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Influence of tree species on continental differences in boreal fires and climate feedbacks

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Wildfires are common in boreal forests around the globe and strongly influence ecosystem processes. However, North American forests support more high-intensity crown fires than Eurasia, where lower-intensity surface fires are common. These two types of fire can result in different net effects on climate as a consequence of their contrasting impacts on terrestrial albedo and carbon stocks. Here we use remote-sensing imagery, climate reanalysis data and forest inventories to evaluate differences in boreal fire dynamics between North America and Eurasia and their key drivers. Eurasian fires were less intense, destroyed less live vegetation, killed fewer trees and generated a smaller negative shortwave forcing. As fire weather conditions were similar across continents, we suggest that different fire dynamics between the two continents resulted from their dominant tree species. In particular, species that have evolved to spread and be consumed by crown fires as part of their life cycle dominate North American boreal forests. In contrast, tree species that have evolved to resist and suppress crown fires dominate Eurasian boreal forests. We conclude that species-level traits must be considered in global evaluations of the effects of fire on emissions and climate.

North America and Eurasia are covered by vast tracts of boreal forest that experience recurrent wildfire. These fires regulate climate and ecosystem dynamics through several pathways. High-intensity crown fires combust large amounts of vegetation and detritus[1,2], and release black carbon aerosols that accelerate melt when deposited on snow and ice[3]. Crown fires kill most trees, altering surface energy budgets and, frequently, species composition for decades[4]. Spring albedo increases considerably after fire in snow-covered areas, leading to regional cooling[5,6]. Whereas most fires in boreal North America are known to be high-intensity crown fires, most in Eurasia are reported to be surface fires[7–12]. Surface fires are expected to have very different impacts as they typically do not kill healthy mature trees and may combust less organic matter[2,8,11,13].

Regional fire dynamics may relate to the distribution of species-specific fire traits[2,12,14]. Only a small number of spruce (*Picea*), pine (*Pinus*) and larch (*Larix*) species dominate the boreal zone[2,13,15]. The predominance of fire in these forests has selected for traits that allow most members of a species to complete a life cycle before being combusted and killed[2]. Divergent adaptations have emerged from this selection pressure, including fire 'embracer', 'resister' and 'avoider' strategies for coniferous trees. Embracers exhibit morphological adaptations that promote high-intensity crown fires such as the retention of lower branches[2,16]. Embracers are generally killed by fires and regenerate immediately from (semi-)serotinous cones that release seeds when burned[13,17]. In contrast, fire resisters suppress crown fires through self-pruning and, in the case of larch, high leaf moisture[12,18,19]. Fire resisters often have thick bark, which protects their cambium and increases their chances of surviving fire[19,20]. Fires tend to be relatively frequent in resister forests, partly owing to low fire-induced mortality[8,9,11]. Fire avoiders, on the other hand, lack fire-adapted traits and tend to occupy wetter environments where fires are infrequent. Under the right conditions, however, avoider canopies will sustain crown fires and the trees are easily killed[2,19,21]. The two boreal continents show a striking divergence in fire strategy: embracers dominate boreal North America and resisters prevail in Eurasia. Deciduous broadleaf trees, such as aspen (*Populus* spp.) and birch (*Betula* spp.), are less flammable and considerably less abundant than conifers on both continents, with their spatial distributions often influenced by post-fire successional dynamics[6,22–25].

Many studies project an increase in boreal forest burned area during the twenty-first century due to higher temperatures and longer growing seasons[26,27]. Boreal forests comprise roughly one-third of global forested area and carbon stocks, and have the potential to feedback to climate change both positively and negatively if disturbance regimes are altered[5,28,29]. Although North American boreal fires are thought to have a cooling effect because of large increases in spring albedo[5], little is known about the climate forcing from Eurasian fires. It has been suggested that plant fire strategies play a role in large-scale fire patterns[2,12], but this has not been quantified using direct observations. Global fire models using generic plant functional types do not account for species-driven differences and may miss important feedbacks. It is therefore of central importance to the scientific, modelling, mitigation and management communities to understand the spatial distribution of fire types, what drives them, and how they interact with climate. Here we investigate these issues using a suite of Moderate Resolution Imaging Spectroradiometer (MODIS) products and ancillary data sets of fire, climate and vegetation dynamics that provide information on various aspects of the fire regime. We reasoned that coherent large-scale differences in fire intensity and severity between the continents would be evident from remote sensing, that these would result in distinctly different post-fire

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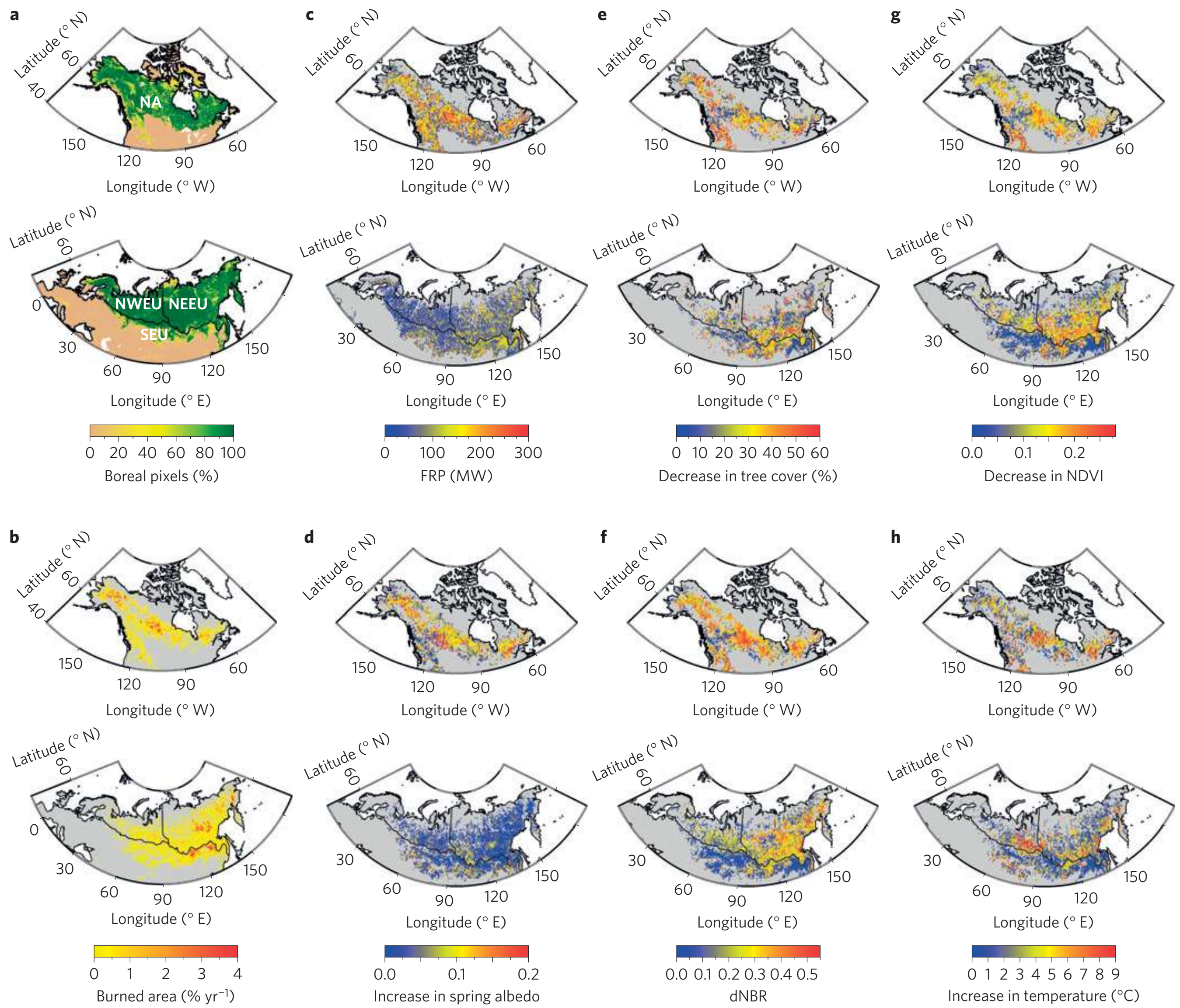

Figure 1 | Maps of the boreal domain and satellite products. a, Percentage of boreal pixels. **b**, Burn fraction from boreal pixels (2001–2012). **c**, FRP (2003–2013). **d**–**h**, Fire-induced changes in spring albedo (2001–2012; **d**), relative tree cover (2001–2009; **e**), dNBR (2001–2012; **f**), NDVI (2001–2012; **g**) and land surface temperature (2003–2012; **h**). Analyses were performed at the native resolution of the MODIS imagery (500 m–1 km) and averaged to 0.5° to produce these maps. Regions in **a** represent North America (NA), northwest Eurasia (NWEU), northeast Eurasia (NEEU) and southern Eurasia (SEU).

surface short-wave forcings, and that species-level fire strategies are the primary drivers.

Differences in fire intensity and severity

As boreal Eurasia shows marked functional diversity, we divided it into three regions on the basis of ecological and climatological characteristics (Fig. 1). Northwest Eurasia contains most of the continent's 'dark taiga' (that is, fire avoiders), experiences a comparatively mild climate, and is heavily influenced by human land use and fire management. This region burned infrequently during 2001–2012 (0.3 Mha yr^{-1}; Fig. 1b and Supplementary Fig. 1). Northeast Eurasia experiences a harsher continental climate and contains large expanses of deciduous larch often growing on shallow soils underlain by permafrost[30]. These forests are sparser, especially towards the Far East, yet burned relatively frequently with an annual burned area (2.0 Mha yr^{-1}) similar to North America (2.1 Mha yr^{-1}). Southern Eurasia is distinguished by topography and relatively high levels of understorey grasses, summer rainfall and human ignitions[31]. Burning was concentrated in late spring in southeastern Russia, with high interannual variability (1.4 Mha yr^{-1}, Fig. 1 and Supplementary Fig. 1).

We consider three timescales of fire dynamics: instantaneous fire behaviour ('fire intensity'), immediate impacts on the environment ('fire severity'), and longer-term ecosystem change ('burn severity'). Fire radiative power (FRP) was employed as a metric of fire intensity. FRP measures the instantaneous release of combustion energy (Supplementary Table 1) determined by fireline intensity and fire line length[32]. High FRP is associated with large, fast, intense fires, all properties known to be greater in crown versus surface fires[1,33]. Consistent with previous work[10,34], mean FRP across boreal Eurasia was 49 ± 4% lower than North America (Figs 1 and 2 and Supplementary Table 2; unless otherwise noted, error bars indicate 95% confidence intervals). We considered five measures of immediate fire severity derived from satellite imagery collected shortly before and after burning (one season to one year). Increase in spring albedo (dAlbedo) is correlated with fire severity as more needles, branches and boles that shade snow are destroyed[35]. dAlbedo was an order of magnitude weaker across Eurasia (85 ± 6%

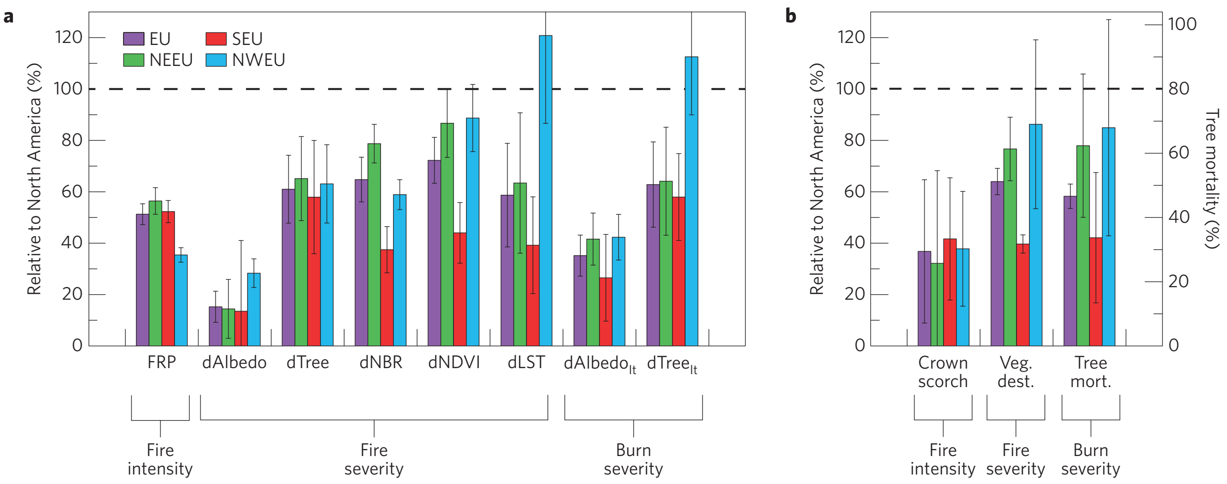

Figure 2 | Regional comparisons of intensity and severity. a,**b**, Satellite products (**a**) and derived metrics (crown scorch, live vegetation destruction, and tree mortality; **b**) categorized by fire intensity, fire severity and burn severity. Regions in the legend represent Eurasia (EU), northeast Eurasia (NEEU), southern Eurasia (SEU) and northwest Eurasia (NWEU). Values are shown relative to North America, and absolute percentages are given for tree mortality in **b**. The North American mean is located on the dashed line for every metric. Uncertainty bars represent 95% confidence intervals. Full descriptions of the abbreviated metrics are given in the text.

less than North America). A related but independent measure is the relative decrease in tree cover (dTree), which was 39 ± 13% lower in Eurasia. Summer-based fire severity metrics, including changes in normalized burn ratio (dNBR), normalized difference vegetation index (dNDVI) and land surface temperature (dLST), were between 28 ± 9% and 41 ± 20% lower in Eurasia. dNBR is sensitive to landscape charring, loss of live vegetation, soil exposure, and reduction in canopy water, dNDVI is sensitive to the destruction of photosynthetic vegetation, and dLST is sensitive to biomass loss through decreased roughness, reduced transpiration, and deposition of char (Supplementary Table 1).

Multi-year responses of spring albedo and tree cover were used as indicators of longer-term burn severity. North American fires caused large immediate decreases in tree cover and increases in spring albedo (Fig. 3, Supplementary Fig. 2 and Supplementary Table 2). Spring albedo continued to rise during the ensuing decade (Fig. 3) because of delayed branch and tree fall and dissolution of char[35]. Although initial increases were much smaller, spring albedo continued to rise by a similar degree in Eurasian regions. This was probably due to post-fire tree mortality and tree fall (Supplementary Fig. 2), which have been documented after surface fires and are thought to result from root and cambium mortality and soil destabilization[8]. When aggregated for post-fire years five and higher, burn severity was 37 ± 17% lower across Eurasia compared with North America using tree cover (dTree$_{lt}$), and 65 ± 8% lower using spring albedo (dAlbedo$_{lt}$) (Fig. 2). Southern Eurasia exhibited the lowest values for all immediate and longer-term severity metrics. We suggest that severity was higher in northwest Eurasia because of a greater proportion of fire avoiders (discussed below), and in Northeast Eurasia because of smaller trees (which increases the susceptibility to cambial kill and crown scorch) and harsher edaphic and climatic conditions for post-fire survival.

Satellite products were transformed and combined into three synthetic metrics better suited for understanding fire ecology and refining global models: an index of crown scorch (fire intensity), live vegetation destruction (fire severity), and percent tree mortality (burn severity; Supplementary Figs 3–5). Crown scorch is related to fire intensity, tree survival and the prevalence of crown fires[33,36], which represents a fundamental difference in fire regimes between the two continents. Consistent with field and modelling studies[7,8,12], our analysis implied that crown scorch was much lower (63 ± 28%) in Eurasia compared with North America (Fig. 2 and Supplementary Fig. 4 and Supplementary Table 2). Vegetation destruction has implications for carbon emissions and biomass stocks, and was 36 ± 5% lower across Eurasia (this is consistent with carbon emissions from ref. 12, in which modelled combustion in central Russia was 35% less than in central Canada). Finally, tree mortality is relevant for successional dynamics and can have a major impact on carbon and energy fluxes[6,37]. Total fire-induced tree mortality was 42 ± 5% lower across Eurasia compared with North America. Similar to the satellite products, derived metrics of fire and burn severity in Eurasia were lowest in Southern Eurasia and highest in northwest Eurasia (Fig. 2).

The consistency of trends across multiple satellite data sets provided compelling evidence for greater fire intensity, immediate fire severity and longer-term burn severity in the boreal forests of North America compared with Eurasia. Further analysis of independent data sources corroborated these conclusions. Active crown fires generate strong convection as they rapidly consume fuel and move across the landscape[2,38]. We therefore expected that fires in boreal North America would inject smoke higher into the atmosphere, spread quicker and grow to larger sizes than in Eurasia. Multi-angle Imaging SpectroRadiometer derived data sets on plume height and MODIS derived data sets on fire spread rate and fire size all confirmed this hypothesis (Table 1 and Supplementary Fig. 6). Our difference estimates are also inclined to be conservative as a greater proportion of low-severity surface fires are probably omitted from the MCD64A1 burned area data set[39] in Eurasia (see Supplementary Section on uncertainty and biases). While previous studies have addressed particular aspects of this phenomenon[10,12], ours is the first to provide a comprehensive assessment of fire behaviour and ecosystem impacts across the circumpolar boreal zone.

Implications for climate feedbacks and modelling

Our results provide evidence that fire-related climate feedbacks from the two continents are decidedly different. It has been shown that fires in North American boreal forests may have an overall cooling effect because of the dominant surface short-wave forcing[5]. Although highly dependent on severity, this can be twice as strong as the other combined biogeochemical and aerosol forcing terms, which are generally positive and scale with carbon emissions. In contrast, fires in boreal Eurasia may be close to climate-neutral

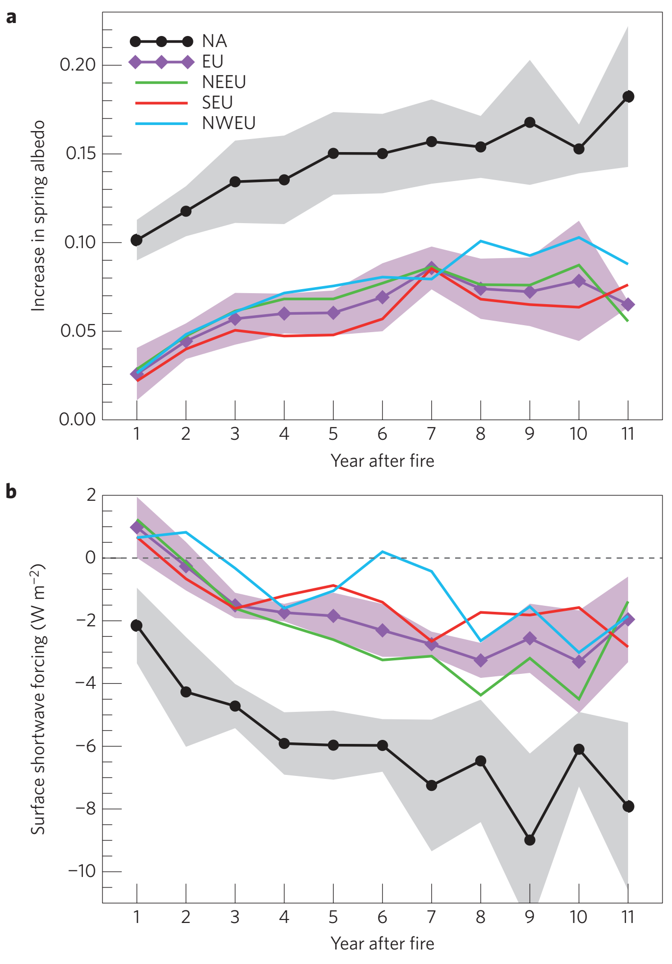

Figure 3 | Differences in post-fire albedo forcing. a,b, Post-fire trajectories of spring albedo (**a**) and annual surface short-wave forcing (**b**) during the first 11 years after fire. Regions in the legend represent North America (NA), Eurasia (EU), northeast Eurasia (NEEU), southern Eurasia (SEU) and northwest Eurasia (NWEU). Shaded areas for North America and Eurasia represent 90% confidence intervals, derived from individual trajectories for each fire year between 2001 and 2005. Forcings in North America are consistent with ref. 5, which calculated an annual mean radiative forcing of −5 to −8 W m^{-2} during the first post-fire decade in Alaska.

or have a warming effect. Whereas vegetation destruction in Eurasia was only 36 ± 5% less than North America, surface short-wave forcing during the initial 11 years after fire was 69 ± 9% weaker (−1.9 ± 0.7 W m^{-2} in Eurasia versus −6.0 ± 1.2 W m^{-2} in North America; Fig. 3). This difference may be even greater when integrated over the entire period of regrowth because forests are predicted to attain their pre-fire albedo quicker after surface fire compared with crown, and reflective deciduous broadleaf species are more common during post-fire succession in North America than Eurasia[9,19,24].

We found that current-generation global fire models do not capture the continental differences described above. The Global Fire Emissions Database version 3 (GFED; ref. 40) and the Community Land Model version 4.5 (CLM; ref. 41) were unable to reproduce continental contrasts in vegetation destruction or tree mortality. CLM, which simulates surface energy fluxes, also misrepresented differences in spring albedo increases from fire (Supplementary Table 3). These and other models that depend on broad plant functional types will misrepresent boreal fire impacts on the land surface and atmosphere, and require further development to reliably project fire–climate feedbacks.

Species effects

What causes these differences in fire dynamics between the two boreal continents? Fire intensity and severity are functions of meteorology, the amount, structure, continuity and moisture content of fuel, and vegetation properties that determine resilience to disturbance. Fire weather indices indicated that fire season meteorological and fuel moisture conditions during our analysis period were generally similar between the continents, and, if anything, were more severe in Eurasia (Table 1 and Supplementary Fig. 7). Long-term climate directly affects fuel amount through productivity and decomposition, yet global fire models using observed climate and generic biome-level plant functional types did not capture the observed continental differences. Instead, we argue that the dominant control comes from the tree species themselves, which have evolved distinct adaptations to fire that, in turn, influence fire behaviour and effects through fuel structure, fuel moisture and susceptibility to mortality[2,13,14].

Most fires in boreal North America occur in mature stands of black spruce (*Picea mariana*), jack pine (*Pinus banksiana*) and white spruce (*Picea glauca*)[2,12,25] (Supplementary Fig. 8). Black spruce and jack pine are fire embracers, and together accounted for 76% of the region's forested burned area. Although white spruce is known to successfully regenerate from seedbanks that survive fire[42], it is considered an avoider. Of lesser importance are lodgepole pine (*Pinus contorta* var. *latifolia*), also considered an embracer, and balsam fir (*Abies balsamea*), classified as an avoider. As these species are frequently found in mixed stands and none exhibit traits that suppress crown fires, fire intensity and severity were consistently high in all these forests (Supplementary Fig. 8 and Fig. 4). The sole resister in boreal North America, albeit a weak one, is American larch (*Larix laricina*). This species contributed to only 0.01% of the region's burned area but exhibited levels of crown scorch, vegetation destruction, tree mortality (Fig. 4 and Supplementary Fig. 8), and all raw satellite products (Supplementary Table 5) that were significantly lower and similar to deciduous broadleaf trees.

In stark contrast to North America, Eurasia is dominated by resisters, primarily Scots Pine (*Pinus sylvestris*) and larch[2,8,9,11,19,24] (Supplementary Table 4 and Supplementary Fig. 8). Avoiders are also found across the continent, such as Norway spruce (*Picea abies*), Siberian spruce (*Picea obovata*), Siberian fir (*Abies sibirica*) and Siberian pine (*Pinus sibirica*). These species occupy less of the landscape and burn much less frequently[2,8,18,19,23]. However, when they did burn, Eurasian avoiders exhibited significantly higher severity metrics than resisters (Supplementary Table 5), particularly those related to crown scorch and tree mortality (Fig. 4 and Supplementary Fig. 8). This helps explain why northwest Eurasia frequently exhibited the continent's highest fire and burn severities: fires in avoider forests comprised 30% of burned area in northwest Eurasia compared with only 6% in the other two Eurasian regions. The divergence in fire strategy between the boreal continents is remarkable: even though both contain small fractions of avoiders, no embracers are found in Eurasia, and the only resister in North America occupies less than 0.4% of the forested landscape. This is particularly surprising given that each genus is represented in both continents and that most of the areas experience analogous climates. The phenomenon argues for wide-scale selection pressure to survive and reproduce in fire-prone environments that resulted in divergent strategies between the continents.

Intensity and severity metrics were not identical between equivalent fire strategy groups in North America and Eurasia. This was probably due to a combination of factors, including mixed forest stands, energetic inertia of fires as they spread across a landscape, disparate data sources for vegetation distributions, mapping errors, and other climate, vegetation and ground surface influences. Nonetheless, this analysis for the first time provides quantitative evidence for the influence of individual species on

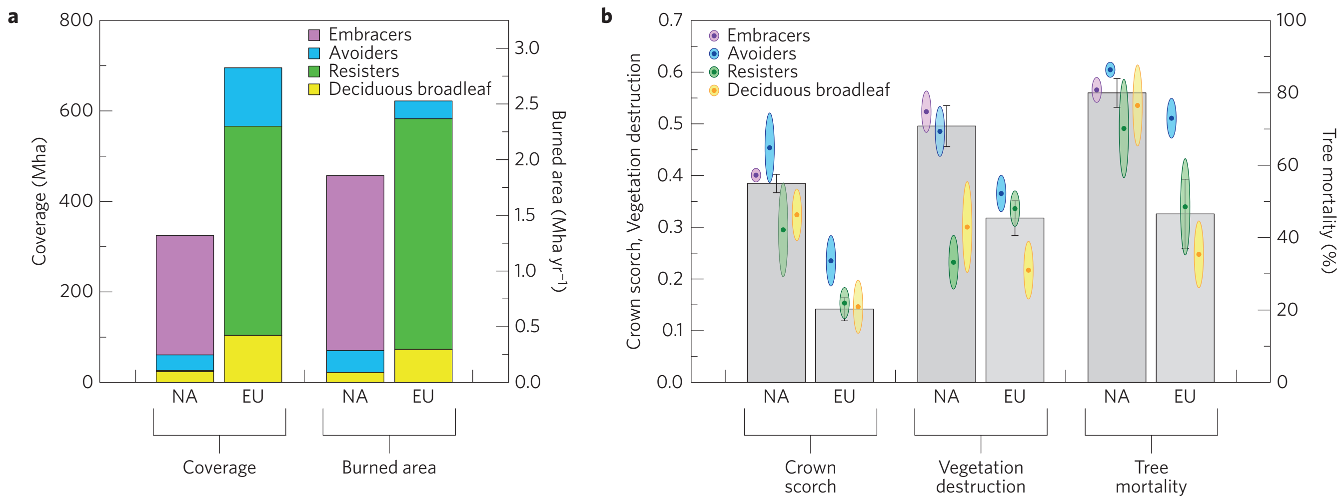

Figure 4 | Effects of fire strategy on fire dynamics. a, Spatial characteristics (aerial coverage and burned area) for North America (NA) and Eurasia (EU). **b**, Derived intensity/severity metrics. Grey bars indicate continental means. Error bars and ellipse heights represent 95% confidence intervals based on annual means. Note that contributions from non-forest areas (16% of total burned area in NA and 28% in EU) and forests classified as mixed deciduous/evergreen in North America (4% of total burned area) are not shown, and that only Russia is included for Eurasia (95% of its burned area).

Table 1 | Supporting observations for continental differences in fire dynamics.

Observation	Metric	North America*	Eurasia
Smoke plume height	Mean (km)	1.45 ± 0.03	1.27 ± 0.03
	Percentage above 1.7 km	29.3	15.4
Fire spread rate†	Area based (ha d^{-1})	77.5 ± 2.6	53.5 ± 0.9
	Length based (m d^{-1})	271 ± 7	243 ± 4
	Pixel based (m d^{-1})	357 ± 1	334 ± 1
Fire size	Mean/median (kha)	2.93/0.17	1.40/0.11
	95% burned area‡ mean/median (kha)	39.1/25.1	19.8/9.4
Fire weather indices§	Initial spread index‖	2.32 ± 0.13	3.18 ± 0.24
	Build-up index¶	36.3 ± 2.5	36.0 ± 2.9
Lightning flashes#	Mean annual frequency (km^{-2} yr^{-1})	1.36 ± 0.06	1.83 ± 0.04

*When applicable, 95% confidence intervals are given. †Geometric means and confidence intervals. ‡Size of largest fires contributing to 95% of 2001–2012 burned area. §Canadian fire weather indices during the fire season from 2000–2010, weighted by the spatial distribution of burned area within each region. Fire season was defined by the three consecutive months of maximum burning, which was April–June for southern Eurasia and June–August for all other regions. ‖Signifies potential rate of fire spread based on wind speed and fine fuel moisture. Higher values in Eurasia were primarily caused by southern Eurasia (Supplementary Fig. 7). ¶Indicative of dry fuel available for combustion. #Lightning flashes weighted by the spatial distribution of burned area within each region, including cloud-to-ground and intra-cloud flashes. More than 98% of flashes occurred between May and September in all regions, and more than 88% occurred between June and August.

large-scale fire dynamics. Moreover, when included with relevant fire weather variables in statistical models of intensity and severity, fire strategy emerged as the dominant predictor variable (see Supplementary Section on species effects).

We identify two potential selection drivers for the dominance of fire resisters in Eurasia. Larch (particularly *Larix gmelinii*) prevail across Siberia in part because of their ability to tolerate the region's extreme winter and poor soils[30,43]. As with other deciduous trees, the leaves of larch have relatively high moisture contents that suppress crown fires. Second, more frequent fires tend to favour resister species, and fire return times are generally shorter in the fire-prone boreal forests of Eurasia compared with North America[2,8,9,44]. Although influenced by vegetation and fire history, high fire frequencies may stem from more natural ignitions: we found that Eurasian boreal forests experienced 35 ± 6% more lightning strikes per unit area between 1995 and 2000 than North American (Table 1 and Supplementary Fig. 6).

We reason that black spruce may be a primary driver of the crown fire regime in boreal North America. Black spruce is both widely distributed and highly flammable[2,45], accounting for 65% of the forested burned area in North America (Supplementary Fig. 8). Black spruce has been dominant during past interglacial cycles and an aggressive pioneer during glacial retreat[46]. Regional fire frequency during the Holocene is strongly correlated with the presence of black spruce, often despite opposing climate trends[47,48]. Over the course of evolution and community assembly, the large, high-intensity conflagrations engineered by black spruce may have selected for other species that were capable of completing a life cycle despite frequent fire mortality. Although further work is needed to disentangle these origins, our observations are consistent with the presence or absence of particular species-level traits driving continental-scale fire patterns. Important future steps are to comprehensively evaluate the combustion of soil organic matter (which constitutes most carbon in these forests), quantify the contribution from peatland fires (which may be substantial[49]), incorporate these fire strategies into Earth system models, and systematically evaluate feedbacks to climate change.

It should not be surprising that strong species effects occur in boreal forests. High-latitude systems exhibit strikingly low species diversity compared with other biomes. As interspecific trait differences are not necessarily averaged out across diverse communities, species-level influences on ecological processes are evident at large spatial scales. The intercontinental differences in fire regimes are arguably as important for global carbon and energy cycling as fire-mediated transitions between tropical forests and savannas[50]. Indeed, they may represent the pre-eminent example of individual species regulating continental-scale biogeochemistry, biophysics and climate feedbacks.

Methods

All analyses of fire intensity and severity were performed using MODIS remote-sensing products (https://lpdaac.usgs.gov/data_access/data_pool) at their native 250 m, 500 m or 1 km resolution. Fire and burn severity metrics were quantified for burned pixels between 2001 and 2012 in the MCD64A1 data set. All data sources are described in detail in the Supplementary Information. Independent products were transformed and linearly combined to derive proxy metrics for crown scorch, live vegetation destruction, and tree mortality. We calculated regional surface short-wave forcings during the first 11 years after fire from monthly albedo trajectories and mean monthly solar insolation from 0.5° Climate Research Unit (CRU) National Centers for Environmental Prediction (NCEP) reanalysis climate data between 2000 and 2010. This reanalysis data set was also used to calculate fire weather indices from the Canadian Fire Weather Index System during fires and the three-month fire season for each region. Individual MODIS fire pixels were aggregated to fire events on the basis of temporal and spatial proximity and used to quantify fire spread rates and sizes. Additional supporting data sets were derived from satellite-based lightning frequency maps and previously compiled smoke plume heights. Combustion was extracted from 0.25° boreal grid cells in GFED for comparison purposes. We also compared vegetation destruction, tree mortality and spring albedo anomalies to CLM, which was run in an uncoupled configuration at 1° with a one-time prescribed fire event. We aggregated national inventory-based forest distribution data sets for Alaska, Canada and Russia to examine the influence of tree species and fire strategy on fire dynamics. Data reported in this paper are available at http://chronos.whrc.org (username 'br_EUvsNA_BorFires', password 'guest').

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Author contributions

B.M.R., J.T.R., M.L.G. and A.J.S. designed research; B.M.R. performed the research; A.J.S. provided Russian vegetation data sets; B.M.R. drafted the paper; J.T.R., M.L.G. and A.J.S. contributed to the interpretation of the results and to the text.

Additional information

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Competing financial interests

The authors declare no competing financial interests.