

RESEARCH ARTICLE

Getting to the root of the matter: landscape implications of plant-fungal interactions for tree migration in Alaska

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Abstract

Context Forecasting the expansion of forest into Alaska tundra is critical to predicting regional ecosystem services, including climate feedbacks such as carbon storage. Controls over seedling establishment govern forest development and migration potential. Ectomycorrhizal fungi (EMF), obligate symbionts of all Alaskan tree species, are particularly important to seedling establishment, yet their significance to landscape vegetation change is largely unknown.

Objective We used ALFRESCO, a landscape model of wildfire and vegetation dynamics, to explore

whether EMF inoculum potential influences patterns of tundra afforestation and associated flammability.

Methods Using two downscaled CMIP3 general circulation models (ECHAM5 and CCCMA) and a mid-range emissions scenario (A1B) at a 1 km² resolution, we compared simulated tundra afforestation rates and flammability from four parameterizations of EMF effects on seedling establishment and growth from 2000 to 2100.

Results Modeling predicted an 8.8–18.2 % increase in forest cover from 2000 to 2100. Simulations that explicitly represented landscape variability in EMF inoculum potential showed a reduced percent change afforestation of up to a 2.8 % due to low inoculum potential limiting seedling growth. This reduction limited fuel availability and thus, cumulative area burned. Regardless of inclusion of EMF effects in simulations, landscape flammability was lower for simulations driven by the wetter and cooler CCCMA model than the warmer and drier ECHAM5 model, while tundra afforestation was greater.

Conclusions Results suggest abiotic factors are the primary driver of tree migration. Simulations including EMF effects, a biotic factor, yielded more conservative estimates of land cover change across Alaska that better-matched empirical estimates from the previous century.

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Introduction

Soil microbes are critical to plant establishment, survival, and growth (Horton and van der Heijden 2008; van der Heijden and Horton 2009; Bever et al. 2010), but rarely has the link between plant-fungal interactions and landscape vegetation change been explored. This is likely due to issues of scale, where microbial composition can vary on the micro-scale (Taylor et al. 2010) and vegetation composition can vary on the landscape or regional scale (Turner 1989). For example, controls over seedling establishment at and beyond current treeline govern both stand development at the range limit of the boreal forest and the potential for migration (Hobbie and Chapin 1998; Harsch and Bader 2011). However, the importance of biotic factors, such as the effect of mycobionts on tree seedling establishment, in understanding treeline dynamics has been largely overlooked. Regional changes in the cover of boreal forest and tundra vegetation can influence the climate system through changes in albedo and carbon storage (McGuire et al. 2001; Chapin et al. 2005; Euskirchen et al. 2009a). Therefore, understanding the ecological factors that influence the position of arctic treeline, the boundary between the boreal forest and tundra, has strong implications for accurately forecasting changes in these ecosystem services.

Ectomycorrhizal fungi (EMF) are obligate symbionts of all boreal tree species in Alaska. These mycobionts are physiologically important to plant performance because they are the conduits of soil resources for host plants, especially during the vulnerable seedling establishment stage (Horton and van der Heijden 2008; Smith and Read 2008). Fungal inoculum is generally not considered limited in soils (but see Peay et al. 2010a). However, at Alaskan treeline low availability of boreal tree compatible fungal inoculum could limit seedling establishment (Hewitt 2014). The transition from boreal forest to tundra across the ecotone corresponds with a shift from dominance of EMF host plants, such as aspen (*Populus tremuloides*), spruce (*Picea* sp.), and birch (*Betula neoalaskana*) trees, to ERM (ericoid mycorrhizal) host plants, such as blueberry and cranberry (*Vaccinium* species) dwarf shrubs, and non-mycorrhizal or AM (arbuscular mycorrhizal) graminoid host plants, with varying densities of EMF dwarf shrubs, such as willow and birch (Read 1991; Gardes and

Dahlberg 1996). EMF composition and abundance has been related to successful seedling establishment both within and beyond the current range limit of host plants in other ecosystems (Perry et al. 1982, 1989; Horton et al. 1999; Nara 2006; Nunez et al. 2009). Across biomes, EMF richness and colonization of seedlings declines with increased distance from forest edge for both native and invasive tree species across fine spatial scales (<1000 m) (Dickie and Reich 2005; Nunez et al. 2009; Peay et al. 2010b, 2012). These isolation-effects on fungal communities persist through stand development (Peay et al. 2010b), which in turn could influence growth of early life-stages of boreal trees that establish beyond current treeline. However, as far as we know, a scaling exercise linking biogeographic patterns of mycobionts to root tips, seedling performance, and forecasts of landscape vegetation transitions has not been accomplished until this study.

Projected changes in treeline position are primarily based on the assumption that high latitudinal and altitudinal forests will respond positively to increases in growing season and air temperatures (Harsch et al. 2009). Changes in fire regime in the boreal forest and tundra biomes are also directly related to a warming climate (Hu et al. 2010; Kelly et al. 2013) and may be a greater driver of species migrations than temperature per se (Dale et al. 2001). In Alaska and western Yukon Territory, fire regime is tightly coupled with tree seedling recruitment, forest species composition, and the northward migration of lodgepole pine (Johnstone and Chapin 2003, 2006; Johnstone et al. 2010). This has led to the hypothesis that fire will likely facilitate afforestation of tundra by killing extant plant competitors and opening up novel, high-quality microsites for establishment (Landhausser and Wein 1993). In contrast, mycobiont communities are often altered post-fire when host plants are killed or there is severe combustion of the upper soil horizons where they are abundant (Dahlberg 2002; Cairney and Bastias 2007; Hewitt et al. 2013; Hewitt 2014). These effects of fire severity on fungal composition can in turn reduce seedling performance (Hewitt 2014).

To explore the impacts of EMF on tree migration in the tundra zone of Alaska we used a landscape model of vegetation dynamics and fire activity. We performed model simulation experiments using the landscape model ALaska FRame-based EcoSystem COde (ALFRESCO) (Rupp et al. 2000, 2001) to

quantify the effects of variability in EMF inoculum potential on state transitions from tundra to forest with climate warming and fire activity. Model simulation results contribute to understanding how mycorrhizal interactions and variability in landscape inoculum potential may influence vegetation transitions and the scope of potential changes in landscape vegetation patterns, landscape flammability, and associated ecosystem services with climate warming at high latitudes.

Methods

Model overview

ALFRESCO is a frame-based spatially explicit state-and-transition model (Starfield et al. 1993) that simulates vegetation succession and fire occurrence across Alaska at a 1 km² resolution and annual time step. The model was originally developed to simulate vegetation state transitions with changes in climate (temperature and precipitation) and fire disturbance (Rupp et al. 2000). The model assumes that vegetation responds primarily to transient changes in climate and fire regime (Starfield and Chapin 1996; Fig. 1). Previous renditions of the model quantified spruce migration in response to changes in climate and fire (Breen et al. 2013; Rupp et al. 2001). Here we developed a mycorrhizal-effects submodel that modifies seedling establishment and growth in relation to transient changes in climate and fire activity to assess the landscape implications of plant-fungal interactions on tree migration.

ALFRESCO simulates wildfire as a stochastic process. It uses a cellular automaton approach for ignition of a 1 km² cell in the model and spread to the surrounding cells. Ignition and spread are determined by the comparison of a randomly generated number and the flammability coefficient of a cell. Flammability is determined by vegetation classification of a cell, age of a cell, and climate parameters. Climate-effects on flammability are a function of weighted monthly mean temperatures and precipitation for the fire season derived from a regression model, for the months of March–September (Rupp et al. 2015).

ALFRESCO simulates vegetation succession and state transitions as deterministic processes. State transitions between vegetation classes are based on

rules for each vegetation type. The initial land cover dataset used for ALFRESCO simulations is a modified version from the North American Land Change Monitoring System from 2005, with aggregated vegetation classes. For earlier versions of ALFRESCO, successional dynamics were parameterized for five major subarctic, arctic, and boreal ecosystem types: upland tundra, black spruce forest, white spruce forest, deciduous forest, and grassland-steppe. The most recent version of the model instituted successional dynamics for distinct shrub and graminoid tundra vegetation classes and refined the migration dynamics by which the graminoid and shrub tundra vegetation classes transition to white spruce forest (Breen et al. 2013). Successional dynamics for shrub and graminoid tundra are probabilistic and influenced by fire history and climate (Breen et al. 2013; Rupp et al. 2015). Burn severity is also a factor in the model, influencing colonization and survival of white spruce in tundra vegetation classes. There are five classes of fire severity in the model: unburned (class 0), low burn severity (class 1), moderate burn severity (class 2), high crown severity with low surface severity (class 3), and high crown severity with high surface severity (class 4). Low, moderate, and high crown severity with low surface severity result in self-replacing successional trajectories for graminoid and shrub tundra; whereas, high crown severity and surface severity fires in shrub tundra can result in the transition from shrub to graminoid tundra (Breen et al. 2013; Rupp et al. 2015). The likelihood of a high crown and surface severity fire occurring decreases from spruce forest to tundra vegetation classes and is discussed further in Breen et al. (2013). Wetland tundra does not burn and is a static vegetation class.

Successional dynamics for the transition from shrub or graminoid tundra to white spruce forest are influenced by fire history and climate (Breen et al. 2013; Rupp et al. 2015). As an overview, a transition to white spruce forest by a 1 km² tundra cell occurs from succession or colonization and infilling (Fig. 2). Colonization of tundra by spruce is a two-step process consisting of seed dispersal and seedling establishment. These processes are influenced by climate and fire history, which affect seedling establishment and growth conditions. Within a given time step, if a fire occurs in a tundra cell trees established in that cell survive based on fire burn severity: 100 % survival (class 1), 50 % survival (classes 2 and 3) and 0 %

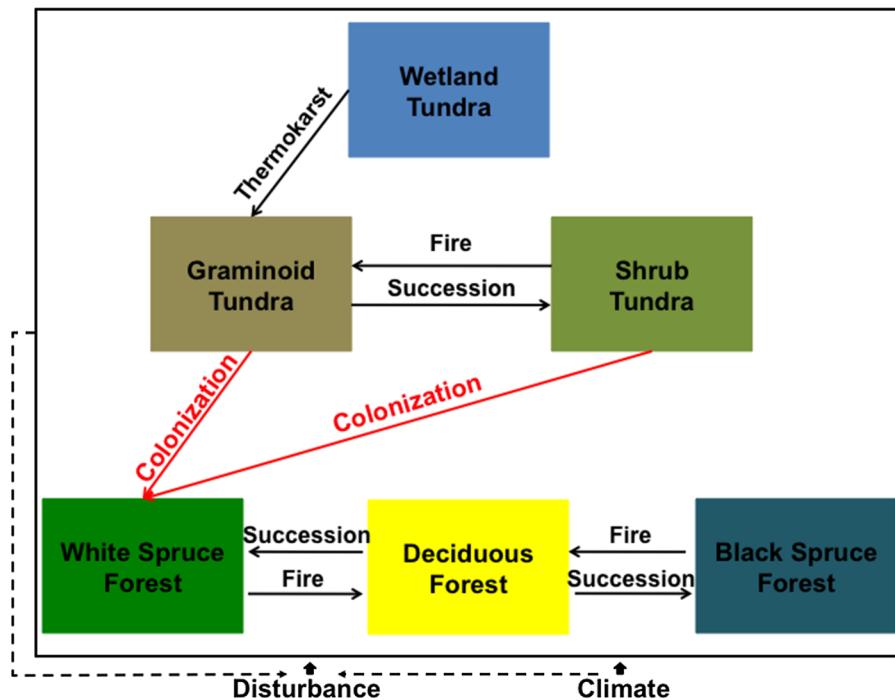


Fig. 1 Conceptual diagram of the processes affecting state transitions in ALFRESCO 2.0. Arrows indicate causal relationships (Breen et al. 2013; Gray et al. 2013; Rupp et al. 2015). We

focus on the effects of EMF inoculum potential on successful colonization of tundra by white spruce seedlings as indicated by red arrows

survival (class 4). The next step in the model is to check whether there is a white spruce forest seed source within an adjacent cell resulting in a 1 km^2 neighborhood (Rupp et al. 2015). If a spruce seed source is present, the model then checks whether conditions are favorable for germination and establishment that are modeled as a single process. Germination and establishment, however, cannot occur independently of seed dispersal so we do not account for a seed bank in the model. We assume white spruce seed viability at its latitudinal and altitudinal limits is limited to the year of dispersal. Climate is suitable for establishment and growth (the next step) when the Summer Warmth Index, the sum of mean monthly temperatures $>0^\circ\text{C}$, is $>31^\circ\text{C}$, and the ten-year moving-average of July temperature is $>10^\circ\text{C}$. If conditions continue to be favorable for growth, then basal area (BA) increases in the cell with time. The basal area growth function follows a normal distribution between 10 and 20 $^\circ\text{C}$, centered on 15 $^\circ\text{C}$, for July mean temperature with a maximum accrual of 2 mm per year. Mean July temperatures <10 and $>20^\circ\text{C}$ result in no growth

accrual, as these July isotherms bound the northern and southern limits of the boreal forest in North America (Larsen 1980). When the basal area of a cell reaches the reproductive threshold [BA = 10 meters $^2/\text{hectare}$ (m^2/ha)], it may act as a seed source for nearby cells. When spruce trees become abundant in the cell and reach a basal area threshold (BA = 20 m^2/ha), the cell transitions to the white spruce vegetation class. In addition to climate, fire severity influences the basal area accumulation in a cell. If a moderate or severe fire does occur, then the spruce basal area of the tundra cell is reduced by 50 % (class 2, 3) or 100 % (class 4) for the shrub or graminoid tundra vegetation classes. In this paper we present our findings from tree migration simulations that incorporate modifications to the tundra-to-spruce state transition to include the effects of mycorrhizal fungi on establishment and growth (Fig. 2) and fire-effects on EMF inoculum potential and plant-fungal interactions detailed below (Fig. 3). This is the first time that mycorrhizal effects (Fig. 3) have been incorporated into ALFRESCO simulations of tundra afforestation (Fig. 2).

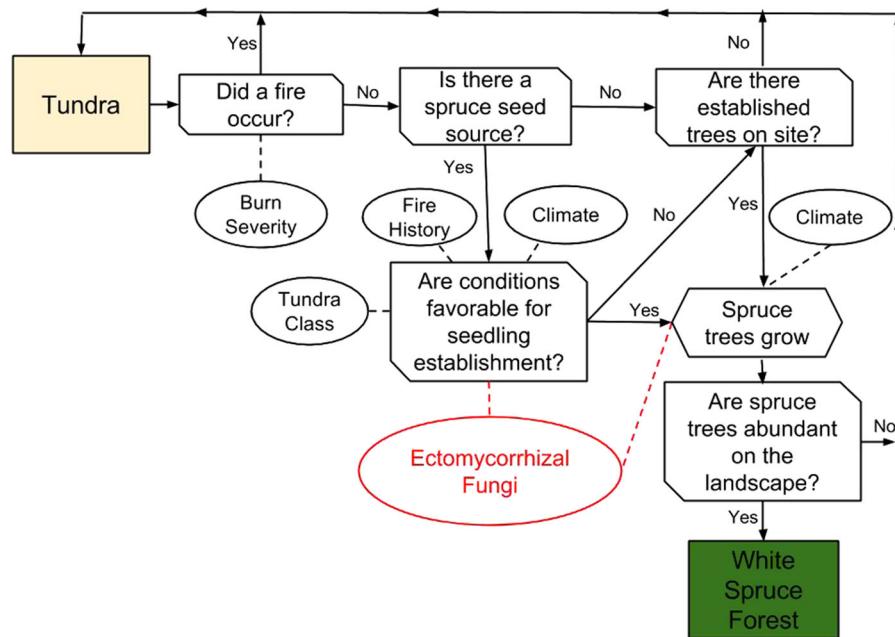


Fig. 2 Conceptual diagram of the processes affecting state transitions from tundra to spruce in ALFRESCO 2.0. Arrows indicate the progression from one step in the transition process to the next step. The pathway to the right represents infilling of a 1 km² cell as long as there are spruce trees in the cell and conditions are favorable. This is indicated by the different

hexagonal polygon. Figure modified from work by the ALFRESCO 2.0 Team (Breen et al. 2013; Gray et al. 2013) to emphasize (in red) the focus of this modeling effort, mycorrhizal effects on tree migration. Red indicates EMF (ectomycorrhizal fungi) inoculum potential modifiers to seedling establishment and growth

Mycorrhizal submodel parameterization

Previous field and greenhouse studies in Alaska have shown that fire alters fungal composition (Hewitt et al. 2013; Hewitt 2014), and post-fire fungal composition influences seedling performance for boreal tree species expected to migrate into tundra with a warming climate (Hewitt 2014). Studies from other biomes show that limited availability of EMF, i.e. lower EMF inoculum potential, reduced seedling establishment, growth, and performance beyond the forest edge (Perry et al. 1982, 1987, 1989; Dickie and Reich 2005; Nunez et al. 2009). Collectively, this suggests that seedling establishment, growth, and migration potential may be limited at and beyond treeline where pre-fire EMF inoculum potentials may be low. In addition, increased wildfire occurrence and severity may exacerbate these limiting effects of plant-fungal interactions on tundra afforestation. We and others have also observed that boreal seedlings can share compatible fungi with EMF tundra shrubs (Reithmeier and Kernaghan 2013; Hewitt 2014).

These findings together suggest that seedling establishment and growth, the most critical step in forest migration, at and beyond current treeline may be constrained by reduced EMF availability due to variability in EMF host-plant densities across different vegetation classes or wildfire effects.

To investigate the regional implications of landscape variability in EMF to land cover change we developed four model parameterizations that represent variation in EMF landscape inoculum potential and its effects on seedling establishment phase and/or early growth (see Table 1 for description of model parameterization naming structure). For one of the model parameterizations seedling establishment and growth were not constrained by EMF (unconstrained inoculum, UI). In the UI parameterization every forest and tundra cell in the model was considered to have an optimum inoculum potential and seedling establishment and growth was unaffected by EMF. In contrast to the UI parameterization, three EMF parameterizations represented variability in inoculum potential across the model domain by deriving EMF inoculum

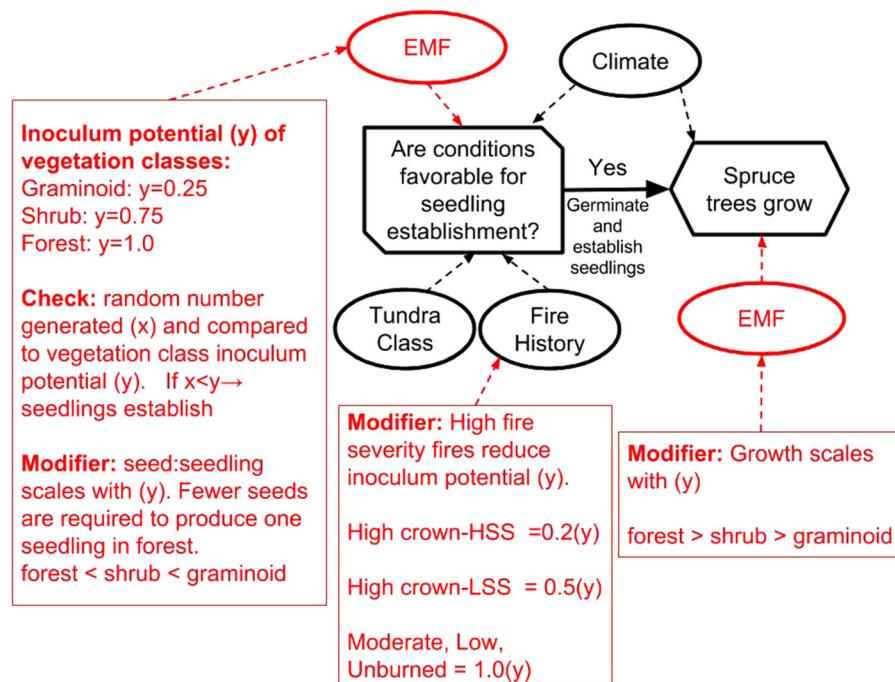


Fig. 3 Conceptual diagram of the influence of mycorrhizal fungi on tree seedling establishment and growth. Red indicates EMF (ectomycorrhizal fungi) inoculum potential modifiers to seedling establishment and growth. The arrows show the progression from addressing ecological factors for one life history stage to the next. Fire-severity classes are as follows: 0 = unburned, 1 = low burn severity, 2 = moderate burn

severity, 3 = high crown severity with low surface severity (LSS), and 4 = high crown severity with high surface severity (HSS). Tundra classes are based on a highly modified output originating from the North American Land Change Monitoring System. We assigned inoculum potential scores to the tundra classes based on shrub densities reported by Viereck et al. (1992)

Table 1 Parameterizations of seedling establishment and growth with variation in the importance of limited EMF inoculum potential on seedling performance

Abbreviated name	Name	Description
UI	Unconstrained inoculum potential	EMF inoculum potential does not vary across the landscape and is not correlated with seedling establishment and growth
CI-E	Constrained inoculum potential—establishment	EMF inoculum potential varies across the landscape and the inoculum potential is correlated with successful seedling establishment
CI-E + STG	Constrained inoculum potential—establishment and short-term seedling growth	EMF inoculum potential varies across the landscape and the inoculum potential is correlated with successful seedling establishment and short-term growth of seedlings. We define short term growth as the accrual of seedling biomass in a 1 km^2 cell up until the cell has reached a basal area of $1 \text{ m}^2/\text{ha}$
CI-E + LTG	Constrained inoculum potential—establishment and long-term seedling growth	EMF inoculum potential varies across the landscape and the inoculum potential is correlated with successful seedling establishment and long-term growth of seedlings. We define long-term growth of seedlings as the accrual of seedling biomass in a 1 km^2 cell up until the cell has reached a basal area of $5 \text{ m}^2/\text{ha}$

potentials from the pre-fire vegetation class of each cell (e.g. highest EMF availability in forest, lowest in graminoid tundra) and the fire history of each cell

(Fig. 3; Table 2). For these three EMF parameterizations, successional dynamics were constrained when EMF availability, inoculum potential, was limited

(Tables 1, 2; Fig. 3). To elaborate, the shrub and graminoid vegetation classifications in ALFRESCO correspond to vegetation communities that differ in their densities of plant functional types (tall and dwarf shrubs, graminoids, and forbs) (Table 2). For example, shrub tundra has a dominant shrub canopy with less abundant forbs and graminoids, whereas graminoid tundra has dominant graminoids and lower densities of shrubs and forbs. EMF inoculum potentials for each vegetation class were derived from EMF shrub densities described in the Viereck et al. (1992) vegetation classification (see descriptions under II. C. 2 for shrub and graminoid tundra communities). To illustrate, Viereck et al. (1992) described shrub tundra as having up to 75 % cover by EMF shrubs (mainly willows and dwarf birch). Because our previous empirical work showed that EMF shrubs in Alaska tundra host EMF compatible with boreal trees (Hewitt 2014) our EMF inoculum potential for shrub tundra vegetation class is 75 % of the inoculum value for white spruce forest vegetation class, which we considered to have full inoculum potential. The percent cover of shrub taxa capable of supporting EMF compatible with boreal tree seedlings is reduced threefold in graminoid tundra compared to shrub tundra (Fig. 3; Table 2). As such, the white spruce forest and tundra classes in simulations of treeline dynamics are viewed as having a gradient of host plant densities that support EMF compatible with boreal tree seedlings (white spruce > shrub tundra > graminoid tundra inoculum potential). The assignment of these inoculum potentials includes several assumptions about the mycobionts: (1) the majority of EMF spores do not disperse far from intact forest (Peay et al. 2010b, 2012), and as such we

consider inoculum potential within a 1 km² cell as independent of vegetation class and fire history of neighboring cells, (2) EMF are generalists and EMF taxa are compatible across multiple boreal tree and tundra shrub taxa (Bent et al. 2011; Reithmeier and Kernaghan 2013; Hewitt 2014), and (3) EMF promote seedling performance (Hoeksema et al. 2010). These broad assumptions are supported by our local findings from empirical field and greenhouse studies after fire in Alaska tundra: (1) post-fire tundra soils were not strong sources of EMF inoculum beyond current treeline (Hewitt 2014), (2) some EMF taxa can survive fire on resprouting tundra shrub vegetation (Hewitt et al. 2013) and colonize establishing boreal tree seedlings (Hewitt 2014), and (3) post-fire mycobionts are correlated with seedling nutrient status and biomass (Hewitt 2014).

We parameterized the effects of fire severity on EMF inoculum potential as part of the fire history modifier to seedling establishment. Of the five burn classes described above, we expect high severity fires, classes three and four, to have a strong effect on inoculum potential. Fire-severity effects on mycobionts are related to the degree to which host plants are killed and the amount of soil combusted (Dahlberg 2002). The high severity fire classes with both low and high surface severity reduce inoculum potential through combustion of soil and killing or reduction of EMF host plant densities. This is in contrast to moderate and low severity fires, which we did not parameterize to have reduced post-fire EMF inoculum potentials. Despite a modest reduction in host plant cover with moderate severity fires (e.g. reduced basal area of spruce trees), there is low surface combustion and no effect on tundra successional dynamics (Breen

Table 2 Derived inoculum scores from vegetation classifications

Model vegetation class	Dominant plant functional types	EMF inoculum potential
Graminoid tundra	Trees absent or sparse; dominant non-mycorrhizal or AM graminoids; lower densities of EMF and ERM shrubs, up to 25 %; moss mat	0.25
Shrub tundra	Trees absent or sparse; dominant tall and dwarf shrubs, up to 75 % (both EMF and ERM hosts); lower densities of non-mycorrhizal or AM graminoids; sparse herbs	0.75
White spruce forest	White spruce overstory; EMF and ERM shrub understory; feather moss mat	1.00

Inoculum potentials reflect dominance of cover by EMF hosts that support EMF compatible with boreal tree seedlings
AM arbuscular mycorrhizal fungi, EMF ectomycorrhizal fungi, ERM ericoid mycorrhizal fungi

et al. 2013; Rupp et al. 2015) and thus we extrapolated that reduction of inoculum potential is minimal. Low-severity fires do not reduce spruce basal area or result in tundra vegetation transitions and do not have surface soil burning (Breen et al. 2013; Rupp et al. 2015). From our previous observations we assume that low or no surface combustion and high potential of resprouting host plants (e.g. after low and moderate severity burning) (Hollingsworth et al. 2013) after fire will maintain pre-fire inoculum potentials (Hewitt et al. 2013; Hewitt 2014).

Three of four EMF parameterizations represent seedling performance constrained by variability in EMF across the model domain. These three EMF parameterizations differ by whether EMF inoculum potential affects seedling establishment and/or seedling growth (Table 1). We limited mycorrhizal effects to seedling stages. In the simulations seedling growth is represented by basal area accrual. We used basal area as a proxy for time and stand development based on site-index curves for white spruce in interior Alaska [i.e. 1 km² cell with BA = 1 m²/ha has small, very young seedlings and 1 < BA < 5 m²/ha has small, young seedlings (Yarie and Cleve 1983)]. The three different EMF parameterizations represent different consequences for seedling performance when EMF inoculum potential is reduced: (1) constraint on seedling establishment (CI-E), (2) constraint on seedling establishment and short-term growth (CI-E + STG) for tundra cells with up to an accrued spruce basal area of 1 m²/ha, and (3) constraint on seedling establishment and long-term seedling growth (CI-E + LTG) for tundra cells with up to a basal area of 5 m²/ha. The quantitative constraints of the EMF parameterizations and establishment and growth are based on the pre-fire inoculum potentials derived from vegetation classes (white spruce = 1.0; shrub tundra = 0.75; graminoid tundra = 0.25 inoculum potential) and fire-severity effects on inoculum potential (high crown severity with high surface severity (class 4) = 0.2; high crown severity with low surface severity (class 3) = 0.5; unburned (class 0), low burn severity (class 1), moderate burn severity (class 2) = 1.0 inoculum potential) described above (Fig. 3). The seedling age and size at which EMF inoculum potential most acutely affects seedling performance is ambiguous in the empirical literature. For example, the literature shows that EMF limitation can hinder seedling establishment (Perry et al. 1982,

1989; Nunez et al. 2009), but if a seedling does establish and has grown beyond sapling phase then it is most likely that growth is not hindered at all by EMF (Collier and Bidartondo 2009). As such a comparison of the outputs of simulations for forest migration with these four EMF parameterizations can serve as a sensitivity analysis of EMF effects on forest migration. The comparison of these simulations represents the full range of possible EMF-effects on stand development from earliest effects (CI-E) to the latest effects (CI-E + LTG) based on what is known from the empirical literature.

Climate and study domain

Simulations of forest migration and landscape flammability across Alaska were driven by two downscaled CMIP3 General Circulation Models (ECHAM5 and CCCMA) that represent the best performing models for the Alaska region (Rupp et al. 2015) and a mid-range emissions scenario (A1B) at a 1 km² resolution (Rupp et al. 2015). Climate forcing from downscaled ECHAM5 outputs represents a warm and dry scenario and the CCCMA represents a scenario with climate conditions warmer than the present but cooler and wetter than ECHAM5.

In Alaska, the latitudinal treeline is the limit of white spruce in the southern foothills of the Brooks Range and Western Alaska. The latitudinal forest-tundra ecotone is gradual, with spruce stand density decreasing over a broad area, and in some localities abrupt where physiographic features limit white spruce growth (Viereck 1979). Our modeling experiments focused on spruce expansion in the tundra zone of Alaska (Fig. 4). The tundra zone in the model includes arctic and subarctic lowland and arctic-alpine tundra from the Brooks Range, North Slope, and western regions of Alaska. The treeline dynamics include two tundra classes (shrub and graminoid) and one forest type (white spruce). We compared land cover estimates from the beginning of the century to those in 2100 (2000–2100). Our general approach was to compare the outputs from model simulations where three different EMF parameterizations have been implemented (CI-E, CI-E + STG, CI-E + LTG) to those that did not include EMF-effects on seedling establishment and stand development (UI) for both GCMs.



Fig. 4 Map of the model domain used in ALFRESCO simulations. We focus our analysis on forest expansion in the tundra zone, which includes arctic and subarctic lowland and alpine tundra

Calibration

For vegetation transitions from tundra to spruce forest model calibration was completed by comparing model simulation results (1900–2005) to empirical studies that estimated changes in vegetation cover. Model simulation results obtained during the calibration phase were a good fit for the historic period (Rupp et al. 2015). Our target transitions were an increase in white spruce forest cover of 5 % (Chapin et al. 2005; Hinzman et al. 2005) and 30 % loss in graminoid tundra due to shrub encroachment (Sturm et al. 2001; Tape et al. 2006; Macias Fauria and Johnson 2008) in the last century. These empirical observations were our calibration transition targets for the historical phase for all model parameterizations (the unconstrained parameterization and three EMF parameterizations) because our simulations should reflect forest encroachment that has been observed in the field where we assume a suite of abiotic and biotic factors, including mycorrhizal fungi, influence successful seedling establishment and growth.

Fire module calibration was accomplished using historical fire activity records across the simulation domain (Rupp et al. 2015). Simulations were evaluated over the 1950–2009 time period, and parameters were adjusted to approximate historical fire sizes, frequency, and number of fires based on historical observations. For metrics of landscape flammability, model simulation results reasonably matched observed (1950–2010) wildfire activity—both cumulative area burned and the cumulative distribution of individual fire size (Gustine et al. 2014).

Results

EMF effects on vegetation transitions

In the tundra zone of Alaska forest cover increased over the simulation period for all parameterizations (Figs. 5, 6) by 8.8–18.2 % depending on model parameterization (Table 1) and driving climate model (Figs. 5, 6). During the time frame from 2000 to 2100,

the simulations run with the constrained inoculum establishment (CI-E) parameterization closely matched those run with the unconstrained (UI) parameterization and resulted in the greatest area of forest that transitioned to forest from tundra compared to the other parameterizations (Figs. 5, 6). For example the median percent change in forest cover from 2000 to 2100 for the CCCMA simulations was 18.25 % for the CI-E parameterization and 18.23 % for UI parameterization. As the duration of the EMF constraint increased (CI-E + LTG > CI-E + STG > CI-E), afforestation rate declined (Fig. 5). Overall, the largest reduction in forest expansion occurred when simulations included effects of variability in inoculum potential on establishment and long-term growth of seedlings (CI-E + LTG). This suggests that additive mycorrhizal effects on establishment and growth constrain forest expansion more than mycorrhizal effects on establishment alone.

Irrespective of the model parameterization (unconstrained or EMF constrained), there was greater forest expansion in the tundra domain for simulations driven by the more moderate warming scenario, CCCMA,

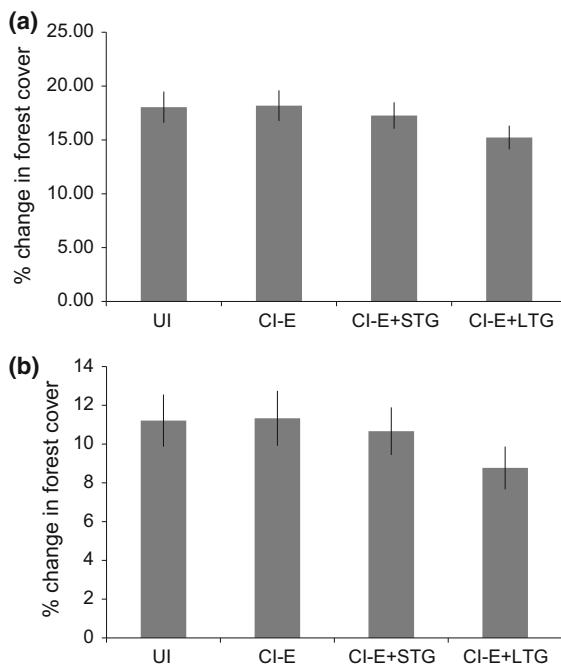


Fig. 5 Percent change in forest cover ($\text{km}^2 \pm \text{SD}$) for four inoculum parameterizations across the tundra zone of the state of Alaska from 2000 to 2100 averaged across 100 model replicates: **a** CCCMA, **b** ECHAM5

than the ECHAM5 GCM. The CCCMA simulations resulted in 6.7 % greater forest expansion by 2100 than the ECHAM5 simulations averaged across all model parameterizations (Fig. 5). Simulations driven by CCCMA had on average 6940 km^2 more forest cover than ECHAM5 simulations by 2100 (Fig. 6).

The majority of forest expansion occurred in the western Brooks Range (Fig. 7). Although there are differences in the extent of tundra conversion among simulations, the geographic domains where spruce expansion occurred remain the same (Fig. 7). For example, maps comparing UI and CI-E + LTG simulations for both the CCCMA and ECHAM5 models show greatest afforestation in northwestern Alaska and a reduction in afforestation in these areas when EMF effects are employed in simulations. Overall, assessment of geographic patterns of afforestation suggest that simulations that incorporate variability in

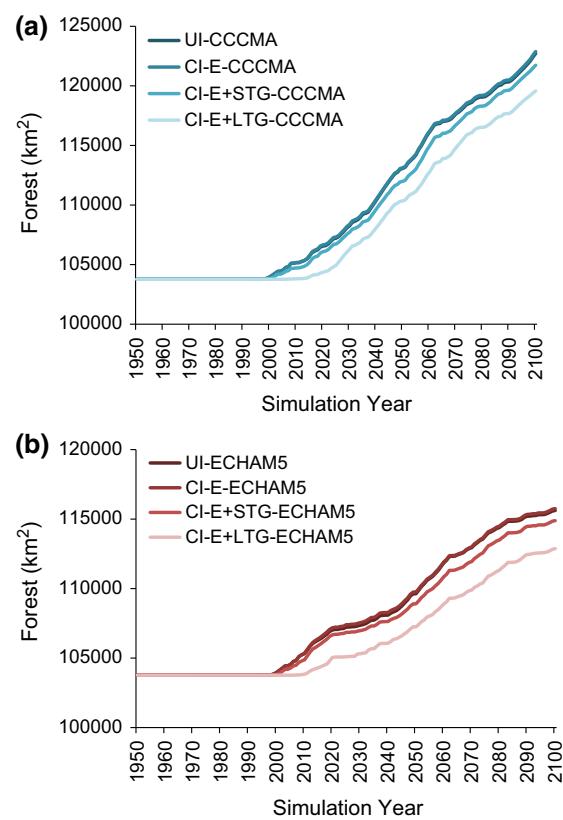


Fig. 6 Forest cover (km^2) across the tundra zone of the state of Alaska for simulations driven by four inoculum parameterizations: **a** CCCMA and **b** ECHAM5 GCMs. Forest cover at each time step is the average of 100 model replicate runs

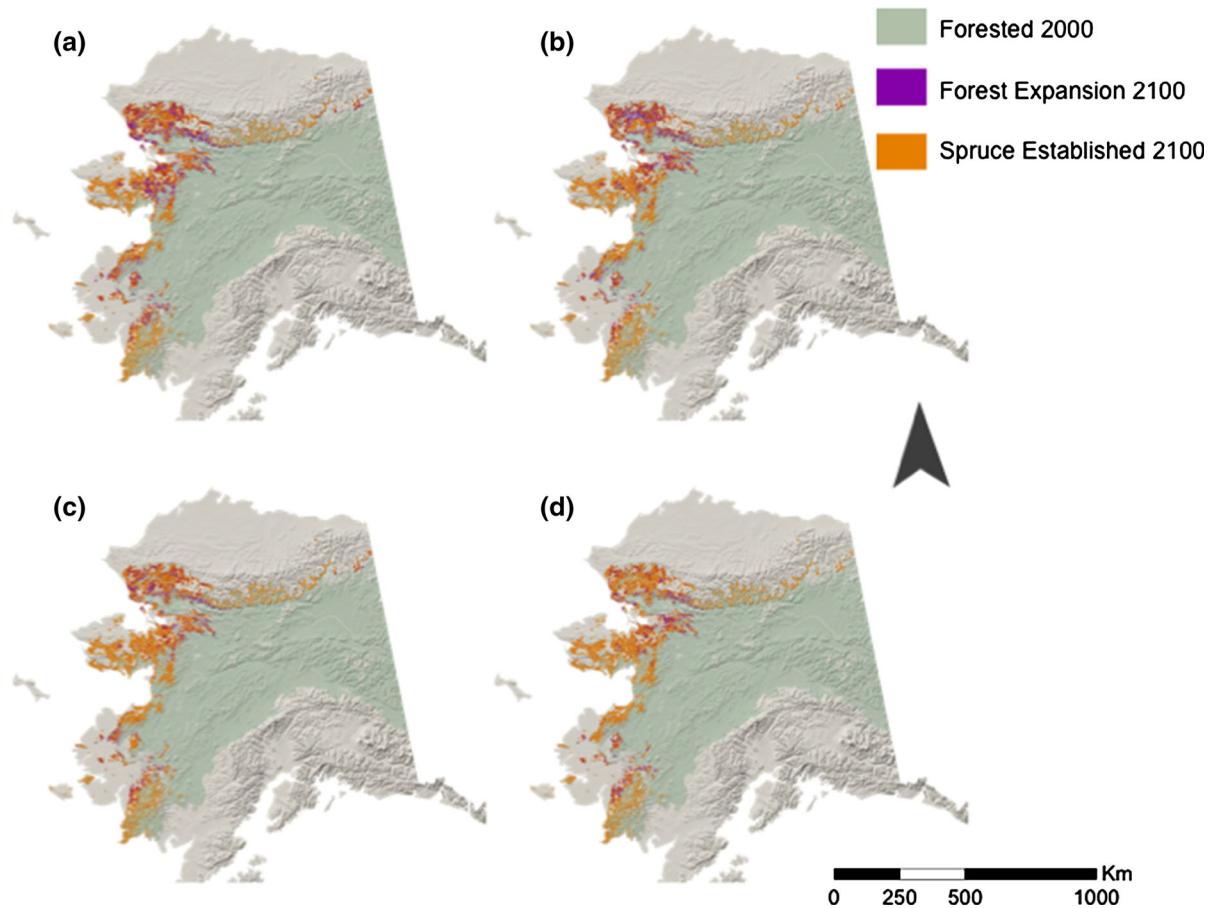


Fig. 7 Comparison of the spatial patterns of landscape-level forest expansion in the tundra zone of Alaska driven by four inoculum parameterizations: **a** UI-CCCMA, **b** CI-E + LTG-CCMA, **c** UI-ECHAM5, and **d** CI-E + LTG-ECHAM5. Effects of variability in inoculum potential on establishment and long-term growth of seedlings (CI-E + LTG) had the largest influence on forest expansion rates for simulations forced with

both climate models. Spruce establishment (*orange pixels*) indicates where spruce has dispersed, but the tundra has not transitioned to forest. Forest expansion (*purple pixels*) indicates where spruce seed has dispersed during model simulations and reached stand maturity. Expansion patterns displayed using the best replicate simulation for the tundra zone (Breen et al. 2013)

inoculum potential appear to influence the magnitude of expansion within geographic localities instead of altering which regions become forested compared with simulations that do not incorporate EMF effects (UI).

Maps differentiating spruce dispersal and establishment (i.e., areas of spruce expansion that have not transitioned to mature forest) from forest expansion [i.e., a tundra cell that has transitioned to a mature spruce stand where the 1 km^2 cell has a basal area consistent with a mature stand ($\text{BA} > 20 \text{ m}^2/\text{ha}$)] illustrate that EMF constraints on establishment and growth have

greater impact on afforestation than dispersal limitation and EMF constraints on establishment alone (Fig. 7). However, the magnitude of forest expansion differed more based on forcing climate model than on inoculum parameterization. Thus, the spatial extent of spruce establishment and forest expansion (Fig. 7) mirror the temporal trends in forest migration (Fig. 6) indicating that climate and the associated fire regime is the primary factor influencing the conversion of tundra to forest, and secondarily limitation in EMF inoculum potential constrains afforestation in simulations across the tundra zone of the state.

Indirect effects of EMF on landscape flammability

In parallel with our investigations of vegetation transitions, we analyzed the indirect effects of mycorrhizal interactions on landscape flammability. Because EMF parameterizations influence afforestation and thus fuel loads, these biotic interactions indirectly affect landscape flammability. For each of the GCMs there is fairly moderate variance in the projected cumulative area burned for each of the four model parameterizations (Fig. 8). Constraining EMF parameterizations (CI-E, CI-E + STG, and CI-E + LTG) resulted in lower fire activity relative to unconstrained parameterizations (UI) regardless of driving GCM by 2100. The parameterizations with the largest negative effect on afforestation (CI-E + LTG) had the most reduced landscape flammability. More specifically, the simulations with unconstrained (UI) parameterizations resulted in 11,974 km² (CCCMA) and 18,045 km² (ECHAM5) more kilometers burned than the CI-E + LTG parameterization for the respective GCM. However, the cumulative area burned for each of the eight simulations was more affected by the abiotic factors, climate and fire, than the indirect effect of variability in EMF on fuels (Fig. 8). For example, cumulative area burned in the tundra was lower by an average of 42,437 km² for simulations using CCCMA than the warmer and drier ECHAM5 model, which is 2 or 3.5 times greater than the difference between UI and

CI-E + LTG parameterizations driven by CCCMA (11,974 km²) or ECHAM5 (18,045 km²), respectively (Fig. 8).

We also observed that after high fire years there are apparent negative feedbacks between lowered fuel loads and subsequent periods of time with lower fire activity. Due to the negative influence of limited EMF on forest expansion, these negative feedbacks between fire activity and fuels seem to be amplified in simulations that are parameterized with constraints on seedling establishment and growth due to low EMF. As an example, notably high fire activity was predicted in the 2001–2050 time period for simulations forced with the ECHAM5 GCM. After the highest peak in fire activity around 2035, variation in cumulative area burned among model parameterizations is more apparent. This may reflect additive fire-effects on plant-fungal interactions and forest expansion, where fire reduces both seedling basal area and EMF inoculum potential.

Discussion

The main objective of these modeling experiments was to evaluate the landscape implications of our understanding of how plant-mycorrhizal interactions influence tundra-to-forest vegetation transitions. Here, we found that, in the tundra zone of Alaska, abiotic drivers, climate and associated fire activity primarily influenced the magnitude of conversion to forest from previously treeless areas. Yet, landscape patterns of spruce expansion and forest development were constrained when we parameterized the model to limit opportunities for positive EMF effects on tree establishment and growth in tundra. Mycorrhizal influence on spruce migration consequently influenced the magnitude of feedbacks between vegetation and fire activity, providing insight into controls over vegetation response to disturbance and directional climate change.

Variability in forest expansion in relation to the model parameterization employed suggests that additive EMF-effects on establishment and biomass accrual of seedlings and saplings, and not seedling establishment alone, will most greatly influence conversion of treeless tundra to forest on a landscape-scale. Historically, carbon limitation due to cold temperatures has been proposed as the main control

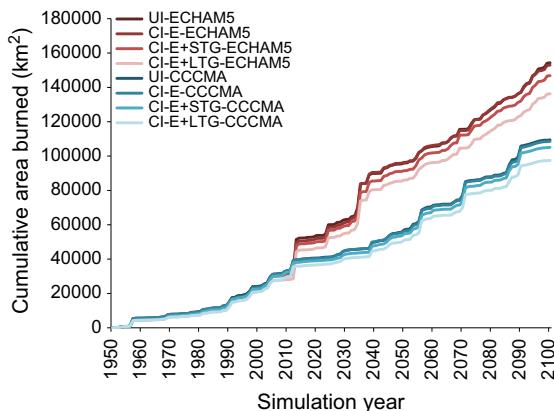


Fig. 8 Mean cumulative area (km²) burned across the tundra zone of the state of Alaska for simulations driven by four inoculum parameterizations and ECHAM5 and CCCMA GCMs. Cumulative area burned is the sum of the area burned within a given year and all previous years starting from 1950 averaged across 100 model replicates

over treeline seedling growth and treeline position (Korner and Paulsen 2004; Hoch and Korner 2012). More recently, nutrient limitation was put forth as a key factor influencing treeline seedling (Sullivan and Sveinbjornsson 2010) and stand development (McNow and Sullivan 2013). Our simulations indicate that stand development is sensitive to both temperature and nutrient limitations and our findings support a hierarchy of factors influencing treeline change. For example, we observed the increased forest cover over the next century for all simulations indicating sensitivity to temperature, and the change in forest cover was greater between driving GCMs than among EMF parameterizations. Yet, *within* a given climate scenario, forest expansion was constrained by a secondary factor, mycorrhizal effects—likely associated with the influence of mycobionts on both nutrient accrual and growth (Smith and Read 2008).

In a global synthesis, Harsch et al. (2009) inferred that disturbance legacies, such as those from fire, would likely not affect the probability of treeline advance. Instead, the positive influence of climate on afforestation would override any negative influence of disturbance on initial recruitment. This hierarchy of controls on treeline advance (climate followed by disturbance legacies followed by biotic factors) is in agreement with our model simulations, where climate ultimately controls afforestation across the landscape, but EMF factors influence the rate and/or magnitude of reaching the climax state of the successional trajectory, in this case spruce forest. Our findings are consistent with several studies showing the importance of biotic factors such as seedbed quality and herbivory (Cairns and Moen 2004; Munier et al. 2010) as secondary filters and climate as the primary filter affecting seedling establishment and growth beyond treeline.

The magnitude of abiotic (such as climate and fire) versus biotic (in our case EMF inoculum potential) effects on afforestation might deviate from our model outputs with the inclusion of EMF dispersal in estimates of inoculum potential. Our best conceptualization of estimated inoculum potential within a 1 km² cell in the model was based on pre-fire vegetation class and fire history in that cell i.e. post-fire fungal survival at the site (1 km² cell) excluding dispersal from adjacent cells. This formulation does not fully capture the biology of the plant-EMF symbiosis. However, we

represent a parsimonious conceptual model of EMF inoculum potential reflective of rationale based on several field experiments showing both local networking of seedlings into intact hyphal networks (Horton and van der Heijden 2008) and dispersal limitation at distances less than 1 km (Peay et al. 2010b, 2012) influencing seedling performance. This representation of inoculum potential at a coarse 1 km² –scale excludes the *potential* positive “rescue effects” of long-distance dispersal of spores on seedling growth and the *known* negative effects of fungal limitation that may constrain seedling growth at scales far below 1 km². Thus, we suggest that our outputs likely result in an underestimate of EMF effects on afforestation despite the exclusion of dispersal in estimates of inoculum potential.

Few studies outside of paleontological research document the magnitude of forest vegetation shifts for comparison to our estimates of vegetation transitions from the model simulations. Paleontological studies suggests that spruce-dominated latitudinal treeline is currently at its farthest, northern Holocene-extent in Alaska (Bigelow et al. 2003). Present-day dendrochronological and satellite-based investigations show increases in forest productivity at the forest-tundra margin under favorable climate conditions (Beck et al. 2011) coupled with observations of young tree cohorts growing beyond the current forest limit (Lloyd and Fastie 2003). Despite the retardation of spruce migration due to effects of mycorrhizal limitation on establishment and growth in our study, simulations of afforestation were greater than observed forest migration and tundra fire activity from empirical studies within the 21st century. Chapin et al. (2005) reported 2.3 % increase in forest cover over a fifty-year time frame. From our study this is most similar to the CI-E + LTG-ECHAM5 simulations with a conversion of 8.8 % tundra to spruce over a one hundred year time frame. In strong juxtaposition to this magnitude of tundra conversion, the CCCMA simulations with the UI and the CI-E parameterization were close to four-fold higher (~18 % tundra conversion) and the ECHAM5 UI simulations over two-fold higher (~11 % tundra conversion) than these empirical estimates. Thus, the inclusion of some restricting parameter on seedling establishment and growth, whether EMF or otherwise, improved the match between historic and projected estimates of tundra conversion. Perhaps most importantly, future

rates of treeline expansion may not reflect what has been observed in empirical studies to date. With this in mind the sensitivity analysis we conducted comparing afforestation for all four model parameterizations for each GCM yields a bracketed range of the extent of forest migration that may occur in the next 100 years. These high projections of state transitions are likely a reasonable estimate given that currently the majority of the model domain is within $\leq 2^{\circ}\text{C}$ threshold of summer temperatures that would likely promote forest expansion and projections of future climate are on average $>2^{\circ}\text{C}$ degrees C by 2100 (Scenarios Network for Arctic and Alaska Planning 2015).

One of the main biophysical feedbacks discussed in relation to treeline shifts and vegetation transitions in the Arctic is the contribution to atmospheric heating. Based on the estimates of changes in atmospheric heating due to changes in forest cover reported in Chapin et al. (2005), we calculated changes in atmospheric heating for the changes in forest cover that we found (Table 3). The most conservative tundra-forest conversion was 0.9 % per decade, from the CI-E + LTG-ECHAM5 simulations. This resulted in a $\sim 0.2\text{ W m}^{-2}/\text{decade}$ increase in atmospheric heating. In contrast, the largest conversion from the CCCMA simulation UI or CI-E parameterizations (resulting in $\sim 1.8\%$ conversion per decade) would result in a $\sim 0.4\text{ W m}^{-2}/\text{decade}$ increase in atmospheric heating. While the contribution of vegetation transitions to atmospheric heating are smaller than that found for a reduced snow season due to climate warming ($\sim 3.3\text{ W m}^{-2}/\text{decade}$; (Chapin et al. 2005; Euskirchen et al. 2009a, 2009b), it is still important to consider these tundra-forest conversions to come to a more complete quantification of the full suite of feedbacks to atmospheric heating.

The implications of vegetation transitions on long-term atmospheric heating for a given climate scenario is contingent on whether the influence of mycorrhizal fungi *retards* the magnitude of transitions or *prevents* afforestation. Our simulations are limited to a century-long time frame ending in 2100. However, other ALFRESCO simulations suggested substantial forest expansion after 4000 years with a 2000 year time lag when climate was $+9^{\circ}\text{C}$ (Rupp et al. 2001). A comparison of long-term simulations out to year 2300 that utilized climate scenarios with variation in radiative forcing (decreased, constant, or increased forcing), suggested that for long-term, directional change to occur in response to climate warming (e.g. sea ice decline), simulations required increased forcing over the simulation period. In contrast, simulations with decreased or constant forcing resulted in stasis or recovery of a given ecological or physical state (Hezel et al. 2014). For scenarios with increased forcing over longer simulation time periods, it seems likely that our mycorrhizal simulations represent a time lag in seedling and sapling growth, with the climax spruce state being reached over time. EMF inoculum would likely increase across the tundra as vegetation types with higher inoculum potential (forest and shrub tundra) respond positively to climate and become more dominant over the simulation time period (see Breen et al. 2013). In contrast, climate scenarios with constant or decreased radiative forcing from climate might yield simulations with vegetation outputs that would converge and the influence of mycorrhizal fungi on vegetation processes would become more pronounced. Given that warming is projected to continue at high latitudes, the most likely extrapolation from our simulations is that the forest will continue to expand into tundra regions of Alaska,

Table 3 Calculated atmospheric heating (Watts m^{-2}) for changes in forest cover from simulated tree migration based on estimates of atmospheric heating reported in Chapin et al. (2005)

Parameterization	% Afforestation		Model: field		$\text{W (m}^{-2}\text{)}$	
	CCCMA	ECHAM	CCCMA	ECHAM	CCCMA	ECHAM
UI	18.04	11.21	3.92	2.44	0.43	0.27
CI-E	18.18	11.33	3.95	2.46	0.43	0.27
CI-E + STG	17.26	10.67	3.75	2.32	0.41	0.26
CI-E + LTG	15.23	8.77	3.31	1.91	0.36	0.21

Model: field is a ratio of the percent change in forest cover from our model outputs compared to the field estimates reported in Chapin et al. (2005) and used to calculate atmospheric heating

influencing feedbacks between the biosphere and the climate system.

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Conflict of interest The authors declare that they have no conflict of interest.

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