



Typhoon diverged forest succession from natural trajectory in the treeline ecotone of the Changbai Mountains, Northeast China

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ABSTRACT

Windthrow is a typical gap phase disturbance that changes forest composition but rarely alter succession trajectories of a forest stand. Catastrophic windthrow such as typhoons is a large but infrequent disturbance that can have long-lasting effects on forest ecosystems. Whether catastrophic windthrow resets successional pathways of forest ecosystems remains inconclusive. We compared forest structure and regeneration patterns between undisturbed and disturbed stands 30 years after a typhoon event in the treeline ecotone of the Changbai Mountains, Northeastern China. Measurements were made using WorldView-1 satellite imaging and fieldwork in two types of large plots, one located in areas affected by the typhoon event and the other in adjacent undisturbed areas. Results showed that community divergence at landscape scale occurred following the typhoon. In non-wind-disturbed stands, forest development followed the successional pathway of both broadleaved and coniferous trees. By contrast, the late-successional coniferous rather than the early successional broadleaved trees occupied the wind-disturbed stands. The alteration mechanism on the forest succession pathway was that herbs formed tall, dense, and persistent mono-dominant thickets after the typhoon, which inhibited the regeneration of broadleaved trees. In contrast to the common knowledge that forest would return to initial successional stage after catastrophic disturbance, we concluded that catastrophic windthrow, different from gap phase windthrow, altered forest successional trajectory.

1. Introduction

Forest disturbances including wind, fire, extreme weather events, biotic disturbances (insect and disease) affect forest composition and dynamics (Attiwill, 1994; Foster, 1988; Shifley et al., 2000). Among these factors, wind disturbance is particularly difficult to characterize because of its uncertain frequency, size, intensity, and damage (Mladenoff et al., 1993). To date, wind disturbance has received increasing attention because the frequency of wind-related damage and mortality in forests has increased, and wind disturbance is expected to increase with global climate change (Allen et al., 2012; He et al., 2002; Seidl et al., 2014). Generally, there are two types of distinct wind disturbances. One, typically known as gap phase windthrow, is a small-scale gap created by downing a few large trees but does not redirect the successional trajectory of the stand (Rich et al., 2007). The other is catastrophic windthrow (CW) which causes large-scale blowdowns, also known as forms of hurricane in the North Atlantic Ocean and the Eastern Pacific Ocean (Heartsill Scalley et al., 2010), typhoon in the

Northwest Pacific Ocean (Yamashita et al., 2002), cyclone in the Southwest Indian Ocean (Dittus, 1985), and tornado in the inlands of North America (Peterson and Rebertus, 1997). CW is a large but infrequent disturbance that can have severe, long-lasting effects on forest ecosystems. Studies have examined the effects of CW on forest dynamics across globe, e.g. New England in the United States (Foster, 1988; Weishampel et al., 2007), Puerto Rico (Heartsill Scalley et al., 2010), and Australia (Murphy et al., 2014). However, it is still inconclusive whether CW may reset successional paths of forests to an initial stage.

Researches on the effect of CW on forest succession mainly focus on the immediate impacts or the first phase (1–15 years) of recovery after the wind disturbance (Arévalo et al., 2000; Holzmüller et al., 2012; Peterson, 2000; White et al., 2015). Some studies found that forest recovery begin with the regeneration of early successional tree species from survived or adjacent stands and gradually grow back to the original track (Lee et al., 2008; Yih et al., 1991). Moreover, increasing relative dominance by shade-intolerant pioneer species are observed as

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disturbance size increases (Peterson and Pickett, 1995). Other studies, however, suggested that CW may disrupt succession by accelerating forest succession by allowing a shift from early successional species to later successional species (Arévalo et al., 2000; Holzmueller et al., 2012; Webb and Scanga, 2001; White et al., 2015). These diverse phenomena demonstrate the complexity of the CW legacy effect and motivate additional research to understand the underlying mechanisms on how CW affected forest succession. Nevertheless, long term monitoring (≥ 30 years) and survey work on forest dynamic after CW was actually the necessary prerequisite to assess the changes on successional paths of forest (Heartsill Scalley et al., 2010; Hibbs, 1983; Xi et al., 2008). Full evaluation of post-wind disturbance forest succession requires understanding of the tree longevity, forest structure, and overstory and understory layer dynamic (Merrens and Peart, 1992).

On 28 August 1986, a typhoon swept through 11,386 hm^2 of forest including the treeline ecotone in the Changbai Mountain National Nature Reserve (CMNNR), northeast China. The exposed, scattered trees and isolated tree islands were susceptible to strong winds, which caused a large area of blowdowns (Guo et al., 2010). Impacts of the typhoon on the forest restoration (Liu, 1997; Zhao et al., 2004), tree regeneration (Guo et al., 2010), and soil nitrogen cycling (Meng et al., 2014) have been investigated, but the impacts on the forest successional trajectories has not been thoroughly evaluated. Theoretically, the expected successional pathway should be that pioneer trees established first after the disturbance at this altitudinal treeline ecotone (Veblen et al., 2001). Recent field survey showed, however, that regeneration of birch trees (e.g., *Betula ermanii*), the pioneer early successional species, was scarce in the disturbed area while later successional species (e.g., *Larix olgensis*) grew extensively (Guo et al., 2010). Thus, forest succession has not followed the pathway known to the region (Zhao et al., 2004).

The CW had complex damaging impacts on different tree species due to differences such as wood strength, tree geometry, and root characteristics (Veblen et al., 2001). However, forest structure in the treeline ecotone is relatively simple, mainly consisting of few broad-leaved and coniferous tree species, which made comparing post-wind disturbance successional trajectories between conditions possible. In this study, we established two types of plots including disturbed and undisturbed stands to study post-wind disturbance forest succession. Thus, although the common knowledge predicts that post-wind disturbance forest recovery would reset forest succession to its original stage (Runkle, 1981, 1985; Whitmore, 1982, 1989), we found that the CW caused forest succession to diverge from its natural trajectory. To understand the underlying mechanisms, we asked three general questions. (1) How the forest structure has been changed by typhoon disturbance in long term (30 years)? (2) What are the regeneration patterns of various trees in undisturbed and disturbed area? (3) What factor determines the alteration on successional pathway of forest? In addition, we also explored whether our finding is exceptional or has the commonness of post-wind disturbance succession in temperate forests elsewhere.

2. Materials and methods

2.1. Study area

The study area ($41^{\circ}57'55''$ – $47^{\circ}58'57''\text{N}$, $127^{\circ}58'57''$ – $128^{\circ}0'11''\text{E}$) was located on the western side of the Changbai Mountains within the CMNNR in Jilin province, Northeast China (Fig. 1). The climate of the study area is characterized by low temperature, heavy precipitation, strong wind, and a short growing season. Annual mean temperatures in the growing season (June to September) range from 3.37 to 8.82 $^{\circ}\text{C}$ (mean 5.87 $^{\circ}\text{C}$). Annual average precipitation ranges from 700 to 1400 mm (Zong et al., 2013). The mean annual radiation is 506.6 $\text{J cm}^{-2} \text{a}^{-1}$. Harsh environmental conditions limit the photosynthetic capability and vegetative growth of plant species. The study

area has typical alpine meadow soil. Recent studies showed that there were no differences in soil organic carbon, and total nitrogen between disturbed and undisturbed area at treeline ecotone (Meng et al., 2014). Hence, we assumed other soil properties between the disturbed and undisturbed sites are similar.

The treeline ecotone is an area of transition (elevation 1700–1850 m) from close canopy forests to open areas where trees are sparsely distributed (Zong et al., 2014). The forest landscape within the treeline ecotone was fragmented and patchy. A reference map of wind disturbance (blue¹ area, Fig. 1) was generated based on field survey data in 1994. Within the treeline ecotone, forest structure was relatively simple due to the harsh environment at high elevations. Major broad-leaved tree species, also known as pioneer species, include low stem densities of mountain birch (*Betula ermanii*) and Korean birch (*Betula costata*). Major coniferous tree species included late-successional species spruce (*Picea jezoensis*) and fir (*Abies nephrolepis*) and early successional species larch (*Larix olgensis*) (He et al., 2002). Alpine treeline ecotone located at the core area of the Changbai Mountain Nature Reserve, within which logging, hunting, and medicinal and commercial plants gathering were totally forbidden. Sporadic fires occurred in lower elevation areas of Changbai Mountains but have not been recorded in our study area (at elevations above 1480 m) because of relatively high precipitation in the growing season and snow cover for the rest of the year (Zong et al., 2013). Lightning does strike down in these areas but rarely starts fires because of the above reasons. Forest diseases and pests events rarely occurred in the treeline ecotone (Hou and Han, 1997). Therefore, we can reasonably believe that there were no other major disturbances in this study area for the known past.

Ground-layer plants, about 36 plant species, 17 associations in total, in the treeline ecotone grew vigorously after the typhoon disturbance and formed dense plant communities (Xue, 2009). Shrubs mainly included *Rosa marretii*, *Rubus feddei*, *Lonicera caerulea*, *Vaccinium uliginosum*, and *Potentilla fruticosa*. Herbaceous plants occupied most of the wind-disturbed area, with an increasing diversity gradient from non-forest stand to understory stand. In non-forest stands, dominant plant species of the tall and dense plant communities mainly included *Deyeuxia angustifolia*, *Erigeron komarovii*, and *Synurus deltoideus*, characterized as fast-growing with high seed production. Herb roots and litter in most stands of the wind-disturbed area formed a 10 cm layer above the soil layer, which has been reported to hinder tree seed germination (Xue, 2009). In the understory stands, dominant plant species mainly included *Geranium baishanense*, *Fragaria orientalis* Losinsk, *Sanguisorba tenuifolia*, *Solidago pacifica*, *Trifolium lupinaster*, *Heracleum moellendorffii*, *Thalictrum tuberiferum*, and *Vicia baicalensis*, which formed various plant communities with low densities.

2.2. Sampling plots and field work

The total area of treeline ecotone in the western slope of the Changbai Mountains affected by typhoon disturbance was about 1450 ha (Niu et al., 2013). To ensure enough sampling area, measurements were made in two types of plots, each having 5.6 ha. Type one included three subplots (W1, W2, W3) located in an area of stands affected by the wind disturbance, and type two included three subplots (N1, N2, N3) in an adjacent undisturbed area that served as a control (Fig. 1). The old growth forest at treeline ecotone of the Changbai Mountains has developed for hundreds of years since the last volcanic eruption at about AD 938, which removed all vegetation in 55 km radius (Liu and Wang, 1993). The forests recovery from seed sources at lower elevation refuges gradually reached the treeline ecotone, we can reasonably believe that successional status of all forest plots were comparable prior to the typhoon disturbance. In addition, examining

¹ For interpretation of color in Fig. 1, the reader is referred to the web version of this article.

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