



Altitudinal patterns illustrate the invasion mechanisms of alien plants in temperate mountain forests of northern China



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ABSTRACT

Alien plant invasions usually cause economic and ecological losses. Currently, exotic plants have already appeared in the understory of mountain forests that are subjected to relatively less human disturbance and are often thought of as a safe shelter for most native plants. This study aims to explore invasions patterns and underlying mechanisms in the understory of Chinese mountain forests. Sixty-three quadrats of 20 m × 30 m were systematically set up along the elevation gradient on Mount Tai and Mount Lao, Shandong Province, China. We examined the variation in alien and native plant richness and composition along the elevation gradient to explore the invasion mechanisms of alien species in mountain forests and analyzed the relationship between alien species richness and environment factors (human disturbance, slope, aspect and canopy density) in both mountains. In contrast to native plants, which presented two different richness patterns along the elevation gradient on Mount Tai and Mount Lao, alien species richness presented a consistent decreasing tendency with increasing elevation, suggesting that mechanisms driving native and alien species richness may be different. While native plants had many specialists at high altitudes and presented an obvious change of chorological groups along the elevation gradient, most alien species distributed in high altitude areas also occurred at lower elevations. All findings indicated that the invasion process in mountain forests is from great majority of alien species that are introduced at low altitude, successively filtered out by worsening climatic conditions and decreasing anthropogenic propagule pressures along the elevation gradient, and a subset of this community spreads upward to high altitude areas. Plots with high exotic species richness were generally subject to high levels of human disturbance. We conclude that approaches of monitoring and managing alien plant species should focus on low elevation areas of mountain forests to prevent invasions of high elevation areas.

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1. Introduction

The invasion of alien plants frequently alters the functioning of ecosystem services (Charles and Dukes, 2007) and leads to a decline in biodiversity (Davis, 2003; Hejda et al., 2009). It has been regarded as one of the great threats to natural ecosystems (Pimentel, 2011). It is generally accepted that disturbed areas near anthropogenic activity are more susceptible to invasion because of higher available resources and higher propagule pressure from exotic species (Davis et al., 2000; Dreiss and Volin, 2013). The understory of mountain forests subjected to relatively less artificial interference and with limited light resource are often thought of as

highly resistant to invasion (Pimm, 1989; Rose and Hermanutz, 2004).

However, in recent years, mountain forests are under great threat from rapidly expanding population, development of agriculture and tourism and the excess exploitation and unreasonable utilization of forest resources. This process enhances the strength of human interference and facilitates the introduction and colonization of alien species in mountain forests (Becker and Bugmann, 2001). At present, growing evidence shows that exotic plants have already appeared in understory of mountain forests (Gilbert and Lechowicz, 2005; Seipel et al., 2012; Dreiss and Volin, 2013). While invasions of mountain forests have been analyzed in many parts of the world (Kueffer et al., 2013), Chinese mountain forests are clearly understudied. In particular, substantial field studies are lacking (Yan et al., 2012). Mountain regions remain among the few terrestrial ecosystems not severely affected by plant invasions,

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especially at high altitude, where harsh climate might limit the spread of alien plants (Haider et al., 2011). However, as the time from introduction increases and global climate changes, non-native plants may extend their distribution ranges and reach new areas in the future (Becker et al., 2005; Haider et al., 2010). Sharing information gained in different mountain regions is important for establishing effective management strategies. Therefore, it is necessary to investigate the plant invasion patterns in the mountain regions in China to fill in the regional gaps.

Altitudinal patterns in mountains provide a suitable model for investigating invasion processes, as across a relatively short geographical range there are large environmental changes, such as climate, geometric constraints (e.g. boundary constraints) (Pineda, 1993; Rahbek, 2005) and intensity of anthropogenic activities (Parks et al., 2005). The two most common altitudinal species richness patterns are hump-shaped and monotonically decreasing patterns (Rahbek, 1995). Several factors are considered to explain those altitude patterns, such as energy constraints, the mid-domain effect (MED), species–area relationship and contemporary and historical ecological forces (Currie, 1991; Hawkins et al., 2003; Hawkins et al., 2005; Lee et al., 2013). An increase in altitude is usually accompanied by harsher environments in wet climates. For instance, temperatures and the length of the growing season is decreasing, while the period of frost and the intensity of ultraviolet light increases with increasing altitude (Körner, 2003). Plants at higher elevations are also a handful of species that possess a narrow climatic range and specialized physiological properties to withstand the harsh environmental conditions. Consequently, species richness decreases as altitude increases.

However, compared to native species, there has been relatively little research on altitudinal richness patterns of alien species. Some studies have found a declining trend in exotic species richness with increasing elevation, at least from middle to high elevations (Pauchard and Alaback, 2004; Daehler, 2005; Alexander et al., 2009; Denslow et al., 2010; Khuroo et al., 2011). The mechanisms of assemblies of flora along elevation gradients may be different between native and alien species. Because native species have had a long time to develop and adapt to the local environment, richness patterns may be influenced by climate, area, topography and evolutionary history (Rahbek, 1997; Kluge et al., 2006; Wang et al., 2007). However, alien plants have been introduced and colonized along the elevation gradient in only a few hundred years, and human activities, such as the introduction and spread of alien species to new habitats, may be more relevant for explicating alien plants richness patterns (Becker et al., 2005; La Sorte et al., 2008). Comparing alien and native species richness patterns and the causal factors behind these patterns could provide insights into the mechanism of the invasion processes of alien plants.

Shandong province is located in the warm temperate zone of China, with a dense human population and rapid economic development. Mount Tai and Mount Lao are two famous scenic spots in Shandong Province, which are likely to be invaded by alien plants due to intensive human pressures (e.g. recreation activities). However, there are few studies about alien plant invasion in Mount Tai and Mount Lao. Most studies just focused on certain alien plants which have caused damage to the environment, for example, *Robinia pseudoacacia* and *Coreopsis grandiflora* (Liang et al., 2008; Lv et al., 2013). In this study we conduct field investigation in two mountain regions (Mount Tai and Mount Lao), which have different climate features, to compare whether altitudinal richness patterns vary between native and alien species, to test whether alien species richness in different climate conditions present a consistent altitudinal pattern and to explore the invasion mechanisms of alien species in the understory of mountain forests to provide important guidance for controlling and managing the invasion of alien plants in mountain forests.

2. Material and methods

2.1. Study area

The study was conducted on Mount Tai, which is situated in the western part of Shandong Province (N36°05′ – N36°15′, E117°5′ – E117°24′) and on Mount Lao which is located in the eastern part of Shandong Province (N36°05′ – N36°19′, E120°24′ – E120°42′). They are both nature reserves in China (Fig. 1).

Mount Tai has a warm temperate continental monsoon climate. The altitude of the main peak is 1532.5 m, which is the highest in Shandong Province. The character of vertical zonality is very clear on Mount Tai. On the top of the mountain, the annual mean temperature is 5.3 °C and the annual mean precipitation is 1124.6 mm. In contrast, at the bottom of the mountain, the annual mean temperature is 12.8 °C and the annual mean precipitation is 715.0 mm. The average frost period lasts 159 d and the extreme minimum temperature is –27.5 °C. Precipitation mainly occurs from June to August. The annual relative humidity is 63%.

Mount Lao is surrounded by the sea on two sides. Its weather belongs to a temperate maritime climate. It is the highest peak on the Chinese coastline at 1132.7 m. The weather is tempered by the ocean, and this region has higher humidity than Mount Tai. The annual relative humidity reaches 73%. Mean annual precipitation increases with elevation from 726.6 mm to 2103.8 mm and is concentrated in the summer. The average frost period is over 186 d and the extreme minimum temperature is –21.2 °C. The mean annual temperature is 11.9 °C.

Mount Tai and Mount Lao were rich in vegetation resources. However, owing to excessive deforestation and grazing, the forest resources fall under serious destroy and the ecological environments deteriorate. Until 1950s, the vegetation was protected by fenced off for afforestation. During several decades' natural succession and reasonable protection, the present forests develop towards a more natural stage. Now, vegetation coverage is over 90% on Mount Tai. There are obvious changes of vegetation types along the elevation gradient, from warm temperate deciduous broad-leaved forests dominated by *Quercus acutissima*, *Quercus variabilis* and *R. pseudoacacia*, to temperate coniferous forests dominated by *Pinus tabulaeformis* and *Platyclusus orientalis*, to cold-temperate coniferous forests dominated by *Larix principis-rupprechtii*, and end with shrub lands. The main forest communities on Mount Lao are temperate coniferous forests and temperate deciduous broad-leaved forests. *Pinus densiflora*, *P. tabulaeformis* and *P. orientalis* were constructive species of the temperate coniferous forests. *Q. acutissima*, *Q. variabilis*, *R. pseudoacacia*, *Pterocarya stenoptera* and *Alnus sibirica* were important components of the temperate deciduous broad-leaved forests.

An alien species *R. pseudoacacia* is widespread in the two study areas. *R. pseudoacacia* is native to North America. It was first introduced to China at the end of the eighteenth century. Due to its rapid growth and hardiness, it had been deliberately introduced to Mount Tai and Mount Lao in 1950s for the purpose of afforestation. It had been mainly planted in the middle and low elevation regions. Alien species *C. grandiflora* had been deliberately cultivated in Mount Lao as an ornamental flower in 1980s. At present, it has established as an escape in the forest understory on Mount Lao.

2.2. Field sampling

Vegetation surveys were conducted from August to September in 2012 and 2013. August and September are the growing seasons with relatively stable species composition and peak appearance of plants. The setup of each plot in plant community investigation

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