Forest dynamics and carbon storage under climate change in a subtropical mountainous region in central China

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Citation: Wu, Y., D. Wang, X. Qiao, M. Jiang, Q. Li, Z. Gu, and F. Liu. 2020. Forest dynamics and carbon storage under climate change in a subtropical mountainous region in central China. Ecosphere 11(3):e03072. 10.1002/ecs2.3072

Abstract. Climate change has been observed to significantly influence forest growth, community composition, and species distribution ranges. These influences in turn will impose continuous impacts on forest production and carbon (C) storage potential. Forests in the subtropical China that are experiencing rapid regeneration and recovery may suffer multiple threats in the face of future climate change. Understanding how climate change may affect forest C sequestration and species dynamics over time will help formulate better management strategies for maintaining forest productivity and biodiversity. Here, we used a forest landscape model (LANDIS-II) to evaluate the long-term effects of current business-as-usual (BAU) management and climate projections (current, RCP4.5, and RCP8.5 climate scenarios; IPCC representative concentration pathways [RCPs] scenarios) on above- and belowground forest C storage and tree species dynamics in the Sangzhi County in the subtropical China. Our simulations showed a fast-growing period of forest total C in the first 70 yr, regardless of climate regime. Moderate climate change (RCP4.5 climate scenario) increased soil organic carbon (SOC) (12%) and detrital C (16%) but reduced live C (5%), contributing to a slight augment of 3% in forest C storage compared to the control climate, while severe climate change (RCP8.5 climate scenario) decreased SOC (16%), detrital C (27%), and live C (12%), resulting in a dramatic reduction of 14% in forest C storage, primarily because severe warming-induced water stress restrained species establishment and regeneration in temperature-sensitive areas like the lower elevations. Meanwhile, nature reserves in the higher elevations could act as “safe islands” by providing suitable conditions for most tree species, but the logging ban caused higher canopy closure, which in turn inhibit the growth and establishment of shade-intolerant species. The results also highlighted the positive responses of native “warm species” to climate warming and suggest that using them to replace some conventional coniferous plantation tree species would better mitigate the future climate change. Poor performance of the current BAU management in maintaining forest productivity and diversity suggests that new climate-adapted management strategies should be designed accordingly.

Key words: aboveground biomass; climate warming; forest landscape model; forest management; LANDIS-II; soil organic carbon; species distribution; subtropical forest.

Received 16 September 2019; revised 12 December 2019; accepted 3 January 2020; final version received 1 February 2020. Corresponding Editor: David M. Bell.

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INTRODUCTION

Forests are important terrestrial ecosystems to store carbon and mitigate global climate change (IPCC 2013), given their great net ecosystem productivity (NEP) and huge carbon storage (both soil and plants; Beer et al. 2010, Pan et al. 2011). Compared to Asian tropical and temperate
forests, East Asian monsoon subtropical forests have a higher NEP (Yu et al. 2014). High nitrogen deposition and “sufficient and synchronous water and heat availability” contribute to fast growth of these subtropical young forests (Yu et al. 2014), and this forest growth may continue for decades (Dai et al. 2016). However, future climate change, especially warming, may cause multiple uncertainties in productivity and species dynamics for subtropical forests (Tan et al. 2012, Dai et al. 2016).

Climate change has been observed to bring risk to biodiversity (Thomas et al. 2004, Heller and Zavaleta 2009, Urban 2015), shift species distribution ranges (Parmesan 2006, Aitken et al. 2008, Franklin et al. 2016), modify disturbance regimes (Dale et al. 2001, Westerling et al. 2006, Seidl et al. 2017), and influence forest growth (Rustad et al. 2001, Ciais et al. 2005, McMahon et al. 2010, Pretzsch et al. 2014). Recent frequent and severe drought events in tropical forests are suggested to be linked to climate warming (Phillips et al. 2009, Lewis et al. 2011), which may increase moisture stress and eventually lead to forest dieback (Malhi et al. 2008, Brien et al. 2015). However, the effects of climate change are not restricted to these observations. Future climate change associated with rising greenhouse gas in the atmosphere could have complex impacts on forest carbon balance. Soil warming experiments, translocation experiments, and model predictions have revealed that warming will cause higher soil respiration and soil organic carbon (SOC) loss (Bronson et al. 2008, Savage et al. 2013, Li et al. 2016). Given the critical role of temperature to metabolic processes, rising temperature in general can accelerate tree growth and bring about higher biomass accumulation (Rustad et al. 2001, McMahon et al. 2010). Longer growing seasons that are correlated with warming climate may allow forests earlier leaf flush (Penuelas and Filella 2009), leading to higher carbon sequestration (Delpierre et al. 2009). However, observed warming in some areas, especially in tropical forests, showed negative effects on tree growth (Clark et al. 2003, Ciais et al. 2005, Feeley et al. 2007), and even shifted a forest ecosystem from carbon sink toward carbon source (Brien et al. 2015). Warming climate may increase both soil evaporation and plant transpiration, decreasing soil water availability and causing water stress. If precipitation could not compensate the loss of soil water under warming, tree growth would be limited (Ciais et al. 2005, Choat et al. 2012, Gustafson and Sturtevant 2013). High temperature in summer may exceed plant species physiological tolerance (Wahid et al. 2007), leading to decline in growth or even death. If future climate warming continues as predicted, drought threats may even extend to low- to midlatitude (20°–40° N) subtropical forests and hinder forest growth (Luo et al. 2008, Wen et al. 2010).

Forests in subtropical China are mostly mountainous forests which contain various ranges of tree species along altitudinal gradients (Fang and Yoda 1990). The climate becomes cooler as elevation rises, causing an altitudinal temperature gradient. Thus, tree species distribution and forest phenology in the mountains tend to strongly depend on elevations (Tang and Ohsawa 1997, Da et al. 2009). In lower elevations, most native tree species can generally establish and regenerate under the warm and wet climate. In higher elevations, cooler climate restricts some warm species due to winter frost, shorter growing seasons, or lower accumulated temperature (Liu et al. 2007, Lenz et al. 2013). However, future climate change may cause tree species range shifts in montane due to spatially changing the climate adaptation ranges of tree species (Lenoir et al. 2008, Choat et al. 2012, Ruiz-Labourdette et al. 2012). Warming climate is expected to mitigate the low-temperature restrictions on species establishment and prolong the growing seasons in higher mountains, but to increase the water stress in lower lands (Liu et al. 2018, Deng et al. 2019). The competition among tree species for soil water may become more intensified. In lower lands, tree species establishment could be limited by soil water availability and temperature tolerance. Thus, tree species may be forced to migrate vertically upward. However, given the rapid rate of climate change projected, tree species will likely suffer adaptational lag between fundamental and realized niches (Davis 1989, Iverson et al. 2004, Aitken et al. 2008), which could potentially reduce forest carbon storage (Scheller and Mladenoff 2005). Besides, warming may also bring about uncertainties to soil C pools because rising temperature could not only change soil C inputs due to root exudates and litter fall, but
also accelerate decomposition of detritus and soils, especially where heterogeneous above- and belowground systems are shaped by complex mountainous terrain. In central China, subtropical mountain forests provide great forestry productions and are expected to play a key role in mitigating global climate change (Yu et al. 2014), but they also risk forest decline under future climate warming. Thus, a further understanding of how subtropical mountain forests may respond to climate change is urgently needed, which will help formulate better management strategies for maintaining forest functions.

Using traditional approaches to explore forested landscape succession in response to climate change is quite difficult. Forest landscape models are useful tools to further understand the effects of climate change and disturbance regimes on forests (Xi et al. 2009). In this study, we used LANDIS-II model to assess the effects of climate projections on forest C storage and tree species dynamics. We especially highlighted the potential impacts of future climate change on forests along altitudinal gradients. We traced the dynamics of C pools and investigated the dynamics of species abundance and forest composition in the Sangzhi County (SZC) in the subtropical forested region in central China. Our study questions were as follows: (1) How may climate change affect long-term carbon dynamics in forest vegetation, detritus, and soils under current forest management? (2) What are the likely impacts of climate change on tree species distribution, migration, and forest composition in mountainous terrain? (3) Will higher mountainous ecoregions become more suitable for tree species to establish in the face of warming climate?

**METHODS**

**Study area**

Our study area is the SZC in Hunan Province in central China (Fig. 1). The county has an area of 347,050 ha which extends across 29°17’31”–29°47’40” N, 109°42’13”–110°45’52” E. The climate is subtropical humid monsoon with cool and dry winter (mean January temperature 5.23°C), and warm and wet summer (mean July temperature 27.68°C). The average annual precipitation is 1425 mm, about 80% of which falls between April and October. The topography is complex mountainous terrain with elevation ranges from 179 to 1882 m. Higher mountains located in the north and northwest of the county while lower hilly lands in the middle and south of the area. The distribution of soil types is highly correlated with elevation. Soils are mainly comprised of Alfisols in mountains and Ultisols in lower hilly lands. The soil texture is generally loamy.

The forests in the county were once dominated by multiple evergreen and deciduous broad-leaved tree species. Starting from the 1950s, timber harvesting had caused vast areas of deforestation in the past several decades. By the 1990s, more than 60% of the forests had been clear-cut and then had been left to self-regeneration. In 1998, government policy changed to forbid deforestation, and to promote plantation establishment. Currently, most of the SZC forests are dominated by *Pinus massoniana* and *Cunninghamia lanceolata* conifer plantations in the lower elevations. Meanwhile, the Badagongshan (BDGS) National Nature Reserve in the higher mountains (mostly >1000 m) is covered mostly by natural and secondary forests with over 700 tree and shrub species. The BDGS forests are currently comprised of either evergreen-deciduous broad-leaf mixed forests dominated by *Cyclobalanopsis multinervis* and *Fagus lucida*, or coniferous and broad-leaved mixed forests dominated by *Tsuga chinensis* and *Cyclobalanopsis multinervis*. The BDGS Nature Reserve is a big resource pool of species and gene diversity providing diverse seeds to surrounding lands.

**LANDIS-II model**

We simulated the dynamics of the SZC forests under climate change using LANDIS-II model. LANDIS-II is a process-based, spatially dynamic forest landscape model that simulates seed dispersal, succession, natural disturbance, management, and climate change effects over the long term (Scheller and Mladenoff 2004, Scheller et al. 2007, 2011b). Across a landscape, the LANDIS-II model simulates a grid of interacting cells that are aggregated into ecoregions with homogeneous climate and soil properties (Scheller and Mladenoff 2005). Within each cell, LANDIS-II simulates tree growth, mortality, and regeneration. Trees are represented as species-age cohorts...
rather than individual trees. Each cell can contain multiple species and species-age cohorts. Within LANDIS-II, seed dispersal is a critical ecological process which allows active cells to interact spatially. An active cell has the probability to receive seeds from adjacent or farther cells which contain mature cohorts. Species probability of establishment ($P_{\text{est}}$) determines the possibility of a tree species to establish in an ecoregion, under the condition that the available light at the site must meet the species’ light requirements (Scheller and Mladenoff 2005, Scheller et al. 2011c).

The Century Succession extension (v 4.0) of LANDIS-II was used to simulate landscape above- and belowground carbon dynamics. The Century Succession extension (Scheller et al. 2011a) is a combination of the CENTURY soil model (http://www.nrel.colostate.edu/projects/century/) and the LANDIS-II Biomass Succession extension (Scheller and Mladenoff 2004), which links aboveground processes of successional dynamics to belowground processes of soil carbon dynamics and root dynamics (Scheller et al. 2011a). The extension simulates growth, regeneration, and mortality of trees, wood and litter aggradation and decay, soil accumulation and decomposition, available nitrogen, and available soil water (Scheller et al. 2011a, 2012). Using the Century Succession extension, time series data of carbon dynamics can be traced within a forested landscape, such as above- and belowground net primary productivity, net ecosystem exchange (NEE), SOC, detrital carbon, and aboveground biomass (AGB) by species (Loudermilk et al. 2013, Kretchun et al. 2014, Martin et al. 2014, Creutzburg et al. 2016, Laflour et al. 2016).

**Model parameterization**

The inputs for LANDIS-II include initial community data, ecoregion configuration, spatial

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**Fig. 1.** Map of study area, the Sangzhi County, China. Colored background shows the elevation band in the mountainous region.
management, species life history attributes and functional traits, and climate data. Given the extent of our study area, we choose a cell resolution of 100 m (1 ha) for our simulations.

According to field investigations, 25 major tree species were selected to simulate vegetation dynamics across the landscape (Table 1). Some of the species dominated in relatively lower hilly lands, while others were more abundant in the higher Nature Reserve. Species life history attributes (Table 1), functional traits, and soil properties were obtained from a 25-ha forest dynamic plot, field samples, academic literature, local scientific reports, and experts (Guo et al. 2013, Xu et al. 2016, Li et al. 2017, Wang et al. 2017). Initial communities were derived from the species and age class information in the seventh forestry resource survey (FRS) data of Hunan Province in 2008.

We divided our study area into six active ecoregions (Appendix S1: Table S1), mainly depending on altitude, climate, and soil properties. Based on the soil data provided by FRS, the digital elevation model data obtained from geospatial data cloud (http://www.gscloud.cn/), and the distribution of vegetation along the elevation, we set up six ecoregions, SZ101 (179–450 m), SZ201 (450–700 m), SZ301 (700–1000 m), SZ401 (1000–1300 m), SZ501 (1300–1600 m), and SZ601 (1600–1882 m). The environmental gradient represented by these ecoregions could help us better understand how plant communities and C pools along altitudinal gradients may respond to climate change.

Spatial management inputs, including maps of management areas and harvest stands, were defined according to ownership information and subcompartment delineation separately from the FRS database. In the SZC, 30% of the area was mapped as protected areas with natural forests, 25.4% as woodlands, 18.2% as plantation forests, and 26.4% as non-forested lands.

**Climate data**

We selected three climate scenarios for this study, with one current climate scenario and two climate change scenarios (Fig. 2). The climate data for current climate scenario were based on 30-yr (1981–2010) monthly averages from the local weather station. The data for climate change scenarios were derived from the HadGEM2-ES climate model (Martin et al. 2011), provided by the Data Distribution Centre of Intergovernmental Panel on Climate Change (IPCC; http://www.ipcc-data.org/). Here, we selected the RCP4.5 (the radiative forcing target level at 4.5 W/m²) scenario and the RCP8.5 (the radiative forcing target level at 8.5 W/m²) scenario as stabilized emission levels (moderate climate change) and high greenhouse gas concentration levels (severe climate change). HadGEM2-ES projects average minimum and maximum temperatures and average precipitation on a monthly basis to the year 2100. The warming tendency from 2010 to 2100 is expected to be 0.26°C/10a for RCP4.5 and 0.58°C/10a for RCP8.5, while the warming trend for the current climate is about 0.13°C/10a. The precipitation from 2010 to 2100 is projected to increase about 49.1 mm/10a for RCP4.5 and 70.1 mm/10a for RCP8.5, while the precipitation trend for the current climate is about 43.5 mm/10a.

In our simulation, climate stayed the same for each simulation year under current climate scenario. The projected climate data were used in climate change scenarios (RCP4.5 and RCP8.5) from 2010 to 2100; then, the last 10-yr (2091–2100) climate data were repeatedly used till the end of simulations (the year 2310). We modified the temperatures corresponding to elevation range, based on the notion that temperatures will decrease 0.6°C for every 100 m elevation rising under humid climate conditions (Lazaridis 2011).

**Disturbance regimes**

Given the fire suppression and high precipitation in our study area, the wildfire probability is extremely low. Local records of forest management also confirmed that few minor fire events occurred in the past 30 yr, mostly caused by human activities such as cigarette ends and campfire, and were rapidly put out. Insect outbreak and windthrow events also rarely occurred due to the subtropical mild climate and high biodiversity in this area. Harvest is the only disturbance which has and will profoundly influence the forests in this area.

Across the forested landscape, we used business-as-usual (BAU) forest management to model anthropogenic disturbance to mimic actual conditions. Business-as-usual strategies balance forestry production, biodiversity
conservation, forest restoration, and carbon sequestration potential. In the simulations, the SZC forests were divided into three types of forest management areas, including protected areas (40.7%), woodlands (34.6%), and plantations (24.7%). Protected areas cover the BDGS National Nature Reserve and other areas with abundant relict and rare species. A logging ban was imposed in protected areas from the beginning to the end of our simulations. Woodlands were forbidden to cut in the first 50 simulation years to prevent soil erosion. After that for every 10 yr, 10% of the woodland stands were cut. Only mature stands with mean maximum age over 40 yr can be selected. The selective harvest only removed economic and fast-growing species but kept protected, relic, and later-successional species. The youngest cohorts of every species were kept to promote regeneration. Plantations were predominated by C. lanceolata and P. massoniana, 15% of which were harvested per 10 yr. In addition, relict and rare tree species (i.e.,

| Species abbr. | Long | Mat | ShT | EfSD | MaxSD | MinJT | MaxAD | MinGDD | MaxGDD |
|---------------|------|-----|-----|------|-------|-------|-------|--------|--------|
| Betuinsi      | 150  | 15  | 1   | 200  | 500   | –12   | 0.2   | 501    | 5202   |
| Betulumi      | 150  | 15  | 1   | 500  | 3000  | –12   | 0.244 | 501    | 6804   |
| Camespit      | 200  | 10  | 4   | 50   | 200   | –7    | 0.228 | 945    | 5979   |
| Carvipimi     | 100  | 10  | 1   | 400  | 1000  | –15   | 0.244 | 501    | 5790   |
| Castsegu      | 150  | 15  | 3   | 50   | 500   | –19   | 0.282 | 1584   | 6249   |
| Cornkous      | 100  | 10  | 2   | 50   | 200   | –10   | 0.273 | 1764   | 6201   |
| Cunnblanc     | 200  | 15  | 2   | 300  | 600   | –12   | 0.244 | 501    | 6999   |
| Cyclgrac      | 300  | 15  | 5   | 100  | 300   | –12   | 0.2   | 600    | 6114   |
| Cyclmult      | 300  | 15  | 5   | 100  | 300   | –8    | 0.186 | 1923   | 5790   |
| Davinvo       | 250  | 15  | 2   | 150  | 500   | –8    | 0.195 | 1191   | 5754   |
| Faguluci      | 300  | 25  | 4   | 100  | 300   | –7    | 0.184 | 1923   | 5790   |
| Lirichin      | 250  | 15  | 2   | 500  | 1000  | –9    | 0.204 | 2094   | 6168   |
| Litselon      | 100  | 8   | 4   | 100  | 300   | –8    | 0.271 | 915    | 6957   |
| Magnoffi      | 200  | 15  | 2   | 50   | 200   | –12   | 0.216 | 501    | 5883   |
| Nyssine       | 250  | 15  | 2   | 100  | 500   | –5    | 0.21  | 2382   | 6393   |
| Padugray      | 150  | 10  | 3   | 50   | 200   | –11   | 0.244 | 681    | 5379   |
| Pinumass      | 300  | 10  | 1   | 300  | 600   | –12   | 0.271 | 600    | 6882   |
| Pter haphe     | 150  | 10  | 1   | 500  | 3000  | –19   | 0.282 | 1446   | 4467   |
| Querserr      | 200  | 15  | 3   | 100  | 300   | –21   | 0.272 | 600    | 6006   |
| Rhodstam      | 100  | 8   | 5   | 100  | 200   | –8    | 0.184 | 2046   | 5769   |
| Rhodsuic      | 150  | 10  | 5   | 100  | 200   | –11   | 0.2   | 615    | 4371   |
| Sassstrum     | 100  | 12  | 1   | 100  | 300   | –8    | 0.219 | 2094   | 6408   |
| Schiparv      | 200  | 15  | 4   | 50   | 200   | –4    | 0.175 | 2478   | 5754   |
| Toxisucc      | 80   | 10  | 2   | 50   | 200   | –17   | 0.296 | 501    | 6999   |
| Tsugchin      | 400  | 20  | 5   | 50   | 150   | –15   | 0.271 | 501    | 6891   |

Notes: EfSD, effective seeding distance (m); Long, longevity (years); Mat, age of maturity (years); MaxAD, maximum allowable drought (0.0–1.0, lower values indicate species whose establishment is more sensitive to drought); MaxGDD, maximum number of growing degree days; MaxSD, maximum seeding distance (m); MinGDD, minimum number of growing degree days; MinJT, minimum tolerable January temperature (°C); ShT, shade tolerance class (1–5, with 1 for the most shade-intolerant and 5 for the most shade-tolerant).
**Data analysis**

Using LANDIS-II model, twenty-five tree species within six ecoregions were simulated over the period of 300 yr (2010–2310) under three climate scenarios (current climate, RCP4.5, and RCP8.5). Each scenario was replicated five times because of the stochastic variability in dispersal, establishment, and disturbance events.

Two aspects were examined to assess how climate change may affect long-term forest carbon storage and tree species dynamics. The first aspect represented the effects of climate change on whole landscape. The second aspect explored how ecoregions along elevational gradients responded to climate change. We traced SOC, live C, detrital C, and species AGB in a time series for the 300-yr simulation across the landscape and within each ecoregion under three climate scenarios. Live C represents the plant C pools, including above- and belowground. Detrital C consists of litter fall, dead wood, and dead root. Besides, we calculated total ecosystem carbon (Total C), which is the sum of SOC, live C, and detrital C pools. We examined the effects of climate change on each C pool and species-specific biomass at simulation year 2310 with a one-way analysis of variance (ANOVA) across the whole landscape and among each ecoregion separately.

All calculations, analysis, and graphics were accomplished using ggplot2 (Wickham 2011, 2014, 2016) library in R v 3.5.2 (R Core Team 2018) and ArcGIS 10.2 for Desktop (ESRI 2013).

**RESULTS**

**Model validation**

It is difficult to validate long-term simulation results for large study areas (Scheller and Mladenoff 2004, 2005). Instead, we validated the simulated AGB at the initial year, since we have the spatial stand volume data from the FRS. We converted the stand volume into AGB through biomass expansion factor (Fang et al. 2001, Dai et al. 2016). We randomly selected about 3000 sampling points spatially covering the whole study area and then compared the simulated AGB and the converted values for validation. The results showed a positive linear correlation between the simulated and observed AGB values ($R^2 = 0.61$, $P < 0.001$), with a root mean square error (RMSE) of 1100.2 g/m², 23.5% of the mean (Appendix S1: Fig. S1). This result indicated that the simulated initial AGB data matched well with the actual stand volume data.

**Climate change impacts on C pools**

In the beginning of the simulations, the total ecosystem C was 98.37 Mg C/ha ($1 \text{ Mg}/\text{ha} = 100 \text{ g/m}^2$), with 87.62% in mineral soil, 11.71% in live biomass (above- and belowground), and 0.67% in detritus (Fig. 3). The total ecosystem C showed a fast accumulation in the first 70 yr (2.06 Mg C·ha$^{-1}$·a$^{-1}$), which was mainly contributed by the increase of live C

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**Fig. 2.** The variation trend of (a) annual mean temperature (°C) and (b) annual total precipitation (mm) under current conditions (1981–2010) and RCP scenarios (2010–2100).

*Davidia involucrata* and *Liriodendron chinense* were forbidden to cut across the whole forested landscape.
(1.91 Mg C·ha\(^{-1}\)·a\(^{-1}\)) regardless of climate change. By the end of the simulations, the projected total ecosystem C increased to 263.92 Mg C/ha under current climate scenario, with 55.12% in live C, 41.13% in SOC, and 3.75% in detrital C. Severe climate change (RCP8.5) decreased SOC (16%), detrital C (27%), and live C (12%), resulting in a reduction of 37.22 Mg C/ha (14.10%) in total ecosystem C storage, compared to the control climate scenario, while moderate climate change (RCP4.5) increased SOC (12%) and detrital C (16%) but reduced live C (5%), contributing to a slight augment of 8.41 Mg C/ha (3.19%) in forest C storage.

The projected C dynamics in each ecoregion showed different effects of climate change along elevational gradients (Fig. 4, Tables 2, 3). For the live C pool, severe climate change showed a detrimental effect in the lower elevations (SZ101 and SZ201), but this negative effect gradually diminished in the middle elevations (SZ301 and SZ401) and even turned into a promote effect in the higher elevations (SZ501 and SZ601), compared to the control climate (Fig. 4b). The effects of moderate climate change on live C were relatively slight. For the SOC and detrital C pools, severe climate change resulted in significant reductions in all ecoregions, while moderate climate change caused evident augments (Fig. 4a, c).

**Climate change effects on species dynamics**

Simulated live C represented the sum of the 25 tree species biomass, which illustrated the rapid growth of the SZC forest in the first 70 yr and the subsequent levelling-off (Fig. 3b). By the end of the simulations, the SZC forest was dominated by *C. lanceolata*, *P. massoniana*, and *L. chinense*, regardless of climate change (Fig. 5). Some shade-intolerant species, such as *Betula luminifera*, *Carpinus viminea*, and *Pterocarya hupehensis*, lost their dominating status after the fast-growing stage and began to decline in the following succession (Fig. 5). In contrast, shade-tolerant species like *C. multinervis*, *F. lucida*, and *T. chinensis* showed a
continued biomass accumulation throughout the succession (Fig. 5).

For most species in our simulations, severe climate change caused lower biomass accumulations (Table 3), while the effects of moderate climate change were minor (Table 2), compared to the control climate (Fig. 5). These effects were particularly pronounced in lower elevations (Fig. 6). Under RCP8.5 climate scenario, some species were forced to shrink to middle and higher elevations, for example, *Castanea seguinii*, *L. chinense*, and *C. multinervis* (Fig. 6). However, warm species like *B. luminifera*, *Litsa elongata*, and *Toxicodendron succedaneum* showed great expansion under climate change scenarios, especially under RCP8.5 climate scenario (Fig. 6). Though climate change influenced the growth of tree species, the dominance of the tree species in each ecoregion was not changed (Fig. 7). The lower elevations were dominated by *P. massoniana*, while in the middle elevations, *L. chinense* became more dominant. Shade-tolerant species, *F. lucida* and *T. chinensis*, dominated in the higher elevations.

Species probability of establishment ($P_{est}$) determines whether a tree species can establish in an ecoregion, each of which was calculated depending on species functional traits and climatic changes. Our simulation results indicated that climate change evidently affected $P_{est}$ of tree species in all ecoregions (Fig. 8). In the lower elevations, climate change reduced $P_{est}$ of all species, including warm species which showed great expansion under RCP8.5 climate scenario (Fig. 8). With the elevation increasing, the negative effects of climate change on $P_{est}$ gradually became minor (Fig. 9). In the higher mountainous ecoregions, $P_{est}$ was evidently increased by projected climate change (Fig. 9).

Fig. 4. Simulated C estimates (g C/m²) of (a) SOC (soil organic carbon), (b) live C (below- and aboveground), (c) detrital C, and (d) total C (SOC + live C + detrital C) in six ecoregions along elevational gradients (from lower lands SZ101 [altitude < 450 m] to higher mountains SZ601 [altitude > 1600 m]) over 300 yr under current climate and two projected climate scenarios (RCP4.5 and RCP8.5).
Table 2. Effects of RCP4.5 climate scenario on C pools and species aboveground biomass at the year 2310.

| Variable                | Whole landscape | SZ101 | SZ201 | SZ301 | SZ401 | SZ501 | SZ601 |
|-------------------------|-----------------|-------|-------|-------|-------|-------|-------|
| Carbon pools (g C/m²)   |                 |       |       |       |       |       |       |
| Detrital C              | 155.79***       | 132.31*** | 160.66*** | 152.50*** | 170.96*** | 188.44*** | 40.72*** |
| Live C                  | -642.39***      | -1663.45*** | -796.75*** | -252.33*** | -238.97*** | -107.96*** | 143.68*** |
| SOC                     | 1341.36***      | 1286.38*** | 1300.08*** | 1573.00*** | 931.64*** | 1387.06*** | 628.54*** |
| Total C                 | 854.75***       | -244.76*** | 663.99*** | 1473.17*** | 863.63*** | 1467.54*** | 812.94*** |
| Species (g biomass/m²)  |                 |       |       |       |       |       |       |
| Betula insigneis        | 1.68***         | 2.87*** | 2.78*** | 2.05*** | -0.65 | -8.57*  | -0.81   |
| Betula luminifera       | 107.90***       | 337.00*** | 124.66*** | 44.83*** | 5.21  | -16.41*** | -0.60   |
| Camellia pitardii       | -30.03***       | -30.26*** | -47.42*** | -18.05*** | -17.43*** | -8.07  | 1.21     |
| Carpinus vinnea         | 63.66***        | 212.02*** | 77.9***  | 17.54*** | -1.29 | -10.63*** | -0.57   |
| Castanea sequinii       | -383.00***      | -736.68*** | -562.27*** | -185.07*** | -88.54*** | -30.49*** | -19.2*** |
| Correa kousa            | 3.09***         | 8.02***  | 4.18***  | 1.20***  | 0.33  | -0.09    | 0.07     |
| Cunninghamia lanceolata  | 5.24            | -352.44*** | 169.49*** | 76.24*** | -199.09*** | -199.01*** | -17.25*** |
| Cyclobalanopsis gracilis| -96.72***       | -33.29*** | -110.43*** | -115.38*** | -31.72 | -139.74*** | -97.15*** |
| Cyclobalanopsis multinervis| -261.02***   | -163.73*** | -306.27*** | -283.54*** | -286.11*** | 59.15  | -38.43*** |
| Davidia involucrata     | -0.92           | -0.03    | 0.73***  | 0.17    | -2.38 | -15.57   | -72.29*** |
| Fagus lucida            | 18.69***        | -0.53*   | -0.99    | 8.21*   | -100.60*** | 474.52*** | 2219.64*** |
| Liriodendron chinense   | 14.96           | -617.05*** | -203.35*** | 309.90*** | 505.09*** | 351.96*** | 76.06***  |
| Lirsea elongata         | 28.71***        | 107.68*** | 39.95***  | -5.01*  | 4.05* | -0.93    | 0.96***   |
| Magnolia officinalis    | -0.12           | 0.09     | 0.64***  | 0.51*   | -3.00** | -4.19*  | -0.41    |
| Nyssa sinensis         | 1.37            | -3.83**  | 1.10     | 4.09*** | 1.44  | 0.10     | 0.00     |
| Padaus grayana         | 26.65***        | 49.60*** | 46.28*** | 8.24*** | 2.28  | -8.45*** | -0.42    |
| Pinus massoniana        | -537.42***      | -1373.69*** | -657.15*** | -280.18*** | -79.73 | -33.72   | -2.74    |
| Pterocarya liaophenensis| -2.81*          | 9.03***  | -4.95    | -1.78  | -7.78** | -18.74** | -1.03    |
| Quercus serrata        | 35.75***        | 153.26*** | 83.03***  | -13.3** | -74.14*** | -74.73*** | -14.40*** |
| Rhododendron stamineum | -2.02***        | -4.12*** | -3.53*** | -0.93*** | 0.50*** | 2.22***  | 4.08***   |
| Rhododendron sutchuenense| -0.24***      | 0.00     | -0.04*** | -0.22*** | -0.80*** | -1.35*   | 0.78***   |
| Sassafras tzumu         | -6.97***        | -30.78*** | -11.82*** | 4.91*** | 0.97* | 0.00     | 0.00     |
| Schinua paeziflora      | -52.18***       | -356.72*** | -3.23    | -3.16  | 1.31  | 2.38***  | 0.00     |
| Toxicodendron succedaneum| 17.63***     | 56.43*** | 21.82*** | 4.96*** | 0.36* | -0.09    | 0.00     |
| Tsuga chinensis        | -26.23***       | 0.00     | 0.00     | -0.02  | -26.83*** | -484.3*** | -899.72*** |

Notes: SOC, soil organic carbon. For the whole landscape and each ecoregion, values are expressed as differences between RCP4.5 and the control climate. Significant differences between the two climate scenarios are indicated by asterisks.

*P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001.

**DISCUSSION**

Our simulation results indicated a fast-growing period of ecosystem carbon in the first 70 yr of the simulation, which is mainly due to the growth and succession of young forests in the SZC as a legacy effect caused by long-time extensive logging from the 1950s to the end of the 1990s. Widespread and intense deforestation left vast areas of young plantations in the lower elevations and small areas of natural and secondary forests in the higher elevations. In the end of the 1990s, the Chinese government had implemented two large-scale forest conservation and restoration programs: The Natural Forest Conservation Program and the Green for Grain Program (Zhang et al. 2000). The first program conserves natural forest through logging bans and afforestation with incentives to forest companies and local stakeholders, while the second one converts agricultural lands on steep slopes to forest and grassland by providing farmers with food and cash subsidies. These two programs have been shown to strongly expand forest area and increase forest productivity (Liu et al. 2008, Fang et al. 2014). As a consequence, the expanded forest could sequester a large amount of C into forest ecosystems, especially in...
Table 3. Effects of RCP8.5 climate scenario on C pools and species aboveground biomass at the year 2310.

| Variable                  | Whole landscape | SZ101 | SZ201 | SZ301 | SZ401 | SZ501 | SZ601 |
|---------------------------|-----------------|-------|-------|-------|-------|-------|-------|
| Carbon pools (g C/m²)      |                 |       |       |       |       |       |       |
| Detrital C                | −267.82***      | −339.30*** | −206.76*** | −264.71*** | −348.86*** | −347.58*** | −503.82*** |
| Live C                    | −1714.38***     | −6425.94*** | −1946.96*** | −404.37*** | 148.70*** | 436.45*** | 694.10*** |
| SOC                       | −1768.35***     | −1777.48*** | −1231.92*** | −1681.58*** | −3136.64*** | −3005.72*** | −3456.66*** |
| Total C                   | −3750.55***     | −8537.32*** | −3385.64*** | −2350.66*** | −3336.89*** | −2916.87*** | −3266.38*** |
| Species (g biomass/m²)    |                 |       |       |       |       |       |       |
| Betula utilisima          | −8.55***        | −2.66*** | −4.40*** | −8.05*** | −22.43*** | −30.43*** | −1.06*  |
| Betula luminesfera        | 538.78***       | 1038.42*** | 833.98*** | 245.13*** | 58.35*** | −32.40*** | −1.28   |
| Carpinus viminea          | −74.49***       | −197.81*** | −128.07*** | 8.69***   | −10.61*** | −25.64*** | −0.76   |
| Castanea sieginnii        | −1347.10***     | −2542.72*** | −1841.51*** | −847.04*** | −267.12*** | −81.66*** | −22.94*** |
| Cornus kousa              | 9.67***         | −9.48*** | 24.30*** | 5.67***  | 1.49***  | 0.75*    | −0.02   |
| Cunninghamia lanceolata   | 423.96***       | −1944.54*** | 1079.60*** | 999.73*** | −57.91*** | −440.32*** | −22.26*** |
| Cyclobalanopsis gracilis  | −204.11***      | −53.03*** | −201.46*** | −264.84*** | −117.13*** | −363.86*** | −1693.95*** |
| Cyclobalanopsis multimeris | −613.97***    | −268.04*** | −722.76*** | −812.86*** | −441.92*** | 231.60*** | −161.31*** |
| Daidia involucrata        | −3.52***        | 0.11**  | 0.09*** | 0.23**   | −8.21***  | −59.93*** | −97.19*** |
| Fagus lucida              | −43.44***       | −2.71*** | −22.50*** | −120.36*** | −371.28*** | 930.76*** | 2984.15*** |
| Liriodendron chinense     | −125.52***      | −2887.26*** | −1026.11*** | 810.75*** | 2748.93*** | 1466.78*** | 83.29*** |
| Litsea elongata           | 304.92***       | 584.77*** | 475.78*** | 129.57*** | 43.55***  | −0.96***  | 3.55***  |
| Magnolia officinalis      | −2.18***        | −0.26*** | −0.96*** | −0.91*** | −8.89***  | −10.41*** | −1.08   |
| Nyssa sinensis            | 4.31***         | −14.98*** | 0.74***  | 16.46***  | 6.50***  | 0.18**   | 0.00    |
| Pseudolarix gigantea      | −43.49***       | −21.32*** | −48.59*** | −50.68*** | −41.25*** | −27.54*** | −0.95*** |
| Pinus massoniana          | −937.96***      | −3214.12*** | −661.97*** | −446.82*** | −466.16*** | −440.76*** | −24.71*** |
| Pterocarya hupensis       | −160.14***      | 0.00***  | −166.58*** | −218.79*** | −205.66*** | −63.64*** | −1.99*** |
| Quercus serrata           | −430.22***      | −441.58*** | −476.00*** | −415.00*** | −393.36*** | −248.10*** | −17.77*** |
| Rhododendron staminatum   | −4.62***        | −5.71*** | −7.19*** | −4.51*** | −0.42*** | 7.36***   | 13.66*** |
| Rhododendron sutchuenense | −1.26***        | 0.00***  | −0.05*** | −0.59*** | −3.86*** | −14.35*** | −5.22*** |
| Sassafraz tsumu           | −5.60***        | −2.90*** | −2.90*** | −5.66*   | 22.70***  | 5.33***   | 0.00    |
| Schima paricifora         | −166.18***      | −683.91*** | −419.22*** | 250.94*** | 22.48***  | 7.96***   | 1.44***  |
| Toxicodendron suckedeanum | 83.30***       | 199.44*** | 124.00*** | 28.49***  | 2.65***   | −0.20***  | 0.00    |
| Tsuga chinensis           | −2.19***        | 0.00***  | 0.00***  | 0.14***  | −11.05*** | −39.96*** | 139.13*** |

**Notes:** For the whole landscape and each ecoregion, values are expressed as differences between RCP8.5 and the control climate. Significant differences between the two climate scenarios are indicated by asterisks.

*P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001.

Research in southern China (Liu et al. 2014). In Hunan Province, subtropical China (Chen et al. 2019), revealed that the C density in forest ecosystems increased from 1996 to 2015, which ranged from 110.3 to 130.8 Mg/ha, with an increment rate of 10.3 Mg/ha per decade. This increasing rate of forest C storage is relatively slower than our simulation results of the first twenty years (2010–2030, 17.95 Mg/ha per decade), mainly because of the differences in tree species composition and forest age. In Hunan forests, the live C pool accounted for approximately 17.3% of the total C storage, and soil C pool and detritus accounted for 78.0% and 2.7%, respectively (Chen et al. 2019). However, our simulated live C pool at the initial year only amounted for 11.71%, mainly due to the young forests (Appendix S1: Fig. S2) caused by past deforestation. Large areas of young forests in our study also resulted in a relatively smaller detrital C pool (0.67%). Furthermore, herbs and shrubs were not modeled in our simulation; therefore,
our results may underestimate the detrital C pool in the SZC. Although the simulated soil C pool in our study (87.62%) seemed to have a larger proportion than that of Hunan forests (78.0%), the values of soil C density were comparable (86.19 Mg/ha for our study and about 90 Mg/ha for Hunan forests). However, apart from the different proportion of C pools, we found similar increasing tendency of forest ecosystem C storage to other empirical studies between subtropical and warm temperate regions of China (Cui et al. 2015, Wang et al. 2018, Chen et al. 2019) and modeling studies in subtropical China (Dai et al. 2016), owing to the forest conservation and restoration policies. Compared to other modeling studies in subtropical and temperate forests (Scheller et al. 2011a, Laflower et al. 2016, Creutzburg et al. 2017), the initial ecosystem C storage of our simulation was much lower, but the increasing rate of our simulated ecosystem C was much faster, mainly due to the legacy effects. A similar study in temperate forest also indicated that the legacy effects could sustain for more than a century and may offset the potentially detrimental effects of climate change on forest growth (Loudermilk et al. 2013).

**Climate change effects on carbon pools**

In our simulation, climate change effects on forest C storage were minor in the first few decades, likely because of the offset by forest growth. As forests mature, negative effects of climate change became more evident, especially under the RCP8.5 scenario. We should carefully examine the long-term effects of climate change since the short-term effects may be masked by legacy effects (Kruhlov et al. 2018). The observed continuous forest growth in recent decades (Tan et al. 2012, Yu et al. 2014) and the restoration expectations in the 21st century (Dai et al. 2016) may not fully reflect the effects of climate change on species establishment and community growth.
composition. In our study, for example, it was not until 2100 that climate change began to show distinct impacts on live C (Fig. 3), particularly in the lower elevations (Fig. 4). However, for some mature forests in temperate America and Canada, climate change effects on forest ecosystems were projected to emerge in the first one or two decades (Duveneck et al. 2014b, Duveneck and Scheller 2015, Creutzburg et al. 2016, Boulanger et al. 2017). There are many simulation cases that climate change may increase AGB and total ecosystem C storage in some cool and wet regions (Thompson et al. 2011, Steenberg et al. 2013, Creutzburg et al. 2017), mainly due to increasing forest productivity in cool months.

Both RCP4.5 and RCP8.5 reduced live C in the SZC but the moderate climate change under RCP4.5 increased detrital C and SOC pools and resulted in a higher ecosystem C storage relative to the control climate. The live C pool increased with plant growth and succession, but decreased with massive tree death. In our study, detrital C is the sum of litter fall, dead wood, and dead root. Litter fall is somewhat relative to live C, whereas dead wood and dead root are more relative to events of harvesting (Swanson 2009) and tree mortality (Busing 2005, Busing and Fujimori 2005). The inconsistency between the changes in live C and detrital C pools under RCP4.5 was likely caused by harvest events and warm-induced mortality, which increased dead wood and root, but reduced live biomass. Additionally, community composition and forest type may also influence litter fall (Liu et al. 2004) and detritus decomposition (Scheller et al. 2011a). Though higher temperature increased the decay rate of detritus, lower moisture due to warmer and relatively drier climate under RCP4.5 (Fig. 2) may surpass the effects of temperature rise alone, and reduce detritus decomposition (Aerts 2006,
Gavazov 2010, Prieto et al. 2019). In our simulation, litter fall was larger under control climate, while RCP4.5 caused greater dead wood and dead coarse root, and the magnitude of dead wood was greater than that of litter fall (Appendix S1: Fig. S3). Since we could not trace how much woody biomass was removed in every harvest event, we could only prudently speculate that harvest events caused more dead wood and dead coarse root under RCP4.5 relative to the control climate. Furthermore, compared to the control climate, RCP4.5 resulted in more B. luminifera, C. viminea, P. hupehensis, and T. succedaneum (Fig. 5, Table 2) that have higher percentage of lignin in leaf and wood (Appendix S1: Table S2). In contrast, the late-
successional species that are more dominant in the control climate, such as *C. multinervis* and *C. seguinii*, have relatively lower percent leaf and wood lignin. As a result, the detritus with higher percent wood and leaf lignin (Cornwell et al. 2008) from the forest communities under relatively warmer and drier RCP4.5 climate scenario is expected to decay slower.

Soil C accumulation is a balance of C input and decomposition. Responses of SOC storage to climate change are complex, since climate could directly affect SOC by changing soil respiration and indirectly change soil C inputs by altering community compositions and above- and below-ground biomass. Though temperature rise may increase the decay rate of SOC in general (Knorr
et al. 2005, Kirschbaum 2006), we found a higher SOC storage with an increment of detrital C under RCP4.5 in our simulation. Severe warming under RCP8.5 reduced detritus and increased soil respiration, resulting in a significantly smaller SOC. In contrast, we found a relatively lowered soil respiration under RCP4.5 (Appendix S1: Fig. S4), mainly because respiration is constrained by lower soil moisture (Schindlbacher et al. 2012, Suseela et al. 2012, Wang et al. 2014) due to moderate warming-induced accelerated soil evaporation and relatively drier climate under RCP4.5 scenario.

**Climate change effects on forests along elevational gradient**

In regions with an elevational gradient, forests usually distribute following a vertical pattern due to variation in environmental conditions. The dynamics of these forests are more complex than those of flat regions, especially under future climate change. However, few simulations of regional forests addressed the vertical dynamics of forest communities and their responses to changing climate (Sundqvist et al. 2013, Hannah et al. 2014, Frey et al. 2016). In our simulation, we defined ecoregions according to elevational differences. We found that future climate change will have strong effects on different ecoregions via changing tree species establishment, plant community composition, and carbon pools.

The dramatic reduction of live C in SZ101 and SZ201 revealed the potential negative impacts of severe warming under RCP8.5 on the lower ecoregions. Severe warming hampered species establishment for most tree species (Figs. 8, 9).
and remarkably changed community composition (Fig. 7) in these temperature-sensitive areas. Some mild climate-adapted species (e.g., C. viminea, C. seguinii, C. multinervis, and P. huperiensis) dramatically declined in the lower ecoregions under RCP8.5 due to limited establishment and depressed growth. Extreme temperature increase in summer under RCP8.5 may exceed tree species physiological tolerance (Wahid et al. 2007), which could be another reason for forest decline in the lower ecoregions. Studies in European mountains indicated that climate change reduced the distribution of cold-adapted species (Gottfried et al. 2012) and may cause an extinction because population dynamics may lag behind climatic changes (Dullinger et al. 2012). In our study, the lower elevations were projected to be the temperature-sensitive areas, where future warming may bring seriously negative impacts on native forest communities. However, some warm species like B. luminifera, L. elongata, and T. succedaneum showed great expansion under climate change scenarios, especially under RCP8.5. Their increments partly mitigated forest decline in the lower ecoregions, but far from reversing the decline through natural regeneration.

In the higher ecoregions, severe warming stimulated forest growth and resulted in higher live C stocks relative to the control climate. This is similar to other studies in temperate forests (McMahon et al. 2010, Dymond et al. 2016), mainly because the climate of the BDGS National Nature Reserve located in higher elevations is characterized by the combination of temperate-like temperature and tropical-like precipitation. Besides, increased minimum temperature in winter may mitigate the low-temperature limits to species establishment and prolong the growing seasons. It is likely that the BDGS reserve could act as a potential safe island for most native species in face of future climate change. However, compared to the rate of climate change, the migration of tree species may be slower (Davis 1989, Iverson et al. 2004) and vary remarkably among species (Parolo and Rossi 2008, Chen et al. 2011). Given the negative effects of landscape fragmentation (e.g., settlements and farms) on seedling dispersal (Honnay et al. 2002, Higgins et al. 2003), tree species in lower elevations may have difficulty to migrate to suitable climate ranges in a few generations (Aitken et al. 2008). Thus, in face of climate change, species conservation strategies like assisted migration need to be further considered (Pearson and Dawson 2005, Vitt et al. 2010, Hewitt et al. 2011, McLane and Aitken 2012).

Across the entire study area, climate change evidently affected tree species distribution and community composition, though the dominant species were not changed for each ecoregion. Reduction of tree species richness commonly occurred in lower and mid-elevational ecoregions under RCP8.5 scenario, indicating that climate change may drive tree species to shrink to smaller suitable habitats. However, we did not see evident upward migration of tree species, probably because the climate change-induced adaptational lag surpassed the ranges that species could migrate in finite simulation duration. Moreover, the spatial range of our ecoregions was another factor that may limit our ability to detect species upward migration. The elevational range of each ecoregion is about 300 m, whereas the upward migration rate of plant species is only about 20 m per decade (Kelly and Goulden 2008, Parolo and Rossi 2008). Finer division at altitudinal ecoregions could be more efficient in exploring tree species upward migration (Bennie et al. 2013).

**Implications on forest management**

Our simulation showed expansions of several species under the current BAU management, especially for relic species and protected species. For instance, L. chinense, a relic species that was firmly protected in all ecoregions, could occupy the opened spaces created by the BAU management, showing continuous expansion throughout the simulation period. However, our research suggests that continuous BAU management may potentially weaken the ability of the BDGS forests to maintain biodiversity over time, because logging ban in the BDGS reserve will form closed forests dominated by shade-tolerant species, which could limit establishment of shade-intolerant species in the higher elevation ecoregions. In our simulation, shade-intolerant species like Betula insignis, D. involucrata, and Magnolia officinalis maintained little abundance and tended to become rarer in all climate scenarios, mainly due to the closed canopy caused by
current management. Undisturbed or least-disturbed forests with closed canopy were indicated to have lower species diversity (Molino and Sabatier 2001, Biswas and Mallik 2010, Shrestha et al. 2013), compared to the forests under intermediate disturbance that could open the closed canopy and provide light and spaces for shade-intolerant species. Thus, the traditional BAU forest management strategies may not match the expectation of long-term biodiversity conservation in the BDGS reserve, especially when considering future climate change. Moderate thinning of relic and shade-tolerant species in the logging ban areas could provide establishment spaces for early successional species, potentially promoting biodiversity conservation (Kerr 1999, Ares et al. 2010, Schweitzer and Dey 2011, Zhou et al. 2016). Our research also discovered that the BAU management performed poorly in maintaining forest biomass under future climate change, especially in the lower ecoregions. About 45% reduction of live biomass in SZ101 under RCP8.5 indicated that the current BAU management may be inappropriate for future forest production and carbon stock in the face of severe climate change. Severe warming caused extremely low species establishment probabilities. As a result, most native tree species except warm species could hardly establish or regenerate in the lower ecoregions, which means that these temperature-sensitive areas could not provide sustainable forest production under current BAU management. Finding alternative harvesting protocols and reducing deforestation (Swanson 2009, Gustafson et al. 2011, Temperli et al. 2012, Duveneck et al. 2014a, Schelhaas et al. 2015) in the lower ecoregions are probably better practices to mitigate forest decline caused by climate change. Another way to alleviate decline in forest biomass is to take advantage of the warm species mentioned above. Planting warm species to partly replace conventional afforestation tree species may promote forest resistance to high temperature and drought (Duveneck and Scheller 2015, Hof et al. 2017). Therefore, we suggest that the BAU management, as a long-term forest management strategy to maintain forest productivity and biodiversity, should be revised to address these issues. Furthermore, given that most forest management strategies at present were developed without considering climate warming, we recommend efficiency assessment of the current management regimes to cope with future climate change.

Uncertainties and limitations

Here, we took main factors into consideration in the simulation, including future climate change, species competition, seed dispersal, and anthropogenic disturbance (BAU management). However, uncertainties in this simulation are inevitable due to data limitations. For instance, (1) the projected climate scenarios caused the largest uncertainty in long-term climate change simulations (Allen et al. 2000, Knutti and Sedlacek 2013). (2) We did not model natural disturbance (e.g., wildfire, windthrow, and insect outbreaks), which generally play a critical role in forest landscape succession (Newton et al. 2011, Lucasch et al. 2018). Particularly, rising temperature and altered precipitation patterns may trigger wildfire, and pest and disease outbreaks in the future (Seidl et al. 2017), although these natural disturbances are not frequent in the SZC forests. (3) Our simulation did not include the impacts of CO2 fertilization or ozone pollution on tree species growth (Isebrands et al. 2001, Pan et al. 2009, Hararuk et al. 2019). (4) The mountainous terrain in the SZC is much more complex than we modeled here. We only took altitude into consideration because the spatial resolution (100 m) in our simulation weakened other topographic factors (e.g., slope and aspect), and the data we obtained could not reflect slope- or aspect-related discrepancies (e.g., soil moisture, temperature, and established communities). (5) Although we considered temperature discrepancies along elevational gradients, we neglected the spatial heterogeneity in terms of precipitation. Projected climate change at regional scale, especially precipitation, can hardly be downscaled to reflect the heterogeneity at landscape scale. The actual precipitation in the higher mountains is larger than we modeled. Thus, our simulation results may overestimate soil moisture stress in the higher mountainous ecoregions. (6) The BDGS reserve in the SZC has high biodiversity and contains much tree species than we simulated. We only selected the dominant and important tree species to cut down redundant simulations. This, however, comes at the expense of reducing the evaluation accuracy at biodiversity. However, our goal was not to precisely predict carbon storage or
species distribution in response to climate change. Rather, we aimed to adequately simulate forest succession, comparing the relative importance of different processes simulated, and evaluating future trends in the face of climate change.

**Conclusions**

Our simulations illustrated the potential threats of future climate warming on forest growth and species establishment in the subtropical mountainous forested regions in central China. The results showed a fast-growing period of ecosystem carbon in the first 70 yr, regardless of climate regime, primarily due to the past extensive logging induced rapid forest regeneration and recovery. Moderate warming slightly increased forest C storage, while severe warming resulted in a dramatic decrease in ecosystem C pool, as a consequence of combined reductions in SOC, detrital C, and live C pools. In the lower ecoregions, the results of reduced live biomass and restrained species establishment indicated that forests with limited regeneration will suffer persistent decline in live biomass after the fast-growing stage. The Nature Reserve in the higher ecoregions could act as safe islands by providing suitable conditions for most tree species in the face of climate warming, but the logging ban caused higher canopy closure, which in turn could inhibit the growth and establishment of shade-intolerant species. The results also highlight the positive response of native warm species to climate warming and suggest that using them to replace some conventional coniferous plantation tree species would better mitigate the future climate change. In order to effectively mitigate the potential threats of climate change on the subtropical forested landscapes, improved management strategies considering sustainable forest production, and efficient carbon management should be presciently designed accordingly.

**Acknowledgments**

Funding was provided by the National Basic Research Program of China (973 Program) (2014CB954004) and the National Natural Science Foundation of China (31700462 and 31870465). We would like to thank Dr. David Bell and the anonymous reviewers for their constructive comments on this manuscript.

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