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Lack of evidence for alternative stable states in Northern Hemisphere forests during the past 8 ka

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Lack of evidence for alternative stable states in Northern Hemisphere forests during the past 8 ka

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E-mail: laura.schild@awi.de**Keywords:** tipping points, forest, paleoecology, climate change, alternative stable statesSupplementary material for this article is available [online](#)**Abstract**

With increased pressure from anthropogenic climate change, boreal forests are suspected to be approaching tipping points which could cause large-scale changes in tree cover and affect global climatic feedback. However, evidence for this proposed tipping is sparse and relies heavily on observations on short time scales from remote sensing data and space-for-time substitutions. Here we make use of an extensive pollen data set including 239 records of large lakes to investigate the existence of alternative stable forest cover states in the boreal forest and its adjacent biomes during the last 8000 years. By using a multimodality measure on time series of reconstructed tree cover we find very little multimodality in pollen data. To test whether this lack of multimodality is caused by limitations in the paleo data set we perform surrogate experiments. Surrogate data with alternative stable states based on the paleo vegetation–climate relationship were generated and significant multimodality was found more often than for the pollen-based tree cover (24.7% and 5.3% respectively). The response of tree cover to climate may, therefore, be more gradual and not as abrupt as would be expected from remote sensing analyses on stability. The apparent alternative stability hypothesized in the analyses of climate–vegetation relationships could be due to the strong spatial heterogeneity of environmental factors and vegetation responses as an artifact of space-for-time substitutions. Even though current and upcoming shifts in the boreal forest are indisputable and a reason for strong concern, these changes could happen gradually without going through large-scale tipping between alternative stable states. To aid adaptation and conservation measures, more knowledge is needed about boreal forest drivers and their spatial heterogeneity.

1. Introduction

Boreal forests play a crucial role in the global climate system through feedback mechanisms related to albedo, evapotranspiration, and substantial carbon storage (Bonan *et al* 1992, Foley *et al* 1994, Snyder *et al* 2004, Chapin *et al* 2005, Bonan 2008, Pan *et al* 2011, Bradshaw and Warkentin 2015, Lin *et al* 2020). In addition, they provide a multitude of other ecosystem services on local scales such as timber production, nutrient cycling and biodiversity (Shvidenko *et al* 2005, Mery 2010, Brandt *et al* 2013). However, the fast rate of anthropogenic climate change is causing

strong shifts and the potential for tipping within the boreal biome is increasingly under discussion as it would entail abrupt biome-wide change with far-reaching consequences for global and regional feedbacks (Bonan *et al* 1992, Lenton *et al* 2008, Armstrong McKay *et al* 2022).

Here, we define a tipping point as a qualitative change that becomes self-perpetuating after crossing a critical threshold (Scheffer *et al* 2001, Armstrong McKay *et al* 2022). Once the transition from one state to another occurs, reversing it can only be achieved by restoring environmental pressures to a state far beyond the initial tipping point; a concept known

as hysteresis (Scheffer *et al* 2001, Lenton *et al* 2008). This is due to an overlap of stable states at the same environmental conditions enforced by stabilizing feedback mechanisms (Scheffer *et al* 2001). The existence of such alternative stable states is thus a prerequisite for tipping to occur. Proposed tipping points concerning the boreal biome include abrupt and irreversible boreal forest dieback at the southern edge and expansion at the northern edge (Foley *et al* 1994, Chapin *et al* 2005, Lenton *et al* 2008, Wang *et al* 2023). The primary feedback mechanism that supports the alternative stability between forested areas and open grasslands at the southern boreal extent is fire, which occurs more frequently in open, arid grasslands and hinders tree establishment (Adams 2013, Pausas and Bond 2020, Seidl *et al* 2020, Burrell *et al* 2021, Sun *et al* 2021). Permafrost serves as an additional feedback driver that may lead to forest loss or shifts in community composition once thawed (Carpino *et al* 2018, Herzsuh 2020, Schulte *et al* 2022, Liu *et al* 2023). At the northern boundary, a feedback involving albedo is hypothesized to result in rising temperatures with increased forest cover, which, in turn, supports the establishment and stability of forests (Chapin *et al* 2005, Scheffer *et al* 2012).

However, boreal tipping points are contested. Some studies suggest that instead of large-scale tipping, gradual change, resilience, and spatial heterogeneity are characterizing boreal forest responses to climate change (Chapin *et al* 2004, Reyer *et al* 2015, Abis and Brovkin 2017, Stralberg *et al* 2020, Hansen *et al* 2021) and in general, evidence for tipping points in the extratropical terrestrial biosphere is scarce (Brook *et al* 2013, Reyer *et al* 2015, Hillebrand *et al* 2020, Pausas and Bond 2020). Yet, some past studies have indicated or postulated boreal tipping points (Soja *et al* 2007, Johnstone *et al* 2010, Scheffer *et al* 2012, Adams 2013, Xu *et al* 2015, Lasslop *et al* 2016, Foster *et al* 2019) and transitions in boreal forests are still being cited as potential tipping elements (Lenton *et al* 2008, Lenton 2012, Armstrong McKay *et al* 2022).

For instance, a multimodal distribution of modern boreal forest cover was detected in remote-sensing data by Scheffer *et al* (2012) and Xu *et al* (2015), indicating the potential existence of three stable states. They proposed that multiple forest cover states might coexist within the same climatic conditions, suggesting the presence of hysteresis and the potential for tipping points in the boreal biome. However, this approach is limited by the space-for-time substitution used in the analysis (substituting spatial climate-biotic relationships for temporal relationships, when long-term observations of sufficient change are not available, e.g. Fukami and Wardle 2005) as the spatial heterogeneity of environmental conditions may inflate the detected hysteresis (van Nes *et al* 2014).

Regardless, significant changes in the boreal forest under anthropogenic climate change have been detected through observations. At the southern extent,

boreal forests increasingly host temperate species and transform from needle-leaved to mixed-leaf communities, especially after fire disturbances (Johnstone *et al* 2010, Mann *et al* 2012, Shuman *et al* 2015, Wu *et al* 2017, Foster *et al* 2019, Baltzer *et al* 2021, Mack *et al* 2021). Local increases of forest area in the north and decreases in the south have been shown both by observations (Soja *et al* 2007, Beck *et al* 2011, Burrell *et al* 2021, Berner and Goetz 2022, Rao *et al* 2023) and modeling studies as a response to climate change (Pearson *et al* 2013, Foster *et al* 2019, Hansen *et al* 2021, Kruse and Herzsuh 2022). Though some studies report a much slower advance of forest in the north than the corresponding retreat in the south (Rotbarth *et al* 2023) and continental patterns differ (Bi *et al* 2013, Lin *et al* 2020, Rees *et al* 2020). Despite these changes, the short duration of observations makes it difficult to confirm the presence of tipping points, as hysteresis has not yet been witnessed, and time series are too short to statistically test for alternative stable states (Scheffer and Carpenter 2003, Dakos *et al* 2012, Clements and Ozgul 2018). The observed changes could, therefore, also be attributed to a gradual response or a potentially reversible threshold response (Brook *et al* 2013, Reyer *et al* 2015).

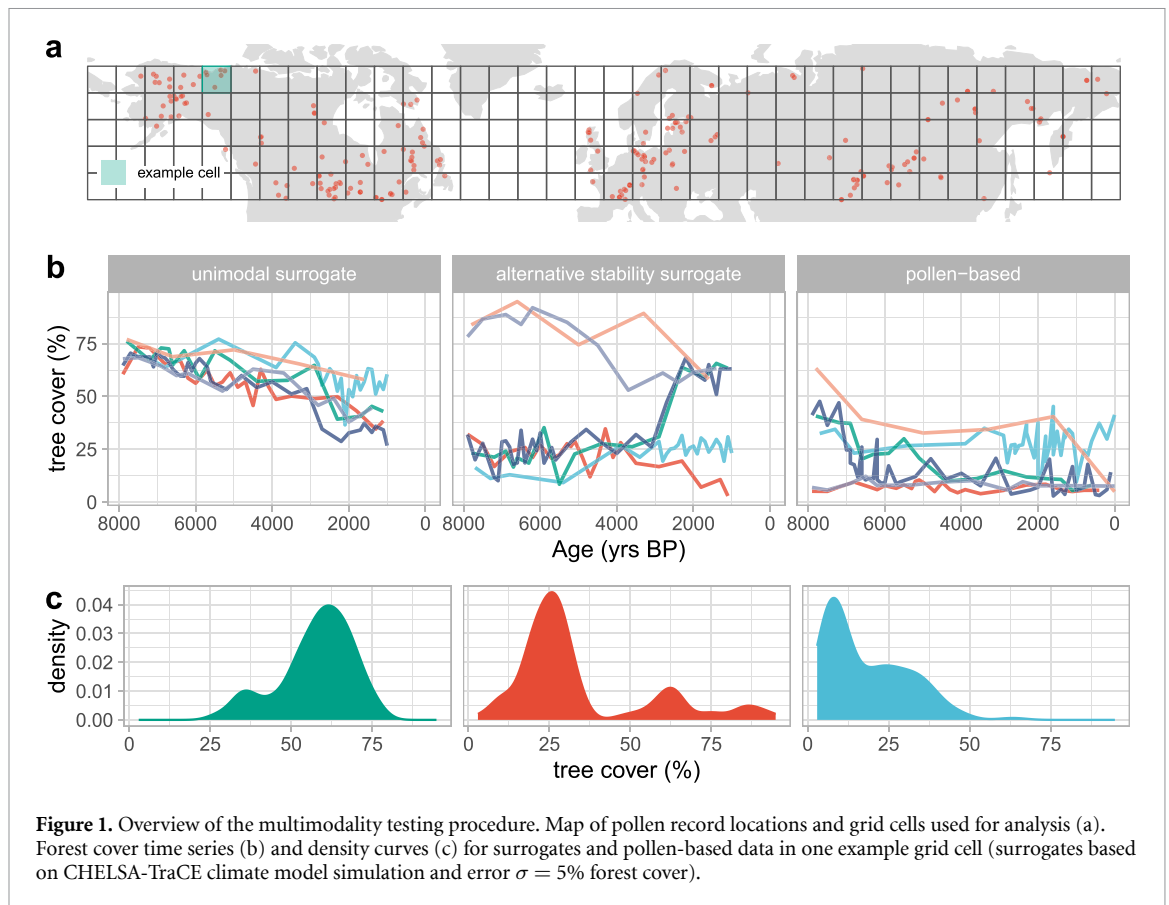
In contrast to the short observational period, sedimentary pollen data provide time series of forest cover reconstructions over several thousands of years and thus offer a unique opportunity to study the temporal stability of forested and non-forested systems in the Northern Hemisphere. Due to local climate change during the Holocene and the availability of pollen data in different climatic zones, they can be used to investigate forest cover states across the climatic space. However, factors such as age uncertainty, irregular temporal resolution, and species-specific biases in pollen compositions have to be accounted for.

Here we make use of a novel, Northern Hemisphere, pollen-based forest cover reconstruction (Schild *et al* 2024) to investigate forest cover dynamics over extensive time scales and assess whether temporal multimodality in pollen-based forest cover during the past 8000 years is consistent with alternative stable states in forest cover. Using pollen-based forest cover time series, we estimate a local multimodality parameter to check for the existence of stable forest cover states in the temporal domain directly, thus avoiding the uncertain space-for-time substitution.

2. Methods

2.1. Paleo forest cover

Reconstructed forest cover time series (<https://doi.org/10.5281/zenodo.13902921>, Schild *et al* 2024) based on the global pollen data set LegacyPollen 2.0 (Herzsuh *et al* 2022, Li *et al* 2024) were used as



paleo forest cover. To consider potential transitions between tundra, steppe, and boreal and temperate forest, we restricted the analysis to the 45° – 70° N latitudinal band, which includes different forested and non-forested systems of the Northern Hemisphere. We utilized 239 pollen records from large lakes for our study (see figure 1(a)) as large lakes provide more reliable vegetation reconstructions. The results of an analysis using all available records do not differ significantly and can be found in the supplementary material. The forest cover data set is based on a vegetation reconstruction using the REVEALS model (Sugita 2007) which takes site and taxon-specific parameters concerning pollen dispersal and deposition into account to resolve biases (Schild *et al* 2024). Revised age modeling and taxonomic harmonization of the pollen data set allow for a cohesive analysis of all records (Herzschuh *et al* 2022, Li *et al* 2022).

2.2. Regional analysis of multimodality

Statistically if alternative stable states are present the distribution of forest cover should be multimodal. Therefore, multimodality in forest cover acts as an indicator for alternative stability (Scheffer and Carpenter 2003). To account for the spatial heterogeneity of environmental factors, we conducted a spatially gridded (5° Latitude \times 10° Longitude) analysis of forest cover multimodality using Hartigan's diptest (Hartigan and Hartigan 1985). For significantly multimodal grid cells, the difference between

modes was calculated using the locmodes function from the 'multimodes' R package (Ameijeiras-Alonso *et al* 2021). A cell continued to be considered multimodal in the analysis if the difference between modes exceeded 5% to only record ecologically different states. We accounted for ecological variability and uncertainties by bootstrapping grid cell results ($n = 500$) and creating a distribution of the average fraction of multimodal cells.

2.3. Surrogate models with ESM climate data

To ensure that an observed lack of multimodality is actually due to a lack of alternative stability and not an exceptionally stable climate, we create two surrogate models: a model based on alternative stability, and a unimodal model representing a gradual ecosystem response. Both models were driven by summer temperature from paleo climate simulations to create forest cover data following the simulated regional climate change during the mid to late Holocene. Three different climate model products were considered: CHELSA- TraCE21k (Karger *et al* 2023), which is a downscaled version (1 km spatial resolution) of the CCSM3-TraCE21k simulation (He 2010), and two simulations using the MPI- ESM 1.2 model (3.7° spatial resolution) with different deglaciation scenarios (Mauritsen *et al* 2019). For each simulation, 100 year mean values for summer temperature (TJJA) were extracted at the pollen record locations for the period between 0 and 8 ka BP. To avoid the

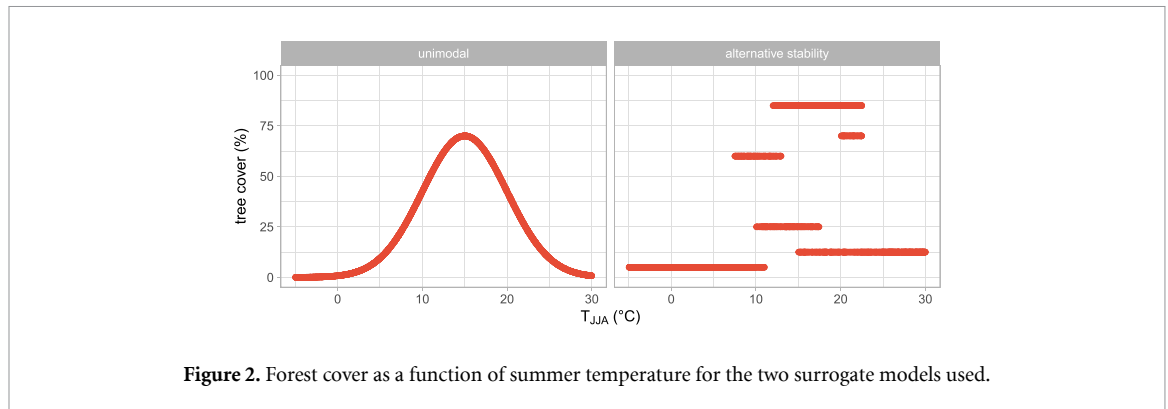


Figure 2. Forest cover as a function of summer temperature for the two surrogate models used.

high uncertainty associated with paleo hydroclimate (Ljungqvist *et al* 2016) we focused on summer temperature following the analysis by Scheffer *et al* (2012).

2.3.1. Alternative stability model

The model based on alternative stability was derived from so-called stability landscapes, which illustrate the stable and unstable states of a system as a function of the driving environmental factor (see figure 2). Here, the stability landscapes considered show stable and unstable forest cover states as a function of summer temperature. Stability landscapes were estimated by tracing the local maxima in the frequency of forest cover at a given summer temperature (Scheffer *et al* 2012). Forest cover data was binned by summer temperatures using overlapping intervals of 1 °C width and a 0.2 °C spacing between 0 °C and 20 °C. In each bin, we estimate a non-parametric probability distribution function for the forest cover using a gaussian kernel with a bandwidth of $(1.06 \times \sigma)/n^{1/5}$ (σ = standard deviation, n = number of forest cover samples in a summer temperature bin, Scheffer *et al* 2012). Local minima and maxima in the density curves were ignored when their amplitude was less than 10% relative to the global maximum. Forest cover values at maxima and minima were recorded as stable and unstable states for a given temperature bin respectively.

Two stability landscapes were created and compared: (1) a contemporary landscape, based on remote-sensing data, and (2) a paleo landscape, based on pollen data. For the modern landscape (2000–2020 CE) MODIS v006 remote sensing forest cover (DiMiceli *et al* 2015) and summer temperature from the Climate Research Unit gridded Time Series v4.06 (CRU TS; Harris *et al* 2020) were collected at 40 000 random points. Points with suspected anthropogenic influence (see table A1) were removed from the analysis. For the paleo stability landscape (0–8 ka BP), pollen-based forest cover and climate data from the CHLSA TraCE21k product were used.

In order to derive a surrogate model for alternative stability in forest cover, we manually simplified the stability landscape by setting temperature boundaries

for stable states (see figure 2 and table A2). As the two landscapes had similar features, we chose to derive the model from the paleo landscape to ensure consistency with the paleo data being investigated. To get a realistic starting value, the initial state is determined by the oldest forest cover for each pollen record (see figure 4). The record then follows the stability landscape as a function of summer temperature, and remains in the current state until the temperature boundary for that state is reached (see table A2). It then transitions to a new state randomly chosen from all possible states at the new temperature, each with equal probability.

2.3.2. Unimodal response

As an alternative hypothesis we assume a gradual response of vegetation to temperature and create surrogate data following a unimodal response. A Gaussian response function was chosen to approximate the observed state space (see equation (1) and figure 2),

$$\text{tree cover} = 70 \times \exp\left(-\frac{(T_{\text{JJA}} - 15)^2}{2 \times 5^2}\right). \quad (1)$$

2.4. Surrogate time series creation

Using the models described above, simulated paleo temperatures were used to create surrogate forest cover time series at all record locations. As we perform this step on 100 year mean summer temperatures, we implicitly account for biome response time (Chapin and Starfield 1997, Svenning and Sandel 2013). Several steps were taken to mimic processes associated with sedimentary paleo data and their effects on variability (similar to Hébert *et al* 2022). (i) Surrogate time series were smoothed using a 1000 year lowpass filter to mimic sediment mixing and bioturbation, then, (ii) the series were sub-sampled to the irregular sample time series of the actual record. Finally, (iii) a normally distributed error term was added to forest cover values to mimic errors on a sample basis and vegetational variability. Our choice of $\sigma_{\text{error term}} \in \{5\%, 10\%, 15\%\}$ reflects our uncertainty in this parameter and spans the typical pointwise uncertainty of pollen-based forest cover reconstructions (Schild

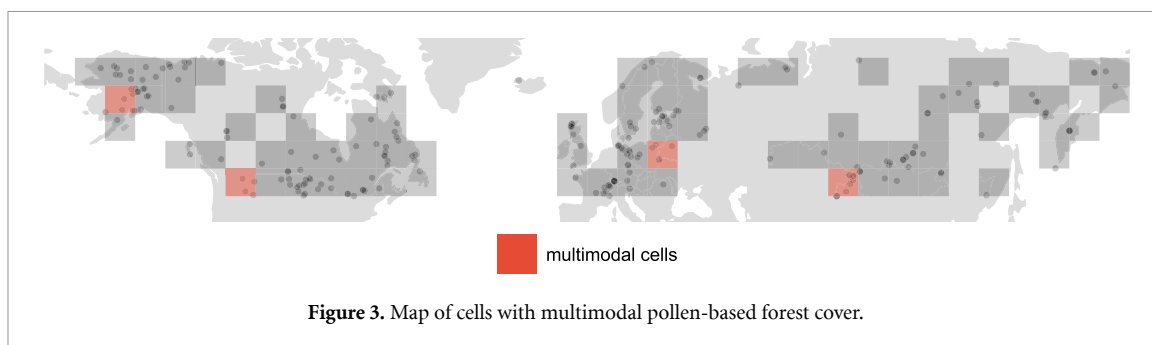


Figure 3. Map of cells with multimodal pollen-based forest cover.

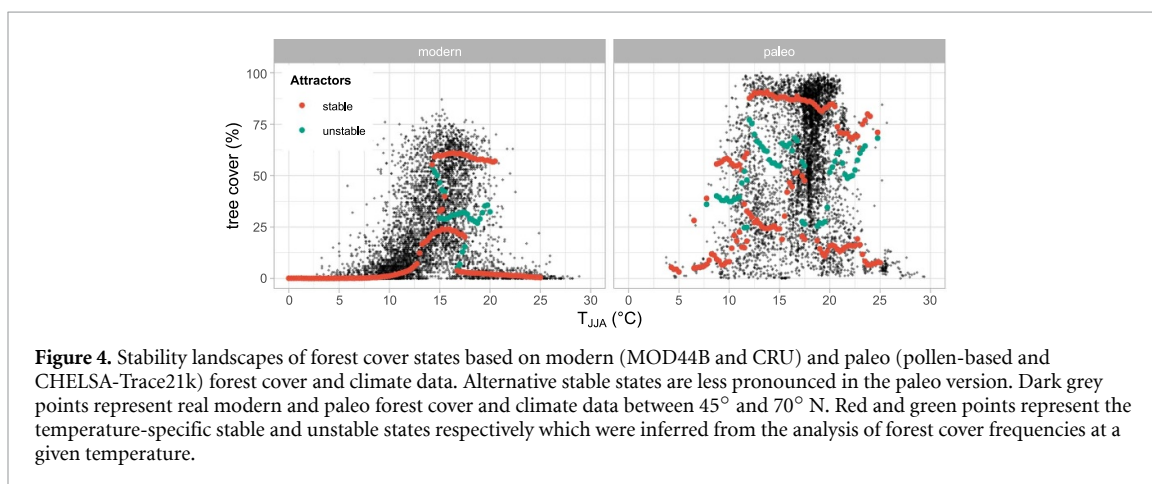


Figure 4. Stability landscapes of forest cover states based on modern (MOD44B and CRU) and paleo (pollen-based and CHELSA-Trace21k) forest cover and climate data. Alternative stable states are less pronounced in the paleo version. Dark grey points represent real modern and paleo forest cover and climate data between 45° and 70° N. Red and green points represent the temperature-specific stable and unstable states respectively which were inferred from the analysis of forest cover frequencies at a given temperature.

et al 2024). By combining the three climate model datasets with the three different error levels, we thus obtained two surrogate ensembles (alternative stability and unimodal) with nine members each. The regional analysis of multimodality was also conducted on the surrogate ensembles and uncertainty was quantified through the spread of results in the surrogate ensembles.

3. Results

3.1. Temporal multimodality in pollen data

The analysis of pollen-based forest cover shows locally significant ($p < 0.05$) multimodality in only 5.3% of the grid cells during the mid- to late Holocene (see figure 3). Most of the grid cells displaying multimodality are located in the southern extent of the study area, with only one multimodal cell above 55° N.

3.2. Stability landscapes

The modern stability landscape shows distinct states (figure 4). Below 12 °C and above 17 °C T_{JJA} a low forest cover state (<5%) is present. An intermediate forest cover state at roughly 20% exists between ~12 °C and ~17 °C and a forested forest cover state (~60%) between 13 °C and 21 °C T_{JJA} .

While the stable states that were identified in the paleo stability landscape are not as smooth as those from the modern landscape, their broad features are

nonetheless similar (figure 4). Low forest cover states (~10%) are again present at the beginning and the end of the summer temperature space but extend more to intermediate temperatures (below 10 °C and above 16 °C). Intermediate stable states are noisy, but resemble the ones observed in the modern data albeit with higher values of forest cover. They cover a slightly wider climate space from ~9 °C to 25 °C and vary between 25% and 75%.

The general shapes of both stability landscapes are similar, but absolute values differ as pollen-based forest cover tends to be higher than remotely sensed forest cover. Hence, the paleo stability landscape was used to generate a model (figure 2) for surrogate forest cover (example in figure 1(b)) to allow bias-free comparison to the reconstructed pollen-based forest cover.

3.3. Temporal multimodality in surrogate data

The fraction of grid cells with temporal multimodality is much higher in surrogates based on alternative stability than in unimodal surrogates or pollen-based data (24.7%, 3.7% and 5.3% average respectively, see figure 5(b)). The frequency of multimodality in pollen-based forest cover is slightly higher than that observed in the unimodal surrogate.

Multimodality in the surrogate based on alternative stability occurs in Europe and in some regions of North America for most of the ensemble (see

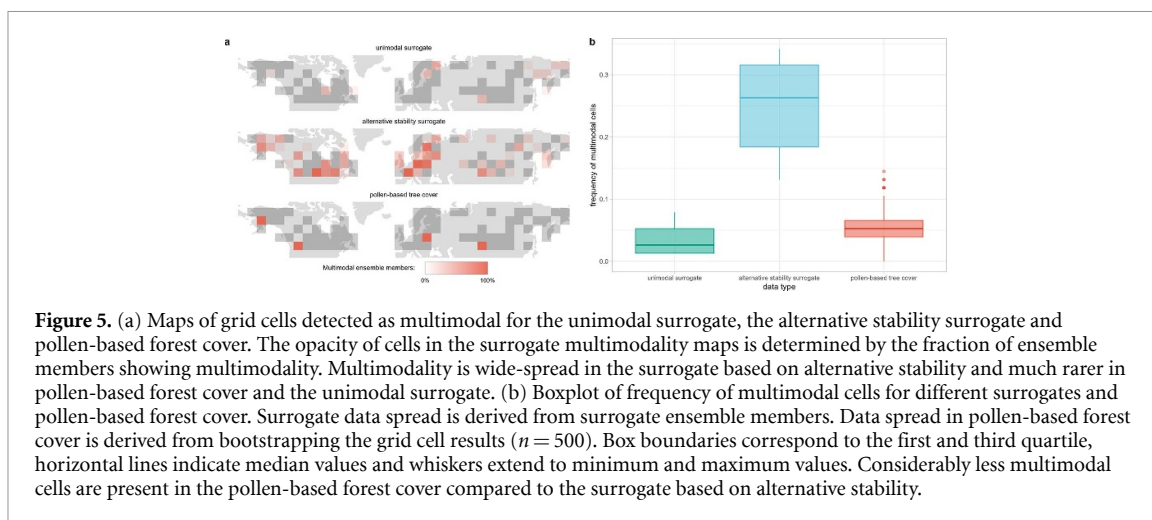


Figure 5. (a) Maps of grid cells detected as multimodal for the unimodal surrogate, the alternative stability surrogate and pollen-based forest cover. The opacity of cells in the surrogate multimodality maps is determined by the fraction of ensemble members showing multimodality. Multimodality is wide-spread in the surrogate based on alternative stability and much rarer in pollen-based forest cover and the unimodal surrogate. (b) Boxplot of frequency of multimodal cells for different surrogates and pollen-based forest cover. Surrogate data spread is derived from surrogate ensemble members. Data spread in pollen-based forest cover is derived from bootstrapping the grid cell results ($n = 500$). Box boundaries correspond to the first and third quartile, horizontal lines indicate median values and whiskers extend to minimum and maximum values. Considerably less multimodal cells are present in the pollen-based forest cover compared to the surrogate based on alternative stability.

figure 5(a)). Grid cells detected as multimodal in the unimodal surrogates are only present in few of the ensemble members.

4. Discussion

Modern stability landscapes using remote sensing data indicate the potential for boreal forest tipping due to overlapping states in space (Scheffer *et al* 2012). An analysis of tipping in time and underlying alternative stability is, however, constrained by the short length of instrumental time series. In our analysis using pollen data, we find a lack of evidence for alternative stable forest cover states in the past 8 ka.

We first constructed a stability landscape from pollen data and found overlapping states akin to landscapes created from modern remote sensing data, which indicates that pollen data can be used for the investigation of temporal stability. If alternative stable forest cover states exist in tundra, steppe, and forest systems, we expect to find them in time on smaller spatial scales where additional environmental conditions (e.g. soil characteristics, precipitation) are more homogeneous and where a changing climate during the Holocene should have caused tipping. States would present as different modes in a distribution of forest cover. This is why we used a multimodality metric to look for alternative stable states in time series of pollen-based forest cover. However, only very few grid cells show multimodality. To discern whether this is due to shortcomings in data, method, or a lack of alternative stability, we employed two surrogate models to construct forest cover time series as null hypotheses to compare the observations against.

The analysis revealed significantly more multimodal grid cells in surrogates based on alternative stability than in unimodal surrogates or pollen-based forest cover. This result indicates that there is a lack of evidence for forest cover in the Northern Hemisphere

to follow alternative stable states and that a smooth, potentially lagging, response to a changing climate—in contrast with the apparent alternative stability visible in both modern and paleo stability landscapes—may be more likely.

Several reasons could explain this discrepancy. One could lie in the multitude of environmental factors and their spatial heterogeneity impacting forest cover dynamics. Boreal forest cover is governed by more drivers than just summer temperature (Bonan 2008, Gauthier *et al* 2015, Abis and Brovkin 2017). Focusing on one driver when the remaining ones are spatially heterogeneous could cause apparent alternative stability in spatial stability landscapes, which could be resolved if other environmental factors are considered (van Nes *et al* 2014, Abis and Brovkin 2017, Wang *et al* 2023). The stabilizing feedback of forest cover with albedo and fire may additionally not be strong enough compared to the other drivers to support alternative stability. Another reason for the spatial-temporal disparity could be the considerable vegetation–climate lag proposed in previous studies (Wu *et al* 2015, Rees *et al* 2020, Dallmeyer *et al* 2022, Kruse and Herzsich 2022, Rotbarth *et al* 2023). Forests not in equilibrium with climate would likely indicate spatial alternative stability while lacking multiple stable states, consistent to the results of our study.

Even though the paleo data used in our analyses contains marked uncertainties, we argue that they exhibit only limited influence on the result of our analyses. Using our surrogate data, we showed that realistic uncertainties on the forest cover reconstruction and the sparse and irregular sampling of the proxy records in time do not prevent distinguishing between the alternative stability and the unimodal hypothesis in our data set. Another key aspect is the considerable source area influencing the pollen record. In the paleo forest cover data set used here, the average relative pollen source radius extends to approximately 150 km and can accommodate many forest

stands (Schild *et al* 2024). Tipping events on smaller scales could, therefore, go unnoticed in the pollen record. However, these localized dynamics are of limited importance concerning the suggested regional to biome-scale tipping and are even anticipated to play a role in stabilizing regional landscapes (Higgins and Scheiter 2012, Rietkerk *et al* 2021, Bastiaansen *et al* 2022).

By using only forest cover as an indicator of forest state, we are unable to assess alternative stable states of different forest communities at the southern edge of the boreal domain, as has been reported for some boreal regions through modeling and remote sensing studies (Mann *et al* 2012, Wang *et al* 2020). Nevertheless, we rarely detect the strong alternative stability between open systems and forest that should also be present based on previous studies (Scheffer *et al* 2012). Additionally, tipping between different forest communities is less severe than tipping between forested and non-forested ecosystems concerning changes in boreal carbon budgets (Mack *et al* 2021).

Lastly, the results we obtained may depend on the climate model based paleo temperature used to create surrogates and stability landscapes. While there are uncertainties related to the modeled paleoclimate (Dallmeyer *et al* 2022), it appears that there is a tendency to regionally underestimate the variability during the Holocene rather than overestimate it (Cheung *et al* 2017, Hébert *et al* 2022, Laepple *et al* 2023). A more variable model climate would lead to more state changes in our surrogates based on alternative stability, resulting in even greater multimodality than what was detected in paleo observations. We also took the model uncertainty into consideration by using multiple simulations to create an ensemble of surrogates based on alternative stability. Still, the spread of results based on the alternative stability ensemble differed markedly from pollen-based results. It is debatable how much these conclusions apply to the 21st century as the late Holocene climate change is not an analog for modern climate change. Not only could the increased rate of change lead to unprecedented vegetation dynamics, but the contrasting directionality could also play a role. Abrupt transitions from forest to steppe are rare with cooling being the dominant trend during the mid to late Holocene and we therefore have higher uncertainties regarding their absence in the Northern Hemisphere. The slower rate of climatic change observed in the Holocene could have also enabled forest communities to adapt compositionally, thus preventing abrupt transitions. A modelling approach considering the observed spatial patterns of overlapping stable states and temporal dynamics, such as lags in vegetation response, could potentially uncover the impact of faster climatic change on forest cover stability.

Despite the undisputable changes ongoing in boreal forests (e.g. Baltzer *et al* 2021, Burrell *et al* 2021, Rotbarth *et al* 2023), the paleoecological evidence analyzed here suggests that forest cover in the Northern Hemisphere, including the boreal biome, does not exist as alternative stable states at the centennial timescales of pollen-based forest cover. Past transitions that occurred seem to have been smoother or between different forest communities, not altering the quantitative forest cover state abruptly. More likely, a mix of environmental drivers, some stabilizing feedbacks and a vegetation–climate lag are the cause for rather local responses in forest cover that need to be considered during conservation and adaptation efforts responding to increasing pressures with ongoing climate change (Pausas and Bond 2020).

5. Conclusion

Boreal tipping is still uncertain as alternative stability of forest cover has only been investigated spatially and not temporally, due to a lack of sufficiently long time series. Here, we analyze pollen-based tree cover time series for the past 8000 years and compare their multimodality to two null hypotheses: a model based on alternative stable states, and involving tipping, generated from the spatial stability landscape and a gradual unimodal climate response. We find that multimodality in pollen-based tree cover is significantly lower than would be expected with alternative stable states. Therefore, our analysis of local forest cover time series suggests that alternative stability is not the main driver for past Northern Hemisphere tree cover dynamics. Instead, spatial heterogeneity of other environmental drivers may cause apparent alternative stability in space. Additional drivers of forest cover and their spatial heterogeneity need to be investigated in modern and paleo datasets to better understand boreal forest climate responses and support conservation and management under climate change.

Data availability statement

The paleo climate data (MPI: <https://doi.org/10.26050/WDCC/PMMXMCRTDIP132>; <https://doi.org/10.26050/WDCC/PMMXMCRTDGP132>; CHLSA-TraCE21k: <https://chelsa-climate.org/chelsa-trace21k/>), modern climate data (CRU TS: https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.06/) and remote sensing landcover data (GLC2000: <https://forobs.jrc.ec.europa.eu/glc2000/data>) are available online. Pollen-based forest cover data is available at Zenodo (<https://zenodo.org/records/13902921>, Schild *et al* 2024). MODIS forest cover and analysis code can be found on Zenodo (<https://doi.org/10.5281/zenodo.10075793>, Schild 2023).

The data that support the findings of this study are openly available at the following URL/DOI: <https://doi.org/10.5281/zenodo.13902921>.

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Author contributions

TL and UH conceptualized the study. LS, RH, UH, and TL developed the analyses. LS implemented the analyses and prepared the original draft under the supervision of RH, UH, and TL. All authors reviewed and edited the manuscript.

Appendix

Table A1. Landcover categories with anthropogenic influence in the GLC2000 (European Commission Joint Research Centre 2003).

Land cover class code	Land cover class name
16	Cultivated and managed areas
17	Mosaic: cropland/tree cover/other natural vegetation
18	Mosaic: cropland/shrub and/or grass cover
20	Water bodies
21	Snow and ice
22	Artificial surfaces and associated areas
23	No data

Table A2. Temperature ranges for alternative stable states in tipping response model.

Forest cover state in %	Summer temperature range in °C
5	<11
60	7.5–13
25	10–17.5
70	20–25
85	12–22.5
12.5	>15

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