Are fire regimes the result of top-down or bottom-up drivers?

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Abstract.
The evolutionary topic we examine here is whether species determine the environment (bottom-up) or if environments shape plant traits (top-down). For the environment, we focus on the fire regime. Many forests are subject to either frequent low-intensity surface fires or less frequent but high-intensity crown fires. What are the ultimate factors controlling these fire regimes? The top-down model proposes that environmental factors controlling productivity and fire frequency shape fire regimes; the bottom-up model attributes them to different plant assemblies. In boreal forests, it is assumed that, because of the similar climate, forests of North America and Eurasia undergo distinct fire regimes (crown-fire and surface-fire regimes, respectively) due to bottom-up forces. We tested the hypothesis that fire regimes are primarily controlled by top-down factors by selecting congeneric species of Pinus and Picea from both continents. Plots dominated by each species were studied using remote sensing data. We then compared environmental conditions where the species occur and found that Eurasian tree species occur in warmer and more productive environments than North American tree species. Our results support the top-down model, which suggests that environmental factors control the surface versus crown fire regime in boreal forests.

Introduction

Two evolutionary mechanisms have been proposed that drive the relation between organisms and their environment. One is that the environment selects for species with appropriate traits (top-down; Van der Valk 1981, Weiher & Keddy 1999). Another is that species generate the appropriate environment for their persistence (bottom-up; Lewontin 2000, Laland et al. 2016). These two mechanisms are also important to understanding drivers that ultimately shape fire regimes (i.e., the characteristic fire activity that prevails in a given area). Despite fire regimes varying considerably depending on their different components (e.g., frequency, intensity, seasonality), broadly speaking, there are two fire regime types: periodic high-intensity crown fires and frequent low-intensity surface fires. What is the ultimate factor determining the predominant type of fire regime in forest ecosys-
tems? The proximal cause (i.e., the phenomenon that is immediately responsible or the ‘how’ explanation) is whether the surface fire is intense enough to transition into the crown (e.g., Van Wagner 1977, Parks et al. 2012); however, here we ask about the factors that control the intensity of fires (e.g., factors that allow the development of ladder fuels and the change in forest structure), which is the ultimate or distal cause (the ‘why’ explanation).

In explaining the distribution of different fire adaptations in the genus *Pinus* it was proposed that ultimately fire regimes were driven by the environment (top-down approach), specifically the combination of site productivity and frequency of ignitions (Keeley and Zedler 1998). Moderately high productivity forests allow trees to outgrow surface fires, and with frequent ignitions, surface fuels do not accumulate, thereby selecting for a particular suite of plant traits. These traits include high tree growth rates and self-pruning that prevent spread of fires from surface fuels to crowns, and a thick basal bark that protect from the heat of surface fires. In contrast, low productivity environments with infrequent fires produce a fuel load conducive to a crown-fire regime. This is linked to a suite of traits such as branch retention that enhance flammability, and serotiny that allows reproduction after crown fires (Keeley and Zedler 1998).

More recently, a bottom-up model has been proposed to explain the ultimate factor determining the predominant type of fire regime in boreal conifer forests (Rogers et al. 2015). This hypothesis was based on observations suggesting that ‘the’ climate across Eurasian boreal forests was similar to that in North American boreal forests. Since the regions are characterized by very different fire regimes (surface vs crown, respectively; Granström & Niklasson 2007, de Groot et al. 2013, Kharuk et al. 2021), those authors concluded that the fire regime was not driven by top-down factors that mediated plant traits, but rather by bottom-up characteristics of the available species pool in each biogeographical region. That is, whereas the top-down model suggests that the environmental difference (productivity) is the key factor determining the fire regime type and plant traits, the bottom-up model attributes the fire regime to differences in community assembly, which in turn is driven by the different biogeographical history (Fig. 1). For the bottom-up model to hold, the key requirement is that growing conditions are the same – and thus, species’ differences must dictate differences in fire regime. Given this key assumption, we can investigate the fundamental controls over boreal fire regimes by comparing growing conditions in the two continents.

Our hypothesis is that the broad-scale variability of forest fire regimes (crown vs. surface fires) is primarily controlled by top-down (environmental) factors. To test this hypothesis, we selected tree species pairs in *Pinus* and *Picea* that occur in the boreal forest of Eurasia (dominated by surface fire regimes; Zackrisson 1977, Granström & Niklasson 2007, Niklasson et al. 2010, Kharuk et al. 2021) and America (dominated by crown fire regimes; de Groot et al. 2013, Rogers et al. 2015) and examined the environmental parameters where they occur. Specifically we chose North American *Pinus* and *Picea* species that do not self-prune and have serotinous cones typical of crown-fire regimes; Eurasian species in these two genera lack serotiny and typically experience surface fire regimes. In fact, there are no serotinous trees in the Eurasian boreal forest. We predict the environmental variability will be greater between continents (within the same genus) than within the continent (for species of the two genera). More specifically, we predict that Eurasian boreal species grow in more productive environments conducive to surface fire regimes whereas North American boreal species are in less productive environments conducive to crown fire regimes. If this is the case, it would support the hypothesis that forest fire regimes are driven by top-down factors rather than by bottom-up factors.
Methods

Species

We selected two pairs of coniferous species that are abundant in the boreal forest: *Picea mariana* and *Pinus banksiana* in North America, and the congeneric *Picea abies* (northern lineage; Lockwood et al. 2013) and *Pinus sylvestris* in Eurasia. These species were selected because they are common and widespread in the boreal forest, occur under contrasted fire regimes, and have different fire-related traits; in addition, they allow congeneric comparisons. Specifically, the two North American species are serotinous and typically retain lower branches that contribute to crown fires, whereas this is not true for the two Eurasian species that commonly burn in surface fires. Of the two Eurasian species, *Pinus sylvestris* is a typical surface fire regime species (Zackrisson 1977, Niklasson et al. 2010) with self-pruning that prevents the continuity of vertical fuels. *Picea abies* at younger ages does not self-prune lower branches but their low flammability allow this species to withstand some surface fires; older trees do prune lower branches (Niklasson et al. 2010). The species selected allowed us to compare closely-related (within genus) taxa between continents (congeneric comparison). This means that many plant traits are similar due to recent common ancestry and thus, it is a way to better isolate the question (climate and fire regimes) from other factors.

We extracted localities (occurrence coordinates) for the four species from the Global Biodiversity Information Facility (GBIF; for discussion on the accuracy of this dataset see, e.g., Beck et al. 2014, Alhajeri & Fourcade 2019) within areas defined as boreal forest from a global map of terrestrial ecoregions (Dinerstein et al. 2017). Using the package ‘rgbif’ (Chamberlin et al. 2023) in the R statistical program (R Core Team 2023), we obtained a total of 13479 GBIF records for the four species. We then cleaned records with duplicate coordinates and excluded those plots that were outside of the species distribution area (e.g., obvious spatial errors or located within human-dominated land covers). Finally, to minimize the potential for spatial autocorrelation, we filtered the records using a minimum separation distance of 1 km (Beck et al. 2014). This yielded 8012 plots for the four species distributed as follows: *Picea abies* (n= 4074), *Picea mariana* (n= 881), *Pinus sylvestris* (n= 2488), *Pinus banksiana* (n= 569).

Fire regime

It is difficult to quantify the difference in fire regime (surface vs crown) between continents. One approach is to evaluate the differences in fire intensity from remotely sensed data, under the expectation of higher fire intensity in the North American boreal forest where crown fires are common (de Groot et al. 2013, Roger et al. 2015, Kharuk et al. 2021). To do so, we extracted the MODIS hotspots (Collection 6 Active Fire Products from Terra satellite, dataset MCD14ML; downloaded from the University of Maryland, USA; period 2002–2022) for a pixel of 0.1 degrees around each plot (8012 locations). We then averaged the fire radiative power (FRP, in MW; an indicator of fire intensity) for those plots with hotspots during that period. This method had limitations (e.g., some understory fires remain undetected, a short time window, and FRP may not only reflect fire intensity), but may still be an indicator of the difference in fire regime in our selected plots.

Environmental information

For each of the 8012 locations, we extracted environmental data from global datasets as follows. We used Google Earth Engine (GEE; Gorelick et al. 2017) to extract net primary productivity and soil
data. Net primary productivity (kgC/m²/year) was obtained from MOD17A3HGF.061 (Terra Net Primary Production Gap-Filled Yearly Global 500m, https://lpedac.usgs.gov/products/mod17a3hgfv061/) and soil properties from SoilGrids data set (https://www.isric.org/explore/soilgrids; 250m resolution, ISRIC World Soil Information). We selected the bottom soil layer as it best reflects the parent material (lithology); top soil layers may be influenced by the vegetation. For climate variables, we used bioclimatic data from Climatologies at High resolution for the Earth’s Land Surface Areas (CHELSA; Karger et al. 2017) mapped at a resolution of 30 arc seconds (i.e., about 0.46 Km at 60° latitude).

Statistical analyses

For each environmental variable, we estimated the variance component, using mixed-effects models where species was a random factor nested within continent. This allowed us to evaluate the amount of environmental variability distributed between continents (i.e., within congeneric species), within continents (i.e., between genera), or with species (i.e., the spatial variability across the species distribution). We used the “nlme” library in R (Pinheiro et al. 2022).

For each environmental variable, we evaluated the differences between species from different continents (North America vs Eurasia) within each genus (Picea and Pinus) by looking at the frequency distribution of each variable. We then compared the means among continents (between species of the same genus) using a maximum likelihood estimation of spatial simultaneous autoregressive lag (SAR); this method explicitly accounted for the spatial dependence between observations (using geographical coordinates of the plots). The SAR models were performed using the R library ‘spatialreg’ (Bivand & Piras 2015).

Unless otherwise stated, figures are displayed for the entire data set (n= 8012), but statistical analyses (variance component, SAR) were performed with 500 randomly selected plots for each species (n= 2000). Different random selections provide very similar results, and thus they are not considered further. When using GBIF data, subsetting for the statistics further reduces the spatial autocorrelation and produces better predictive models (Beck et al. 2014).

Results

Remotely sensed hotspots varied in FRP between continents, but not between species of the same continent (Table 1); they also vary greatly within each species. The frequency distribution suggests that, for the species considered, fires in the Eurasian forests have lower FRP than North American species (Fig. 2); the differences between continents were significant (Table 2).

Primary productivity, climatic variables related to temperature, and soil pH showed the strongest variability between continents, while the variability between species within the same continent was low (Table 1). There was also considerable variability within species as those species covered large areas in the boreal region. Precipitation-related variables varied substantially across the species’ distributions, with little remaining variability between continents. The variability between species co-occurring in the same continent was very low for all variables (Table 1). Thus, the environmental conditions where the species occurred were more different between continents (within genus) than within continents (between genus).
Eurasian *Picea* and *Pinus* species grow in higher productivity sites under warmer conditions and with a lower annual temperature range than North American ones (Fig. 3, Fig. S1). They also occur on sites with lower soil pH (Fig. 3). Thus, the environmental niches of the congeneric species living in different continents are different (Fig. S2). Mean differences between continents, when considering the spatial structure of the plots, are significant for all variables except for annual precipitation (Table 2). All environmental variables showed a high and positive spatial autoregressive coefficient (Rho > 0.59; Table 2). Some spatial autocorrelation remained in the residuals for some of the variables (Table 2).

**Discussion**

North American boreal forests show more intense fires than Eurasian boreal forests, in agreement with their different fire regimes (crown vs surface fires, respectively; Roger et al. 2015). These different fire regimes within a given biome (the boreal forest) have puzzled ecologists given their presumed similarity in environmental conditions (de Groot et al. 2013, Roger et al. 2015, Archibald et al. 2018, Kharuk et al. 2021). The regional similarity in climates has led to the proposal that the differences in fire regimes are due to a bottom-up mechanism - such that species with different traits (from different biogeographical pools) generate different fire regimes (Rogers et al. 2015). The results of our investigation, however, show some environmental differences between the continents, thereby supporting an alternative hypothesis that the broad-brush approach of comparing continental climates has confounding effects when addressing fire regimes. At a broad scale, these regions may have similar climates (Rogers et al. 2015); however, there is substantial variation when considering the localized environmental factors that characterize the species distributions. That is, some widespread species in the American boreal forest inhabit environments that are significantly different from those in common species in Eurasia, despite the overall climate similarity between continents.

Our results demonstrate that congeneric pairs of *Pinus* and *Picea* species with different character trait syndromes and subject to different fire regimes between American and Eurasian boreal forests occupy significantly different environments on the two continents. Specifically, boreal Eurasian species occur in warmer and more productive environments with a lower temperature range throughout the year than the North American boreal trees. These more productive environments provide better growing conditions for conifers to grow faster and taller, thus limiting the ability of surface fires to spread to their crowns (*Pinus sylvestris*; fire tolerator syndrome; Niklasson et al. 2010, Keeley 2012, Pausas 2015); or to quickly develop a low-flammability structure, especially in wetter microsites (*Picea abies*; fire avoider; Ohlson et al. 2011). The self-pruning in *Pinus sylvestris* further limits surface fire from reaching the crowns. The current higher incidence of lightning flashes in Eurasia (Rogers et al. 2015), if consistent throughout the past, may have also contributed to a high fire frequency, which in turn maintained low fuel levels and surface fires. In contrast, North American conifers are highly flammable and grow in less productive environments; thus, they typically lack a gap in vegetation between surface and crown fuels; so fires easily reach the crown. In such conditions, conifers have evolved serotinous cones to successfully reproduce under crown-fire regimes (fire embracer or postfire seeder syndrome). On the other hand, no serotinous species are known to occur in the Eurasian boreal forests. The two fire regimes are maintained by feedback processes such as those driven by flammability-related traits (dashed lines in Fig. 1; Schwilk 2003, Pausas et al. 2017). That is, the high flammability of trees of North American species (branch retention; high proneness to crown-fire) contrasts with the low flammability of Eurasian species (self-pruning; low proneness to crown-fire), and this contrast enhances the divergence between
North American and Eurasian fire regimes. This dynamic interplay is evident at the ecological scale (surface fires consume lower branches and enhance the vertical gap) and the evolutionary scale (driving divergent trait selection between fire regimes) and stabilizes the system into two contrasted fire regimes. Once the two systems are established, those feedbacks could potentially maintain the two fire regimes in similar environments, as suggested by some niche overlap (Fig. 1 and 2).

Overall, the top-down explanation of the contrasting fire regimes is more parsimonious than the bottom-up explanation. That is, the ultimate cause of divergent fire regimes between continents is the difference in environmental conditions that generate different evolutionary dynamics rather than the difference in assemblages due to biogeographical history (Fig. 1). That is, the subcontinental variability in top-down factors is a key to understanding the different fire regimes and associated plant traits between continents. The proximal cause (the ‘how’ explanation) is obviously driven by the accumulation of flammable fuel ladders in the North American boreal forests (Parks et al. 2012) as has been reported in many other coniferous forests (Covington & Moore 1994, Ireland et al. 2012). We further contend that, at a broad scale, fire regimes are largely driven by environmental factors that control both site productivity and fire frequency (e.g., Keeley and Zedler 1998, Bradstock 2010, Pausas & Keeley 2021).

The fact that variability is higher between congeneric species (from different continents) than between coexisting species from different genera suggests that, in boreal forests, the fire regime is a strong evolutionary force that makes the ancestral niche evolutionary labile (low niche conservatism; allopatic speciation). This is despite the general tendency in plants for niche conservatism (Prinzing et al. 2001), and supports the idea of evolutionary feedbacks between fire regimes and plant traits. In fact, our results suggest that fire regimes have generated a convergence in niche and fire traits (e.g. serotiny) between different genera. This is similar to what we observed in Mediterranean-climate regions (MCRs), where there are many cases of convergent evolution of fire traits in different lineages (Keeley et al. 2012). While some phylogenetic constraints may generate differences (especially when comparing Northern and Southern MCRs), the influence of top-down processes is strong enough to produce similar fire regimes and many instances of convergent evolution in MCRs.

An important consideration in determining variation in fire regimes, as in any other ecological process, is the scale of analysis (Falk et al. 2011). Our investigation, and the example of MCRs above, focused on broad-scale controls of contrasting fire regimes that are maintained at evolutionary scales and suggest the importance of top-down factors. However, bottom-up factors can be influential at smaller scales where two fire regimes may coexist in the same climate (i.e., within the same species pool). For instance, in forest-savanna landscape mosaics, shade produced by forest trees is associated with high moisture and low wind and favors low fire activity in forests, while in neighboring savannas, the higher light and wind generate drier conditions that maintain frequent fires and flammable grasslands (Charles-Dominique et al. 2018, Pausas & Bond 2020). The two co-occurring biomes (forest and savannas) have plants with markedly different traits. That is, at small spatial scales, vegetation feedbacks can drive different fire regimes in a given environment (Staver et al. 2011, Dantas et al. 2016) but are unlike to biogeographical differences.

One of the limitations of our study is the use of a biased sampling of the species distribution (from GBIF records). However, we have minimized the possible sampling bias by (1) excluding GBIF records that were closer than 1 Km; (2) selecting 500 randomly plots (subsetting) for the statistics (e.g., Beck et al. 2014), and (3) considering the spatial pattern in analyses (SAR models, Table 2). The observed patterns are strong and consistent in two pairs of species, suggesting that the potential remaining sampling bias is unlikely to affect the conclusions. We have analyzed the occurrence of
surface vs crown fire; however, there is a significant variability in fire regime within each of these
types (e.g., in frequency and intensity) that also deserves analysis. Small-scale variability in climate,
topography, and fuel distribution are likely to be responsible for such variability (Parks et al. 2012,
small spatial scales could also override environmental controls (e.g., Syphard et al. 2017).

While surface and crown fires may be the dominant fire regimes characterizing each continent
(boreal Eurasia vs boreal America, respectively), both continents are large and diverse and therefore
environmentally heterogenous. As such, there is evidence of crown fires in some areas of Eurasian
boreal forests (Kuuluvainen & Rouvinen 2000) and surface fires in some areas of American boreal
forests (Hauser 2008). In addition, although serotiny is absent in Eurasian forests, North American
boreal forests also host non-serotinous trees, including species of pine (e.g. *Pinus resinosa*; a thick-
barked tree with self-pruning, living under surface fires; Hauser 2008) and spruce (*Picea glauca*;
a fire-sensitive tree that colonizes postfire if the recurrence is not too high; Abrahamson 2015). Local
factors (e.g., sandy soils in *Pinus resinosa* habitats) are important for driving fire regimes at finer
scales, allowing the persistence of these other species in pockets of these continents. This is why we
focused on species distributions, i.e., subcontinental variability, to explain the difference in plant
traits between continents. By focusing on congeneric *Picea* and *Pinus* that are widespread, inhabit
different continents, and have different traits (serotinous/non-serotinous in North America/Eurasia),
we could restrict our analysis to the species and geographies that were relevant to our question.

We conclude that, at broad scales, the distribution of surface and crown fires across the boreal forest
is controlled by top-down (environmental) factors and maintained by eco-evolutionary dynamics.

**Data statement**

The paper does not present any new data; all data used were sourced from publicly available
databases as indicated in the Methods section.

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**Author contributions**

JGP and JEK designed the study, ADS compiled most of the data, JGP analyzed the data and wrote
the first draft. All authors contributed significantly to the final version of the manuscript.

**References**

U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire


Table 1. Variance component estimates (scaled to 0-1) for environmental variables between continents (within genus), between species of the same continent (i.e., between genera), and within species. The last column (Figure) indicates the corresponding figure where the frequency distribution is displayed. Values are estimated from 500 randomly selected plots for each of the four species. For each variable (i.e., by rows), the highest values are in bold and the lowest in italics.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Between continent</th>
<th>Between species (same continent)</th>
<th>Within species</th>
<th>Figure</th>
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<td>0.110</td>
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Table 2. Results of the comparisons of the means between continents for each variable and genus, using spatial simultaneous autoregressive lag models (SAR). Shown are the p value of the comparison, the spatial autoregressive coefficient (Rho), and the Lagrange Multiplier test for residual autocorrelation. The data for these comparisons is displayed in Fig. 3, 4, and S1. In all cases, the comparison between a linear model and this SAR model is significant (LR test <0.001) suggesting that including the spatial component improved the model. **** p < 0.0001; ns p > 0.05

<table>
<thead>
<tr>
<th>Variable</th>
<th>Picea Model</th>
<th>Rho</th>
<th>Residuals</th>
<th>Pinus Model</th>
<th>Rho</th>
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Figures

**Figure 1.** Simplified scheme of the two evolutionary mechanism mechanisms explaining the relationship between plants (light green boxes) and their environment (gray boxes). The top-down mechanism (left) suggests that there is a variability in environmental factors (e.g., productivity in different continents) that generates different fire regimes, which assemble different communities with different plant traits. The bottom-up mechanism (right) suggests that the different biogeographical history (in a given environment, e.g., boreal climate), assembles different communities with different plant traits that subsequently generate different fire regimes. Flammability traits (e.g., branch retention vs self-pruning) may feed back to fire regime (dashed lines) enhancing the difference between crown and surface fire ecosystems. For plant traits, serotiny and branch retention are examples of traits associated with crown fires, while thick basal bark and self-pruning are associated with surface fires. Red and green arrows are different pathways (e.g., different productivity, fire regime, community, and traits) related to crown and surface fire regimes.
Figure 2. Mean fire radiative power for each plot (log-scale), an indicator of fire intensity as detected from MODIS remote sensors. The figures show the comparison between continents for *Picea* (*P. abies* in Eurasia and *P. mariana* in North America) and *Pinus* (*P. sylvestris* in Eurasia and *P. banksiana* in North America).
Figure 3: Frequency distributions of three environmental variables for each species. The figures show the comparison between continents for *Picea* (*P. abies* in Eurasia and *P. mariana* in North America) and *Pinus* (*P. sylvestris* in Eurasia and *P. banksiana* in North America). NPP = Net primary productivity. The difference between congeneric species (i.e., between continents) is shown in Table 2. For more environmental variables, see Figures S1 in the Supplementary Material).