

Alternative tree-cover states of the boreal ecosystem: A conceptual model

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Abstract

Aim: Previous analyses of remotely sensed data detected the multimodality of the tree-cover distribution of the boreal forest, and identified areas with potentially alternative tree-cover states. This paper aims at investigating the causes of multimodality and multistability of the boreal forest, their influence on the asymmetric tree species distribution between Eurasia and North America, and whether multistability could be associated with recent greening trends in leaf area index (LAI) and normalized difference vegetation index (NDVI).

Location: Eurasian and North American boreal forests.

Time period: 2000–2010.

Major taxa studied: Boreal forest plant functional types.

Methods: We employ a conceptual model based on tree species competition to simulate the sensitivity of tree cover to stochastic disturbances and to changes in environmental factors. We include different plant functional types based on survival adaptations, and force the model with remotely sensed environmental data. We analyse the model as a dynamical system. We use metrics from statistics and information theory to compare the detection of alternative tree-cover states and greening trends in LAI and NDVI.

Results: We find that multimodality and multistability can emerge through competition between different plant functional types. Additionally, our model is able to reproduce the asymmetry in tree species distribution between Eurasia and North America. Moreover, changes in permafrost distribution can be associated with phenomenological bifurcation points of the model. Finally, we find that the detection of multistable areas is not affected by recent vegetation trends, whereas shifts between alternative states could have affected the greening trends.

Main conclusions: Tree-cover multistability in the boreal region can emerge through competition between species subject to periodic disturbances. Changes in permafrost thaw and distribution could be responsible for the asymmetry in tree species distribution between North America and Eurasia. Climate change and permafrost degradation could cause shifts in tree-cover states and dominant species. Recent vegetation greening trends in multistable areas could have been affected by shifts between alternative states.

KEYWORDS

alternative stable states, boreal forest, climate change, conceptual model, ecosystem shifts, greening trends, multistability, tree cover

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1 | INTRODUCTION

The tree-cover distribution of the boreal forest exhibits three alternative modes: low tree cover, open woodland and forest (Scheffer, Hirota, Holmgren, Nes, & Chapin, 2012; Xu, Medvigy, & Rodriguez-Iturbe, 2015). These states, corresponding to remotely sensed tree-cover fraction values below 20%, between 20 and 45%, and above 45%, respectively, have been suggested to reflect the presence of alternative stable states acting as attractors (Scheffer et al., 2012). Following the detection of multimodality of the boreal forest, it has been shown that, in c. 95% of the cases, environmental conditions uniquely determine the tree-cover state among the three dominant modes (Abis & Brovkin, 2017). Nonetheless, areas with potentially alternative tree-cover states under the same environmental conditions have also been identified, as in Figure 1, reinforcing the hypothesis of the presence of alternative stable states (Abis & Brovkin, 2017). These areas encompass 1.1 million km², and correspond to possible transition zones with a reduced resilience to disturbances.

However, the detection of alternative tree-cover states under the same environmental conditions could have been affected by pre-existing vegetation trends caused by climate change. In fact, the recent analysis by Zhu et al. (2016) showed a general “greening” of the Earth, that is, an increase in leaf area index (LAI) and normalized difference vegetation index (NDVI). While for tropical and temperate regions it was possible to attribute this phenomenon mostly to increased levels of CO₂ concentrations, this was not the case for the northern high latitudes, where the changes in vegetation were attributed in large part to climate change and “other factors”. Both phenomena involve differences in vegetation patterns, and they could be mutually

dependent. On the one hand, greening and browning trends may be associated with transitions between different stable tree-cover states. On the other hand, the detection of multistability could be influenced by greening trends in the vegetation caused by other environmental factors. Furthermore, the mechanisms underlying the existence of possible multiple stable tree-cover states are still unknown.

Within this paper, we investigate the relationship between multistability and vegetation trends, and whether alternative tree-cover states and multimodality of the tree cover can be explained through a simple competition mechanism incorporating different plant functional types (PFTs) and environmental factors. In particular, we present and make use of a conceptual dynamical model capable of capturing the multimodality and multistability of the boreal ecosystem. Additionally, our model allows us to investigate the sensitivity of the total tree cover, and its underlying PFT distribution, to changes in environmental variables. Furthermore, to understand whether the detection of greening trends and the emergence of alternative vegetation states are mutually dependent, we employ the concept of mutual information for clusters (MI; Vinh, Epps, & Bailey, 2010) and the Spearman’s rank-order correlation.

Changes in climate and environmental conditions are likely to play a more prominent role in future decades (Coumou & Rahmstorf, 2012; IPCC, 2013; Johnstone et al., 2010; Orlowsky & Seneviratne, 2012), affecting the resilience of forests, and possibly pushing them towards tipping points (IPCC, 2013; Reyer et al., 2015). In particular, environmental and climate changes are impacting the boreal latitudes at a higher rate and intensity than other regions on Earth, as surface temperature at high latitudes has been increasing approximately twice as fast as the global average (IPCC, 2013). As the boreal

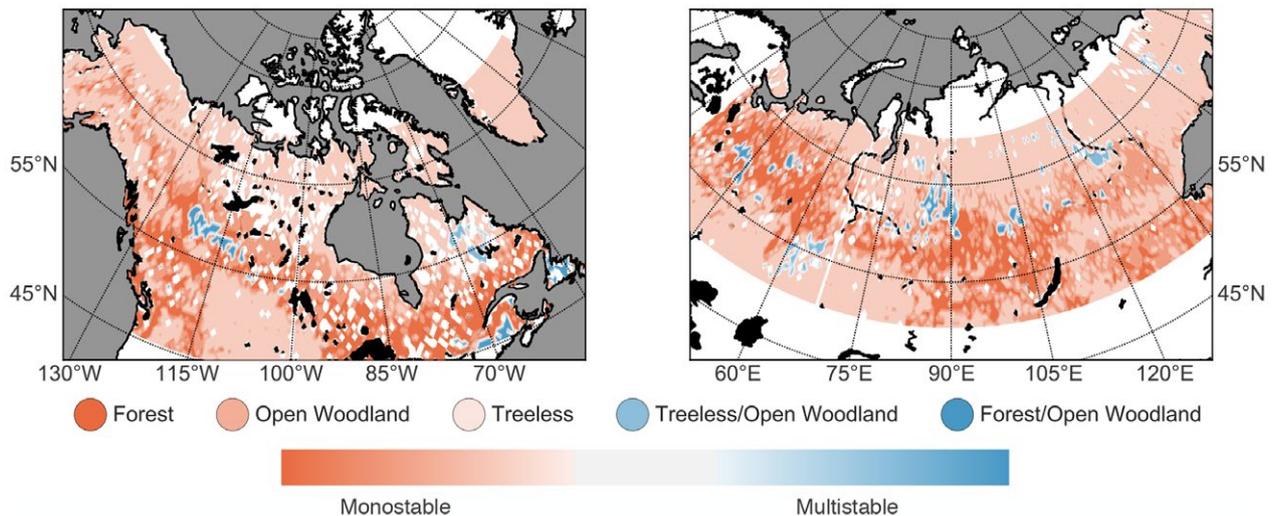


FIGURE 1 Distribution of possible alternative tree-cover states areas, adapted from Abis and Brovkin (2017) figure 3, CC BY 3.0. Regions coloured in orange represent monostable areas, shaded according to the three dominant vegetation modes inferred from remote sensing: Forest, Open woodland and Treeless (Abis & Brovkin, 2017; Scheffer et al., 2012). These modes correspond to remotely sensed tree-cover fraction values above 45%, between 20% and 45%, and below 20%, respectively. Regions in shades of blue correspond to multistable areas, where alternative tree-cover states are found under the same environmental conditions. Multistable regions are divided into Treeless/Open woodland and Forest/Open woodland. The former comprises grid cells where, under the same environmental conditions, the tree-cover fraction values are either below 20%, or between 20% and 45%. The latter, instead, encompasses grid cells with tree-cover fraction values either above 45%, or between 20% and 45%

forest covers c. 30% of the global forested area, it is important to deepen our understanding of the dynamics of the boreal ecosystem with respect to alternative stable tree-cover states.

Despite its low diversity of tree species, the boreal forest's tree-cover distribution depends on interactions between several factors and feedbacks (Bonan, 1989; Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015; Heinselman, 1981; Hare & Ritchie, 1972; Shugart, Leemans, & Bonan, 1992; Soja et al., 2007). At the same time, boreal trees have a high functional diversity (Wirth, 2005), that is, the diversity of species' traits (Tilman & Lehman, 2001). Notably, boreal trees possess distinct fire adaptation traits to ensure survival of the species in case of wildfires (Gill, 1981; Wirth, 2005). These traits, in turn, can be grouped into five separate plant functional types [fire PFTs in Wirth (2005), and simply PFTs in the following]: resister, endurer, avoider, embracer and invader, corresponding to either survival (resister, endurer and avoider) or dispersal (embracer and invader) strategies (Wirth, 2005). Strikingly, there is a peculiar asymmetry in the distribution of these PFTs between the North American and Eurasian boreal forests. On the one hand, embracer species are absent from Eurasia, whereas resister species, such as *Pinus sylvestris* and *Larix sibirica*, constitute the majority of the forest. On the other hand, resister species are almost absent from North America, and embracer species, such as *Picea mariana* and *Pinus banksiana*, occupy most of the forested areas (Wirth, 2005; M. Flannigan, 2015; Rogers, Soja, Goulden, & Randerson, 2015).

The distribution of PFTs is associated with very different fire regimes within the boreal area, with implications for nutrient and carbon cycling (Wirth, 2005; M. Flannigan, 2015). Moreover, PFTs differ in other phenological properties, such as their average albedo, whether they are shade tolerant or not, and their evapotranspiration regimes (Wirth, 2005). However, as of today, there is no consensus on the reasons behind such asymmetry (Rogers et al., 2015; M. Flannigan, 2015). In this respect, we contribute to the debate by including in our conceptual model separate competing PFT populations, namely resisters, avoiders and embracers, as they dominate the boreal landscape (Wirth, 2005). We then employ the model to study their response to different environmental conditions, in particular to changes in permafrost distribution, in areas with potentially alternative stable tree-cover states, as identified in Abis and Brovkin (2017), and to determine which factors could affect the asymmetric distribution of PFTs between Eurasia and North America.

2 | METHODS

2.1 | Material

To set up our model and study PFT competition and tree-cover dynamics in the boreal forest, we make use of seven globally observed environmental datasets, as summarized in Table 1. In particular, PFT distributions are taken from the Canadian National Forest Inventory

TABLE 1 Summary of variables and datasets

Variable	Acronym	Units	Origin	Reference
Percentage tree-cover fraction	TCF	%	0.05° MODIS MOD44B V1 C5 2001–2010; 0.05° Landsat GFC Tree-Cover product 2000–2015	Townshend et al. (2010); Sexton et al. (2013)
Decadal normalized difference vegetation index trend	NDVI trend	%	0.05° MODIS MOD13C1 VI 2000–2015	Didan (2015)
Decadal leaf area index trend	LAI trend	%	500 m MODIS MOD15A2 LAI 2000–2015	Myneni et al. (2015)
Mean annual rainfall	MAR	mm/year	CRU TS3.22 Precipitation 1998–2010	Harris et al. (2014)
Mean spring soil moisture	MSSM	mm	CPC Soil Moisture 1998–2010	van den Dool et al. (2003)
Permafrost zonation index	PZI	–	Global Permafrost Zonation Index Map	Gruber (2012)
Fire frequency	FF	fires/year	GFED4 Burned Area 1996–2012; Canadian National Fire Database 1980–2014	Giglio, Randerson, and Werf (2013); Canadian Forest Service (2014)
Growing degree days above 0 °C	GDD0	°C/year	NCEP Reanalysis (NMC initialized) 1998–2010; CRU TS3.22 Temperature 1998–2010	Kalnay et al. (1996); Harris et al. (2014)
Tree-species distribution	TSD	%	Canadian National Forest Inventory	Beaudoin et al. (2014)

Note. Percentage tree-cover fraction indicates the proportion of land per grid cell covered by trees. Normalized difference vegetation index (NDVI) is calculated from the visible and near-infrared light reflected by vegetation to quantify density of plant growth. Leaf area index (LAI) is defined as one-sided green leaf area per unit ground area in broadleaf canopies and as one-half the total needle surface area per unit ground area in coniferous canopies. Trends in LAI and NDVI are calculated with respect to the baseline observations of the year 2000. Mean annual rainfall corresponds to the mean cumulative precipitation in millimetres over a year. Soil moisture is measured as water height equivalents in a 1.6-m soil column. Permafrost zonation index shows the probability of a grid cell having permafrost existing only in the most favourable conditions or nearly everywhere. Fire frequency is the average number of fire events per year. Growing degree days above 0 °C correspond to the sum of the mean daily temperatures at 2 m height above 0 °C through a year, using 6-hr measurements. Tree species distribution indicates the percentage composition for the major tree species groups of Canada at 250-m resolution.

(Beaudoin et al., 2014), whereas for tree-cover fraction we make use of the 0.05° MODIS MOD44B V1 C5 2001–2010 (Townshend et al., 2010) and Landsat GFC Tree Cover 2000–2015 (Sexton et al., 2013) products. Furthermore, to include the dependence of tree-cover fraction on environmental variables, the model takes as input four environmental factors based on the work of Hare and Ritchie (1972), Woodward (1987), Bonan (1989), Bonan and Shugart (1989), Shugart et al. (1992), Kenkel, Walker, Watson, Caners, and Lastra (1997) and Abis and Brovkin (2017). These factors are: growing degree days above 0 °C (GDDO – °C/year) calculated from the NCEP/NCAR reanalysis 1998–2010 (Kalnay et al., 1996) and from the CRU TS3.22 1998–2010 dataset (Harris, Jones, Osborn, & Lister, 2014); mean annual rainfall (MAR – mm/year) from the CRU TS3.22 1998–2010 dataset (Harris et al., 2014); mean spring soil moisture (MSSM – mm) from the CPC Soil Moisture 1998–2010 dataset (van den Dool, Huang, & Fan, 2003); and permafrost distribution obtained as Permafrost Zonation Index (PZI – unitless) from the Global Permafrost Zonation Index Map (Gruber, 2012). The role of these environmental variables within the boreal ecosystem has been extensively studied in the past and it is beyond the scope of this paper. For more details see for instance Benninghoff (1952); Hare and Ritchie (1972); Rowe and Scotter (1973); Woodward (1987); Bonan (1989); Skopp, Jawson, and Doran (1990); Havranek and Tranquillini (1995); Way and Oren (2010); Flannigan (2015); Abis and Brovkin (2017).

The MODIS tree-cover dataset has certain biases and limitations, and, as has been pointed out, it may not be useful for differentiating over small ranges of tree cover (less than c. 10%) at its highest resolution (Hansen et al., 2003; Gerard et al., 2017), as the use of classification and regression trees (CARTs) to calibrate the dataset might introduce artificial discontinuities (Hanan, Tredennick, Prihodko, Bucini, & Dohn, 2014). For this reason, we employ MODIS tree-cover fraction data at a coarser resolution (0.05°, subsequently re-projected to 0.5°), and we compare results with the use of the Landsat Tree Cover dataset. Within this setup, we assume that the dataset products are suitable for our investigation (Prof. R. Myneni, July 2017).

Environmental and climate conditions in the boreal forest have different distributions in North America and Eurasia (Abis & Brovkin, 2017). To preserve continuity of patterns and to separate areas with different characteristics, for example, due to oceanic influence, we divide the boreal area into four regions, as in Abis and Brovkin (2017), using approximately the Canadian Shield and the Ural Mountains as middle boundaries for North America and Eurasia. Namely, Western North America (45–70 N, 100–170 W), Eastern North America (45–70 N, 30–100 W), Western Eurasia (50–70 N, 33–68 E) and Eastern Eurasia (50–70 N, 68 E–170 W). Moreover, to evaluate whether the model is able to capture alternative tree-cover distribution patterns, we further divide multistable regions in Eastern North America and Eastern Eurasia. As reported in Figure 2, we separate Eastern North America between north and south of 51.25 N, and Eastern Eurasia between east of 91.75 E, west of 91.75 E but south of 61.75 N and west of 91.75 E but north of 61.75 N.

2.2 | Greening trends analysis

To compare multistable regions with greening and browning trends in the boreal area, we employ the MODIS C6 NDVI and LAI 2000–2015 Trend datasets, supplied by Ranga Myneni and Taejin Park (Didan, 2015; Myneni, Knyazikhin, & Park, 2015). These datasets, as reported in Table 1, describe trends in LAI and NDVI during the growing season period with respect to the baseline observations of the year 2000. NDVI is calculated from the visible and near-infrared light reflected by vegetation to quantify density of plant growth. LAI is defined as one-sided green leaf area per unit ground area in broadleaf canopies and as one-half the total needle surface area per unit ground area in coniferous canopies. The goal is to determine whether there is a causal relationship between the environmental conditions causing multistability, as in Abis and Brovkin (2017), and the corresponding greening or browning trends in vegetation. To this avail, we compute the MI metric over multistable regions using either environmental or trends data as the clustering property.

Mutual Information for Clusters is a measure built upon fundamental concepts from information theory, quantifying the amount of

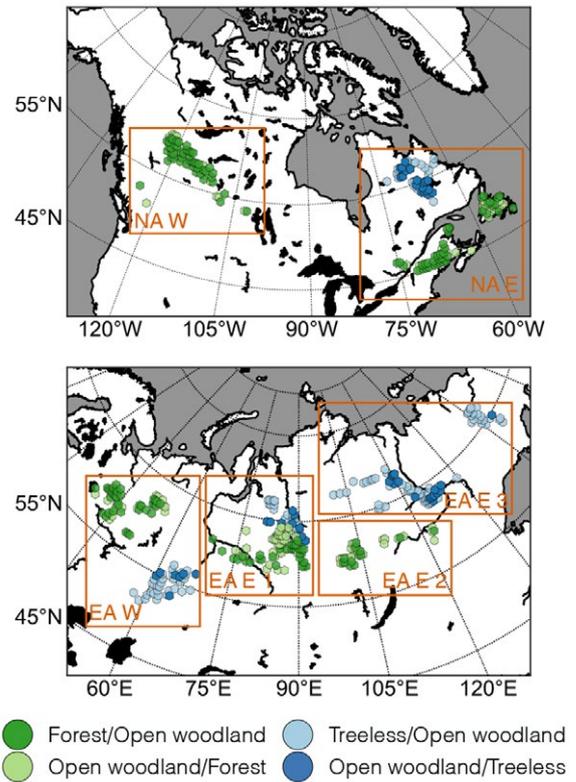


FIGURE 2 Division of multistable regions according to geographic location: Western North America (NA W), Eastern North America (NA E), Western Eurasia (EA W), Eastern Eurasia Area 1 (EA E 1), Eastern Eurasia Area 2 (EA E 2), Eastern Eurasia Area 3 (EA E 3). Multistable grid cells are coloured according to the remotely sensed vegetation state. For example, Forest/ Open woodland indicates grid cells that are currently in Forest state but could shift to Open woodland. Adapted from Abis and Brovkin (2017) figure 3, CC BY 3.0

information shared between clusterings, that is, segmentations of a set of elements into subsets with similar properties. Possible MI values range from 0 to 1, the former corresponding to absolute no gain in knowledge, and the latter to total redundancy between the two datasets. In our analysis, the main set is composed by multistable gridcells clustered either according to the environmental conditions underlying them, or to the value of the LAI and NDVI trends. Hence, MI provides a measure of how much information on alternative tree-cover states is gained by looking at the greening trends data and vice versa. Specifically, MI values close to 0 signify that there is no link between the conditions causing multistable states and the greening trends, that is, they are independent and share no information. Thus, observing one clustering will not augment our knowledge of the other one. On the contrary, values close to one indicate that there is a significant overlap in the conditions determining the vegetation state and the greening trends, meaning that the two clusterings share significant information. A more detailed discussion regarding MI can be found, for instance, in Vinh et al. (2010).

More specifically, to make use of the MI metric, we employ a procedure divided into three steps. First, we create a reference case. Second, we compute the value of the MI metric in multistable regions (multistable case). Third, we compare multistable and reference values.

To create the reference case, we divide the circumboreal area into four sub-areas, namely Eastern North America, Western North America, Eastern Eurasia and Western Eurasia, as in Abis and Brovkin (2017). Next, for each sub-area, we randomly select grid cells covering the same extent as the multistable regions found in that sub-area.

Subsequently, for each random sample, we create three clusterings: one according to the value of the LAI trend, one according to the NDVI trend and one according to the environmental conditions found in each grid cell. The reference case is then defined as the value of the MI metric between the LAI and the environmental conditions clusters, and between the NDVI and the environmental conditions clusters.

The multistable case is computed in a similar way. For each sub-area, we select all the multistable grid cells and then, as in the reference case, we create three clusterings: one according to the value of the LAI trend, one according to the NDVI trend and one according to the environmental conditions. The multistable case is defined as the value of the MI metric between these clusters, as in the reference case, but with the difference that only multistable grid cells are used. Finally, we compare the values of the MI metric obtained in the reference and multistable cases in each sub-area.

2.3 | Conceptual model

In a similar fashion to Van Nes, Hirota, Holmgren, and Scheffer's (2014) work on savanna–forest transitions in the subtropics, we employ a conceptual model to explain tree-cover dynamics with respect to the main environmental factors playing a role, namely growing degree days, precipitation, soil moisture and permafrost distribution (see Section 1), in areas where alternative tree-cover states are

possible according to Abis and Brovkin (2017). Within this framework, the aim of our model is to investigate whether alternative tree-cover states and multimodality of the tree cover can be explained through a simple competition mechanism incorporating different PFTs and environmental factors. Tree succession and gap dynamics have already been largely and thoroughly investigated (Bonan, 1989; Bonan & Shugart, 1989; Chapin III et al., 2004, 2006; Johnstone & Chapin, 2003; Kenkel et al., 1997; Schulze, Wirth, Mollicone, & Ziegler, 2005; Ustin & Xiao, 2001) and are not aspects we included in our study.

The model consists of three equations describing the dynamics of three populations (x_1 , x_2 and x_3) competing for resources: x_1 and x_2 represent the percentage (%) of two boreal PFTs with different survival adaptations, that is, different PFTs among embracers, resisters and avoiders, whereas x_3 represents generic non-tree species, such as shrubs, also as a percentage. The total tree-cover fraction (%) is then expressed as the sum $x_1 + x_2$ of the two competing PFTs corresponding to trees. The model is based on the concept of ecological competition as described in Y. M. Svirezhev and Logofet (1983) [see also Y. Svirezhev (2000); Y. M. Svirezhev (2008); Van Nes et al. (2014)] using Lotka–Volterra type equations. Each population is allocated a niche depending on the environmental carrying capacity, that is, the amount of a given PFT the environment can sustain. We assume the carrying capacities K_i , $i = 1, 2, 3$, to be functions of precipitation, permafrost, soil moisture, and nutrient availability, whereas the growth functions (or expansion rates) r_i , $i = 1, 2, 3$, depend only on the growing degree days above 0 °C (g) (Way & Oren, 2010). Additionally, we included a nonlinear loss term, as in Van Nes et al. (2014), representing disturbances to vegetation, such as wildfires (Holmgren, Scheffer, & Huston, 1997; Rietkerk & van de Koppel, 1997; Scheffer et al., 2012). The equations are as follows:

$$\begin{aligned}\frac{dx_1}{dt} &= r_1(g)x_1C_1(x_1, x_2, x_3) - D_1(x_1)\xi(t) \\ \frac{dx_2}{dt} &= r_2(g)x_2C_2(x_1, x_2, x_3) - D_2(x_2) \\ \frac{dx_3}{dt} &= r_3(g)x_3C_3(x_1, x_2, x_3) - D_3(x_3)\end{aligned}\quad (1)$$

with

$$r_i(g) = r_L + rp_i \cdot g,$$

$$C_i(x_1, x_2, x_3) = \left[1 - \frac{\alpha_{i1}x_1 + \alpha_{i2}x_2 + \alpha_{i3}x_3 + \alpha_{im}}{K_i(m, p, s)} \right]$$

$$D_i = m_{if}x_i \frac{h_{if}^2}{h_{if}^2 + x_i^2} \beta(t), \quad i = 1, 2, 3$$

$$K_3(m, p, s) = K_3(m, p, s),$$

$$K_i(m, p, s) = \zeta(t) + K_i(m, p, s),$$

$$\zeta \sim \mathcal{U}(0, 10), \quad \beta \sim \text{Bernoulli}(0.5), \quad \xi \sim \mathcal{U}(0.7, 1)$$

and where $k_i(m, p, s)$, $i = 1, 2, 3$, is a second-degree polynomial taking as input mean annual rainfall (m), permafrost distribution (p) and soil moisture (s). All coefficients, parameters and variables are

summarized in Table 2. The response of PFTs to fire is modelled via the disturbance term D_i , which takes into account the different fire adaptations strategies, that is, survival and avoidance of damage for resisters and avoiders, and crown fire promotion to increase seed dispersal for embracers (Wirth, 2005). For simplicity, we represent disturbances as stochastic events causing a loss of vegetation (higher mortality). As the large wildfires that burn most of the area are caused by lightning (Johnson, Miyanishi, & Bridge, 2001; Nash & Johnson, 1996), we assume that the frequency of disturbances is modulated only by the stochastic variable β , which has a Bernoulli distribution, whereas the intensity of disturbances depends on the proportions of PFTs. In particular, the different fire adaptations strategies of PFTs correspond to different maximum damage rates from disturbances (m_{if}), which are lowest for resisters and highest for embracers. Additionally, fire damage to resisters is modulated in intensity with the stochastic variable ξ , which follows a uniform distribution (\mathcal{U}), simulating their fire suppression capability. This means that, even though the probability of a stochastic disturbance is the same for all populations, resisters can effectively suppress disturbances and further reduce the damage rate. Furthermore, as the fire recurrence interval increases towards the tree line and depends heavily on the moisture balance, with dry sites having a higher fire frequency than wet ones (Bonan & Shugart, 1989), we assume fire frequency to be lower in the shaded and wetter conditions associated with a fully covered forest. For these reasons, the disturbance term D_i is designed to decrease after a fixed threshold (h_{if}), corresponding to the lower boundary of the forest state (45% tree-cover fraction). The competition coefficients α_{ij} are determined and optimized to fit the distribution of tree species and PFTs over Canada (Beaudoin et al., 2014) by assuming the equations of the model as in ecological equilibrium, that is, the left-hand side is assumed to be approximately zero. Finally, to deal with the lack of a suitable dataset, the stochastic variable ζ represents nutrient availability in the soils, following a uniform distribution, in an approach similar to Xu, Holmgren, et al. (2015). Other coefficients are based on literature values (Van Nes et al., 2014). It is important to note that the Canadian Forest Inventory contains all three PFTs, including a small percentage of resisters.

These resister species possess the same survival adaptations present in Eurasian resisters [see, for instance, Arno and Fischer (1995); Scher (2002); Wirth (2005); Beaudoin et al. (2014); Rogers et al. (2015)]. This allowed us to run the model on both continents, even though the calibration was performed with data for North America only.

2.4 | Model calibration and analysis

Although there are five main PFTs in the boreal area, the majority of the forested area is dominated by only three of them, namely resisters, embracers and avoiders (Rogers et al., 2015; Wirth, 2005). Furthermore, due to the asymmetry in species distributions between continents, only avoiders are present in both North

America and Eurasia, whereas embracers are virtually absent from Eurasia and resisters from North America (except for a small population). For this reason, we employ our model to simulate competition between two of these three PFTs at a time, in any possible combination.

The coefficients of the model are optimized to fit tree species distributions from the Canadian Forest Inventory (Beaudoin et al., 2014) corresponding to the three major PFTs (see Supporting Information Section S1 for details). The fitting is performed over randomly selected grid cells where the different PFTs are present, both in and out of possible multistable regions, assuming the equations are in equilibrium, that is, the derivatives are set to be approximately zero. The model is then forced with environmental data for both continents as in Table 1. With the calibrated model, we perform simulations for all possible multistable regions, as in Figure 2, and run them with different initial conditions (different proportions of competing PFTs) until all populations reach stable configurations where only small fluctuations due to stochastic disturbances happen and the system can be considered in equilibrium.

TABLE 2 Description of coefficients, parameters and state variables

Symbol	Description	Value/Range	Units
x_i	Tree-cover fraction composed by i-th PFT	0–100	%
r_i	Growth rate function of i-th PFT	0–1	per dt
r_L	Growth rate base	0.5	per dt
rp_i	Growth rate temperature component	–.5–+.5	per dt
g	Normalized growing degree days above 0°C	0–1	–
a_{ij}	Competition coefficient of PFT i over j	0–1	–
a_{im}	Normalization factor for i-th PFT	–	–
K_i	Total carrying capacity for i-th PFT	0–100	%
k_i	Environmental carrying capacity for i-th PFT	0–100	%
ζ	Stochastic capacity due to nutrient availability	0–10	%
m	Normalized mean annual rainfall	0–1	–
p	Permafrost zonation index	0–1	–
s	Normalized soil moisture	0–1	–
m_{if}	Loss rate due to disturbances for i-th PFT	0–1	per dt
h_{if}	Threshold tree cover for increased fire mortality	0–100	%
β	Stochastic disturbance factor	0/1	–
ξ	Fire suppression factor	0.7–1	–

Note. PFT = plant functional type.

The total tree-cover fraction is then obtained as the sum of the different populations of competing trees. Note, however, that our model is not meant to accurately describe the tree-cover fraction distribution of the boreal forest, but only its multimodality and multistability. All simulations are performed in MATHEMATICA version 11.0.1.0 (Wolfram Research, Inc., 2016).

As a next step, we study how the number of critical points of the dynamical system changes depending on the four environment-dependent parameters, r_1 , r_2 , K_1 and K_2 , that is, the growth rates and carrying capacities. To do so, we make use of results on parametric polynomial systems and discriminant varieties from Lazard & Rouillier (2007), which are built on the theory of Gröbner bases (Buchberger & Winkler, 1998). We employ MAPLE 2015.0 (Maple Inc, 2015) to determine the number of equilibria of the system in the cases where only one PFT is present, that is, equilibria in which either x_1 or x_2 is equal to zero, with any given combination of parameters. Afterwards, we numerically explore the existence of “mixed” solutions, in which both x_1 and x_2 are non-zero. Next, we study the eigenvalues of the Jacobian matrix of the system to determine the stability of each equilibrium, both in the case with and without stochastic terms, in all possible multistable regions. To do so, we employ environmental data as in the simulations performed in MATHEMATICA. Finally, we perform a sensitivity analysis to changes in environmental variables and compare parameters from North America and Eurasia.

3 | RESULTS

3.1 | Greening trends

Results of the comparison between greening trends and alternative tree-cover states are reported in Table 3. We find that LAI and NDVI trends in multistable areas in North America are always non-significant (not shown), and hence we excluded North America from Table 3. On the other hand, trends in multistable regions in Eurasia are significant and more pronounced. Moreover, we find that, in the reference cases over Eurasia, the average value of the MI metric is c. .47. However, when using only grid cells from multistable regions, the average MI metric drops to c. .14 for Eastern Eurasia and c. .11 for Western Eurasia.

By employing other measures or tests, we obtain similar results (see Supporting Information Section S2 for further details and additional tables). For instance, as reported in Table 4, the Spearman's rank-order correlation coefficients (r_s) between LAI/NDVI trends and environmental conditions causing alternative tree-cover states do not show a significant correlation.

3.2 | Model performance

We evaluate model simulations in multistable regions as illustrated in Section 2.1. The modelled tree-cover fraction distribution shows a good fit with observations with a χ^2 goodness-of-fit test value of 2.29 (with critical value 106.39 for 95% confidence)

testing the hypothesis that modelled and observed distributions do not differ significantly, and a K-sample Anderson–Darling test (Scholz & Stephens, 1987) value of -0.51 , implying that the null hypothesis that the two samples come from the same distribution cannot be rejected. A summary of the simulated tree-cover distributions over each area is represented in Figure 3, together with kernel density estimates to depict modal peaks. When considering the entire Eurasian area, the model shows a tree-cover distribution similar to the one reported in Xu, Holmgren, et al. (2015), with three main modes, as depicted in Figure 3a. Looking at the details in each subregion reveals the presence of different distribution modes. Western Eurasia exhibits two separate modes, as in Figure 3c, one at intermediate tree cover, greater than 20%, and one at high tree cover, above 50%. The first area in Eastern Eurasia, depicted in Figure 3d, has a first modal peak below 20% tree cover, followed by a smoother central one at intermediate tree cover and a third modal peak at tree cover around 60%. The second area, Figure 3e, exhibits two clear modes, one around 20% tree cover and one at 45%. The third and last area shows two clear modes, one below 10% tree cover and one around 25%, as can be seen in Figure 3f. The simulated tree-cover distribution in North America also shows three modes, located at low, intermediate and high tree-cover values, with a significant amount of treeless grid cells, as depicted in Figure 3b. In particular, tree cover in Western North America is bimodal, with a peak at 20% and one at 50% values, as reported in Figure 3g. Finally, the distribution of tree cover in Eastern North America, represented in Figure 3h, shows three separate modes, with peaks at values smaller than 20%, around 30% and above 55%, corresponding, respectively, to treeless, open woodland and forest states.

3.3 | Model asymmetry

The simulated distributions of embracer and resister trees exhibit an asymmetric behaviour between North America and Eurasia. In particular, as depicted in Figure 4 for Western North America and Eastern Eurasia Area 1 (EA E 1), with environmental conditions from North America, embracer species show a pronounced peak at high tree-cover values (greater than 45%, as in Figure 4a), whereas in Eurasia, the peak corresponds to treeless or very low tree-cover states (less than 10%, as in Figure 4b). On the other hand, simulated resister species show a treeless peak in North America (not shown), and two peaks in Eurasia, one corresponding to open woodland states and one to forest states, as in Figure 4c.

3.4 | Number of equilibria

The competition between embracers and resisters yields a varying number of critical points depending on the environment-dependent parameters r_1 , r_2 , K_1 and K_2 . In particular, the model can have one, two or three equilibria when one of the two PFTs is not present, as depicted in Figure 5. At low values of K_2 and r_2 , three equilibria with only embracer trees are possible, whereas with high values of

TABLE 3 Mutual information for clusters (MI) values calculated using trends in leaf area index (LAI) and normalized difference vegetation index (NDVI) against environmental conditions determining alternative tree-cover states (ATS) computed over multistable regions

Region	MI (LAI, ATS)		MI (NDVI, ATS)	
	Ref	Multistable	Ref	Multistable
Eastern Eurasia	.43	.10 (76%)	.42	.18 (56%)
Western Eurasia	.50	.13 (73%)	.53	.09 (82%)

Note. MI is a measure that quantifies the amount of information, in the sense of information theory (Vinh et al., 2010), shared between clusterings, that is, segmentations of a set of elements into subsets with similar properties (in this case similar greening trends and similar environmental conditions). MI values close to 0 signify that there is no link between the conditions causing multistable states and greening trends. On the contrary, values close to 1 indicate that there is an almost complete overlap in the conditions determining the vegetation state and the greening trends. The reference (Ref) case is computed by selecting random grid cells, from the entire region, covering the same area as the multistable case. Numbers in parentheses represent the percentage of change from the reference to the multistable case. Greening trends over multistable areas in North America are non-significant. Hence, results for North America are not reported here (see Supporting Information Table S2 for a more comprehensive overview).

K_2 but low values of r_2 , or low values of K_2 but high values of r_2 , two equilibria exist. With high values of both parameters, and with any value of r_2 but very low values of K_2 , only one equilibrium is possible. Results for K_1 and r_1 , with resister trees only, follow the same type of pattern; however, with very low values of either r_1 or K_1 , only one equilibrium is possible. Additionally, it is possible to find mixed equilibria in which both x_1 and x_2 are non-zero, as depicted in Figure 6 with fixed growth rates r_1 and r_2 . The other cases, that is, competition between avoiders and either embracers or resisters, yield qualitatively the same results (not shown).

3.5 | Stability of solutions

The eigenvalues of the Jacobian matrix of the model depend on the choice of the four environment-dependent parameters K_1 , r_1 , K_2 and r_2 , requiring a numerical algorithm to determine their sign and making a comprehensive visualization not feasible (see Supporting Information Section S3 for detailed information). Nonetheless, it is possible to group results into four qualitatively different cases. The first is the trivial case in which the only stable equilibrium is the null one, that is, $x_1 = x_2 = 0$. The second case, additionally, has a second stable equilibrium where either $x_1 \neq 0$ or $x_2 \neq 0$. The third case, instead, has one additional equilibrium with $x_1 \neq 0$, and one with $x_2 \neq 0$. The fourth case, finally, corresponds to the trivial case, with the addition of a mixed equilibrium where both $x_1 \neq 0$ and $x_2 \neq 0$.

The first case can only be obtained with parameters allowing for only one equilibrium of x_1 and x_2 , corresponding to white areas of Figure 5. The second case corresponds to parameters that allow for only one equilibrium for one PFT, and three equilibria for the other

TABLE 4 Spearman's rank-order correlation coefficients (r_s) between leaf area index trends (LAI) and environmental conditions determining alternative tree-cover states (ATS), and between normalized difference vegetation index trends (NDVI) and ATS, over multistable regions

Region	r_s (LAI, ATS)	r_s (NDVI, ATS)
Eastern Eurasia	-.06	.19
Western Eurasia	-.29	-.28

Note. As greening trends over multistable areas in North America are non-significant, only results for Eurasia are reported (see Supporting Information Table S3 for a more comprehensive overview).

one, that is, a white area in one figure and a dark area in the second one. The third case requires parameters allowing for three equilibria of both PFTs. The fourth case can only be found with parameters allowing for mixed equilibria, as in Figure 6.

Furthermore, we find that permafrost, as a parameter determining K_1 and K_2 , induces a bifurcation, that is, a change in the number or type of stable solutions of the model. In particular, we find that, when forcing the model with permafrost distribution from Eurasia but environmental conditions from North America, different stable solutions appear with higher permafrost presence. Moreover, for the case of resister and embracer trees, the stable equilibria with only embracers cease existing and the model shifts to mixed equilibria where resisters are the dominant PFT (not shown, see Supporting Information Section S4.1).

4 | DISCUSSION

The recently detected greening trends (Zhu et al., 2016) and multistable areas of the boreal ecosystem (Abis & Brovkin, 2017) could potentially be linked by a causal relationship. Specifically, the detection of alternative tree-cover states could be influenced by pre-existing greening trends, and greening trends could be affected by a previous shift between alternative states in a multistable region that resulted in a sudden tree-cover change. Moreover, the extent of trends in North America and Eurasia adds seemingly contradicting evidence to the argument. On the one hand, LAI and NDVI trends in multistable regions over North America are non-significant, suggesting that there is no connection between trends and alternative states in this area. On the other hand, as summarised in Table 3, LAI and NDVI trends in multistable areas over Eurasia are more pronounced, hinting at a possible link with transition zones between vegetation states.

In agreement with the latter hypothesis, the value of the MI metric over randomly selected grid cells over Eurasia is c. .5, as reported in Section 3.1. This indicates that the environmental conditions analysed in our study are a major determinant for the greening trends, and does not come as a surprise. In fact, vegetation in the boreal area is influenced by environmental conditions, temperature in particular, which have been changing drastically due to anthropogenic activity (IPCC, 2013), affecting the detected trends.

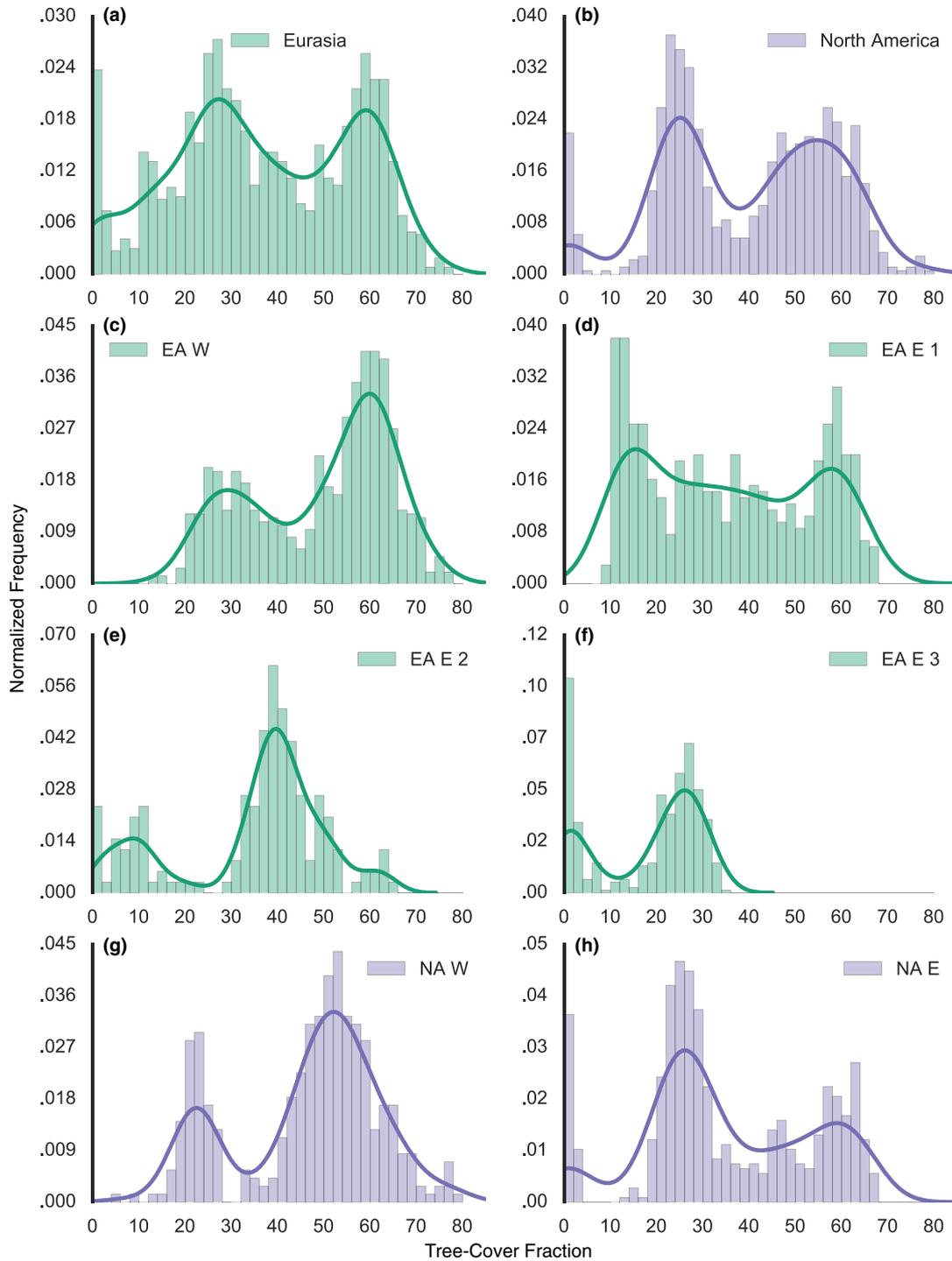


FIGURE 3 Modelled tree-cover distribution over Eurasia (a) and North America (b). (c) to (f) represent the modelled tree-cover fraction distribution over the four sub-areas of Eurasia, whereas (g) and (h) represent results in the two sub-areas of North America, as depicted in Figure 2. Green-coloured histograms are related to Eurasia, purple ones to North America. The lines correspond to the modal peaks obtained from kernel density estimates. The x axis always represents the tree-cover fraction values, divided into bins of equal size (2%), whereas the y axis corresponds to the normalized frequency of each tree-cover fraction bin. NA W = Western North America; NA E = Eastern North America; EA W = Western Eurasia; EA E 1 = Eastern Eurasia Area 1; EA E 2 = Eastern Eurasia Area 2; EA E 3 = Eastern Eurasia Area 3

However, the MI metric drops almost to 0 when including only multistable grid cells, as reported in Table 3 and corroborated by the Spearman's rank-order correlation coefficients r_s of Table 4, indicating that LAI and NDVI greening trends in these areas are not

associated with environmental conditions. This, in turn, suggests that the detected trends could have been affected by shifts between alternative tree-cover states under the same environmental conditions. Vice versa, as greening trends in multistable regions over

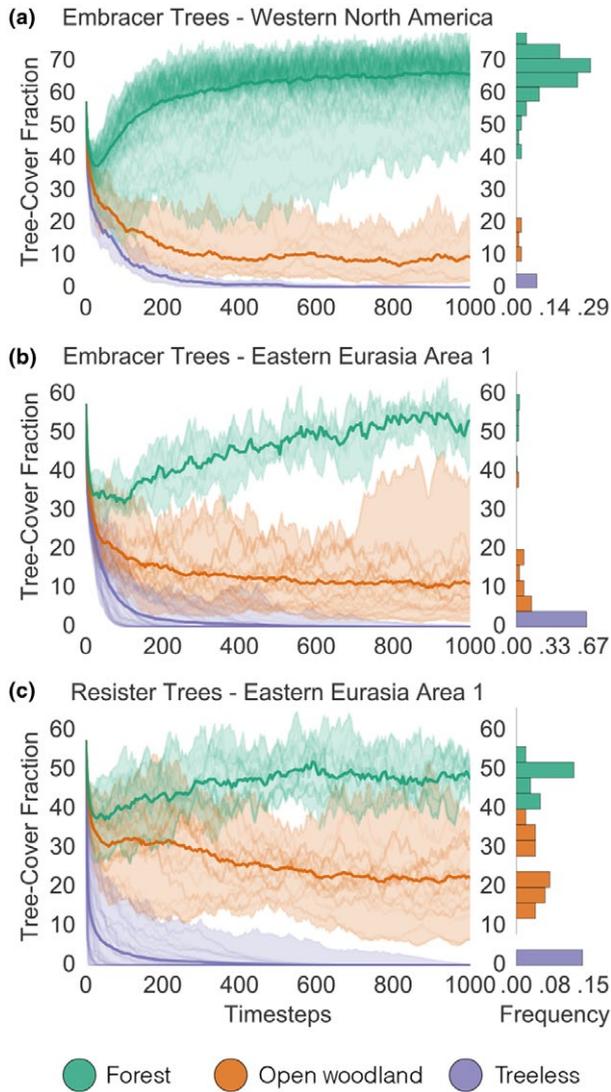


FIGURE 4 Simulated dynamics of embracer species over Western North America (a) and Eastern Eurasia Area 1 (b), and dynamics of resister species over Eastern Eurasia Area 1 (c). Left panels represent the evolution of initial population for 1,000 timesteps. Each line corresponds to a set of conditions for the four parameters K_1 , K_2 , r_1 and r_2 , which are determined using forcing values for the regional environmental conditions as in Table 1. Each plot is coloured according to the final vegetation state attained: purple for Treeless, orange for Open woodland and green for Forest. Thicker lines correspond to the evolution of the mean state in each shaded area. The histograms on the right represent the normalized frequency of the final tree-cover fraction distribution attained

North America are non-significant, and environmental conditions are not linked to LAI and NDVI trends over multistable regions, we conclude that the detection and existence of multistable areas are not affected by vegetation trends, that is, high greening/browning trends do not imply the detection of a multistable region.

Zhu et al. (2016), using factorial simulations with several ecosystem models, suggested that CO_2 fertilization effects can explain 70% of the observed greening trend at a global level. However, when

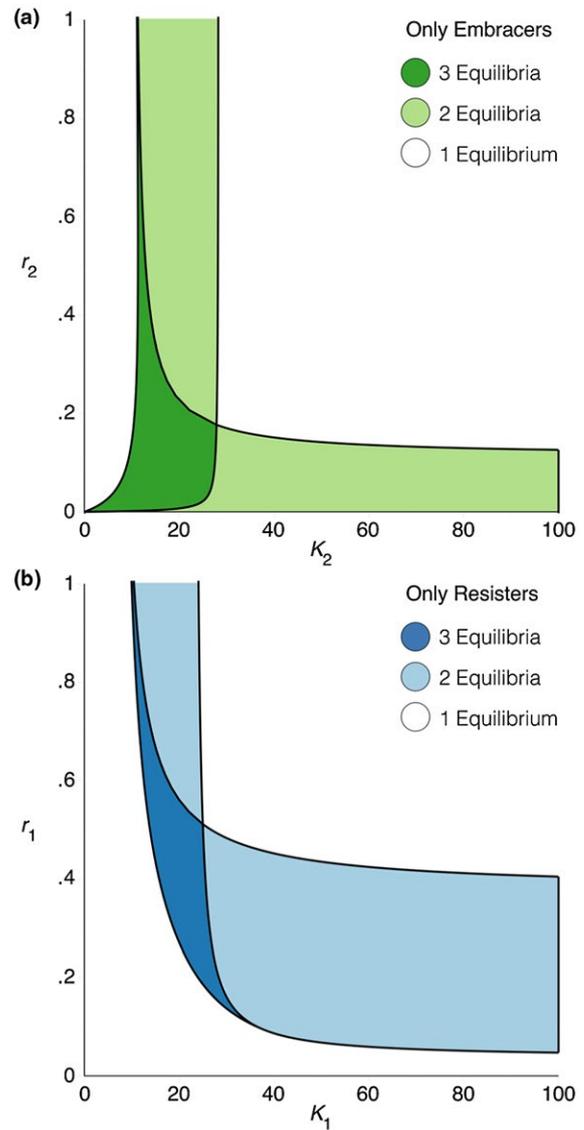


FIGURE 5 Dependence on the environment-dependent parameters K_i and r_i of the number of equilibria with only embracer trees (a) and only resister trees (b). Both plots correspond to competition between embracer and resister trees. Depicted equilibria have a null resister population in (a), and null embracer population in (b)

focusing on the boreal region, they concluded that changes in vegetation could be attributed in large part to climate change and “other factors.” In line with these results, our analysis suggests that shifts between alternative tree-cover states might have played a significant role in determining vegetation trends over multistable areas in Eurasia. Nonetheless, there are missing factors in our analysis, such as trends in CO_2 and nutrients, for example, nitrogen, which play an important role in determining vegetation trends, and that could explain why the value of the MI metric for the reference case is not c. 1. Furthermore, the recent analysis of Sulla-Menashe, Woodcock, and Friedl (2018) showed that greening and browning trends over Canada seem to reflect disturbance–recovery dynamics instead of

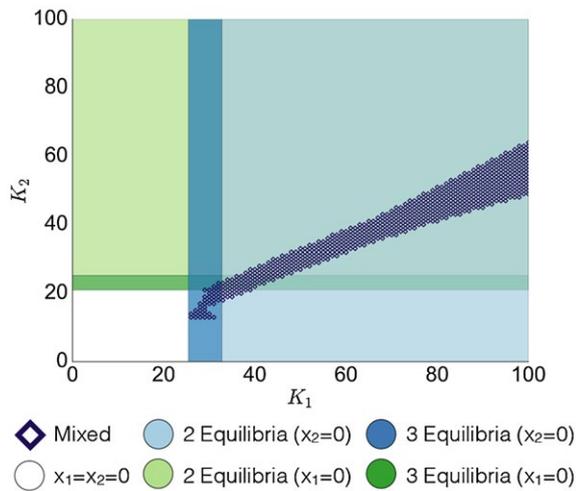


FIGURE 6 Dependence of the number of critical points on environmental carrying capacities K_1 and K_2 , with fixed growth parameters, $r_1 = .68$ and $r_2 = .12$, using embracer and avoider species. Cases where either $x_1 = 0$ or $x_2 = 0$ are marked as coloured regions, whereas dark diamonds represent mixed equilibria where both x_1 and x_2 are non-zero

climate change impacts, and that observed NDVI changes are often limited to small geographic locations. These results are in agreement with our MI metric analysis, as fire occurrence is part of the environmental variables employed in our study. Nonetheless, the fact that in multistable areas in Eurasia the MI metric drops almost to 0, even when considering fire frequency, suggests that these areas lie outside of the expected ecological response to climate change. As we shall discuss, this hypothesis is reinforced by results from our conceptual model, which show how changes in tree cover depend not only on climate change and fire regime, but also on the competition between different fire PFTs, which is connected to both aspects. Thus, in follow-up studies it would be useful to look deeper into the link between multistability, greening trends and wildfires. In particular, to project future effects of climate change, and to increase the predictive power of our conceptual model, it will be important to include the role of increased levels of CO_2 and a more realistic representation of forest fires. Nevertheless, our findings illustrate that shifts in the vegetation of the boreal ecosystem can be linked to environmental variables that are deeply affected by climate change.

Our conceptual model is able to reproduce the multistability of boreal tree cover suggested by the data, as shown in Figure 3. The modelled alternative stable states are markedly dependent on the parameters of the system, corresponding to environmental conditions, to the disturbance regime and to the fire-specific traits of the different PFTs, as illustrated in Figures 5 and 6. From the climate point of view, this hints at the fact that the stability of the boreal forest is linked in a nonlinear way to environmental conditions, and can shift abruptly under a slowly changing environment. In particular, our analysis suggests that the number of alternative stable tree-cover states depends primarily on the competition between PFTs

with different adaptations to disturbances and on the feedbacks between tree cover and permafrost.

Results from Sections 3.4 and 3.5 represent three scenarios. First, in the case where three equilibria of the same PFT are possible, as in Figure 5, only two will be stable. Hence, if the system is perturbed from the state with positive tree cover, it will either recover to the same vegetation state, or collapse to a treeless state, as intermediate states are unstable. Second, when two equilibria of the same PFT are possible, only one of the two can be stable, as in Figure 5. Changing environmental conditions could reverse which one is stable, causing a rapid shift, or revert the system to the case with three equilibria. Third, in the case where mixed equilibria are possible, as in Figure 6, the vegetation can follow any of the previous pathways, with the addition of a stable mixed tree-cover state. In this scenario, a perturbed system in mixed equilibrium could either recover, switch to a state in which only one PFT is present, or collapse completely.

The three scenarios introduced above imply that, as environmental conditions vary, the resulting modelled alternative tree-cover states can either have different tree-cover fractions, different PFT compositions or both. This latter distinction is important because the dynamics of the boreal forest in terms of successional changes and carbon cycling is primarily driven by wildfires (Beck et al., 2011; Bond-Lamberty, Peckham, Ahl, & Gower, 2007; Viereck, 1973), which additionally help to regulate climate and ecosystem dynamics (Rogers et al., 2015). The dominant control of fire dynamics, in turn, comes from the vegetation composition, which influences fire behaviour and effects through fuel structure, fuel moisture and susceptibility to mortality (Flannigan, 2015; Rogers et al., 2015). For this reason, even though fire weather indices are similar between continents, most fires in embracers-dominated North America are high-intensity crown fires, whereas most fires in resisters-dominated Eurasia are surface fires (Flannigan, 2015; de Groot et al., 2013; Rogers et al., 2015; Wooster & Zhang, 2004). This differentiation of alternative states in terms of PFTs and associated fire regimes suggests that the extent of multistable areas with low resilience estimated in Abis and Brovkin (2017) might be a conservative one. In fact, in their approach, vegetation was treated only in terms of tree-cover fraction without information on the PFT composition and its effects on wildfires. Hence, alternative states with similar tree-cover fraction states but different PFTs could not have been detected, nor could alternative states with different fire regimes due to the vegetation composition. In this context, our results from Sections 3.4 and 3.5 indicate that biome shifts between alternative states with different PFT compositions are also possible in both continents, implying that the extent of multistable areas might be greater than previously thought. Additionally, this suggests that transitions between multistable states can affect not only the magnitude of feedbacks with the environment, that is, different albedo and evapotranspiration values (Brovkin, Raddatz, Reick, Claussen, & Gayler, 2009), but also the function of the boreal forest.

This is of particular relevance as the boreal forest is expected to experience a rapid temperature increase during the 21st century,

with a connected increase in fire frequency and fire size (Héon, 2014). Furthermore, possible shifts between alternative states with different PFTs would have important repercussions on the climate, as boreal forests contain a third of the terrestrial carbon stocks (Crowther et al., 2015; Gauthier et al., 2015). A higher fire intensity will lead to substantial higher carbon emissions, and to changes in the albedo of the land surface, with an impact on surface temperatures, as the high-intensity crown fires associated with embracers are more likely to kill trees with low albedo, thus increasing reflectivity of land more than a fire suppressed by resisters (Rogers et al., 2015; M. Flannigan, 2015). In our conceptual model, the multistability of the boreal forest and the asymmetry in PFT distribution between continents are driven by the distribution of environmental conditions and by competition. Additionally, as we employed a stochastic disturbance regime that does not differentiate between continents, our results suggest that the dominant PFT is determined by adaptations to other key environmental conditions, permafrost thaw in particular. However, the goal of our study is towards alternative tree-cover states, and the magnitude of these implications and feedbacks cannot be studied with our model, as it does not include any coupled process nor does the disturbance scheme employed take into account differences in fuel characteristics. Moreover, in a real ecosystem, shifts in forest composition will additionally depend on the possibility of species invasions and seedling establishment, which, in turn, involve different strategies and plant traits (Grotkopp, Rejmánek, & Rost, 2002; Herron, Martine, Latimer, & Leicht-Young, 2007). For this reason, in follow-up studies, it would be useful to look deeper into the coupling between environment, climate and alternative tree-cover states.

Permafrost, the condition of soil when its temperature remains below 0 °C continuously for at least 2 years, influences vegetation in several ways and, according to our results of Section 3.5, plays a key role regarding multistability. Permafrost can impede infiltration and regulate the release of water from the seasonal melting of the active soil layer, inhibit water uptake and root elongation, restrict nutrient availability, and slow down organic matter decomposition (Bonan & Shugart, 1989; Woodward, 1987). Furthermore, permafrost thaw can guarantee a constant supply of water during the growing season. For these reasons, soil temperature and soil moisture are two of the primary factors determining vegetation patterns (Bonan & Shugart, 1989).

Surface warming due to climate change will dramatically impact regions underlain by permafrost, and cause widespread permafrost thaw (Camill, 2005; IPCC, 2013). Permafrost thaw in well-drained sites produces warmer and drier soil conditions, favourable for afforestation, whereas thaw in poorly drained sites can result in wetter and cooler conditions dominated by *Sphagnum* species (Camill, 2005). At the same time, permafrost degradation and warmer conditions have been observed to promote an increase in shrub abundance and encroachment, at the expenses of other biomes (Myers-Smith et al., 2011).

In this context, our results from Section 3.5 additionally suggest that permafrost might be responsible for the asymmetry in PFTs

between continents, and that permafrost thaw might induce changes in the dominant PFT, causing shifts between different tree-cover types. In fact, in areas extensively underlain by permafrost, such as Siberia, forests are capable of developing because of the specific root strategies of the plants within them (Jackson et al., 1996; Sugimoto, Yanagisawa, Naito, Fujita, & Maximov, 2002) and their adaptations to the additional summer moisture provided by the melting of permafrost (Nadezda, Gerald, & Elena, 2006). Thus, in a changing ecosystem, resisters dominating these areas might lose their competitive advantage over other PFTs due to the same survival traits that allowed their establishment. Hence, we hypothesize that permafrost degradation in Eurasia might not only lead to a northwards expansion of vegetation, but also to the loss of stability of resister communities, with the possibility of regional tree-cover shifts.

Clearly, our conceptual model is not fully representative of the complex dynamics determining the boreal forest's distribution and composition. In fact, despite its low diversity in tree species, the boreal forest's structure depends on interactions between a multitude of factors, including precipitation, air temperature, solar radiation, nutrient availability, soil moisture, soil temperature, presence of permafrost, depth of forest floor organic layer, forest fires, insect outbreaks, grazing from herbivores, understory composition, soil microbes, and more (Bonan, 1989; Gauthier et al., 2015; Van Der Heijden, Bardgett, & Straalen, 2008; Heinselman, 1981; Hare & Ritchie, 1972; Nilsson & Wardle, 2005; Shugart et al., 1992; Soja et al., 2007). For instance, soil fertility is in great part driven by the understory vegetation, with consequences on plant growth and tree seedling establishment (Bonan & Shugart, 1989; Nilsson & Wardle, 2005). Accumulation of organic matter and carbon can be promoted by increased nitrogen deposition, which, at the same time, might decrease forest growth through its effects on soil processes (Mäkipää, 1995). Moreover, nitrogen does not only limit plant growth in the boreal forest (Mäkipää, 1995), but it also affects herbivore grazing (Ball, Danell, & Sunesson, 2000), influencing indirectly the cycling of soil nutrients and plant regeneration (Wal, 2006). Furthermore, our model does not incorporate explicitly the passing of time, which is needed to represent in detail forest succession after disturbances (Bergeron & Dubue, 1988; Van Cleve & Viereck, 1981).

In order to simulate in depth the complex dynamics of the boreal forest, a more comprehensive coupled climate vegetation model would be needed. Our goal, however, is to explore whether a conceptual mechanism, such as the competition between tree species with different survival adaptations, can explain the detected multimodality and multistability of the boreal forest (Scheffer et al., 2012; Xu, Holmgren, et al., 2015; Abis & Brovkin, 2017) with respect to steady alternative tree-cover states. Hence, we intentionally kept our model simple, so that we could control its different components. This, additionally, serves the purpose of highlighting the importance of certain factors, such as permafrost and fire adaptations, and their role in determining the boreal forest's stability. Furthermore, results from our study suggest that these key components should be included in global dynamic vegetation models if they are to capture

and reproduce the nonlinear dependence between tree cover and environmental conditions at high latitudes.

The boreal forest, with about 0.74 trillion densely distributed trees (Crowther et al., 2015) encompassing almost 30% of the global forest area, is an ecosystem of key importance in the Earth system. Currently, climate change is impacting the boreal ecosystem more rapidly and intensely than other regions on Earth, and its surface temperature has been increasing approximately twice as fast as the global average (IPCC, 2013). As our analysis shows, changes in the disturbance regime and in the dynamics and distribution of permafrost could have profound implications for the stability of the boreal forest. Incidentally, surface temperature is deeply connected to these factors, as its warming can increase the frequency and extent of wildfires (M. D. Flannigan, Logan, Amiro, Skinner, & Stocks, 2005; Balshi et al., 2009; Johnstone et al., 2010), promote insect outbreaks (Volney & Fleming, 2000), and modify permafrost thawing and the hydrological cycle (Camill, 2005; Osterkamp, 2007; Osterkamp & Romanovsky, 1999; Schuur et al., 2009). As the number of modelled alternative tree-cover states varies depending on such environmental conditions (see Section 3.4), a slow rise in surface temperature could increase the extent of multistable areas, with the risk of abrupt vegetation shifts.

However, the majority of current global models is not able to reproduce intrinsic alternative vegetation states (Van Nes et al., 2014). The inclusion of fire as an interactive process in dynamic global vegetation models, such as JSBACH-SPITFIRE, makes it possible to simulate the intrinsic multistability of savanna regions (Lasslop, Brovkin, Reick, Bathiany, & Kloster, 2016). Our findings of Sections 3.4 and 3.5 suggest that, for the boreal ecosystem, multistability ensues from the interplay between different PFTs, wildfires and environmental conditions such as permafrost, soil moisture and soil nutrients. Hence, in order for coupled climate vegetation models to predict alternative tree-cover states in high latitudes, it is recommendable to include such interplay.

5 | CONCLUSIONS

Through the use of the MI metric, we conclude that the detection of multistable areas of the boreal forest is not affected by the recent greening trends of LAI and NDVI. Vice versa, shifts between alternative tree-cover states could have influenced the detected greening trends.

We developed and applied a conceptual model based on competition between PFTs with different survival adaptations to disturbances. We find that multistability of the tree cover in the boreal region can emerge through competition, and that alternative states can differ both in tree-cover fraction and PFT composition.

The stability of the modelled boreal forest equilibria depends on environmental conditions, particularly permafrost distribution, highlighting the fundamental role of permafrost thaw and degradation in a changing climate. Additionally, our analysis suggests that asymmetry in tree species distribution between North America and Eurasia

could be associated with bifurcation points due to the presence of permafrost.

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DATA ACCESSIBILITY

All data necessary to reproduce the paper are provided in the Supporting Information, and are also stored within the publication repository of the Max Planck Society at <http://hdl.handle.net/21.11116/0000-0002-AA10-C> (please contact Carola Kauhs at carola.kauhs@mpimet.mpg.de in case of issues).

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