal type was the sole predictor in the AICc-best model (Table S4), with an effect opposite to that predicted by the FDE. Mycorrhizal type also exhibited a modest effect size (0.34), although the 95% confidence interval for its coefficient overlapped zero (Table 1). The null (no predictor) model was within 2 AICc units of the AICc-best model, and should therefore be considered the most parsimonious, plausible model, given the data.

Environmental buffering

We found limited support for EB: mycorrhizal type was included in the AICc-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 > 0.4 (Table 2).

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

<table>
<thead>
<tr>
<th>Prediction</th>
<th>Dataset</th>
<th>Response variable</th>
<th>Predictor</th>
<th>Standardized coefficient (95% confidence limits)</th>
<th>RIb</th>
</tr>
</thead>
<tbody>
<tr>
<td>EB₁</td>
<td></td>
<td>Trailing-boundary distribution</td>
<td>Climate velocity</td>
<td>0.46 (0.027, 0.893)</td>
<td>0.753</td>
</tr>
<tr>
<td>Prediction</td>
<td>Dataset</td>
<td>Response variable</td>
<td>Predictora</td>
<td>Standardized coefficient (95% confidence limits)</td>
<td>Rb</td>
</tr>
<tr>
<td>------------</td>
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<td>--------------------------------------------------</td>
<td>----</td>
</tr>
<tr>
<td></td>
<td></td>
<td>contraction rate</td>
<td>Cold</td>
<td>-0.37 (-0.803, 0.060)</td>
<td>0.524</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(m yr⁻¹)</td>
<td>sensitivity</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mycorrhizal</td>
<td>-0.33 (-0.747, 0.094)</td>
<td>0.448</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>type</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13 ectomycorrhizal (EM) &amp;</td>
<td>13 EM host genera (n = 13)</td>
<td>Maximum contraction rate</td>
<td>Host</td>
<td>0.38 (-0.234, 0.996)</td>
<td>0.249</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>height</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed mass</td>
<td>-0.15 (-0.653, 0.348)</td>
<td>0.185</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Shade</td>
<td>0.07 (-0.394, 0.525)</td>
<td>0.137</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>tolerance</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed mass</td>
<td>-0.40 (-1.027, 0.237)</td>
<td>0.251</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Host</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>receptivity</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Climate</td>
<td>0.37 (-0.263, 1.005)</td>
<td>0.225</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>velocity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prediction</td>
<td>Dataset</td>
<td>Response variable</td>
<td>Predictora</td>
<td>Standardized coefficient (95% confidence limits)</td>
<td>RIb</td>
</tr>
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<td>-------------------------------------------------</td>
<td>-----</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Shade tolerance</td>
<td>Shade</td>
<td>0.27 (−0.370, 0.918)</td>
<td>0.144</td>
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<tr>
<td></td>
<td></td>
<td>Cold sensitivity</td>
<td>Cold</td>
<td>−0.09 (−0.793, 0.623)</td>
<td>0.097</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maximum height</td>
<td>Maximum</td>
<td>0.09 (−0.591, 0.776)</td>
<td>0.086</td>
</tr>
</tbody>
</table>

- a Bold text indicates predictor variables whose confidence intervals for parameter estimates exclude zero, and RI > 0.60.
- b Relative variable importance.

We found no support for EB₂: 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 Figs 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:

1. Support for host receptivity as a predictor of distribution expansion rates among EM host genera (FDE₁) 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).

2. Support for host receptivity as a predictor of distribution expansion rates among EM host genera (FDE1) is strongest when analyzing time periods associated with maximum sample size (i.e. 13 EM host genera vs 11 genera; Fig. S5).

3. Seed mass has a consistently negative effect on distribution expansion rates among EM host genera (FDE1) 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 analyzed (Fig. S5).

4. 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 FDE2: 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.

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

6. Mycorrhizal type has a consistently negative effect on distribution contraction rates among EM and AM host genera (EB1), which reflects slower contraction rates among EM hosts compared to AM hosts, but the strength of the effect varies among time period analyzed (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 postglacial (16–7 ka bp) distribution expansion and contraction rates among woody North American plant genera. We tested hypotheses that propose roles for biotic interactions, specifically below-ground 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 (1) interactions with mycorrhizal fungi and seed mass moderated leading-boundary distribution responses to geohistorical climate change, and (2) climate velocity had a detectable influence on trailing-boundary contraction rates only, when analyzing 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 & Horton, 2009), and the potential for EM fungi to assist in plant establishment and survival outside of their current range (e.g. Reithmeier & Kernaghan, 2013; Nuñez & Dickie, 2014).

Consistent with the findings of Lankau et al. (2015), we found no support for prediction FDE$_2$, that is 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. By contrast, AM fungi display low diversity (Davison et al., 2015) and lower root colonization (Soudzilovskaia et al., 2015) in such ecosystems. Second, nitrogen limitation increases with latitude (Gill & Finzi, 2016), being particularly acute in postglacial 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 c. 190 to 265 ppmv between 18 and 7 ka bp (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 favorable.

**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 16 000 and 7000 years before present (ka bp) among tree genera for 13 ectomycorrhizal (EM) (right panels) and 10 arbuscular mycorrhizal (AM) (left panels) host genera. Genus richness in each grid cell was calculated by summing the number of overlapping core distributions. Ice sheet extents (grey) are 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 the Materials and Methods section).
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 & Horton, 2009; Lankau et al., 2015). However, counter to Lankau et al. (2015), our tests of EB1 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 AICc-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 & Horton, 2009; Simard et al., 2012). Hence, in EB2, 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), and 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, 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 & 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 7 ka bp (see their fig. 4). This can be attributed to methodological differences: Ordonez & 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 Fig. S9, climate velocity is a significant predictor of biotic velocity in only one of the four time-periods: 12–10 ka bp. Our sensitivity analyses are largely consistent with this finding (Figs S5–S8): if we focus solely on the 12–10 ka bp period, climate velocity emerges as the sole significant predictor of (1) leading-boundary distribution expansion rates among AM and EM taxa (prediction FDE₂), (2) trailing-boundary distribution contraction among AM and EM taxa (prediction EB₁), and (3) trailing-boundary distribution contraction among EM taxa (EB₂). The only prediction for which climate velocity does not gain support is FDE₁.

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). First, maximum rates of distribution expansion and contraction occurred in different time periods for different plant genera (Fig. S1). For instance, nine
of 23 plant genera exhibited maximum rates of distribution expansion outside of the 12–10 ka bp period, and maximum rates of distribution contraction were distributed across all four time-periods (Fig. S1). Second, despite the 12–10 ka bp period exhibiting the most rapid overall change in climate (Ordonez & Williams, 2013), maximum rates of climate velocity occurred in different time periods for different genera (Fig. S1). For example, six of 23 plant genera exhibited maximum rates of leading-boundary climate velocity outside the 12–10 ka bp period, and 10 of 23 genera exhibited maximum rates of trailing-boundary climate velocity outside the 12–10 ka bp period (Fig. S1). Lastly, the number of time periods for which velocity estimates could be calculated varied among plant genera (Table S2). By calculating for each genus a weighted average of velocities across all time periods, we maximized data use and thus statistical power, while simultaneously accounting for the varied precision of estimates among genera. For example, focusing solely on the 12–10 ka bp period would reduce the number of tree genera from 23 to 18. In our sensitivity analyses we explored alternative combinations of time periods, but we place greatest credence in our main analyses for the reasons outlined above.

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

For decades, ecologists have debated the relative importance of climatic and biotic controls on species distributions and the timescales at which plant distributions are in dynamic equilibrium with climate (Davis, 1986; Prentice et al., 1991). By analysing the roles of climate and biotic factors simultaneously, we found that the importance of
climate as a driver of distributional changes was context-dependent among North American tree genera. Climate velocity was the primary determinant of postglacial distribution contraction rates at trailing boundaries, whereas biotic interactions, specifically mycorrhizal associations, and seed mass were the primary determinants of distribution expansion rates at leading boundaries. Thus, our findings indicate that inter-taxon variation in climatic sensitivity, dispersal-related plant traits, and biotic interactions – particularly mycorrhizal symbioses – acted together to modulate plant responses to the rapid climate changes accompanying the last deglaciation.

**Acknowledgements**

We thank M. A. Gorzelak, M. M. Hart, R. W. Jackson, M. D. Jones, J. Klironomos, N. G. Swenson and M. Zobel for their comments on earlier versions of the manuscript, and our colleagues at UBC and the University of Reading for discussions of the concepts presented here. N. G. Swenson provided guidance on coding for the phylogenetic analyses. Angela Moles kindly provided seed mass and plant height data. J.P. and S.W.S. are funded by the Discovery Grants program of the Natural Sciences and Engineering Research Council, Canada. B.J.P. was initially funded by a Discovery Grant held by S.W.S. J.W.W. was supported by the National Science Foundation (DEB-1353896, DEB-1257508). A.O. was initially supported by the European Research Council (ERC-2012-StG-310886-HISTFUNC) held by Jens-Christian Svenning. The authors declare no conflicts of interest.

**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. analyzed 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 all other analyses; A.O. produced Fig. 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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