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RESEARCH ARTICLE

The impact of typhoon on post-volcanic-eruption forest landscape recovery: a study in Changbai mountain through 300 years of historic landscape reconstruction

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Abstract
Context Study of interplay of disturbance and forest succession is key to understand forest landscape dynamics, especially under changing climate and disturbance regimes. However, most such studies are from small spatial and temporal scales, and thus may be limited to generalize at large scales.

Objectives We investigate how typhoons affected forest dynamics at stand and landscape scales, whether the impacts differ among forest biomes, and whether a post-volcanic forest landscape could ultimately reach equilibrium under typhoon disturbances.
Methods We used landscape modelling to spatially reconstruct the time-series (1710–2010) for the post-volcanic-eruption forest landscapes driven by forest succession and typhoon in Changbai Mountain, China. We compared aboveground biomass (AGB), climax tree species importance value, degree of recovery, and landscape pattern between northern (with typhoons) and southern and western Changbai Mt. (without typhoons).
Results The effects of typhoon disturbances were minimal when forests were young (before ~1810) but gradually increased as tree grew and forest recovered. The response of forest biomes to typhoon varied, which can be attributed to individual species traits. With recurring typhoons landscape did not reach an equilibrium until 2010. However, the effects of typhoons on landscape pattern gradually stabilized after 1960, suggesting landscapes with typhoons may eventually reach a steady state.
Conclusions Typhoons have long-lasting and cumulative effects that varied with successional-stages and forest biomes. Landscape under infrequent, large disturbances is nonequilibrium in the short term, but may ultimately reach equilibrium over long time periods. Historical landscape reconstruction reveals fuller spectrum of interplays of typhoons and succession.

Mia M. Wu and Xianghua Zou have contributed equally to this work as joint first authors.

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Keywords Typhoon disturbance · Landscape equilibrium · Forest landscape dynamics · LANDIS PRO

Introduction

The classic paradigm of landscape equilibrium suggests that forest ecosystems after disturbance would develop along expected successional pathways towards landscape equilibrium (Whittaker 1953; Bormann and Likens 1979). The concept of landscape equilibrium was developed by Bormann and Likens (1979) and Turner et al. (1993). It suggests that a seral stage at a local place may change over time, but over a sufficiently long time, the proportion of each seral stage on the landscape becomes relatively constant. Shifting mosaic steady state further suggests that while the proportions may become stable but the locations (patches) of various seral types may shift over time. Scientists have increasingly reported alternative paradigms in which disturbance may cause forest ecosystems to diverge from expected successional trajectories to develop alternative pathways (Wu and Loucks 1995; Mori 2011). Depending on disturbance regime (intensity, frequency, size), this divergence may result in landscapes that are expected to reach equilibrium, to evolve into dynamic steady states, or to remain at non-equilibrium (Turner et al. 1993). Understanding the interplay of disturbance regime and landscape dynamics is essential to anticipating future landscape changes, especially under alternative climate and disturbance regimes (Huang et al. 2021).

Wind disturbance is a stochastic process that can range from small and frequent to large and infrequent events (Lorimer and White 2003; Meigs and Keeton 2018). Correspondingly, landscape responses vary widely to these varied disturbance regimes (Boose et al. 1994; Everham and Brokaw 1996; Turner 2010). Commonly, small, frequent wind disturbances such as windthrow occur at stand scales, at which canopy trees are blown down to create small gaps for the establishment of early successional, light-demanding tree species (Marra et al. 2018). This gap-scale disturbance has little effect on forest successional pathways at landscape scales, because the forest landscape ultimately would reach equilibrium characterized by predominant old-growth forests with small pockets of early successional tree species (Brokaw and Scheiner 1989; Chambers et al. 2013). However, large, infrequent wind disturbances, such as hurricanes and typhoons, span a large spatial extent, often with long return intervals. Where they occur, they greatly alter forest landscapes by creating large openings (Foster et al. 1998). Recurrent hurricanes can create a complex landscape pattern consisting of forest patches of varying ages and sizes at different forest successional stages. In some cases, large wind disturbances may trigger different forest successional pathways and impede a forest landscape from reaching an equilibrium state (Nagel et al. 2014; Čada et al. 2016).

Forest dynamics following wind disturbance are partly dependent on tree species response to the disturbance. On one hand, major differences exist among tree species in their susceptibility to wind disturbance, which is related to species-specific traits such as morphology, wood structure, and age (Foster and Boose 1992; Canham et al. 2001; Xi and Peet 2011). Generally, early successional species are characterized as light-demanding, fast-growing, short-lived, and of low wood density. They are typically more vulnerable to wind disturbance than slow-growing, long-lived, and shade-tolerant species (Foster 1988b; Rich et al. 2007). Additionally, forest recovery after wind disturbance is related to tree species' ability to regenerate and eventually be recruited into the canopy (Papaik and Canham 2006; Xi et al. 2008). Many studies found that shade-intolerant species tend to recruit rapidly in large open areas from high-severity wind disturbance (Xi et al. 2008; Kosugi et al. 2016), whereas shade-tolerant species thrive following low or moderate severity wind disturbance in mixed-species forests (Harcombe et al. 2009; Meigs and Keeton 2018). Therefore, given the variation among species in response to varied wind disturbances, it is likely that different forest types would differ in their response to wind disturbance.

Detecting whether post-disturbance landscapes reach an equilibrium, steady state or a non-equilibrium state requires examination of long-term forest dynamics over large spatial extents (Baker 1989). Such a task is hindered by the intractability of the driving factors since any contemporary landscape is the outcome of complex interactions and cumulative effects of the disturbance, environment, and forest succession. Consequently, previous studies have largely relied on post-disturbance inventory and monitoring, which span relatively short time periods

(Harcombe et al. 2002; Meigs and Keeton 2018). Forest landscape models (FLMs) may bridge the gap by integrating theories of forest stand dynamics and disturbance ecology with limited field data and disturbance history data (Wang et al. 2013, 2014). FLMs are designed to incorporate trees' species-specific demographic processes such as seed dispersal, establishment, growth, mortality, and competition, at the stand scale and the interaction with wind disturbances at landscape scales (He 2008; Wang et al. 2013, 2014). FLMs can be parameterized at a historic time and simulate forest succession forward with rigorous verification and validation (Wu et al. 2020). By doing so, we can dismantle the individual forces and reassemble them to reconstruct historic landscape series.

In this study, we analyzed the long-term effects of typhoon disturbances by spatially reconstructing a time series of historic forest landscapes and typhoon disturbance regimes using a FLM. In particular, we addressed: (a) how long-term typhoon disturbances affected forest dynamics at the stand and landscape scale; (b) whether the impacts of typhoon disturbances differ among forest biomes; and (c) whether the forest landscapes could ultimately reach equilibrium or non-equilibrium states under typhoon disturbances. The outcome of the study helps to gain insight into large, infrequent disturbances and their impacts on forest landscape dynamics.

Approach and methods

Study area

Our study area was on Changbai Mountain, northeast China, bordering North Korea (Fig. 1). The climate varies by elevation with a temperate continental climate regime at low elevations (530 m) ranging to a polar climate regime at the mountaintop (2691 m). The annual mean temperature decreases from 7 °C at low elevations to 3 °C at high elevations, and the annual precipitation increases from about 760 mm at low elevations to about 2000 mm at the mountaintop. Vegetation types in this region correspond to the elevational zones, with mixed Korean pine-broadleaf forests at low-elevation zones (530–1100 m),

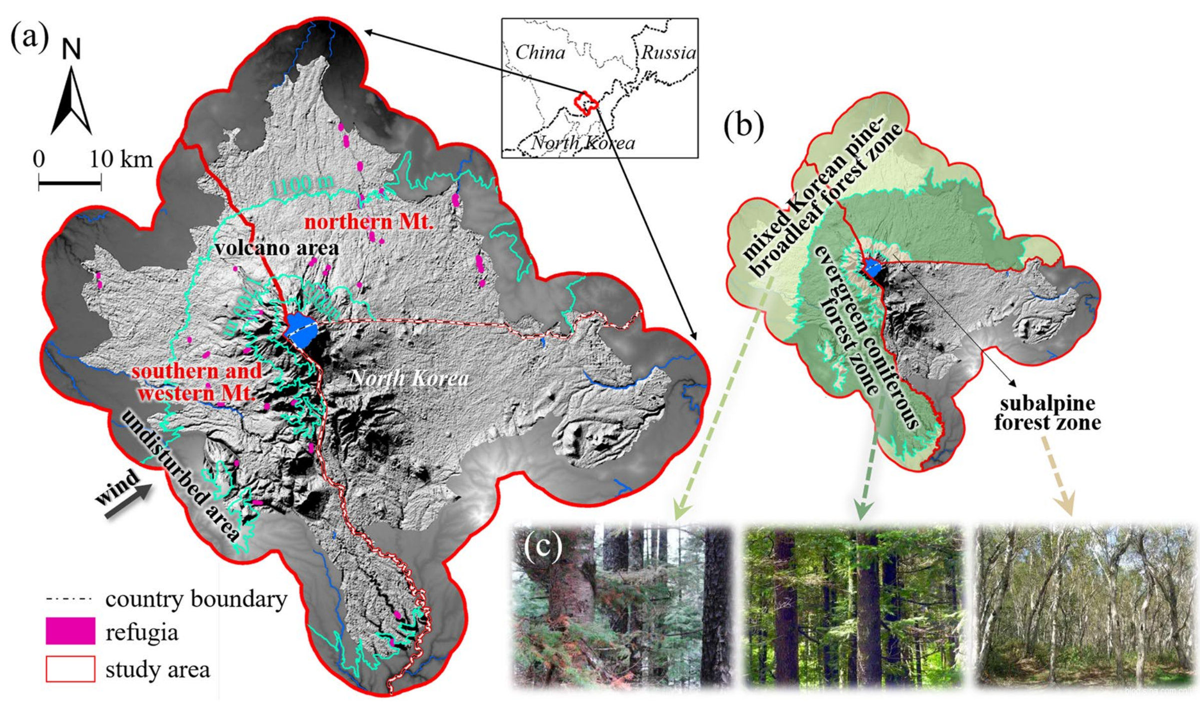

Fig. 1 The study area in Changbai Mountain bordering North Korea (**a**). The bright grey represents the volcano destroyed area and dark grey is a 15 km-width undisturbed area. Current forests in the study area have evolved into three vertical forest zones by altitude (**b**). Snapshots of the dominant forests in each forest zone (**c**)

evergreen coniferous forests at mid-elevation zones (1100–1700 m), subalpine forests at higher-elevation zones (1700–2100 m), and alpine tundra at the highest elevation zones (above 2100 m). The dominant overstory tree species include Korean pine (*Pinus koraiensis* Siebold and Zucc.), basswood (*Tilia amurensis* Rupr), and maple (*Acer mono* Maxim) at low-elevation zones; jezo spruce (*Picea jezoensis* Siebold and Zucc.) and Manchurian fir [*Abies nephrolepis* (Trautv.) Maxim] at mid-elevation zones; and mountain birch (*Betula ermanii* Cham) at higher-elevation zones. Within their corresponding elevation zones, these tree species are either late-successional and shade-tolerant species or climatic climax species (e.g., mountain birch). In addition, the other common shade-tolerant tree species include elm [*Ulmus davidiana* Planch. var. *japonica* (Rehd.) Nakai] and ash (*Fraxinus mandshurica* Rupr). Other shade-intolerant species include Asian white birch (*Betula platyphylla* Suk), aspen (*Poplus davidiana* Dode), Mongolian oak [*Quercus mongolica* (Fisch) Ledeb.], and Olga Bay larch (*Larix olgensis* A. Henry).

A Plinian eruption occurred in 946 A.D., well-known as the 'Millennium Eruption' with a volcanic explosivity index of 7 on Changbai Mt. (Horn and Schmincke 2000; Wei et al. 2003; Iacovino et al. 2016). The eruption destroyed most plants within a ~50-km-radial area. The undisturbed habitat below the eruption area and isolated refugia within the eruption area served as sources of seed (Fig. 1). The size of matrix seed sources and the location of remnant seed sources were determined in Wu et al. (2020) with a reference to a study of Mount St. Helens (Antos and Zobel 1986).

After hundreds of years of recovery, forests landscape reached equilibrium at each elevation zone on northern Changbai Mt. This was because it had not been affected by major natural and human disturbances due to its remoteness and relatively high precipitation (760–2000 mm). The forests had been under natural succession ever since the millennium volcano eruption and have already reached a climax condition (Qian 1983). However, such equilibria were not apparent on southern and western Changbai Mt. where early successional forests were frequently mosaicked within mature forests, because of prevailing southwest typhoons. For instance, on 28 August 1986, Typhoon Vera landed on southern and western Changbai Mt., destroying 11,386 ha of forest and creating large openings spanning across all three elevation zones (Guo et al. 2010).

Overall approach

Volcanic ash and erosion after the Millennium Eruption hindered forest recovery, since the substrate after the eruption was unsuitable for tree survival and establishment for the first few hundred years (Xu and Liang 2010). This was reaffirmed by field inventories within the volcano-disturbed area that reported tree ages were no more than 300 years and decreased with increasing altitude. This indicated that tree species establishment and colonization from the lower matrix seed sources and remnant seed sources did not start prior to 1710 s (Zhao 1984; Xu and Liang 2010). Consequently, we reconstructed the historic forest landscapes within the volcano-disturbed area from 1710 to 2010, which was sufficiently long to study the forest landscape recovery.

We assumed that the surrounding matrix forests beyond the volcano blast zone had been in an old-growth stage for the last 300 years. This assumption was made based on Zhao (1984) who analyzed charcoal records from the pre-eruption forests and found that pre-eruption forest vegetation was nearly the same as the current old-growth forests with typical stand structure of live and dead trees. This condition suggested that the protected matrix forests adjacent to the volcano-disturbed area had reached the late-successional stage at the time the volcano eruption occurred. Afterward, due to rare human disturbances (due to the remoteness) and natural disturbance (due to relatively low altitudes not exposed to typhoons and high precipitation which eliminated fire), the matrix forests had been under natural succession ever since the volcanic eruption. In addition, our own field investigation in matrix forests and those of others (Hao et al. 2008; Shao 2011) also confirmed that the matrix forests had the old-growth characteristics including old stand age, canopy closure, and dominant climax tree species. Thus, we concluded that it was reasonable to parameterize the initial (1710 s) forest composition using contemporary old-growth data from the volcano-undisturbed area.

We derived historical typhoon disturbances by combining remote sensing images and field inventory data. Since typhoons are the only disturbance that could reset forest succession in this area, without typhoons forests would success to the old-growth stage and uniformly distribute in all climatic zones such as we reported in the protected sides of Changbai Mt. (Wu et al. 2020). Thus, forest patches at early and mid-successional stages can reveal historical typhoon events. These forest patches were identified in remote sensing images and their stand ages (the time of typhoon events) were determined by field inventory data, which was consistent with previous studies (Yang and Xie 1994; Shao et al. 1996). Our approach to determine the historical typhoon regime was analogous to those used to characterize stand-replacing fire regime (Johnson 1992). From all the typhoons inferred (a total of 11), we calculated mean disturbance size (3771.5 ha, i.e., 5.4% of this region) and the mean wind return interval (500 years).

We evaluated the effects of typhoon on forest recovery in Changbai Mt. by comparing forest dynamics between northern Changbai Mt. and southern and western Changbai Mt. Here, we assumed that influencing factors other than typhoon disturbances are identical between northern Changbai Mt. and southern and western Changbai Mt. Location proximity leads to similar climatic and edaphic conditions among them. In addition, abundant precipitation has led to fire events being rare in this region. Further, strict forest protection policies and remoteness resulted in little human disturbance in the study area. Therefore, without typhoon disturbance, forests on both the northern side and southern and western side would follow the same successional trajectories and develop into mature forests in each respective climatic zone, with any differences attributed to primarily typhoon disturbance. This assumption has also been confirmed by Jin et al. (2020) and Liu (1997) who reported that the landscape mosaics in the forested zones in the southern and western side that differed from northern side were resultant from typhoon disturbances. In our simulations, we assigned the same model parameters (e.g., species life-history attributes) except wind parameters, and thus, the simulated differences reflected the effects of typhoon regime [see below for detail parameterization and simulation for wind disturbance (typhoon)].

LANDIS PRO model and parameterization

We used a forest landscape model, LANDIS PRO, to reconstruct the spatial-temporal dynamics of the historical forest landscape and typhoon disturbances in Changbai Mountain from 1710 to 2010 using a 10-year time step with 20 replicates. LANDIS PRO records tree density and size information by species and age cohort at each pixel (Wang et al. 2013). It simulates tree species demographic processes including growth, aging, sprouting, seed dispersal, establishment, competition, and mortality, which are driven by species-specific life history traits (i.e., longevity, age of reproductive maturity, shade tolerance, and seed dispersal distance, among others), which were obtained from previous studies (Liang et al. 2012; Dijak et al. 2017). LANDIS PRO simulates forest stand dynamics including four development stages: stand initiation, stem exclusion, understory reinitiation, and old-growth (Wang et al. 2013). Stand (pixel) dynamics are regulated by available growing space which is determined using a relative stand density index based on the density and size of trees at a site (Wang et al. 2013). LANDIS PRO simulates seed dispersal following Clark et al. (1999) dispersal algorithms which use a shape coefficient to adjust dispersal curves corresponding to individual species. For example, animal-dispersed species are slightly thin-tailed with relatively short dispersal distances and broad densities, while wind-dispersed species are relatively fat-tailed with longer dispersal distances and narrow densities. LANDIS PRO can spatially and temporally output numbers of trees by species and age cohort for each pixel and the entire landscape.

Wind disturbance is a spatially contiguous landscape process. When it occurs, where it occurs, and how large it occurs are not deterministic. Thus, LANDIS PRO uses probabilistic approach including mean return interval and mean size and standard deviations and the lognormal distribution to stochastically simulate wind disturbance. These statistic parameters are derived from historical wind disturbance events (remote sensing and field inventory data in this study). Wind is simulated as a top-down disturbance, where species susceptibility increases with age and size (Mladenoff and He 1999). In Changbai Mountain, typhoons occur almost exclusively on the west and south sides of Changbai Mountain. As a strong wind disturbance, it can destroy almost all the trees (few small trees survived). To account for the stochasticity in wind disturbance, we conducted 20 model replicates and we chose one representative for illustration (Fig. S1). Therefore, typhoons would occur randomly over the landscape following the size distribution. Simulated results of forest landscape dynamics were generated from the 20 replicates with means and standard deviations.

To better capture the environmental heterogeneity in LANDIS simulations, the entire landscape was stratified into multiple land types derived by overlaying GIS layers of climate, soil, and terrain. Thus, each land type captured the coarse-scale climatic pattern (elevation zones) and fine-scale topography and soil (pixels). Within a given land type, potential species assemblages were quantified by species establishment probabilities (SEP) and resource availability was quantified as maximum growing space occupied (MGSO). SEP and MGSO values for each land type were derived from the LINKAGES ecosystem process model from prior studies (Hao et al. 2001; He et al. 2002; Liang et al. 2012).

We modeled the 12 most abundant tree species in the study region (Table 1); collectively those species accounted for over 90% of aboveground forest biomass (Hao et al. 2008; Shao and Deng 2000). We parameterized the initial tree species composition based on an inventory of 45 old-growth field plots (20 m × 20 m) located in the matrix seed source areas surrounding the volcano impact zone. The inventories were conducted in 2010 and 2014, and they recorded the number of trees and their diameters by species.

Model calibration and result validation

To calibrate model parameters and validate the simulated results, we surveyed 135 plots by recording the number and diameter of trees by species in 2010 and 2014. We used 2/3 of the plots for model calibration by iteratively adjusting model parameters (e.g., age-DBH relationships by land type, the number of seeds and maximum DBH per species) until there were no significant differences (paired t-tests, $p > 0.05$) between the 2010 s inventory data and the 2010 simulated values of tree species basal area and density by each elevation zone. We then used the remaining 1/3 of the plots to independently validate the simulation results at year 2010 (Fig. S2). To ensure the intermediate simulated processes (1710–2010), i.e., forest development processes, are credible, we evaluated the simulated forest development trajectories with and without typhoon disturbance using Ginrich (1967) stocking charts (Fig. S4) (Wang et al. 2014). In addition, we showed species-level forest recovery trajectories. Based on the species-specific attributes (i.e., early/mid-/late- successional species), we verified whether the simulated tree species trajectories and turnovers measured by basal area and density were supported by the theories of stand development (Fig. S5) (Oliver and Larson 1996; Wang et al. 2014).

Data analysis

We developed criteria to characterize the process of forest recovery (*recovered*, *recovering* and *unrecovered*). Forest recovery after large disturbances is often characterized by increased biomass and/or successional change (e.g., from stand initiation with pioneer species to mid-successional then late-successional stage with medium and shade tolerant species). Therefore, we used aboveground biomass (AGB) and species composition to characterize the degree of forest recovery.

We quantified biomass recovery at a given pixel (*i*th stand) as the ratio of the actual aboveground biomass (AGB_i) to the maximum aboveground biomass (AGB_{max}) that can be reached within the climatic zone. We quantified species composition at a given pixel (*i*th stand) using the *importance value* (IV) of late-successional or climax species. IV is measured as these species' basal area/total basal area + these species' tree number/total tree number, ranging from 0 to 2. Thus, we defined degree of stand recovery (DSR) at stand *i* as $DSR_i = AGB_i / AGB_{max} + IV_i/2$.

Table 1 The dominant species and their relative abundance in our study area

Species	Korean pine	Basswood	Maple	Spruce	Fir	Mountain birch
Relative abundance (%)	9.8	9.0	9.5	19.5	14.2	5.6
Species	Elm	Ash	White birch	Aspen	Oak	Larch
Relative abundance (%)	4.3	2.9	4.8	4.0	3.3	6.9

We classified the stand *i* as *recovered* when its AGB reached the average AGB at the late-simulation stages when the AGB became stabilized (i.e., last 30 years of the simulation, the average AGB value was approximately equal to 0.45 of AGB_{max} in our study area) and IV/2 > 0.66 according to Seidl et al. (2014), indicating species composition is at the late successional stage, that is, DSR > 0.45 + 0.66 = 1.11. Likewise, we classified a given stand as *unrecovered* when its AGB did not even reach the average AGB for the initial 100 to 150 years of the simulation when stands were mostly occupied by pioneer species and these species thrived to mature forest conditions (the average AGB value was approximately equal to 0.4 of AGB_{max}) and there were no late-successional or climax species (IV = 0), that is, DSR < 0.4. Therefore, based on DSR we classified forest recovery into three categorical levels: *unrecovered* (DSR < 0.40), *recovering* (DSR 0.40–1.11), and *recovered* (DSR > 1.11, i.e., AGB and IV/2 reached the level of late-successional or climax stages of recovery) (Table 2).

We calculated the absolute effects of typhoons by comparing AGB, IV, and DSR values for northern Changbai Mt. with those of typhoon-impacted southern and western Changbai Mt. We used a spatially stratified sampling scheme to randomly select pixels (stands) from each forest zone in northern Changbai Mt., as well as in the typhoon-disturbed southern and western Changbai Mt. Additionally, we analyzed the mean post-disturbance stand recovery for all typhoon events in each forest zone to assess the responses of stands to wind disturbances.

To assess the degree of forest recovery at the landscape level, we designed an index, degree of landscape recovery (DLR), which measures the proportion of recovered stands in each forest zone. Moreover, we also measured the aggregation index (AI) to assess the effects of typhoon disturbances on forest landscape pattern. AI measures the level of aggregation of the landscape with value ranging from 0 to 100. AI values decrease with increasing level of fragmentation (He et al. 2000) (Table 2).We evaluated landscape dynamics (equilibrium/nonequilibrium) by monitoring the dynamics of the proportions of the patches at different recovery stages (*unrecovered*, *recovering*, and *recovered*). Specifically, when the proportions of the patches of different recovery stages became constant, we regarded the landscape as having reached the equilibrium.

Results

Effects of typhoon disturbance at the stand scale

In the initial decades (before ~1810) of the modeled forest landscape recovery, the trajectories of AGB, IV, and DSR were similar in undisturbed (on northern Changbai Mt.) and disturbed stands (on southern and western Changbai Mt.) for each forest zone (Fig. 2). Seedling recruitment increased in the open area while each species reached its native elevational zone driven by seed dispersal. AGB, IV, and DSR all increased progressively after 1710 in the mixed Korean pine-broadleaf forest zone and the evergreen coniferous forest zone (Fig. 2a–f). Similar increases were observed from about 1760 in the subalpine forest zone (Fig. 2g–i). There was little difference (close to 0) in the three measures before ~1760 in the mixed Korean pine-broadleaf forest zone and the evergreen coniferous forest zone and before ~1810 in the subalpine forest zone (except for IV) (Fig. 2j–l). Typhoon disturbances showed little effect on AGB, IV, and DSR at the stand level, because juvenile trees were less susceptible to wind disturbance due to their

Table 2 Definitions, and equations of metrics for measuring stand and landscape recovery

Metric	Definition	Equation	Notes
AGB	Aboveground biomass	Sum of all tree aboveground biomass	≥ 0
IV	Importance value of late-successional or climax species	(Basal area/total basal area) + (tree number/total tree number) of the species	0–2 (2 most important)
DSR	Degree of stand recovery	$DSR_i = AGB_i/AGB_{max} + IV_i / 2$	0–2 (2 highest degree)
DLR	Degree of landscape recovery	DLR_j = area (recovered stand)$_j$/total area$_j$	0–1 (1 highest degree)
AI	Aggregation index	From He et al. (2000)	0–100 (100 most aggregated)

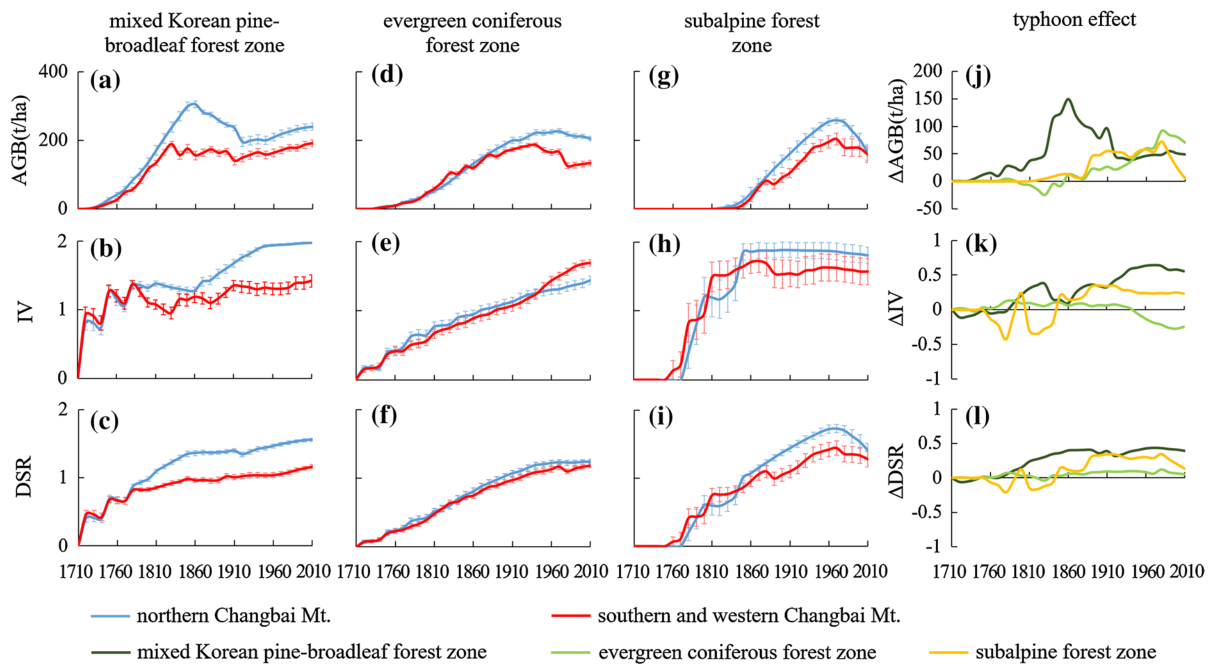

Fig. 2 Trajectories of the reconstructed aboveground biomass (AGB), importance value (IV) of late-successional and climax tree species, and degree of stand recovery (DSR) from disturbed and undisturbed the stands (pixels) by forest. Error bars are marked as mean ± confidence interval and the number of pixels randomly select in column 1, 2, and 3 are 220, 500, and 50, respectively). The differences (Δ) in ABG, IV, and DSR between disturbed and disturbed stands are shown in the last column (j, k and l)

smaller canopies and less exposed volume compared with large tall trees.

The differences in AGB between the northern Changbai Mt. (protected) and southern and western Changbai Mt. (disturbed) showed similar patterns for all three forest zones, with the differences initially non-existent, then increasing, and later decreasing (Fig. 2a, d, g). However, the timings at which the pattern showed changes (e.g., from no differences to increasing or decreasing differences) varied by forest zone. The timing for when the difference started to increase was circa 1750 in the mixed Korean pine-broadleaf forest zone, and delayed for about 80 years in the evergreen coniferous forest zone, and 130 years in the subalpine forest zone. The difference in timing reflected the mechanisms of seed dispersal, in that seed from matrix seed sources colonized the mixed Korean pine-broadleaf forest zone first, followed by the evergreen coniferous forest zone, and then subalpine forest zone. Likewise, the timing when the difference started to decrease was circa 1860 in the mixed Korean pine-broadleaf forest zone, and 1980 in the evergreen coniferous forest zone and subalpine forest zone. Especially, for the mixed Korean pine-broadleaf forest zone, the differences gradually leveled off after 1920 (Fig. 2a). Thus, the decrease in differences lasted no more than 60 years for each forest zone, suggesting the time span of the legacy effects of typhoons.

As simulated forest succession progressed, the effects of typhoon disturbances on species composition (IV) and forest recovery (DSR) differed among forest zones. For the mixed Korean pine-broadleaf forest zone and the subalpine forest zone, as late-successional and climax species gradually became dominant, typhoon-caused mortality of these species increased in disturbed stands (on southern and western Changbai Mt.) Consequently, the differences in IV and DSR showed a general increase with some fluctuations in response to typhoons from 1770 in the mixed Korean pine-broadleaf forest zone and from 1850 in the subalpine forest zone (Fig. 2k, l). As the effects of typhoon disturbances stabilized after 1940, so did these differences. However, for the evergreen coniferous forest zone, the differences in IV were stabilized and minor (less than 0.1) until 1950 (Fig. 2k). As forest growth progressed and typhoon events accumulated over time, the IV of disturbed stands in the southern and western Changbai Mt. even surpassed that of undisturbed stands in the northern Changbai Mt. in the evergreen coniferous forest zone after 1950, and the difference in IV gradually decreased to a minimum (−0.3) at 2000. Typhoon disturbances increased the IV of spruce but decreased AGB, which led to similar DSR (the difference < 0.1) throughout the simulation (Fig. 2l).

Effects of typhoon disturbance at the landscape scale

The landscape-level recovery emerged from the cumulative effects of the stand-level recovery. The recovery process started mainly from the matrix seed sources found at low elevations outside the volcano impact zone and gradually moved to higher elevations, showing a striped encroachment pattern. It was not until year 1760 that recovered sites were visible along the north and south borders of the volcano-disturbed landscape (Fig. 3a, b, c). The landscape recovery spanned centuries as the expanding, striped pattern showed the recovering sites becoming recovered throughout 1710–2010 (Fig. 3). The area occupied by recovering patches showed a decrease after 1890 in northern Changbai Mt. and after 1950 in southern and western Changbai Mt. (Fig. 4). In addition, the scattered remnant seed sources played an important role in forest landscape recovery as the spotted recovering and recovered patches started to form around those remnant patches about one hundred years into the forest landscape simulation (1810) (Fig. 3d). These patches gradually coalesced with the recovered patches that originated from matrix seed sources and this increased landscape connectivity beginning 200–250 years into the reconstruction (Fig. 3e, f).

The evidence of typhoon impacts was clear on the landscape. Typhoon disturbance effects became clearly visible 150 years into the simulated landscape recovery and resulted in forest fragmentation. Across the landscape, typhoons created a mosaic of

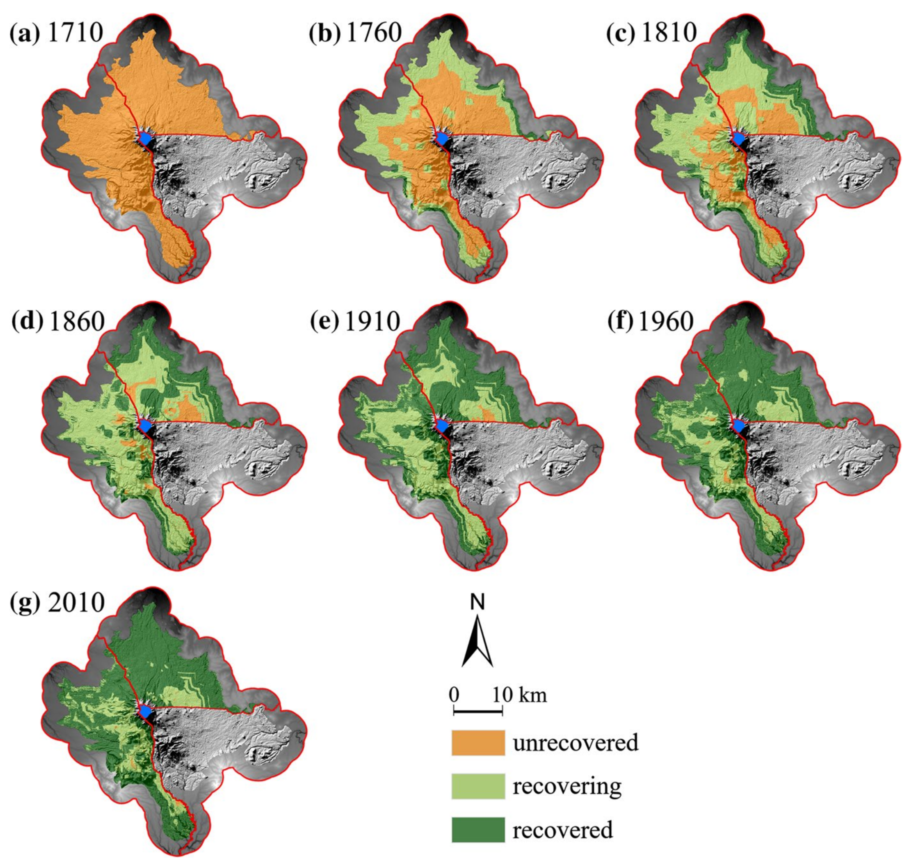

Fig. 3 The degree of stand recovery (DSR) pattern at 1710, 1760, 1810, 1860 s, 1910, 1960, and 2010 in northern Changbai Mt. and southern and western Changbai Mt.

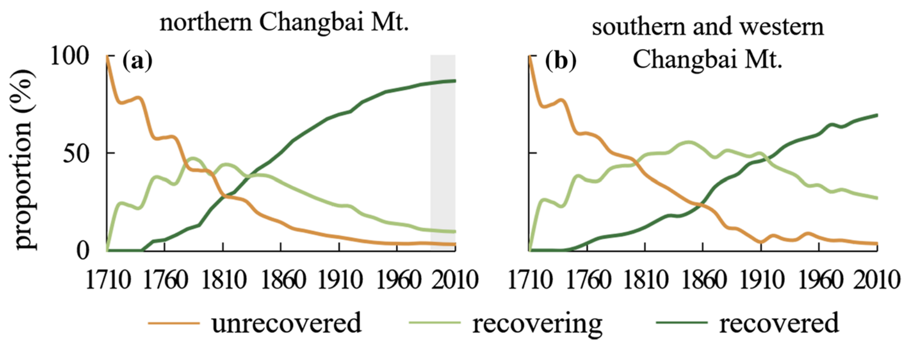

Fig. 4 The proportions of patches in different recovery stages

stand conditions by setting some of the recovered forest sites in southern and western Changbai Mt. back into an unrecovered (or newly regenerated) state. In contrast, northern (protected) Changbai Mt. experienced no typhoon disturbance, and consequently by 2010 most of the northern landscape had evolved into a highly connected landscape of recovered forest. However, southern and western Changbai Mt. continued to show a forest landscape mosaic with many pockets of unrecovered and recovering forest area scattered within the matrix of recovered forests (Fig. 3g). Specifically, the proportions of patches in different recovery stages became stabilized by 1990 in northern Changbai Mt., of which the proportion of recovered patches reached approximately 90%. However, due to typhoon disturbances, the proportion of recovered patches in southern and western Changbai Mt. was still increasing, reaching only 70% by 2010 (Fig. 4).

Forest landscape patterns showed similar dynamics among the three forest zones. In the initial year of recovery, the landscape was homogeneous, with no or little forest cover. DLR were essentially zero and AI reached the maximum in all forest zones (Fig. 5a–h). Subsequently, as unrecovered sites gradually moved to the recovering or even recovered stage, DLR started to increase and AI gradually decreased caused by increasing landscape heterogeneity. Due to little effect of typhoon disturbance in the early decades of the simulation, the differences in DLR and AI were minimum for each forest zone except for the subalpine forest zone where the changes in DLR and AI values were delayed until 100 years after the start of recovery (Fig. 5g–h). Later, as the area of

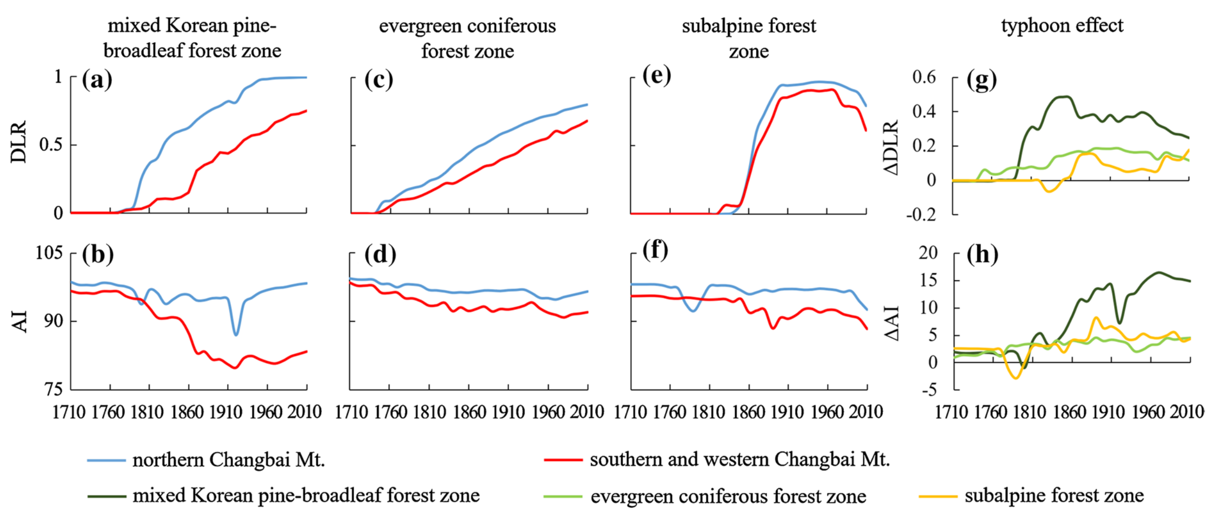

Fig. 5 Trajectories of the reconstructed degree of landscape recovery (DLR) and aggregation index (AI) from northern Changbai Mt. (protected) and southern and western Changbai Mt. (disturbed) by forest. The differences (Δ) in DLR and AI between northern Changbai Mt. and southern and western Changbai Mt. are shown in the last column (g, h)

recovered sites increased over time, the effects of typhoon disturbances became more apparent, and the differences in DLR and AI between northern Changbai Mt. (protected) and southern and western Changbai Mt. (disturbed) increased. The differences in the mixed Korean pine-broadleaf forest zone were greater than that observed in other forest zones from around 1810. Later, as the forests were nearly recovered and the landscape patterns became relatively stable, the difference in DLR gradually became stabilized from around 1900. The difference in AI also were relatively stable with only with minor fluctuations from around 1960, and the effects of typhoons on the forest landscape became relatively constant at late stages of recovery.

Discussion

We reconstructed historic forest landscapes and typhoon disturbances over the past 300 years (1710–2010) for Changbai Mountain, during which the forests were recovering from the 946 A.D. volcano eruption. Even in the northern Changbai Mt. where typhoon was absent, recovery is ongoing as forests grow towards the maximum capacity and age (quantified by MGSO in LANDIS) (Wang et al. 2014). In the exposed mountain sides (western and southern Mt.), forest recovery follows the general trend of post-volcanic eruption forest succession. Thus, by comparing forest dynamics between northern Changbai Mt. and southern and western Changbai Mt, we removed the common trend of post-volcanic eruption forest succession and revealed the impacts of typhoon disturbance on forest composition, ecosystem functioning, and landscape pattern. This work, to our knowledge, is among few attempts that evaluate quantitatively the long-term effects of typhoons on forest landscapes. Long-term studies are essential to understanding cumulative effects of large, infrequent disturbances that have a long-lasting imprint on forest ecosystems (Weishampel et al. 2007; Turner 2010; Seidl et al. 2014). In addition, the large spatial extents spanning multiple forest zones in our study allowed us to examine the variation among forest biomes in their response to typhoon disturbances.

Our results suggested that typhoons have long-lasting effects that significantly affect forest composition, biomass, and landscape pattern. Results showed that forests experiencing high biomass loss induced by typhoons take decades to recover like those reported for hurricanes (Fig. S6) (McNulty 2002; D'Amato et al. 2017). The forest openings created by hurricanes disproportionally favor some tree species over others, causing shifts in species composition (Harcombe et al. 2009; Xi et al. 2019), further altering forest successional trajectories. In addition to such stand-scale effects, we found that typhoons increase landscape heterogeneity in ways also reported for hurricanes (Foster 1988a; Boose et al. 2001; Platt et al. 2015). Thus, large, infrequent wind disturbances, such as typhoon or hurricane, play important roles in the wind-prone forest ecosystems. Especially, typhoons are a common disturbance in Eastern Asia while their impacts have been rarely studied on temperate forests (Saito 2002; Wu et al. 2019). Our work confirmed what is known about large disturbances derived mostly from other disturbances such as fire and added typhoon to the literature body.

At the stand scale, the effects of typhoon disturbances on forest recovery varied with forest successional stages. As expected, typhoons showed roughly increasing effects at early recovery stage for each forest biome. In addition to increasing susceptibility of trees to wind disturbances over succession (due to increasing tree size) (Foster and Boose 1992; Sharitz et al. 1993), recurring typhoons caused compounding effects. When the intervals between typhoons were less than the recovery time for affected forests, multiple disturbance events worked synergistically and exerted greater pressure for forest change. Other studies also reported the cumulative effects of repeated disturbances in forest ecosystem dynamics (Busing et al. 2009; Menges et al. 2011; Turner et al. 2019; Kim et al. 2020) reported that successive hurricane disturbances could induce greater change to the forest structure and function than a single hurricane. As forests grew into mature or old-growth states, the effects of typhoons on forest recovery gradually stabilized. Long-term examination of typhoons' roles is essential for understanding forest response to regimes of large, periodic disturbances in different successional stages, since this information is difficult to obtain from short-term studies.

The response of different forest biomes to typhoon disturbance varies. Recurring typhoon disturbances resulted in lower aboveground biomass (AGB) in disturbed stands than undisturbed stands among the three biomes, but the degree of reduction varied. The largest decrease was found in the mixed Korean pine-broadleaf forests, followed by the evergreen coniferous forests, and subalpine forests. This was because AGB of these biomes decreases in this order. Forests with higher AGB usually suffer more loss from typhoon disturbance. Correspondingly, the time for recovery from typhoon disturbance is longer in the forests with high biomass loss (Fig. S6). Additionally, we found that occurrence of typhoons caused a decrease in the importance of late-successional/climax species in mixed Korean pine-broadleaf forests and in subalpine forests, but an increase in the evergreen coniferous forest at the late recovery stage (when most forests reached old-growth/mature stages). This discrepancy depends on specific-species biological attributes and their response to wind disturbance. Our simulated results demonstrated that in the mixed Korean pine-broadleaf forests and alpine forests, pioneer tree species are white birch, aspen, and larch, which are rapidly recruited in the large openings created by typhoons. This resulted in a decrease in dominance of late-successional/climax species, causing species composition shifts and species diversity to increase. Likewise, the phenomenon was widely reported in other forest ecosystems with severe disturbances (Xi 2015; Kosugi et al. 2016). For example, Xi et al. (2008) reported a dramatic increase in light-demanding hardwood species in pine stands after a hurricane hit the Duke Forest in North Carolina USA. However, spruce, which is primarily in the evergreen coniferous forest zone, is a late-successional species but grow well under full sunlight. Moreover, because of seed source limitations, other pioneer species (aspen and birch) could not reach the spruce-fir forest biome. Thus, spruce exhibited abundant regeneration after disturbances. Similar regeneration patterns have been observed for European Norway spruce (Svoboda et al. 2010; Novakova and Edwards-Jonasova 2015). Therefore, taking into account species' biological attributes is essential to understanding the response of forest ecosystems to large disturbances as different responses of forest biomes to typhoon disturbances are because of the different biological attributes.

Theoretically, equilibrium can be precisely defined, but it is not straightforward when applied to real ecosystems (DeAngelis and Waterhouse 1987). Empirical studies suggest that landscape equilibrium is more likely to occur in ecosystems where disturbance effects are not severe enough to significantly change the successional trajectory (Shugart 1984; Picket and White 1985). The northern Changbai Mt. is one such ecosystem, where forests have not been subject to strong natural and human disturbance and progressed steadily along the expected successional pathways and landscapes gradually reached an equilibrium state. Especially, our simulated results suggested the proportions of forests at different recovery stages stabilized around 1980 in the northern Mt., while the proportion of recovered forests reached approximately 90%. These results were derived from model simulations, yet the deliberate model design incorporating key ecological processes and theories, as well as rigorous validation and verification of simulation results, increase the credibility of the simulated forest dynamics for our study area. Likewise, other studies have suggested that quasi-equilibrium conditions could occur in old-growth forests with relatively small, recurring disturbances (Brokaw 1985; Shinneman and Baker 1997; Shugart 1984). In many forest ecosystems, disturbance regimes are complicated with highly variable disturbance intensity, frequency, and size, which could cause available successional pathways and lead ecosystems to nonequilibrium conditions, such as typhoon disturbances in the western and southern Changbai Mt.

Results showed that landscape patterns in southern and western Changbai Mt. (disturbed by typhoons) exhibited general departures from the protected northern Changbai Mt. Under the influence of typhoon disturbances, southern and western Changbai Mt. had low proportions of recovered forest patches and high proportions of recovering patches than the undisturbed northern Changbai Mt. Landscapes in southern and western Changbai Mt. never reached an equilibrium as the proportions of different successional stages were constantly changing. Nonequilibrium for landscapes experiencing infrequent and large disturbances (e.g., hurricanes, wildfires) has been widely reported in other studies (Baker 1989; Nagel et al. 2014; Čada et al. 2016). Notably, the effects of typhoon disturbances on landscape patterns gradually stabilized after 1960, which suggested that with longer timeframe the landscape will continue to shift toward a quasi-equilibrium condition, having less area in recovered patches and more area in recovering patches than those of northern Changbai Mt. Consistently, Chambers et al. (2013) found that ecosystem and community attributes of hectare-scale plots presented continuous dynamic departures from a steady-state condition (i.e., were in a small-scale nonequilibrium state), while a shifting mosaic of steady-state forest conditions still can occur over a relatively large temporal-spatial scale. Therefore, equilibrium of landscapes under infrequent, large disturbances requires long timeframes of study.

The examination for the long-term effects of strong wind disturbance regime is important for understanding current forest landscape patterns and anticipating future changes. This is especially important under global climate change, while disturbance regimes are expected to change with increasing intensity and frequency (Thomas et al. 2004; Vanderwel and Purves 2014). The new disturbance regimes are likely to have a greater impact on forest ecosystems. For instance, the disproportionate effects of disturbances on species may result in greater shifts in species composition. More frequent and severe disturbances may lead to more fragmented forest landscapes and cause forests to diverge from current successional trajectories to develop alternative pathways (Webster et al. 2005; Turner 2010).

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

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