Sensitivity of forest composition and productivity to climate change in mixed broadleaved-Korean pine forest of Northeastern China

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Abstract

Temperate forest is one of the largest forest biomes and is undergoing remarkable shifts in forest composition and ecosystem productivity under warming climates. However, there are considerable uncertainties when predicting future dynamics of temperate forest ecosystems partly because of the uncertainties in future climate predictions. Sensitivity analysis provides an effective mean to evaluate the uncertainties in the predicted forest responses to climate change. Here we evaluated the sensitivity of forest composition and productivity to climate change in the mixed broadleaved-Korean pine forest, a keystone temperate forest type in northeast China. In this study, we used a process-based forest dynamic model, FORMIND, to simulate and predict the response of the mixed broadleaved-Korean pine forest under climate change based on plant functional types (PFTs), and we performed model calibration using forest investigation. We then designed a factorial experiment to quantify the sensitivity to temperature and precipitation of forest composition and ecosystem productivity. Results showed that the uncertainty in future climate predictions could result in divergent responses of forest composition and ecosystem productivity to climate change over the 21st century. The response of PFTs to climate (temperature and precipitation) varied in terms of aboveground biomass. Both shade-tolerant and shade-intolerant PFTs exhibited higher sensitivity (**>** 80% for most of the PFTs) to temperature than precipitation, yet they responded oppositely to climate warming with shade-tolerant PFTs generally increasing but shade-tolerant PFTs decreasing. Moderate shade-tolerant PFTs showed higher precipitation sensitiveness (**>** 50%). Such differences in response and sensitivity of PFTs to climate change are related to PFTs' competitiveness. Ecosystem productivity exhibited a higher sensitivity (≥ 50%) to temperature than to precipitation. There was more increase in ecosystem respiration than gross primary productivity (GPP) under warming climate, leading to a decrease in carbon sequestration and net ecosystem exchange (NEE). Our study addresses the importance of evaluating the sensitivity of a forest ecosystem model to climate change, which is relatively less studied. The insight

from the study may help design effective forest management strategies to cope with future climate change.

Keywords: climate sensitivity; aboveground biomass; net ecosystem exchange; FORMIND model

1. Introduction

Temperate forest is an important component of terrestrial ecosystems. With carbon reservoirs up to over 50 Pg C (Thurner et al. 2014), these forests play an important role in regulating the global carbon cycle and mitigating climate change (Bonan 2008; Piao et al. 2009). Temperate forests are sensitive to changing climates and have been undergoing remarkable and significant shifts in forest composition (Taylor et al. 2017; Thom et al. 2017). Consequently, ecosystem productivity associated with the composition change along with tree growth, carbon consumption, and tree respiration, is also expected to change (Boisvenue and Running 2006; Brzostek et al. 2014). The fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC5) predicted that annual average temperature will increase by 0.5-8.9 ℃ and precipitation will increase by 2.5-76.2%, in the middle and high latitudes of northern hemisphere in the 21st century (IPCC 2013). The potential forest responses to climate change may be considerably varied across a broad range of climate projections (Ahlström et al. 2012; Huang et al. 2021). Accurate evaluation of temperate forest responses to future climate change is of great importance with respect to coping with global changes, designing adaptable forest management strategies, and maintaining its biodiversity.

The mixed broadleaved-Korean pine (*Pinus koraiensis* Sieb. et Zucc.) forest is most significant among temperate forest ecosystems in northeast China because of its broad distribution and rich species diversity (Krestov et al. 2015). Research suggests that species composition of mixed broadleaf-Korean pine forest could shift from pine- to broadleaf-dominated under warming climates (He et al. 2005; Lyu et al. 2017; Shao et al. 2003; Zhang et al. 2014). For example, many studies report that warming could

potentially favor broadleaf species, such as *Quercus* and *Acer* (He et al. 2005; Kim et al. 2020). The enhanced competitive capacity of the broadleaf species could promote their growth and colonization, leading to an increase in their proportion and biomass in the forests (He et al. 2005; Shao et al. 2003). Meanwhile, dendrochronological studies show that temperature is a predominant factor affecting the growth of Korean pine (Lyu et al. 2017; Wang et al. 2019). Elevated temperature along with the prolonged growing season can benefit the establishment of Korean pine and cause an expansion of their leading edge (Li et al. 2011). Furthermore, studies found a synergistic effect of heat and moisture on the growth of Korean pine (Zhuang et al. 2017). Particularly, increased precipitation can strengthen the positive effects of warming on Korean pine, while decreased precipitation can weaken the growth due to drought stress (Cao et al. 2019; Wang et al. 2019; Zhuang et al. 2017). Thus, the discrepancies in the responses of mixed broadleaf-Korean pine forest to climate change may obscure our understanding of the response of the forest ecosystem to climate change.

The mixed broadleaved-Korean pine forest is also expected to significantly change its ecosystem productivity under warming climate (Qiu et al. 2014; Wang et al. 2019; Zhou et al. 2011). However, the direction of this change is uncertain. Generally, it is thought that relatively low temperature is a major constraint to tree growth in this forest (Cao et al. 2019). Warming should therefore increase the period of photosynthesis by prolonging the growing season, leading to increases in tree growth, forest biomass, and productivity, and further promoting carbon sequestration in the ecosystem (Cao et al. 2019; Cao et al. 2018; Zhou et al. 2011). Yet, other studies report that higher temperatures, especially when accompanied by an asynchronous increase in precipitation, may lead to higher evapotranspiration, slower tree growth, decreased forest biomass and productivity, and lower sequestrated carbon (Liang et al. 2016; Wang et al. 2019). Additionally, elevated temperature could also increase maintenance respiration, further reducing ecosystem productivity (Wang et al. 2019). Increased drought events under higher temperatures could also result in a shift from carbon sink to carbon source in the mixed broadleaved-Korean pine forest (Lee et al. 2021; Peng et

al. 2009).

In this study, we investigate the response of the mixed broadleaf-Korean pine forest of Northeast China to climate warming. We used the process-based forest growth model FORMIND to simulate forest dynamics under various climate scenarios. The model simulates tree growth and forest development, as well as carbon dynamics, dependent on climatic conditions. Thus, FORMIND could evaluate the sensitivity of forest ecosystems to climate change. Sensitivity analysis provides an effective mean to evaluate the uncertainties in forest responses to climate warming (Huang et al. 2021). It can also quantify how variations of climate variable such as temperature and precipitation affect the projected results. The objectives of this study are to (1) develop a FORMIND modeling framework for the mixed broadleaved-Korean pine forest, (2) examine the forest dynamics in response to future climates, and (3) quantify the sensitivity of forest composition and productivity to potential changes in temperature and precipitation in the mixed broadleaved-Korean pine forest of northeastern China.

2. Methods and materials

2.1 Study site

The study focuses on the temperate forests of the Changbai Mountain, northeast China, bordering North Korea (Fig. 1). Our study site (42°23′N, 128°05′E) is located in the old-growth mixed broadleaf-Korean pine forest. The mixed broadleaf-Korean pine forest is a typical temperate forest type of China. The elevation is about 800 m a.s.l. Climate is a moist temperate climate with long, cold winter and short, warm summer. The average temperature is 2.8 °C, and the average annual precipitation is about 700 mm with a wet season from June to September. There are a variety of tree species, and six dominant species of which represent 90% of total basal area, including *Pinus koraiensis* Siebold & Zucc., *Tilia amurensis* Rupr., *Acer mono* Maxim., *Quercus mongolica Fisch*. ex Ledeb., *Fraxinus mandschurica* Rupr., and *Ulmus davidiana* Planch. var. *japonica* (Rehd.) Nakai.

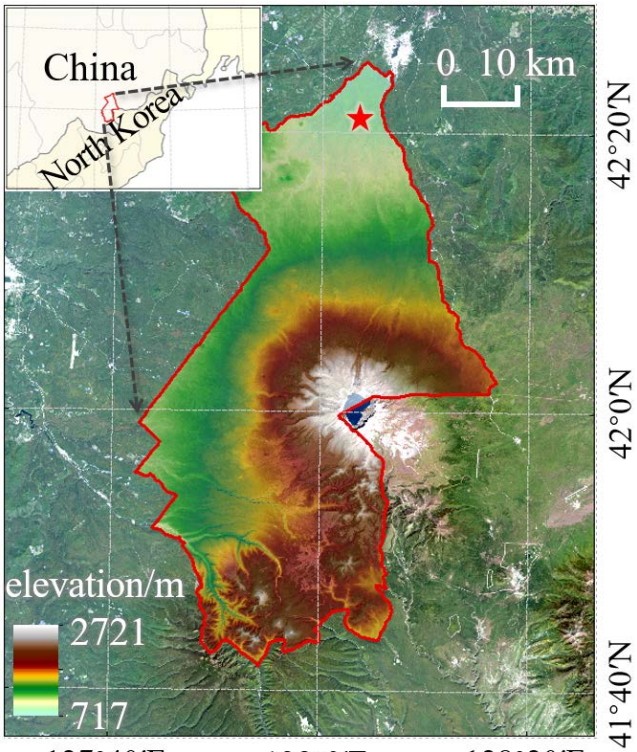

Figure 1. The location of study site. The red line and the red star indicate Changbai Mountains Nature Reserve (CMNR) and study site, respectively.

2.2 Inventory data

In 2004 a 25-ha (500 m × 500 m) permanent plot was established in our study site, which is located within the Changbai Mountain Nature Reserve (CMNR) (Hao et al. 2008). The plot consists of a multi-layered uneven-aged forest with a dominant tree layer of approximately 300 years and an average height of about 26 m. The plot has an average elevation of 801.5 m, ranging from 791.8 m to 809.5 m asl. The terrain of the plot is generally flat with the exception of some undulating areas. Since the establishment of permanent plot, all trees in the plot were censused in five-year intervals. For each tree with a diameter at breast height (DBH) ≥1 cm, the coordinates, species names, DBH, tree height, and crown width were measured and recorded. Thus, average basal area and tree density in the plot can be derived. The successive tree census also allowed us to capture tree regeneration, growth, and mortality.

2.3 Climate data

To assess the sensitivity of forest to climate change, we collected current and future climate data in our study site. The current weather data is derived from the meteorological station within the study site, which collects hourly temperature, precipitation, solar radiation, wind speed, and relative humidity from 2004-2019. Future climate (temperature and precipitation) data (2015-2100) is derived from CMIP6 global climate models (GCMs) over the 21st century (https://esgf-node.llnl.gov/projects/cmip6/), which are based on simulations of the Earth's climate system. Future climate predictions (2015-2100) of this region largely indicated that both temperature and precipitation will exhibit increasing trends, but at different magnitudes. Thus, we chose four typical climatic scenarios (CESM2-WACCM SSP245, CESM2-WACCM SSP370, CNRM-ESM2 SSP245, and CNRM-ESM2 SSP585), representing warmer and wetter, much warmer and wetter, warmer and much wetter, and much warmer and much wetter climate at the end of 21st century (2080-2100), respectively, relative to current condition, which can capture the potential future climate change characteristics (Table 1, Fig. S1). Moreover, the chosen future climate scenarios whose predictions in 2015 are closest to the weather data of the meteorological station. All selected climate scenarios have inherited daily climate variability and consequently annual variability similar to the current climate data (e.g., greatest precipitation occurs in the summer and snow in the winter). Specifically, we used the PRISM (parameter-elevation regressions on independent slopes model) interpolation method (Daly et al. 2002) that included elevation of Changbai Mountain to spatially interpolate the future climate data for our study site.

Table 1. The characteristics of current climate and future climate scenarios at the end of 21st century.

climate scenario	**average T (℃)**	**average annual P (mm)**	**ΔT (℃)**	**Δ annual P (mm)**	**climate characteristic**
current	3.7	705.1	-	-	-

(2005-2015)					
CESM2-WACCM SSP245 (2080-2100)	7.1	1162.5	3.4	457.4	warmer and wetter
CESM2-WACCM SSP370 (2080-2100)	9.1	1155.9	5.4	450.8	much warmer and wetter
CNRM-ESM2 SSP245 (2080-2100)	6.3	1278.0	2.6	572.9	warmer and much wetter
CNRM-ESM2 SSP585 (2080-2100)	9.3	1290.5	5.6	585.4	much warmer and much wetter

Note: ΔT and Δannual P represent the changes in annual mean temperature and annual precipitation between current (2004-2019) and future climate conditions at the end of 21st century (2080–2100), respectively.

2.4 FORMIND Model

The FORMIND model is a processed-based, individual-oriented, spatially explicit forest model, which was designed for simulating the dynamics of species-rich forest communities. It divides the simulated forest area into patches (20 m × 20 m) interacting by seed dispersal and tree falling. Within each patch, FORMIND simulates tree demographic processes, including tree growth, recruitment, competition, and mortality, which are mainly controlled by the availability of light and space. Tree biomass growth is determined with respect to a carbon balance as a result of photosynthesis and respiration, which regulates the increments in tree height, stem diameter, stem volume, and leaf area. In FORMIND, seeds are stochastically distributed among the patches, and new seedlings can establish under suitable light conditions (Fischer et al. 2016). Both seed survival and establishment can be influenced by climate change, which

consequently regulates forest regeneration. Tree competition takes place for light owing to shading effects, as well as for space owing to expanded canopies. Tree mortality is associated with weakened tree growth (related to climate), enhanced competition for space (e.g., self-thinning), death of large trees and their falling, as well as background mortality due to stochastic events, which can be simulated stochastically. The FORMIND model does not simulate asexual reproduction (e.g., sprouting, layering) that many trees are capable of and that is important in more disturbance-prone forest ecosystems. Since the study location is not generally affected by these perturbations, this limitation should not have an appreciable impact on our simulations and we have thus chosen to exclude this regeneration process. More model details are available in the supplementary materials.

The FORMIND model is capable of simulating forest carbon dynamics (Bohn et al. 2014; Fischer et al. 2016). Based on physiological processes such as photosynthesis and respiration, it analyzes the local carbon fluxes among atmosphere, vegetation, and soil to estimate gross primary productivity (GPP), respiration of the forest (including living biomass and dead biomass) and the soil, and net ecosystem exchange (NEE). NEE is calculated as the difference between the ecosystem GPP and the total respiration by the forest and soil. Thus, a positive NEE represents increasing carbon stocks, while a negative NEE represents decreasing carbon stocks.

2.5 Model parameterization

FORMIND simulates forest dynamics based on plant function types (PFTs) which represents the groups of tree species with similar traits. Here, according to physiological attributes including maximum potential tree height and light requirement (shade-tolerance), we classified the species in our area into seven PFTs (Table 2). We determined the maximum potential tree height classes by referring to the criteria from Groeneveld et al. (2009), together with the vertical structure (i.e., height layers) of the forest in the study site. We conducted the parameterization of the FORMIND model by defining environmental variables as well as model parameters describing tree

establishment, mortality, geometry, and biomass production. In this study, we defined the allometry relations for tree geometries (e.g., diameter-height relationships) for each PFT from the aforementioned permanent plot encompassing a range of sizes and ages of trees (Table S2). Specifically, we recorded DBH and height for each individual tree every five years (2004-2019). Furthermore, the seed number of each PFT is determined from the published results in the study site (Qian et al. 2019). The environmental parameters and variables include those related to light condition, soil, and climate. The parameters referring to light condition and soil were obtained from related literature and field investigation. The climatic parameters were derived from the climate station (current climate) and CMIP6 future predicted data (see above) in the study site, such as temperature, precipitation. Here, we did not simulate CO2 concentration since we opted to simplify the parameterization. The parameters related to mortality and biomass production for each PFT were estimated from multiple successive censuses (2004-2014 by every five years). In order to better reproduce each PFT's growth dynamic, we also inventoried an early successional forest plot (24 ha), whose data were used as references point to adjust the diameter growth change parameters. The plot (42°22′N, 128°00′E) is dominated by white birch (*Betula platyphylla* Suk.) and aspen (*Populus davidiana* Dode), and is located near the study site. Within the plot, the geographic coordinates, height, and DBH of all trees (DBH ≥ 1 cm) were recorded. In this study, we performed simulations based on PFTs rather than on individual tree species, since parameters at the tree species level may introduce uncertainties without gaining more significant insights.

Table 2. Seven plant functional types (PFTs) divided by shade-tolerance and potential maximum height class of tree species in the mixed broadleaved-Korean pine forest

PFT	**shade-tolerance class***	**potential maximum height (H_{max}) class****	**tree species**
S1H2	1	2	*Betula platyphylla* Suk., *Betula costata* Trautv., *Populus*

			davidiana Dode, *Syringa reticulata* subsp. *amurensis* (Ruprecht) P. S., *Phellodendron amurense* Rupr.
S1H3	1	3	*Populus ussuriensis* Kom., *Quercus mongolica* Fisch. ex Ledeb.
S2H2	2	2	*Maackia amurensis* Rupr. et Maxim., *Ulmus laciniata* (Trautv.) Mayr.
S2H3	2	3	*Ulmus davidiana* Planch. var. *japonica* (Rehd.) Nakai, *Fraxinus mandshurica* Rupr.
S3H1	3	1	*Sorbus pohuashanensis* (Hance) Hedl., *Sorbus alnifolia* (Sieb. et Zucc.) K. Koch
S3H2	3	2	*Acer mono* Maxim., *Acer mandshuricum* Maxim., *Acer triflorum* Komarov, *Malus baccata* (L.) Borkh., *Tilia mandshurica* Rupr. et Maxim.
S3H3	3	3	*Pinus koraiensis* Sieb. et Zucc., *Tilia amurensis* Rupr.

Note: *Shade-tolerance class: 1: least shade-tolerance; 2: middle shade-tolerance; 3: most shade-tolerance. **Potential maximum height (H_{max}) classes: 1: $H_{max} \leq 15$ m; 2: 15 m < $H_{max} \leq 25$ m; 3: $H_{max} > 25$ m.

2.6 Model simulation

We simulated forest succession on 25 ha over a period of 585 years with a 1-year time step, initializing with bare ground. During the first 500 years, forest dynamics were simulated in the stable climatic conditions to allow forest to reach a steady state (corresponding to the current old-growth forests) , which is designed for the model spin-up to reach equilibrium (Fig. 2). We then ran the model for the next 85 years (which correspond to years 2015-2100, i.e., CMIP6 projection period) to simulate future forest dynamics under the predicted climatic scenarios (see “climate data” section) in order to evaluate the sensitivity of the forest to future climate changes. Generally, under uncertain future climate changes, forest attributes will exhibit three possible scenarios: “status quo” (the relatively stable current forest condition) as the null hypothesis, and

either higher or lower levels as alternative outcomes (Fig. 2). Additionally, we also included a simulation scenario with no future climate change as baseline. In this study, we performed the simulation for 10 replications. Not all simulation results will be presented in this paper, please see the supplemental materials section for these outcomes.

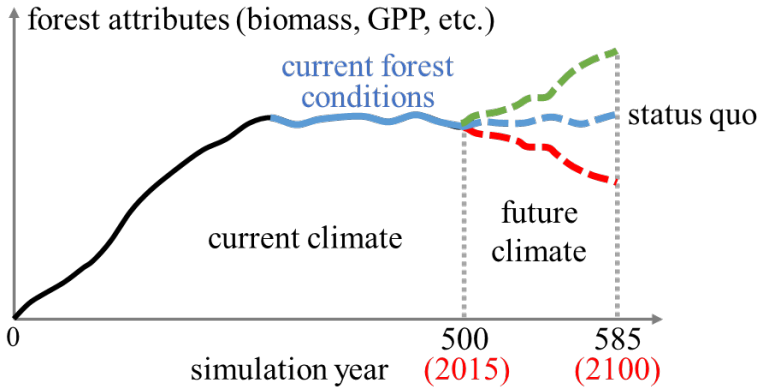

Figure 2. Schematic diagram of forest stand development initialized from bare land. Under future climate, there are three possible scenarios of forest attributes (such as biomass, GPP), including "status quo" (the relatively stable current forest condition) as the null hypothesis, and either higher or lower levels as alternative outcomes.

2.7 Model calibration

For model calibration, we compared the simulated mature forests with the corresponding field observations. Based on the assumption that forests can reach the equilibrium state in the late-successional stage under the stable climate conditions (Bormann and Likens 1979; Turner et al. 1993), we regarded that the simulated forest reached maturity and stabilized after 300 simulation years. Thus, the simulated mature forest attributes were averaged over the 300-500 years. Field observation values were the averages from 2004-2014 surveys in the study site (25 ha). We conducted model calibration by iteratively adjusting the model parameters that cannot be directly determined, such as light response curves and minimum light intensity required for seed ingrowth (Table S2) until we were able verify that there was no significant difference between the simulated results and the field observations (25 ha, mentioned above) in

terms of tree density and basal area for each PFTs for all trees. Here, the measured and estimated basal area for each PFT can be calculated from the average of the basal area of all trees for each PFT. Model calibration also involved comparing the simulated results at the early-successional stage against forest inventory data (an early-successional forest plot near the mixed broadleaved-Korean pine forest plot) (see Supplementary, Fig. S3). The two-step calibration processes ensured that calibrated model is capable of reproducing the current mixed forest conditions.

2.8 Climate sensitivity

We quantified the sensitivity of forest dynamics in response to future climate change by the four CMIP6 scenarios (section "climate data"). These scenarios can lead to a factorial experiment for two independent climate variables at two levels: temperature (warm and warmer at the end of 21st century) and precipitation (wet and wetter at the end of 21st century). For the future scenarios, we used daily values of temperature and precipitation of the corresponding CMIP6 climate scenarios during 2015-2100. We analyzed final states in the simulated forest under the CMIP6 future climate scenarios by the averaged values over the last 20 years (2080-2100) to evaluate the sensitivity of the forest to future climate change.

2.9 Data analysis

For all climate scenarios, we assessed the forest composition through the aboveground biomass (AGB) of each PFT, and ecosystem productivity through gross primary productivity (GPP), net productivity (NPP), total respiration (Rt), autotrophic respiration (Ra), heterotrophic respiration (Rh), and net ecosystem exchange (NEE). Moreover, we regarded the above variables as the response variables when quantifying the sensitivity of forest composition and productivity in response to climate change for the end of 21st century (2080-2100). We quantified the sensitivity of the response variables to climate change through determining relative importance of each climatic variable, by calculating the proportion of the total variance in the response variables

explained by each climatic variable using two-way ANOVA (Analysis of Variance) based on Type III sums of squares.

3 Results

3.1 Model validation

Current field inventory data and simulated data exhibited no significant differences in either total basal area or density by each PFT (paired t-tests, df = 6, $p < 0.05$) (Fig. 3). This showed that the simulated forest composition and structure using the FORMIND model are representative of our field-based example of the mixed broadleaved-Korean pine forest.

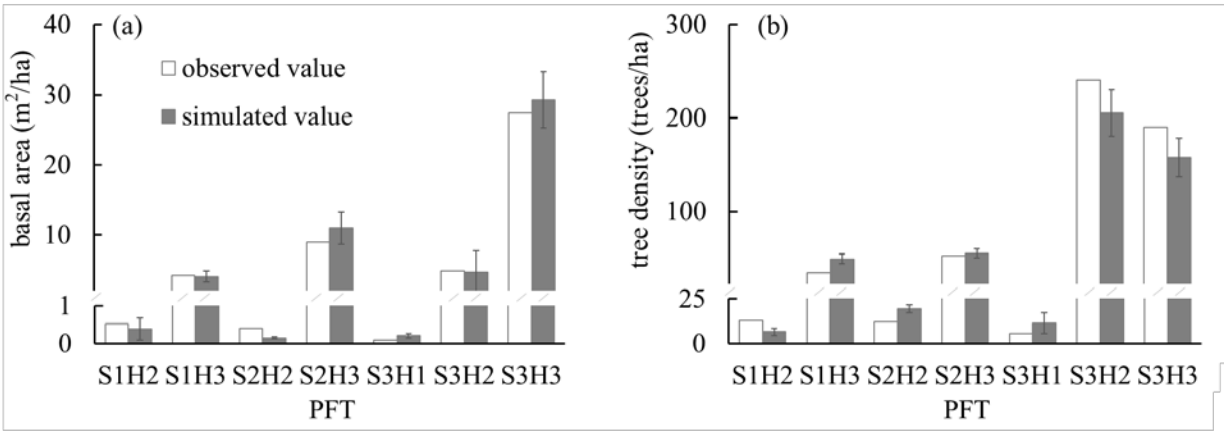

Figure 3. Comparison between simulated basal area (a) and tree density (b) in 2015 and observed data in 2010s for each PFT.

The simulated forest development pathways of all PFTs showed that shade-intolerant PFTs (S1H2 and S1H3) initially sharply increased but then decreased in AGB, and finally get gradually replaced by mid-tolerant and tolerant PFTs (e.g., S2H3, S3H2, and S3H3), which exhibited gradual increases and stabilized after 300 years of the simulation (Fig. S4). The PFTs with both relative shade tolerance and a higher potential maximum height (S3H3, S3H2, and S2H3), became dominant at the steady state (more than 90% of total AGB) (Fig. S4). Thus, simulated forest trajectories using the FORMIND model were consistent with forest stand development theory (Oliver and Larson 1996), which increased our confidence in the ability of the calibrated

FORMIND model to effectively represent long-term forest dynamics for the study site.

3.2 Forest dynamics under future climates

Generally, total AGB showed patterns of gradual increase under all future climate scenarios, from 317.0 t/ha to 331.4±3.0 t/ha from 2015 to 2100 (Fig. 4). The largest increase in total AGB occurred in the CNRM-WACCM SSP245 scenario (warmer and wetter), and the smallest increase occurred in CESM2-ESM2 SSP245 scenario (warmer and much wetter) (Fig. S5). Notably, the seven PFTs have divergent responses in their AGB to future climate change. Specifically, for some of the PFTs, including S3H3 and S2H3, AGB gradually increased over the 21st century under future climates, with an increase of 15.2±4.2 t/ha (182.2 – 197.4±4.2 t/ha during 2015-2100) and 5.3±0.6 t/ha (72.7 – 78.0±0.6 t/ha during 2015-2100) by 2100, respectively. Shade-intolerant PFTs (S1H2, S1H3), exhibited decreases in AGB with 1.9±0.4 t/ha (5.3 – 3.4±0.4 t/ha) and 2.4±1.3 t/ha (34.8 – 32.4±1.3 t/ha) from 2015 to 2100. Other PFTs, like S3H2, S2H2, and S3H1, kept relatively stable during the years 2015-2100 (Fig. 4).

The increases in temperature and precipitation also resulted in noticeable changes in ecosystem productivity over the 21st century. NEE showed an overall slight decline from 0.3 t C/ha/yr in 2015 to 0.3±0.1 t C/ha/yr in 2100, respectively (Fig. 4). The largest decrease occurred in CNRM-ESM2 SSP585 scenario (much warmer and much wetter) with 0.2 t C/ha/yr, while the smallest decrease occurred in CNRM-ESM2 SSP245 scenario (warmer and much wetter), with 0.0 t C/ha/yr (Fig. S6). NPP showed slight increase under the four future climate scenarios, with 3.6 t C/ha/yr in 2015 to 3.9±0.2 t C/ha/yr in 2100. The largest NPP occurred in CNRM-ESM2 SSP245 scenario (warmer and much wetter) (3.8 t C/ha/yr), while the smallest NPP occurred in CESM2-WACCM SSP245scenario (warmer and wetter) (3.7 t C/ha/yr) (Fig. S6). Additionally, under the four climate change scenarios, GPP and respiration (Rt, Ra, and Rh) presented slow increases of 1.7±0.6 (GPP), 1.8±0.6 (Rt), 1.4±0.5 (Ra), and 0.4±0.1 (Rh) tC/ha/yr, respectively, during 2015-2100 (Fig. 4). The largest increase occurred in CNRM-ESM2 SSP585 scenario (much warmer and much wetter), while the smallest increase in

CESM2-ESM2 SSP245 scenario (warmer and much wetter) (Fig. S6).

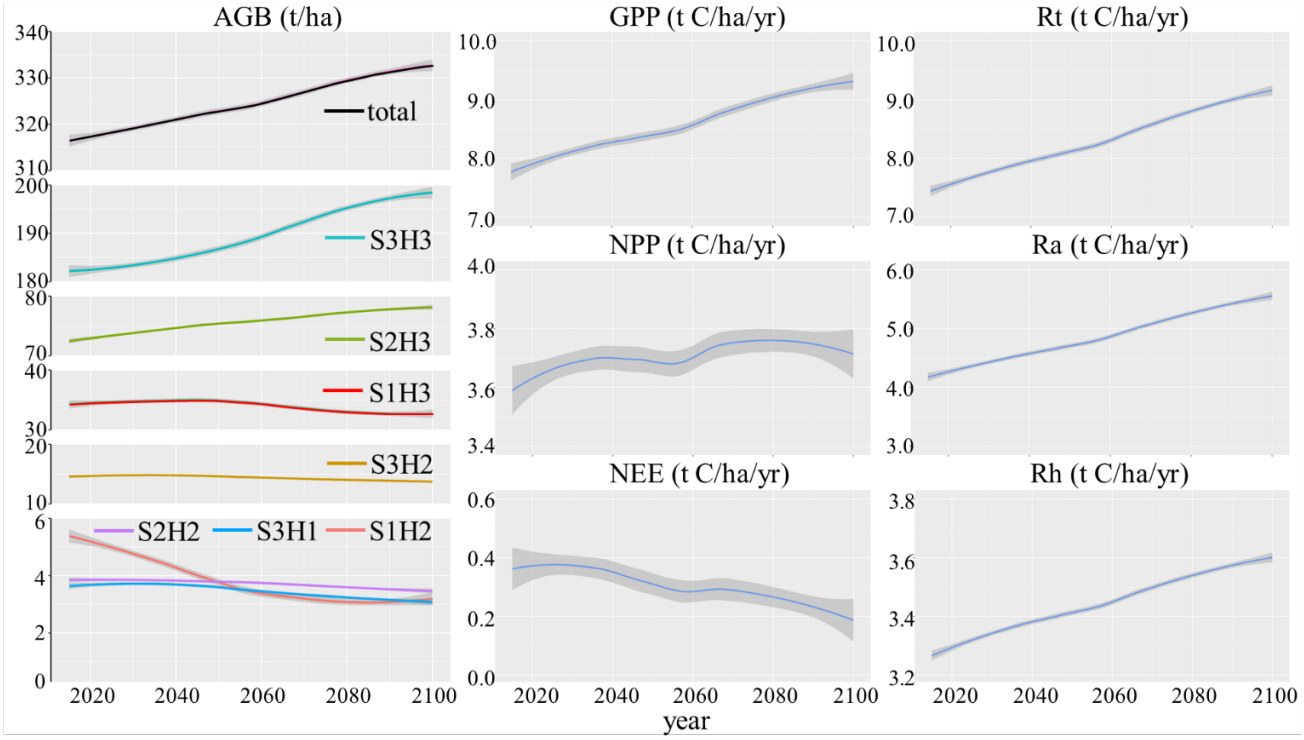

Figure 4. The dynamics of average of aboveground biomass (AGB) of individual PFTs, total AGB, NEE, GPP, NPP, Rt (total respiration), Ra (autotrophic respiration), and Rh (heterotrophic respiration) during the simulated years 2015-2100 across all climate scenarios. Grey shading represents the 5%–95% confidence interval (mean ± 2se (standard error)).

3.3 Sensitivity of individual PFTs to climate

The sensitivity of seven PFTs to climate (temperature and precipitation) varied. Compared to precipitation, most of the PFTs were more sensitive to temperature in terms of AGB, including S1H2, S1H3, S3H1, S3H2, and S3H3. Especially, for S1H2, S3H1, and S3H2, temperature explained >80% of total variation in AGB (Fig. 5). For S1H3 and S3H3, temperature and its interaction with precipitation explained >65% of total variation in AGB. However, AGB of mid shade-intolerant PFTs (S2H2 and S2H3) was more sensitive to precipitation than temperature, with precipitation explaining 56.0% and 86.9% of total variation in their AGB, and temperature explaining 44.0 % and 7.6%,

respectively (Fig. 5).

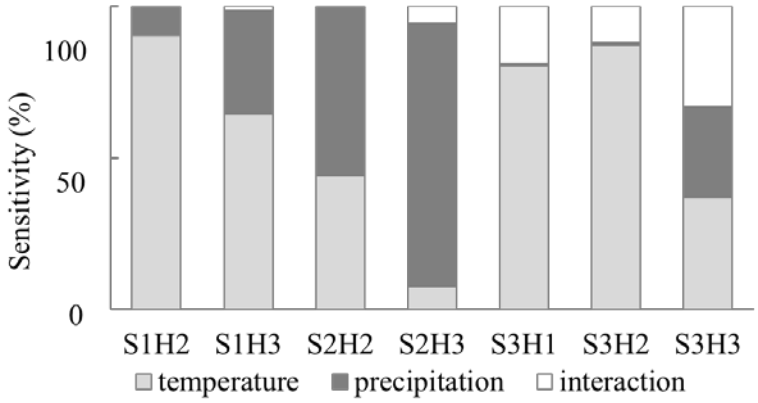

Figure 5. The sensitivity of individual PFTs to temperature, precipitation, and their interaction in terms of aboveground biomass (AGB).

3.4 Sensitivity of the forest ecosystem to climate

Total AGB exhibited a higher sensitivity to temperature explaining 49.6% of its total variation, than to precipitation explaining only 7.7% (Fig. 6a). Meanwhile, ecosystem productivity also exhibited a higher sensitivity to temperature than precipitation. For GPP, NPP, and NEE, temperature explained 87.8%, 56.7%, and 66.1% of their total variation, respectively, exceeding that explained by precipitation (11.4%, 40.5%, and 2.7%) (Fig. 6b-d). Likewise, respiration (Rt, Ra, and Rh) was also more sensitive to temperature than precipitation, with >80% of total variation explained by temperature (Fig. 6e-g).

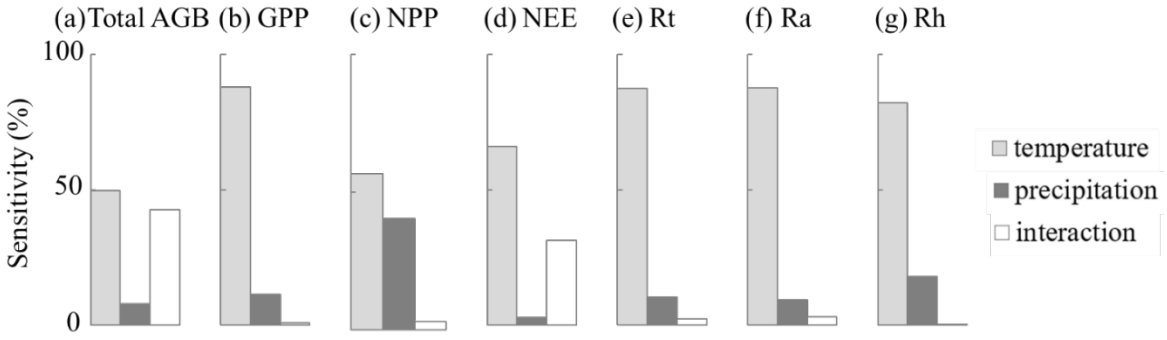

Figure 6. The sensitivity of total aboveground biomass (AGB), GPP, NPP, NEE, Rt, Ra, and Rh to temperature, precipitation, and their interaction.

4 Discussion

This study is one of the few attempts to apply dynamic forest models, here specifically FORMIND, to the mixed broadleaved-Korean pine forest – an important temperate forest in northeast China. Simulated forest dynamics showed that intolerant pioneer tree species sharply increased in AGB at early successional stages, afterwards decreased gradually, and finally were replaced by dominant and climax tree species (mid shade-tolerant and shade-tolerant tree species). The simulated forest successional trajectories followed the theories of classic forest stand dynamics (Oliver and Larson 1996), which are consistent with the simulated dynamics of other forest ecosystems (Fischer et al. 2016; Groeneveld et al. 2009). We focused on the AGB dynamics of individual PFTs (which can reflect the compositional differences through PFT dominance) and on ecosystem productivity under four representative future climate scenarios, and evaluated the sensitivity of this forest ecosystem to climate. We found that the uncertainty in future climate predictions can lead to inconsistent responses of forest composition and ecosystem productivity to climate change. The sensitivity of the forest to temperature and precipitation differed within both – plant function type (PFT) composition and ecosystem productivity. Our study addresses the importance of evaluating the sensitivity of forest ecosystems to climate change, which is relatively less studied. The insight from the study may help designing effective forest management strategies to cope with future climate change.

Our results suggest that the simulated forest composition and structure of the mixed broadleaved-Korean pine forest by the FORMIND model (starting from bare ground to year 2015) reflected the currently observed forest conditions. Moreover, the simulated results, with an NEE of 0.3-0.6 t C/ha/yr in ~2015 (Fig. S6), indicated that currently the forest is still a carbon sink, which agrees with the observations and other simulations at this forest site (0.3-1.8 t C/ha/yr) (Guan et al. 2006; Saigusa et al. 2013; Tang et al. 2009; Wang et al. 2006; Xie et al. 2020). Moreover, our simulated result is consistent with other studies in temperate forest worldwide. For example, a study of estimated

NEP (which is generally considered to be close to NEE) from improved individual-based forest ecosystem model (FORCCHN) showed that NEP in mixed broadleaved-coniferous forests from 1982 to 2011 were 0.4 t C /ha/yr (Zhao et al. 2019). Forest observation exhibited that the average NEP for unmanaged temperate and boreal forests more than 200 years old was 1.3 ± 0.6 t C /ha/yr, indicating a slight net C sink (Gundersen et al. 2021), which is close to our simulation result. The above results confirmed that the FORMIND model performs well in simulating the forest dynamics in the studied mixed broadleaved-Korean pine forest. Overall, we found that both biomass and productivity of the mixed broadleaved-Korean pine forest will show an increasing trend under future climate change, which is similar to the predicted results of other temperate forest in northeastern United States (Wang et al. 2017), further supporting the promoting effects of climate warming on forest carbon accumulation.

Our results revealed that there are divergent responses of the PFTs to temperature and precipitation over the 21st century in the mixed broadleaved-Korean pine forest. The simulated AGB of PFTs is generally more sensitive to temperature than to precipitation. This is mainly due to the climate of the study site (Changbai Mountain) with low temperatures and abundant precipitation (Yang 1981), where tree growth is more responsive to temperature increases. In our study, we found that the least shade-tolerant and the most shade-tolerant PFTs exhibited a higher sensitivity to temperature than precipitation, but they showed opposite responses. The most shade-tolerant PFTs (e.g., Korean pine, basswood) gradually increased in AGB with warming climates, while the least shade-tolerant PFTs (such as birch, aspen, oak) gradually decreased. This discrepancy is related to the tree species' biological traits, which affect the species establishment and survival (Craine and Dybzinski 2013). A tree's ability to increase its growth under more favorable climates is also confounded by its competition capability that varies significantly among species (Ford et al. 2017). In our study area, future increases in temperature and precipitation would create a more suitable environment for tree growth. However, the shade-tolerant PFTs with strong competitiveness will gain advantages over other PFTs and occupy more space. In particular, recent studies

based on both, model simulation and tree chronology, also confirmed that shade-tolerant species, such as Korean pine, was highly temperature sensitive and showed a positive relationship between radial growth and temperature (Lyu et al. 2017; Wang et al. 2019). However, because of the diminished available space and enhanced tree competition resulted from the growth and establishment in shade-tolerant PFTs, AGB of shade-intolerant PFTs with weak competitiveness suffers, even though these PFTs are also favored under the warming climates. Noteworthily, moderate shade tolerant PFTs, such as ash and elm group, exhibited lower sensitivity to temperature than precipitation, and the simulated dynamics in their AGB remain largely stable with slight fluctuations. This is because their ecological niches are mostly in the middle between shade-tolerant and shade-intolerant PFTs, allowing them to be less sensitive to climate change. Therefore, under anticipated climatic conditions in the future, species composition in mixed broadleaved-Korean pine forest may tend to evolve towards increasing in shade-tolerant PFTs but decreasing shade-intolerant PFTs. Notably, this change in forest composition is mainly caused by climate change rather than succession, as the current forest, i.e., mature forest dominated by mid- to late-successional species, has been already in a stable state, i.e., the successional climax under the current climate. Certainly, drought induced by high temperature may limit the increase in forest biomass (Allen et al. 2010; Ma et al. 2012).

We found that ecosystem productivity exhibited a higher sensitivity to temperature than precipitation in the mixed broadleaved-Korean pine forest. This is consistent with recent studies based on carbon flux observation (Yu et al. 2008; Yu et al. 2005), which shows that the low temperature limits tree growth in this forest ecosystem. Future warming can prolong the growing season and increase tree photosynthesis, thereby enhancing forest ecosystem productivity (Keenan et al. 2014; Oberbauer et al. 2007). Our simulation results also found that GPP will increase under future climate scenarios over the 21st century. Meanwhile, our results also suggest that ecosystem respiration demonstrated a high sensitivity to temperature, which is consistent with recent studies (Jiang et al. 2005; Wen et al. 2006; Yu et al. 2005). We found that ecosystem respiration

showed a gradual increase under the warming climates. This is resulted from the elevated temperature that increases plant and soil respiration rates (Atkin and Tjoelker 2003; Davidson and Janssens 2006). Although increasing precipitation may increase soil water content, promoting plant growth and soil respiration, and thus increasing ecosystem GPP and respiration (Beer et al. 2010; Chen et al. 2013; Wang et al. 2004), the intensity of the effect is relatively weak due to abundant precipitation in our study site. We did not find synchronous response of GPP and respiration to climate change in this study. Instead, we found that respiration increases more strongly than GPP (photosynthesis) under the warming climates. This could lead to a reduced carbon sequestration and decreased NEE, which may even change the forest ecosystem from a carbon sink to a carbon source under the higher temperature increase scenarios. Thus, the differences in the response and sensitivity of photosynthesis and respiration to climate change may alter future ecosystem carbon dynamics.

Our study that evaluates and quantifies the sensitivity of forest ecosystems to climate change is crucial in predicting the evolution of ecosystems under future climate change. Under future warming and precipitation conditions, our simulated results showed that the aboveground biomass of the forest increases over the 21st century, accompanied by increases in abundance of shade-tolerant tree species. This suggests that forest demand of management for promoting shade tolerant species could be naturally met under the future climate conditions in our study area. However, there were some limitations in the model simulation. The FORMIND model we used can only simulate seed-based tree regeneration without asexual reproduction and disturbance, which may partly limit the capability of the model when predicting future forest dynamics. We will further explore and discuss these limitations in future work.

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