Thresholds for boreal biome transitions

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Although the boreal region is warming twice as fast as the global average, the way in which the vast boreal forests and tundras may respond is poorly understood. Using satellite data, we reveal marked alternative modes in the frequency distributions of boreal tree cover. At the northern end and at the dry continental southern extremes, treeless tundra and steppe, respectively, are the only possible states. However, over a broad intermediate temperature range, these treeless states coexist with boreal forest (∼75% tree cover) and with two more open woodland states (∼20% and ∼45% tree cover). Intermediate tree covers (e.g., ∼10%, ∼30%, and ∼60% tree cover) between these distinct states are relatively rare, suggesting that they may represent unstable states where the system dwells only transiently. Mechanisms for such instabilities remain to be unraveled, but our results have important implications for the anticipated response of these ecosystems to climatic change. The data reveal that boreal forest shows no gradual decline in tree cover toward its limits. Instead, our analysis suggests that it becomes less resilient in the sense that it may more easily shift into a sparse woodland or treeless state. Similarly, the relative scarcity of the intermediate ∼10% tree cover suggests that tundra may shift relatively abruptly to a more abundant tree cover. If our inferences are correct, climate change may invoke massive nonlinear shifts in boreal biomes.

remote sensing | tipping point | resilience | permafrost | wildfire

The boreal forest is one of the most extensive biomes on Earth. Together with tundra, it is warming more rapidly than other biomes—approximately twice as fast as the global average (1). Warming has already caused extensive thawing of permafrost, accompanied with changes in hydrology, which are likely driving changes in vegetation, wildfires, and insect outbreaks (2, 3). Despite these major changes, the potential response of boreal systems to further climate change is poorly understood. One of the big questions is whether boreal biomes will change gradually, as assumed by most dynamic vegetation models (4, 5), or might have tipping points where changing conditions can invoke critical transitions.

Many factors, including fire, insects, climate, permafrost, and human land use, play a role in vegetation dynamics in the boreal region (2, 3, 6, 7). However, although detailed studies have revealed separate mechanisms, an understanding of large-scale stability properties and dynamics cannot easily be constructed from these separate elements. To address the question of potential critical transitions, we therefore complement the existing studies by analyzing the distribution of tree cover densities on continental scales. Tree cover is admittedly a rather crude descriptor of the vegetation state. However, it is one of the most defining characteristics not only for the structure of the landscape, but also for functional characteristics such as carbon storage and albedo.

Our central goal is to determine whether the frequency distribution of tree cover is a smooth unimodal function of one or more environmental variables or instead shows distinct modes that represent preferential states that occur more frequently than expected by chance. Multimodality of the frequency distribution of the state of a system can result from multimodality of underlying environmental drivers or from the existence of alternative stable states in the system (8). Alternative stable states imply tipping points and the potential for critical transitions (9) and have basins of attraction separated by repelling intermediate states. Frequency distributions of states can be informative about these properties because—given that stochastic events frequently perturb a system—a collection of snapshots will reveal the system to be more often close to the attractors (the alternative stable states) than around the repellors (the intermediate unstable states) (10, 11). Moreover, the system will be more frequently around states that are more resilient in the sense that they have a larger basin of attraction (see *SI Appendix*, Fig. S1 and *SI Text* for further background). Sharp transitions can happen even if environmental conditions change gradually in systems with alternative attractors. The positive feedbacks that cause the alternative stable states amplify change driving the system in a runaway fashion to an alternative state once a critical threshold is exceeded (9).

For our study, we used the Moderate Resolution Imaging Spectroradiometer (MODIS) dataset of remotely sensed estimates of tree cover in 500 × 500 m blocks between latitudes 45°N and 70°N. We relate these patterns to mean annual precipitation and mean July temperature (both averaged for the period 1961–2002) and to other known correlates of boreal tree cover. The frequency distribution of boreal tree cover across the globe is markedly multimodal (Fig. 1). In addition to forest and virtually treeless conditions, there are two distinct “savanna-like” woodland states: one with sparse (approximately 20%) tree cover and a denser one (approximately 45% cover). The four modes are particularly clear in Eurasia where the largest part of the world’s boreal region is found (*SI Appendix*, Fig. S2*A*). In North America, the sparse savanna is less pronounced and the overall distribution is best described by three modes (*SI Appendix*, Fig. S2*B*).

The frequency at which different tree cover states occur varies strongly with temperature (*SI Appendix*, Fig. S3). Treeless tundra dominates at low temperatures, whereas a distinct treeless steppe dominates at high temperatures. Over a range of intermediate temperatures, these treeless states coexist with boreal forest and two different open-woodland states. Of those two open-woodland states, the sparser one is found on average at somewhat lower temperatures with more continuous permafrost (*SI Appendix*, Fig. S4). The probability of finding boreal forest also increases with precipitation, and the combination of temperature and precipitation explains the distribution of boreal forest better than either of those factors alone (*SI Appendix*, Fig. S5). Although the relationship of boreal tree cover to precipitation, temperature, permafrost, and other factors has been widely discussed (12, 13), the conspicuous multimodality we find has not been reported, although it is in fact consistent with the classical observation that distinct biomes can be found under similar climatic conditions (14).

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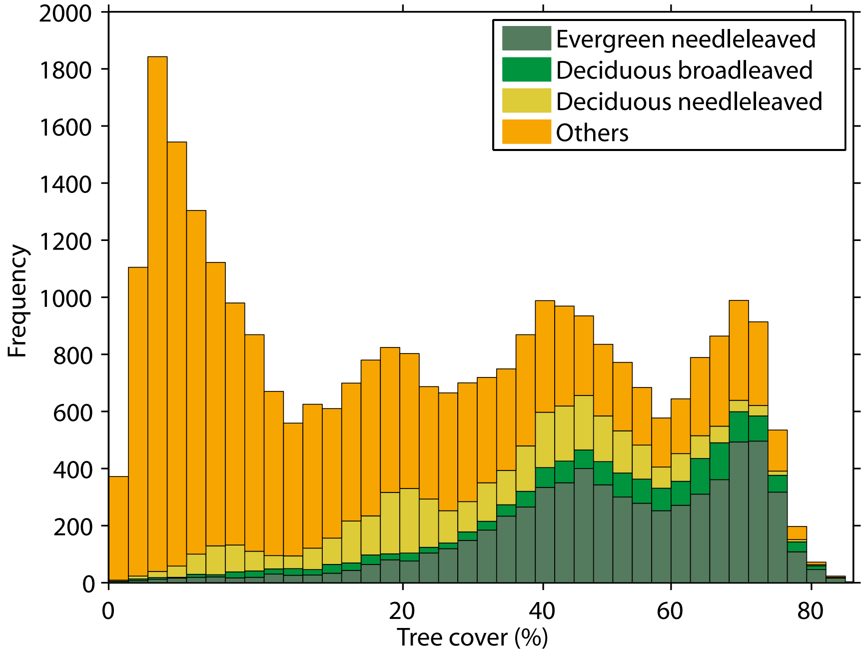

Fig. 1. Frequency distribution of tree cover in the boreal zone (45°N–70°N) in 500 × 500 m grid cells. There are four distinct modes corresponding to forest, dense savanna-like woodland, sparse savanna-like woodland, and a treeless state (tundra or steppe). Tree cover percentage values have been transformed through the arcsine-squared-root transformation.

Multimodal abundance distributions can be caused by multimodality of environmental conditions (8), but in our dataset, both precipitation and temperature have smooth unimodal frequency distributions (*SI Appendix*, Fig. S6), and tree cover is a smooth function of temperature, precipitation, and their interaction (*SI Appendix*, Fig. S5). We were also unable to find indications that multimodal patterns of other potential drivers such a soil, topography, or permafrost would explain the patterns. Another possibility would be that the savanna-like woodland states would represent a transient recovery phase from disturbances such as fire or insect outbreaks. However, the occurrence of the same mode across the two continents would require a synchronized massive disturbance episode for which there is no evidence (15, 16). Therefore, it seems likely that the conspicuous modes are the result of a nonlinear response of these ecosystems to environmental conditions. As explained earlier, in this interpretation, the fact that intermediate tree cover levels separating forest, woodlands, and treeless states are relatively uncommon suggests that such intermediate states represent unstable situations. Stochastic forces will cause the system to be in such states occasionally, but the intrinsic instability of these states causes them to be transients. More precisely, assuming the probability distribution of states to result from the interplay of environmental stochasticity and a tendency of the system to move away from unstable situations ("repellors") and toward stable states ("attractors") one can estimate "stability landscapes" from the data (10) (*SI Appendix*, Figs. S1 and S7). We use this technique to explore how the possible alternative states might depend on temperature (*SI Appendix*, Figs. S7 and S8 and *SI Text*). The results support the view that boreal forest and woodlands are distinct alternatives to the treeless steppe and tundra states over an intermediate temperature range (Fig. 2). This analysis reveals that boreal forest shows no decline in tree cover toward its limits. Instead, our results suggest that it becomes less resilient in the sense that it may more easily shift into a woodland or treeless state.

Discussion

There is inevitable uncertainty when it comes to inferring dynamical systems properties from observed patterns. Certainly, multimodality in the frequency distribution of states cannot be considered full proof of the existence of alternative stable states. As argued, the alternative interpretation that the pattern would result from multimodality of environmental conditions or synchronized recovery from a massive perturbation episode seems unlikely, leaving a nonlinear response of the system to environmental conditions as a prime candidate. The degree to which alternative states overlap with respect to an observed environmental variable (the inferred hysteresis in the response to this variable) is not easily inferred from data. Variation in unobserved driving variables will tend to inflate inferred hysteresis, whereas a large-scale positive feedback between tree cover and the observed environmental variable (e.g., precipitation or temperature) may cause real hysteresis to climatic change to be larger than inferred (17).

Despite such uncertainties, multimodality suggests the existence of positive feedbacks that drive the system away from unstable states. Our results thus raise the question which mechanisms could cause such positive feedbacks. Fire is a major driver of boreal vegetation dynamics, especially in drier periods or areas (e.g., continental interiors) (18–20). Wildfire might therefore account for the apparent instability at approximately 60% tree cover in the boreal forest, just as in the tropics (11, 21, 22). In tropical systems, as tree cover increases, beyond some point flammability decreases, which further promotes increase of tree densities in a runaway positive feedback toward closed forest. By contrast, if tree cover falls below a critical density, increased flammability may kill tree seedlings and cause runaway change toward an open landscape. Similarly, many closed boreal forests (ranging from broadleaf deciduous to tall-statured needleleaf dominated; Fig. 1) may be less flammable than more open woodlands, where lack of light competition leads to retention of lower branches (ladder fuels), and penetration of light and wind to the ground surface can dry understory mosses and lichens sufficiently within 24 h to support wildfire (23–26). Contiguous stands of this sort support extensive fires (27). However, closed boreal forests are not immune to fire. In fact, under dry windy conditions, closed boreal forests can be just as flammable as more open woodlands, causing flammability to rise up to a tree cover of 75% and remain constant for higher tree covers

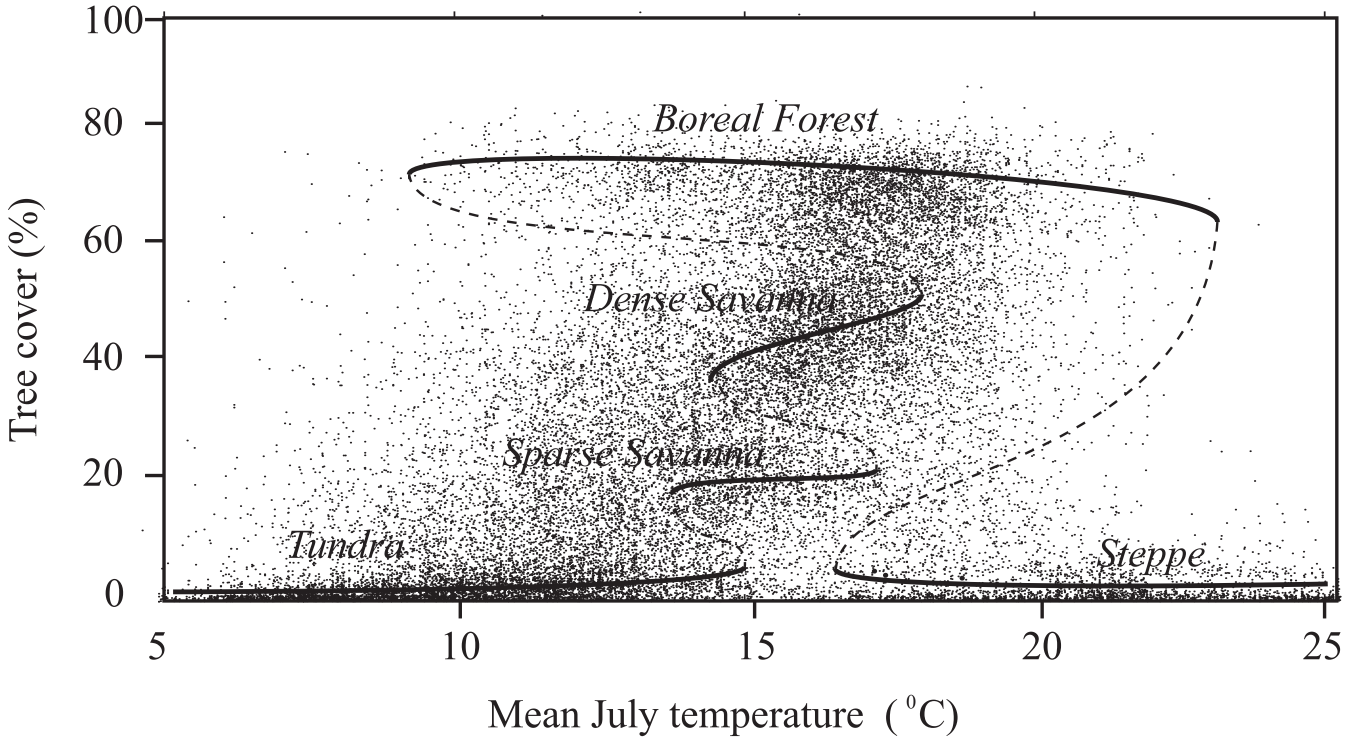

Fig. 2. Relationship between mean July temperature averaged for the period 1961–2002 and the approximate position of alternative stable states of boreal tree cover (solid curves) inferred from minima in the computed stability landscapes (*SI Appendix*, Fig. S7) computed from the data (*SI Appendix*, *SI Text* and Fig. S7). The dashed curves correspond to maxima in the computed stability landscape that separate the basins of attraction of the alternative stable states. Dots represent the tree cover and mean July temperature in the grid cells we analyzed.

(25). In addition to fire, insect outbreaks, windfall, and browsing are important drivers of boreal tree dynamics (3) and may be part of feedback loops because they are themselves likely affected by tree cover, but how the interplay of such forces and other factors might lead to alternative stable states in tree cover remains to be resolved.

At the northern end of the range, low temperature is a likely limiting factor to tree growth. A virtually treeless tundra is found at low temperatures (Fig. 2), which may be related to short growing seasons (28) and to the permafrost soils where water-logging restricts tree growth. Through changes in both energy budget (greater energy absorption; refs. 5 and 29) and wildfire (greater fire probability; ref. 30), trees increase heat input to soils on a regional scale. This effect implies a positive feedback as the resulting permafrost thaw further favors trees, suggesting that continued warming could cause abrupt forestation of northern treeline areas, as is already observed in some situations (28, 31, 32).

In addition to mechanisms explaining the tipping points at the northern and southern forest boundaries, the mechanisms causing the separation of the treeless and the two woodland states are less obvious. A virtually treeless state can be an alternative attractor if harsh conditions prevent establishment of seedlings unless ameliorated by the facilitative effects of existing trees (33). The fact that distinct treeless modes coexist with forest and woodland over a broad range of conditions suggests that such strong Allee effects must be at play. It is intriguing that, particularly in Eurasia, two distinct woodlands are found. The sparse type occurs especially in continental areas with continuous permafrost and saturated soils found, for instance, in peatlands (e.g., the Ob Depression in central Siberia), poorly drained ice-rich loess (yedoma) soils of eastern Siberia, and the Canadian Shield (34). One possibility is that this particular woodland type is related to local landscape features such as elevated microtopography (hummocks) or thaw-related breaks in the surface organic mat that alter water flow and nutrient distribution and provide a mineral seedbed that allows limited tree establishment (31). There is growing evidence showing that trees may trigger self-facilitating mechanisms in these local structures (35).

Clearly we cannot yet fully resolve the nature of underlying mechanisms that cause the boreal biome to have distinct tree-cover states. However, our results suggest that, rather than showing gradual responses, these boreal ecosystems will tend to shift relatively sharply between alternative states in response to climate change. The actual speed of transitions will depend on the mechanisms at play. Limited seed availability and slow hydrological changes could result in relatively slow transitions. However, in southern continental areas, changes such as warming-induced drought stress (12, 36), insect outbreaks, and fire could result in catastrophic collapse into a treeless steppe consistent with observations (3). Change will also differ depending on the local trends in climate. Although trees in continental parts of the southern border of boreal forest may experience increased drought stress, precipitation will likely increase in more maritime southern boreal zones (e.g., in Scandinavia or Labrador) (37), perhaps leading to an expansion of forest (38, 39). The scenarios of change are perhaps most difficult to infer at the northern end of the boreal range. However, rapid pulses of tree recruitment are often observed in warm episodes (28) consistent with our results, suggesting that increased temperature could result in distinct shifts in tree cover from tundra to forest or savanna-like woodland. Overall the observations in the boreal region are consistent with the finding that extreme climate events such as droughts or very rainy years may trigger shifts between alternative vegetation states because they can trigger pulses of tree recruitment or mortality that further affect disturbance regime and the positive feedbacks maintaining a particular vegetation state (40, 41).

The massive character of the potential transitions we envision for the boreal region have profound consequences for plant, animal, and the indigenous human populations that have lived for millennia in boreal ecosystems. The vast extent of the boreal region also implies that such potential transitions could create substantial feedback effects to the climate system. Unraveling the mechanisms that drive the potential instabilities suggested by our study will be challenging and will most likely require large-scale field experiments, coupled to mechanistic models and deeper analysis of field patterns. Also, reconstructions of the biome shifts that have occurred during the Holocene Thermal Maximum (28) and high-resolution satellite monitoring data may help to get a better insight into the character and timing of the imminent transitions we foresee for the boreal region.

Methods

Material and Geo-Information Processing. We studied tree cover distributions in terrestrial areas not dominated by human activity within the latitudinal belt defined between 45°N and 70°N. All collected datasets were resampled to ∼500 m. The following maps (databases) were selected:

i) Tree cover percentage map from the MOD44B Collection 3 product (42) at 500-m resolution, computed based on data collected from October 31, 2000, to December 9, 2001. It comprises the canopy cover percentage derived from MODIS satellite measurement of canopy reflectance. This estimator has not been specifically trained for boreal systems, potentially implying some error, although it has been found quite accurate in a broad range of ecosystems worldwide (42). We used the Global Land Cover 2000 (GLC2000) map (43) to filter out areas undergoing human activities or areas covered by water (categories 16–18 and 20–23). GLC2000 classes were also used to classify tree composition for each state depicted in histograms [evergreen needle-leaved, ref. 4; deciduous broadleaved, refs. 2 and 3; deciduous needle-leaved, ref. 5; and others (remaining classes, including mixed forest)].

ii) Mean annual precipitation and mean July temperature values were extracted from the Climate Research Unit's high-resolution monthly data (44). This dataset is based on climatic observations from meteorological stations interpolated at a resolution of 0.5° (∼55 × 55 km). We computed mean annual precipitation based on data for the period 1961–2002 (Fig. 3).

iii) The circumpolar permafrost data and the ground-ice data taken from the National Snow and Ice Data Center (45) were used to assess the effect of permafrost on the frequency distributions of trees within the selected zone. This dataset presents three main classifications of permafrost: extension (continuous, discontinuous, sporadic, isolated, or nonexistent); abundance of ground ice in the upper 20 m (low, medium, or high); and terrain/overburden specifications (lowlands/highlands, thick/thin overburden layer).

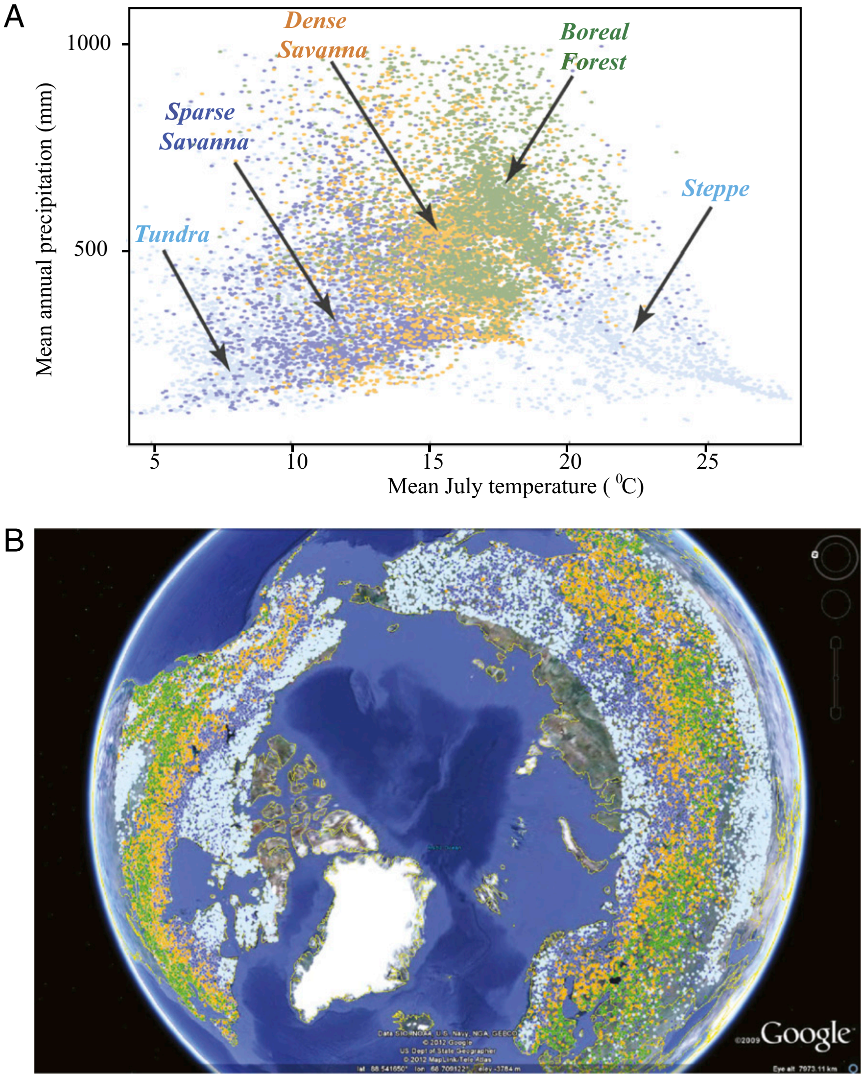

Fig. 3. Distribution of boreal forest, dense savanna-like woodland, sparse savanna-like woodland (forest tundra), and the treeless tundra and steppe states as a function of mean July temperature (°C) and mean annual precipitation (mm·yr^{-1}) both averaged for the period 1961–2002 (*A*) and the geographical distribution of these states (Copyright 2011, Google Earth) (*B*).

We used a random sample of ~0.01% of the total number of pixels, which means North America and Eurasia were represented by 15,000 and 21,000 random points, respectively. From these samples, we excluded the GLC2000 classes described above (item 1) and built a dataset of 29,893 points for further analysis. Geoprocessing steps were carried on in ArcGis 10.0, and data extraction/statistical analysis was performed by using Matlab R2011a and SPSS Statistics 17.

Analysis of Multimodality. We used latent class analysis to statistically test the number of modes of the tree cover frequency distributions (*SI Appendix*, Fig. S3). This technique can fit several frequency distributions to the data. We used the MATLAB/stats routine gmdistribution (Matlab/stats version R2011a) that uses an expectation-maximization procedure to find the best fit for a certain number of normal distributions. We compared the fit of the models with 1–6 classes by using a parsimony criterion (i.e., a goodness-of-fit criterion that punishes for each parameter of the model). For this comparison we used the Bayesian information criterion (BIC; *SI Appendix*, Table S1). Before analysis, the fractions of tree cover were arcsine square-root transformed to approach normal distributions, and a random subsample of 10,000 points from the GIS data were taken.

Computation of Stability Landscapes from the Data. To compute stability landscapes directly from the data (Fig. 2 and *SI Appendix*, Figs. S8 and S9), we used a method developed by Livina et al. (10) to compute the height of the stability landscape (i.e., the potential). The basic assumption is that there is an underlying stochastic system with a potential function:

$$dz = -U'(z)dt + \sigma dW,$$

where $U(z)$ is the potential function, z is the state variable (here tree cover), σ is the noise level, and dW is a noise term (Wiener process). The corresponding Fokker–Planck equation connects the probability density to the potential of this model. From this equation it can be shown that the potential U can be derived as (see ref. 10 for details):

$$U = -\frac{\sigma^2}{2}\log(p_d),$$

where p_d is the empirically derived probability density function. In our case, it was difficult to estimate the noise level σ, but because we were only interested in a qualitative estimation of the potential, we scale the potential to the noise level (U/σ^2). By following ref. 10, we estimated the probability density by using the MATLAB function ksdensity with a standard bandwidth of $h = 1.06\ s/n^{1/5}$ (s = SD of the dataset, and n is the number of data points).

We used a Gaussian kernel-smoothing window to calculate an approximate potential for each precipitation value. Because we have no independent estimates of the SD of the noise (10), we expressed the potential in units of σ and interpret it only qualitatively. We smoothed the potential by applying Gaussian weights (window size 5% of the temperature range) to the ksdensity routine (11). We estimated the equilibrium values by determining the local minima and maxima of the probability density function numerically. We detected the minima and maxima in an automated way, filtering out small local patterns by neglecting humps that were smaller than a threshold value (0.0007).

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