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RESEARCH ARTICLE

Future forest dynamics under climate change, land use change, and harvest in subtropical forests in Southern China

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Abstract
Context Subtropical forests have and will continue to face tremendous pressure from various disturbances, which have the potential to alter forest composition, structure, and function. Forest dynamics relate to spatial patterns, ecological processes, and their interactions. However, integrating forest ecosystems and land systems has seldom been attempted in southern China.
Objectives We explore the spatiotemporal response and trajectories of forest dynamics at different scales under climate change, harvesting, and land-use disturbances in the near future.
Methods We simulated forest landscape dynamics by integrating a forest landscape model (LANDIS-II), an ecosystem model (PnET-II), and a land change model (CA-Markov) for 2010 to 2050. We identified changes in forest composition, aboveground biomass, and landscape patterns under individual and integrated scenarios, including a control scenario, climate change, harvesting, and land-use change for tree species, ecoregions, and forest types.
Results For forest composition, the forest area continued to increase, and coniferous forests increased approximately 3.7 times that of broad-leaved forests. Harvesting reduced aboveground biomass, with a reduction of 30.3% in comparison to the control scenario. The integrated disturbances showed a greater impact on the forest landscape. Landscape fragmentation increased, showing that the patch density increased by 52.3% (control scenario), 46.2% (climate change), 118.4% (harvest), 55.0% (land use change) and 139.5% (integrated scenarios), respectively.
Conclusions Our results suggest that climate change will contribute to forest growth, especially for coniferous forests. Harvesting will reduce forest area and aboveground biomass. The interaction between human activities and climate change contributes to diminished forest expansion and increased landscape fragmentation.

Keywords Forest dynamics · Forest disturbances · Climate change · Land use · Model integration · Subtropical forests

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Introduction

Global forests are under tremendous pressure from various natural and anthropogenic disturbances (Espírito-Santo et al. 2014; Seidl et al. 2017) that have led to forest loss and degradation over the past 25 years (FAO 2016; Houghton and Nassikas 2018). These multiple, complex disturbances affect the structure, composition, and function of forest ecosystems at the community and population levels (Dale et al. 2001; Wardle et al. 2011; Giam 2017) and threaten the continuous provision of ecosystem services at local, landscape, and global scales (Seidl et al. 2016). Moreover, increases in population and demand for land resources will result in further deforestation and conversion of forested areas in the near future (Rudel et al. 2005; Drummond and Loveland 2010). The landscape scale is very suitable for addressing the cumulative effects of various disturbances in forests, and landscape dynamics can be used to explore the interactions between spatial patterns and ecological processes in forest ecosystems and to inform strategies for forest management (Azevedo et al. 2014). In fact, many studies have paid considerable attention to relatively long-term trends in forest landscapes (He et al. 2017). However, applying the most recent information about the range of possible impacts on forest landscapes as well as their larger ecological consequences will also be critical for landscape management and planning in the near future, especially in areas with high forest coverage, rapid increases in population, and rapid economic development.

Forests in southern China are typically subtropical, serving as an important base for forestry and hosting vast tree plantations (Ma et al. 2016). In southern China, climatic conditions play an important role in the formation of the forested biome, and the region is home to many tree species and forest types, such as subtropical coniferous forests, deciduous forests, and evergreen broad-leaved forests. These forests are important for maintaining the carbon balance, as most species cycle large amounts of water and carbon, which leads to high productivity in this area (Wen et al. 2006; Li et al. 2018). However, the composition, distribution, and successional trajectory in modern subtropical forests are highly impacted by human activities. Especially in the hilly red soil region, subtropical forests have experienced unprecedented and extensive deforestation, which resulted in the rapid loss of forest cover during the latter half of the twentieth century. However, in the beginning of the twenty-first century, the Chinese government implemented a series of policies aimed at large-scale forest restoration and conservation, including the Natural Forest Conservation Program and the Grain for Green program (Chen et al. 2015). Although there has been massive investment and effective execution of these policies, which have contributed to increases in forest cover at the national level, some areas are still experiencing a large amount of forest loss due to rapid increases in urban sprawl and lumber demands (Seto et al. 2012; Viña et al. 2016). In addition, recent studies have shown that, the risks to forests posed by climate change (CC) will mostly be concentrated in the southern subtropical and tropical regions of China, risks which are particularly notable under the high-emissions scenario Representative Concentration Pathway (RCP) 8.5 (Scholze et al. 2006; Yin et al. 2018). Therefore, it is necessary to carry out sustainable forest management and recovery modeling under complex disturbances for subtropical forest.

Forest disturbances induced by natural and human activities are complex and interacting (Seidl et al. 2017). The sensitivity of forests to CC has been well studied, in terms of spatial distribution, biomass aggregation, and other indirect influences (Dale et al. 2001; Schuur 2003). Studies have shown that most forests are sensitive to the shift in spatial distribution and composition in response to global CC (Parmesan and Yohe 2003; Kelly and Goulden 2008). In addition, variations in temperature, precipitation, and CO_2 concentrations will alter the net primary productivity and carbon stocks of regional forests (Norby et al. 2005). Although these changes are more prominent in boreal forests, tropical and subtropical forests are also sensitive to ongoing CC (Giam 2017). Human activities affect forest landscapes mainly through the two most prevalent land use disturbances: forest transitions and deforestation. Unlike the effects of CC, the conversion of forests to agriculture and urban land have more immediate ecological impacts (Wu et al. 2017a). Land use change, such as urban sprawl and road construction, leads to habitat fragmentation (Lai et al. 2009; Sheng et al. 2010). Timber harvest is another primary forest management activity, and alternative forest management practices have a remarkable effect on the forest landscape. For example, the size, shape, and cycle of harvesting units influences habitat connectivity and fragmentation, which determines the forest pattern as well as critical ecosystem functions (Fraser et al. 2013). However, forest disturbance regimes are dynamic and occur dependently (Scheller and Mladenoff 2005; Wu et al. 2017b). Specifically, changes in land use patterns affect forest dynamics through their interaction with forest management practices and a changing climate (Thompson et al. 2011). Therefore, it is important to explore the degree to which future forest dynamics will change under multiple disturbances.

Quantifying simulated forest dynamics under various disturbances is a challenging but critical task, which is progressing toward methods with increased detail, complexity, and spatial extent (Shifley et al. 2017). On one hand, forest dynamic change is complicated and systematic. Changes in forest composition result in changes in forest landscape patterns and affect forest function (Grimm et al. 2013; Robinson et al. 2013). On the other hand, most forest changes that arise from interactions between human and natural systems are complex (Liu et al. 2007). Spatial simulation modeling is an important technique for exploring the effects of coupled natural and human processes in forested landscapes (Wimberly et al. 2012). Forest landscape models (FLMs) and land change models (LCMs) are two key classes of models that can be used to analyze natural and anthropogenic disturbances (He et al. 2017). Through integration or coupling, these models can simulate disturbance events, reconstruct historical landscape patterns, and project future forest composition and ecosystem services under different scenarios. FLMs, such as LANDIS-II, focus on landscapes where forests are the dominant land cover, and have been widely applied to examine the influence of disturbances on long-term broad-scale dynamic changes in forest ecosystems (Scheller et al. 2007). However, FLMs are not well-suited to simulating land-use change (Thompson et al. 2016). In contrast, LCMs can simulate transitions between forests and other categories (Azizi et al. 2016). In previous studies, FLM and LCM models have been combined to project forest landscape dynamics. Syphard et al. (2007) integrated a forest landscape model (LANDIS) with an urban growth model to simulate the effects of urban development and disturbances from fires on the distribution of vegetation in southern California, United States. They focused primarily on the expansion of the wildland-urban interface. Similarly, Thompson et al. (2011) coupled LANDIS-II with a method for assessing land use change to simulate future scenarios for regional land use and harvesting dynamics in Massachusetts, United States. Their simulation showed that increases in forest biomass due to CC were more than offset by land use change from primarily forest conversion to urban uses. Following this study, they developed an extension for the LANDIS-II model to further integrate spatially and temporally explicit representations of land use and other forest disturbances into simulations (Thompson et al. 2016). These studies indicate that the integrated landscape modeling approach is an effective way to analyze many complex forest dynamics, which may have the potential to aid in conservation strategies, and to sustain the development of local communities.

Our objectives are to project forest dynamics under CC, harvesting, and land use change disturbances in the subtropical areas of China. We aim to answer the following questions: How will the forest composition, aboveground biomass (AGB), and landscape patterns change under CC, harvesting, and land use change disturbances in the near future? Is there a difference in the responses of different forest types to CC and various disturbances? What are the interactions between CC, harvesting, and land use change disturbances at the landscape scale? Moreover, from the perspective of natural restoration, we will explore the major effects of different ecological processes and disturbances on different ecological regions, and then provide relevant measures and suggestions for sustainable forest management. In order to answer these questions, we used the LANDIS-II forest landscape model, the PnET-II forest ecosystem process model, and the CA-Markov land change model using loose coupling to simulate spatial interactions under alternative scenarios from 2010 to 2050.

Methods

Study area

We simulated forest composition, AGB, and changes in landscape patterns within Taihe County (26.45°N–26.98°N, 114.95°E–115.33°E), located in the south-central Jiangxi Province of southern China (Fig. 1).

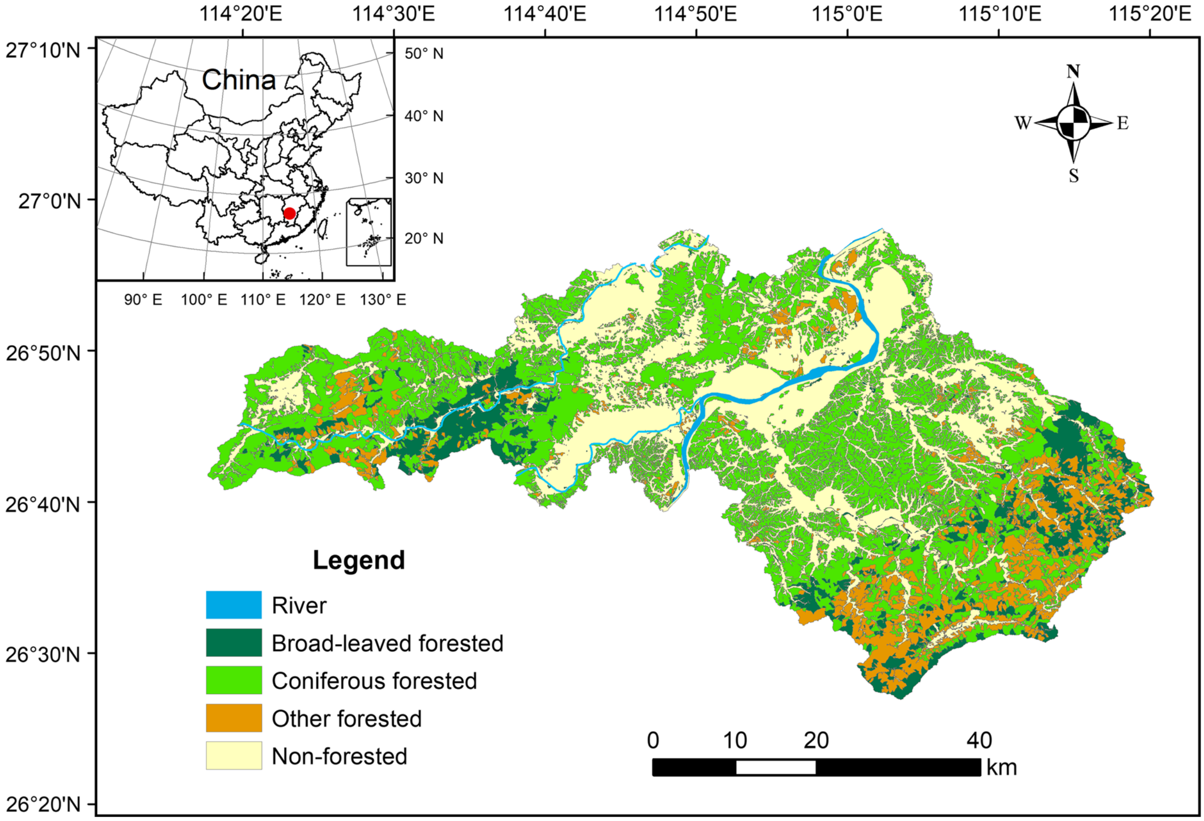

Fig. 1 Location and forest landscape types of the study area

The total area of Taihe County is 266,700 ha, with forest covering approximately 62% of the total area. The topography is characterized by rolling hilly terrain, with elevations ranging between 9 and 1129 m. Soils are fairly homogeneous and are dominated by red soil (South Hilly Scientific Expedition, Chinese Academy of Sciences 1982). The region has a subtropical monsoon climate with mild winters (the mean January temperature is 6.5 °C) and warm summers (the mean July temperature is 29.7 °C). The mean annual precipitation is ~ 1400 mm, with approximately 60% of precipitation falling between March and June (Wu et al. 2017b). In the last 5 years, the population of Taihe County increased by roughly 37,700 people (6.73%), while the GDP of the county increased from 100.48 billion yuan in 2012 to 167.87 billion yuan in 2017. In the context of this growth, the annual production value from forestry increased by 2.5 times, from 2.46 billion yuan in 2012 to 6.15 billion yuan in 2017 (Statistics Bureau of Taihe County 2013b, 2018). Rapid regional economic development accelerated the expansion of urban built-up land; this is evident in the trend in building construction area, which increased by 6.6 times, from 177,000 to 1175,700 m^2 over the last 5 years (Statistics Bureau of Taihe County 2013b, 2018).

The forest landscape is characterized by subtropical coniferous and broadleaved forests, which include 18 abundant tree species. The subtropical coniferous forests are comprised of masson pine (*Pinus massoniana*), slash pine (*Pinus elliottii*), Chinese fir (*Cunninghamia lanceolata*), and Chinese weeping cypress (*Cupressus funebris*). The broadleaved forests include camphor tree (*Cinnamomum camphora*), zhennan (*Phoebe zhennan*), crenate gugertree (*Schima superba*), beautiful sweetgum (*Liquidambar formosana*), Chinese sassafras (*Sassafras tzumu*), evergreen chinkapin (*Castanopsis eyrei*), myrsinaleaf oak (*Cyclobalanopsis gracilis*), fortune chinabells (*Alniphyllum fortunei*), farges evergreen chinkapin (*Castanopsis fargesii*), longpeduncled alder (*Alnus cremastogyne*), faber oak (*Quercus fabri*), shinybark birch (*Betula luminifera*), chinaberry (*Melia azedarach*), and poplar (*Populus deltoids*). In addition, there are a few other forest types found in the region, such as bamboo and forests comprised of economically productive tree species, for example orange trees and tea bushes. These types were not considered in our simulation because of their distinct physiological features and specific management practices in comparison to the dominant tree species. Owing to anthropogenic disturbances, the forest landscape has experienced many cycles of decreases in size followed by recovery during the past half century. In the early 1950s, forest cover accounted for 55% of the land area, however forest cover dropped to its lowest point at 31.3% in 1980 due to unrestrained logging that began in the 1960s. Following this, a series of forest protection policies were implemented, which were then organized by state-owned forestry farms (Editorial Committee of Chorography of Taihe County 2013). According to forest inventory data published in 2010, planted forest cover expanded, and the forest coverage recovered to 61.2%. The subtropical coniferous plantations became dominated by masson pine, slash pine, and Chinese fir, which covered 112,608 ha and were mostly distributed in the flatland area of the basin.

We selected this specific study area, Taihe County, as an appropriate area to study the forest landscape dynamics for several reasons. Firstly, the natural conditions of our study area are regionally representative of subtropical forests in southern China. Climatic conditions (subtropical monsoon climate), soil texture (red soil) and landforms (hills) are the most typical physical geographical features in this region. Moreover, the study area has the most common tree species and important forest types (broad-leaved forests and coniferous forests) in southern China (Liu et al. 2014b). The forest coverage rate is high. Lastly, a large area of plantations were harvested and managed by local forestry farms. Harvesting is the main cause of forest disturbance. Furthermore, the rapid economic development and population growth in our study area have gradually brought about conflicts between forest land and non-forested land, especially for urban construction land. In summary, we believe that this study area is appropriate for addressing the research questions posed by this study, and may therefore yield results that are beneficial for the subtropical forests in southern China.

Climate data

To simulate future changes in forest landscape dynamics, we considered both current climactic conditions as well as a high-emissions CC scenario (RCP 8.5). In the scenario without CC, the averages for monthly temperature and precipitation data were provided by the local meteorological station and compiled for a 30-year period (1980–2010) for our study area (http://data.cma.cn/). We assumed that the climate would stabilize after the initial simulation year. For the scenario accounting for CC, we used a high-emissions projection for 2010 to 2050. The CC scenario downscaled climate data based on RCP 8.5 (Riahi et al. 2011). The RCP 8.5 simulations were carried out using the Coupled Model Intercomparison Project Phase 5 (CMIP5) framework proposed by the World Climate Research Programme (IPCC 2013). In this study, the RCP 8.5 projections were interpolated to a smaller grid of 30 arc seconds, or approximately 1 km by the MarkSimGCM weather generator (http://gisweb.ciat.cgiar.org/MarkSimGCM/). We used monthly downscaled projections of maximum temperature, minimum temperature, and precipitation from 17 general circulation models (GCMs) to produce the average. Based on this, we predicted an approximate 2.0 °C increase in monthly maximum and minimum temperatures, and a 53 cm increase in annual precipitation by the year 2050. CO_2 concentrations were derived from the RCP Database (http://tntcat.iiasa.ac.at:8787/RcpDb). In the scenario without CC, we assumed that CO_2 remained constant at 388.82 ppm. In the scenario accounting for CC, CO_2 concentrations increased linearly to 544.04 ppm by the year 2050. The photosynthetically active radiation (PAR) observation data was derived from the Qianyanzhou ecological station and the Chinese FLUX Observation and Research Network (http://www.chinaflux.org/enn/). Because there was low rate of PAR change ($<$ 5%/10a) in our study area between 1961 and 2007 (Zhu et al. 2010), we hypothesized that the PAR remained unchanged in both scenarios.

Simulation models and parameterization

We simulated forest dynamics by integrating a spatially interactive landscape model, LANDIS-II v6.1 (Scheller et al. 2007) (http://www.landis-ii.org/), with the PnET-II v5.1 ecosystem process model (Aber and Federer 1992; Aber and Driscoll 1997), and the CA-Markov land use and land cover change model. LANDIS-II is a cell-based spatially dynamic forest landscape model that simulates disturbances, seed dispersal, and forest succession (Scheller et al. 2007). LANDIS-II is designed for simulating forest landscape changes over mesoscales (10^4–10^7 ha) by tracking species-age cohorts (Mladenoff and He 1999). The cell resolution was set to 100 m. Within each cell, competition between cohorts and biomass accumulation was driven by unique species life-history attributes—specifically, the species establishment probability (SEP), the maximum aboveground net primary production (ANPP), and spatial heterogeneity and disturbances. The community composition of the forests was initialized using data from a forestry resource survey gathered by a sub-compartment division of Jiangxi Province in 2010 that included 61 forest communities.

The landscape was divided into an inactive region and four ecoregions with similar ecological conditions within the study area (Fig. 2). The inactive region was non-forested land or bamboo and economic forests. These four ecoregions were divided by geomorphic properties under different elevations, which closely related to tree species growth and distribution. Ecoregions 1 to 4 were divided by elevation gradients, represented as small hills (under 100 m), medium hills (100–250 m), high hills (250–500 m), and mountains (above 500 m), respectively. In terms of natural conditions, temperature that decreased with increasing elevation was the dominant climatic factor affecting ANPP in our study area (Dai et al. 2015a). Thus, the ecoregions under different elevations are assumed to be homogenous in terms of climatic conditions. In terms of human activities, the landform conditions under different elevations also affect land use and specific planting practices, and then affect ecological processes, such as succession and disturbances.

Furthermore, the 18 most abundant tree species were included in the modeling. The parameters selected related to the attributes of the species life history that were obtained from a literature review (He and Liu 1989; Editorial Committee of Forest of China 2000; Mi et al. 2008; Dai et al. 2016; Ma et al. 2016), as well as from plot investigations, and in consultation

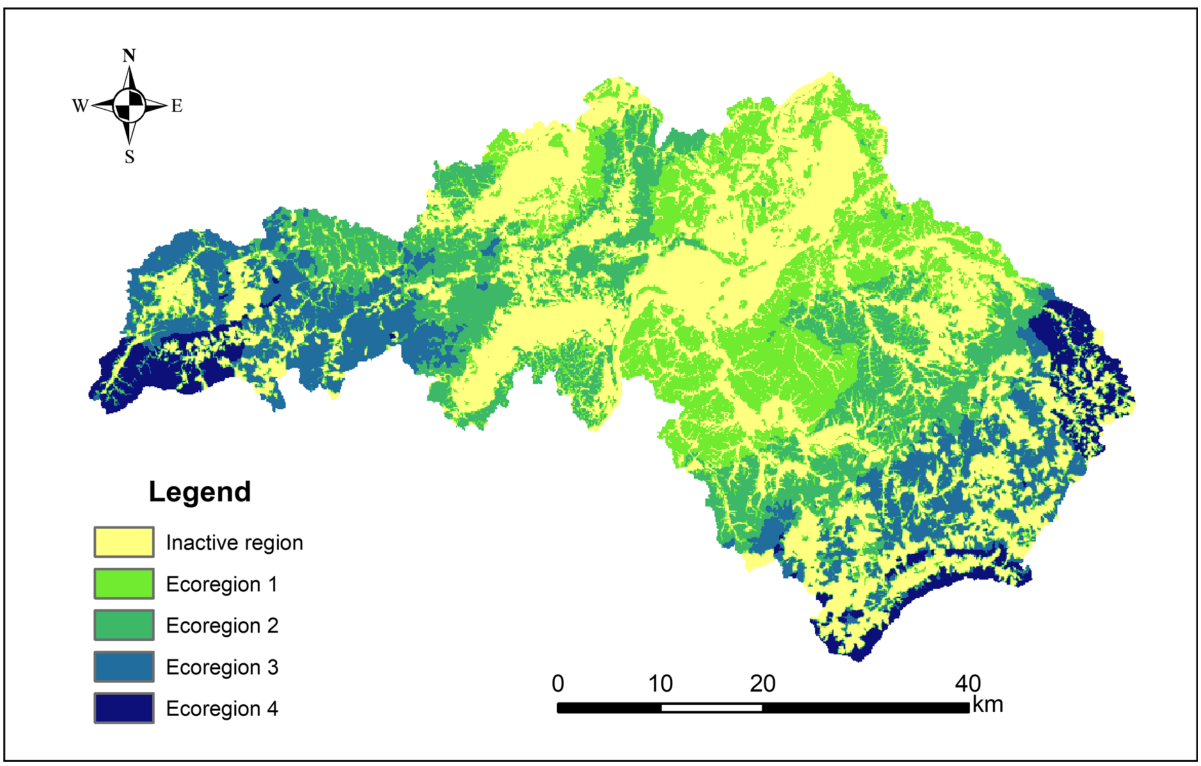

Fig. 2 Ecoregions for the study area

with local experts in forest ecology (Table 1). The ANPP and SEP inputs for LANDIS-II were initialized using the PnET-II model for each tree species in each ecoregion.

There are several options for the succession and disturbance modules included in LANDIS-II. We selected 5-year time steps to project the effect of CC, harvesting and land use change on the forest landscape. We used the Biomass Succession v3.2 extension to simulate natural forest succession by calculating competition among cohorts, the gain and loss of living and dead biomass, seed dispersal, and the process of seedling establishment (Scheller and Mladenoff 2004). The succession extension employed an ANPP that was calculated using PnET-II for each species to simulate cohort biomass accumulation. PnET-II is a process-based model used for carbon and water balance in forest ecosystems (Aber and Federer 1992). This model can simulate changes in ANPP due to climate by applying adjustable factors, including light (dependent on the input of PAR), temperature (dependent on the temperature input), water availability (dependent on the precipitation input), the water vapor deficit, and CO_2 concentration.

By coupling the PnET-II with the Biomass Succession extension of LANDIS-II, we could also address the effects of CC on forest succession. We calculated the ANPP and SEP using PnET-II (Xu et al. 2009)

Table 1 Species life history attributes for species simulated within the study area based on Dai et al. (2016) and Wu et al. (2017a, b)

Species	Common name	Longevity (years)	Sexual maturity (years)	Shade tolerance	Seed dispersal effective distance (m)	Seed dispersal maximum distance (m)	Vegetative reproduction probability
Cunninghamia lanceolata	Chinese fir	200	10	1	200	500	0.6
Cupressus funebris	Chinese weeping cypress	500	35	2	70	200	0.4
Pinus massoniana	Masson pine	200	10	1	200	500	–
Pinus elliottii	Slash pine	200	10	1	200	500	–
Schima superba	Crenate gugertree	300	20	5	20	200	0.6
Cinnamomum camphora	Camphor tree	1000	15	4	50	120	0.5
Phoebe zhennan	Zhennan	1000	50	5	40	120	0.5
Castanopsis eyrei	Ever evergreenchinkapin	200	20	5	50	120	0.6
Castanopsis fargesii	Farges evergreenchinkapin	150	30	5	60	250	0.6
Quercus fabri	Faber oak	120	15	4	20	200	0.6
Cyclobalanopsis multinervis	Myrsinaleaf oak	200	7	4	20	50	0.4
Liquidambar formosana	Beautiful sweetgum	130	8	3	100	375	0.8
Betula luminifera	Shinybark birch	100	15	2	150	400	0.5
Alnus cremastogyne	Longpeduncled alder	125	5	3	15	60	0.5
Alniphyllum fortunei	Fortune Chinabells	120	15	2	250	500	0.4
Sassafras tzumu	Chinese sassafras	120	20	3	50	150	0.5
Melia azedarach	Chinaberry	80	5	2	200	400	0.3
Populus	Poplar	90	10	2	150	500	0.5

under CC scenario RCP 8.5 and given current climate conditions. The parameters selected for the PnET-II were based on inputs for each species, and environmental factors were acquired from a literature review and via observation. The site-specific water-holding capacity (WHC) was obtained from the Qianyanzhou ecological station. The species-specific parameters were obtained from previous studies; these included foliar nitrogen concentration (FolNCon) (Yu et al. 2014), the minimum temperature for photosynthesis (PsnTMin) (China 2000; Wu 1984), the optimum temperature for photosynthesis (PsnTOpt) (He and Liu 1989), and water use efficiency (WUE) (Sheng et al. 2011).

Timber harvesting was simulated using the Biomass Harvest v3.0 extension (Gustafson et al. 2000). The forest landscape was divided into management areas, which were comprised of collections of stands with specific harvesting prescriptions. These various prescriptions were stochastically selected and determined which stands qualified for harvest and defined the order in which stands would be harvested. Separate prescription rankings were derived for each management area, beginning with harvesting in the highest ranked stand and proceeding down the ranked list of stands until the percentage of area in the management area had been cut. In our simulation, there were five forest management areas (Appendix I in supplementary material), and the corresponding harvest prescriptions were derived from the local forest management policies. Several harvesting criteria were set for each management area, including the percentage of harvesting area, stand rankings, harvesting minimum ages and harvesting species. Specifically, the forest landscape harvested 5% of forest area per 5 years for each management area. Stands within each management area were harvested in rank order with three types: economic importance, random and maximum cohort age. For economic importance, slash pine was assigned a relative higher economic value than masson pine, which indicated that slash pine was set at highest priority for harvest in that management area. For random, stands in a management area were randomly selected for harvest. For the maximum cohort age, the oldest stands were harvested first in a management area. In term of harvesting minimum ages, the harvesting events occurred until the specific tree species reached the age of economic maturity, which was the minimum age of merchantability. The specific harvested tree species for each management area are given in Table 2. Some locally protected species, such as camphor tree and zhennan, were not chosen to harvest. In addition, no planting was simulated. The specific harvesting prescriptions are shown in Table 2.

Forest conversion was simulated using the Land Use Plus (LU +) version 1.1 extension (Thompson et al. 2016). LU + is a disturbances extension that is compatible with the Biomass Succession extension, which results in representations of corresponding land use and changes in AGB. LU + can integrate independently-derived maps that depict land use or land cover change into the LANDIS-II simulations. The extension requires a series of categorical or thematic raster maps, where the map codes represent land use types. We used the CA-Markov model to conduct the simulation for land-use change to generate the thematic raster maps. The forest conversion sites were delineated between two time steps for the land use and land cover map.

We used the CA-Markov module in the IDRISI 17.0 software package (Clark Labs 2006) to simulate and ultimately predict changes in future spatial–temporal patterns of land use. To parameterize the CA-Markov model, land-use survey datasets for 2005 and 2010 were used as the initial inputs to determine the transition rules for predicting the land-use patterns in the near future. This geospatial data was obtained from the land and resources survey from the department of land and resources in Jiangxi Province, China. The land use maps were created for every 5 years for 2015–2050, and were used as the inputs for the LU + extension in LANDIS-II. We also designed two scenarios for land use change by modifying the transfer matrix, specifically current land use and a rapid urban development scenario. The transfer matrix for the current land use scenario was derived from actual land survey data. From 2005 to 2010, built-up land increased from 15,484 to 15,913 ha. According to the general plans for land use in Taihe County, the built-up land area will reach 17,173 ha by the year 2020, and the rate of urban expansion will be 1.5 times the current scenario. We assumed a relatively more extreme urban development scenario in which the expansion rate of built-up land would be double that of the current land use scenario. Once a site was allocated as converted to built-up land, that site was restricted to converted land and could not revert back to forest at a later time.

Table 2 Forest harvesting prescriptions in different management area

Management areas	Harvesting area (%)	Stand rankings	Harvesting minimum ages (year)	Harvesting species
I	5	Economic importance	15	Slash pine
				Masson pine
II	5	Maximum cohort age	15	Chinese fir
III	5	Maximum cohort age	20	Crenate gugertree
				Ever evergreenchinkapin
				Farges evergreenchinkapin
				Faber oak
				Myrsinaleaf oak
				Beautiful sweetgum
				Shinybark birch
				Longpeduncled alder
IV	5	Random	15	Clear cut
V	5	Maximum cohort age	50	Ever evergreenchinkapin
				Farges evergreenchinkapin

Calibration and validation

Quantitative validation for a modeling study given large spatial scales and long time periods may be challenging, especially in terms of projections for future conditions (Dai et al. 2015b). In this study, we both calibrated and assessed the behavior of the model by comparing the initial conditions through a literature review, field data, and in consultation with forestry experts. Furthermore, the outputs of ANPP based on PnET-II were compared with a previous study we conducted, which used the CASA simulation model (Dai et al. 2015a). The results of the different forest types were generally consistent for the first year. In the land use simulation, the spatial consistency was checked using the Kappa spatial correlation statistic (0.9287) between the actual and simulated maps of the 2010 land use categories. In LANDIS-II, the AGB, age structure, and forest composition in the initial year was evaluated by comparing simulated data with the results of previous simulation studies (Dai et al. 2016). In addition, the model harvesting scenario was consistent with local expert opinion and local forestry administration.

Experimental design

We simulated forest landscape change for a 40-year period (from 2010 to 2050), using one control scenario and six disturbance scenarios. We simulated forest dynamics for only 40 years by considering the tradeoff of temporal effects between land use and CC. Land use changes are greatly affected by policy that may change with the regional economy, population, and other environmental factors. Longer simulation times will result in an increase in uncertainty. However, it is worth noting that this period can also reflect an overall trend of CC in the near future. The alternative scenarios included three aspects: CC, direct anthropogenic disturbances, and integrated disturbances. Specifically, the scenarios were: (a) control scenario (CS), (b) CC, (c) harvesting (Harv.), (d) current land use (CLU), (e) rapid development of urban land use (RLU), (f) climate change-harvest-current land use (CC-Harv.-CLU) and (g) climate change-harvest-rapid development of urban land use (CC-Harv.-RLU). The CS was set to simulate natural forest succession under current climate conditions without disturbances. The RCP 8.5 scenario was used to depict CC. The simulation results were output in 5 year time steps to examine the effects of CC, harvesting, and land use change, as well as AGB and landscape patterns.

We simulated the eighteen predominant species in the integrated PnET-II and LANDIS-II model for four ecoregions. The outputs from the LANDIS-II were grouped into two forest types, specifically broad-leaved forests and coniferous forests, to assess the differences in response to various individual and collective disturbances. We analyzed the different responses of forest type, ecoregions, and species levels to disturbances in forest composition, AGB, and landscape patterns. To study how these natural and anthropogenic disturbances affect forest landscape patterns, the landscape was classified as consisting of eighteen tree species and non-forested land. The spatial pattern of the landscape and influence on the class level (species level) and landscape level were expressed by the patch density (PD), which reflects landscape fragmentation; the largest patch index (LPI), which reflects dominance and connectivity; and the aggregation index (AI), which reflects the potential responses of different species and the forest landscape to human activities.

Results

Forest composition

The results of our simulation showed that the area of different forest types continuously increased under all scenarios (Fig. 3 and Appendix II in supplementary material). On average, the area of coniferous forests increased was about 3.7 times that of broad-leaved forests among all scenarios. For broad-leaved forests, the forest area showed a 54% increase under the CS scenario between 2010 and 2050. CC was beneficial for the growth of broad-leaved forests, which increased from 21,475 to 33,084 ha (60% increase). Harvesting had little effect on broad-leaved forests, especially after 2030. The impact of land use change on broad-leaved forests was negligible, and no big differences were shown between the CLU and RLU scenarios. Under the integrated scenarios, the forest growth of broad-leaved forests first increased and then decreased before 2025. Subsequently, the forest area increased stably. The growth in forest area was much greater for coniferous forests than for broad-leaved forests, although the growth rate was generally slow after 2025. Under the CS scenario, the coniferous forests area increased by 48,062 ha, which was about four times greater than of broad-leaved forests. CC had little effect on the coniferous forest. Harvesting led to a loss of area for coniferous forests; in 2050, this type of forest was 17,893 ha smaller in area than the under the CC scenario. The effect of land use change on coniferous forests was more varied; the RLU scenario resulted in more forest land conversion than the CLU scenario.

In terms of the responses of different ecoregions, the changes in the forest area of four ecoregions between 2010 and 2050 are shown in Fig. 4. It was found that Ecoregion 1 had the most dramatic change in forest area, accounting for approximately half of the changes for all scenarios. The forest area under different scenarios showed different responses; the range between the lowest (CC + Harv. + RLU) and the highest (CC) area values of Ecoregion 1 was 13,023 ha in 2050. The change of forest area in

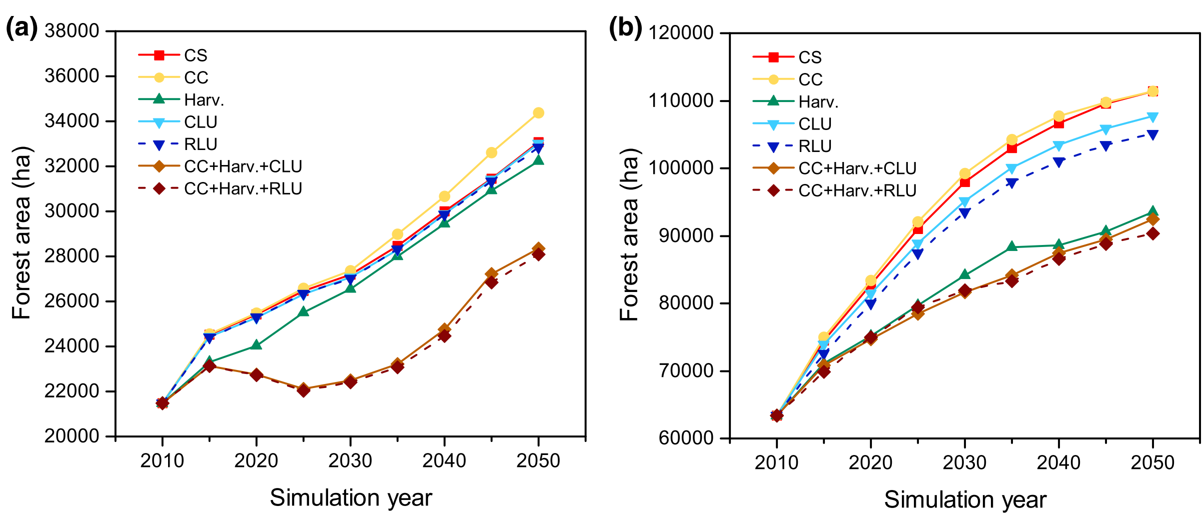

Fig. 3 Responses of forest area of broad-leaved forests (**a**) and coniferous forests (**b**) to multiple scenarios over the 40-year simulations

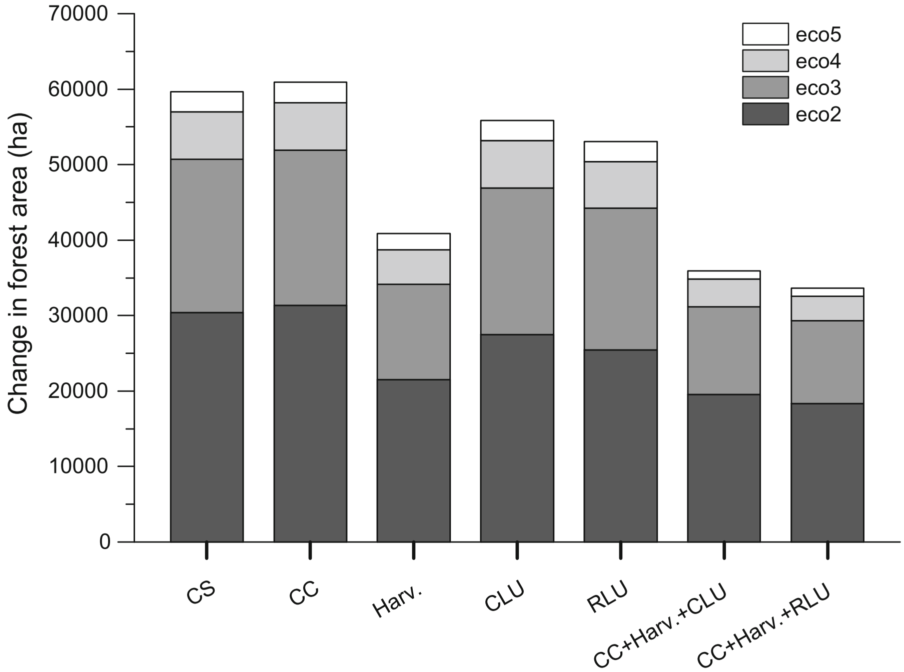

Fig. 4 Change in forest area for the four ecoregions under multiple scenarios between 2010 and 2050

Ecoregion 2 accounted for an average of 33.4% of change in forest area under all scenarios. The degree of forest area change gradually reduced in Ecoregion 3 and Ecoregion 4, accounting for 10.7% and 4.3% of the total forest area change, respectively.

The response of forest composition at the species level is shown in Fig. 5. We selected five representative tree species, which accounted for the majority of the tree area in 2010, to represent the change in forest area between 2010 and 2050. Chinese fir experienced an average increase of 18,101 ha under all scenarios.

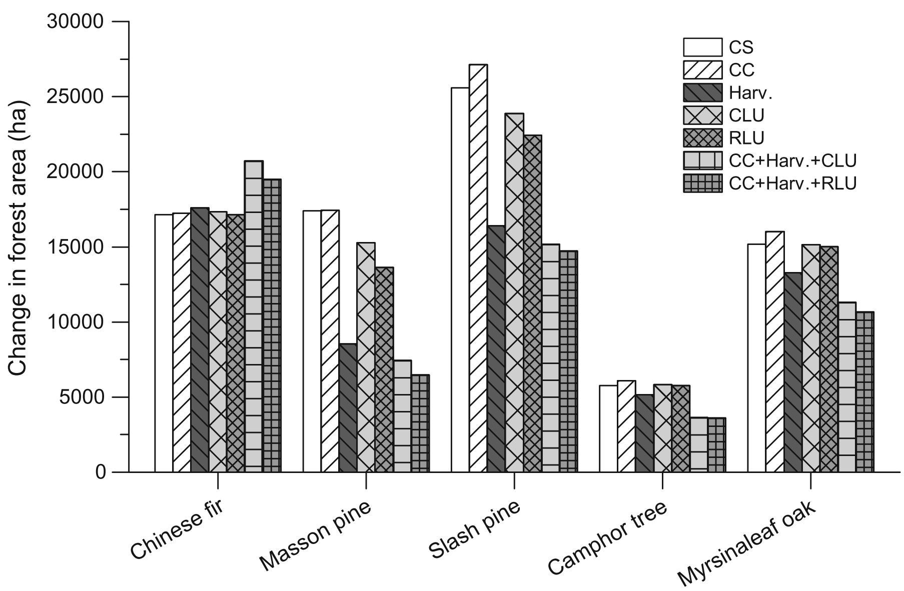

Fig. 5 Change in forest area of five important species under multiple scenarios between 2010 and 2050

In comparison to other species, it was not sensitive to disturbances; however, the area of Chinese fir under the integrated disturbances was larger than that under other scenarios. The largest increase in landscape presence was slash pine, which had an increase of 27,138 ha under the CC scenario and showed better resilience to CC under RCP 8.5. Harvesting had an important effect on the forest area of masson pine and slash pine, which were reduced 8842 ha and 9196 ha compared to the CS, respectively. Although not as extensive as harvesting, land use changes also had a certain impact on these two coniferous species. The converted forest area of masson pine and slash pine under RLU was greater than that under CLU, and the responses of camphor tree and myrsinaleaf oak to multiple disturbance scenarios were largely consistent. The integrated disturbances had a greater impact on forest composition.

Forest aboveground biomass

Forest AGB responded to harvesting and the integrated disturbances. The total forest AGB under Harv., CLU and RLU was 30.3%, 40.6% and 42.8% less than under the CS in 2050, respectively; as with forest composition, broad-leaved and coniferous forests exhibited divergent responses to multiple experimental scenarios (Fig. 6). Though the trend was consistent with the change in forest area, differences in the response existed, especially for broad-leaved forests. In the harvest scenario, the AGB of broad-leaved forests increased by 1.92 Tg during the simulation, and there was 1.86 Tg less than the CS at year 2050. The AGB of broad-leaved forests exhibited minimal changes under the integrated scenario in comparison to other scenarios, and during the period 2025–2040 was even less than the initial AGB. For coniferous forests, AGB was 0.25 Tg higher under the CC scenario than under the CS in 2050. The AGB of coniferous forests under the CLU and RLU scenarios increased by 109% and 103% in the period between 2010 and 2050, respectively. The results showed that the AGB of coniferous forests increased slightly with harvesting, from 4.31 Tg in 2010 to 6.40 Tg in 2050. Under the integrated scenario, AGB under the current land use scenario increased by 1.99 Tg (46%) from 2010 to 2050. With rapid urban development, AGB under the integrated scenario increased by 1.75 Tg (41%).

In terms of impacts in different ecoregions, the changes in forest AGB are shown in Appendix III in the supplementary material. Interestingly, Ecoregions 1 and 2 changed greatly during the simulation. CC had a positive effect on AGB in all ecoregions. Harvesting had the largest impact on Ecoregion 1 and the smallest impact on Ecoregion 4. Compared with the CS, the effect of land use mainly affected Ecoregion 1. In Ecoregion 4, AGB even decreased during the

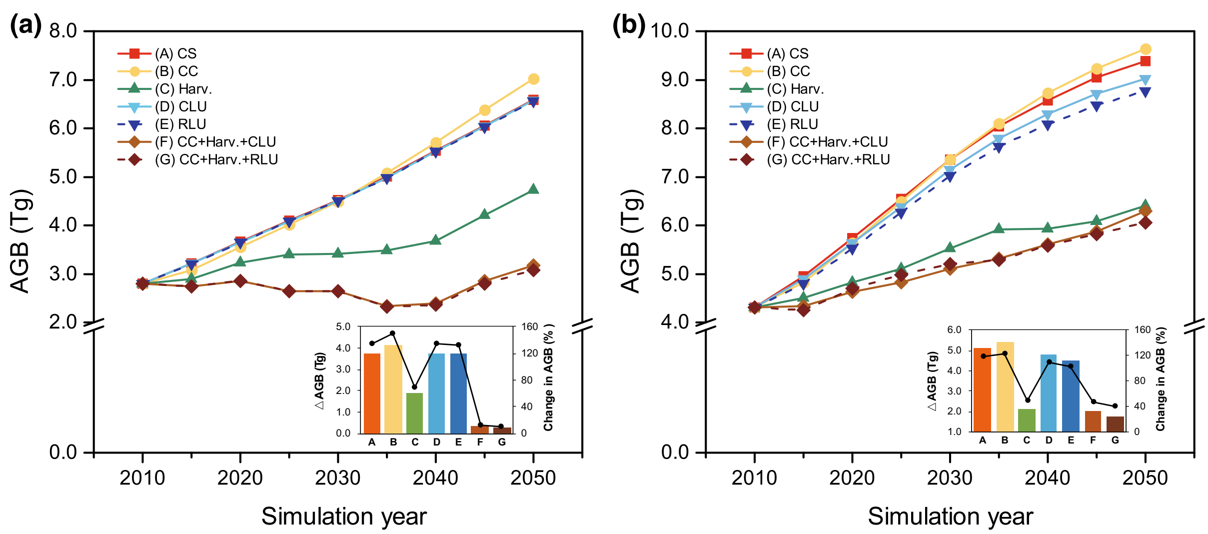

Fig. 6 Response of forest aboveground biomass of broad-leaved forests (a) and coniferous forests (b) to multiple scenarios from 2010 to 2050

simulation. At the species level, slash pine and myrsinaleaf oak had the most change in AGB, as shown in Fig. 7. For myrsinaleaf oak, AGB increased by 2.96 Tg under CC over the simulation period; in particular, the effect of the integrated disturbances was notable: 0.63 Tg under current land use and 0.56 Tg with rapid urban development. Different tree species responded more strongly to harvesting, with the exception of camphor tree. In addition, the changes in AGB for eighteen species are shown in Appendix IV in the supplementary material.

In terms of spatial distribution, AGB was spatially heterogeneous due to forest growth, succession, seed dispersal, and multiple disturbances between the initial biomass in 2010 and the simulated biomass in 2050 (Fig. 8). The spatial pattern of AGB was consistent with forest landscape types. The distribution area of broad-leaved forests had a higher AGB than any other landscape type for each disturbance scenario. In the central region, the increased AGB was due to the rapid growth of the coniferous plantation, which mainly represented masson pine and slash pine. The AGB in the west of the study area showed relatively lower value zones; these areas were mainly composed of Chinese fir. The land use change happened in the central region, where forest conversion took place. Harvesting reduced the AGB and increased spatial heterogeneity, especially in the central region. Compared with the CS, there was an appreciable reduction in the AGB of the overall forest landscape under the integrated disturbances.

Forest landscape pattern

The results for landscape-level metric changes in the study area are shown in Fig. 9. Between 2010 and 2050, PD increased over the simulation and showed different levels under different scenarios. Specifically, the PD increased by 52.3% (CS), 46.2% (CC), 118.4% (Harv.), 55.0% (the average of CLU and RLU), and 139.5% (the average of two integrated scenarios), respectively. It revealed that the degree of landscape fragmentation increased with the increase of human disturbances. The PD at the landscape level was most strongly influenced by harvesting, and was not sensitive to climate and land use change. As a result, the largest patch was non-forested land at the landscape level during the simulation, and the LPI showed a downward trend under all scenarios. The LPI at the landscape level was more sensitive to multiple disturbances, especially to land use change. Under the harvesting scenario, the LPI showed a fluctuation change, indicating the periodic effect on the forest landscape pattern. In terms of the AI, the results showed a downward trend, reflecting a declining tendency for similar landscape types to be adjacent,

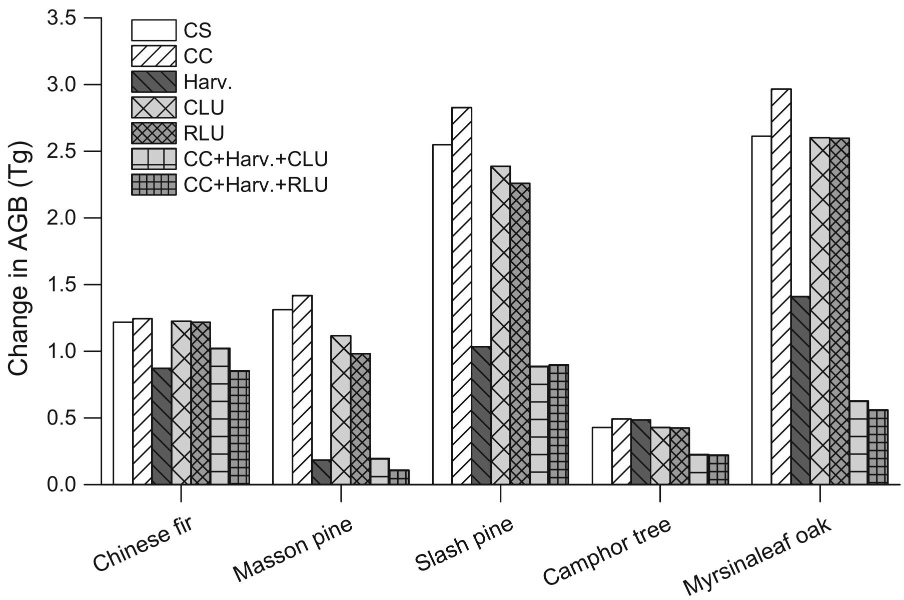

Fig. 7 Change in forest AGB for five important species under multiple scenarios between 2010 and 2050

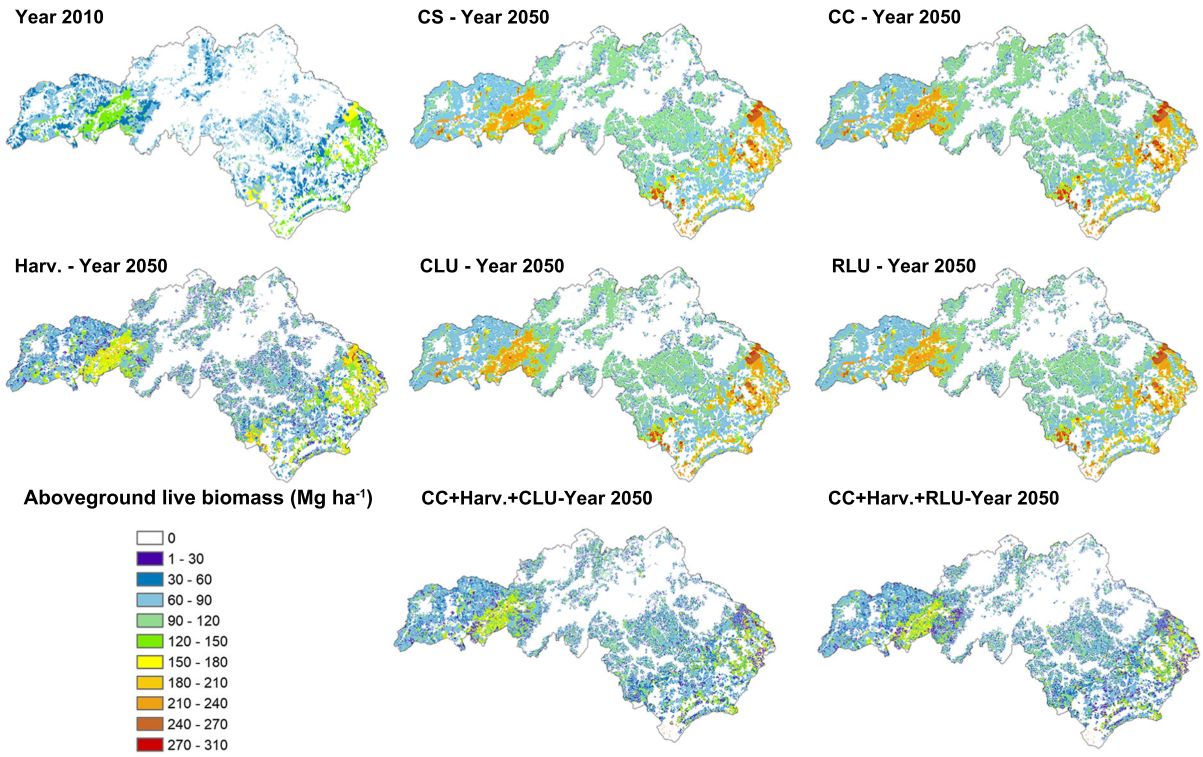

Fig. 8 Spatial distribution of forest aboveground biomass based on the response to climate change, harvest, and land use change scenarios in Taihe County

especially under the harvesting scenario. The AI showed the greatest decrease, from 86.01 to 76.53, under the integrated scenario; this indicates that different disturbances compounded landscape complexity and reduced connectivity between different tree species.

At the species level, the change in landscape metrics showed a more complex response between 2010 and 2050 (Appendix V in supplementary material). In terms of PD, the broad-leaved species, such as camphor tree, shinybark birch, Chinese sassafras, and chinaberry, showed a clearer increase than the coniferous tree species. In contrast, the PD for faber oak, myrsinaleaf oak, and poplar showed a slight decline. In terms of LPI, Chinese fir was insensitive to different disturbances, and showed an average 345% increase under all scenarios between 2010 and 2050. Slash pine and camphor tree responded strongly to the harvesting. For the AI, some broad-leaved tree species showed a dramatic decrease, such as shinybark birch, chinaberry, and evergreen chinkapin. Some tree species responded differently to multiple disturbances. Poplar was mainly affected by land use change, and showed an increase in AI under the CC and harvesting scenarios, but a decrease under the land use change and integrated scenarios.

Discussion

Forest landscape dynamics

Our simulation results individually and collectively described the response of forest composition, biomass, and landscape patterns to CC, harvesting, and land use change disturbances in the near future. In the absence of disturbances, the total forest area and AGB showed an increasing trend due to natural succession, indicating that the current climatic conditions of the study area may benefit forest growth and expansion in the near future. The early successional coniferous species, such as Chinese fir, masson pine, and slash pine, showed a greater range of expansion than the broad-leaved species, which can be explained by seed

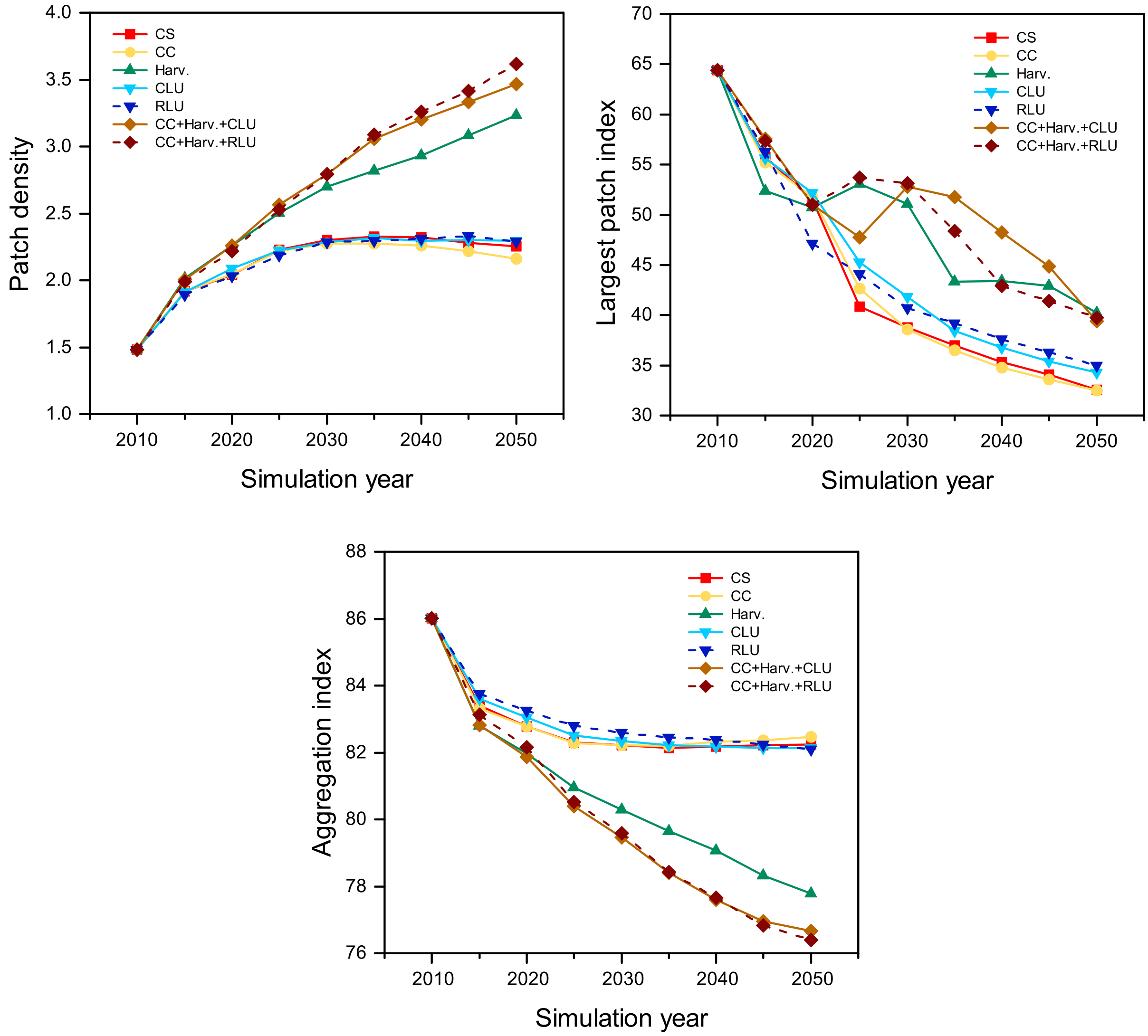

Fig. 9 Changes in landscape metrics (PD, LPI, AI) at the landscape level under multiple scenarios during the simulation

dispersal and density-dependence at the stand level for the subtropical forest (He and Mladenoff 1999; Ma et al. 2016). Though the maximum seed dispersal distances play a small role in the lowlands (Corlett 2009), the effective seed dispersal distance for coniferous species was wider than for the broad-leaved forests in our study area. In addition, the relatively fixed density at the stand level for plantation may promote forest expansion (Rudel 2009). Forest AGB in our simulation was measured in terms of ANPP, existing biomass, and aboveground mortality (Acker et al. 2002). Our results suggested that AGB would increase over the simulation period, revealing that the biomass accumulation process was primarily dominated by forest productivity. Although age structure was not simulated in our study, we can still estimate that most species did not reach the age-related mortality point (half of the species' lifespan), at which point the removal of live AGB begins (Scheller and Mladenoff 2004). Moreover, due to the physiological tolerances of different tree species, coniferous and broad-leaved species responded differently in terms of productivity, rate of biomass accumulation, species richness, and distribution pattern; these results are similar to those found by other studies (Nagaike 2002; Chmura et al. 2017; Song et al. 2017).

In contrast to natural succession, CC and human disturbances may drive the forest landscape dynamics away from stable conditions. Previous studies have found that temperature is the dominant climatic factor affecting the productivity of tree species in this area (Dai et al. 2015a). Therefore, we only modeled forest landscape change under the relatively extreme scenario of RCP 8.5 (i.e., 2.0 °C increase in temperature by 2050). Although CC did not have a large influence on the forest landscape, recent warming contributed to the expansion of forest area and AGB accumulation for both coniferous and broad-leaved forests, and this finding agrees with the results of previous studies (Mi et al. 2008; Liu et al. 2014c; Dai et al. 2016). Compared with CC, the impacts of human activities on forests are potentially more dramatic (Kulakowski et al. 2011; Thompson et al. 2011). As expected, harvesting greatly reduced forest area and AGB in our simulation, especially for the coniferous forests. This is because most of the coniferous forests are plantations that are mainly used for wood production. Thus, some harvesting criteria were prone to preferential harvesting for coniferous forests, such as stand rankings and harvesting age. In addition, harvesting may also affect the dynamics of ecosystem carbon allocation and carbon concentrations (Zheng et al. 2008). Differences in responses between coniferous and broad-leaved forests to land use disturbances came from the spatial area of action for forest conversion. The forest conversion mainly occurred in the peri-urban area where coniferous forests dominated. In addition, the growing impact of land use change on coniferous forests is due to the expansion of urban land. Our results showed that the compounded effects of CC and human activities contribute to diminished forest expansion and AGB accumulation. Regarding interactions between different spatial processes, harvesting plays the leading role in forest dynamics, and far offsets the positive effects of CC in the near future. The main reason for this is that harvesting is the most direct human activity on forest dynamics. In regard to the large-scale synchronization of disturbances, timber harvesting and land use change may have no lag effect compared with CC (Bertrand et al. 2011).

For the forest landscape pattern, forest fragmentation increased with the intensity of human disturbance. This finding is agrees with the results of studies in south-central Siberia (Gustafson et al. 2010) and in Puerto Rico (Gao and Yu 2014). The increased forest fragmentation is associated with habitat loss and impacts on species population dynamics (Wiegand et al. 2005). In contrast to the results for increased fragmentation caused by urban expansion in other literature (Irwin and Bockstael 2007; Miller 2012; Gao and Yu 2014), our results showed that land use change, even under the rapid urban development scenario, contributes less to forest fragmentation. We believe that the simulated urban expansion mainly occurred in the peri-urban area where cultivated land and garden plots are primarily distributed in our study area. The transition in land use patterns was mainly between the non-forested areas (Appendix VI in supplementary material). Affected by topography, slope, and soil moisture, the "urban amenities-cropland-forestland" gradient pattern of land use has a long history in the hilly area of southern China (Liu et al. 2014a) and other areas (Robinson et al. 2013). In addition, our results showed that landscape connectivity was closely related to human activities, which would be expected to negatively impact the biodiversity of forest ecosystems (Barlow et al. 2016; Giam 2017). Forest landscape dynamics can not only affect forest structure and function, but also play an important role in providing ecosystem services (e.g., biodiversity, carbon sequestration, water yield, soil retention). Provisioning (timber production), regulating (habitat conservation), and even cultural services (aesthetics and recreation) of forest ecosystems can benefit human well-being and represent the economic value of the forest landscape. In the future, more attention should be paid to the ecosystem services related to human welfare, and those that may inform forest management.

Sustainable forest management based on natural restoration

Forest recovery is an important issue for current and future China, especially for the southern region, where forest loss has occurred more frequently in the past 10 years (Viña et al. 2016). The rapid growth of forestry economic production has increased the demand for forest harvesting, and this change has appeared in other parts of southern China in the past few years (Liu et al. 2014b). In this context, we should take advantage of the rich hydrothermal conditions in the southern China and conduct management based on natural restoration. Ecologists have recognized that disturbances and recovery processes overlap in both spatial and temporal dimensions (Chazdon 2008). Our results showed the major effects of ecological processes and disturbances on different ecoregions. The ecoregions that were divided by landforms with different elevations were recognized to have relatively homogenous ecological conditions (including climate, soil, and slope). In the absence of disturbances, these ecoregions act on the forest communities and play a decisive role in the habitat of different species, shown as the difference in the SEP. This is the basis for the natural restoration of the forest landscape. In addition, our ecoregions (landforms) are associated with land use and other human activities. For instance, urban construction land and agricultural land are usually built in plain areas, which are conducive to life and agricultural production. Plantations are also closer to the towns, owing to the cost of transportation roads.

In order to restore forests from the perspective of natural restoration, we simulated the disturbances for different ecoregions and then presented several relevant measures and suggestions for sustainable management. For Ecoregion 1, our results showed that both harvesting and land use change had an impact on forests, and harvesting played a larger role in forest dynamics. This area had the greatest loss of forest area under the harvest and land use change scenarios during the simulations, thus, ensuring that forest areas will be a top priority for Ecoregion 1. For residents in terms of land use, residential and farming areas should concentrate on plain areas and avoid occupying forest land. For Ecoregion 2, land use had less impact on forests, and harvesting is still dominant. This area showed the most AGB removed by harvesting. This is because that the slash pine were dominantly distributed, and had a higher economic importance in the stand rankings for harvesting. Thus, we suggest that attention should be paid to the forest regeneration patterns and forest product processing. Ecoregion 3 mainly distributed Chinese fir and broad-leaved forests. Land use had almost no effect in this area. Thus, the forest management should focus on optimizing community structures and reducing artificial pure forests, and then realizing forest natural regeneration. For Ecoregion 4, several local native tree species, such as camphor tree and zhennan, should be protected and developed by the implementation of protection policies. We believe that these suggestions are applicable not just for our study case, but also for other areas facing similar problems in southern China.

Uncertainties and limitations

Owing to the complexity of forest dynamic change, studying forest landscape change under individual disturbances may lead to an underestimation of the potential magnitude of change (Gustafson et al. 2010). The simulation environment and these disturbances were based on consultations with local forestry experts and the literature (Lai et al. 2009; Li et al. 2009; Sheng et al. 2010; Ma et al. 2016). However, there are some unavoidable limitations and uncertainties associated with our simulations. Firstly, a definitive validation of simulated results by comparison to the field study observations will not be possible for the projected results from our study. Although attempts to validate long-term predictions using varying methods have been made (Ma et al. 2017), their application to complicated anthropogenic disturbances is difficult. Secondly, there were limitations in terms of data acquisition, including the projected climatic change data, potential land use change data, and long-term forestry inventory data. Some underlying individual extreme weather events were not included, which were expected to have exacerbated differences in the responses. Meanwhile, the simulation ran only one replicate of each scenario that did not capture the stochasticity around succession and disturbance. Thirdly, there were limitations in terms of modeling potential human activities (Ren et al. 2014). Because of the uncertainty of human activities, it is still difficult to estimate the future trajectories of human behavior in a changing environment that mirror human decision-making, cognition, and behavior (Robinson and Brown 2009). Finally, the feedback mechanisms between different models were not included in our integrated simulation, which may have led to uncertainties.

Despite limitations and uncertainties, we still have confidence in our results based on the following points. Firstly, the input data for these models were reasoned and relatively accurate. Most of the data—including current climate, land use, and initial forest communities—were derived from field investigations and consultation with local forestry experts. Furthermore, the relevant parameters have been validated in previous studies (Dai et al. 2016; Wu et al. 2017a).

Secondly, the models we used have been subjected to extensive testing and applications in many studies (Xu et al. 2009; de Bruijn et al. 2014; Xiao et al. 2016; Creutzburg et al. 2017). For example, the sensitivity of parameters and uncertainties of the core model LANDIS-II have been previously analyzed (Xu et al. 2009; Simons-Legaard et al. 2015). In terms of variability among model runs, our previous studies for this area have been simulated with multiple replicates, which showed that the differences among each run under CC, harvesting and land use change were quite small (Wu et al. 2017a, b). Meanwhile, the low stochastic variation in forest area and AGB for each replicate were also found in other literature (Duveneck and Scheller 2016; Ma et al. 2017). Thus, we selected only one replicate for the analysis. Thirdly, our study was based on several reasonable assumptions. For example, we did not consider fire, wind, insects, and the interaction between different disturbances in our simulation because these may be not the key driving factors in the forest dynamics of the subtropical forest (Luo et al. 2014; Ma et al. 2016). In addition, we assumed that the harvest regime remained unchanged in the future. In fact, forest landscape change is slow-acting, with long-term results (Shen et al. 2013). We only simulated the forest landscape dynamics for the next 40 years, and believe that a longer simulation would increase uncertainties. Finally, we believe that our simulated results were rational under these various scenarios, and we made some attempts to validate the results for the initial year. We drew several conclusions based on the design of the experiment, rather than the accuracy of the prediction, although we want to reflect real-world changes. Overall, the above points strongly support the use of our methodology and the robustness of our results.

Conclusions

We conclude that the interactions between CC, harvesting, and land use change events will have a remarkable effect on forest composition, biomass, and landscape pattern over the next 40 years. In our model, CC promoted forest growth, though not dramatically within the time range of our study. Natural and anthropogenic determinants played different roles in terms of forest dynamics both spatially and temporally. Specifically, our results demonstrated that harvesting and land use will contribute to the complexity of forest dynamics, resulting in the loss of forest area, declining levels of AGB, and increases in fragmentation, which may have feedbacks in terms of forest succession and ecological processes. The responses of tree species, forest types, and forest landscapes can help to understand the drivers of forest dynamics at different scales and can be more conducive to near-term forest and land use management and planning. Our model showed that the current harvest strategy will have the greatest impact on the forested landscape, mainly altering the coniferous tree species and plantations. Moreover, our results showed that the interaction between human activities and CC contributes to diminished forest expansion. Our results can help to understand the driving forces of subtropical forest landscape dynamics and the interactions between complex spatial processes. Furthermore, our findings have practical implications for sustainable forest management in the near future.

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References

Aber JD, Driscoll CT (1997) Effects of land use, climate variation, and N deposition on N cycling and C storage in northern hardwood forests. Global Biogeochem Cycles 11(4):639–648

Aber JD, Federer CA (1992) A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. Oecologia 92:463–474

Acker SA, Halpern CB, Harmon ME, Dyrness CT (2002) Trends in bole biomass accumulation, net primary production and tree mortality in *Pseudotsuga menziesii* forests of contrasting age. Tree Physiol 22:213–217

Azevedo JC, Perera AH, Pinto MA (2014) Forest landscapes and global changes: challenges for research and management. Springer, New York

Azizi A, Malakmohamadi B, Jafari HR (2016) Land use and land cover spatiotemporal dynamic pattern and predicting changes using integrated CA-Markov model. Global J Environ Sci Manag 2(3):223–234

Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, MacNally R, Thomson JR, Ferraz SFDB, Louzada J, Oliveira VHF, Parry L, Solar RRDC, Vieira ICG, Aragão LEOC, Begotti RA, Braga RF, Cardoso TM, de Oliveira RC, Souza CM, Moura NG, Nunes SS, Siqueira JV, Pardini R, Silveira JM, Vaz-de-Mello FZ, Veiga RCS, Venturieri A, Gardner TA (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535(7610):144–147

Bertrand R, Lenoir J, Piedallu C, Riofrío-Dillon G, de Ruffray P, Vidal C, Pierrat JC, Gégout JC (2011) Changes in plant community composition lag behind climate warming in lowland forests. Nature 479(7374):517–520

Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320(5882):1458–1460

Chen YP, Wang KB, Lin YS, Shi WY, Song Y, He XH (2015) Balancing green and grain trade. Nat Geosci 8(10):739–741

Chmura DJ, Modrzyński J, Chmielarz P, Tjoelker MG (2017) Plasticity in seedling morphology, biomass allocation and physiology among ten temperate tree species in response to shade is related to shade tolerance and not leaf habit. Plant Biol 19(2):172–182

Corlett RT (2009) Seed dispersal distances and plant migration potential in tropical East Asia. Biotropica 41(5):592–598

Creutzburg MK, Scheller RM, Lucash MS, LeDuc SD, Johnson MG (2017) Forest management scenarios in a changing climate: trade-offs between carbon, timber, and old forest. Ecol Appl 27(2):503–518

Dai EF, Li SY, Wu Z, Yan HW, Zhao DS (2015a) Spatial pattern of net primary productivity and its relationship with climatic factors in Hilly Red Soil Region of southern China: a case study in Taihe county, Jiangxi province. Geogr Res 34(7):1222–1234 **(in Chinese)**

Dai EF, Wu Z, Wang XF, Fu H, Xi WM, Pan T (2015b) Progress and prospect of research on forest landscape model. J Geogr Sci 25(1):113–128

Dai EF, Wu Z, Ge QS, Xi WM, Wang XF (2016) Predicting the responses of forest distribution and aboveground biomass to climate change under RCPs scenarios in southern China. Global Change Biol 22(11):3642–3661

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM (2001) Climate change and forest disturbances. Bioscience 51(9):723–734

de Bruijn A, Gustafson EJ, Sturtevant BR, Foster JR, Miranda BR, Lichti NI, Jacobs DF (2014) Toward more robust projections of forest landscape dynamics under novel environmental conditions: embedding PnET within LANDIS-II. Ecol Model 287:44–57

Drummond MA, Loveland TR (2010) Land-use pressure and a transition to forest-cover loss in the eastern United States. Bioscience 60(4):286–298

Duveneck MJ, Scheller RM (2016) Measuring and managing resistance and resilience under climate change in northern Great Lake forests (USA). Landscape Ecol 31:669–686

Editorial Committee of Chorography of Taihe County (2013) Chorography of Taihe County. China Local Records Publishing, Beijing **(in Chinese)**

Editorial Committee of Forest of China (2000) Forest of China. China Forestry Publishing House, Beijing **(in Chinese)**

Espírito-Santo FDB, Gloor M, Keller M, Malhi Y, Saatchi S, Nelson B, Oliveira Jr RC, Pereira C, Lloyd J, Frolking S, Palace M, Shimabukuro YE, Duarte V, Mendoza AM, López-Gonzalez G, Baker TR, Feldpausch TR, Brienen RJW, Asner GP, Boyd DS, Phillips OL (2014) Size and frequency of natural forest disturbances and the Amazon forest carbon balance. Nat Commun 5:3434

FAO (2016) Global Forest Resources Assessment 2015: how are the world's forests changing. FAO, Rome

Fraser JS, He HS, Shifley SR, Wang WJ, Thompson FR (2013) Simulating stand-level harvest prescriptions across landscapes: LANDIS PRO harvest module design. Can J For Res 43(10):972–978

Gao Q, Yu M (2014) Discerning fragmentation dynamics of tropical forest and wetland during reforestation, urban sprawl, and policy shifts. PLoS ONE 9(11):e113140

Giam XL (2017) Global biodiversity loss from tropical deforestation. Proc Natl Acad Sci USA 114(23):5775–5777

Grimm NB, Chapin FS, Bierwagen B, Gonzalez P, Groffman PM, Luo YQ, Melton F, Nadelhoffer K, Pairis A, Raymond PA, Schimel J, Williamson CE (2013) The impacts of climate change on ecosystem structure and function. Front Ecol Environ 11(9):474–482

Gustafson EJ, Shifley SR, Mladenoff DJ, Nimerfro KK, He HS (2000) Spatial simulation of forest succession and timber harvesting using LANDIS. Can J For Res 30:32–43

Gustafson EJ, Shvidenko AZ, Sturtevant BR, Scheller RM (2010) Predicting global change effects on forest biomass and composition in south-central Siberia. Ecol Appl 20(3):700–715

He K, Liu RL (1989) Encyclopedia of Chinese agriculture: forestry volume. China Agriculture Press, Beijing **(in Chinese)**

He HS, Mladenoff DJ (1999) The effects of seed dispersal on the simulation of long-term forest landscape change. Ecosystems 2:308–319

He HS, Gustafson EJ, Lischke H (2017) Modeling forest landscapes in a changing climate: theory and application. Landscape Ecol 32(7):1299–1305

Houghton RA, Nassikas AA (2018) Negative emissions from stopping deforestation and forest degradation, globally. Global Change Biol 24(1):350–359

IPCC (2013) Climate change 2013: the physical science basis. Contribution of working group I to the Fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York

Irwin EG, Bockstael NE (2007) The evolution of urban sprawl: evidence of spatial heterogeneity and increasing land fragmentation. Proc Natl Acad Sci USA 104(52):20672–20677

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci USA 105(33):11823–11826

Kulakowski D, Bebi P, Rixen C (2011) The interacting effects of land use change, climate change and suppression of natural disturbances on landscape forest structure in the Swiss Alps. Oikos 120(2):216–225

Labs Clark (2006) IDRISI geographic information systems and remote sensing software. Clark Labs, Worcester

Lai JS, Mi XC, Ren HB, Ma KP (2009) Species-habitat associations change in a subtropical forest of China. J Veg Sci 20:415–423

Li L, Huang ZL, Ye WH, Cao HL, Wei SG, Wang ZG, Lian JY, Sun IF, Ma KP, He FL (2009) Spatial distributions of tree species in a subtropical forest of China. Oikos 118(4):495–502

Li J, Wang ZL, Lai CG, Wu XQ, Zeng ZY, Chen XH, Lian YQ (2018) Response of net primary production to land use and land cover change in mainland China since the late 1980s. Sci Total Environ 639:237–247

Liu JG, Dietz T, Carpenter SR, Alberti M, Folke C, Moran E, Pell AN, Deadman P, Kratz T, Lubchenco J, Ostrom E, Ouyang ZY, Provencher W, Redman CL, Schneider SH, Taylor WW (2007) Complexity of coupled human and natural systems. Science 317(5844):1513–1516

Liu JY, Kuang WH, Zhang ZX, Xu XL, Qin YW, Ning J, Zhou WC, Zhang SW, Li RD, Yan CZ, Wu SX, Shi XZ, Jiang N, Yu DS, Pan XZ, Chi WF (2014a) Spatiotemporal characteristics, patterns, and causes of land-use changes in China since the late 1980s. J Geogr Sci 24(2):195–210

Liu SR, Wu SR, Wang H (2014b) Managing planted forests for multiple uses under a changing environment in China. NZ J For Sci 44(Suppl 1):S3

Liu YP, Yu DY, Xun B, Sun Y, Hao RF (2014c) The potential effects of climate change on the distribution and productivity of *Cunninghamia lanceolata* in China. Environ Monit Assess 186(1):135–149

Luo X, He HS, Liang Y, Wang WJ, Wu ZW, Fraser JS (2014) Spatial simulation of the effect of fire and harvest on aboveground tree biomass in boreal forests of Northeast China. Landscape Ecol 29:1187–1200

Ma L, Lian JY, Lin GJ, Cao HL, Huang ZL, Guan DS (2016) Forest dynamics and its driving forces of sub-tropical forest in South China. Sci Rep 6:22561

Ma J, Xiao XM, Bu RC, Doughty R, Hu YM, Chen BQ, Li XP, Zhao B (2017) Application of the space-for-time substitution method in validating long-term biomass predictions of a forest landscape model. Environ Modell Softw 94:127–139

Mi N, Yu GR, Wen XF, Sun XM, Wang SS (2008) Responses of subtropical conifer plantation to future climate change: a simulation study. Chin J Appl Ecol 19(9):1877–1883 **(in Chinese)**

Miller MD (2012) The impacts of Atlanta's urban sprawl on forest cover and fragmentation. Appl Geogr 34:171–179

Mladenoff DJ, He HS (1999) Design and behavior of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff DJ, Baker WL (eds) Spatial modeling of forest landscape change: approaches and applications. Cambridge University Press, Cambridge

Nagaike T (2002) Differences in plant species diversity between conifer (*Larix kaempferi*) plantations and broad-leaved (*Quercus crispula*) secondary forests in central Japan. Forest Ecol Manag 168:111–123

Norby RJ, DeLucia EH, Gielen B, Calfapietra C, Giardina CP, King JS, Ledford J, McCarthy HR, Moore DJP, Ceulemans R, De Angelis P, Finzi AC, Karnosky DF, Kubiske ME, Lukac M, Pregitzer KS, Scarascia-Mugnozza GE, Schlesinger WH, Oren R (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. Proc Natl Acad Sci USA 102(50):18052–18056

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421(6918):37–42

Ren Y, Deng LY, Zuo SD, Luo YJ, Shao GF, Wei XH, Hua LZ, Yang YS (2014) Geographical modeling of spatial interaction between human activity and forest connectivity in an urban landscape of southeast China. Landscape Ecol 29(10):1741–1758

Riahi K, Rao S, Krey V, Cho C, Chirkov V, Fischer G, Kindermann G, Nakicenovic N, Rafaj P (2011) RCP 8.5—a scenario of comparatively high greenhouse gas emissions. Clim Change 109(1–2):33–57

Robinson DT, Brown DG (2009) Evaluating the effects of land-use development policies on ex-urban forest cover: an integrated agent-based GIS approach. Int J Geogr Inf Sci 23(9):1211–1232

Robinson DT, Sun SP, Hutchins M, Riolo RL, Brown DG, Parker DC, Filatova T, Currie WS, Kiger S (2013) Effects of land markets and land management on ecosystem function: a framework for modelling exurban land-change. Environ Modell Softw 45:129–140

Rudel TK (2009) Tree farms: driving forces and regional patterns in the global expansion of forest plantations. Land Use Policy 26(3):545–550

Rudel TK, Coomes OT, Moran E, Achard F, Angelsen A, Xu JC, Lambin E (2005) Forest transitions: towards a global understanding of land use change. Global Environ Change 15(1):23–31

Scheller RM, Mladenoff DJ (2004) A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol Model 180(1):211–229

Scheller RM, Mladenoff DJ (2005) A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. Global Change Biol 11(2):307–321

Scheller RM, Domingo JB, Sturtevant BR, Williams JS, Rudy A, Gustafson EJ, Mladenoff DJ (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol Model 201(3–4):409–419

Scholze M, Knorr W, Arnell NW, Prentice IC (2006) A climate-change risk analysis for world ecosystems. Proc Natl Acad Sci USA 103(35):13116–13120

Schuur EAG (2003) Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. Ecology 84(5):1165–1170

Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA (2016) Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J Appl Ecol 53(1):120–129

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D, Petr M, Honkaniemi J, Lexer MJ, Trotsiuk V, Mairota P, Svoboda M, Fabrika M, Nagel TA, Reyer CPO (2017) Forest disturbances under climate change. Nat Clim Change 7:395–402

Seto KC, Guneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity

and carbon pools. Proc Natl Acad Sci USA 109(40):16083–16088
Shen Y, Santiago LS, Ma L, Lin GJ, Lian JY, Cao HL, Ye WH (2013) Forest dynamics of a subtropical monsoon forest in Dinghushan, China: recruitment, mortality and the pace of community change. J Trop Ecol 29(02):131–145
Sheng HAO, Yang YS, Yang ZJ, Chen GS, Xie JS, Guo JF, Zou SQ (2010) The dynamic response of soil respiration to land-use changes in subtropical China. Global Change Biol 16(3):1107–1121
Sheng WP, Ren SJ, Yu GR, Fang HJ, Jiang CM, Zhang M (2011) Patterns and driving factors of WUE and NUE in natural forest ecosystems along the North-South Transect of Eastern China. J Geogr Sci 21(4):651–665
Shifley SR, He HS, Lischke H, Wang WJ, Jin WC, Gustafson EJ, Thompson JR, Thompson FR, Dijak WD, Yang J (2017) The past and future of modeling forest dynamics: from growth and yield curves to forest landscape models. Landscape Ecol 32(7):1307–1325
Simons-Legaard E, Legaard K, Weiskittel A (2015) Predicting aboveground biomass with LANDIS-II: a global and temporal analysis of parameter sensitivity. Ecol Model 313:325–332
Song HJ, Xu YD, Hao J, Zhao BQ, Guo DG, Shao HB (2017) Investigating distribution pattern of species in a warm-temperate conifer-broadleaved-mixed forest in China for sustainably utilizing forest and soils. Sci Total Environ 578:81–89
South Hilly Scientific Expedition, Chinese Academy of Sciences (1982) Natural resource and agricultural regionalization in Taihe County. Energy Press, Beijing **(in Chinese)**
Statistics Bureau of Taihe County (2013b) Statistical Communiqué of the Taihe County on the 2012 National Economic and Social Development. http://pub.jian.gov.cn/jxth/gddt/tjsj/201310/t20131010_1736107.htm. Assessed 3 Sept 2018 (**in Chinese**)
Statistics Bureau of Taihe County (2018) Statistical Communiqué of the Taihe County on the 2017 National Economic and Social Development. http://www.jxth.gov.cn/contents/39/64771.html. Assessed 3 Sept 2018 (**in Chinese**)
Syphard AD, Clarke KC, Franklin J (2007) Simulating fire frequency and urban growth in southern California coastal shrublands, USA. Landscape Ecol 22(3):431–445
Thompson JR, Foster DR, Scheller RM, Kittredge D (2011) The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. Ecol Appl 21(7):2425–2444
Thompson JR, Simons-Legaard E, Legaard K, Domingo JB (2016) A LANDIS-II extension for incorporating land use and other disturbances. Environ Modell Softw 75:202–205
Viña A, McConnell WJ, Yang HB, Xu ZC, Liu JG (2016) Effects of conservation policy on China's forest recovery. Sci Adv 2:e1500965
Wardle DA, Bardgett RD, Callaway RM, Van der Putten WH (2011) Terrestrial ecosystem responses to species gains and losses. Science 332(6035):1273–1277
Wen XF, Yu GR, Sun XM, Li QK, Liu YF, Zhang LM, Ren CY, Fu YL, Li ZQ (2006) Soil moisture effect on the temperature dependence of ecosystem respiration in a subtropical *Pinus* plantation of southeastern China. Agric For Meteorol 137(3–4):166–175
Wiegand T, Revilla E, Moloney K (2005) Effects of habitat loss and fragmentation on population dynamics. Conserv Biol 19(1):108–121
Wimberly MC, Boyte SP, Gustafson EJ (2012) Understanding landscapes through spatial modeling. Springer, New York
Wu ZL (1984) Chinese fir. China Forestry Publish House, Beijing
Wu Z, Dai EF, Ge QS, Xi WM, Wang XF (2017a) Modelling the integrated effects of land use and climate change scenarios on forest ecosystem aboveground biomass, a case study in Taihe County of China. J Geogr Sci 27(2):205–222
Wu Z, Ge QS, Dai EF (2017b) Modeling the relative contributions of land use change and harvest to forest landscape change in the Taihe County, China. Sustainability 9(5):708
Xiao JT, Liang Y, He HS, Thompson JR, Wang WJ, Fraser JS, Wu ZW (2016) The formulations of site-scale processes affect landscape-scale forest change predictions: a comparison between LANDIS PRO and LANDIS-II forest landscape models. Landscape Ecol 32(7):1347–1363
Xu C, Gertner GZ, Scheller RM (2009) Uncertainties in the response of a forest landscape to global climatic change. Global Change Biol 15(1):116–131
Yin YH, Ma DY, Wu SH (2018) Climate change risk to forests in China associated with warming. Sci Rep 8:493
Yu QZ, Wang SQ, Shi H, Huang K, Zhou L (2014) An evaluation of spaceborne imaging spectrometry for estimation of forest canopy Nitrogen concentration in a subtropical conifer plantation of southern China. J Resour Ecol 5(1):1–10
Zheng H, Ouyang ZY, Xu WH, Wang XK, Miao H, Li XQ, Tian YX (2008) Variation of carbon storage by different reforestation types in the hilly red soil region of southern China. Forest Ecol Manag 255(3–4):1113–1121
Zhu XD, He HL, Liu M, Yu GR, Sun XM, Gao YH (2010) Spatio-temporal variation characteristics of photosynthetically active radiation in China in recent 50 years. J Geogr Sci 20(6):803–817