Environmental Conditions for Alternative Tree Cover States in High Latitudes

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Abstract. Previous analysis of the vegetation cover from remote sensing revealed the existence of three alternative modes in the frequency distribution of boreal tree cover: a sparsely vegetated treeless state, an open woodland state, and a forest state. Identifying which are the regions subject to multimodality, and assessing which are the main factors underlying their existence, is important to project future change of natural vegetation cover and its effect on climate.

We study the impact on the tree cover fraction distribution (TCF) of eight globally-observed environmental factors: mean annual rainfall (MAR), mean minimum temperature (MTmin), growing degree days above 0°C (GDD0), permafrost distribution (PZI), mean spring soil moisture (MSSM), wildfire occurrence frequency (FF), soil texture (ST), and mean thawing depth (MTD). Through the use of generalised additive models, conditional histograms, and phase-space analysis, we find that environmental conditions exert a strong control over the tree cover distribution, generally uniquely determining its state. Additionally, we find that the relationship between tree cover and environment is different within the four boreal regions here considered, namely Eastern North Eurasia, Western North Eurasia, Eastern North America, and Western North America. Furthermore, using a classification based on MAR, MTmin, MSSM, PZI, FF, and ST, we show the location of areas with potentially alternative tree cover states under the same environmental conditions in the boreal region. These areas, although encompassing a minor fraction of the boreal area (~5%), are of interest for a more detailed analysis of land-atmosphere interactions.

1 Introduction

Forest ecosystems are a fundamental component of the Earth, as they contribute to its biophysical and biogeochemical processes (Brovkin et al., 2009), and harbour a large proportion of global biodiversity (Crowther et al., 2015). However, changes in species composition, structure, and function are happening in several forests around the world (Phillips et al., 2009; Lindner et al., 2010; Poulter et al., 2013; Reyer et al., 2015b). These changes originate from a combination of environmental changes, such as CO_2 concentration, drought, and nitrogen deposition (Hyvönen et al., 2007; Michaelian et al., 2011; Brouwers et al., 2013; Brando et al., 2014; Reyer et al., 2015a), and local drivers, both anthropogenic and not, such as forest management, wildfires, and grazing (Volney and Fleming, 2000; Malhi et al., 2008; Barona et al., 2010; DeFries et al., 2010; Bond and Midgley, 2012; Bryan et al., 2013). Environmental and climate changes, as well as extreme events, are likely to play a more prominent role in future decades (Johnstone et al., 2010; Orlowsky and Seneviratne, 2012; Coumou and Rahmstorf, 2012; IPCC, 2013), affecting

the resilience of forests - i.e., the ability to absorb disturbances maintaining similar structure and functioning (Scheffer, 2009) - and possibly pushing them towards tipping points and alternative tree cover states (IPCC, 2013; Reyer et al., 2015a), potentially inducing ecosystem shifts (Scheffer, 2009).

Increasing attention has been given to the response of ecosystem to past climate changes (Huntley, 1997; Huntley et al., 2013), and to ecosystems exhibiting potential alternative tree cover states under the same environmental conditions, as key factors to a deeper understanding of forest resilience. To such avail, in this paper, we investigate the relationship between environment and remotely-sensed tree cover distribution within the boreal ecozone. Through the use of generalised additive models (GAMs), conditional histograms, and phase-space analysis, we assess whether alternative stable tree cover states are possible in the boreal forest, and under which environmental conditions. Hence, understanding the mechanisms underpinning them is a key point to assess future ecosystem changes (Reyer et al., 2015a).

In this context, it has recently been hypothesised that tropical forests and savannas can be alternative stable states under the same environmental conditions. A stable state being the state an ecosystem will return to after any small perturbation (May, 1977). Evidence for bistability in the tropics has been inferred through fire exclusion experiments (Moreira, 2000; Higgins et al., 2007), field observations and pollen records (Warman and Moles, 2009; Favier et al., 2012; de L. Dantas et al., 2013; Fletcher et al., 2014), mathematical models (Staver and Levin, 2012; van Nes et al., 2014; Baudena et al., 2014; Staal et al., 2015), and satellite remote sensing (Hirota et al., 2011; Staver et al., 2011a, b; Yin et al., 2015).

One key evidence is that the tree cover distribution in the tropics is trimodal (Hirota et al., 2011). In fact, multimodality of the frequency distribution can be caused by the existence of alternative stable states in the system (Scheffer and Carpenter, 2003). In the case of the tropics, multimodality could be an artefact of satellite data processing (Hanan et al., 2014), however, it has been suggested that this issue is not of major importance (Staver and Hansen, 2015). The proposed mechanism responsible for the forest-savanna bistability is a positive feedback between tree cover and fire frequency. The same mechanism has also been employed to explore the potential of multiple stable states in a global dynamic vegetation model (Lasslop et al., 2016). Per contra, it has been suggested that trimodality of the tree cover distribution is not necessarily due to wildfires, since it can be achieved through nonlinearities in vegetation dynamics and strong climate control (Good et al., 2016). The picture is far from complete, as there is evidence that other environmental factors might play a fundamental role in controlling the tree cover distribution (Mills et al., 2013; Veenendaal et al., 2015; Staal and Flores, 2015; Lloyd and Veenendaal, 2016).

In a similar fashion, multimodality of the tree cover distribution has recently been detected within the boreal biome (Scheffer et al., 2012). The boreal forest is an ecosystem of key importance in the earth system, as it encompasses almost 30% of the global forest area and comprises about 0.74 trillion densely distributed trees (Crowther et al., 2015). Despite a low diversity of tree species, boreal forest's structure and composition depend on interactions between precipitation, air temperature, available solar radiation, nutrient availability, soil moisture, soil temperature, presence of permafrost, depth of forest floor organic layer, forest fires, and insect outbreaks (Kenneth Hare and Ritchie, 1972; Heinselman, 1981; Bonan, 1989; Shugart et al., 1992; Soja et al., 2007; Gauthier et al., 2015). The boreal ecozone is highly sensitive to changes in climate and can affect the global climate system through its numerous feedbacks, the most important ones related to albedo changes, soil moisture recycling, and the

carbon cycle (Gauthier et al., 2015; Steffen et al., 2015). However, the dynamics of the boreal ecosystem regarding gradual changes and critical transitions are not yet understood (Bel et al., 2012; Scheffer et al., 2012).

Previous analysis of the vegetation cover from remote sensing revealed the existence of three alternative modes in the frequency distribution of boreal trees (Scheffer et al., 2012; Xu et al., 2015): a sparsely vegetated treeless state, an open woodland "savanna"-like state, and a forest state. These three modes could represent alternative stable states, hence, identifying which are the regions subject to multimodality, and assessing which are the main factors underlying their existence, is important both to understand boreal forest dynamics, and to project future changes of natural vegetation cover and their effect on climate.

We do acknowledge that vegetation and climatic variables are linked through a more differentiated set of interactions than just mean annual rainfall, fire frequency, and forest cover. Henceforth, to improve our understanding of the boreal ecosystem dynamics, we investigate the impact of eight globally-observed environmental variables (EVs) on the tree cover fraction (TCF) distribution. To do so, we make use of satellite products spanning the time period up until 2010, incorporating both spatial and temporal information in our analysis, and taking into account the past variability of the boreal ecosystem. Furthermore, we investigate whether the three observed vegetation modes could represent alternative stable tree cover states. To such avail, we adoperate generalised additive models (GAMs), conditional histograms, phase-space analysis, and statistical tests.

2 Methods and Materials

2.1 Environmental Variables Datasets

We study the impact on the tree cover fraction distribution of eight globally-observed environmental variables (EVs): mean annual rainfall (MAR), mean minimum temperature (MTmin), growing degree days above 0°C (GDD0), permafrost distribution (PZI), mean spring soil moisture (MSSM), wildfire occurrence frequency (FF), soil texture (ST), and mean thawing depth (MTD). These factors are chosen based on the work of Kenneth Hare and Ritchie (1972), Woodward (1987), Bonan (1989), Bonan and Shugart (1989), Shugart et al. (1992), and Kenkel et al. (1997), and they are summarised in Table 1.

The tree cover dataset has certain biases and limitations: it underestimates shrubs and small woody plants, as the product was calibrated against trees above 5m tall (Bucini and Hanan, 2007), it never resolves 100% tree cover, it is not well-resolved at low tree cover (Staver and Hansen, 2015), and may not be useful for differentiating over small ranges of tree cover (less than c.10%) (Hansen et al., 2003), as the use of classification and regression trees (CARTs) to calibrate the dataset might introduce artificial discontinuities (Hanan et al., 2014). Regarding the particular case of the northern latitudes, an evaluation of the accuracy of the MODIS VCF product pointed out that the dataset may not be suitable for detailed mapping and monitoring of tree cover at its finest resolution (500m per pixel), especially for tree cover below 20%, and that there might be a systematic bias over the Scandinavian region (Montesano et al., 2009). To overcome these limitations, we employ MODIS VCF data at a coarser resolution (0.05°, subsequently re-projected to 0.5°), we aggregate for most of the analysis tree cover values into three bins encompassing the 0–20, 20–45, 45–100 percent ranges, and we exclude gridcells over Scandinavia from the analysis.

In our analysis, we investigated the use of an alternative dataset for MTmin, namely the CRU TS3.22 tmn product, for the years 1998–2010 (Harris et al., 2014). This dataset has a finer resolution and provides a more detailed picture of the ecosystem,

Table 1. Variables and datasets summary.

Variable	Origin	Reference
Percentage tree cover fraction (TCF)	0.05° MODIS MOD44B V1 C5 2010 product	Townshend et al. (2010)
Mean annual rainfall (MAR)	CRU TS3.22 Precipitation dataset 1998–2010	Harris et al. (2014)
Mean seasonal soil moisture (MSSM)	CPC Soil Moisture dataset 1998–2010	van den Dool et al. (2003)
Mean minimum 2m temperature (MTmin)	NCEP/NCAR Reanalysis 1998–2010	Kalnay et al. (1996)
Permafrost zonation index (PZI)	Global Permafrost Zonation Index Map	Gruber (2012)
Fire frequency (FF)	GFED4 burned area dataset 1996–2012; Canadian National Fire Database 1980–2014	Giglio et al. (2013); Canadian Forest Service (2014)
Growing degree days above 0°C (GDD0)	NCEP Reanalysis (NMC initialized) 1998–2010	Kalnay et al. (1996)
Soil texture type (ST)	improved FAO soil type dataset	Hagemann and Stacke (2014)
Mean thaw depth (MTD)	Arctic EASE-Grid Mean Thaw Depths	Zhang et al. (2006)
Surface elevation	Global 30-Arc-Second Elevation Dataset	U.S. Geological Survey (1996)
Land cover type	Global Land Cover 2000 product (GLC2000)	GLC2000 database (2003).

albeit affected by a cold bias over Canada (see CRU TS 3.22 release notes, Harris et al. (2014)). Nonetheless, it shows similar patterns to the NCEP/NCAR product. The two datasets are heavily linearly correlated, although the CRU tmn product shows lower temperatures, especially over East North Eurasia and East North America. Since our analysis is independent of variables shifts, results obtained using the CRU tmn product are essentially the same (see supplementary material).

5   All datasets are re-projected using CDO (version 1.7.0) on a regular rectangular latitude-longitude grid at 0.5° resolution, and divided into four main areas using approximately the Canadian Shield and the Ural Mountains as middle boundaries for North America and Eurasia: Western North America (45° N–70° N and 100° W–170° W), Eastern North America (45° N–70° N and 30° W–100° W), Western North Eurasia (50° N–70° N and 33° E–68° E), and Eastern North Eurasia (50° N–70° N and 68° E–170° W). This is done in order to preserve continuity of patterns for the environmental variables and to separate areas with

10   different characteristics, e.g. due to oceanic influence. Note that most of Europe is excluded beforehand due to the high levels of human activity (Hengeveld et al., 2012) and to a possible bias in MODIS data (Montesano et al., 2009). Subsequently, data are filtered to restrict the analysis on areas with minimum anthropogenic influence and where altitude does not play a significant role (Staver et al., 2011b). Areas to exclude are identified using the Global 30-Arc-Second Elevation dataset and the Global Land Cover 2000 product; they correspond to sites that are either bare or flooded (codes: 15 and 19–21), subject to

15   intensive human activity (codes: 16–18 and 22), or with elevation greater than 1200m. The resulting datasets comprise 5848 gridcells for Eastern North Eurasia (EAE), 1559 for Western North Eurasia (EAW), 1775 for Eastern North America (NAE), and 3094 for Western North America (NAW).

Within this setup, we assume that the dataset products are suitable for our investigation.

2.2 Data Analysis

After filtering and dividing the dataset, we confirm the multimodality of the tree cover distribution in high latitudes, as found by Scheffer et al. (2012) and in line with results from Xu et al. (2015), by optimising the fitting of different sums of Gaussian functions over the TCF distribution (not shown). Next, we group all data gridcells according to the modal peaks into three

5 states: "treeless", where TCF is smaller than 20%, "open woodland", with TCF between 20% and 45%, and "forest", where TCF is greater than 45%. The ensuing data analysis is aimed at two main purposes: to ascertain the impact of EVs on the TCF, and to assess whether different vegetation states can be found under the same set of EVs.

First, we evaluate the impact of the eight environmental factors on the TCF distribution using Generalised Additive Models (Miller et al., 2007). GAMs are data-driven statistical models able to handle non-linear data structures (Hastie and Tibshirani,

10 1986, 1990; Clark, 2013); their purpose is to ascertain the contributions and roles of the different variables, thus allowing a better understanding of the systems (Guisan et al., 2002). Each GAM test provides an estimate of the proportion of TCF distribution that can be explained through a smooth of one or more EVs (Staver et al., 2011b) - for instance, the formula $TCF = s_1(MTmin) + s_2(MAR)$ is used to assess the contribution of minimum temperature and precipitation on the tree cover fraction distribution. For each region, we repeatedly apply GAMs including different combinations of variables, and - to

15 determine whether the sample size influences the results - we use in turn either multiple random samples of 500 gridcells each, multiple random samples of 1000 gridcells each, or all the gridcells.

Subsequently, we analyse the conditional 2-dimensional phase-space between the EVs to visualise whether intersections of vegetation states in each phase-space are possible or not. To do so, we perform a kernel density estimation (KDE) of the joint distribution between the two EVs, conditioned to whether ot not the corresponding data belong to the treeless, open woodland,

20 or forest state, and we plot the KDE together with the EVs histograms. Kernel density estimates are used to approximate the probability density function underlying a set of data (Silverman, 1981, 1986).

Next we look at the 6-dimensional phase-space formed by mean annual rainfall, mean spring soil moisture, mean minimum temperature, permafrost distribution, wildfire frequency, and soil texture, and we divide it into classes in the following manner. First, for every region, we divide the domain of each EV into bins. To do so, we compute the 10th and 90th percentile of

25 the three vegetation states with respect to MTmin, MSSM, MAR, PZI, and FF. Then, for the same EVs, we select the second lowest 10th and second highest 90th percentiles; these two values are the boundaries of the first and last bin, while the range in between them is equally divided into bins: 5 for MTmin, MSSM, and MAR, and 3 for FF and PZI, as exemplified in Fig. 1 for MTmin; ST is instead divided according to the clay, sand, and loam groups. By doing so, we separate the range of an EV where overlaps between the KDEs of the vegetation states are more likely to happen, from ranges where only one vegetation state is

30 more likely to be found (respectively the central bins and the two most external ones). Second, we consider the partition of the 6D phase-space among the EVs generated by the so computed bins. Each element of this partition is defined as a class, i.e., a class is a set of bins for the EVs. The idea behind this analysis is to split the 6D EVs space into classes where EVs could be considered equal for all geographical gridcells. The question, then, is whether the tree cover could be different under the same environmental conditions.
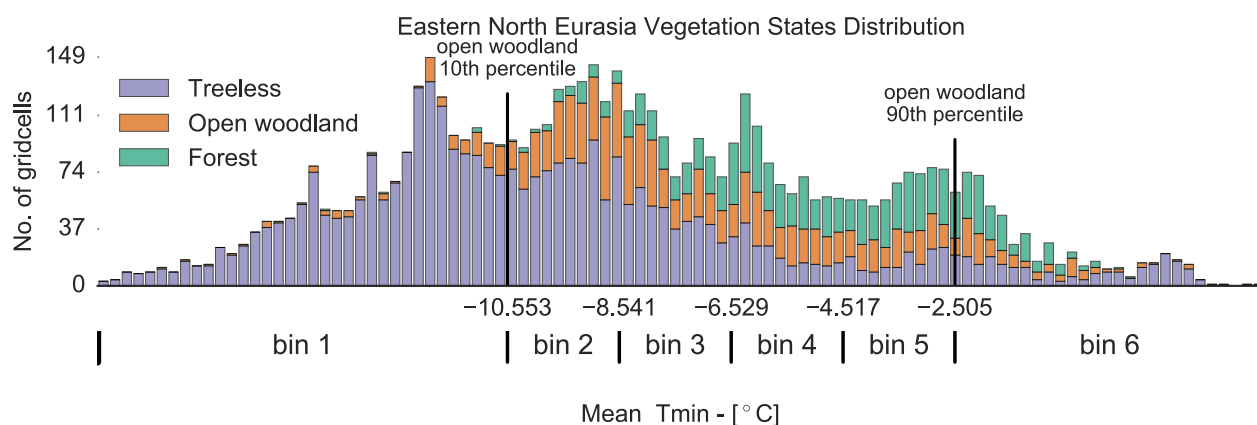
Figure 1. Bin division of MTmin for Eastern North Eurasia. The boundaries of the first and last bins are calculated using the second lowest 10th percentile and second highest 90th percentile of the three vegetation states, with respect to the EV in use, having in mind that only one vegetation state is generally found below or above this thresholds, respectively. The remaining space is subdivided uniformly.

Afterwards, to assess our research question, we associate every gridcell of the boreal area with its vegetation state and with the class corresponding to its EVs values. Subsequently, we select two types of areas of interest, that correspond to possible alternative states:

- equivalent tree cover states, defined as gridcells with different vegetation state but same EVs class, e.g., an open woodland gridcell and a forest gridcell, where all the environmental variables are in the same bins;

- fire disturbed (FD) tree cover states, defined as gridcells with different vegetation state, where the EVs are in the same bins, except for wildfire frequency, e.g., a forest gridcell with low fire frequency and an open woodland gridcell with higher fire frequency but with the remaining EVs in the same bins.

Within this last step, to take into account internal variability and the continuous evolution of the ecosystem, we consider only environmental classes that appear significantly, with a frequency above certain thresholds (generally at least 1% of the gridcells with the same vegetation state). Furthermore, we test the multimodality of the TCF distribution over gridcells with equivalent and fire disturbed tree cover states. To assess this, we employ the Silverman's test against the hypothesis of unimodality (Silverman, 1981; Hall and York, 2001). Finally, to ascertain the variability of the ecosystem, we compute the standard deviation of the TCF distribution for the period 2001–2010 over the same alternative states gridcells, and we compare it with the distributions of the alternative states.

The entire analysis is carried out using Python 2.7.10, IPython 4.0.1, and RStudio 0.99.441.

3 Results

3.1 GAM Results

A summary of GAMs results using random samples of 1000 gridcells is reported in Table 2. GAMs analysis using all the gridcells or random samples of 1000 gridcells yields similar results, with explained deviances for the former case in between the extremes of the latter, and always with statistical p-value< 0.0001. On the other hand, using samples of 500 gridcells can increase the explained portion of TCF distribution at the expenses of statistical significance, due to higher p-values, and larger-scale applicability.

Table 2. Summary of GAMs performed using random samples of 1000 gridcells each. The ranges represent the spread of results obtained with different samples. Statistical p-values are < 0.0001 for every case. Percentages of explained deviance are a measure of the goodness of fit of each GAM (McCullagh and Nelder, 1989; Agresti, 1996).

Variables	Deviance of TCF Explained - %			
	EA_E	EA_W	NA_E	NA_W
MAR	24–30	28–38	51–57	28–36
MSSM	12–20	20–29	43–53	11–21
MTmin	36–44	23–31	70–75	36–43
PZI	38–45	10–17	69–75	31–37
FF	2–9	15–20	8–13	11–19
GDD0	49–57	40–51	70–74	24–34
ST	9–18	26–35	42–52	9–15
MTD	21–33	27–37	39–46	18–30
MAR+MSSM	26–31	29–41	56–62	31–38
MTmin+GDD0	53–60	43–54	73–77	42–50
PZI+FF	42–48	34–42	70–76	34–42
All	60–67	52–58	80–85	59–65

The impact of EVs on the TCF distribution depends on the region of interest. Furthermore, the percentage of explained TCF distribution is reduced ($\sim 40\%$ maximum combined deviance explained) if we perform the analysis on broader regions than the ones here considered, i.e., on the entire boreal area at once or on the single continents. We hypothesise this is caused by the different species distribution across the regions. For instance, North America is mainly dominated by "fire embracer trees", promoting high-intensity crown fires, whereas Eurasia is populated by "resister trees" in its driest regions, i.e., Eastern North Eurasia, where only surface fires are common, and fire avoiders in Western North Eurasia, which burn less frequently due to the wetter climate of this region (Wirth, 2005; Rogers et al., 2015). As a result, despite the environmental variables having

different distributions, the general response of the tree cover distribution in the four regions is similar, but the impact of each individual EV varies within the regions.

GDD0 and MTmin are the EVs with the greatest influence on the TCF distribution, with a combined effect ranging from 42 to 77%, in line with literature, as temperature is the main limiting factor for boreal forest (Bonan and Shugart, 1989). The
5 next EV in order of importance is PZI, with an impact ranging from 10–17% to 69–75% depending on the southern extent of continuous permafrost. Water availability, as expressed through the combined effect of MAR and MSSM, explains 26 to 62% of the TCF distribution. The two variables have a similar influence when considered alone, although MAR has always a greater impact. The impact of wildfires depends on the region of interest, with FF contributing the lowest in Eastern Eurasia and the highest in Western Eurasia, 2–9% and 15–20% respectively. Soil related variables, namely ST and MTD, have a similar impact,
10 generally around 30%.

The environmental variables are not independent of each other, and hence the combined impact of multiple variables does not correspond to the sum of the single terms. For instance, permafrost presence, MTmin, and GDD0, are highly correlated, and their combined effect is only slightly greater than the effect of each factor alone. Overall, the combined effect of all the EVs contributes to 52–67% of the TCF distribution, with the exception of Eastern North America, where the cold temperatures,
15 permafrost distribution, and rainfall gradients, clearly dominate the tree cover distribution and make up for almost 80% of it (omitted from Table 2). We obtain similar results when combining temperature related EVs (GDD0, MTmin) with water related ones (MAR, MSSM).

We hypothesise the unexplained percentage of TCF distribution can be linked mainly to three possible causes. First, missing factors in the evaluation, for instance insect outbreaks, which are linked to climate and play an important role in the boreal
20 forest dynamic (Bonan and Shugart, 1989), or grazing from animals (Wal, 2006; Olofsson et al., 2010). Second, deficiencies in the datasets used, such as the underestimation of fire events in the boreal region (Mangeon et al., 2015), and the limited timespan of satellite observations, as fire return intervals in high latitudes can exceed 200 years (Wirth, 2005). Third, as shown later, the presence of areas where the system is in different alternative stable states under the same environmental conditions.

3.2 Phase-space results

25 Phase space plots for MAR versus MTmin, and MSSM versus GDD0 in Eastern North Eurasia are shown in Fig. 2. Combining together EVs in phase-space, it is possible to locate peaks in the distributions of the vegetation states. As for the case of GDD0, where low values clearly denote a peak in the distribution of the treeless state. Unfortunately, GDD0 does generally not separate well between the vegetation states in the central area of its distribution, and even combining it with other variables, a clear picture does not emerge. For this reason, and for its high correlation with MTmin (Pearson's correlation coefficient
30 $0.78 < r < 0.94$), GDD0 is not used in the classification. Similarly, MTD is also excluded.

In many phase-space regions, environmental conditions support only a single "dominant" vegetation state, as in Fig. 2b. Nonetheless, peaks of the KDEs are not always completely disjoint, and it is possible to find intersections between the KDEs of the different vegetation states, as if Fig. 2a, meaning that the same environmental conditions can lead to different vegetation states, hinting at possible alternative states. Results vary by region, and a complete description of all the combinations between

variables is beyond the scope of this paper. Suffices to say that extremes in the distributions of EVs are generally associated with a single vegetation state, as in Fig. 2b, whereas intermediate values allow for both single states and intersections, Fig. 2b and 2a, respectively. However, these intersections consider only two EVs at a time and they provide only part of the total picture. Results from the classification described and discussed in Sections 2.2 and 3.3 cover all the EVs at once.
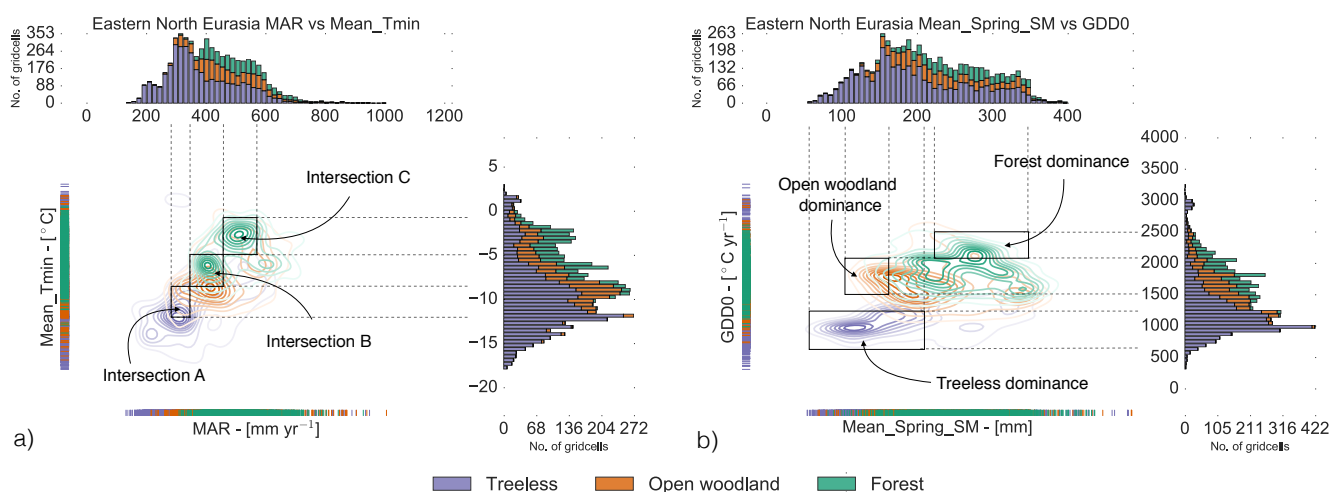
Figure 2. Representation of the KDEs of the three vegetation states in the phase-space generated by MTmin and MAR (a), and MSSM and GDD0 (b), for Eastern North Eurasia. The isolines describe the probability of finding the three vegetation states under the specified EVs regimes. Intersections in phase-space represent areas with different vegetation states under the same environmental conditions (a), whereas areas with only one dominant state hint at the unimodality of the underlying distribution (b).

3.3   6D phase-space classification results

Associating to every gridcell a class based on the values of the environmental variables reveals that in most cases there is a uniquely determined vegetation state for every class of EVs. However, a number of classes allow for different vegetation states, namely either treeless and open woodland, or forest and open woodland. Gridcells belonging to these classes are called equivalent tree cover states. Furthermore, by selecting gridcells corresponding to classes differing only in the fire regime, we can isolate fire disturbed tree cover states, where wildfires played a major role in the timespan covered by the satellite observations. A summary of the possible vegetation states found in the system is provided in Table 3. Equivalent tree cover states gridcells and fire disturbed tree cover states gridcells are represented in Fig. 3 and they cover approximately ~5% of the total boreal area. Specifically, each class contains on average 29 gridcells. Note that we excluded classes containing less than 1% of the gridcells corresponding to each vegetation state. Equivalent tree cover states can be found in every region, with a total of 14 different EVs classes related to them, whereas fire disturbed (FD) states appear consistently only in Eastern North Eurasia, and consist of 5 EVs classes, of which 4 are also related to equivalent tree cover states. All 19 classes are reported

in Table 4. Qualitative indexes for the EVs, except for ST and PZI, represent the bin into which the variable's value falls in the classification, as described in Section 2.2; the order is: very low, low, medium-low, medium-high, high, very high. Soil texture is described as belonging to the sand, loam, or clay group. Permafrost is described as sparse, discontinuous, frequent, or continuous. Each EV class contains two possible vegetation states, e.g., forest and open woodland, that are consistently

5 found under the same specified environmental regimes.
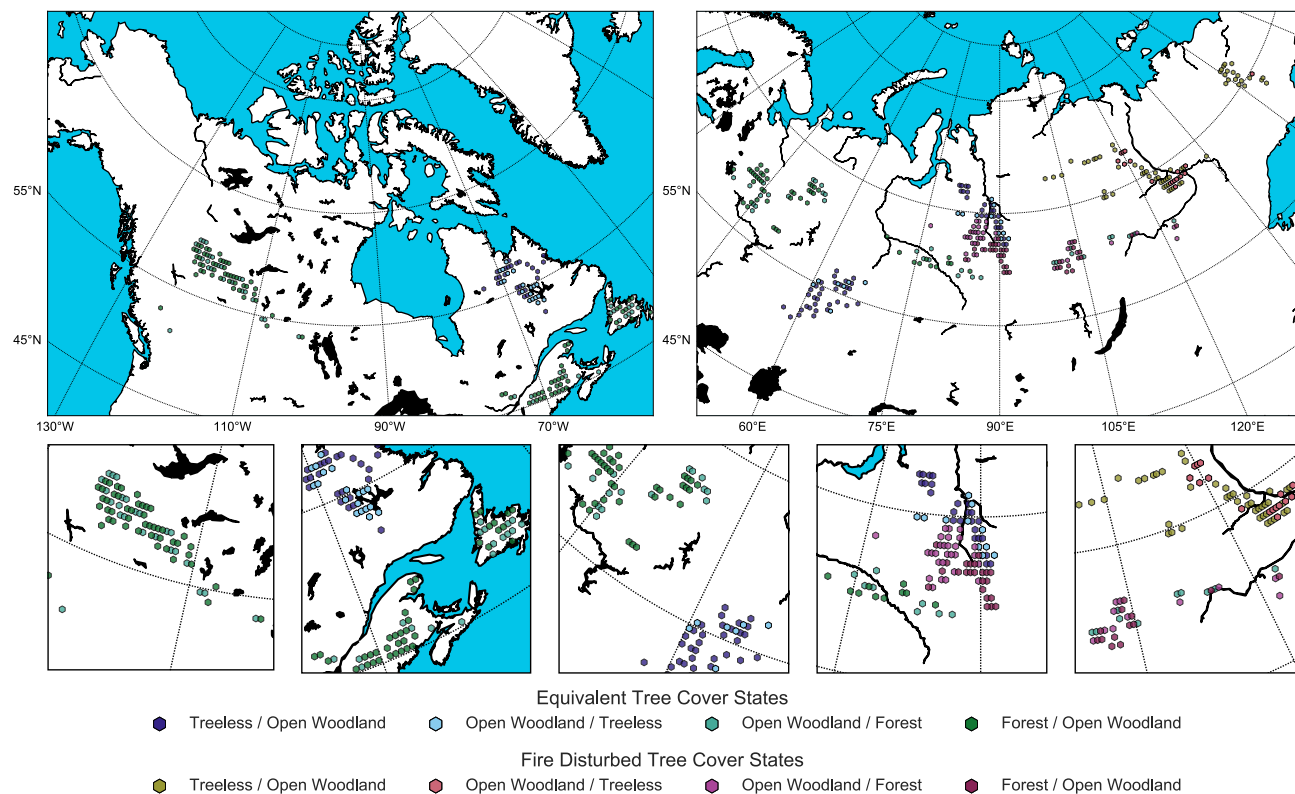
Figure 3. Possible alternative tree cover states over North America (left) and North Eurasia (right). The bottom five panels represent a close-up of the areas of interest ordered from West to East. Legend to be interpreted as follows: for every entry in the legend, the first name refers to the observed vegetation state in a specific gridcell, the second name corresponds to the possible alternative state found elsewhere under the same environmental conditions.

Table 4 and Figure 3 pinpoint the conditions and locations, respectively, of the possible alternative tree cover states in the boreal area. Results of the Silverman's tests on the distributions of the alternative open woodland and treeless gridcells, and the one of the alternative open woodland and forest gridcells confirm their bimodality, as shown in Fig. 4. Each Silverman's test assesses the hypothesis that the number of modes of each distribution is ≤ 1. The tests show that the minimum number of modes,

10 for both cases, is two, with p-values smaller than 0.001 and 0.01, respectively. Furthermore, by fitting these distributions using KDEs, we estimate the distances between the peaks of the distributions, and we compare them with the standard deviation of

Table 3. Summary of possible vegetation states. Fire disturbed states have a higher fire regime than the indicated counterpart.

Type of state	Vegetation states		
Single stable	Treeless (TCF<20%)	Open woodland (20%≤TCF<45%)	Forest (TCF≥45%)
Equivalent tree cover	Treeless - Open woodland	Forest - Open woodland	
Fire disturbed (FD) tree cover	Open woodland - FD Treeless	Forest - FD Open woodland	Open woodland - FD Forest

Table 4. Classes related to equivalent tree cover states and fire disturbed (FD) tree cover states. The qualitative marks are always relative to the extremes of the EVs distributions in the region of interest, and represent the bins into which the phase-space is subdivided.

Region	Case & Vegetation states	FF	ST	PZI	MAR	MSSM	MTmin
NA_W	1 Forest - Open Woodland	medium-low	loam	sparse	medium-high	medium-low	medium-high
	2 Forest - Open Woodland	medium-low	clay	sparse	medium-high	medium-low	medium-high
NA_E	3 Treeless - Open Woodland	very low	sand	frequent	low	high	medium-high
	4 Treeless - Open Woodland	very low	sand	continuous	very low	medium-high	medium-low
	5 Forest - Open Woodland	very low	sand	sparse	very high	very high	very high
EA_W	6 Treeless - Open Woodland	very high	loam	sparse	high	very low	very low
	7 Forest - Open Woodland	very low	sand	sparse	medium-high	high	high
	8 Forest - Open Woodland	very low	loam	sparse	high	high	medium-low
EA_E	9 Treeless - Open Woodland	very low	loam	frequent	medium-low	very high	high
	10 Treeless - Open Woodland	medium-low	loam	continuous	very low	low	very low
	11 Forest - Open Woodland	very low	loam	frequent	medium-low	medium-low	medium-low
	12 Forest - Open Woodland	very low	loam	frequent	medium-high	very high	high
	13 Forest - Open Woodland	medium-low	loam	frequent	medium-high	very high	high
	14 Forest - Open Woodland	very low	loam	frequent	high	high	high
FD EA_E	15 Open Woodland - FD Treeless	very low	loam	continuous	very low	low	very low
	16 Open Woodland - FD Treeless	medium-low	loam	continuous	very low	low	very low
	17 Open Woodland - FD Forest	very low	loam	frequent	medium-high	very high	high
	18 Forest - FD Open Woodland	very low	loam	frequent	medium-low	medium-low	medium-low
	19 Forest - FD Open Woodland	very low	loam	frequent	medium-high	very high	high

the TCF distribution during the 2001–2010, as a measure of variability. The minimum distance between the peaks is 18.19 percentage points (note that TCF is measured as a percentage), whereas the average standard deviation for the alternative states

gridcells is 5.77 percentage points, with only one gridcell possessing a variability greater than 18 percentage points, as shown in Fig. 5. Henceforth, the bimodality of the alternative states distributions is not influenced by the variability of the TCF.
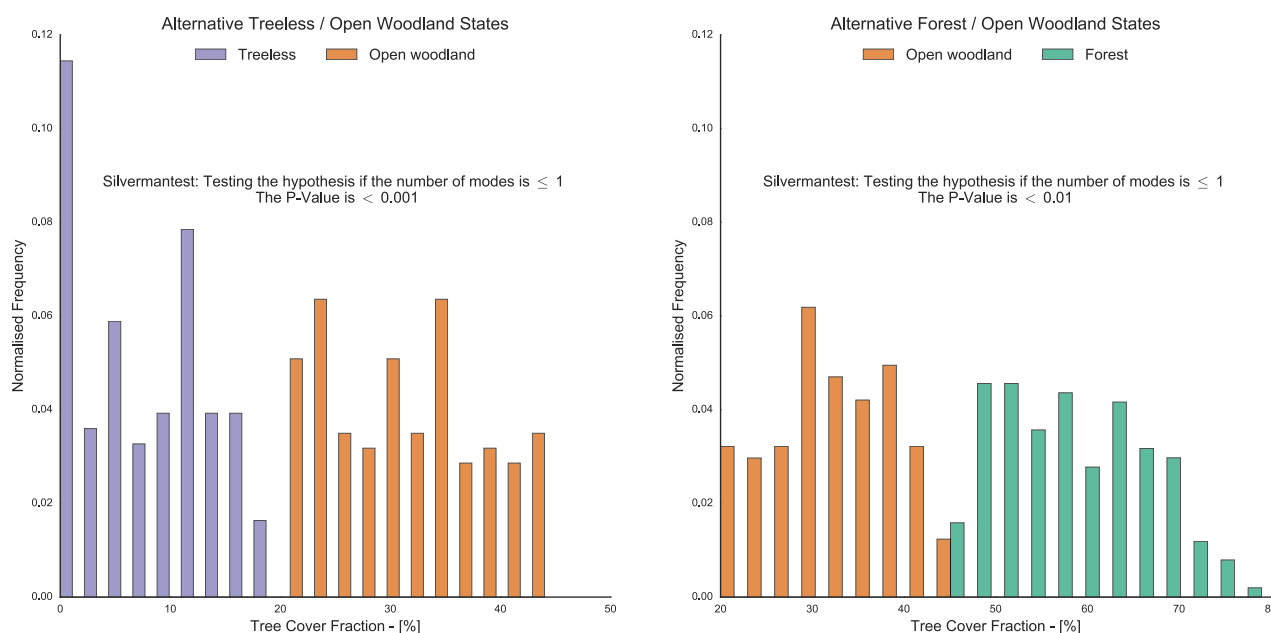
Figure 4. TCF Distribution over the gridcells where equivalent or fire disturbed open woodland and treeless states are found (left), and where equivalent or fire disturbed open woodland and forest states are found (right). For each case the Silverman's test verifies the hypothesis that the distribution is unimodal.

Notably, equivalent tree cover states generally fall into two categories: either they possess intermediate values for the environmental variables, or they have contrasting ones. For instance, case number 1 in Table 4 is characterised by medium or

5   intermediate values for all the environmental variables, whereas case number 6 shows high values for FF and MAR, but very low for MSSM and MTmin. The first category, with intermediate values, can be associated with transition zones, when passing from a EV class where only a single vegetation state is dominant, to a class where another state is dominant. As a result, the observed TCF distribution can oscillate between the two states. The second category, on the other hand, relates to classes where at least one of the environmental variables has a value contrasting with the remaining ones. For instance, in case 8, PZI, MAR,

10   MSSM, and ST, all possess values generally associated with forest states, however, MTmin is low, preventing tree growth. This possibly creates a limit cycle where the ecosystem alternates between the different alternative states. Fire disturbed tree cover states, instead, can be grouped into three categories. The first category is represented by classes where the vegetation state with the lowest tree cover is disturbed by fire, and the one with highest tree cover corresponds to one of the existing equivalent tree cover states (case 16, 18, and 19). The second category is the opposite: the vegetation state with the highest tree cover is

15   disturbed and the one with the lowest tree cover is found among the equivalent tree cover states (case 17). The third category
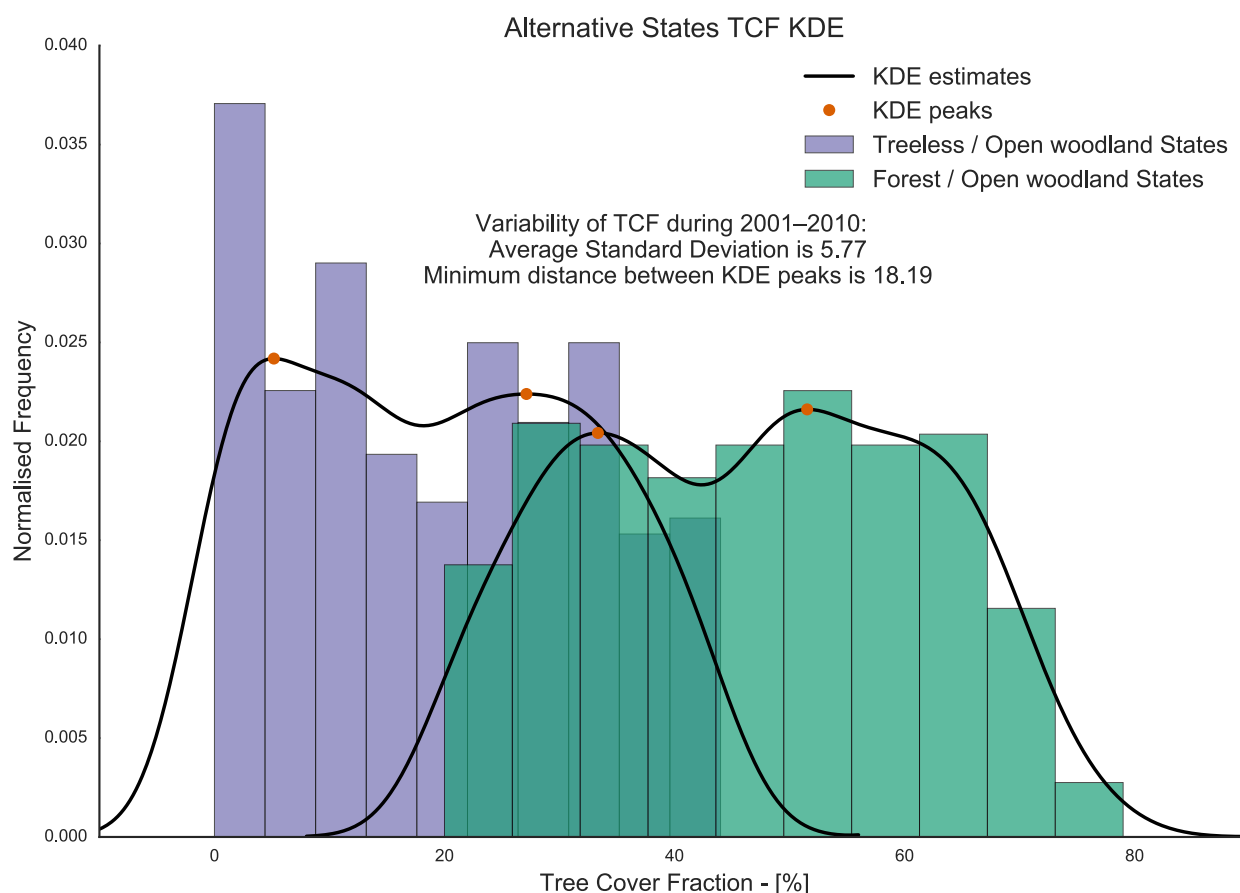
Figure 5. KDE fittings of the TCF distribution for gridcells where alternative states are found, showing the bimodality of the underlying distributions and the locations of their peaks. The variability of the TCF distribution for the period 2001–2010 is computed using the standard deviation of the distribution.

corresponds to the first one, but neither of the vegetation states is found among equivalent tree cover classes (case 15, although very similar to case 10).

Classification results suggest that environmental variables exert a strong, albeit sensitive, control over the tree cover distribution. Depending on the conditions, only one of the three possible vegetation states is attained. However, in transition zones with intermediate or contrasting conditions, it is possible to find multiple vegetation states with the same environmental regimes. In such zones, disturbances could shift the system between the possible alternative states. In this sense, fire is part of the environment both as a variable (Wirth, 2005; Schulze et al., 2005) and as a disturbance. Strong fire events in transition zones can determine which of two alternative states the system will fall into. On the other hand, changes due to fire events in a stable

area should be reabsorbed with time, unless they are so dramatic to produce changes in another main environmental variable, creating a new transition zone.

4 Discussion

Minimum temperatures and growing degree days are the most influential environmental variables for the boreal TCF distribution, as can be seen in Table 2. Nonetheless, their combined effect does not fully explain the tree cover distribution, as a more diverse set of variables and feedbacks plays a role. By linking tree cover distribution to a 6D phase-space formed by environmental variables, we show that under most environmental conditions, the TCF distribution is uniquely determined, i.e., is unimodal, suggesting a strong control of the vegetation by means of the environment. In this sense, the three different modes of the boreal tree cover distribution (Scheffer et al., 2012; Xu et al., 2015) represent three distinct stable tree cover states that do not generally appear under the same environmental conditions. However, we find areas where the TCF distribution is bimodal under the same environmental conditions, suggesting the existence of possible alternative states, as depicted in Fig. 3. These areas are characterised by either intermediate or contrasting environmental conditions, possibly creating limit cycles that allow alternative tree cover states. Furthermore, these areas seem to exhibit a reduced resilience, since disturbances, such as wildfires, appear to be able to shift the vegetation from one state to the other, as in the case of fire disturbed tree cover states.

Environmental conditions control the tree cover distribution in high latitudes, pushing its vegetation towards three distinct tree cover states. This hints at the presence of feedbacks between the vegetation and the environment able to stabilise the vegetation cover in three different ways. However, the environment is influenced by the forest cover state through albedo, water evapotranspiration (Brovkin et al., 2009), and nutrients recycling. Thus, changes in climate and environmental variables will trigger feedbacks from the vegetation that can either further amplify or dampen the initial changes. In particular, areas of reduced resilience where alternative tree cover states are found, i.e., what we call transition zones, will be affected. As the classification results suggest, environmental variables drive the ecosystem towards seemingly stable states and away from intermediate unstable ones, resulting in the multimodality of the tree cover. Thus, disturbances in transition zones could cause a rapid ecosystem shift regarding tree cover. Henceforth, it is important to better understand the interplay between environmental variables and tree cover.

Additionally, there are other factors playing a role in the dynamics of the boreal forest, both at local and larger scales. For instance, the understory vegetation acts as an important driver of soil fertility, influencing decomposition, nutrient flow and availability, plant growth, and tree seedling establishment (Bonan and Shugart, 1989; Nilsson and Wardle, 2005). Under increased nitrogen deposition, accumulation of organic matter and carbon may increase in boreal forest (Mäkipää, 1995). At the same time, its effects on the forest floor and soil processes might decrease forest growth (Mäkipää, 1995), thus hindering carbon storage. Despite its importance, there is a lack of knowledge regarding the impact of understory interactions at large spatial scales, and the contribution of climate change drivers such as nitrogen deposition and global warming (Nilsson and Wardle, 2005). For this reasons we could not take it into account in our study. Another missing factor is nitrogen (N). Plant growth in the boreal forest is thought to be generally N limited (Mäkipää, 1995). This is supposedly due to the slow mineralisation of

soil organic nitrogen and the assumption that most plants are incapable of using organic nitrogen (Näsholm et al., 1998). In fact, nitrogen cycling in the boreal forest is regulated to a great extent by soil fungi (Fierer and Jackson, 2006). Additionally, herbivore grazing is also influenced by N fertilisation (Ball et al., 2000), with the potential to affect feedbacks involving soil nutrient cycle and plant regeneration (Wal, 2006). However, globally-distributed datasets for N availability and grazing

5   pressure suitable for our analysis are not yet available. Local topography also plays a role, as the low solar elevation angle at high latitudes accentuates the effect of ground characteristics such as slope and aspect (Rydén and Kostov, 1980; Bonan and Shugart, 1989; Rieger, 2013). South-facing slopes are warmer and drier than north-facing ones (Bonan and Shugart, 1989), and these differences are proportional to the slope gradients. Therefore, topography indirectly influences vegetation and forest productivity, by affecting two major factors controlling them, namely temperature and soil moisture, that we took into account

10 in our analysis. Finally, micro-topography, such as shelter from boulders, can increase resistance to disturbances by creating small-scale refugia (Schmalholz and Hylander, 2011), thus locally increasing the resilience of the forest.

In the context of climate change, understanding transition zones at large scales is necessary for assessing future projections of vegetation cover. Climate change is impacting the boreal area more rapidly and intensely than other regions on Earth; for instance, surface temperature has been increasing approximately twice as fast as the global average (IPCC, 2013). Temperature

15 is a key variable in this region, as it is connected with tree growth and mortality cycles, with permafrost thawing and the hydrological cycle, and with disturbances, such as wildfires and insect outbreaks (Assessment, 2005; Wolken et al., 2011; Johnstone et al., 2010; Scheffer et al., 2012; D'Orangeville et al., 2016). Particularly, air and surface warming can increase the frequency and extent of severe fires (Flannigan et al., 2005; Balshi et al., 2009; Johnstone et al., 2010), and promote more favourable conditions for insect outbreaks (Volney and Fleming, 2000). At the same time, climate change influences the

20 resilience of boreal forest stands (Johnstone et al., 2010), making them more susceptible to abrupt shifts due to disturbances. As temperature increases and permafrost thaws, it is more likely to find intermediate conditions where alternative tree cover states are possible. For instance, a study on the southern part of the eastern North America boreal forest has shown that an increased disturbance regime, together with the superimposition of fires and defoliating insect outbreaks, can cause a shift between alternative vegetation states (Jasinski and Payette, 2005). Furthermore, there is strong evidence that certain types of

25 extreme events, mostly heatwaves and precipitation extremes, are increasing under the effect of climate change (Orlowsky and Seneviratne, 2012; Coumou and Rahmstorf, 2012). Such events could foster areas with contrasting environmental conditions, further weakening the stability of the boreal ecosystem, and increasing its susceptibility to shifts.

5   Conclusions

Eight environmental variables datasets, namely mean annual rainfall, mean minimum temperature, growing degree days above

30 0°C, permafrost distribution, mean spring soil moisture, wildfire occurrence frequency, soil texture, and thawing depth, are used to investigate the multimodality of the tree cover distribution of the boreal forest. Through the analysis of generalised additive models, we find that the environment exerts a strong control over the tree cover distribution, forcing it into distinct tree cover states. Nonetheless, the tree cover state is not always uniquely determined by the variables at use. Furthermore,

the response of vegetation to the environment varies in the four regions considered: Eastern North America, Western North America, Eastern North Eurasia, and Western North Eurasia.

By means of a classification, we analyse the 6D phase-space formed by mean annual rainfall, mean minimum temperature, permafrost distribution, mean spring soil moisture, wildfire occurrence frequency, and soil texture. We find several environ-

5 mental conditions under which alternative tree cover states are possible, broadly falling into two categories: with contrasting environmental features, e.g. high rainfall but low temperature, or with intermediate environmental values. In our opinion, these conditions favour competition between different tree cover states by limiting tree reproduction and growth. In regions under these environmental conditions, the tree cover exhibits a reduced resilience, as it can shift between alternative states if subject to forcing.

10 Fire is an intrinsic component of the boreal ecosystem, with an essential role in biodiversity maintenance and stand succession. At the same time, wildfires can contribute to alternative tree cover states as a disturbing agent. In regions of reduced resilience, in fact, fires can shift the tree cover from one vegetation state to another under the same EVs. Hence, we hypothesise that a strong disturbance could permanently change the state of the ecosystem, by the combined effect of a shift in tree cover and its potential feedbacks on the environment.

15 We find that regions with possible alternative tree cover states encompass only a small percentage of the boreal area (∼5%). However, since temperature and temperature-related environmental variables - such as permafrost distribution - exert the strongest control on the tree cover distribution and its modes, temperature changes can greatly affect forest resilience. Therefore, under a changing climate, regions allowing for alternative tree cover states could expand both in frequency and extent.

20 In the context of climate change, a gradual expansion of transition zones with reduced resilience could lead to regional ecosystems shifts. As climate in the boreal area is related to tree cover through numerous biogeophysical feedbacks, such as changes in albedo and transpiration, these shifts could have a significant impact not only on the structure and functioning of the boreal forest, but also on its climate.

Author contributions. Both authors designed the research; B. Abis performed the research; both authors contributed to the discussion and

25 interpretation of the results; B. Abis wrote the first draft of the manuscrip and both authors contributed to its final draft.

Acknowledgements. We would like to thank the Integrated Climate Data Center (ICDC, icdc.cen.uni-hamburg.de) of University of Hamburg for helping with the retrieval of datasets. We thankfully acknowledge Gitta Lasslop for helping us review the manuscript, and Fabio Cresto Aleina for his useful comments. We also thank the International Max Planck Research School on Earth System Modelling (IMPRS-ESM) for supporting this work.

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