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# Present-day and future contribution of climate and fires to vegetation composition in the boreal forest of China

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**Abstract.** Climate is well known as an important determinant of biogeography. Although climate is directly important for vegetation composition in the boreal forests, these ecosystems are strongly sensitive to an indirect effect of climate via fire disturbance. However, the driving balance of fire disturbance and climate on composition is poorly understood. In this study, we quantitatively analyzed their individual contributions for the boreal forests of the Heilongjiang Province, China, and their response to climate change using four warming scenarios (+1.5°, 2°, 3°, and 4°C). This study employs the statistical methods of Redundancy Analysis (RDA) and variation partitioning combined with simulation results from a SErgey VERsion Dynamic Global Vegetation Model (SEVER-DGVM), and remote sensing datasets of global land cover (GLC2000) and the third version of Global Fire Emissions Database (GFED3). Results show that the vegetation distribution for the present day is mainly determined directly by climate (35%) rather than fire (1–10.9%). However, with a future global warming of 1.5°C, local vegetation composition will be determined by fires rather than climate (36.3% >29.3%). Above 1.5°C warming, temperature will be more important than fires in regulating vegetation distribution although other factors such as precipitation can also contribute. The spatial pattern in vegetation composition over the region, as evaluated by Moran's Eigenvector Map (MEM), has a significant impact on local vegetation coverage; for example, composition at any individual location is highly related to that in its neighborhood. It represents the largest contribution to vegetation distribution in all scenarios, but will not change the driving balance between climate and fires. Our results are highly relevant for forest and wildfires' management.

**Key words:** boreal forests; China; climate change; dynamic global vegetation models (DGVMs); fires; individual contribution.

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## Introduction

The boreal forest, as one of the important flammable ecosystems around the world, occupies 30% of the global forest areas (Gauthier et al. 2015). The vegetation structure and distribution are influenced by many factors. It is widely considered that climate, especially temperature and precipitation, directly controls the vegetation composition and distribution (Scheiter and Higgins 2009); hence, vegetation classifications are mainly based on such climate variables (e.g., Holdridge life zones [Holdridge 1947]). Temperature impacts the vegetation growth and distribution by changing the rates of photosynthesis, respiration, regulating phenology, tissue growth, regeneration, and mortality processes (e.g., frost damage). Plant Function Types (PFTs), which are assigned different bioclimatic limits (e.g., minimum coldest month temperature and maximum coldest month temperature), will determine whether they are able to survive and regenerate based on the climatic conditions. In addition to temperature, precipitation controls vegetation distribution by changing the water balance of the ecosystem (Stephenson 1990). Recent research indicates that annual rainfall is the dominant factor in regulating the relative distribution of global tropical forests and savannas (Hirota et al. 2011). Although climate is undoubtedly an important driver in regulating vegetation structure, within a single climate zone, different combinations of species can exist together, suggesting a decoupling of climate and vegetation, which means that other controls are also important in determining the local vegetation composition within any biome (Murphy and Bowman 2012, Scheffer et al. 2012).

Furthermore, vegetation distribution is indirectly determined by changes in the local disturbance regimes (Weber and Flannigan 1997, Dale et al. 2001, Gauthier et al. 2015). Fire is a particularly important natural disturbance and has a significant impact on the extent of forest cover in the flammable boreal forest ecosystems, helping to shape the vegetation structure and accelerate the natural carbon cycle (Bowman et al. 2009). Moreover, fires instantaneously link the atmosphere and biosphere by carbon emissions and have strong feedbacks to climate. In addition, fires will impact the climate by changing biophysical characters of the land surface, for example, albedo. Currently, all sources of fires (landscape and biomass combustion) cause $CO_2$ emissions (2–4 PgC/yr) equivalent to around one-third of emissions from fossil-fuel combustion (~10 PgC/yr; Van der Werf et al. 2006, Bowman et al. 2009, Le Quéré et al. 2015).

Dynamic global vegetation models (DGVMs) are important tools to simulate potential vegetation and carbon cycles in the terrestrial ecosystems. Meanwhile, DGVMs integrate biophysical, physiological, and ecological processes on a large scale, including vegetation physiology, phenology, vegetation dynamics, and competition. Vegetation distribution, carbon pools, and carbon fluxes are typically simulated at $0.5° \times 0.5°$ spatial resolution. The area unit of the model is a grid cell, and vegetation distribution in each grid cell is described as the fraction of different PFTs, or Foliage Projective Cover (FPC). Competition, as an important part of vegetation dynamics, is the most widely documented biotic factor affecting vegetation range by changing range limits and thus may impact range shifts (Ettinger and HilleRisLambers 2017). Zielinski et al. (2017) suggested that competition for resource was a significant control on "warm-edge" limits based on large-scale non-invasive surveys and home range data (Zielinski et al. 2017). Resource competition among PFTs in DGVMs, including water, light, nutrients, and individual response to disturbance (e.g., fire), impacts their relative FPC in each grid cell yearly (Sitch et al. 2003). Competition of woody PFT individuals depends on carbon gain, which depends on water, nutrients and light. Carbon gain is allocated to crowns and competition takes place as a self-thinning when potential FPC summed over all PFTs exceeds 1. We assume there are no differences for competition from leaves, roots, and wood in DGVMs, although the main use of carbon gain in roots is for fecundity and growth (Dybzinski et al. 2011). Carbon pools subdivided by PFTs exist in each grid cell, including leaves, sapwood, heartwood, fine roots, a fast and a slow decomposing above-ground litter pool, and a below-ground litter pool. Soil carbon pools in each grid cell collect the inputs from the litter pools of PFTs residing in the grid cell, and carbon fluxes connect terrestrial ecosystems and atmosphere, including net primary production (NPP) of PFTs, soil heterotrophic respiration, and combustion emissions.

In particular, when fire models have been incorporated into DGVMs, fire regime and vegetation–fire interactions can be represented (Scheiter et al. 2013, 2015, Bachelet et al. 2015, Wu et al. 2015). According to the DGVM simulations, forest cover (around 80–100% of tree cover) would more than double from 26.9% to 56.4% in a world without fire (Bond and Keeley 2005). Existing research revealed that some flammable ecosystems (including boreal forests, eucalypt woodlands, shrublands, grasslands, and savannas) are actually determined by fires (Bond et al. 2005). However, there is a difficulty in isolating the controls on vegetation distribution (Mills et al. 2006) and a limited number of studies have focused on analyzing the driving balance between fire disturbance and climate on boreal forests. For example, Bond-Lamberty et al. (2007) explored the impact of environmental factors in driving the carbon balance of central Canadian boreal forests based on factorial experiments; they proved that the carbon balance of this area was determined by changes of fire disturbance between 1948 and 2005. Similarly, Weber and Flannigan (1997) illustrated that compared with the direct impact of climatic change, the change of fire regime might be more important in driving or facilitating vegetation distribution changes, migration, shift, and extinction. In addition, Bergeron and Dansereau (1993) ascribed the difference in composition of the Canadian boreal forest to varying fire cycles. Besides, boreal biosphere interactions with climate, fire disturbance, insect disturbance, and permafrost were assessed by Scheffer et al. (2012) and Soja et al. (2007) based on historical predictions. Furthermore, Scheffer et al. (2012) described thresholds for boreal biome transitions based on satellite data and multi-models, suggesting the change of tree cover was strongly dependent on temperature. Factorial experiments have been widely used to quantify the individual contributions of environmental factors. Generally, the indicators or objects of factorial experiments are usually one type of independent variable, for example, leaf area index (Mao et al. 2013, Zhu et al. 2016), terrestrial evapotranspiration (ET; Jiafu et al. 2015), net biome production, NPP, and vegetation dominance (Bond-Lamberty et al. 2007). However, in this study, we are devoted to analyzing whether the vegetation distribution in boreal forest ecosystems, described by fractional cover/FPC of different plant functional types, is mainly determined by climate or fires and quantifying their individual contributions. Multiple vegetation types exist in the boreal forest of China, for example, needle-leaved evergreen and deciduous conifers and deciduous broadleaf species. Under this circumstance of multiple vegetation types and their properties, we adopt instead the statistical methods of Redundancy Analysis (RDA) and variation partitioning to explore the above-mentioned questions.

Global warming is likely to significantly impact the stability and health of boreal forests (Gauthier et al. 2015). The Paris Agreement aims to control the global warming below 2°C and to pursue efforts to achieve a limit of 1.5°C (Hulme 2016). Therefore, in this study, we aimed to explore the questions of the potential change of vegetation distribution and fire regime in the boreal forest ecosystems of China, the driving balance between climate and fire disturbance, and quantify their distinctive contributions to biome composition in six scenarios, including two present-day scenarios and four different global warming targets (1.5°, 2.0°, 3.0°, and 4.0°C, relative to pre-industrial climate).

## Materials and Methods

### Study area

The study area is located in Heilongjiang Province between 42°30′–51°20′ N and 121°40′–128°30′ E in northeast China, covering an area of around $4.54 \times 10^5$ km$^2$. The summers are usually hot and humid, while the winters are cold and dry. The annual average temperature is between $-4$ and +5°C from north to south, and the annual precipitation ranges from 400 to 700 mm from west to east (Zhang et al. 2015). The main vegetation types include evergreen needleleaf forest (ENF), deciduous needleleaf forest (DNF), deciduous broadleaf forest (DBF), and cultivated and managed areas/grassland (see Fig. 1b and Appendix S1: Table S2) based on GLC2000 (Bartholomé and Belward 2005). Existing research shows that historically, the most common fire type was frequent, low-intensity surface fires mixed with infrequent stand-replacing fires in this area, and burnt area was usually large with fire return interval ranging from 30 to 120 yr and the average number of fires was 317 per year during 1980–1987 (Xu et al. 1997, Liu et al. 2012). However, after a catastrophic fire which was occurred in 1987 in this area, burning a total area of 1.3 Mha, forest harvesting and fire suppression have changed the fire regime of this area. Currently, fire regime is characterized by infrequent but more intense fires and larger burnt area, with a fire return interval of more than 500 yr (Chang et al. 2008, Liu et al. 2012). The total number of grid cells in Heilongjiang Province is 216 at the $0.5° \times 0.5°$ spatial resolution.

### Data and tools

*Present-day PFT coverages and burnt area simulation.*—SEVER-DGVM, which is an intermediate-complexity DGVM and is developed from the Lund–Potsdam–Jena Dynamic Global

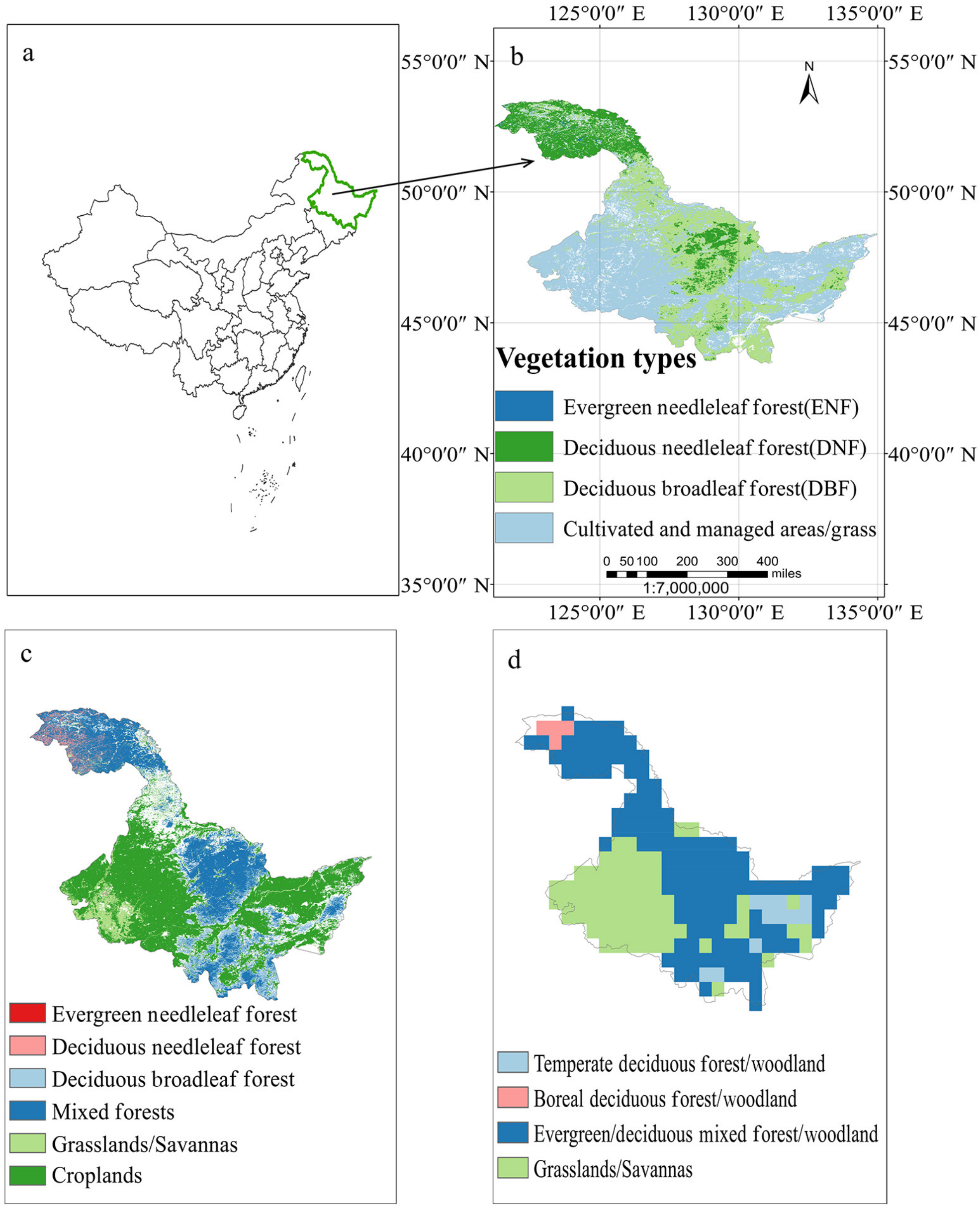


Fig. 1. Location and main vegetation types in Heilongjiang Province. The sources of datasets are (a) Administrative divisions of China, (b) GLC2000, (c) 0.5-km MODIS-based global land cover climatology, and (d) global potential vegetation dataset.

Vegetation Model (LPJ-DGVM; Sitch et al. 2003) with much improvement for high latitudes (Venevsky and Maksyutov 2007), for example, including a daily time step description for dynamics of soil temperature, potential ET, and fire disturbance, is used to simulate PFT coverages. Meanwhile, burnt area is simulated by Glob-FIRM (Global FIRe Model; Thonicke et al. 2001), which is incorporated into SEVER-DGVM. Here, some simplifying hypotheses are made. First, fire occurrence is only dependent upon fuel load and litter moisture (i.e., the amount of dry material available), which combines both the influence of climate and vegetation. Ignition is assumed to take place sooner or later, without specific consideration. Secondly, fire effects are mainly driven by the length of the fire season and the PFT-dependent fire resistances. Thirdly, we assumed that the smallest burnt area in each grid cell is 250 ha and fire intensity is not considered in this study.

All input datasets were provided at a $0.5° \times 0.5°$ spatial resolution. We used NCEP/NCAR (National Centers for Environmental Prediction/National Center for Atmospheric Research) Reanalysis data (http://www.esrl.noaa.gov/psd/) as the input climate data in SEVER-DGVM, including daily temperature, precipitation, and shortwave radiation during 1957–2002, which were downscaled to a 0.5° grid based on Kalnay et al. (1996). The soil physical and thermodynamic characteristics were determined by simplified FAO soil dataset (FAO 1991). We used historical observed $CO_2$ concentration from 1957 to 2002 (Meinshausen et al. 2011). The global DGVM applications often misrepresent vegetation dynamics on a regional scale (Seiler et al. 2014). Therefore, a PFT parameterization, suitable for Eurasian boreal forests, was used here, based on Khvostikov et al. (2015). A typical simulation with SEVER-DGVM started from "bare ground" (no plant biomass present) and "spined up" 1012 yr until approximate equilibrium was reached with respect to carbon pools and vegetation cover. We used climate data during 1957–2002 repeated 22 times, and a prescribed constant atmospheric $CO_2$ concentration of the year 1957 was used. The present-day simulation by SEVER-DGVM is run in the transient phase 1957–2002 with historical changes in atmospheric $CO_2$ and climate.

*Future PFT coverages and burnt area projection induced by climate change.*—Four different global warming targets (1.5°, 2.0°, 3.0°, and 4.0°C, relative to pre-industrial climate) were used in modeling the response of future PFT coverages and burnt area to climate change. We selected 22 general circulation models (GCMs) of Coupled Model Intercomparison Project Phase 5 (CMIP5) (see Appendix S1: Table S1), which have been bias-corrected, to project the future climate data in this study though the number of GCMs actually used changed depending on different global warming targets (see Table 1). The year, when a specific global warming target was reached, from the multi-model ensemble was recorded (see Table 1 and Appendix S1: Table S1). Daily precipitation and temperature used in SEVER-DGVM for each global warming target were the integrated climate data from the GCMs when the specific global warming target was reached. Here, we ignored the future climatic inter-annual variation and used a simple method to recycle the daily precipitation and temperature of the target year in each warming scenario for the future simulations (starting from 2002) (see Table 1). Daily shortwave radiation values used in SEVER-DGVM were kept the same values with the year 2002. $CO_2$ concentration data in different global warming targets during running years were from the RCP8.5 emission scenario (Riahi et al. 2007). Soil data and parameters needed in SEVER-DGVM stayed the same as present day.

Table 1. Future SEVER-DGVM simulation in different global warming targets.

| Global warming target | No. GCMs used | Year when warming target was reached | Running years |
|---|---|---|---|
| Temperature + 1.5°C | 22 | 2026 | 24 |
| Temperature + 2.0°C | 22 | 2040 | 38 |
| Temperature + 3.0°C | 18 | 2063 | 61 |
| Temperature + 4.0°C | 13 | 2085 | 83 |

*Note:* DGVM, dynamic global vegetation model; GCMs, general circulation models.

### *Validation of present-day PFT coverages and burnt area*

The accuracy of simulated PFT coverages against current remote sensing products is an important component to reduce the uncertainty of terrestrial biogeochemistry to climate change (Poulter et al. 2011). Three independent datasets were used for validation of present-day PFT coverages in Heilongjiang Province. Firstly, we selected an observed potential vegetation dataset by Ramankutty and Foley (1999), which was based on satellite data at $0.5° \times 0.5°$ spatial resolution and includes 15 categories of vegetation. Four main categories were extracted for Heilongjiang Province (see Fig. 1d). Secondly, in order to obtain the latest land cover which also considers human disturbance on forests in study area, we used a 0.5-km MODIS-based global land cover climatology (Broxton et al. 2014), which was based on 10 yr (2001–2010) of Collection 5.1 MCD12Q1 land cover type data as compared with potential vegetation datasets (see Fig. 1c). We found that the large grasslands and savannas areas were actually replaced by cropland. However, our study is mainly focused on forest ecosystems. What is more, cropland and grassland are usually assessed as the greatest uncertainty in PFT classification (Poulter et al. 2011). Therefore, we extracted the forest areas based on the grasslands/savannas category in Fig. 1d. Finally, we used GLC2000, which was based on SPOT 4 satellite and provides the year 2000 global land cover, to validate the present-day distribution of different PFTs from the simulation of SEVER-DGVM. Although GLC2000 contains 17 different global categories of vegetation, only four main categories were used for validation in Heilongjiang Province (see Fig. 1b). Using the PFT mapping methods in DGVMs by Poulter et al. (2011), GLC2000 datasets were first reclassified into phenology-based categories consistent with the PFTs used in SEVER-DGVM (see Appendix S1: Table S2). And then, three main forests (DNF, DBF, and ENF) were translated to a spatial resolution of 0.5° by summing the area of each PFT class within corresponding 0.5° grid cell and dividing by the grid cell area (Poulter et al. 2011).

In recognition of fires as a large-scale and important agent of change in earth system, it has led to the development of long-term, spatially and temporally explicit global burnt area datasets based on satellite (Justice et al. 2002, Roy et al. 2008, Giglio et al. 2009, 2013, Randerson et al. 2012, Boschetti et al. 2015). The third version of Global Fire Emissions Database (GFED3; Giglio et al. 2010) was used to validate the burnt area simulated by SEVER-DGVM in this study. Global Fire Emissions Database provides global monthly burnt area estimates in 0.5° spatial resolution from July 1996 to mid-2009. We first used Glob-FIRM to compare the similarity of the annual burnt area between GFED3 and SEVER-DGVM during 1996–2002 using a Student's *t* test, and then over the same period, we conducted a monthly burnt area validation (see Appendix S1).

### *Quantifying individual contributions*

Contributions of climate and fire to explaining present-day vegetation distribution were detected by two independent experiments. One was based on the observed remote sensing dataset, and the other was dependent upon the simulation by SEVER-DGVM and Glob-FIRM which successfully reproduce contemporary vegetation distribution and fire regimes. The latter was also applied in the global warming scenario simulations (see Table 2).

We selected Plant Function Types Coverages (PFTC) of the last year of the simulation period as the response variable and mean annual burnt area (BA, ha), simulated by Glob-FIRM, as the explanatory variable, representing the impact of fires. Mean annual temperature (MAT, °C), mean annual shortwave radiation (MAR, W/m$^2$), and mean annual precipitation (MAP, mm) were used to be the climatic explanatory variables. Mean annual burnt area (BA, ha) in Glob-FIRM is determined by PFT specific soil moisture and flammability threshold and, thus, depends on MAT and MAP in a non-linear way.

First, we exclude explanatory variables with strong covariation. Redundancy analysis, whose aim is to explore a series of linear combinations of the explanatory variables that can best explain the variation in the response variables (Borcard et al. 2011*a*), and variation partitioning were used to quantify the individual contributions of

Table 2. Data used to produce RDA in different experimental designs.

| Scenarios | PFTC | BA | MAT | MAP | MAR | Periods |
|---|---|---|---|---|---|---|
| Present-day 1 | GLC2000† | GFED3‡ | NCEP/NCAR | NCEP/NCAR | NCEP/NCAR | 1957–2002 |
| Present-day 2 | SEVER-DGVM | Glob-FIRM‡ | NCEP/NCAR | NCEP/NCAR | NCEP/NCAR | 1957–2002 |
| Temperature + 1.5°C | SEVER-DGVM | Glob-FIRM | NCEP/NCAR | NCEP/NCAR | NCEP/NCAR | 2002–2026 |
| Temperature + 2.0°C | SEVER-DGVM | Glob-FIRM | NCEP/NCAR | NCEP/NCAR | NCEP/NCAR | 2002–2040 |
| Temperature + 3.0°C | SEVER-DGVM | Glob-FIRM | NCEP/NCAR | NCEP/NCAR | NCEP/NCAR | 2002–2063 |
| Temperature + 4.0°C | SEVER-DGVM | Glob-FIRM | NCEP/NCAR | NCEP/NCAR | NCEP/NCAR | 2002–2085 |

*Notes:* BA, mean annual burnt area; DGVM, dynamic global vegetation model; GFED3, The third version of Global Fire Emissions Database; MAR, mean annual shortwave radiation; MAP, mean annual precipitation; MAT, Mean annual temperature; PFTC, Plant Function Types Coverages; RDA, redundancy analysis. All the data are provided at a 0.5° × 0.5° spatial resolution. The number of samples is 216.

† The year of PFTC in the "present-day 1" scenario is the projected year of land cover in GLC2000 product.

‡ The periods for GFED3 and Glob-FIRM are 1996–2002, which are the overlapping years between GFED3 and present-day simulation.

climate and fires to the vegetation distribution in the boreal forest ecosystem of China in different scenarios. The data used to produce RDA are shown in Table 2. Second, we used the R package "vegan" version 2.3-2 (Oksanen et al. 2015) to build RDA sequence: rda (formula = PFTC ~ BA + MAT + MAP + MAR). Next, we produced forward selection and collinearity test to determine critical factors. Collinearity test on explanatory variables was based on Variance Inflation Factors (VIF), and it is considered that there is little/no collinearity when VIF < 4. Finally, we tested the RDA results using "Permutable test" with 999 runs. R package "vegan" version 2.3-2 was also applied in variation partitioning, which was shown as Venn diagrams by R package "VennDiagram" version 1.6.17 (Chen and Boutros 2011). Here, we only focused on the impacts of climate and fires on the vegetation distribution; the contributions of other controls (e.g., soil and human activities) were described as residuals.

Spatial structures play a crucial role in the analysis of ecological data. If external forcings (e.g., climatic, physical, and chemical) are spatially structured, biomes that are actually controlled by these factors will be spatially structured at many scales (Borcard et al. 2011*b*). This can be confirmed by autocorrelation of quantitative biome characteristics in space, which is referred to as spatial pattern (Borcard et al. 2011*b*). In order to analyze individual contributions of vegetation spatial pattern, climate, and fire in regulating vegetation distribution, we used variation partitioning and Moran's Eigenvector Map (MEM) spatial analysis method (Dray et al. 2006), which was based on sets of variables describing spatial structures in the way of deriving from the coordinates of the samples or from the neighborhood relationships among samples and could model structures at multiple scales and allowed the modeling of any type of spatial structures (Borcard and Legendre 2002), by R package "vegan" version 2.3-2 (Oksanen et al. 2015). However, a linear trend in vegetation distribution should be considered as a source of variation if the test for response data was significant (Borcard et al. 2011*b*). The whole explanatory variables were standardized firstly. All calculations were based on RStudio version 0.99.489 software environment (RStudio 2015).

## Results

### *Present-day PFT coverages and burnt area distribution*

We simulated PFT coverages in forest areas of Heilongjiang Province in 2002 and compared them with the main forest types from GLC2000 (see Fig. 2a). We found that simulated PFT coverages were relatively consistent with GLC2000 for

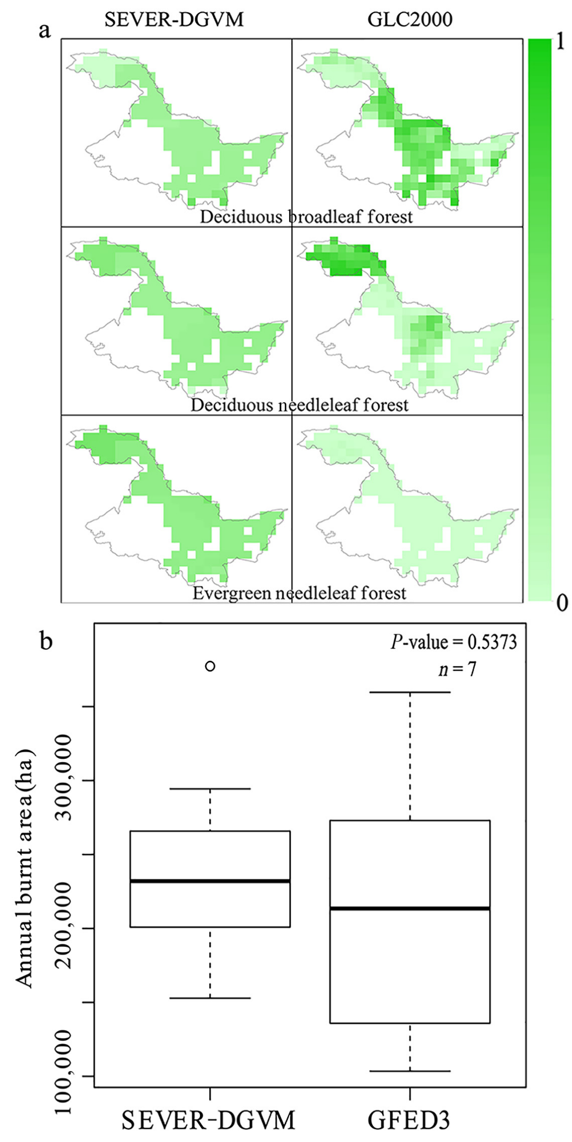


Fig. 2. (a) Present-day Plant Function Type coverages and (b) mean annual burnt area during 1996–2002 in forest areas of Heilongjiang Province. DGVM, Dynamic global vegetation model; GFED3, The third version of Global Fire Emissions Database.

categories DBF and DNF, especially in the northwest parts of the Heilongjiang Province. However, a large difference existed for ENF and we only captured the ENF distribution in the northwest; these might be the results of the misclassification in GLC2000 between ENF and mixed forests in other parts of the study areas. Based on remote sensing products (see Fig. 1c, d), we find that large areas of mixed forests are actually distributed in Heilongjiang Province, which has been proved by the vegetation atlas of China (Tan et al. 2007). Also, mixed forests were twice as large in extent as DNF in this area (Xiao et al. 2002).

The results of the validation in the BA between GFED3 and simulated by SEVER-DGVM are shown in Fig. 2b. We suggest that the simulated total burnt area reproduced GFED3, and Student's $t$ test demonstrated that there was not a significant difference between SEVER-DGVM and GFED3 at the 90% confidence level ($t$ = 0.63512, $n$ = 7, df = 12, $P$ = 0.5373). Monthly burnt area comparison is described in Appendix S1: Fig. S1.

### *Present-day individual contributions of climate and fire in regulating PFTC*

First, we use the "present-day 1" experiment to quantify present-day individual contributions of climate and fire in regulating PFTC. The correlation analysis between climate and fire factors revealed that MAR and MAT had a strong relationship (adjusted $R^2$ = 0.91) (see Appendix S1: Fig. S2). Considering the ecological meanings, we excluded MAR from the explanatory variables. Thus, MAP, MAT, and BA are the explanatory variables in regulating PFTC in the boreal forest ecosystems of Heilongjiang Province, China.

Results from a Principal Component Analysis (PCA) showed that the first two components (PCA1 and PCA2) could together explain 77.8% of the total variation. The RDA for PFTC and explanatory variables demonstrated that RDA1 and RDA2 were able to explain 35.5% of the total variation. Then, forward selection revealed that MAP, MAT, and BA were the significant factors in determining PFTC ($P$ = 0.015); meanwhile, none had obvious collinearity among explanatory variables (VIF < 4). Next, the "Permutable test" of the RDA results was significant ($F$ = 40.436, df = 3, $P$ < 0.001) and all the canonical axes were significant as well. The adjusted bimultivariate redundancy statistic ($R^2$) was 0.3550. The RDA results are shown in Fig. 3a. Similarly, experiment results from "present-day 2" are shown in Fig. 3b. The RDA results are described as "triplot," including

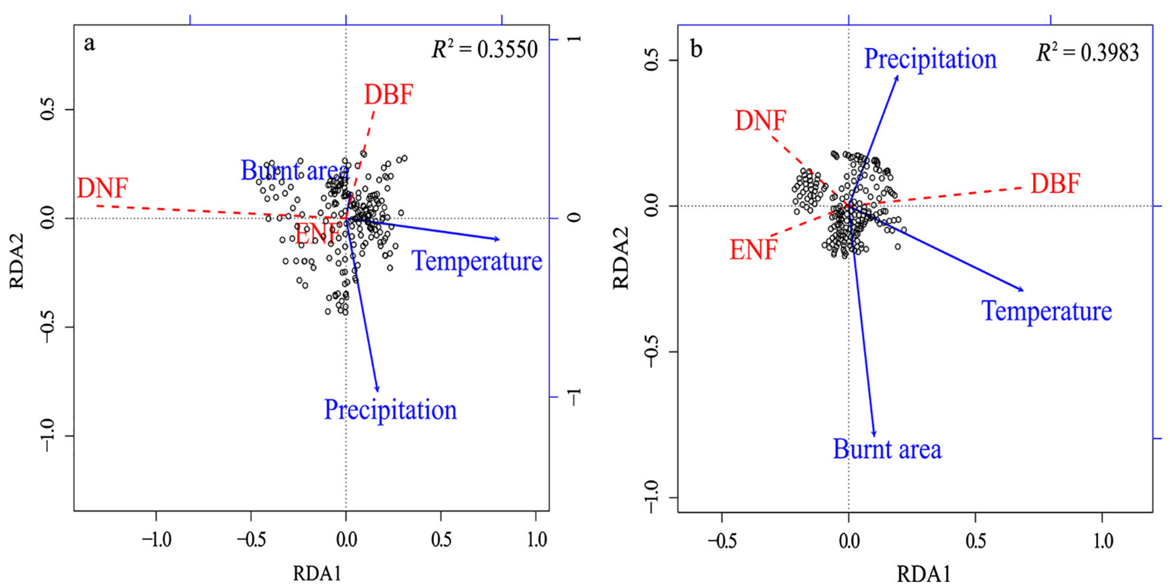


Fig. 3. Correlation triplot based on a redundancy analysis (RDA) depicting the relationship between the selected climate and fire variables and the variation of coverages among different Plant Function Types. (a) Present-day 1; and (b) present-day 2. DNF, deciduous needleleaf forest; ENF, evergreen needleleaf forest; DBF, deciduous broadleaf forest.

three different entities: sites, response variables (without arrowheads, red), and explanatory variables (with arrowheads, blue). The "triplot" was interpreted as "scaling 2—correlation biplot," in which the angles between variables (explanatory and/or response variables) reflect their correlations. We found that DNF distribution was negatively related to temperature, while temperature would contribute to the growth of DBF as well. Meanwhile, fire would decrease the distribution of flammable DNF according to both present-day experiments. However, the influence of precipitation on biome composition was uncertain in these two scenarios.

Variation partitioning illustrated that fire and climate factors could explain 35.5% of the total variation in PFTC from "present-day 1." Furthermore, fires alone could only explain around 1%, while climatic individual contributions were around 35.8% of the total variation (see Fig. 4a). Here, we ignored the minus values and it could be considered as zero, for the joint contributions of explanatory factors, which indicated that the explanatory variables did worse than random normal variables (Borcard et al. 2011*a*). Moreover,

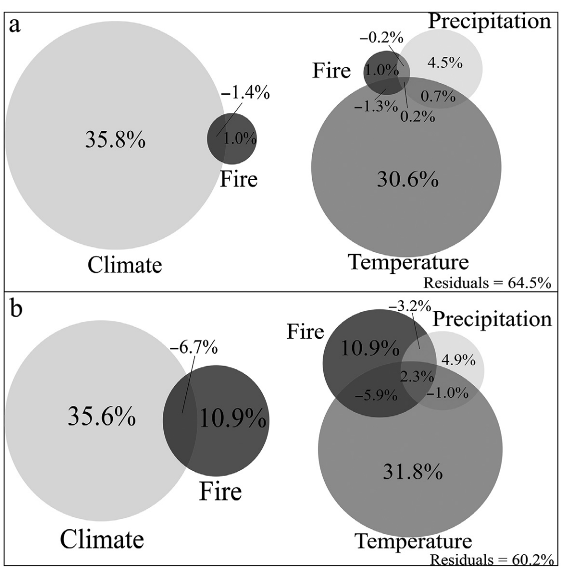


Fig. 4. Individual contributions of fires and climate in regulating Plant Function Types Coverages in (a) "present-day 1" and (b) "present-day 2" (left: Climate consists of comprehensive effects of temperature and precipitation; right: individual effects of temperature and precipitation).

temperature was much more important than precipitation in regulating the PFTC (30.6% >4.5%). All the results were significant ($P$ < 0.001) based on permutation tests.

Next, based on the experiment "present-day 2," we found that 39.8% of the total variation could be explained by climate and fires in determining vegetation distribution (see Fig. 4b). Different from "present-day 1," fire could describe 10.9% of the total variation based on modeling. However, individual contributions of climate factors did not change a great deal. Therefore, based on two independent present-day experiments, the results illustrate that the distribution of boreal forests in China is more determined by climate rather than fires; meanwhile, the response of vegetation is more sensitive to temperature than precipitation at the present day. Even though the contribution of fire in regulating PFTC is strongly dependent on the data source and accuracy of burnt area, changing from 1% to 10.9% in our study, climate contributes around 30%, largely driven by temperature, to the distribution of vegetation in boreal forests of China.

### *Spatial pattern in regulating PFTC*

Spatial pattern over the region is important in the analysis of individual contributions of fires and climate factors in regulating local vegetation distribution; that is, one can interpret this as the importance of the vegetation in the surrounding area for the composition at a specific location. Essentially it gives an indication of the level of spatial homogeneity in vegetation across the region, and its importance for determining local vegetation cover. Based on the "present-day 1" scenario, there is a strong linear trend in the spatial distribution of vegetation ($F$ = 57.121, df = 2, $P$ < 0.001). After detrending the data (Borcard et al. 2011*b*), the MEM spatial analysis showed that spatial pattern could explain 82.0% of the distribution of vegetation. Spatial scale and regression analysis help to analyze whether the spatial pattern of vegetation distribution is related to environmental factors (climate and fire disturbance in this study) at different scales. The different scales here are defined as the significant MEM variables map according to the scales of the patterns they represent. And the results illustrated that the vegetation distribution was significant at the broad scale ($F$ = 19.066, df = 11, $P$ < 0.001) and produced two significant canonical axes to explain the spatial pattern. The first canonical axis was significant to MAP ($R^2 = 0.3033$, $P < 0.001$), while the second canonical axis was significant to BA, MAT, and MAP ($R^2 = 0.2229$, $P < 0.001$). However, there were no obvious spatial differences at medium and fine scales ($P > 0.05$). The reason might be that at finer spatial scale, vegetation often displayed properties of inertia, contingency, and hysteresis, most frequently because of climatic variability across multiple timescales and the episodic nature of disturbance and establishment (Jackson 2013).

A similar analysis was produced for the "present-day 2" scenario. Variation partitioning results are shown in Table 3. Spatial pattern has a strong impact on the quantitative analysis of the individual contributions of fire and climate factors to PFTC. Fires, climate, and spatial information could explain around 90% of the total variation. Compared to the small influence of fire disturbance (0–4.2%), climate could explain around 30% of the total variation. However, as an important source of variation, the linear trend in vegetation spatial distribution itself cannot be ignored. Therefore, we should consider spatial information, including spatial pattern and trend in vegetation distribution when we quantify the contributions of explanatory variables even if there is no significant influence on the driving balance between climate and fires. Here, the fact that contributions of fires, climate, spatial pattern, and trend might add up to more than 100% is the reason to consider the overlap among individual factors.

Table 3. Individual contributions (%) of fires, climate, and spatial pattern on PFTC in present-day and warming scenarios.

| Scenarios | Fire | Climate | Spatial | Trend | Residuals |
|---|---|---|---|---|---|
| Present-day 1 | 0 | 34.5 | 88.4 | 34.3 | 11.2 |
| Present-day 2 | 4.2 | 28.9 | 83.6 | 42.0 | 13.6 |
| Temperature + 1.5°C | 36.3 | 29.3 | 89.7 | 32.7 | 7.4 |
| Temperature + 2.0°C | 7.2 | 42.1 | 90.1 | 45.1 | 8.5 |
| Temperature + 3.0°C | 3.4 | 62.3 | 90.4 | 59.5 | 8.6 |
| Temperature + 4.0°C | 5.6 | 59.4 | 93.7 | 55.9 | 5.3 |

*Note:* PFTC, Plant Function Types Coverages. Individual contributions had included the joint contributions (Fire: fire contributions; Climate: climate contributions; Spatial: spatial pattern contributions; Trend: the linear trend of PFTC contributions; Residuals: the contributions that could not be explained).

### *Future PFT coverages and burnt area projection induced by climate change*

Climate change, especially global warming, is simulated to significantly impact vegetation distribution, possibly leading to important biome-level changes (Gauthier et al. 2015). PFT coverages projections for four different global warming targets (1.5°, 2°, 3°, and 4°C) are shown in Fig. 5. We find that the dominant forests in Heilongjiang Province are ENF in the present day, which is consistent with actual vegetation distribution, such as *Pinus koraiensis*, *Pinus sylvestris* var. *mongolica*, *Picea koraiensis*, and *Abies nephrolepis*. Besides, DBF occupies large areas as well, such as *Juglans mandshurica* and *Quercus mongolica Ledeb*. In response to climate change, the biome composition would change in different scenarios. When temperature increased, DNF would decrease from the south to the north until "temperature + 4°C"; almost no DNF existed in this area. ENF would increase at lower temperature increases; however, above 2°C, large areas of ENF would be replaced by temperate forests. Meanwhile, as temperature increased, DBF would start to shift from the south to the north until the time when temperature increased by 3°C; DBF would be the most dominant PFT in this region. There are also some minor areas of grass distributed in the transition areas between boreal forests and temperate vegetation. This is in line with the evidence that there would be a gradual northward migration of temperate deciduous tree species into the boreal region (Gauthier et al. 2015). There are also some minor areas of grass distributed in the transition areas between boreal forests and temperate vegetation.

Climate change would also change the fire regime, in particular burnt area. We used GlobFIRM to simulate the spatial distribution of BA in Heilongjiang Province. As shown in Fig. 6, compared to the present-day burnt area, climate change would lead to a decrease in BA. When temperature increased by 1.5°C, the areas most disturbed by wildfires are centered in the areas with large flammable boreal forests, such as DNF and ENF (see Fig. 5). However, when temperature increased by more than 2°C, BA decreases rapidly and hotspots of wildfires move from the south to the north, which is consistent with the shift from boreal forests to temperate forests. That is, the wildfires induced by global warming are strongly

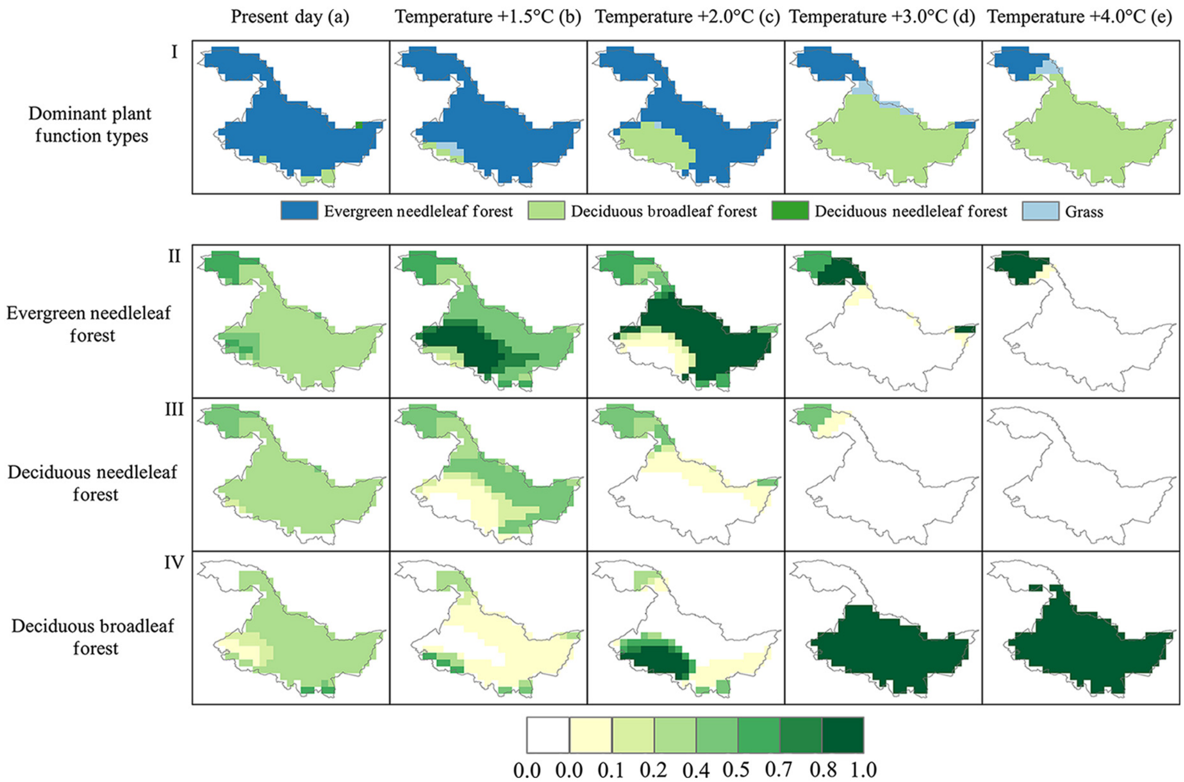


Fig. 5. Plant Function Type (PFT) distribution simulated by SEVER-DGVM in Heilongjiang Province, China. (a) Present day; (b) temperature increase by 1.5°C; (c) temperature increase by 2.0°C; (d) temperature increase by 3.0°C; (e) temperature increase by 4.0°C; and (I) dominant PFTs; tree cover in each grid cell: II, III, IV.

dependent on the PFTs and flammability of the vegetation. In addition, although global warming will decrease precipitation compared to the present day, there is a slight increase in precipitation when temperature increases from +1.5° to +4°C (see Appendix S1: Fig. S3), which might lead to the decrease in burnt area in different scenarios.

### *Individual contributions of climate and fire in regulating PFTC induced by climate change*

Results of the correlation analysis among explanatory variables (MAP, MAT, MAR, and BA) in regulating PFTC for the four different scenarios are shown in Appendix S1: Fig. S4. Similar to the present-day scenarios, we excluded MAR from the explanatory variables. Redundancy analysis results from the four global warming experiments are shown in Fig. 7. Deciduous needleleaf forest, as one type of main flammable forest, was strongly and negatively related to burnt area and temperature in all scenarios. With temperature increasing, precipitation would firstly contribute to the growth of DNF, but when temperature increased by 2°C, precipitation would limit the distribution of DNF. The growth of DBF is strongly dependent on temperature and more DBF will exist in a warmer world, which is consistent with Fig. 5. In addition, when the temperature increased by higher than 2°C, temperature and precipitation would be the dominant limitation factors in regulating ENF. Redundancy analysis results are significant by permutation test ($P < 0.001$).

Variation partitioning can be applied to analyze the individual contributions of climate factors and fires in regulating PFTC in different warming scenarios quantitatively (see Fig. 8). Compared to fire influence, generally climate factors are more important in regulating PFTC, whose individual contributions are larger than fires' except the scenario of "temperature +1.5°C" (Fire 36.3% >Climate 29.3%). When temperature increased by 1.5°C, the vegetation distribution of Heilongjiang Province would be mainly determined by fires rather than climate. When

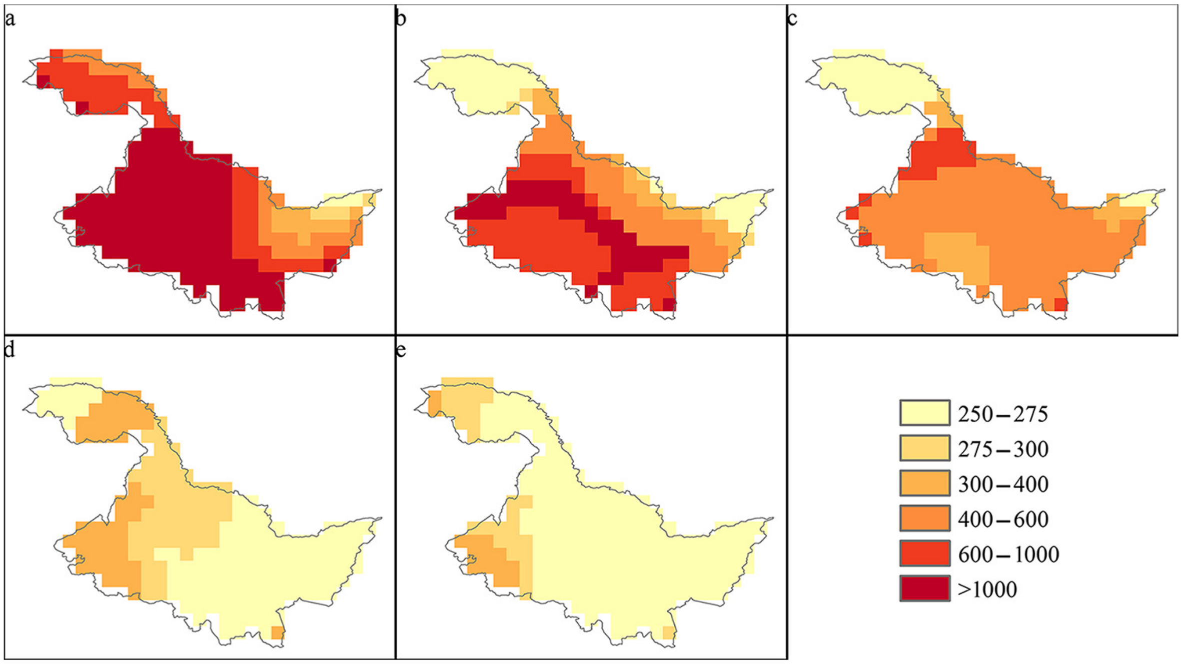


Fig. 6. Mean annual burnt area (ha) spatial distribution simulated by Glob-FIRM in Heilongjiang Province, China. (a) Present day; (b) temperature increase by 1.5°C; (c) temperature increase by 2.0°C; (d) temperature increase by 3.0°C; and (e) temperature increase by 4.0°C.

temperature increased by higher than 1.5°C, the individual contributions of climate would be much larger than the contributions of fires. What is more, we found temperature to be more important than precipitation in regulating PFTC. All the results from permutation tests were significant ($P < 0.001$).

### *Spatial pattern in regulating PFTC induced by climate change*

We cannot ignore the impact of the spatial pattern when analyzing the individual contributions of climate and fire disturbance factors to the PFTC under a changing climate. The results of MEM spatial analysis are also shown in Table 3. Results show how spatial pattern represents the largest contribution to regulating PFTC for the whole four scenarios; that is, the vegetation distribution is strongly dependent on the spatial difference. Except the scenario of "temperature +1.5°C," the other three scenarios showed that climate factors were more important than fires on PFTC. When temperature increased by 1.5°C, the vegetation distribution was strongly dependent on wildfires (Fire 36.29% >Climate 29.31%), which is consistent with the results in Fig. 8. All the permutation test results were significant ($P < 0.001$).

## Discussion

### *Climatic, weather, and fire impacts on forest ecosystems*

Climatic change is likely to exert a strong influence on plant physiology and vegetation coverage (Betts et al. 2000). Temperature will affect biome composition via impacts on plant physiological processes, especially photosynthesis (Collatz et al. 1991) and respiration (Tjoelker et al. 2001). Besides, temperature, combined with growing degree days, has a significant influence on plant phenology and growing season length (Chen and Pan 2002, Tao et al. 2006). Precipitation controls vegetation distribution by impacting water supply, ET, and runoff, leading to the water balance change of the ecosystem (Stephenson 1990). Generally, savanna would be replaced by the forest when annual precipitation exceeds around 1500 mm/yr (Lewis 2006). Moreover, Hirota et al. (2011) implied that actually the

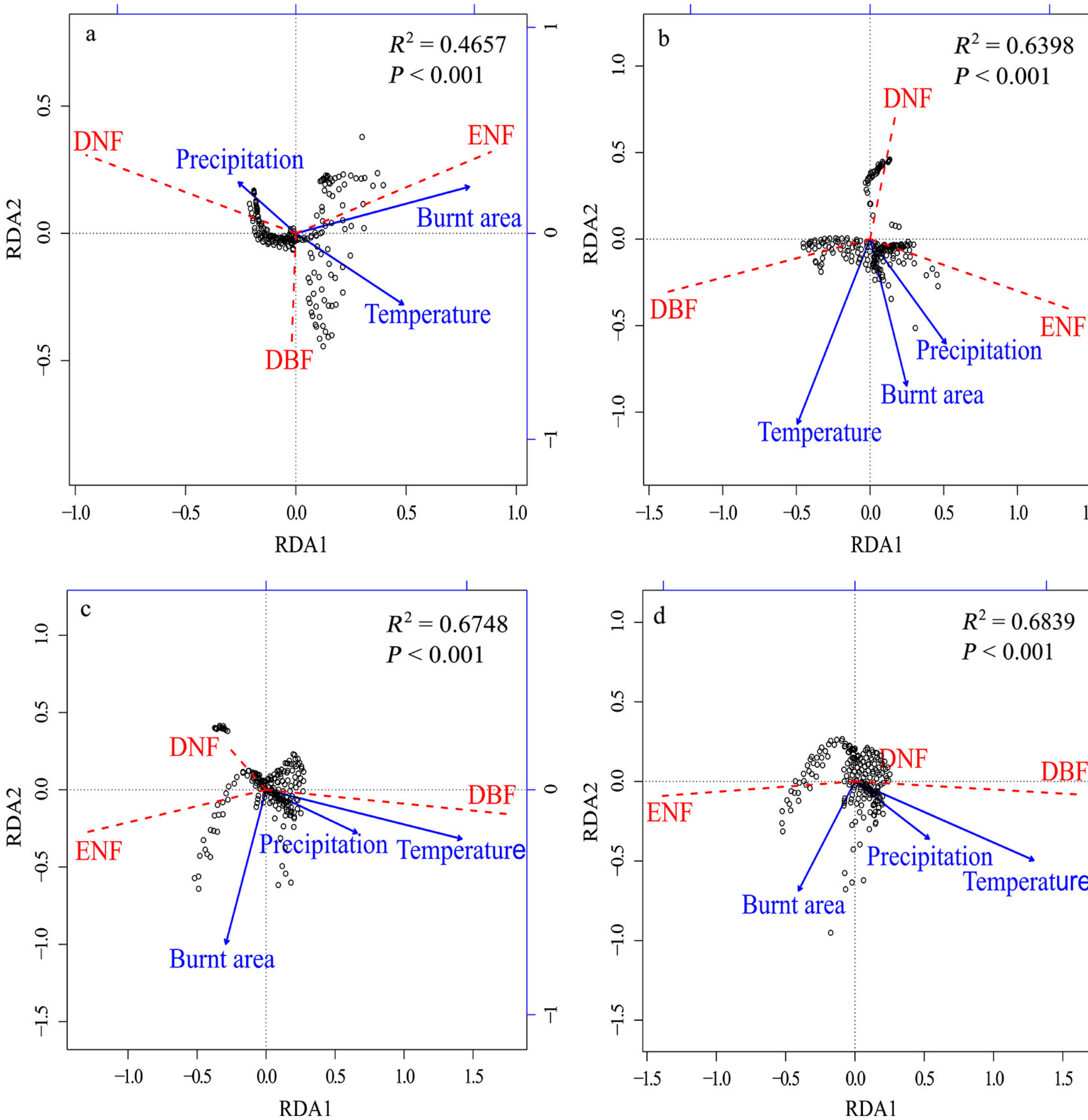


Fig. 7. Correlation triplot based on a redundancy analysis (RDA) depicting the relationship between the selected climate and fire variables and the variation of coverages among different Plant Function Types. (a) Temperature increase by 1.5°C; (b) temperature increase by 2.0°C; (c) temperature increase by 3.0°C; and (d) temperature increase by 4.0°C. For the expansions of the abbreviations used in the Figure 7, refer the caption of Figure 2.

global tropical forests and savannas are controlled by annual precipitation. In addition, the boundaries of boreal forests are modified by precipitation as influenced by oceans and mountains (Volney and Fleming 2000). Drought stress, which is strongly related to precipitation and temperature, will also impact biome composition (Allen and Breshears 1998). Different from the long-term impact from climate, generally the impact of weather happens in a short period of time. For example, climate determines what will probably grow well in a given area, but plants can still be damaged or killed by extreme weather. The impact of weather is always related

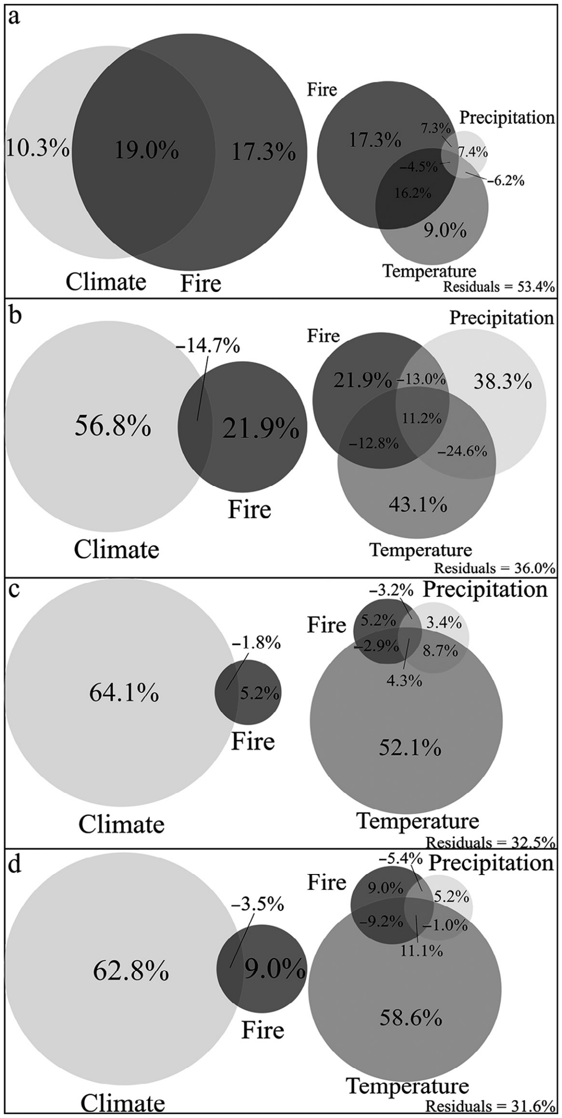


Fig. 8. Individual contributions of fires and climate in regulating Plant Function Types Coverages (climate consists of comprehensive effects of temperature and precipitation). (a) Temperature increase by 1.5°C; (b) temperature increase by 2.0°C; (c) temperature increase by 3.0°C; and (d) temperature increase by 4.0°C.

to extreme weather evens, for example, drought, flood, and storm, which would strongly impact the vegetation composition (Parmesan et al. 2000). Besides, weather-related stress can also make plants more susceptible to disease and insect problems. However, vegetation will also modify weather by changing surface albedo, transpiration and evaporation of water vapor, aerodynamic effects, and emission of hydrocarbons whose oxidation can form aerosol particles (Brown et al. 2005). Extreme, large-scale weather events are likely to trigger ecosystem-level disturbance, for example, wildfires, which may affect the species composition and diversity (Parmesan et al. 2000).

Fire is an important and necessary natural disturbance in forest ecosystems, especially for flammable communities (e.g., boreal forests, grasslands, savannas, and Mediterranean shrublands). All of these fire-prone ecosystems cover around 40% of the world's land surface (Bond et al. 2005). Fires help to shape global biome distribution and maintain the structure and function of fire-prone communities. Meanwhile, climate plays a decisive impact on vegetation growth and distribution, which is also an important factor for vegetation classification around the world (Raich and Schlesinger 1992, Cramer et al. 2001, Nemani et al. 2003, Parmesan and Yohe 2003, Zhengqiu et al. 2015). Bond et al. (2005) suggested that some flammable ecosystems were actually determined by fires. However, few studies focus on the analysis of the actual contributions of fire to ecosystems later.

Our quantitative analysis further supplements Bond's ideas on a regional scale. Regardless of spatial pattern, similar to climate impact, fires also have a substantial impact on vegetation distribution. Contributions of climate to the vegetation distribution are larger than contributions of fires for the present-day boreal forests (around 35% vs. 1–10.9%; see Fig. 4). The reasons might be that the climate influence is a long-term and permanent process, which has been widely considered as the dominant factor for vegetation growth and distribution by the ecologists. Thus, the local vegetation has adapted to the local climatic environment and vegetation coverages and will remain stable under normal growth unless encountering sudden disturbance, such as wildfires. Fire will not only change directly the forest distribution, but will also affect subsequent (postfire) nutrient availability, soil moisture, soil temperature, rates of mineralization, and light availability, and all of these potential influences will lead to competition among vegetation (Mills et al. 2006). What is more, vegetation coverages will not change a great deal once vegetation is established and occupies the area in a certain climatic environment. But fires will kill plants and decrease PFTC quickly, especially in the flammable ecosystems, and heat-stimulated germination is globally widespread in numerous fire-prone ecosystems (Bond and Keeley 2005), making fire the necessary condition for growth and distribution of vegetation in these ecosystems. This might be another reason why fires will have a decisive impact on vegetation components. However, fire occurrence is also dependent on the regional climatic conditions to some degree, such as temperature and precipitation (Liu et al. 2012), and this might be an important reason to explain the larger contribution of climate than fires. Although Mills et al. (2006) suggested that there might be a danger when we use fire to account for the existence of the vegetation state because fire is not an ultimate cause, fire has been treated as a separate effect to explore quantitatively contributions of controls to carbon balance and biome composition (Bond-Lamberty et al. 2007, Soja et al. 2007, Murphy and Bowman 2012). In addition, the contribution of fire is uncertain in the two independent present-day experiments (1% vs. 10.9%). This might be the reason for the accuracy of the projections of burnt area and ENF, and the latter is quite different between DGVM simulation and GLC2000 land cover dataset (see Fig. 2a). Although the evaluation of the annual burnt area is acceptable in Fig. 2b, there are differences in spatial distribution in burnt area.

### *Other controls in regulating vegetation distribution*

Many controls, including soil, topography, insect outbreak, permafrost, and human activity, also play important roles in vegetation distribution and dynamics in the boreal region, in addition to climate and fire disturbance (Murphy and Bowman 2012, Scheffer et al. 2012). We find large residuals (around 60%) exist in this study, which means that there are other controls that are beyond the scope of our study. However, it does not mean these factors are not important. Bond (2008) used the terms "bottom-up" and "top-down" to classify the controls into resource-based (e.g., water, nutrient) and disturbance-based (e.g., fire, insects). As mentioned earlier, water availability is related to climate. Nutrient availability is strongly dependent on soils, and it provides a large nutrient pool (such as soil organic matter) to facilitate the growth and productivity of the forests, which in turn impact rates of succession (Bond 2008, Murphy and Bowman 2012). However, in this study, the soil may not be the dominant control, and Chen et al. (2015) also proved that the vegetation–atmosphere carbon fluxes (Gross Primary Productivity [GPP], Ecosystem Respiration [ER], Net Ecosystem Production [NEP]) in the Northern Hemisphere were not significantly related to soil factors ($R = -0.11$ to 0.14, $P > 0.05$). In addition, large areas of permafrost exist in Heilongjiang Province, which is an important control on vegetation and soil carbon dynamics as well by influencing hydrology and soil thermal conditions in boreal forests (Jiang et al. 2016); meanwhile, permafrost is quite sensitive to climate change (Ran et al. 2012). Recent trends of continuous and island permafrost degradation in northeast China are pushing boreal ecosystems into a disequilibrium state. This may influence the relative role of climate factors and fires in determining vegetation distribution. Recent thaw of permafrost in northeast China can be relatively fast. So, winter baseflow at two watersheds in permafrost area of northeast China had a distinct annual increasing trend, 1–2%, and lagged MAT increase by only two years (Duan et al. 2017). However, the area where these processes are happening is relatively small and does not change our "present-day" results significantly. Similar to fire, insect outbreaks alter the accumulation and distribution of vegetation and strongly disrupt and redirect succession in forest ecosystem (McCullough et al. 1998). Moreover, human activities in forest areas impact not only vegetation composition and forest structure (e.g., deforestation and forest management), but also ecological processes, nutrient availability, and biodiversity (Josefsson et al. 2009). However, the controls as noted earlier are actually interacting with each other in a complicated manner in boreal forests (Soja et al. 2007, Murphy and Bowman 2012); for example, the influence of topography affects vegetation state by impacting water, nutrient availability, and fire activity.

### *PFTs vs. Species*

The vegetation distribution is described as the fraction of different PFTs from the simulation of SEVER-DGVM or the classification of GLC2000 remote sensing product. Although using PFTs, which are widely used in DGVMs and earth system models, as vegetation classification can help us to easily broaden the study area and provide larger scale vegetation composition, the limitations of PFTs are also obvious. Modelers define PFTs to account, in a very general way, for the variation of structure and function among plants (Sitch et al. 2003). Especially, fixed values of leaf-level traits such as carboxylation capacity and nitrogen content per unit leaf area to PFTs do not adequately describe the plasticity of such traits and the variation within PFTs (Prentice and Cowling 2013). Therefore, the new trend in local- and global-scale simulations of vegetation dynamics is to replace the "static" representation of functional diversity with trait continua, that is, incorporating functional trait variation into DGVMs (Fyllas et al. 2017). Meanwhile, species-level analysis has been widely used in the studies of vegetation compositions and their impact factors (Bond-Lamberty et al. 2007, Soja et al. 2007, Mitchell et al. 2017). Rogers et al. (2015) used remote sensing imagery, climate reanalysis data, and field inventories to evaluate the differences in boreal fire dynamics between North America and Eurasia and their main drivers based on the species level and found the difference of fire regime between two regions and then suggested that species-level traits should be considered in the evaluation of fire impacts and response to climate change. However, the difference of fire regime is inferred from the large different species between two regions. Although the analysis based on species level provides the insights into a smaller spatial scale and closer to the fire itself, many other impact factors relevant to species level, such as the impact of soil organic matter, peatland fires, permafrost, the runoff in the forest, and the interactions between different species, should be also considered.

### *Climate change impacts on PFTC*

Climate change impacts the boreal forest health and plant physiology (Piao et al. 2008). Conceivably, boreal forests are more sensitive to climate change than other biome communities (Magnani et al. 2007, Pan et al. 2011, Bradshaw and Warkentin 2015, Steffen et al. 2015). Under a globally averaged prediction of a warming of 4°C, boreal regions would experience temperature increased from 4° to 11°C, which will lead to boreal functional groups being replaced by other more temperate PFTs, such as woodland/shrubland biomes (Scheffer et al. 2012, Gauthier et al. 2015). In our study, we further analyzed the future PFT distribution in four different global warming scenarios (see Fig. 5). Our results suggest that boreal forests in Heilongjiang Province will face a severe challenge to be replaced by other biomes due to climate change. The fastest increasing biomes will be thermophilic PFT, such as DBF, which quickly reacts to temperature.

Climate change will also impact the PFTC by altering global fire regime (Jolly et al. 2015). However, there is great uncertainty on fire regimes in boreal forests of northeast China (Liu et al. 2012). Fire frequency, burnt area, and severity are projected to increase considerably induced by warming (Héon et al. 2014, Gauthier et al. 2015). However, based on a statistic model between fire activity and different environmental controls, Krawchuk et al. (2009) predicted that fire would decrease in this region. In our simulation, burnt area will be the greatest when temperature increased by 1.5°C, because vegetation combustion is dependent not only on temperature but on fuel characters as well. Compared to temperate forests, boreal biomes, such as DNF, are more flammable and can provide more fuels to potential fires (see Fig. 5). Meanwhile, the precipitation is lowest in this scenario (see Appendix S1: Fig. S3). The relative importance of fire and climate change acts in a non-linear way between +1.5° and +4°C with a general decrease in fire influence with a small increase thereafter (see Table 3). This can be explained by the appearance of a small patch of ENF forest substituting grasslands in the most northern mountainous part of Heilongjiang Province (see Fig. 5). Furthermore, human disturbance and simulation uncertainty should be considered as well (Syphard et al. 2007, Knorr et al. 2014).

This is the first time research which has focused on whether the future boreal forests in China will be determined by fires or climate and their individual contributions to vegetation distribution. Our study suggests that the present-day boreal forest ecosystem of China is mainly determined by climate rather than fire disturbance. However, climate change may change the driving balance between climate and fires. When temperature increases by 1.5°C relative to pre-industrial climate, the boreal forest will be mainly determined by fires. It is likely due to a peak in coverage by flammable PFTs (DNF), which accelerate fire spread. What is more, climate change will impact the temperature sensitivity of Soil Organic Carbon (SOC) decomposition (Karhu et al. 2010) and further influence the fire regime by changing fuel loads. However, when the temperature increases by higher than 1.5°C, climate will be the dominant factor in regulating PFTC, according to our study. We also find that the individual contribution of temperature is generally greater than that of precipitation. The reason might be that boreal forests are more sensitive to global warming than other ecosystems (Gauthier et al. 2015) and because of their physiological and ecological characters. The influence of precipitation on vegetation is based on changing water balance of ecosystems, involving in multi-processes, including ET, which is also strongly dependent upon temperature. Other uncertainties, including model uncertainty (Jiang et al. 2012, Verheijen et al. 2015), climate data uncertainty (e.g., underling climate models have considerable disagreements in precipitation values, which may significantly impact the results) and RDA methods' uncertainty are not the focus of this study.

## Conclusion

The vegetation distribution in the present-day boreal forest of Heilongjiang Province, China, is mainly determined by climate rather than fire disturbance. Climate can explain around 35%, while fire contributes 1–10.9% to the distribution of vegetation. Climate change, especially global warming, will have a strong impact on PFT coverages and fire regime, such as the burnt area. In addition, boreal forests will contract in the future in response to rising temperatures, while DBFs will progress rapidly until they become the dominant vegetation in Heilongjiang Province. Meanwhile, climate change will change the driving balance between climate and fires in local biome distribution. When temperature increases by 1.5°C, the local biome distribution will be determined by fires rather than climate (36.3% >29.3%). In other scenarios, temperature will be more important than fires in regulating vegetation distribution although other factors such as precipitation can also contribute. Spatial pattern has a significant impact on biome composition (representing the largest part of the total variation) but will not change the driving balance between fires and climate in determining vegetation distribution. Our results are highly relevant for forest and wildfires' management.

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## Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1917/full