

Disentangle the effects of environment and disturbance on landscape dynamics using LANDIS forest landscape model

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ABSTRACT

Forest landscapes pattern and development are affected by environment and disturbance. Disentangling their effects is important to understanding current landscape and predicting future changes. Such studies are limited by short-term observation and sparse disturbance-history data. Spatially-explicit forest landscape modeling represents a solution to these limitations. Here, we reconstructed the 300-year-time-series (1710–2010) of post-volcanic-eruption forest landscapes experiencing periodic-typhoons in Changbai Mountain, China, using LANDIS forest landscape model. We used a factorial simulation design to quantify the main and interactive effects of environment and typhoon on forest landscape recovery. Results showed environment had dominant effects (>80%) on early recovery (1710–1760), suggesting early forest development follows deterministic community-assembly processes governed by environment. However, as forest matured, disturbance became dominant (>50%) at later-recovery stages (1860–2010). This study showed that historical landscape reconstruction reveals the full spectrum of interplays of environment, disturbance, and succession in forest ecosystems, which may not be captured by short-term studies.

Software availability

Software name: LANDIS PRO. Developer: GIS and Spatial Analysis Laboratory at the University of Missouri-Columbia in collaboration with the USDA Forest Service Northern Research Station.

Operating system: Windows. Program languages: C, C++. Cost: Free.

Availability: Source code, executable, and model documentation are publicly available and can be cloned from the GitHub repository at <https://github.com/landispro>.

1. Introduction

The formation of forest ecosystems across a landscape is affected by factors (e.g., environment (climate, terrain, and soil, etc.), disturbance) across a range of spatial and temporal scales (Oliver and Larson 1996; Svenning and others 2006; Garzon-Lopez and others 2014; Li and others 2016). Climate is a dominant factor regulating distribution of forest

ecosystems at regional scales (Pearson and Dawson 2003; Siefert and others 2012; Osland and others 2017). Under stable climatic conditions, tree species gradually assemble into specific communities to adapt to regional climate (Clements 1916, 1936; Weiher and Keddy 1999), and thus forests success along the determined pathways to reach vegetation-environment equilibriums (i.e., late successional/climax stages) (Bazzaz 1991; Weiher and Keddy 1999; Turner 2010). At landscape scales, disturbances are common processes that disrupt the deterministic succession pathways in forest ecosystems (Flynn and others 2010; Johnstone and others 2010; Marra and others 2018; Huang and others 2017). Vegetation-environment equilibrium is predicted to occur only in systems with small and infrequent disturbances, while large and frequent disturbances often lead to high variations in landscape pattern between pre- and post-disturbances and may even shift forest ecosystem successional pathways (Turner and others 1993; Turner 2010). Environment encapsulates regional-scale climate and *in situ* terrain and soil to interact with site-scale processes to determine tree

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species occurrence, composition, and distribution at broad scales (Chesson 1986; Snyder and Chesson 2004; Meier and others 2010; Cadotte and Tucker 2017).

The complex interactions between extrinsic ecological factors (i.e., environment, disturbances) and inherent ecological processes (i.e., succession, competition) at various temporal-spatial scales, may result in unknown and intractable changes in forest landscapes over time (McCook 1994; Oliver and Larson 1996; Kasel and others 2017; Lucash and others 2018). Understanding and separating the interacting effects of environment and disturbance on forest ecosystems across the landscape is important to understanding current forest landscapes and predicting future changes. However, such a task is challenging because the current forest landscape is the product of the interactive and cumulative effects of stochastic disturbances, environment, and forest succession across space. Studies of this sort are frequently limited by relatively short observations (e.g., several decades) of changes in forest landscapes and spatially sparse disturbance-history data (e.g., paleoecological and dendrochronological) (Wimberly and Spies 2001; Franklin and others 2006).

Spatially explicit reconstruction of historical landscapes over time can be used to assess the effects of environment and disturbance. Forest landscape models (FLMs) are an effective tool for such tasks since they are designed to simulate forest dynamics at site scales with disturbance at landscape scales, while incorporating variable environments across the landscape (He 2008; Wang and others 2013; Wang and others 2014a). FLMs simulate forest dynamics formed in time from a historical starting point, which can be derived from historical data, and are driven by the theories of forest stand dynamics and disturbance ecology (Wu and others 2020; Xu and others 2020). The theories presented in Oliver and Larson (1996) generalizes forest development pattern and mechanism with and without disturbances. The reconstructed forest landscapes can be benchmarked using current field data and forest patterns to check not only the end product but the intermediate processes are defensible (Wang and others 2014b). By spatially-explicit reconstruction of historical landscapes, the effects of environment and disturbance and their interaction on a forest landscape can be separately quantified using a factorial simulation design.

Changbai Mountain experienced a massive volcanic eruption in 946 AD (Iacovino and others 2016). The eruption removed almost all forests in a ~50 km radius and forced forest succession to restart (Zhao 1984; Liu and others 1995). To date, forest zonation has developed on the north side of Changbai Mountain, with temperate, boreal, and alpine dwarf forest ecosystems growing along elevational zones that correspond to their latitudinal distributions (Yang 1981; Xu and others 2004). However, such vertical forest zones have not developed on the west and south sides of the mountain, which are disturbed by periodic typhoons that might have been prevailing even before the volcanic eruption. With succession and disturbance history after the volcanic eruption, Changbai Mountain presents an ideal platform to reconstruct its historical landscapes and reveal the effects of typhoon and environment on forest landscape recovery.

In this study, we reconstructed the post-eruption forest landscape of Changbai Mountain in Northeast China using LANDIS PRO forest landscape model. LANDIS PRO forest landscape model is designed to simulate forest dynamics at landscape scales, while incorporating variable environments across the landscape (He, 2008). Recently, a series studies used LANDIS PRO to investigate forest landscape dynamics under various environments and disturbance regimes and quantify the effects of disturbance, environment, and forest succession. For example, Wang and others (2019) predicted future forest landscape dynamics to quantify the effects of climate change and timber harvest on forest dynamics. Huang and others (2021) and Duan and others (2021) simulated forest landscape dynamics affected by fire and insect disturbances in the context of future climate change, and both studies quantified the direct and indirect effects of climate change to future disturbance regimes. In the context of these studies, this study focused on the influence of

environment and typhoon on the development of post-volcanic eruption forest landscape. Our study is a complement to Wang and others (2019), Huang and others (2021), and Duan and others (2021) in quantifying the effects of various drivers on forest landscape change. Specifically, we hypothesized that 1) environment exerts dominant roles in the early stage of post-volcanic-eruption forest landscape recovery and its role reduces as forests reach the mid and late successional stages; 2) the effects of typhoon increase over time, and will overtake the environment to become dominant in the later recovery stage; and 3) recurrent typhoons weaken the spatial pattern of forest-climate equilibrium and lead to fragmented forest landscapes.

2. Approach and methods

2.1. Study area

Our study area was in Changbai Mountain of China side, with elevations ranging between 780 and 2,652 m (41°28'–42°28'N, 127°32'–128°52'E) (Fig. 1a). As elevation increases, the average climate shifts from temperate monsoon to cold zone, with corresponding long, severe winters and short, warm summers. The annual mean temperature ranges from 7 °C at low elevations to 3 °C at high elevations, while the annual precipitation increases from about 760 mm at low elevations to about 2,000 mm at the mountain top. Distinctive ecosystems correspond with elevation, with mixed Korean pine and broadleaf forests dominating the low-elevation zone (mixed Korean pine-broadleaf forest zone) (780–1100 m), evergreen coniferous forests dominating the mid-elevation zone (evergreen coniferous forest zone) (1100–1700 m), subalpine forests typifying the higher elevation zone (subalpine forest zone) (1700–2100 m), and tundra at the highest elevation zone (above 2100 m). The region contains fairly high levels of plant diversity. In the mixed Korean pine-broadleaf forest zone, the overstory is dominated by Korean pine (*Pinus koraiensis* Siebold and Zucc.), basswood (*Tilia amurensis* Rupr), maple (*Acer mono* Maxim), elm (*Ulmus davidiana* Planch. var. *japonica* (Rehd.) Nakai), ash (*Fraxinus mandshurica* Rupr). In the evergreen coniferous forest zone, the dominant tree species include jezo spruce (*Picea jezoensis* Siebold and Zucc.) and Manchurian fir (*Abies nephrolepis* [Trautv.] Maxim). In the subalpine forest zone, mountain birch (*Betula ermanii* Cham) is the dominant tree species. There are scattered early successional patches dominated by Asian white birch (*Betula platyphylla* Suk), aspen (*Populus davidiana* Dode), Mongolian oak (*Quercus mongolica* [Fisch.] Ledeb.), and Olga Bay larch (*Larix olgensis* A. Henry). The above tree species account for >90% of stand volume in the region (Hao and others 2008; Shao and Deng 2000). In the old-growth forests in this region, coarse woody debris forms 39%–56% of total aboveground detritus (i.e., litter, fine wood, and coarse woody debris), and the ratio of coarse woody debris to live tree mass is 0.04–0.07 (Harmon and Hua 1991) with the total mass of coarse woody debris from 7.9–16.2 Mg/ha in the mixed Korean pine and broadleaf forests (Harmon and Hua 1991) to about 53.4 Mg/ha in the evergreen coniferous forests (Zhou and others 2011).

Our study area included the area disturbed by Millennium Eruption that occurred 946 A.D. (Iacovino and others 2016) and the adjacent undisturbed area extending 15 km down-slope. The spatial extent of the areas affected by the volcanic eruption were determined from previous studies (Fig. 1) (Wu and others 2020), which was approximately 3.8×10^5 ha. Forest recovery after the volcano eruption relied largely on seed sources and seed dispersal (McClanahan 1986; Tautenhahn et al., 2016). The undisturbed habitats below the eruption area and isolated refugia within the eruption area served as sources of seed (Fig. 1). We regarded the undisturbed area (at lower elevations surrounding the eruption area) as matrix seed source area, which linked to the eruption area via seed dispersal and gene flow. We referred to the surviving seed sources in the refugia as remnant seed sources. The size of matrix seed sources and the location of remnant seed sources were determined in Wu and others (2020) with a similar study from Mount St. Helens (Antos and Zobel

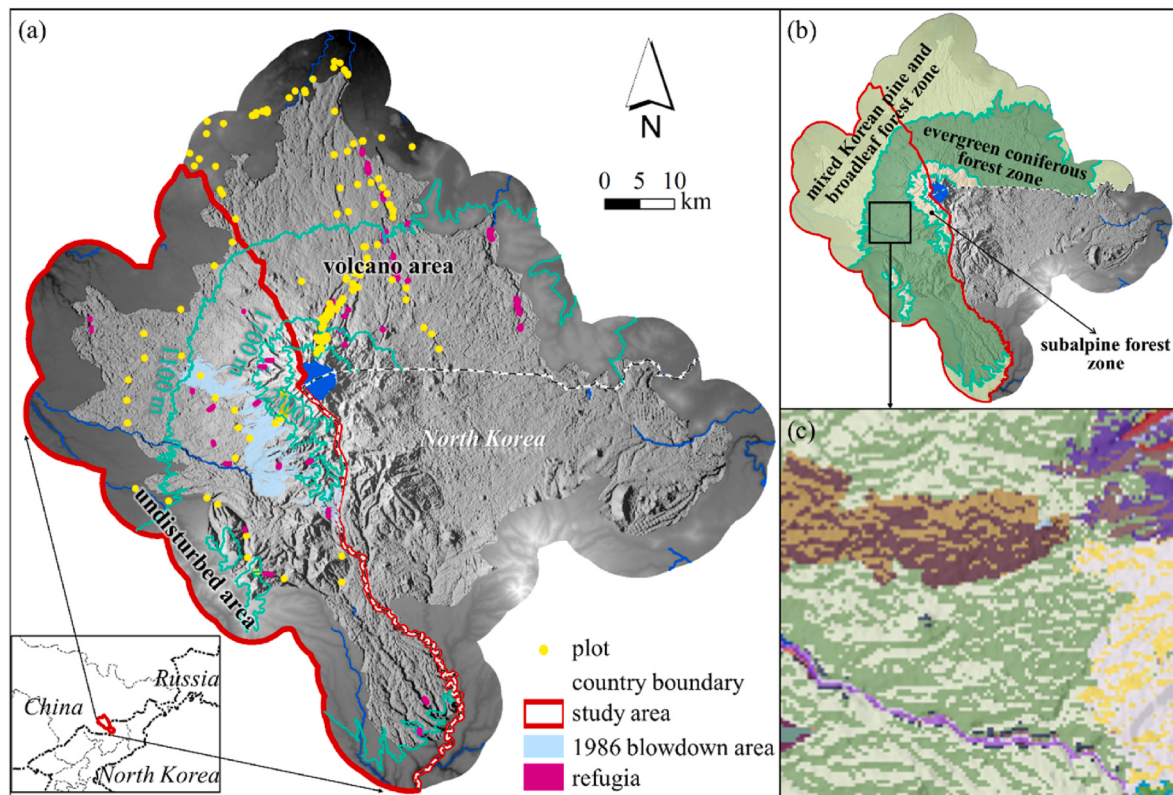


Fig. 1. (a) The study area includes China sides of Changbai Mountain bordering North Korean in the east. The bright grey represents the volcano destroyed area and dark grey is a 15 km-width undisturbed area. (b) Current forests on the study area have evolved into three vertical forest zones by altitude. (c) A closeup look of environment (small homogeneous units in different shapes and colors).

1986).

2.2. The assumptions for historical conditions

Field investigations in the eruption area show that the forest stand age is less than 300 years and decreases with increasing elevation (near the volcano crater) (Xu and Liang 2010). This evidence suggests that tree species established less than 300 years ago then moved upwards, and thick volcanic ash from the Millennium Eruption and erosion hinder tree establishment and survival for the first ~700 years after the eruption. Evidence elsewhere in Northeast China suggests that post-volcanic-eruption forest recovery has lagged for centuries after volcanic eruption since volcanic ash and erosion prohibited trees from establishment. For instance, the Wudalianchi volcano in northern China erupted in 1720 and the volcanic area is still dominated by lichen and brush (Zhang and others 2005). In the low-altitude areas of Changbai Mountain, Zhao (1984) found dead larch (an early successional species) stumps about 200 years in the current 100-year Korean pine-broadleaf forests (late-successional forests), confirming that the early successional species colonized around 1710 and were replaced by mixed Korean pine-broadleaf forests around 1910. The establishment in high elevation areas were even later. Xu and Liang (2010) found that the age of mountain birch (an early successional species) in the area above 1500 m asl. was less than 200 years (colonized around 1810) and decreased with increasing altitude, and only 90 years (colonized around 1920) at 2000 m. They also concluded that the current forest vegetation is the first regeneration after the eruption in Changbai Mountain. Based on this evidence, we hypothesized that few trees establishment and colonization during the first ~700 years due to volcanic ashes and erosion, and the forest colonization started about 300 years ago.

Palaeoecological studies of historical climate reconstruction in Changbai Mt. found that climate has been relatively stable with only

some fluctuations over past 300 years, except for the warming from 1980s (Shao and Wu 1997; Du and others 2018). In addition, Xu and others (2018) reported few significant changes in tree species composition and structure in the old-growth forests during the warming period (1981–2016) in Changbai Mt. Thus, there seems to be no significant impact of the later climate warming on shaping current forest landscape, and it is reasonable to assume that the climate has remained stable during the development of current forest landscape. Moreover, the current geomorphology of Changbai Mt. was formed from the Millennium Eruption in 946 AD, and thus the terrain is also considered to be relatively stable. Additionally, the successful colonization of tree species from around 300 years ago implies that the erosion of volcanic ash from the Millennium Eruption had largely completed and tree establishment started for the past 300 years. Based on the above evidence, we assumed that environment was relatively stable during the development of forest landscape over the past 300 years. Additionally, because of the absence of typhoons at the low elevation in the matrix seed source area, it is reasonable to assume that undisturbed forests in matrix seed source area have reached vegetation-climate equilibrium reflective of historical forests in 1710s. Charcoal study confirmed that pre-eruption forest composition (Korean pine, fir, spruce, larch, basswood, birch, and ash) was nearly the same as the current forests (Zhao 1984). Thus, we can use the current old-growth forests to represent the 1710 forests in the matrix forests. Additionally, to evaluate the uncertainties associated with this assumption, we conducted a sensitivity analysis on the initial conditions (species composition and structure) of the old-growth forests and found that $\pm 30\%$ changes in dominant species abundance in the matrix forests did not significantly affect the reconstructed forest landscapes (see Supplements).

2.3. The framework for reconstructing post-volcanic-eruption forest landscapes

In this study, we present a novel framework for reconstructing post-volcanic-eruption forest landscapes. To our knowledge, there are few studies of spatial and temporal reconstruction of historical landscapes of past centuries. Such a work involves using a forest landscape model that tracks spatially explicit information of parent tree location and abundance, seed dispersal, forest dynamics and succession, and environment heterogeneity. The novelty of our framework includes integrating old-growth forests and disturbance history data with theories of forest stand dynamics and disturbance ecology through LANDIS PRO forest landscape model. We also validated the reconstructed landscapes against contemporary forest inventory data and classified remote sensing data and verified the intermediate trajectories of stand dynamics against theories of stand dynamics.

2.4. LANDIS PRO model

LANDIS PRO is a raster-based landscape model that tracks the number of trees by species and by age cohort within each pixel (Wang and others 2013; Wang and others 2014a). It integrates species-, stand-, and landscape-scale processes (e.g., wind) to simulate forest succession dynamics over large spatial and temporal scales (Wang and others 2014a). LANDIS PRO simulates forest succession by accounting for species-specific demographic processes, which are driven by the species vital attributes (i.e., longevity, age of reproductive maturity, shade tolerance, seed dispersal distance, stand density index), and species establishment probability (SEP) and maximum growing space (MGSO) for each environment. In this study, we modeled the 12 most dominant tree species (mentioned above). We derived the species biological attributes from previous studies, and SEP and MGSO based on ecosystem process model (LINKAGES model) (He and others 2002; Liang and others 2012, 2014).

2.5. Environmental data and historical typhoon regimes

In this study, environment represents the assembly of various physical variables at various spatial scales, that encapsulates regional-scale climate and *in situ* terrain (including multiple terrain factors) and soil. Thus, environment in our study encapsulates slope, aspect, and elevation as well as soil and climate. The effects of environment on post-volcanic-eruption forest recovery refer to how given configurations of environmental factors (climate, terrain, and soil combinations) regulate the forest succession and landscape formation. Environment was derived from elevation zones corresponding to climate zones superimposed with topography (30 m digital elevation model) and soil (1 km resolution). Soil data included thickness of soil layers, soil texture, field capacity, soil organic matter, and soil nitrogen content, which derived from China Soil Database (<http://www.soil.csdb.cn>). Thus, the environment covered the entire study area as numerous small homogeneous units with similar environmental conditions (i.e., climate-terrain-soil conditions) (Fig. 1c). We classified the whole area into 168 climate-topography-soil types (which were derived from the overlay of climate, terrain, and soil layers). For at each climate-terrain-soil type we derived SEP, which represents the response of species to the environment. The higher SEP indicates the stronger adaptability of species to the environment, and easier establishment and colonization of tree species in this environment type.

Information referring to early typhoon disturbances was not readily available for the past 300 years. Thus, we determined the historical typhoon regime by combining remote sensing data and field inventory. First, we identified historical typhoon disturbances by interpreting Landsat TM/ETM+ images from 1980 to 2016 (<https://earthexplorer.usgs.gov/>). Since there were no other stand-replacing disturbances except typhoon, the early successional patches scattered in the matured

forests were deemed to be historical typhoon patches. These patches were readily identified from the remote sensing images due to their distinct characteristics in the surrounding matrix (Shao and others 1996). There were 140 typhoon patches identified with small patches occurred much more frequently than large ones following lognormal distribution (Supplement Figure S2, S3). They covered 26799.3 ha or 19.3% of the region (Supplement Figure S2). Next, we conducted extensive field investigations on >50% of the identified patches to determine stand age, which reflects the time typhoon occurred. There were 114 plots of white birch-aspen forests, 129 plots of larch forests, and 91 plots of meadows (Supplement Figure S2). The oldest typhoon events could be dated back to 1900 (110 years ago), suggesting that all the typhoon patches identified are typhoons occurred within the last 110 years. Typhoon patches of the same occurrence year were counted as one typhoon event. We calculated mean disturbance size using the typhoon patches with known time since disturbance, which is 6968.3 ha or about 5.0% of the study area. We calculated mean typhoon return interval, which is 555.6 year following the approach from Johnson (1992). To extrapolate the typhoon regime to the 300 years (1710–2010), we calculated that the typhoon disturbed area was 54.0% (300/555.6) of the region with 11 (54.0%/5.0%) main typhoon events. The 1986 typhoon recorded a maximum sustained wind of about 30 m/s (Guo and others 2015), which resulted in >80% tree mortality as a result of uprooting (Xue 2009), and 1.21 million cubic meters of fallen wood covering 71.2% of the forest stock in the windfall area (Yu and Han 2016). Thus, we assumed the similar intensity and severity for other typhoons in this study. Especially, to avoid the circular use of the historical typhoon data, the disturbance parameters (mean return interval, mean disturbance size, etc.) were inputted to LANDIS, which replicated 20 times to capture the stochastic behavior of typhoons.

2.6. Experimental design

We designed 2×2 factorial experimental modeling scenarios for environment (realistic heterogeneous vs. hypothetical homogenous environment) and typhoon (recurrence vs. absence) to evaluate the individual and interactive effects of these factors. The treatment combinations resulted in four simulation scenarios: homogeneous environment without typhoon (NN), heterogeneous environment with recurrent typhoons (ET), heterogeneous environment without typhoon (EN), and homogenous environment with recurrent typhoons (NT). The ET scenario was realistic, which was regarded as baseline scenario, while the remaining three scenarios were unrealistic but used to complete the factorial model simulation design to quantify the effects of typhoon and environment on forest landscapes. This design assumed that environment and typhoon were the two dominant extrinsic factors that affected forest landscape dynamics, and typhoon is the main natural disturbance to forest ecosystem in our study area. Typically, the forest landscape dynamics are affected by various disturbances, which may include wildfire, harvest, in addition to typhoon. However, these disturbances, such as wildfire and harvest, have been insignificant in our study area. Wildfires rarely occurred, and if occurred they are at very small scales due to the relatively high humidity (abundant precipitation) and long snow-covered season. Large-scale timber harvest has been absent due to low human density, high elevation, and remoteness of the region. Based on the realistic scenario, we simulated the remaining three scenarios by disregarding environment or/and typhoon while fixing other factors. For the scenarios with homogenous environment, we assumed that there is a uniform environment across the entire study area, where all pixels were assigned the same species establishment probabilities (SEPs). The SEP value for each species was the average across all ecoregions. For each species, the life attributes were kept the same among all simulation scenarios (e.g., homogeneous environment and heterogeneous environment). For the scenarios with heterogeneous environment, we determined the suitability of each environment by species. For the scenarios with typhoons, we incorporated the

reconstructed typhoon regime in the simulation. For each scenario, we simulated spatio-temporally explicit forest dynamics (1710–2010) at 10-year interval with 20 replicates. Additionally, the intrinsic factors included tree establishment, growth, mortality, competition, and seed dispersal, referred as forest dynamics, which are the underlining forces simulated in all scenarios. However, the fundamental assumption here is that the simulated forest dynamics can reconstruct the post-volcanic succession dating back to ca. 900 AD. For this, we used the LANDIS PRO forest landscape model that is designed to simulate forest dynamics at species and stand scales and interactions with environment and disturbance.

In this study, the reconstructed forest landscape (the realistic scenario in our simulation design) has gone through the verification and validation processes (see below), suggesting that the reconstructed landscape credibly captured the spatiotemporal trajectories of forest landscape change of the past 300 years (Wu and others 2020). In our current study framework, the effects of disturbance on environment are not included. Indeed, typhoon disturbance can temporarily alter the environment by increasing light availability through removing forest canopy, reducing evapotranspiration, and increasing soil water. However, from a long-term perspective (e.g., decades), environmental conditions should remain relatively constant under the stable climate. In our study, we measured the effects of environmental factors by species establishment probability (SEP, see above). We assumed that SEPs remain unchanged before and after disturbance because our study is based on a long-term simulation.

2.7. Field inventory for LANDIS PRO model parameterization and result verification

We measured a total of 2055 trees (diameter >5 cm) at 41 old-growth sites (20 × 20 m), and recorded the species and size by each tree. This information was used to parameterize the initial species composition of matrix forests in 1710. We calibrated model parameters and validated the simulated results using 135 20 × 20 m sample plots surveyed in 2010 and 2014. Each plot recorded the number of trees of by species and diameters. We used 2/3 of the data for model calibration and 1/3 of the data for result validation. To calibrate the model, we iteratively adjusted model parameters, such as age-DBH relationships by environment, the number of seeds and maximum DBH per species, until there were no significant differences (paired t-tests, $p > 0.05$) between the 2010 simulated species basal area and density and the 2010s inventory plots in different elevation zones. To validate the results, we compared the remaining 1/3 2010s forest inventory data to the simulated results in 2010 (Figure S5). To ensure simulated forest patterns were reasonable, we compared the simulated distribution of forests types in 2010 with the forest cover type derived from remote sensing classification (Shao and others 1996) (Figure S6). To ensure the intermediate results (1710–2010) were credible, we evaluated the simulated forest development trajectories with the expected trajectories using Gingrich stocking charts (Figure S7).

2.8. Data analysis

We classified tree species into four groups based on tree species assembly and distribution: Korean pine and broadleaf species group (including Korean pine and mid/late-successional broadleaf species such as maple, ash, basswood, and elm), spruce and fir group, mountain birch group, and early successional species group (including white birch, aspen, and larch, which are mainly related to historical typhoon and scattered in the study area). The first three groups are specialists, which represent specific tree species assembly within each forest zone, while the last species group is a generalist. Because the distribution and abundance of early successional species group are relatively small, we did not analyze the species group individually. In addition, we divided the forests into young (<30 years), near-mature (30–70 years), mature

(70–120 years), and old-growth (>120 years) age groups within each pixel. To analyze the forest landscape pattern, we determined the combination of tree-species groups and age groups at each pixel, resulting in 16 possible forest types (4 tree-species groups × 4 age groups, ex., young Korean pine and broadleaf forests).

We used basal area and tree density of each species group (except for the early successional species group, since it was uncommon), as response variables to analyze forest dynamics at the stand (pixel) level. The two attributes, basal area and tree density, reflect the size and abundance of tree species. They are the two most common measurements in field-based forest inventory. Other forest attributes, e.g., biomass, carbon stock, are derived these two attributes. We used contagion (CONTAG) index as the response variable to evaluate forest landscape patterns (Li and Reynolds 1993). CONTAG represents the degree of clumping of patches that considers all patch types present in a landscape affected by both the dispersion and interspersed of patch types, which ranges from 0 to 100 (Li and Reynolds 1993). This metric was selected to assess patch diversity and sensitivity to fragmentation.

We estimated the absolute effect sizes and relative effects of environment, typhoon disturbance, and their interaction on the above response variables in early (1710–1760), middle (1760–1860), and late (1860–2010) recovery periods, respectively. We estimated the effect size of environment alone as the difference between scenarios EN and NN (Scenario EN - Scenario NN), the effect size of typhoon disturbance alone as the differences between scenarios NT and NN (Scenario NT - Scenario NN), and the combined effect as the difference between scenarios ET and NN (Scenario ET - Scenario NN). The size of the interaction effect was calculated as the difference between the combined effects and the sum of the separate main effects of these two factors. Through the experimental modeling design, we used repeated measures ANOVA (analysis of variance) to quantify the relative effects of environment, typhoon disturbance, and their interactions by partitioning the proportion of total variation explained based on Type III sums of squares (Girden 1992). We used the “relaimpo” package (Grömping 2006) in R statistical software to compute the relative effects.

3. Results

3.1. Result verification

The reconstructed forest landscapes tracked the trajectories of basal area and density for all simulated species (Fig. 2a). The simulated recovery pathways were supported by forest stand development theory (Fig. S7) ensuring that the intermediate dynamics between 1710 and 2010 were realistic. Spatially, the simulated distribution of various forests types in the ET scenarios (realistic) in 2010 matched the distribution of current forest types (Figure S6). The simulated 2010 results showed high agreements with the current observed basal area and tree density in each elevation zone (Fig. 2b and c). Especially, the paired t-tests results for species basal area at 2010 were $t = 1.07$, $df = 11$, $P = 0.31$ at low-elevation zone, $t = 1.78$, $df = 11$, $P = 0.10$ at mid-elevation zone, and $t = 1.46$, $df = 11$, $P = 0.17$ at higher elevation zone; the paired t-tests results for density at 2010 were $t = 0.16$, $df = 11$, $P = 0.87$ at low-elevation zone, $t = 1.54$, $df = 11$, $P = 0.15$ at mid-elevation zone, and $t = -1.00$, $df = 11$, $P = 0.34$ at higher elevation zone. Thus, the end of the 300-year simulation in 2010 reasonably represented forest composition and structure in 2010s.

3.2. The effects of environment and typhoon

Basal area. Relative effects of environment in the early recovery stage (1710–1760), were overwhelming (97%) on total basal area of all species while the relative effects of typhoon were minimum (3%) (Fig. 3a). From the 1760 onward, as tree size and forest cover increased over the landscape, the relative effects of environment on total basal area decreased to 28% and the relative effects of typhoon increased to 72%,

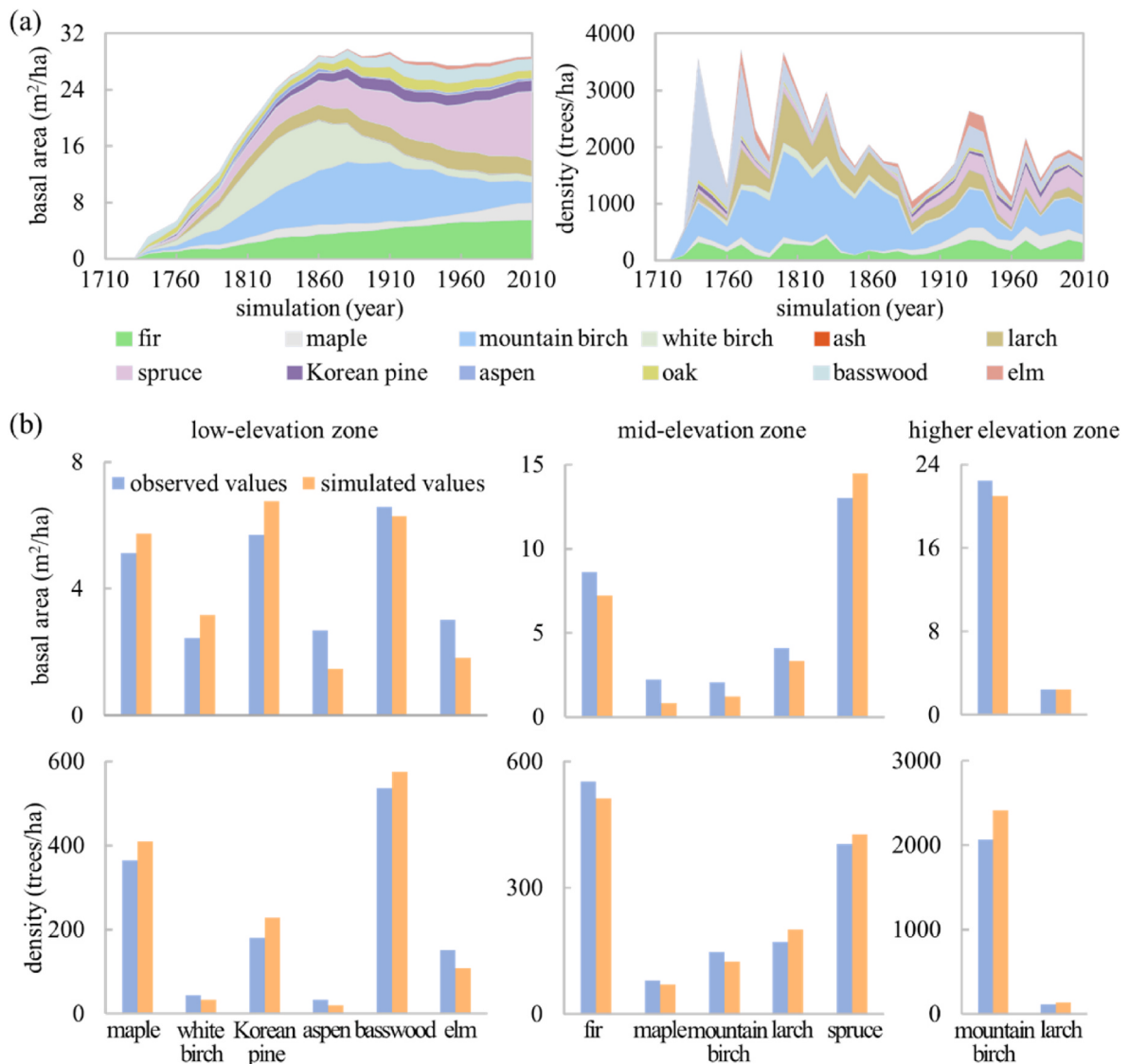


Fig. 2. (a) The basal area and tree (DBH > 10 cm) density in the ET scenario (realistic) for each tree species. (b, c) Comparison of the 2010 simulated basal area and density of major tree species for the realistic scenario (ET) with field data in three elevation zones.

surpassing environment in the mid recovery stage (1760–1860) (Fig. 3a). For each specialist species group in general, the relative effects of both environment and disturbance on its basal area varied similarly to their effects on total basal area of all species, while relative effects of typhoon remained lower than or close to those of environment throughout 300-year period (Fig. 3b–d).

The absolute effect sizes of both environment and typhoon disturbance generally coincided with the relative effects on total basal area for all tree species. Environment had a far greater effect size (0.43 m²/ha) than typhoon (~0) in the early recovery stage (1710–1760) (Fig. 3e). The effect sizes of environment on total basal area decreased to 0.26 m²/ha in the late recovery stage (1860–2010). The effect size of typhoon increased to 0.67 m²/ha, and surpassed environment in the mid recovery stage (1760–1860) (Fig. 3e). At the species group level, typhoons had a negative effect on the basal area in the Korean pine and broadleaf species group and the mountain birch species group because of strong wind-induced mortality among the large, old trees (Fig. 3f and h). However, typhoon had a positive effect on spruce and fir species group (Fig. 3g) because of the widespread regeneration of light-demanding spruce seedlings in the areas affected by typhoons.

Density. Environment had large effects on total tree density in the

early recovery stage (1710–1760), and the relative effect was 98% (Fig. 3i). As forests steadily recovered, the relative effect of environment gradually decreased over time and became increasingly important (40%) in the late recovery stage (1860–2010) (Fig. 3i). For each specialist species group, the relative effects of both environment and typhoon on tree density varied consistently with those on total density of all species. The relative effects of environment were over 80% in the early recovery stage (1710–1760), and then they decreased over time. The combination of the relative effects of typhoon disturbance and its interaction with environment increased over time and exceeded the relative effects of environment (except for the Korean pine and broadleaf species group, for which the combined effects were nearly equivalent to the effect of environment) in the late recovery stage (1860–2010) (Fig. 3j–l).

The absolute effect sizes of both environment and typhoon disturbance generally coincided with the relative effects on total density for all tree species. Environment had a far larger effect size (1745.6 trees/ha) than typhoon (14.1 trees/ha) in the early recovery stage (1710–1760) (Fig. 3m). The effect size of environment on total density decreased to 342.9 trees/ha in the late recovery stage (1860–2010). The effect size of typhoon increased to 357.8 trees/ha, and surpassed environment in the

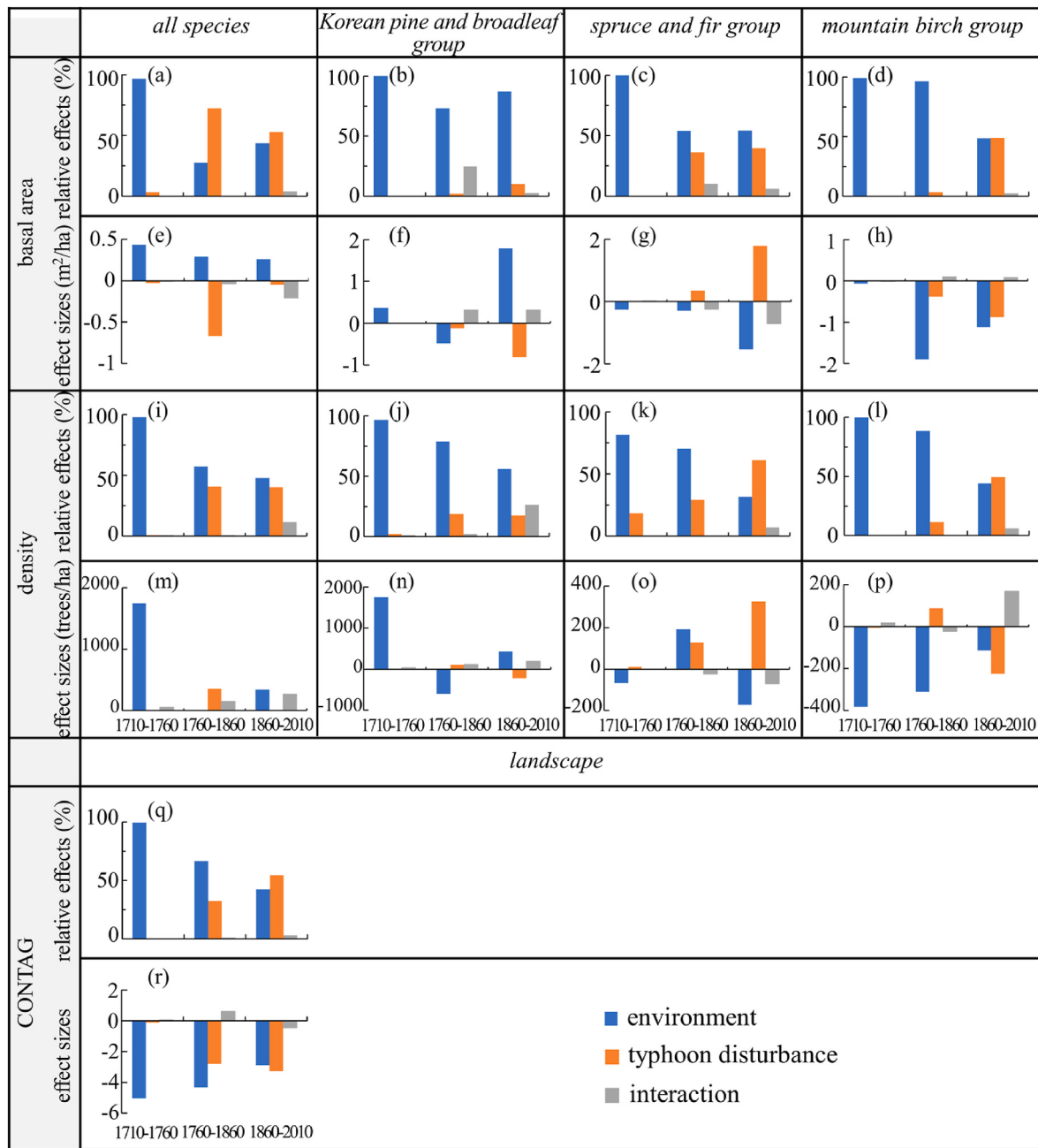


Fig. 3. The relative effects (a-d, i-l, q), and the effect sizes (e-h, m-p, r) of environment, typhoon disturbance, and their interaction on the total basal area and density of each specialist species group, as well as CONTAG.

mid recovery stage (1760–1860) (Fig. 3m). After a typhoon event, seedlings regenerated at a rate greatly exceeding tree mortality, resulting in an increase in tree density for each specialist species group in the mid-recovery stages (reflected by positive effects of typhoon on tree density) (Fig. 3m–p).

Landscape fragmentation. Environment had an overwhelming effect on CONTAG with the relative effect reaching 99% in the early recovery stage (1710–1760) (Fig. 3q). From the 1760 onward, typhoon disturbance became increasingly important in shaping the forest landscape. In the late recovery stage (1860–2010), typhoon exerted a dominant effect on CONTAG, and its relative effect reached 52% (Fig. 3q).

The absolute effect sizes of both environment and typhoon disturbance generally varied consistently with their relative effects (Fig. 3r). The effect sizes of environment decreased from 5.0 in the early recovery stage (1710–2010) to 2.9 in the late recovery stage (1860–2010)

(Fig. 3r). Meanwhile, the effect sizes of typhoon increased from ~0 in the early recovery stage (1710–2010) to 3.3 in the late recovery stage (1860–2010). Especially, both environment and typhoon disturbance showed negative effects on CONTAG (Fig. 3r) with the landscape being more fragmented (smaller CONTAG value) under typhoon disturbances.

4. Discussion

We presented an empirical case study of reconstructing historical forest landscapes and the disturbance regime using a forest landscape model. The composition, structure and spatial patterns of the reconstructed forest ecosystem reasonably represented current forest conditions after a 300-year reconstruction. Historical field data did not exist for a full verification of the reconstructed succession trajectories. Thus, the trajectories were verified against the expected stand dynamics based

on forest successional theory and an understanding of the natural regeneration dynamics of the study site (Oliver and Larson 1996; Wang and others 2014b). Moreover, fluctuations in stand dynamics where total basal area decreased and total density increased corresponded to typhoon events, which confirmed that the patterns of forest disturbance and recovery for typhoons were captured. After 300 years of recovery, the forests have differentiated into the three forest zones corresponding to climatic zones (Fig. 4), suggesting that environment captured broad-scale forest distribution patterns. The above verifications suggested the validity of the reconstructed historical forest landscapes and disturbance regimes.

Environment was shown as the dominant factor controlling forest ecosystem composition, structure, and landscape patterning during the early stage of forest recovery (1710–1760). Although spatially explicit dispersal limitation and niche partitioning via environmental filtering was seen as the ultimate process responsible for the recovery (Fig. 4), environment constrained the establishment and growth (Plotkin and others 2002; Shen and others 2013; Kraft and others 2015). Within each elevation zone, the environments suited one group of species over the other, leading to an expected community assembly and stand structure (Xu and others 2004; Lebrija-Trejos and others 2010; Kraft and others 2015). Environment drove the leading and trailing edges of the species' distributions towards certain elevation zones (corresponding to climatic zones) where they thrive, thus regulating the spatial distribution of the specialist tree species. This is congruent with previous findings that environmental heterogeneity exerts the dominant influence on shaping forest patterns (Harms and others 2001; Prada and Stevenson 2016).

However, a study of second-growth forests suggested that the effects of environment immediately after the disturbances may not be as dominant but would increase because of legacy effects of long-term land-use and two major hurricanes (Hogan and others 2016). Our results further implies that early development of forest ecosystem tends to be a deterministic community-assembly process and provides evidence that niche differences among species shape forest patterns (Kraft and others 2008; Chase and Myers 2011).

Our results showed that the dominance of environment declined in the later stages associated with the increased effect sizes of typhoon disturbance. Once forests reach the mid- and late-successional stages, their composition generally remains stable, and thus the effects of environment decrease. In our case, the increasing relative importance of typhoon disturbance was resulted from their cumulative effects over time. However, some studies have claimed that the impact of environment conditions increase with succession (Harrelson and Matlack 2006; Campetella and others 2011). This conclusion may have resulted from studies conducted within a relatively short timeframe, like the early recovery stage in this study, which would limit the understanding of the cumulative effects of disturbance or other factors.

We were able to spatially simulate that the effects of typhoons on forest ecosystem composition, structure, and landscape pattern through the reconstruction. Results showed that early in recovery period, low tree density and small tree diameters (low height) made forests less susceptible to typhoons. As tree density decreased and diameter increased, forest ecosystems became more susceptible to typhoon damage (Rich and others 2007; Lin and others 2020). The reconstructed

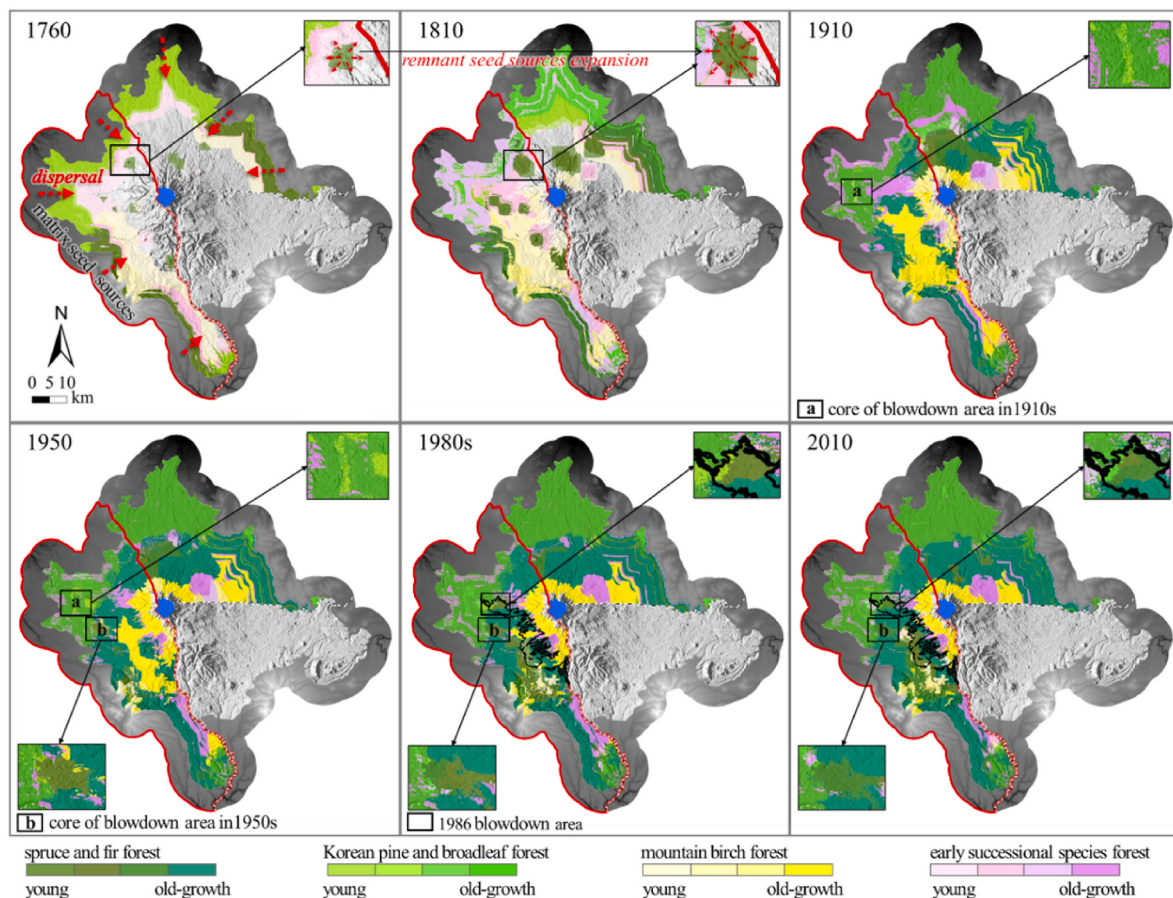


Fig. 4. The snapshots showing forest landscape recovery driven by seed dispersal and typhoons illustrated by stand age in the realistic scenario (ET). Top left: Seedlings are recruited into the open areas around matrix and remnant seed sources. Top middle: The recruited trees pause to mature before producing new seeds to colonize surrounding areas, causing the striped dispersal pattern and the further upward encroachment and outward expansion. Top right to bottom row: forest type gradually succeeds to into vertical zones matching current distribution. Three typhoon events (in 1910, 1950, and 1986) are illustrated, where early successional, young patches are shown (with cumulative disturbances) embedded within the surrounding old-growth forests.

forest landscapes revealed that typhoons had lasting impacts on forest composition and structure for up to many decades. For instance, the 1910 typhoon damaged older stands causing widespread mortality with affected forests changing from old to near-mature forests, which were not recovered by 1950, while the 1950 typhoon occurred that further reduced forest age, and its legacy remained beyond 2010. Likewise, the impact of 1986 typhoon persisted through 2010 (Fig. 4). When the recovery time from a disturbance exceeds the intervals between successive disturbances, multiple stochastic disturbance events will overlap in space, and create a complex landscape pattern as a result of the cumulative effects of disturbances (Turner 2010). Other studies have also reported the compound effects of successive disturbances on forest ecosystems (Busing and others 2009; Menges and others 2011; Turner and others 2019). For example, the cumulative effects of repeated hurricanes could change biomass and carbon balances (Busing and others 2009), and cause greater damage to the forest structure and function than a single disturbance event (Kim and others 2020, 2019). Similarly, McLaren and others (2019) reconstructed the historical hurricanes over 155 years in two tropical montane rainforests in Jamaica, and also confirmed the cumulative effects of successive hurricanes on forest structure and diversity. Studies like ours involving 300-year landscape reconstruction offered a long-term perspective of the cumulative effects of disturbance. The time-dependent cumulative effects highlighted the importance of historical disturbances in shaping current forest landscapes.

Recent studies reported that climate change alters the frequency and intensity of disturbances, which indirectly affects forest landscapes (Huang and others 2021; Duan and others 2021). However, in our study, the effects of climate change on disturbance regimes and forest recovery have not been considered. Previous studies of historical climate in Changbai Mt. found that climate has been relatively stable over the past 300 years, except for the warming after 1980s (Shao and Wu 1997; Du and others 2018). So far, there was only one typhoon event recorded in 1987 that destroyed large areas of forest (Guo and others 2015). Thus, although climate change can alter the frequency and intensity of disturbance such as fire (Huang and others 2021; 2018), we hypothesized that the interactions of climate change and typhoon have been stable since our study focused on the historical landscapes. Additionally, Xu and others (2018) reported few significant changes in forest composition and structure in the old-growth forests during the warming period (1981–2016) in Changbai Mt. Thus, there was no significant impact of the later climate warming on the forest landscape. Thus, our results should not be altered due to recent climate warming and the potential indirect effects of warming climate on typhoon disturbance.

Our study is among the few that quantify the relative contribution of environment and typhoon disturbance over large spatial and temporal scales. There are increasing concerns about the impact of global climate change and associated disturbance regime change on forest ecosystems (Vanderwel and Purves 2014; Lin and others 2020). Knowledge about the relative impacts of environment and disturbance allows us to disentangle the two factors and examine their interactive effects. This is especially important under changing environmental and disturbance regimes, because changes in disturbance regimes predicted under climate warming, such as increased disturbance intensity and frequency, might lead to greater changes in forest ecosystem composition, structure, and landscape pattern (Johnstone and others 2010; Turner and others 2019; Lin and others 2020).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envsoft.2022.105513>.

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