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# Snow damage to the canopy facilitates alien weed invasion in a subtropical montane primary forest in southwestern China

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ABSTRACT

Climate-mediated disturbance often promotes the invasion of non-native species, which impact local ecosystems by altering community structure and composition. In subtropical forests, the formation of canopy gaps, which allow for rapid regeneration in the understorey, strongly affects successional dynamics. However, the role of canopy gaps in promoting invasive species into forest interiors has not been extensively studied. We examined the relationship between canopy disturbance and the germination of *Ageratina adenophora* (Asteraceae), a non-native branched herb species, using seedling population data from a 20-Ha forest dynamics plot in southwest China. The species was first recorded in 2015, after extensive snow-damage to the forest canopy. Our hypothesis was that canopy gaps increase light availability on the forest floor, thereby facilitating the germination and subsequent invasion by the non-native branched herb into the forest interior. Field measurements of the Leaf Area Index before and after the snow damage was combined with measurements of canopy gaps and associated light conditions. Biotic factors (tree seedling species richness, herb species richness and herb coverage), abiotic factors (elevation, slope, convexity and soil moisture), and the density and spatial distribution of *A. adenophora* were also measured ten months after the snow damage. Seedling germination experiments were conducted in the lab to test the relationship between light availability and the germination of the invasive branched herb, showing the branched herb to be light demanding. Using spatial statistical methods, we found significant relationships between densities of recruiting *A. adenophora* and canopy gaps, with high densities of the invasive branched herb recruiting into gap areas. We conclude that light availability shapes the distribution of *A. Adenophora* in the understorey in this subtropical evergreen montane forest. Our results illustrate that disturbances leading to canopy damage can promote the establishment and proliferation of invasive understorey species in forest interiors, providing a rapid route to colonization.



## 1. Introduction

Climate change and biological invasions are two important drivers affecting native community composition and ecosystems around the world (Vilà et al., 2011; Valladares et al., 2015). Previous studies have shown that extreme climate events may increase the probability of species invasion success (Diez et al., 2012). In many forests, canopy gaps created by climate-mediated disturbances promote regeneration, sometimes favoring alien weeds that can more-readily respond to illumination changes in the understorey (Qi et al., 2014; West et al., 2014; Long et al., 2015). Large-scale forest canopy disturbances due to hurricanes (Zimmerman et al., 1995; Comita et al., 2009; Shiels and Gonzalez, 2014), droughts (Gitlin et al., 2006) and snow damage (Lafon, 2004; Wu et al., 2011) are projected to become more frequent and severe under climate change (IPCC, 2013). Thus, analyses of invasions of non-native understorey species and their relationships to disturbance events are important for understanding invasion processes and possible impediments to forest natural successional trajectories.

Colonization opportunities are improved after disturbance due to increased resource availability, possibly promoting the invasion of non-native plant species (D'Antonio et al., 1999; Sher and Hyatt, 1999; Davis et al., 2000; Hierro et al., 2006; Catford et al., 2012). For example, in Hawaii, extreme drought led to widespread mortality among dominant native woody plants, facilitating the invasion of non-native grasses (Lohse et al., 1995). In a Bangladesh

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tropical forest, the number of exotic species had a significant positive correlation with anthropogenic disturbance, illustrating the potentially high risk of invasion by weed species in recovering secondary forests (Uddin et al., 2013). Furthermore, a meta-analysis also showed strong evidence that non-native plant species benefit from disturbance (Jauni et al., 2015), and a large number of previous studies have demonstrated that open environments favor such invasions. For example, abandoned farmlands, roadsides, and the edges of fragmented forests contain higher abundances of invasive species (Brothers and Spingarn, 1992; Pauchard and Alaback, 2006; Flory and Clay, 2009).

In forest understories, well-developed and dense forest structure limits propagule dispersal (Cadenasso and Pickett, 2001) and establishment (Lin and Cao, 2009). This causes the understorey to be strongly aggregated in space (Pellissier et al., 2013; Song et al., 2014; Baeten et al., 2015; Murphy et al., 2016), with the highest densities of non-native species in the first several meters from the forest edge (Lin and Cao, 2009). However, these species may already be present in the soil seed bank in more interior areas of the forest (Lin et al., 2006; Lin and Cao, 2009). If canopy disturbance occurs, light availability in the understorey is increased and interspecific competition is reduced (Corbin and D'Antonio, 2004; Christen and Matlack, 2009), potentially providing an ideal opportunity for invasive species to become established (Catford et al., 2012; Thomas and Moloney, 2015). Indeed, transplant experiments have suggested that canopy disturbance is a key factor that promotes the establishment of two non-native lowland shrubs in a mixed-conifer forest (Stevens and Latimer, 2015). A study in a northeastern American temperate forest showed that ephemeral disturbances significantly increased the populations of two invasive plant species (*Alliaria petiolata* and *Microstegium vimineum*) in the understorey (Eschtruth and Battles, 2014). However, there are few studies documenting how exotic species invade high-elevation primary forests, because such invasions are historically less common.

Globally, montane regions are thought to experience relatively low plant invasion rates (Daehler, 2005; Klinger et al., 2006; Zhang et al., 2015; Petitpierre et al., 2016). Montane ecosystems experience a range of relatively harsh climatic conditions, low rates of disturbance, and low propagule supply when compared to typical lowland forests (Willis and Hulme, 2002; Daehler, 2005). As temperature and precipitation conditions shift due to climate change, and natural and human-induced disturbances increase, the immigration of invasive species to montane ecosystems may increase (Averett et al., 2016). Therefore, there is a need to better understand the dynamics of montane forests as they relate to increased risk of invasion by nonnative plant species (Hellmann et al., 2008; Pauchard et al., 2009).

To better understand the population dynamics and quantify the potential invasion risk of invasive species to montane forests, we measured how a nonnative branched herb species invaded a primary montane forest in southwestern China following climate-mediated disturbance. In November 2015, we observed the initial invasion of *A. adenophora* into a high-elevation primary subtropical evergreen forest after severe snow damage. *Ageratina adenophora* (Sprengel) R. King & H. Robinson (syn. *Eupatorium adenophorum* Sprengel), a Mexican perennial branched herb (maximum height 2 m) in the family Asteraceae, is one of the worst invasive species in China and Southeast Asia (Ding et al., 2008). This species was first reported as invasive in Yunnan province and has since spread across southwest China in lowland areas, but has been limited in its colonization of high-elevation subtropical areas. The individuals of this species can decrease defense allocation and increase growth, which can help it quickly colonize open areas (Feng et al., 2011). Moreover, *A. adenophora* can secrete active allelochemicals through root exudates and leaf litterfall that can negatively influence the native plant community (Yang, 2006; Yang et al., 2013), allowing it to quickly alter understorey community composition of the forest, and change forest composition and structure over the long term. We tested how *A. adenophora* responds to increased light levels in a controlled setting, and examined the spatial pattern of colonization of the invasive branched herb in the forest in relation to canopy gap openings caused via climate-mediated disturbance.

## 2. Material and methods

### 2.1. Study area

The Ailaoshan Forest Dynamics Plot (FDP; 24°32′10″N and 101°01′40″E) was established in 2014 in the Ailaoshan National Nature Reserve following the tree census methods of the Center for Tropical Forest Science (Condit, 1998), where all self-supporting plant stems $\geq$1 cm diameter at breast height (dbh) are tagged, identified to species and mapped. The plot is located in evergreen broadleaved forest dominated by two species in the Fagaceae family, *Castanopsis wattii* and *Lithocarpus xylocarpus*. The mean annual precipitation is 1931 mm, 85 percent of which falls between May and October (Gong et al., 2011). Elevation within the plot ranges from 2430 to 2580 m above sea level (Fig. S1). The average annual temperature is 11.3 °C and monthly average temperatures ranging from 5.7 °C in January to 15.6 °C in July (Wu et al., 2014).

### 2.2. Data collection

#### 2.2.1. Sample plots

Snow damage to the canopy of the forest occurred between January 9th and 11th 2015, during a 3-day cold spell with a minimum temperature of −2 °C. During this time, roughly 40 cm of snow fell on the plot, resulting in broken branches on many canopy trees. Starting in February 2015, a total of 500 seedling plots (2 m × 2 m) were established, one in the center of each 20 m × 20 m quadrat in the 20-ha plot. In each seedling plot all tree seedlings (defined as any plant with basal diameter <1 cm) were tagged, measured and identified to species. A complete re-census of seedlings was conducted in November 2015, 10 months after the snow damage, especially noting the presence of *A. adenophora*. We recorded the abundance of *A. adenophora* present in each seedling plot. Species richness and coverage of other herbs in each seedling plot were also recorded. We use tree seedling species richness, herb species richness and herb coverage as the biotic variables in our analyses, described below.

#### 2.2.2. Canopy openness and environmental variables

Canopy openness was measured after the snow damage during the second seedling census in November 2015, using a digital camera (Nikon Coolpix 4500, Nikon Corporation, Japan) with fisheye lens (Nikon FC-E8 Fisheye Converter, Nikon Corporation, Japan) to take hemispherical photographs (Queenborough et al., 2009). All pictures were taken from the center of the 20 m × 20 m quadrat at 1.3 m height during moderate cloud cover or low sun. The images were analyzed using a software Gap Light Analyzer Version 2.0 (Frazer et al., 1999), in which canopy openness was quantified as the fraction of the image not occupied by vegetation cover (Wu et al., 2016). To compare the change of canopy openness, the Leaf Area Index was also quantified at 9 points in the center and along the two diagonal lines in a 1 ha plot, before snow damage in December 2010 and after snow damage in November 2015, providing a rough proxy for change in canopy openness (Martens et al., 1993; White et al., 2000; Frazer et al., 2000). We used LAI-2000