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

Xiaoyang Song [a,b], James Aaron Hogan [c], Calum Brown [d], Min Cao [a,*], Jie Yang [a,*]

[a] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 666303 Yunnan, China
[b] University of Chinese Academy of Sciences, 100049 Beijing, China
[c] International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL 33199, USA
[d] School of Geosciences, University of Edinburgh, Edinburgh EH8 9XP, United Kingdom

ARTICLE INFO

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.

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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

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 nega-

tively 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 ≥ 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

Plant Canopy Analyzer (PCA, Li-Cor, Lincoln, NE, USA) to estimate the leaf area index. The PCA measured light captured by a fisheye lens.

We measured four other abiotic variables at the landscape scale to quantify environmental heterogeneity: soil moisture, elevation, slope and convexity at the 20 m scale. Soil moisture (per volume) was measured with a soil conductivity probe meter (Theta probe MPM-160B, ICT International Proprietary Limited, Armidale, Australia) at the end of rainy season in November and the end of dry season in May, for both 2015 and 2016. Measurements were taken at the center of each seedling plot, where the litter and humus layer was removed prior to insertion of the soil moisture probe 5 cm below the surface. Soil moisture readings were recorded at three randomly selected points within each seedling plot and then averaged. For each 20 m × 20 m quadrat, elevation was calculated as the mean of the elevation of its four corners. Slope was the mean angular deviation from horizontal of each of the four triangular planes formed by connecting three corners at a time using the calc.slope() function in the CTFS R package (Condit, 2013). Convexity was calculated as the difference between the mean elevation of the focal quadrat and the mean elevation of the eight surrounding quadrats. For edge quadrats, convexity was calculated as the difference between the elevation of the focal quadrat center and the mean elevation of the four corners (Condit, 2013).

2.2.3. Laboratory experiments

To investigate the role of light-limitation in the germination of *A. adenophora*, we collected the seeds of *A. adenophora* near our FDP in Ailaoshan and conducted germination experiments. These experiments were conducted in the laboratory using two opaque incubators, which allowed for the control of temperature and light conditions (MGC-350HP-2 instrument, Yiheng Shanghai, Shanghai, P.R. China). In each incubator light was provided by 10 warm white fluorescent bulbs (Philips E27, 8 W). Five light bulbs each were situated on the left and right sides of each incubator. We gave a 12 h light/12 h dark period treatment in each incubator. Six pots containing seeds of *A. adenophora* were tightly covered with shade netting and positioned in the incubators, and one pot was added as a control treatment, lacking any shade cover. We manipulated light availability to seedlings at seven irradiance levels. Decreasing irradiance levels were created by covering pots with increasing numbers of black mesh layers (0, 1/2, 3/4, 1, 2, 3 and 4; 1/2 and 3/4 were created by cutting the mesh), allowing full light, 10%, 8%, 6%, 3%, 2%, and 1.5% of light penetration into the pot, respectively, through the mesh at the top of the pot (pot sides were opaque). The light penetration was measured using the same methodology as measuring canopy openness, using hemispherical photographs. Each treatment included five replicates of 25 seeds placed on the surface of filter paper moistened with distilled water in 60 mm diameter Petri dishes. Percent germination of seeds was recorded after 18 days with protrusion of the sprouting radicle being the criterion for germination.

2.3. Data analysis

2.3.1. Spatial autocorrelation tests for both canopy openness and A. adenophora density

Using *A. adenophora* abundances at the spatial scale of seedling plot placement (i.e., a 20 m × 20 m sampling grid, positioned at the center of each quadrat), we used bivariate interpolation to estimate the species densities across the 20 ha plot, and then mapped the spatial abundance distribution of this species across the entire plot. The same method was used to map the spatial pattern of canopy openness, using the canopy openness data generated from the hemispherical photographs. The main objective was to see if the spatial pattern of *A. adenophora* distribution and canopy openness were spatially correlated across the plot. We used Moran's Autocorrelation coefficient (Moran's *I*) to test whether spatial autocorrelation existed between values of canopy openness and observed *A. adenophora* densities for the study area (Cliff and Ord, 1981). Spatial analyses were carried out in the 'spatstat' package (Baddeley and Turner, 2005) in R 3.0.3 (R Development Core Team, 2015).

2.3.2. Relationship of biotic and abiotic environment to A. adenophora densities: comparing two models

We conducted an ordinary least-squares (OLS) regression model (Wilkinson and Rogers, 1973) to estimate the effect of biotic and abiotic conditions on the abundance of recruited *A. adenophora* seedlings. This simple linear model ignores spatial autocorrelation. For purposes of model comparison, we conducted a spatial simultaneous autoregressive (SAR) model (Dormann et al., 2007) to estimate the effect of environmental conditions on the abundance of *A. adenophora*. The SAR model differs from simple linear regression in that it incorporates a spatial autoregressive coefficient. The SAR model form is:

$$y = \rho Wy + X\beta + \lambda W\mu + \varepsilon$$

where y is the vector of observations of the response variable, in this case the *A. adenophora* standardized abundance in each seedling plot; X is the explanatory matrix of biotic and abiotic variables (including canopy openness, soil moisture, elevation, slope, convexity, tree seedling species richness, herb species richness, herb coverage); ρ is a model slope vector associated with the response variable; β is a model slope vector associated with the explanatory variables; λ is the spatial autoregressive coefficient; μ is the spatially-dependent error term; W is the spatial-weighted matrix that indicates whether the quadrats are neighbors or not; and ε is a random error term. W takes a value of 1 if quadrats are immediate vertical or horizontal neighbors and 0 otherwise.

Prior to fitting the linear models, both response variables and explanatory variables were standardized (by subtracting the mean value of the variable and dividing by 1 standard deviation) to stabilize the variance and improve normality of the residuals before fitting the models. Finally, we used Moran's test for spatial autocorrelation to evaluate spatial patterns of *A. Adenophora* abundances on the residuals of the two regression models (Cliff and Ord, 1981). Analyses were carried out in the 'spatstat' package in R 3.0.3 (Baddeley and Turner, 2005; R Development Core Team, 2015).

2.3.3. Employing the Torus translation

As a second approach, we used torus-translation tests (Harms et al., 2001) on the relationship between spatial structure of canopy openness and density of *A. adenophora*. This allowed us to statistically test this relationship and to check for bias in results for spatial autocorrelation via the regression methods. In our case, the torus translation shifts the canopy openness map in in the four cardinal directions by one column or row of 20 m × 20 m quadrats at a time, and calculates the correlation between interpolated values of canopy openness and seedling density. In addition to each possible translation for the entire FDP, three additional maps were generated: a 180° rotation, a mirror image, and a 180° rotation of the mirror image. A total of 1999 unique canopy openness translation maps resulted, each differing from the true, untranslated map of canopy openness. The value of the canopy openness assigned to each quadrat therefore differed between each of the 1999 possible maps, providing new null estimates of the strength of correlation between canopy openness and density of *A. adenophora*. The observed relationship between canopy openness and density of *A. adenophora* was compared to the frequency distribution of expected values generated from the torus translations, using a 5%

significance level (equivalent to significant positive or negative correlation measured by $0.025 \geq R^2 \geq 0.975$ of the expected values).

2.3.4. T-test and linear regression

We conducted a t-test to detect whether there is significant difference of leaf area index before and after snow damage. For the lab experiments, we calculate the mean number of germination of A. adenophora seeds in each pot. General linear regression was used to test for a significant linear relationship between germination numbers and light availability, excluding the full light (i.e., control) treatment. All analyses were conducted in R 3.0.3 (R Development Core Team, 2015).

3. Results

We found severe damage to the canopy structure of Ailaoshan FDP following the January 2015 snow storm, based on Leaf Area Index measurements. The LAI declined significantly after this storm (t = −7.13, p < 0.01; Fig. S2), with the average leaf area index decreasing from 3.85 ± 0.51 before the storm to 2.21 ± 0.47 afterwards. From the hemispherical photographs, canopy openness was 13.65 ± 4.22% following the snowstorm, with a significant positive spatial autocorrelation in openness (Moran's I = 0.4081; p < 0.01), with the openness being greatest (>20%) in the east and southwest parts of FDP. The north part of the plot had the most-intact primary canopy structure with canopy openness values of <5% (Fig. 1A).

We recorded 347 A. adenophora individuals in 91 seedling plots (18.2% of seedling plots) in the survey of 500 seedling plots. Among these 91 seedlings plots, the average abundance was 3.81 ± 0.39 individuals, with a maximum abundance of 22 individuals (Fig. 1B). Significant positive spatial autocorrelation was found within the A. adenophora population (Moran's I = 0.2108; p < 0.01). Abundances had patchy distributions in the center and northern parts of the FDP and the densities were highest in the southern part of the plot. The torus translation test showed that the correlation between canopy openness and density of A. adenophora was significant (P = 0.0005).

Results of the SAR and OLS models both revealed that only canopy openness had a significant positive effect on the abundance of A. adenophora. The other three biotic factors (tree seedling species richness, herb species richness and herb coverage) and four abiotic factors (elevation, slope, soil moisture and convexity) showed no significant relationships with the abundance of A. adenophora. Most parameter estimates with high values in the OLS model were reduced in the SAR model. In contrast to the OLS regression (Moran's I = 0.165; p < 0.01), inspection of the residuals from the SAR model showed no significant autocorrelation (Moran's I = −0.002; p = 0.495).

For the lab experiments, linear regression results showed there was a significant positive correlation between germination and light availability (r^2 = 0.7344, p = 0.029) (Fig. 2).

4. Discussion

We documented a novel outbreak of a strongly invasive alien branched herb in the interior of a primary montane forest following snow damage to the forest canopy. Snow damage changed forest structure by directly damaging tree branches, canopy crowns and occasionally tree trunks, leaving a patchwork of forest gaps of differing sizes (Rhoads et al., 2002; Olthof et al., 2003; Wu et al., 2011). Leaf cover decreased significantly as a result, and high light conditions in the understorey (Fig. S2) promoted the germination of the invasive species (Fig. 1). By exploring the effect of biotic and abiotic factors on the abundance of A. adenophoa, alongside a lab-based germination experiment, we found A. adenophoa to be highly sensitive to light-availability, performing best in high light conditions (Fig. 2).

A significant positive correlation between the abundance of A. adenophora and canopy gaps indicates that the seed germination of the invasive species is light-limited (Table 1). Low light availability is regarded as one of the most important environmental limitations for non-native species invading into forest interiors (Brothers and Spingarn, 1992). We supposed that the damage to the canopy structure, as a result of a strong snow storm, increased the light availability in the understorey which stimulated the germination of A. adenophora seeds from the soil seed bank to establish populations in newly opened areas.

We showed how soil seed banks in primary forests at high elevation may be at high risk for accumulating propagules of non-native species, which could invade to alter forest composition and structure after disturbance, eventually creating novel communities (Lin et al., 2006; Lin and Cao, 2009). A previous study demonstrated that large numbers of A. adenophora seeds (246.7 per m^2 in the rainy season and 155.3 per m^2 in the dry season) occur in the soil seed bank in the Ailaoshan primary forest (He, 2000). However, we found no A. adenophora plants during the two surveys in 2007 and 2014 in Ailaoshan FDP. Although the study of He (2000) was conducted just outside the FDP, these findings suggest that A. adenophora seeds are likely to exist in the FDP but had previously failed to germinate due to a lack of suitable conditions. Our research further suggests that light-limitation is the main factor inhibiting the establishment of A. adenophora in this forest (Table 1 and Fig. 1). Germination does not appear to be constrained by other biotic or abiotic factors (though it remains possible, if unlikely, that some unmeasured factors play a role). Generally, canopy disturbance is thought to be the most important prerequisite of alien plant invasion success in forests (Eschtruth and Battles, 2009). Closed canopies ensure light limitation that prevents the germination of the seeds of many invasive species (Qi et al., 2014). Light increase in the understorey following canopy damage often promotes the germination and establishment of invasive species (West et al., 2014). Our results are largely in agreement with a recent study that found that canopy damage caused by large-scale herbivore outbreaks increases the population of two invasive plant species Alliaria petiolata and Microstegium vimineum (Eschruth and Battles, 2014). Additionally, transplant experiments have shown that canopy openness promotes the establishment of invasive plant species (Stevens and Latimer, 2015). Our results suggested that invasive species may first invade the soil seed bank and wait for optimal environmental conditions to germinate and establish populations.

As climate change accelerates, extreme weather events are predicted to become more severe and frequent (Orlowsky and Seneviratne, 2012; Zhang et al., 2013), which could weaken the ecological resilience of forest ecosystems and produce alternative stable ecosystem states (Lebourgeois et al., 2010). Disturbance to the canopy may also reduce interspecific competition between invasive and native species, which in turn may increase the opportunities for non-native species to germinate and establish in the forest community beyond canopy gaps (Davis et al., 2000; Corbin and D'Antonio, 2004). Therefore, we assumed both the low temperature during snowfall and the destruction of many canopy branches might have negative influence on the native understorey community, which also might promote the establishment of A. adenophora. The ability of this species to invade the high elevation primary forest successfully could increase if the frequency and severity of disturbance events increases.

Although we found a significant positive correlation between A. adenophora density and canopy openness, there were still some
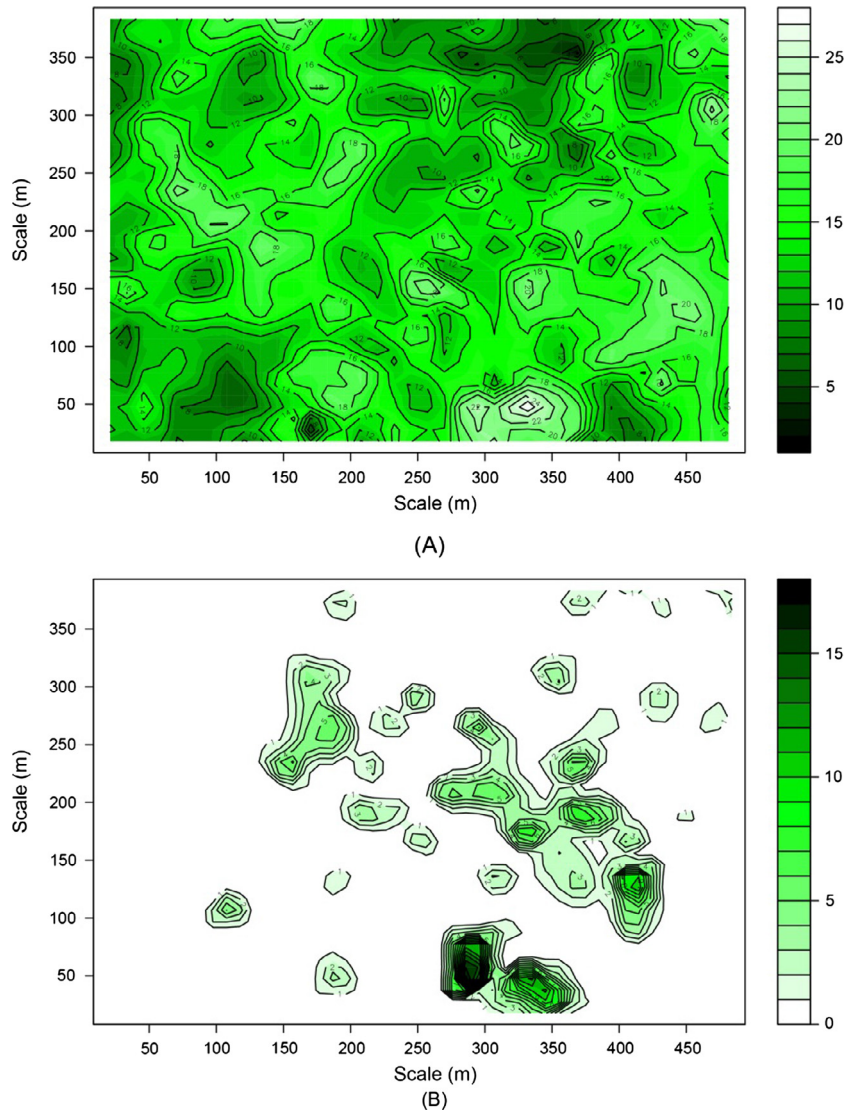
(A)

(B)

Fig. 1. The spatial distribution of canopy openness and the abundance of *A. adenophora* in the FDP. (A), canopy openness (%) conditions in the FDP. Highest canopy openness, over 25%, is in the southeastern part, while the lowest canopy openness areas, less than 10%, can be found in the northern and southwestern parts. (B), the spatial density distribution of *A. adenophora* in the FDP. Highest density can be found in the southeastern part, and most of *A. adenophora* is distributed in the center of the FDP.
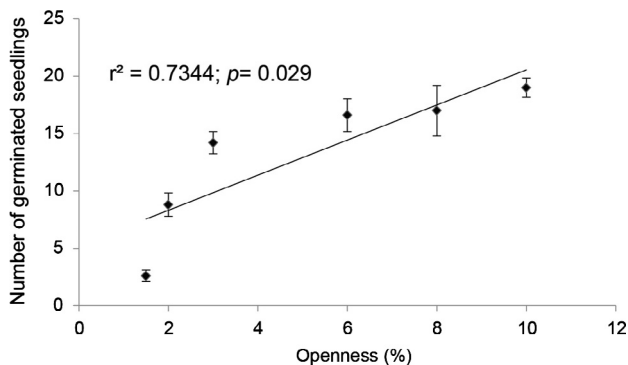

Fig. 2. The correlation between germination number of *A. adenophora* and light availability (Error bars represent standard error of number of germinated seedlings).

areas with an open canopy that had few individuals (Fig. 1), suggesting that other factors in addition to light availability affect the capacity for this species to colonize light gaps. One possible

reason is that the complex structure of forest communities can limit seed dispersal (Cadenasso and Pickett, 2001). The seeds of *A. adenophora* are characterized as having feathery 'parachutes' dispersed by wind, which leads to dispersal limitation in well-developed forest interiors (Devlaeminck et al., 2005). When spatial autocorrelation was taken into account, the explanatory power of canopy openness was weaker using the SAR model than the OLS model (Table 1). The OLS model residuals showed significant spatial autocorrelation (Moran's $I = 0.165$; $p < 0.01$), indicating that spatial arrangement (i.e. dispersal limitation) may have affected the spatial distribution pattern of *A. adenophora*. Seed availability is obviously an important limiting factor for the invasion of alien species (King and Buckney, 2001; Pauchard and Alaback, 2006), and the soil seed bank may have lacked *A. adenophora* seeds in some areas, resulting in fewer or no individuals even when canopy openness increased. We suspect that following the snow damage, the more open forest structure could promote the dispersal of *A. adenophora* seeds, thereby providing another mechanism for colonization by the non-native branched herb.

Typically, forests at high elevations exhibit slow growth rates. Forest canopies of montane forests are slow to recover from distur-

Table 1
The correlation between *A. adenophora* abundance and environmental factors (biotic and abiotic) using spatial simultaneous autoregressive (SAR) model and Ordinary least-squares (OLS) regression models.

Parameter	SAR model				OLS model			
	Estimate	SE	Z	p	Estimate	SE	Z	p
(Intercept)	0.372	0.11	3.393	**0.001**	0.714	0.096	7.464	**<0.001**
Canopy openness	0.374	0.098	3.807	**<0.001**	0.523	0.105	4.996	**<0.001**
Soil moisture	−0.016	0.111	−0.144	0.885	−0.002	0.125	−0.013	0.99
Elevation	−0.003	0.127	−0.021	0.983	0.05	0.16	0.314	0.754
Slope	0.077	0.138	0.558	0.577	0.011	0.163	0.069	0.945
Convexity	−0.02	0.091	−0.223	0.824	−0.046	0.107	−0.434	0.665
Tree seedling species richness	0.158	0.102	1.548	0.122	0.187	0.113	1.647	0.1
Herb species richness	0.067	0.096	0.702	0.483	0.122	0.106	1.146	0.252
Herb coverage	0.115	0.097	1.188	0.235	0.131	0.11	1.195	0.233

P values <0.05 are shown in bold.

bance, often taking decades to fully close. *A. adenophora* can quickly colonize gap areas, due to decreasing defense allocation and increasing growth following the disturbance event (Feng et al., 2011). Moreover, active allelopathic chemicals that *A. adenophora* possesses can negatively influence the native plant community, through root exudates and leaf litterfall (Yang, 2006; Yang et al., 2013). The invasion distribution of the species therefore has the potential to quickly cover the understorey and prevent the seeds of native tree species from germination, reducing regeneration and creating a dramatically increased potential for native biodiversity loss in this forest.

5. Conclusions

The increase in anthropogenic activities in high elevation forests, coupled with new climate change threats (e.g., increased frequency and intensity of disturbance, changes in temperature and precipitation, and increased exposure and susceptibility to pests and pathogens) are decreasing forest resistance to changes in community composition and structure. In this study, we document the establishment of the invasive species *A. adenophora,* in the understorey of a high elevation subtropical forest following severe snow damage to the canopy. The density of this invasive species increased with increasing canopy openness. Dispersal limitation may also influence the density of this invasive species in the understorey. We suggest that long-term monitoring should continue to better document the sustained effects of *A. adenophora* in the forest community. Management intervention (e.g., mechanical removal or use of herbicide) may be necessary, however at this point we conclude that such efforts should be delayed until longer-term demographic information on invading populations of the species is obtained.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.02.031.

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