Perspectives in Plant Ecology, Evolution and Systematics 21 (2016) 1–13

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Research article

Linking spatiotemporal disturbance history with tree regeneration and diversity in an old-growth forest in northern Japan

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ARTICLE INFO

Article history:
Received 17 March 2015
Received in revised form 11 April 2016
Accepted 13 April 2016
Available online 3 May 2016

Keywords:
Tree rings
Disturbance
Spatial pattern
Forest regeneration
Forest dynamics
Dwarf bamboo
Tropical cyclones

ABSTRACT

Knowledge of long-term spatiotemporal effects of disturbances on forest structure, tree regeneration and species composition is key for understanding forest dynamics and predicting future forest responses to climate change. Here, we explore the spatiotemporal impact of disturbances of different severities on tree recruitment and diversity in species-rich oak-fir-maple forest in Hokkaido, a typhoon-prone area in northern Japan, over the past 230 years. The forest disturbance history was reconstructed by growth-release analysis from more than 45,500 tree rings of 385 trees belonging to 15 species. A mixed severity disturbance regime was prevalent over the study period. Altogether, 310 major and 293 moderate growth releases were identified. These were both temporally and spatially localized, with 80% of events detected in only four time periods: 1775–1784, 1815–1839, 1880–1909 and 1950–1979. Disturbances were followed by major recruitment pulses, each lasting around 30 years. Dendrochronological reconstructions alone indicate that severe (i.e. high proportion of releases), infrequent disturbances control tree regeneration and forest development (from oak-dominated forests to mixed-stand with higher proportion of shade-tolerant tree species). However, a combination of temporal and spatial pattern analysis revealed that less severe disturbances, creating small gaps, promote higher density and diversity of recruitment (altogether 19 tree species recorded) compared with severe disturbances. The latter create large forest gaps which became overgrown by dwarf bamboo and suppress tree regeneration. These results provide evidence that severe disturbances interacting with a strong biotic understory filter (as dwarf bamboo), can disrupt forest ecosystem dynamics by significantly reducing the extent and diversity of tree recruitment. Our findings are important as most climate models predict an elevated intensity of typhoons in Northeast Asia. We conclude that a combination of temporal and spatial analyses, as presented here, is necessary to disentangle the complex drivers of long-term forest dynamics.

1. Introduction

Natural disturbances play an essential role in shaping forest structure and species composition across the globe (Altman et al., 2013a; Fraver et al., 2009; Chambers et al., 2013; Papaik and Canham, 2006). It is essential for the understanding of forest dynamics to reconstruct historical disturbances, determine disturbance regimes and characterize their spatiotemporal effect in different forest types and regions. Knowledge of natural disturbance dynamics, and recognition of their spatiotemporal changes, are important to both applied and theoretical ecology (Altman et al., 2013b; Fraver et al., 2009).

The intensity and frequency of disturbance influences the size and spatiotemporal distribution of the forest gaps they create, which consequently affect the subsequent growth and regeneration of trees. Furthermore, the structure and composition of a forest has an important role in determining the consequences of a disturbance of a given intensity. The subsequent regeneration and composition of plant species that colonize an area beneath the disturbed canopy is controlled both by abiotic and biotic factors (Everham and Brokaw, 1996). There is ongoing discussion about the effects of disturbances of different severities on forest structure and

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http://dx.doi.org/10.1016/j.ppees.2016.04.003
1433-8319/

the "optimum" gap size (i.e. most suitable) for tree regeneration and tree diversity (e.g. Albanesi et al., 2008; Kern et al., 2013; Lorimer, 1989; Romme et al., 1998). Some studies describe lower diversity or forest regeneration in large gaps (Kern et al., 2013; Qin et al., 2011), while others showed the opposite trend (Naaf and Wulf, 2007). However, several studies have recently shown that mixed severity disturbance regimes are common in various forest ecosystems (e.g. Khakimulina et al., 2015; Odion et al., 2014). The variation in disturbance severity enables the coexistence of species with different ecological strategies (Loehle, 2000). Some species can grow very slowly for extended periods beneath the canopy (shade-tolerant species) whereas other species can grow beneath the canopy for only limited periods (light-demanding species) (Mori and Takeda, 2004; Rentch et al., 2003). The former group can persist for a long time beneath the canopy and can wait for a disturbance event to attain canopy status. Light-demanding tree species usually show rapid initial growth, but after a few years without a disturbance, growth declines and the trees die. However, large gaps (i.e. multi-tree falls) also present an opportunity for ecological invasion of strong herbaceous competitors and the consequent suppression of forest diversity (Baret et al., 2008; Burnham and Lee, 2010). Different preferences for regeneration niches occur due to various life strategies. The trade-offs between species' physiologically based life-history traits seems to be the most important factor for the mortality and community abundance of individual species (Kobe and Vriesendorp, 2011). Heterogeneous light requirements and variable growth strategies play a key role in species coexistence (Gravel et al., 2010; Valladares et al., 2012).

Most studies exploring the effects of disturbances on forest dynamics have focused on either the temporal or the spatial scale of past disturbances. However, relatively few studies have linked these two aspects, especially at smaller scales, while at broader scales some studies do exist (see e.g. Tepley and Veblen, 2015; Trotsiuk et al., 2014). The missing connection between temporal and spatial aspects is evident in dendrochronological studies, despite the fact that they can provide high temporal and very high spatial resolution data when compared with other methods (Frelich, 2002). Recent progress in the methods of spatial analysis of marked point patterns (Illian et al., 2008; Wiegand and Moloney, 2014) provides an excellent tool for the combination of spatial aspects of forest dynamics with the results of temporal dendroecological reconstruction of past disturbances. Regardless, only a few studies have tried to connect temporal and spatial patterns in forest dynamics (Duncan and Stewart, 1991; Samonil et al., 2013; Shimatani and Kubota, 2011; Splechtna et al., 2005; Zielonka et al., 2010) and these studies focused on one tree species, forests with only a few tree species (especially mountain forests in central Europe), or specific disturbance events. Hence, the results of such studies have limited application; the real potential for forest ecology of connecting these techniques remains largely unrealised. Connection of high temporal resolution with detailed spatial data enables new insight into forest dynamics and can uncover long-term changes affecting small-scale processes (e.g. forest regeneration).

One of the best opportunities for studying disturbances is offered by old-growth temperate forest ecosystems because their longevity enables the reconstruction of past disturbances (e.g. Altman et al., 2013a). However, old-growth forests without human impact are relatively rare in the temperate regions of the northern hemisphere (Peterken, 1996). Until now, most of the knowledge about disturbance regimes in temperate regions came from studies in North America and Europe, with Asia remaining, to a certain extent, neglected. Temperate forests of Northeast Asia (Japan, Korea, Russia, and China) cover over 930,000 square kilometres and represent the most diverse temperate forests on Earth (White, 1983).

The temperate forests of Northeast Asia are shaped by tropical cyclones, which are one of the most common disturbances affecting large areas in the northern hemisphere (hurricanes in the North Atlantic Ocean and the Northeast Pacific Ocean or typhoons in the Northwest Pacific Ocean). Recent studies have documented an increase in tropical cyclones over the past few decades (Coumou and Rahmstorf, 2012; Emanuel, 2013; Holland and Bruyere, 2014) and a surge in their future intensity is also predicted (Grinsted et al., 2013; Murakami et al., 2013). Unfortunately, instrumental measurements of tropical cyclones usually only go back a few decades (Park et al., 2011; Wu et al., 2005), with very few going further back in time (Altman et al., 2013a).

A key compositional component of temperate forests in Eastern Asia is understory dominance of native dwarf bamboo. Understory bamboo species do not occur exclusively here, but are also common in other subtropical and tropical forests around the world (Giordano et al., 2009; Van Goethem et al., 2013). Dwarf bamboo forms dense clumps by vigorously extending their rhizomes and competes intensively with other understory species (e.g. Abe et al., 2002; Dolezal et al., 2009; Montti et al., 2011; Tabarelli and Mantovani, 2000; Tomimatsu et al., 2011), which influences forest regeneration (e.g. Abe et al., 2002; Dolezal et al., 2009). Specifically, high coverage of dwarf bamboo minimizes light availability for the vegetation beneath it and thus limits tree establishment (Royo and Carson, 2006). Furthermore, canopy disturbances are known to increase dwarf bamboo biomass and limit subsequent tree regeneration (Noguchi and Yoshida, 2005; Wang et al., 2009).

The aim of this study was to explore the frequency, severity and spatial distribution of disturbances and their impacts on forest regeneration and diversity in an oak-fir-maple forest, which represents a widespread vegetation type in Northeast Asia. Our aims were to (1) reconstruct the disturbance history by means of tree rings and determine the disturbance regime, (2) link the temporal and spatial pattern of tree recruitment and diversity to disturbance events and their severity, and (3) explore the role of understory bamboo cover in these processes by measuring bamboo coverage beneath three different light conditions (undisturbed, partly open, and removed tree canopy).

We hypothesise that forest dynamics are controlled by infrequent, severe typhoons, which cause regeneration pulses and bring about major compositional changes. Furthermore, because forest understory vegetation is dominated by dwarf bamboo, we hypothesise that bamboo will take better advantage of larger gaps. This dynamic will restrict tree regeneration in large gaps created by severe disturbances, while intermediate disturbances that partly reduce both the tree and bamboo canopies will promote tree-seedling regeneration and hence forest diversity in smaller gaps.

2. Materials and methods

2.1. Study area

The study was conducted in a natural, conifer-hardwood mixed forest in the Uryu Experimental Forest of Hokkaido University (44°20′N, 142°15′E, 380 m a.s.l.; Fig. S1) in Hokkaido, northern Japan. During 1956–2010, the mean annual temperature and precipitation was around 3.3 °C and 1409 mm, respectively (from Meteorological Report at Moshiri Observatory at Uryu Experimental Forest, Hokkaido University). The mean daily temperature during the coldest months (January and February) was −11.5 °C and for the warmest month (August) +18.4 °C. The snow-cover season extends over half the year, with snow depth around 2–3 m. The climate of Northeast Asia is strongly influenced by cold air masses from Siberia in winter and monsoons and tropical storms or typhoons from the northern Pacific Ocean in summer. The main