

Roles of disturbance and demographic non-equilibrium in species coexistence, inferred from 25-year dynamics of a late-successional old-growth subalpine forest

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Abstract

We investigated compositional and demographical characteristics of major tree species in an old-growth subalpine forest in central Japan, based on a 25-year study. The stand is minimally disturbed and thus canopy structure is fairly stable. During the census, species dominance ranks in terms of both number and basal area were maintained. But, proportion of population size of major species within community significantly differed, and reflecting limited or no recruitment, declines in population size were found for all species including highly shade-tolerant *Abies*, suggesting demographic non-equilibrium in this forest community. This is because, according to each species' regeneration attributes, disturbances fluctuating in space and time are required for persistence of their populations. So, competitive exclusion of other dominants by *Abies* spp., proposed as a mechanism of succession in several subalpine forests, seems unlikely. In addition to such non-equilibrium process, life-history differences among dominants, expressed as the equilibrium concept, are also greatly involved in species persistence because trade-offs of mortality and abundance/recruitment were observed between species. However, juvenile recruitment is closely related to canopy dynamics and disturbances, so that species persistence and resultant coexistence cannot be fully explained only by such differential demography. Here, it is specifically notable that not only current disturbance regimes but also ancient disturbance histories are both fundamentally of paramount importance for community maintenance and species coexistence. Populations and communities are fluctuating on the template shaped by both ancient and recent disturbances, and hereby, even in the late-successional forest, they are demographically non-equilibrium. Thus, further careful consideration is needed to evaluate complexity of the role and variability of natural disturbances in old-growth forest ecosystems.

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1. Introduction

Recently, much attention has been paid to natural disturbance, one of primary determinants of structure and dynamics of tree populations and communities in various forested ecosystems (e.g., Romme and Knight, 1981; Runkle, 1982; Denslow, 1987; Spies and Franklin, 1989; Veblen, 1989; Duncan, 1993; Veblen et al., 1994; Taylor et al., 1996; Shinneman and Baker, 1997; Parish et al., 1999; Łaska, 2001; Franklin et al., 2002; Gutiérrez

et al., 2004; Mori and Takeda, 2004b; Woods, 2004; Worrall et al., 2005). Along a gradient of succession, old-growth forests are generally close to the end point, very far from stand-initiating disturbances (Aplet et al., 1988; Kneeshaw and Gauthier, 2003; Mosseler et al., 2003). These forests are sometimes characterized by minimum-scale dynamics at the scale of single-tree standing mortality (Lertzman, 1992; Antos and Parish, 2002b; Mori and Takeda, 2004b; Worrall et al., 2005), so that their state are often expressed as 'stable' and/or 'undisturbed'. However, even in these late-successional systems, potential importance of disturbances has been gradually recognized, such as legacies of infrequent catastrophic large disturbances (Shinneman and Baker, 1997; Kulakowski et al., 2003; Worrall et al., 2005). Spatially and temporally fluctuating disturbances create resource/environment heterogeneity (Grubb, 1977), regulating

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regeneration and coexistence of tree populations within a forest community (Duncan, 1993).

Differential life-history among dominants is also considered as another important aspect of coexistence in old-growth forests. To detect species differences in ‘regeneration niches’ (Grubb, 1977), which arise in earlier regeneration stages (Brokaw and Busing, 2000), juvenile life-history in relation to regeneration habitat has been the main focus in many forests, but in some forests a convincing evidence of coexistence could not be explained alone by the concept of niche partitioning among juveniles (Sipe and Bazzaz, 1995; Poorter et al., 2005). Also, many studies have mentioned the importance of differences in adult lifespan to offset differences in fecundity, recruitment and survivorship of juveniles (Shmida and Ellner, 1984; Veblen, 1986a,b; Lertzman, 1992; Lusk and Smith, 1998; Taylor et al., 2006). Therefore, consideration of differential life-history traits including the stages from juveniles to adulthood is also informative to further clarify community dynamics in old-growth forests (Lusk and Smith, 1998).

In boreal and subalpine regions of the Northern Hemisphere, well-developed forests, characterized by late-successional conifer species, such as fir (*Abies*) and spruce (*Picea*), are very often observed (e.g., Franklin et al., 1979; Aplet et al., 1988; Kubota et al., 1994; Kneeshaw and Bergeron, 1996; Taylor et al., 1996; Messier et al., 1999; Chokkalingam and White, 2001; Worrall et al., 2005). In these forests, species coexistence has been inferred from the disturbance-induced ‘non-equilibrium hypothesis’ and ‘equilibrium hypothesis’ based on the different life-history strategies. Generally, *Picea* dominate in the older age classes but often lack the younger age classes, whereas *Abies* are typically represented by many young trees and a gradually declining number of trees in successively older age classes (e.g., Antos and Parish, 2002b). According to the non-equilibrium model, since greater abundance of *Abies* juveniles may imply a gradual shift in dominance from *Picea* towards *Abies*, large-scale disturbances, which are more favorable to *Picea* regeneration (Peet, 1981; Antos and Parish, 2002b; Mori and Takeda, 2003, 2004b,c), are essential to prevent the competitive exclusion of *Picea* by *Abies* (Day, 1972; Peet, 1981). On the other hand, the equilibrium model is based on the fact that *Abies* show a higher recruitment in the understorey and therefore abundant juveniles in the stands, but suffer from a higher mortality and shorter adult lifespan, and vice versa for *Picea* (Oosting and Reed, 1952; Veblen, 1986b; Yamamoto, 1993; Kubota et al., 1994; Taylor et al., 1996, 2006); due to these alternative differences, the relative proportion of *Abies* and *Picea* in the overstorey remains relatively constant (Veblen, 1986b). A similar life-history strategy is also applicable to persistence of other long-lived conifer species, hemlock (*Tsuga*) (e.g., Lertzman, 1992; Miyadokoro et al., 2003).

Recently, in addition to such fundamental importance of the species differential life-history including both juveniles and adults, a concept that forests are a product of disturbances reflecting a continuum of intensities and thereby a complete equilibrium is unlikely has been gradually recognized also in *Abies*–*Picea* forests (Worrall et al., 2005). In the *Abies*–*Picea*

forests of Colorado, Aplet et al. (1988) reported that the stands exhibited a historical influence of catastrophic disturbance and showed a progressive change following disturbance. However, long-term quantitative evidence on demography and dynamics of each population are quite rare, causing still controversy about the coexistence mechanism in these coniferous forests. The necessity of direct, long-term observation for validation of hypotheses in late-successional communities has been often referred to (Veblen, 1986a; Bakker et al., 1996), but Woods (2000) pointed out that few studies of late-successional stands, irrespective of forest type, have quantified actual empirical rate of changes in tree populations and communities over more than a decade.

In an old-growth subalpine forest in central Japan, which for a very long time has been only minimally affected by disturbances, Mori and Takeda (2004b) suggested that not only life-history traits, but also larger disturbances are essential for coexistence of *Picea jezoensis* var. *hondoensis* with two *Abies* species (*Abies mariesii* and *Abies veitchii*). However, it is still unknown whether, with a lack of major disturbances, *Abies* populations are demographically stable enough to continue to dominate and can eventually exclude others including *Picea*. Notably, in late-successional old forests, judging from all-sized and/or all-aged structures of dominating, highly shade-tolerant species, such as *Abies*, they are often considered to be quite stable and demographically equilibrium. Ideally, this should be confirmed by long-term research, only which can detect their actual demographic dynamics. Here, based on recruitment and mortality data obtained from a 25-year research project, we aim to interpret population and community dynamics in a late-successional, old-growth subalpine forest. The major questions are following: (1) ‘Are there any evidences that shade-tolerant dominants would replace other co-dominants?’ and (2) ‘Are populations/community demographically in the state of equilibrium?’ Based on the above, we discuss the detailed role of natural disturbances on community dynamics in the old-growth forest.

2. Methods

2.1. Study site

The study forest is located within a subalpine forest (altitude 2050 m, 35°56′N, 137°28′E) on Mt. Ontake (3067 m high) in central Japan. Annual precipitation from 1984 to 2004, recorded near the study site, ranges from 1395 to 3607 mm and the average is 2385 mm. Snow covers the forest floor from mid November or early December to late May or early June, and maximum snow depths from 1995 through 2005 recorded near the study plot ranges from 165 to 240 cm. Average annual temperature is about 3–4 °C. The vegetation features of subalpine forests on Mt. Ontake were described by Franklin et al. (1979).

The study forest mainly consists of four coniferous species, *Abies mariesii* Masters, *Abies veitchii* Lindley, *Picea jezoensis* var. *hondoensis* (Sieb. Et Zucc.) Carrière and *Tsuga diversifolia* (Maxim.) Masters, and one hardwood species, *Betula ermanii*

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