

Research

Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems

Rupert Seidl, Juha Honkaniemi, Tuomas Aakala, Alexey Aleinikov, Per Angelstam, Mathieu Bouchard, Yan Boulanger, Philip J. Burton, Louis De Grandpré, Sylvie Gauthier, Winslow D. Hansen, Jane U. Jepsen, Kalev Jõgiste, Daniel D. Kneeshaw, Timo Kuuluvainen, Olga Lisitsyna, Kobayashi Makoto, Akira S. Mori, Deepa S. Pureswaran, Ekaterina Shorohova, Elena Shubnitsina, Anthony R. Taylor, Nadezhda Vladimirova, Floortje Vodde and Cornelius Senf

R. Seidl (<https://orcid.org/0000-0002-3338-3402>) ✉ (rupert.seidl@tum.de), J. Honkaniemi and C. Senf, Univ. of Natural Resources and Life Sciences (BOKU) Vienna, Wien, Austria. RS and CS also at: Technical Univ. of Munich, Freising, Germany. RS also at: Berchtesgaden National Park, Berchtesgaden, Germany. JH also at: Natural Resources Inst. Finland (Luke), Helsinki, Finland. – T. Aakala and T. Kuuluvainen, Dept of Forest Sciences, Univ. of Helsinki, Finland. – A. Aleinikov, Center for Forest Ecology and Productivity, Russian Academy of Sciences, Moscow, Russia. – P. Angelstam, Faculty of Forest Sciences, Swedish Univ. of Agricultural Sciences, Skinnkatteberg, Sweden. – M. Bouchard, Forest Research Branch, Quebec Ministry of Natural Resources, Quebec, QC, Canada. – Y. Boulanger, L. De Grandpré, S. Gauthier and D. S. Pureswaran, Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Québec, QC, Canada. – P. J. Burton (<https://orcid.org/0000-0002-5956-2716>), Univ. of Northern British Columbia, Terrace, BC, Canada. – W. D. Hansen, Earth Inst., Columbia Univ., New York City, NY, USA. – J. U. Jepsen, Norwegian Inst. for Nature Research, Fram Centre, Tromsø, Norway. – K. Jõgiste and F. Vodde, Estonian Univ. of Life Sciences, Tartu, Estonia. – D. D. Kneeshaw, Dept of Biological Sciences, Center for Forest Research, Univ. of Quebec at Montreal, Montreal, Canada. – O. Lisitsyna, Dept of Geology, Tallinn Univ. of Technology, Tallinn, Estonia. – K. Makoto, Field Science Center for Northern Biosphere, Hokkaido Univ., Horonobe, Japan. – A. S. Mori (<https://orcid.org/0000-0002-8422-1198>), Graduate School of Environment and Information Sciences, Yokohama National Univ., Yokohama, Japan. – E. Shorohova, Saint-Petersburg State Univ., University Embankment, St Petersburg, Russia, and Forest Research Inst. of the Karelian Research Centre, Russian Academy of Science, Petrozavodsk, Russia. – E. Shubnitsina, 'Yugyd Va' National Park, Vuktyl, Komi Republic, Russia. – A. R. Taylor, Natural Resources Canada, Canadian Forest Service – Atlantic Forestry Centre, Fredericton, NB, Canada. – N. Vladimirova, 'Denezhkin Kamen' Nature Reserve, Severouralsk, Sverdlovsk region, Russia.

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Disturbance regimes are changing in forests across the world in response to global climate change. Despite the profound impacts of disturbances on ecosystem services and biodiversity, assessments of disturbances at the global scale remain scarce. Here, we analyzed natural disturbances in boreal and temperate forest ecosystems for the period 2001–2014, aiming to 1) quantify their within- and between-biome variation and 2) compare the climate sensitivity of disturbances across biomes. We studied 103 unmanaged forest landscapes with a total land area of 28.2×10^6 ha, distributed across five continents. A consistent and comprehensive quantification of disturbances was derived by combining satellite-based disturbance maps with local expert knowledge of disturbance agents. We used Gaussian finite mixture models to identify clusters of landscapes with similar disturbance activity as indicated by the percent forest area disturbed as well as the size, edge density and perimeter–area-ratio of disturbed patches. The climate sensitivity of disturbances was analyzed using Bayesian generalized linear mixed effect models and a globally consistent climate dataset. Within-biome variation in natural disturbances was high in both boreal and temperate biomes, and disturbance patterns did not vary systematically with latitude or biome. The emergent clusters of disturbance activity in the boreal zone were similar to those in the temperate zone, but boreal landscapes were more likely to experience high disturbance activity

than their temperate counterparts. Across both biomes high disturbance activity was particularly associated with wildfire, and was consistently linked to years with warmer and drier than average conditions. Natural disturbances are a key driver of variability in boreal and temperate forest ecosystems, with high similarity in the disturbance patterns between both biomes. The universally high climate sensitivity of disturbances across boreal and temperate ecosystems indicates that future climate change could substantially increase disturbance activity.

Keywords: boreal forest, climate variability, disturbance regimes, remote sensing, spatial patterns, temperate forest

Introduction

Disturbances shape vegetation structure, composition and distribution around the globe (Franklin et al. 2002, Virtanen et al. 2010, Ding et al. 2012). Agents such as fire, wind and insect outbreaks are key drivers of natural ecosystem dynamics (Turner 2010). Disturbance events happen abruptly, but can have lasting impacts on ecosystems (Yue et al. 2016, Thom et al. 2018). Especially in long-lived systems such as forests, disturbance-mediated alterations of the demographic structure of tree populations can prevail for decades to centuries (Schurman et al. 2018). Such disturbance-created patterns contribute to landscape heterogeneity (Burton et al. 2008), which – in combination with the species-rich early seral habitats resulting from natural disturbances (Swanson et al. 2011) – fosters biological diversity and determines ecosystem functioning (Mori et al. 2018).

Growing evidence suggests that the natural disturbance regimes of the world's forests are changing in response to climate change (Pureswaran et al. 2015, Trumbore et al. 2015, Seidl et al. 2017). In many parts of the world, such as in North America and Europe, disturbance activity has already increased strongly over the past decades (Seidl et al. 2014, Westerling 2016). Further increases in disturbance frequency and severity are expected for the coming decades as climate continues to change (Seidl et al. 2009, Wotton et al. 2010, Moritz et al. 2012).

These ongoing changes in natural disturbance regimes are of concern for policy makers and ecosystem managers because disturbances have a predominately negative impact on ecosystem service supply (Thom and Seidl 2016, Boucher et al. 2018). Increasing natural disturbances can, for instance, counteract policies aiming to mitigate climate change via increased carbon storage in forests (Kurz et al. 2008). Moreover, changes in forest disturbance regimes could fundamentally alter the organization and assemblage of the earth's vegetation. Biomes are primarily differentiated via dominant vegetation types, which, in turn, can strongly be modified by the prevailing disturbance regime (Mucina 2019). Wildfire – vegetation feedbacks are, for instance, important determinants of grassland – forest ecotones around the globe (Hoffmann et al. 2012, Cowling and Potts 2015). Climatically altered disturbance regimes could thus tip the scales between adjacent biomes and facilitate major changes in the global distribution of vegetation (Gauthier et al. 2015).

Due to their fundamental importance for ecosystem structure and functioning, disturbances have also come into the

focus of the global vegetation modeling community. The development of dynamic global vegetation models (DGVMs) has progressed greatly in recent years (Fisher et al. 2018), and increased consideration of tree demography in these models now allows them to simulate disturbances (Kautz et al. 2018). However, global reference data sets to benchmark the disturbance regimes emerging from such simulations remain largely missing to date. Furthermore, whether the disturbance–climate relationships used in large-scale models are consistent across biomes remains unclear.

Hampering a quantitative understanding of global forest disturbance regimes is the fact that disturbances are defined, measured and analyzed differently in different ecosystems around the globe. Despite a long-standing plea for generalization in disturbance ecology (White and Jentsch 2001) and a growing body of research on forest disturbances, the ability to directly compare between local studies remains limited. The proliferation of remote sensing approaches for assessing forest disturbances (Kennedy et al. 2014, Senf et al. 2017) offers great potential in this regard, as satellite-based remote sensing products provide a disturbance quantification that is consistent across the globe. Consequently, the first large-scale analyses of forest disturbances have emerged in recent years. Yet, these analyses have largely focused on within-biome variation in disturbances (Cohen et al. 2016, Senf et al. 2018, Sommerfeld et al. 2018, Kulha et al. 2019), or focused on a single disturbance agent (Kautz et al. 2017, Marini et al. 2017), while investigations across biomes covering the entire disturbance regime remain scarce.

A key limitation for the application of current remote sensing approaches in the context of disturbance ecology remains their inability to distinguish between different agents of forest disturbance. At the global scale, human land-use is a key disturbance agent of forest canopies (Curtis et al. 2018). Distinguishing changes in natural ecosystem dynamics from changes in human land-use thus remains a key challenge when working with remotely sensed disturbance data. Protected areas and areas of minimal human intervention offer important insights in this regard, serving as reference sites for the analysis of patterns emerging from natural processes. We here build on a previously established global network of unmanaged forest landscapes for the temperate zone (Sommerfeld et al. 2018). In this contribution we extend this network by more than doubling the number of landscapes and almost tripling the area covered by these landscapes in order to – for the first time – quantify inter- and intra-biome

differences in recent natural disturbances of boreal and temperate forests.

Our main objective was to compare recent natural disturbances in forest ecosystems between the boreal and temperate biomes. Specifically, we asked whether 1) between-biome differences in disturbance activity (jointly described here by four indicators, namely the percent forest area disturbed as well as the size, edge density and perimeter–area-ratio of disturbed patches) are greater than within-biome differences. Biomes are primarily identified via differences in dominant vegetation, and the associated differences in tree traits confer differences on the susceptibility of forests to natural disturbances (e.g. varying flammability of broadleaved-dominated and conifer-dominated forests). However, also disturbance–vegetation feedbacks are important drivers of abrupt vegetation changes at biome boundaries (Hoffmann et al. 2012, Moncrieff et al. 2015, Dantas et al. 2016). We thus expected distinctly different disturbance patterns between the temperate and boreal biome. Furthermore, we asked whether 2) disturbance regimes in the boreal biome differ from their counterparts in the temperate biome with regard to their climate sensitivity (i.e. the response of disturbance activity to variation in climate). Climate sensitivity is strongly driven by the prevailing disturbance agent and the underlying mechanisms determining disturbance activity (e.g. fuel moisture in the context of fire (Flannigan et al. 2016) and climate-mediated insect population dynamics in the context of insect outbreaks (White 2015)). As wildfire and insect outbreaks are the main agents of disturbance across boreal and temperate forests we tested the hypothesis that disturbances respond similarly to variation in temperature and precipitation. Specifically, we expected that warmer and drier than average conditions will facilitate disturbance activity throughout the boreal and temperate biome (Seidl et al. 2017).

Material and methods

A network of unmanaged forest landscapes

To address the inter- and intra-biome disturbance variation in forests of the boreal and temperate zone we here extended a previously compiled dataset of 50 temperate forest landscapes (Sommerfeld et al. 2018) to the boreal biome. We generally followed the biome delineation suggested by Olson et al. (2001), who combined a number of major previous biogeographic maps, integrating information from more than 1000 biogeographers, taxonomists, conservation biologists and ecologists from around the world. We compiled information for 53 unmanaged landscapes in seven countries spanning the circumpolar boreal forest biome, covering an area of 20.3×10^6 ha (median landscape size: 57 714 ha). Criteria for landscape selection were 1) a contiguous polygon of at least 2000 ha that 2) has not been influenced by management during the study period 2001–2014 (Sommerfeld et al. 2018). Landscapes thus include core zones of protected areas (e.g. cat.

I or II according to the International Union for Conservation of Nature) as well as natural areas without formal protection status that have not been influenced by management interventions (based on the assessment of local experts). For each of the study landscapes we combined remotely sensed disturbance information (see next section) with field-based ecological knowledge from local experts. Specifically, information on dominant disturbance agents was collected from experts via a questionnaire, ranking them in decreasing order of importance (Supplementary material Appendix 1). Experts were identified via their publication record on the topic of forest disturbances for the selected areas, and all consulted experts also contributed to the analysis and interpretation of the data (Supplementary material Appendix 2).

Overall, the combined dataset of temperate and boreal landscapes analyzed here consisted of 103 landscapes with a total area of 28.2×10^6 ha, covering a wide climatic gradient with mean annual temperatures ranging from -15.1°C to 14.8°C and annual precipitation sums between 289 mm and 2315 mm. The dataset spans a latitudinal gradient from 35.73°N to 70.55°N and from 36.20°S to 51.04°S , and contains landscapes from five continents and both the northern ($n = 81$) and southern ($n = 22$) hemispheres (Fig. 1).

Disturbance data and landscape pattern analyses

We retrieved global forest cover change maps from Hansen et al. (2013) for the period 2001–2014 (updated ver. 1.2). They mapped forest canopy change at a 30 m resolution consistently across the globe based on Landsat satellite data. Only areas stocked with trees > 5 m height are considered forest, and only high severity disturbances (i.e. events where a disturbance leads to a complete or near complete removal of canopy trees at the level of a 30 m pixel) are mapped. Pixels are analyzed for disturbances independently of their neighboring pixels, and only the first disturbance of a pixel during the study period is considered. The dataset includes forest cover changes regardless of the agent causing the disturbance (Curtis et al. 2018). By studying unmanaged landscapes we here focused on natural disturbances.

The global forest cover change map was cropped to each study landscape, and four metrics of recent disturbance activity were calculated, using an eight-neighbor rule for defining adjacency between pixels, and considering all disturbances throughout the period 2001–2014. Metrics were selected to capture the extent and spatial patterns of disturbances, and pertain to two different spatial scales: at the landscape scale, we derived 1) the percent of the forest area disturbed (calculated as the total number of pixels disturbed relative to all forested pixels, and indicating the level of recent disturbance activity) and 2) the edge density of all disturbed patches within the forest area of a landscape (calculated by summing the length of all edges of disturbance-created patches and relating it to the total forest area, indicating the level of fragmentation of closed forest canopies caused by recent disturbances). At the scale of disturbed patches within a landscape we calculated

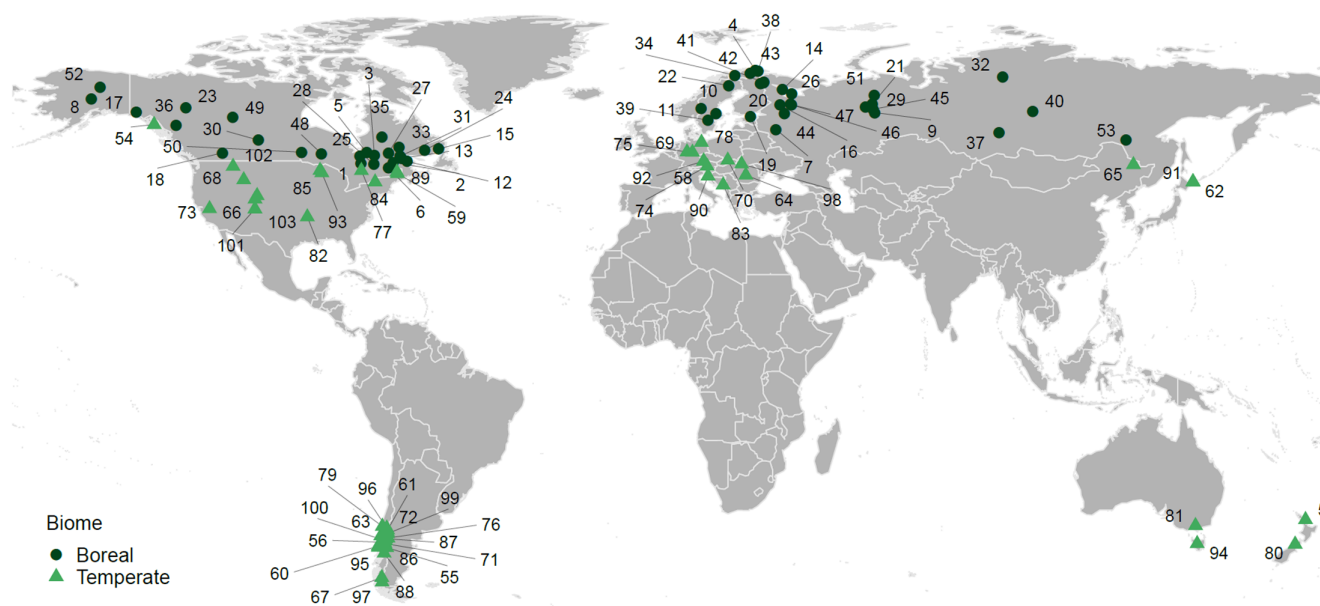


Figure 1. Global distribution of the 103 study landscapes. Biomes were generally delineated based on Olson et al. (2001) and further amended by assessments of local experts. See Supplementary material Appendix 2 for details on each landscape.

3) the area-weighted mean patch size (derived as the mean size of disturbed patches weighted by their size, and indicating the average extent of a disturbance-created patch) and 4) the area-weighted mean perimeter–area-ratio of disturbed patches (calculated as the ratio between patch edge length and patch size weighted by patch size, and describing the spatial complexity of patches). We used area-weighted patch metrics rather than arithmetic mean values across patches because the distribution of disturbance patches is highly skewed and area-weighted indices better represent the expected value that would be encountered when randomly sampling points on the landscape (Turner and Gardner 2015). The metrics calculated here are identical to those used in Sommerfeld et al. (2018) to characterize variation in natural disturbances within the temperate forest biome.

We analyzed the four disturbance metrics across absolute latitude using ordinary least squares regression, testing for broad biogeographical trends. Subsequently, we used unsupervised clustering via Gaussian finite mixture models (Fraley and Raftery 2007) to identify clusters of landscapes characterized by similar disturbance activity based on the four disturbance metrics described above. The number of clusters most strongly supported by the data was identified via the Bayesian information criterion (BIC). To address our first research question (between- versus within-biome variation) we compared the clusters of disturbance activity identified for the boreal biome to those previously described for the temperate biome (Sommerfeld et al. 2018). Comparisons included analyses at the level of the four disturbance metrics, as well as analyses in climate space (here defined by mean annual temperature and mean annual precipitation for the period 1960–1990, acquired from the WorldClim database ver. 1.4).

Climate-sensitivity of disturbances

In order to investigate the climate sensitivity of disturbances (research question two) we used Bayesian generalized linear mixed effect models (GLMM), relating the annual area disturbed in each landscape to temperature anomaly, precipitation anomaly and their interaction. Climate anomalies were expressed as z-scores by subtracting the mean and dividing by the standard deviation from each annual value for 2001–2014. As the annual area disturbed is often highly skewed (and models are thus likely to be over-dispersed), and as disturbance data are frequently characterized by excessive zeros (i.e. years without disturbance), we used a negative binomial error distribution with a log link-function. Climate information was acquired from global NCEP/NCAR Reanalysis 1 data via the RNCMP interface (Kemp et al. 2012). We fitted one GLMM per disturbance activity cluster (identified via the unsupervised clustering described above) and biome, with random intercepts and slopes among landscapes. Our model structure thus accounted for the widely varying landscape sizes within each biome–cluster combination. Joint posterior distributions for all model parameters (temperature anomaly, precipitation anomaly, their interaction and the dispersion parameter of the negative binomial model) were fitted using Monte-Carlo Markov Chain methods implemented in Stan (Carpenter et al. 2017). We put mildly regularizing $N(0, 10)$ priors on the intercept and slope parameters (temperature anomaly, precipitation anomaly and their interaction), reducing the risk of over-fitting. For the dispersion parameter we used a weakly-informative $\text{Exp}(1)$ prior, and for the variance–covariance matrix of the random intercept and slopes we used a regularizing LKJ(1) prior. As temperature and precipitation might have lagged effects on disturbance activity, we considered different lags from one to three years in relating temperature and precipitation anomalies

to annual area disturbed. We first fitted models for all lags and subsequently weighted the posterior distribution by model performance (i.e. a model averaging approach; McElreath 2016). We used a leave-one-out cross-validated estimate of the expected log predictive density, which is similar to using information criteria, but preferable in most settings (Vehtari et al. 2017). Finally, we tested whether each model fitted the data by performing posterior predictive checks. Posterior predictive checking is a simulation-based approach where random draws from the model are compared to the observed data. If the model is well specified, there should be no bias between random draws (here implemented with $n=4000$) and observed data.

Results

Inter- and intra-biome variation in disturbance patterns

Within-biome variation in recent natural disturbance activity was high in both the temperate and boreal biomes.

The proportion of landscape area disturbed over the 14 yr study period varied by three orders of magnitude in both biomes, indicating that some landscapes were heavily affected by disturbances while others were only very little disturbed (Fig. 2). Within-biome variation was even larger for the area-weighted mean patch size of disturbances, spanning nearly five orders of magnitude in both biomes. For all four indicators of disturbance activity, the within-biome variation did not differ between temperate and boreal biomes. Disturbance activity was thus not a strong discriminant between biomes, and all four disturbance indicators did not vary significantly over latitude (Fig. 2). Latitudinal trends were also not significant when analyzed at the level of individual continents (Supplementary material Appendix 3 Fig. A3.1).

Clustering the boreal study landscapes based on our four metrics of disturbance activity resulted in four distinct groups, the first three of which were remarkably similar to the groups previously identified for the temperate zone (Sommerfeld et al. 2018) (Table 1, Fig. 3). Landscapes in the first cluster had low disturbance activity, with a small

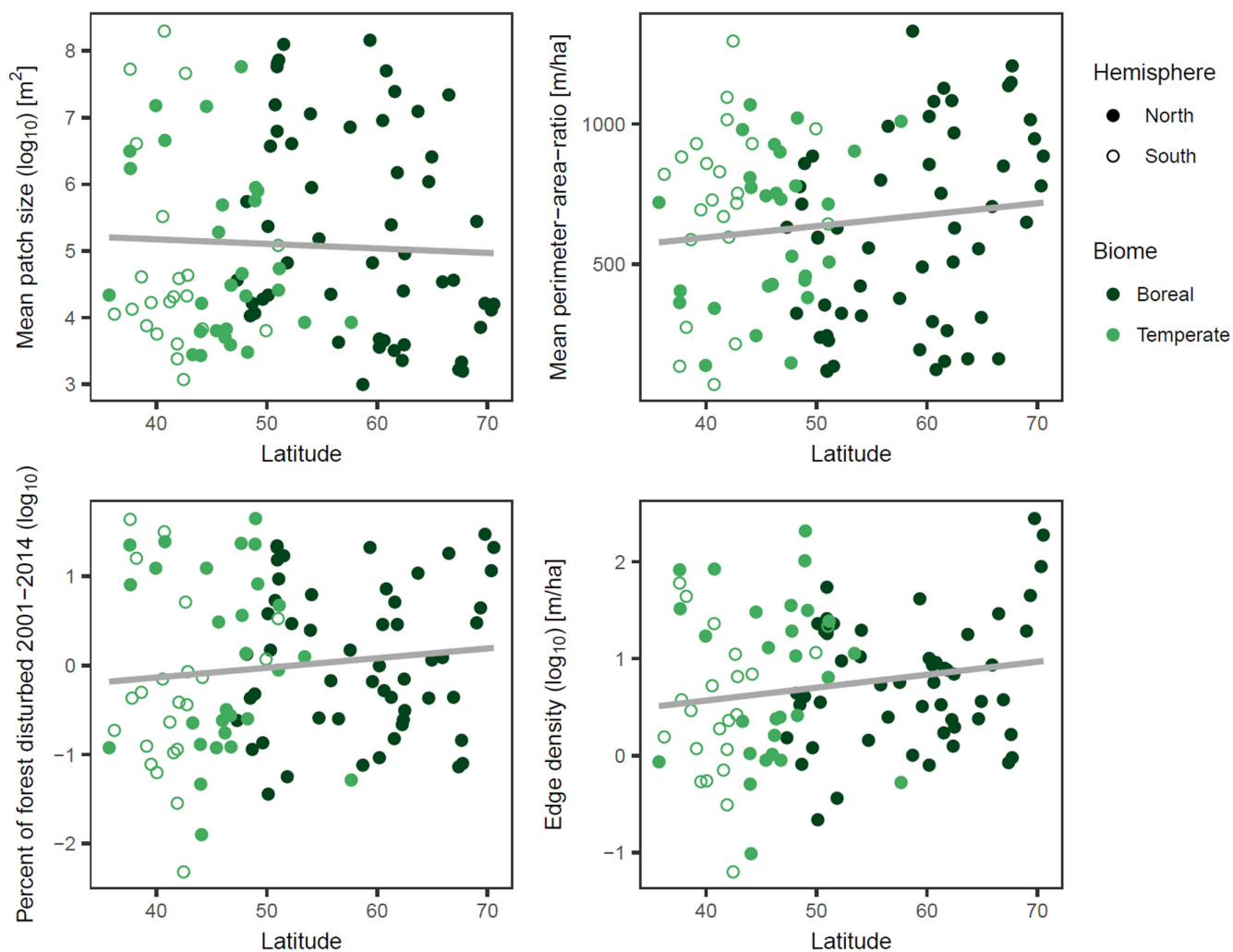


Figure 2. Variation of disturbance metrics over absolute latitude. Each point represents a study landscape (see Supplementary material Appendix 2 for details). Grey lines indicate linear latitudinal trends. None of the slopes were significantly different from zero at $\alpha=0.05$.

Table 1. Clusters of disturbance activity in boreal and temperate forests landscapes 2001–2014.

	All	Disturbance activity			
		Low	Moderate	High	Diffuse
Boreal					
Landscapes [n (%)]	53 (100%)	10 (18.9%)	19 (35.8%)	20 (37.7%)	4 (7.5%)
Total forest area [ha (%)]	9 119 654 (100%)	194 723 (2.1%)	2 420 362 (26.5%)	6 500 170 (71.3%)	4399 (< 0.1%)
Mean annual temperature ^{1,2} [°C]	-1.3 ± 0.5	0.7 ± 2.3	-1.3 ± 1.9	-2.4 ± 1.1	-1.3 ± 1.6
Mean annual precipitation ^{1,2} [mm]	687 ± 32	614 ± 43	796 ± 117	665 ± 108	464 ± 37
Mean percent of forest area disturbed ¹ [%]	4.93 ± 2.02	0.32 ± 0.20	0.69 ± 0.46	8.87 ± 3.34	16.84 ± 10.92
Mean edge density ¹ [m ha ⁻¹]	20.2 ± 12.7	3.4 ± 2.0	4.6 ± 2.8	17.5 ± 5.9	152.2 ± 104.1
Area-weighted mean patch size ¹ [ha]	1214.3 ± 807.1	0.3 ± 0.1	13.0 ± 11.2	3205.0 ± 1853.7	1.3 ± 0.4
Area-weighted mean perimeter–area-ratio ¹ [m ha ⁻¹]	616.6 ± 93.3	1110.9 ± 66.8	687.4 ± 56.4	244.1 ± 41.3	907.3 ± 98.0
Dominant disturbance agent ³ [occurrence in % of landscapes]	fire (35%), wind (23%)	wind (35%), pathogens (18%)	wind (35%), fire (31%)	fire (58%), defoliators (13%)	defoliators (100%)
Temperate					
Landscapes [n (%)]	50 (100%)	18 (36.0%)	23 (46.0%)	9 (18.0%)	–
Total forest area [ha (%)]	3 970 922 (100%)	788 986 (19.9%)	1 216 364 (30.6%)	1 965 572 (49.5%)	–
Mean annual temperature ^{1,2} [°C]	5.5 ± 0.5	6.5 ± 1.3	5.6 ± 1.2	3.7 ± 2.9	–
Mean annual precipitation ^{1,2} [mm]	1335 ± 75	1508 ± 252	1244 ± 180	1220 ± 427	–
Mean percent of forest area disturbed ¹ [%]	6.10 ± 3.12	0.31 ± 0.17	4.61 ± 4.17	21.50 ± 7.68	–
Mean edge density ¹ [m ha ⁻¹]	18.8 ± 10.0	2.9 ± 1.6	21.7 ± 18.9	43.2 ± 17.7	–
Area-weighted mean patch size ¹ [ha]	812.6 ± 847.6	0.7 ± 0.2	24.2 ± 17.3	4451.0 ± 4085.8	–
Area-weighted mean perimeter–area-ratio ¹ [m ha ⁻¹]	668.3 ± 81.0	960.1 ± 54.8	617.3 ± 56.5	215.3 ± 65.2	–
Dominant disturbance agent ³ [occurrence in % of landscapes]	wind (32%), fire (20%)	wind (45%), fire (12%)	wind (33%), fire (18%)	fire (39%), bark beetles (28%)	–

¹ Mean ± 95% confidence interval across landscapes.² Climate for the period 1960–1990.³ Dominant disturbance agents are derived by an expert ranking of disturbance agents in order of their importance for each landscape. Here we report the two most important disturbance agents per category, and the percentage of landscapes in which they occur. See Supplementary material Appendix 1–2 for details.

proportion of the forest area affected by disturbance, small disturbed patches, low edge density yet high patch complexity (as indicated by the perimeter–area-ratio of the disturbed patches). Disturbance activity progressively increased in the second and third group (moderate and high disturbance activity clusters), with increases in the proportion of the landscape disturbed, disturbed patch size and edge density, and corresponding decreases in perimeter–area ratio of disturbed patches (Table 1, Fig. 3). While temperate and boreal forests aligned well for the first three clusters of disturbance activity, a fourth group of landscapes emerged in the boreal zone that did not have an equivalent in the temperate biome. This diffuse disturbance activity cluster had a high proportion of the landscape area disturbed 2001–2014, but disturbances were characterized by many small and complex patches rather than by a few very large patches (Fig. 3).

The disturbance agents affecting a landscape varied more strongly with disturbance activity clusters than with biome and climate. Landscapes in the low disturbance activity cluster were mainly affected by wind and pathogens, while the

high disturbance activity cluster was strongly dominated by wildfire in both biomes (Table 1). The diffuse cluster, occurring only in the northern boreal zone of Europe (Fig. 4), was dominated by defoliators on deciduous trees (mostly *Betula* sp.). Landscapes with high disturbance activity had a tendency of being cooler and drier than other landscapes, yet the climatic differences between the northern and southern hemispheres were stronger than the differences between the temperate and boreal biome in the northern hemisphere (Fig. 5).

While patterns of disturbances were similar in the temperate and boreal forest, the distribution of landscapes across these patterns varied strongly with biome. In the boreal zone, 37.7% of the study landscapes (representing 71.3% of the forest area) were in the high disturbance activity cluster; high disturbance activity was thus the most prevalent disturbance pattern in the boreal zone during the 2001–2014 study period. In contrast, only 18.0% of the landscapes (representing 49.5% of the forest area) experienced high disturbance activity in the temperate zone, indicating a higher prevalence

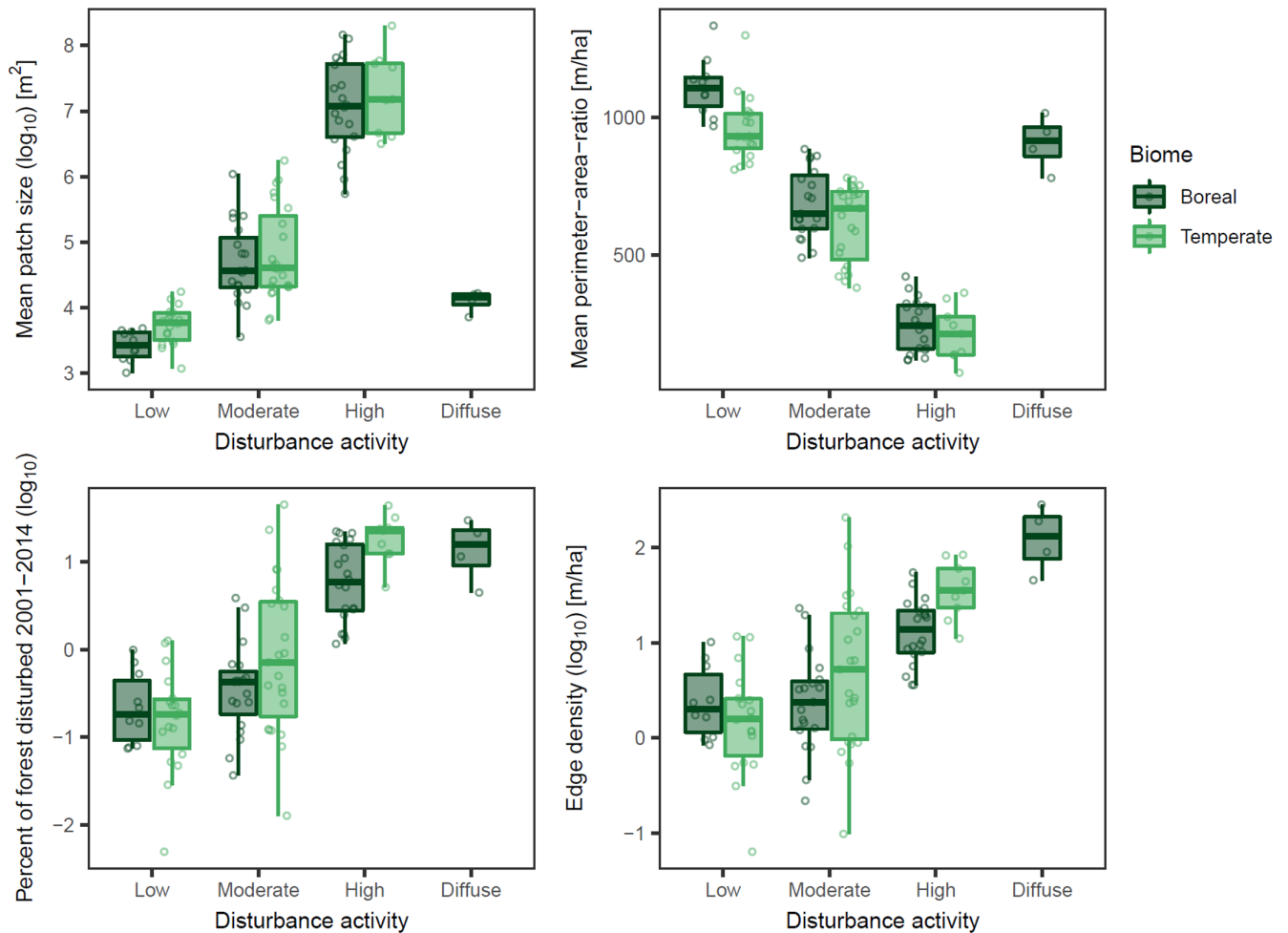


Figure 3. Clusters of disturbance activity 2001–2014 in the temperate and boreal forest biome, derived via Gaussian finite mixture models. Boxes indicate the interquartile range, whiskers extend to the 1% and 99% quantiles.

of low and moderate disturbance activity in temperate compared to boreal forests (Table 1).

Climate sensitivity of recent disturbance regimes

Climate sensitivity of disturbances varied distinctly with disturbance activity cluster. Landscapes with low disturbance activity were more sensitive to variation in precipitation than temperature. In contrast, disturbances strongly increased in response to warmer than average conditions in landscapes experiencing high disturbance activity, when these coincided with drier than average years (Fig. 6). General patterns and lag times of climatic drivers were consistent across biomes (see also Supplementary material Appendix 3 Fig. A3.2). The strongest differences in climate sensitivity between temperate and boreal forests were detected for landscapes with moderate disturbance activity. These landscapes responded more strongly to warm and dry years in the boreal zone than their temperate counterparts. Climate sensitivity was not analyzed for the diffuse disturbance activity group due to the limited number of observations in this group.

Discussion and conclusions

Key findings

Natural disturbances are among the most climate-sensitive processes in forest ecosystems (Lindner et al. 2010) and are expected to respond strongly to ongoing climatic changes (Seidl et al. 2017). Climate change is a global phenomenon, yet its impacts on ecosystems can vary widely. It is thus important to quantify differences in climate sensitivity to understand where climate impacts might be particularly severe. Here we tested for differences in the climate sensitivity of natural disturbances between the boreal and temperate forest biome. We hypothesized that forest disturbance activity is particularly sensitive to warmer and drier than average conditions. Our results confirmed that high disturbance activity in boreal and temperate forests was consistently associated with warmer and drier than average conditions. This finding is related to the fact that high disturbance activity is strongly tied to wildfires in both biomes, with wildfires being particularly sensitive to warming and drying (Abatzoglou et al. 2018).

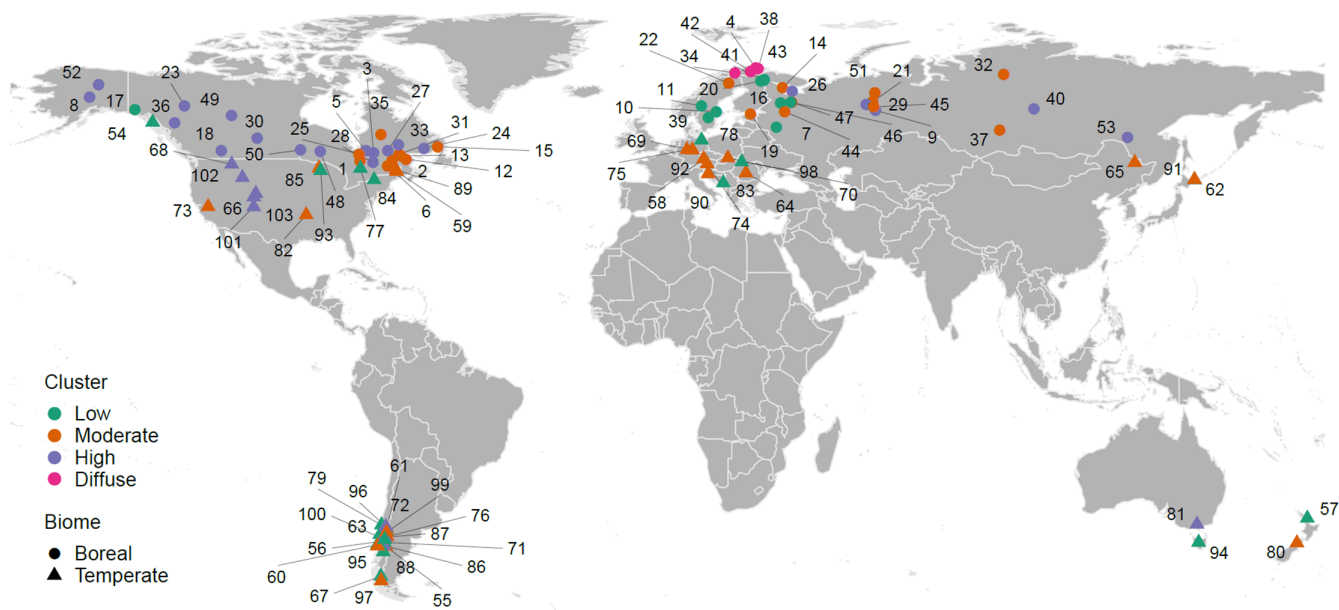


Figure 4. Global distribution of the four clusters of disturbance activity identified. For landscape IDs and meta-information on each landscape see Supplementary material Appendix 2.

Climate sensitivity between biomes was similar for landscapes with high disturbance activity, underlining that large fire events are consistently linked to warm and dry climatic conditions. A further factor contributing to similarities between biomes in areas with large disturbance activity could be that large disturbance events are increasingly decoupled from climate once they exceed a given size (e.g. with fire creating its own fire weather, and insect disturbances being decoupled from climate when population densities are high (Peters et al. 2004, Raffa et al. 2008)).

Assessing inter- and intra-biome variation in ecological patterns provides a quantitative baseline for the assessment of future changes in disturbances in response to climate change. Such baselines are particularly important for natural disturbances, as disturbance regimes are highly variable and any attempt to detect changes needs to distinguish them from the inherent variability of the system (Mori 2011). Here we for the first time quantified natural disturbance patterns across a wide range of boreal and temperate forests, highlighting that

tremendous within-biome variability is indeed a key characteristic of natural disturbance regimes across the globe. This variability in space and time results in a wide variety of structural patterns in forest ecosystems, and thus fosters their biological diversity (Burton et al. 2008, Mori et al. 2018).

Disturbances are important drivers of vegetation dynamics at biome boundaries in tropical ecosystems, with disturbance–vegetation feedbacks contributing to the formation of alternative biome states (Hoffmann et al. 2012, Moncrieff et al. 2015, Dantas et al. 2016). We here tested the hypothesis that disturbances are also an important factor differentiating temperate and boreal forests, expecting distinctly different disturbance regimes in the two biomes. Our data did not support this hypothesis, with disturbance patterns varying little across latitude, and similar disturbance activity groups emerging for both biomes in an unsupervised cluster analysis. Specifically, areas of high disturbance activity in the temperate zone had similar disturbance characteristics as such areas in the boreal zone. Furthermore, also in the boreal zone a sizeable share

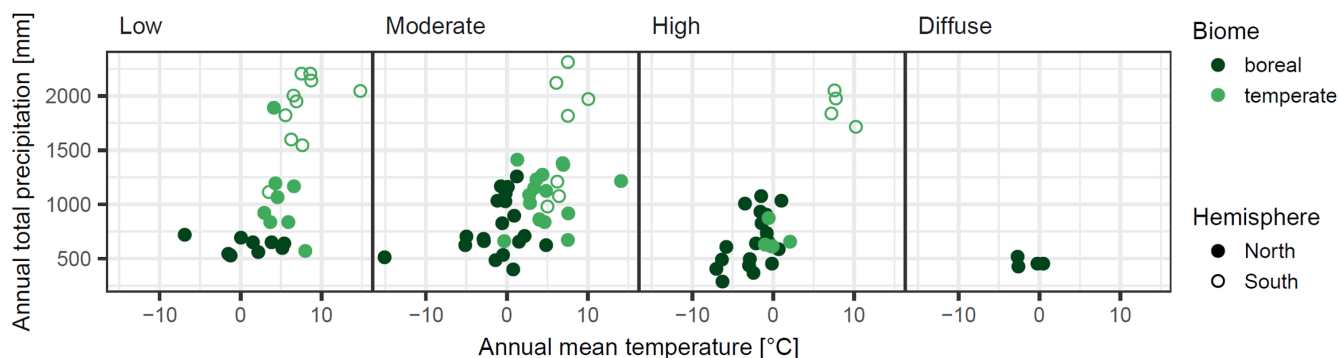


Figure 5. Location of the study landscapes in climate space for the four global clusters of disturbance activity.

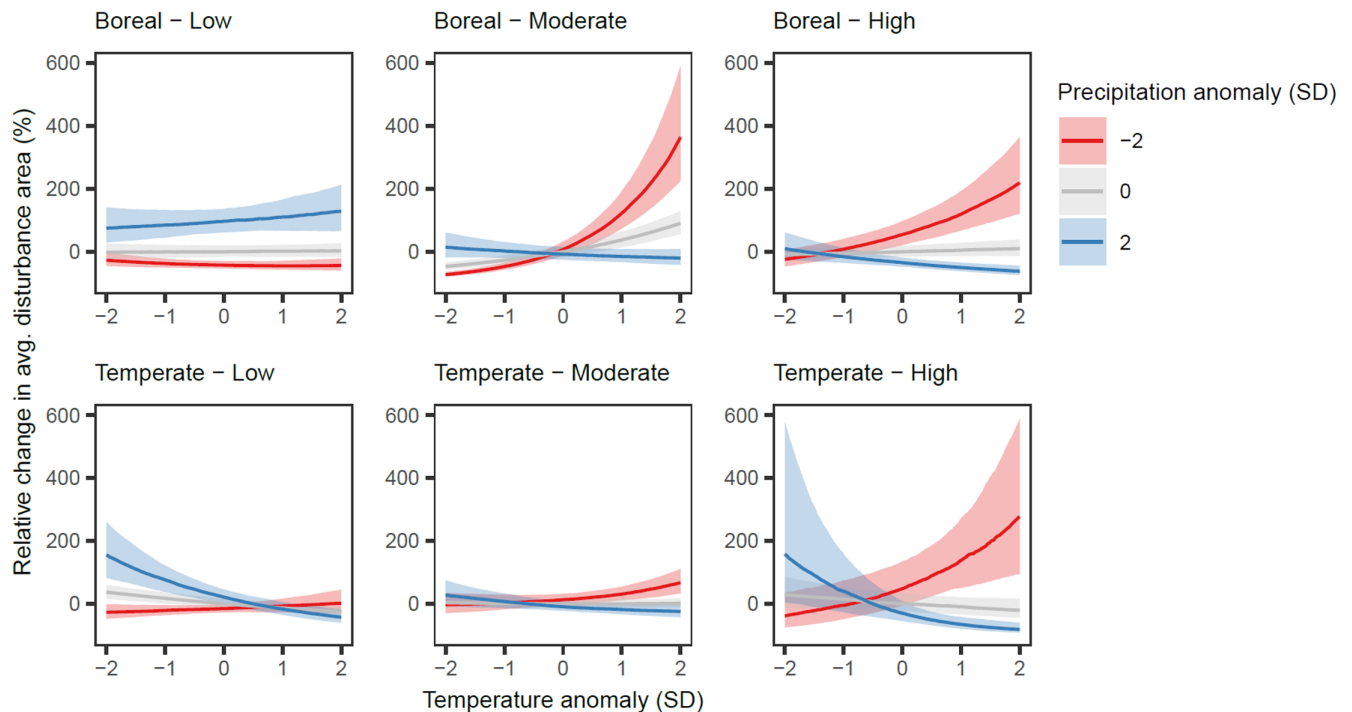


Figure 6. Predicted change of disturbed area relative to the mean in response to variation in temperature and precipitation for two biomes (rows) and three disturbance activity clusters (columns). Anomalies for temperature (x-axis) and precipitation (colors) are expressed in units of standard deviation (SD), with a value of zero indicating average conditions.

of landscapes experienced only very low disturbance activity during the 14-yr study period. While disturbance activity clusters were similar in the boreal and temperate zone, their prevalence differed between biomes, with boreal landscapes being more frequently associated with high disturbance activity than their temperate counterparts.

Limitations

An important limitation of our approach lies in the nature of the remotely sensed data used here (Hansen et al. 2013). First, our study period (2001–2014) is comparatively short for studying rare events such as natural disturbances. We aimed to address the resultant stochasticity by studying disturbances across a large spatial extent, compiling a set of forest landscapes distributed throughout the globe. Nonetheless, future work should further scrutinize our findings, e.g. by making use of the full length of the Landsat observation period (at least from 1984 onwards), which would more than double the temporal scope of the analysis (Cohen et al. 2016, Senf et al. 2018). A further limitation related to our data arises from the fact that the forest definition applied here only identifies vegetation canopies of > 5 m in height as forests (Hansen et al. 2013). Particularly in the northern boreal biome this threshold means that many ecosystems that would still be characterized as forests in the field are outside of the scope of our remote sensing-based analysis (Guindon et al. 2018). More work on the disturbance regimes of the circumpolar northern boreal forest is thus needed to better contextualize our

findings regarding the diffuse disturbance activity cluster. A third limitation is the focus on stand-replacing (at the grain of a 30×30 m pixel) disturbances, which is not able to fully account for the complexities of natural disturbance regimes in forest ecosystems, e.g. with regard to stands only partially affected by disturbance. Systems with low- to moderate-severity and/or mixed-severity disturbance are prevalent around the globe (Perry et al. 2011, Meigs et al. 2017). The resultant live tree legacies play an important role for the recovery from disturbances (Jõgiste et al. 2017), yet they cannot be satisfactorily described with the data used here. Moreover, due to limitations in detection, some disturbance types (e.g. insect defoliation) might be underrepresented in the dataset analyzed here. Also, metrics such as the perimeter–area-ratio can be biased in coarse raster data (Bogaert et al. 2000). Finally, it is important to note that despite our relatively large sample the variability of natural disturbances in the boreal and temperate biome might not be fully captured in our data. Unmanaged landscapes in the temperate zone are frequently also smaller than their counterparts in the boreal zone, which could induce a bias in our inter-biome comparison. The resultant undersampling of rare, large events in the temperate zone does, however, further support our finding of large disturbances being prevalent in both biomes (cf. Table 1).

Implications

Our results underline that natural disturbances are strongly climate-sensitive processes. Specifically, we highlight that

forest disturbances are likely to increase under warmer and drier conditions in boreal and temperate forests (Seidl et al. 2017). This finding of high climate sensitivity underlines the need for robust projections of future disturbance regimes in order to gauge their impacts on ecosystems and the services they provide to society (Scheller et al. 2018, Seidl et al. 2019). In this context our finding of consistent climate sensitivity of disturbances across biomes has important implications for ongoing efforts to improve disturbance modeling in DGVMs (Chen et al. 2018, Kautz et al. 2018), indicating that well-parameterized models might be applicable not only within biomes but also across biome boundaries. Furthermore, our finding of high inter-biome variability can serve as an important benchmark for pattern-oriented modeling of disturbance (Grimm and Railsback 2012).

A key element explaining intra-biome differences in disturbance activity are the prevailing disturbance agents. This underlines the importance of determining locally important disturbance agents to understand (and subsequently predict) disturbance regimes. It also suggests that the introduction of new disturbance agents (e.g. invasive alien pests (Hudgins et al. 2017)) can have a considerable impact on the disturbance regime (and its climate sensitivity). While distinguishing between human and natural causes of canopy disturbances is already possible via remote sensing (Guindon et al. 2014, Curtis et al. 2018), resolving different natural disturbance agents remains challenging. Here, we successfully combined local expert knowledge with large-scale remote sensing products, which can increase the inferential potential of remote sensing data for ecological questions. In conclusion, our analysis highlights remarkable similarities in disturbance patterns across boreal and temperate forest ecosystems (e.g. with regard to their spatial patterns and climate sensitivity), yet also underlines the considerable variation inherent to natural disturbances. While this variation is a challenge for assessing and predicting disturbance change, it is an important factor contributing to the diverse nature of forest ecosystems.

Data availability statement

Data on forest disturbances were derived from the global forest change data set (Hansen et al. 2013) available at <<https://earthenginepartners.appspot.com/science-2013-global-forest>>. Data on temperate forest landscapes were taken from Sommerfeld et al. (2018) and are published in full in their Supporting information. Data on boreal forest landscapes were derived by means of a questionnaire (Supplementary material Appendix 1), and is published in full in Supplementary material Appendix 2.

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References

- Abatzoglou, J. T. et al. 2018. Global patterns of interannual climate–fire relationships. – *Global Change Biol.* 24: 5164–5175.
- Bogaert, J. et al. 2000. Alternative area–perimeter ratios for measurement of 2D shape compactness of habitats. – *Appl. Math. Comput.* 111: 71–85.
- Boucher, D. et al. 2018. Current and projected cumulative impacts of fire, drought and insects on timber volumes across Canada. – *Ecol. Appl.* 28: 1245–1259.
- Burton, P. J. et al. 2008. Large fires as agents of ecological diversity in the North American boreal forest. – *Int. J. Wildl. Fire* 17: 754.
- Carpenter, B. et al. 2017. Stan: a probabilistic programming language. – *J. Stat. Softw.* 76: 1–32.
- Chen, Y.-Y. et al. 2018. Simulating damage for wind storms in the land surface model ORCHIDEE-CAN (revision 4262). – *Geo-sci. Model Dev.* 11: 771–791.
- Cohen, W. B. et al. 2016. Forest disturbance across the conterminous United States from 1985 to 2012: the emerging dominance of forest decline. – *For. Ecol. Manage.* 360: 242–252.
- Cowling, R. M. and Potts, A. J. 2015. Climatic, edaphic and fire regime determinants of biome boundaries in the eastern Cape Floristic Region. – *S. Afr. J. Bot.* 101: 73–81.
- Curtis, P. G. et al. 2018. Classifying drivers of global forest loss. – *Science* 361: 1108–1111.
- Dantas, V. de L. et al. 2016. Disturbance maintains alternative biome states. – *Ecol. Lett.* 19: 12–19.
- Ding, Y. et al. 2012. Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. – *Oikos* 121: 1263–1270.
- Fisher, R. A. et al. 2018. Vegetation demographics in earth system models: a review of progress and priorities. – *Global Change Biol.* 24: 35–54.
- Flannigan, M. D. et al. 2016. Fuel moisture sensitivity to temperature and precipitation: climate change implications. – *Clim. Change* 134: 59–71.
- Fraley, C. and Raftery, A. 2007. Model-based methods of classification: using the mclust software in chemometrics. – *J. Stat. Softw.* 18: 6.

- Franklin, J. F. et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. – *For. Ecol. Manage.* 155: 399–423.
- Gauthier, S. et al. 2015. Boreal forest health and global change. – *Science* 349: 819–822.
- Grimm, V. and Railsback, S. F. 2012. Pattern-oriented modelling: a ‘multi-scope’ for predictive systems ecology. – *Phil. Trans. R. Soc. B* 367: 298–310.
- Guindon, L. et al. 2014. Annual mapping of large forest disturbances across Canada’s forests using 250 m MODIS imagery from 2000 to 2011. – *Can. J. For. Res.* 44: 1545–1554.
- Guindon, L. et al. 2018. Missing forest cover gains in boreal forests explained. – *Ecosphere* 9: e02094.
- Hansen, M. C. et al. 2013. High-resolution global maps of 21st-century forest cover change. – *Science* 342: 850–853.
- Hoffmann, W. A. et al. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. – *Ecol. Lett.* 15: 759–768.
- Hudgins, E. J. et al. 2017. Predicting the spread of all invasive forest pests in the United States. – *Ecol. Lett.* 20: 426–435.
- Jõgiste, K. et al. 2017. Hemiboreal forest: natural disturbances and the importance of ecosystem legacies to management. – *Ecosphere* 8: e01706.
- Kautz, M. et al. 2017. Biotic disturbances in Northern Hemisphere forests – a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. – *Global Ecol. Biogeogr.* 26: 533–552.
- Kautz, M. et al. 2018. Simulating the recent impacts of multiple biotic disturbances on forest carbon cycling across the United States. – *Global Change Biol.* 24: 2079–2092.
- Kemp, M. U. et al. 2012. RNCEP: global weather and climate data at your fingertips. – *Methods Ecol. Evol.* 3: 65–70.
- Kennedy, R. E. et al. 2014. Bringing an ecological view of change to Landsat-based remote sensing. – *Front. Ecol. Environ.* 12: 339–346.
- Kulha, N. et al. 2019. At what scales and why does forest structure vary in naturally dynamic boreal forests? An analysis of forest landscapes on two continents. – *Ecosystems* 22: 709–724.
- Kurz, W. A. et al. 2008. Risk of natural disturbances makes future contribution of Canada’s forests to the global carbon cycle highly uncertain. – *Proc. Natl Acad. Sci. USA* 105: 1551–1555.
- Lindner, M. et al. 2010. Climate change impacts, adaptive capacity and vulnerability of European forest ecosystems. – *For. Ecol. Manage.* 259: 698–709.
- Marini, L. et al. 2017. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. – *Ecography* 40: 1426–1435.
- McElreath, R. 2016. Statistical rethinking: a Bayesian course with examples in R and Stan. – CRC Press.
- Meigs, G. W. et al. 2017. More ways than one: mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. – *For. Ecol. Manage.* 406: 410–426.
- Moncrieff, G. R. et al. 2015. Intercontinental divergence in the climate envelope of major plant biomes. – *Global Ecol. Biogeogr.* 24: 324–334.
- Mori, A. S. 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. – *J. Appl. Ecol.* 48: 280–292.
- Mori, A. S. et al. 2018. β -Diversity, community assembly and ecosystem functioning. – *Trends Ecol. Evol.* 33: 549–564.
- Moritz, M. A. et al. 2012. Climate change and disruptions to global fire activity. – *Ecosphere* 3: 49.
- Mucina, L. 2019. Biome: evolution of a crucial ecological and biogeographical concept. – *New Phytol.* 222: 97–114.
- Olson, D. M. et al. 2001. Terrestrial ecoregions of the world: a new map of life on earth. – *Bioscience* 51: 933.
- Perry, D. A. et al. 2011. The ecology of mixed severity fire regimes in Washington, Oregon and northern California. – *For. Ecol. Manage.* 262: 703–717.
- Peters, D. P. C. et al. 2004. Cross-scale interactions, nonlinearities and forecasting catastrophic events. – *Proc. Natl Acad. Sci. USA* 101: 15120–15125.
- Pureswaran, D. S. et al. 2015. Climate-induced changes in host tree–insect phenology may drive ecological state-shift in boreal forests. – *Ecology* 96: 1480–1491.
- Raffa, K. et al. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. – *Bioscience* 58: 501–518.
- Scheller, R. M. et al. 2018. Interactions among fuel management, species composition, bark beetles and climate change and the potential effects on forests of the Lake Tahoe basin. – *Ecosystems* 21: 643–656.
- Schurman, J. S. et al. 2018. Large-scale disturbance legacies and the climate sensitivity of primary *Picea abies* forests. – *Global Change Biol.* 24: 2169–2181.
- Seidl, R. et al. 2009. Modelling bark beetle disturbances in a large scale forest scenario model to assess climate change impacts and evaluate adaptive management strategies. – *Reg. Environ. Change* 9: 101–119.
- Seidl, R. et al. 2014. Increasing forest disturbances in Europe and their impact on carbon storage. – *Nat. Clim. Change* 4: 806–810.
- Seidl, R. et al. 2017. Forest disturbances under climate change. – *Nat. Clim. Change* 7: 395–402.
- Seidl, R. et al. 2019. What drives the future supply of regulating ecosystem services in a mountain forest landscape? – *For. Ecol. Manage.* 445: 37–47.
- Senf, C. et al. 2017. Remote sensing of forest insect disturbances: current state and future directions. – *Int. J. Appl. Earth Observ. Geoinform.* 60: 49–60.
- Senf, C. et al. 2018. Canopy mortality has doubled in Europe’s temperate forests over the last three decades. – *Nat. Commun.* 9: 4978.
- Sommerfeld, A. et al. 2018. Patterns and drivers of recent disturbances across the temperate forest biome. – *Nat. Commun.* 9: 4355.
- Swanson, M. E. et al. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. – *Front. Ecol. Environ.* 9: 117–125.
- Thom, D. and Seidl, R. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. – *Biol. Rev.* 91: 760–781.
- Thom, D. et al. 2018. Legacies of past land use have a stronger effect on forest carbon exchange than future climate change in a temperate forest landscape. – *Biogeosciences* 15: 5699–5713.
- Trumbore, S. et al. 2015. Forest health and global change. – *Science* 349: 814–818.
- Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. – *Ecology* 91: 2833–2849.
- Turner, M. G. and Gardner, R. H. 2015. Landscape ecology in theory and practice. Pattern and process. – Springer.
- Vehtari, A. et al. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. – *Stat. Comput.* 27: 1413–1432.
- Virtanen, R. et al. 2010. Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological

- disturbance, productivity and diversity. – *Global Ecol. Biogeogr.* 19: 810–821.
- Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. – *Phil. Trans. R. Soc. B* 371: 20150178.
- White, P. S. and Jentsch, A. 2001. The search for generality in studies of disturbance and ecosystem dynamics. – *Prog. Bot.* 62: 399–449.
- White, T. C. R. 2015. Are outbreaks of cambium-feeding beetles generated by nutritionally enhanced phloem of drought-stressed trees? – *J. Appl. Entomol.* 139: 567–578.
- Wotton, B. M. et al. 2010. Forest fire occurrence and climate change in Canada. – *Int. J. Wildl. Fire* 19: 253.
- Yue, C. et al. 2016. How past fire disturbances have contributed to the current carbon balance of boreal ecosystems? – *Biogeosciences* 13: 675–690.

Supplementary material (available online as Appendix ecog-04995 at <www.ecography.org/appendix/ecog-04995>). Appendix 1–3.