

The Effects of Landscape Structure and Stand-Scale Factors on *Dendroctonus Valens* Damage Under *Disturbance Conditions* in North China

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Research

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Abstract

Background

In recent years, the red turpentine beetle (*Dendroctonus valens*, RTB), an invasive pest species has spread northward along the distribution of pine forests, forming a potential threat to healthy pine forests in North China. Previous studies have shown that natural (e.g., fire) and human (e.g., felling) disturbances can significantly promote bark beetle damage. However, few studies have considered the effect of multi-scale factors on bark beetle damage under disturbance conditions. Here, we investigated RTB damage (entrance holes) in 98 forest stands with and without disturbance (fire or stolen felling) in the Heilihe National Nature Reserve, Inner Mongolia, which is considered to be in the early stage of RTB outbreak. We assessed the effects of forest landscape structure (forest proportion and host connectivity) and stand-scale characteristics on RTB damage under different disturbance conditions (presence or absence). In addition, we also explored the effects of fire and stolen felling disturbance on RTB damage and the significant differences between them.

Result

Disturbance (i.e., fire and stolen felling) could significantly promote the occurrence of RTB and there was no significant difference between the two types of disturbance. In the absence of disturbance, small stand-scale factors (i.e., aspect and canopy cover) played important roles in the prediction of RTB damage. In the presence of disturbance, forest proportion within a radius of 250 m was the main factor affecting RTB invasion. Higher forest coverage could reduce the migration of RTB from the surrounding environment to the disturbance area, thus reducing RTB damage. In addition, we observed a positive relationship between elevation and RTB invasion.

Conclusion

Landscape structure and stand-scale factors had different effects on RTB invasion under different disturbance conditions. This study not only provides new insights into understanding the roles played by multi-scale factors in RTB damage but also assists in the implementation of pest management programs.

Background

Bark beetle outbreaks are significant natural disturbance in forest ecosystems worldwide (Coops et al., 2006; Negrón et al., 2009; Seidl et al., 2015). Such outbreaks have important ecological impacts on wildlife, forest succession, water quality, forest timber supply, and forest leisure and entertainment functions (Abbott et al., 2009; Klutsch et al., 2009; Mezei et al., 2014). Since 1998, serious outbreaks of red turpentine beetle (*Dendroctonus valens*, RTB), an exotic invasive pest, have occurred in many

provinces of China, which indirectly caused economic loss of totaled ¥8.1 billion (Zhao et al., 2002; Xu et al., 2006). In recent years, RTB has spread northward along the distribution of pine forests, forming a potential threat to healthy pine forests in North China (Yan et al., 2005; Cheng et al., 2015). While RTB outbreaks have led to a large area of continuous tree mortality, beetles are selective in their attack strategy in the initial invasive stage, leading to a patchwork of tree mortality across the forest landscape (Nelson et al., 2006; Bone et al., 2013). Identifying the factors that promote RTB outbreaks in the early stage of invasion is crucial for forest managers to predict and mitigate RTB damage.

Climate change and increasing human activities are alternating the frequency and severity of the disturbances (e.g., wildfires, logging, and bark beetle outbreaks) on forests, thereby increasing the possibility of disturbance interactions (Komonen and Kouki, 2008; Raffa et al., 2008; Seidl et al., 2016). One kind of disturbance may amplify or dampen the possibility and severity of another disturbance through positive or negative feedback (Hart et al., 2015). Many studies have made great progress in exploring the interaction between bark beetle outbreak and other disturbances such as fire (David et al., 2012; Kulakowski and Jarvis, 2013; Westlind and Kelsey, 2019), gap felling (Komonen and Kouki, 2008; Toivanen et al., 2009; Hekkala et al., 2020), and storm (Schroeder, 2009; Havašová et al., 2017). These disturbances can injure pine bole tissues to release ethanol + 3-carene and monoterpene kairomones, which can attract RTB in the surrounding environment to feed (Kelsey and Westlind, 2017, 2018). In addition, the preference of bark beetles to some tree (e.g., tree diameter) or gap characteristics (e.g., the distance from the gap) at the disturbance site was also studied (Komonen and Kouki, 2008; Kulakowski and Jarvis, 2013). However, few research has focused on the effect of multi-scale ecological drivers (i.e., forest landscape structure and stand attributes) on bark beetle damage in the presence of disturbance.

The dispersal flight of bark beetles depends on their population density (Barclay et al., 2005). In the endemic population phase, bark beetles respond to pheromones and fly in a short distance mainly within the canopy to locate new hosts and mate. In the epidemic population phase, when suitable habitats are exhausted or when beetles enter unfavored habitats, bark beetles may rise above the canopy and follow the wind to travel a long distance to new habitats (Jones et al., 2019). Short-distance dispersal events are more common than long-distance dispersal events. Many studies have shown that landscape structure (e.g., the connectivity of host trees and forest fragmentation) can affect the dispersal flight of insect defoliators during the host-searching and colonization processes (Campbell et al., 2008; Castagneyrol et al., 2019; Wang et al., 2019). This effect of forest structure is applicable to the short-distance dispersal flight of bark beetles (Hansen et al., 2016). However, some studies have pointed out that the effects of landscape structure, a large-scale variable, on host selection of bark beetles vary with the degree of pest damage (Raffa et al., 2008; Simard et al., 2012). For example, in the early stage of bark beetle invasion, the main factors affecting bark beetle damage may be small-scale factors such as tree vigor, tree size, and stand characteristics (Graf et al., 2012; Netherer & Nopp-Mayr, 2005; Pasztor et al., 2014), while forest landscape structure may not play an important role. Considering that most of the studies on bark beetle damage were conducted during the outbreak stage when massive and continuous tree mortality was observed; thus, this view has not been well proved (Simard et al., 2012; Seidl et al., 2015).

The main purpose of this study was to investigate the effects of multi-scale factors including forest proportion, host connectivity, and stand-scale characteristics on RTB damage in the early stage of invasion. In addition, we also evaluated the significance of fire and stolen felling on promoting the hazard caused by beetles and investigated the differences between them by comparing with stands without disturbance. We hypothesize that (1) fire and stolen felling would significantly promote RTB damage and there would be significant differences between the two types of disturbance according to a previous study (Hekkala et al., 2020); (2) In the absence of fire and stolen felling, stand-scale characteristics would be the main factors affecting RTB invasion in the early outbreak stage compared with landscape structure; (3) In the presence of fire and stolen felling, stands with a higher forest proportion would suffer less damage from RTB as forest canopy could affect the migration of RTB from the surrounding environment to the disturbance site.

Methods

Study area

The study area is located in the Heilihe National Nature Reserve (118°27'; 41°24') of Inner Mongolia Province in North China, covering an area of about 27,638 hectares and rising from 750 m to 1,200 m above sea level. The mean annual precipitation and temperature of this area are 470 mm and 6°C, respectively (China Meteorological Data Service Center, 2021). This area is characterized by the presence of forest patches where the most common tree species is Chinese pine (*Pinus tabulaeformis*, the host tree of RTB), interspersed with larch (*Larix principis-rupprechtii*), some broad-leaved tree species, and grasslands. The remaining landscape is characterized by agricultural lands and urban areas.

With the northward spread of RTB from Shanxi Province, RTB was found in the Heilihe Nature Reserve for the first time in 2017 (Tang et al., 2019). In recent years, owing to the abundant host resources and lack of natural enemies, the occurrence of RTB was found in many places of this area. However, due to the short invasion history, the Heilihe National Nature Reserve is considered in the early stage of RTB outbreak with 1%-5% trees having a red crown (White et al., 2005). In addition, fire and stolen felling are the most common and widespread ecological disturbances in this area. Extensive RTB damage is observed in the forest stands where these disturbances occur.

Site Selection And Field Sampling

May and August are the flight periods of RTB, during which the temperature is suitable for their feeding and spread (Zhan et al., 2020). A total of 98 sample plots, in which the trees showed a continuum of degree of RTB damage, were randomly selected and investigated in August of 2019 and 2020, including 68 plots affected by neither fire nor stolen felling, 15 plots affected by fire, and 15 plots affected by stolen felling (Fig. 1). For the sample plots disturbed by stolen felling, a small number of *P. tabulaeformis* (about 3 to 10 trees) were felled, which would not affect the measurement of stand-level factors such as canopy

density (described below). The dead pine trees suffered high-severity fire would not attract bark beetles due to their poor physiological conditions, while low-severity fire increases susceptibility of lodgepole pine to mountain pine beetle (Kulakowski and Jarvis, 2013). Therefore, for the sample plots disturbed by fire, we selected those at the edge of the fire scene in 2019 and 2020. Most of the pine trees in our sample plots possess a partially burnt trunk, with green needles remain in the tree crown. The forest stands suffered fire and stolen felling disturbances are shown in Fig. 2.

We used a GPS receiver (Garmin eTrex 309x, Beijing, China) to record the coordinates of sample plots with an accuracy of < 3 m. In each plot, the diameter at breast height (DBH), species name, and status (infected or uninfected) of each tree with a DBH > 8 cm were recorded. As for the canopy density of the sample plots, we used the canopy projection method to calculate canopy closure (Bunnell and Vales, 2011). Soils of the 20-cm depth were collected at four corners and the central point of each plot and mixed well, and the Kjeldahl method was used to obtain soil total nitrogen content (Simard et al., 2012; Bao and Jiang, 2013). We recorded the topographic characteristics, including elevation, aspect, and slope for each sample plot. Aspect was converted into a south-west-ness index ranging between - 1 and 1 in the subsequent multivariate statistical analysis (Beers et al., 1966). In addition, we used a digital elevation model (DEM) (Aster GDEM 30 m resolution, 2021) to calculate the total radiation of each plot from April to August each year. RTB penetrates the base or shallow roots of pine trees and feeds on phloem tissue, forming funnel-shaped entrance holes in the trunk base (Fig. 2). Therefore, we recorded the number of RTB entrance holes in the sample plots to represent the damage degree, which was used as a response variable in model construction statistics.

Forest Landscape Structure

We acquired two remote sensing images of Gaofen-2 (China Center for Resources Satellite Data and Application, 2020) covering the whole study area in September 2017 to calculate the forest landscape structure of the buffering zone with a radius of 250 m around each sample plot. The buffering zone with a radius of 250 m is a suitable scale for the bark beetle's response to disturbances (Komonen and Kouki, 2008). We used the random forest algorithm (Breiman, 2001) to classify land cover types based on remote sensing images, and the classification accuracy was 81.54% at 1-m resolution (Table S1). Land cover types were classified into six categories: Chinese pines, larches, broad-leaved trees, grasslands, farmlands, and residence communities. The conifer and broad-leaved trees were assigned as forests and other categories as open habitats (non-forests). Finally, we measured the percentage of total forest coverage in the buffering zone area with a radius of 250 m around the sample plot at the landscape level (Castagneyrol et al., 2019; Wang et al., 2021). In addition, we also measured the AI index of forests and COHESION index of Chinese pine patches to indicate the degree of forest fragmentation and connectivity of host patches, respectively (Bone et al., 2013; Seidl et al., 2015; Wang et al., 2019). In order to avoid the influence of spatial overlap on the representativeness of these landscape variables, the sampling points were spaced at least 500 m apart. Moreover, the forest coverage of the buffering zone was maintained between 13% and 98% to ensure the reasonable distribution of these landscape variables. All landscape-

and stand-level variables used for data analysis are shown in Table 1. The detailed descriptions of remote sensing image preprocessing, classification, and landscape index calculation are available in Supplementary Materials.

Statistical analysis

The two-year survey data were divided into non-disturbance group, fire disturbance group, and stolen felling disturbance group for statistical analyses. First, due to the poor normality of the data, a nonparametric Kruskal–Wallis test with post hoc was used to test the significant difference between different disturbance groups using the “Kruskal” function of the R package agricolae. Since no significant difference in the damage degree of RTB was found between fire and stolen disturbance plots, these two groups were combined into a single disturbance group in the following analyses.

Prior to constructing models, we measured multicollinearity among the variables (Table 1). Spearman’s correlation test showed that there was a strong correlation between the AI index and forest proportion ($R = 0.74$; Supporting Information Fig. S2). As the AI index has been shown in previous research (Bone et al., 2013) to affect mountain pine beetle-caused tree mortality, we removed this index from explanatory variables in subsequent analyses. The variance expansion factor (VIF) of models was calculated to evaluate the collinearity between remaining nine explanatory variables. The result showed the VIF values were less than 2, indicating that the collinearity between explanatory variables was low.

To explore the effects of forest landscape structure and stand-level factors on RTB damage under different disturbance conditions, we analyzed the data in two ways. First, we used generalized linear mixed models (GLMMs) and the data obtained from non-disturbance group (68 sample plots) to explore the factors affecting RTB damage. In the GLMMs, time was set as a random effect, stand- and landscape-scale variables were set as fixed effects. Second, since most of the sample plots disturbed by fire or stolen felling investigated in 2019 showed no random effect, we employed generalized linear models (GLMs) to explore the factors affecting RTB damage using the data of disturbance group. The data were the sum of 15 plots disturbed by fire and 15 plots disturbed by stolen felling. Furthermore, a preliminary analysis (overdispersion test) showed that our data were over dispersed, so we employed the negative binomial error distribution and log link function, which would provide better parameter estimates than the Poisson distribution (Zuur et al., 2009). Explanatory variables in all models were log-transformed to facilitate the model’s convergence.

For model simplification, the information-theoretic approach based on Akaike’s information criterion (AICc) corrected for small-sized sample was applied to remove non-significant terms (Grueber et al., 2011). We used the “dredge” and “get.models” functions in the R package MuMIn (Bartoń, 2019) to generate all possible models and selected the top ranked models with a $\Delta AICc$ value (i.e., $AICc - AICc_{min}$) < 2 (Bloom et al., 2021). Model averaging was performed to produce the Akaike weight of the top ranked models and model-averaged partial regression coefficient for each variable. The relative importance of a variable was not based on P -values, but rather quantified by the sum of the Akaike weights of each top

model in which this variable appeared. A variable that showed up in many of the models with large weights would receive a high importance value. Finally, we calculated the marginal R^2 (R^2_m) and conditional R^2 (R^2_c) to assess the proportion of variance explained by fixed effects and by both the fixed and random effects to provide absolute values for the goodness-of-fit of the best-fit model (minimum AICc value) using the “r.squaredGLMM” function implemented in the R package MuMIn.

Significant and important variables identified by the models with and without disturbance were grouped in the same direction (for aspect) or at equidistant intervals (for canopy cover, forest proportion, and elevation), and a nonparametric Kruskal–Wallis test with post hoc was conducted for each variable. Although the variables identified by models could significantly affect RTB damage, the purpose of this analysis was to clarify which group(s) of variables differed from the others, and to help forest managers effectively monitor and control RTB outbreaks.

Table 1
List of explanatory variables used in model analysis

Variable category	Variable	Scale of measurement	Variable description
Stand-level factors	DBH (cm)	plot	Stand mean DBH
	Canopy cover (%)	plot	Degree of canopy closure
	Slope (°)	plot	Stand slope
	Aspect (°)	plot	Stand orientation
	Elevation (m)	plot	Stand elevation
	Total N (g/kg)	plot	Total nitrogen of soil
	Solar radiation	plot	Total solar radiation from April to August
Forest structure factors	Forest proportion	Landscape	The proportion of forest area within a radius of 250 m
	AI	Landscape	The fragmentation degree of forest
	COHESION	Landscape	The connectivity of host patches

Results

Effects of fire and stolen felling on RTB damage

The average number of RTB entrance holes in the non-disturbance group, the stolen felling disturbance group, and the fire disturbance group was 21.65, 107, and 119.47 (SE = 3.71, 19.77, and 25.67), respectively. The results of nonparametric tests showed that the number of RTB entrance holes in the fire

and stolen felling disturbance groups was significantly higher than that in the non-disturbance group ($P < 0.001$). Fire and stolen felling could significantly promote RTB damage (Fig. 3); however, there was no significant difference in the number of RTB entrance holes between the fire disturbance group and the stolen felling disturbance group ($P = 0.985$).

Plots under non-disturbance conditions

Aspect showed a significant positive relationship with RTB damage (Table 2). RTB damage increased gradually as stands' aspect changed from northeast to southwest ($P = 0.005$; relative importance = 1; Fig. 4a). Canopy cover exhibited a negative effect on RTB damage, which decreased with the increase of canopy cover ($P = 0.03$, relative importance = 1; Fig. 4b). Elevation and solar radiation were present in the optimal model, but these two factors did not significantly affect the occurrence of RTB. Similarly, in non-disturbance forest stands, the forest structure factors were not able to predict the occurrence of RTB (Table 2).

Plots disturbed by fire and stolen felling

The average number of RTB entrance holes in the disturbance group was 113.23 (SE = 15.96). Forest proportion was the most important factor that significantly affected RTB damage among all variables ($P = 0.01$, relative importance = 1; Table 2). The exponentially negative relationship between RTB damage and forest proportion indicated that with the increasing forest patches, stands disturbed by fire or stolen felling were less vulnerable to RTB outbreak (Fig. 5a). In addition, elevation was found important under disturbance conditions, with a positive relationship with RTB invasion ($P = 0.03$, relative importance = 0.48; Fig. 5b).

Nonparametric test for important variables

Based on the results obtained from modeling, we divided significant variables into groups (Fig. 6). The Kruskal–Wallis test results showed that the number of RTB entrance holes was significantly higher in the sample plots facing south compared with those facing the north and east directions (Fig. 6a). The number of RTB entrance holes was significantly higher in the stands with canopy cover less than 30% than those with canopy cover more than 40% (Fig. 6b). In the presence of disturbance, stands with forest proportion more than 80% could significantly reduce the degree of RTB damage compared with other groups (Fig. 6c). RTB damage in the stands with an elevation above 1000 m was significantly severe than that in the stands with lower elevations (Fig. 6d).

Table 2

Summary of the model averaging procedure assessing effects of stand- and landscape-scale factors on RTB damage under disturbance and non-disturbance conditions

	Estimate	Std. error	z-value	P-value	Relative importance	R ²
Non-disturbance condition						0.36 (0.43)
Intercept	8.04	4.20	1.90	0.058		
Canopy cover	-10.14	4.60	2.17	0.030*	1.00	
Aspect	0.94	0.33	2.83	0.005**	1.00	
DBH	-2.62	1.43	1.81	0.071	0.49	
Total N	7.99	6.89	1.14	0.254	0.19	
Solar radiation	-0.91	1.11	0.80	0.421	0.13	
COHESION	-0.80	1.02	0.78			
Disturbance condition						0.34
Intercept	1.47	8.81	0.17	0.869		
Forest proportion	-2.15	0.82	0.17	0.01*	0.68	
Elevation	5.46	2.48	2.11	0.03*	0.48	
DBH	2.61	1.56	1.60	0.14	0.22	
Slope	-1.24	0.81	1.46	0.144	0.08	
Note: * represents significant differences at the 0.05 level, ** represents significant differences at the 0.01 level. The model's R ² in the non-disturbance conditions represents the marginal R ² (conditional R ²).						

Discussion

Effects of fire and stolen felling on RTB damage

In line with our first hypothesis and many previous studies (Komonen and Kouki, 2008; Toivanen et al., 2009; Westlind and Kelsey, 2019), we found that fire and stolen felling can significantly promote RTB invasion. The aggressive behavior of RTB under disturbance conditions can be attributed largely to their sensitivity to ethanol and monoterpenes (such as 3-carene) produced in stressed woody phloem (Kelsey and Westlind, 2017, 2018).

Hekkala et al. (2020) has shown that the number of recently attacked spruce in gap-cut stands increased significantly compared with that of burnt stands. This finding contrasts with our study in which no

significant difference was observed between felled and burnt stands. This phenomenon may be related to the sampling time after fire and fire intensity. In general, after three years of fire, the burnt forest stands are less attractive to bark beetles due to the decrease in the concentration of attractive volatiles (Westlind and Kelsey, 2019). Moreover, the stands burnt by high intensity fire are not favored by bark beetles due to the destruction of stem phloem (Kulakowski and Jarvis, 2013). The sample plots in our study were located at the edge of burnt stands within one to two years after fire, which were characterized as low-intensity fire. In addition, a small amount of fallen trees in plots disturbed by stolen felling could still attract a large number of RTBs to harm the fallen and surrounding healthy pine trees. It is worth noting that the current forest management strategies to deal with RTB damage mostly focus on hanging traps or clearing burnt woods in forests after fire, while ignoring the strong attraction of fallen woods after stolen felling to RTB. The new control strategy should simultaneously consider the attraction of woods in forests under natural (e.g., fire) and human disturbances (e.g., stolen felling) to RTB.

Impacts of stand characteristics on RTB damage in the absence of disturbances

Previous studies have shown that bark beetle damage is affected by both beetle pressure and forest susceptibility (Nelson et al., 2006; Raffa et al., 2008). Similar to the studies of Nelson (2006) and Bone (2013), we only considered forest susceptibility (without considering beetle pressure) in our research, which may also be the attribution of the low R^2 values obtained from generalized models. The purpose of our study was to explore the role of landscape structure and stand-scale factors in forest susceptibility assessment during the early stage of RTB invasion. The obtained results supported our hypothesis that stand characteristics were the main factors affecting RTB invasion in this stage.

The factors affecting bark beetle damage are associated with the stage of outbreak (Simard et al., 2012). In the endemic population phase, stand-scale attributes, such as tree vigor, tree size, and canopy density, determine the outcome of bark beetle damage (Jakus et al., 2011; Lausch et al., 2011; Mezei et al., 2014). When bark beetle population increases, landscape-level factors, such as host connectivity and forest structure, outperform in predicting stand sensitivity (Simard et al., 2012; Seidl et al., 2015). The connectivity of host patches is the key for bark beetles to locate their hosts quickly in the outbreak period when the population density is high, while in the period when the population density is low, bark beetles prefer to damage stands at a small scale due to the widespread of hosts (Raffa et al., 2008; Seidl et al., 2015). Bone et al. (2013) found that forest structure (AI index) played different roles in different stages of the mountain pine beetle outbreak, and forests with low fragmentation were more seriously damaged in the late stage of outbreak. All the above results are consistent with our findings. In the early stage of RTB invasion, the factors affecting RTB damage were mainly small-scale stand factors, such as aspect and canopy cover, while large-scale landscape factors did not play a role in the early stage of RTB invasion (Table 2).

We found that aspect played an important role in predicting RTB damage (Table 2). South-facing stands showed a higher degree of RTB damage compared to stands facing other directions. South-facing stands are more sensitive to bark beetles, because higher levels of solar radiation may reduce tree vitality and

increase beetle survival (Coops et al., 2006; Lausch et al., 2011). Stands with lower canopy closure are more likely to be attacked by bark beetles, because relatively higher temperatures in such stands are more attractive to bark beetles (Netherer and Nopp-Mayr, 2005; Pasztor et al., 2014). Therefore, it is believed that aspect and canopy density are associated with solar radiation and stand temperature, respectively, and the significant role solar radiation plays during bark beetle invasion has also been revealed in many other studies (Kautz et al., 2013; Chen et al., 2014; Mezei et al., 2019). However, we did not observe a high relative importance in solar radiation in our study, which was present in the optimal model but was not significant. A possible explanation may be that the effect of extremely high radiation on RTB invasion is neutralized by the long-term cumulative radiation calculation (April to September).

Effects of forest proportion and elevation on RTB damage in the presence of disturbance

In line with our third hypothesis, forest proportion could significantly affect RTB invasion in the presence of disturbance conditions compared with the non-disturbance condition. The average distance of RTB dispersal flight in forests is beyond 500 m (Jones et al., 2019). Within a radius of 250 m, the forest structure with a high proportion of open habitats (non-forest areas) was conducive to RTB dispersal from the surrounding areas to disturbed forests rich in ethanol and monoterpenoid volatiles. However, under non-disturbance condition, RTB prefers to randomly select weak host trees in situ for feeding and mating, which is also the reason why landscape indicators could not alter the preference of RTB in selecting the hosts in the early stage of outbreak (Raffa et al., 2008; Walter and Platt, 2013). Hekkala et al. (2020) explored the effects of the proportion of broad-leaved trees and spruce forests within a radius of 500 m around disturbed plots on the abundance of *Ips typographus*. Although the above landscape indicators did not perform well in regression models, they showed a trend (negative correlation) consistent with that observed in our study. Therefore, the present study, which emphasizes the potential importance of disturbance and landscape structure during RTB spread, not only contributes to expanding the understanding of the roles large-scale factors play under different disturbance conditions but also assists in the implementation of pest management programs.

Low-altitude areas are susceptible to bark beetle invasion in the early stage of beetle outbreak, while the low temperature accompanying high-altitude stands could slow down the development of larvae, thus reducing the generation number of bark beetles. (Lausch et al., 2011; Logan & Powell, 2001). However, during the outbreak period, the activity range of bark beetles shifts to high-altitude areas due to the limitation of host resources in the low-altitude areas (Gregory et al., 2017). In this study, elevation did not exhibit significant effect on RTB damage in the absence of fire or stolen felling, which may possibly be attributed to the relatively small range of elevations of our study areas. However, forest stands with an elevation above 1000 m were more seriously damaged by RTB in the presence of fire or stolen felling. The possible reason may be that the attractive volatiles released by disturbed stands in high-altitude areas could spread around more easily.

Conclusion

In this study, we explored the effects of fire and stolen felling and multi-scale factors on RTB damage in 98 forest stands in the Heilihe National Nature Reserve. We found that fire and stolen felling could significantly promote the occurrence of RTB and there was no significant difference between the two types of disturbance. In the absence of disturbance, small-scale stand factors (aspect and canopy cover) play an important role in the prediction of RTB damage. In the presence of disturbance, landscape structure (forest proportion) and elevation could significantly affect RTB damage. Our results expand the understanding of the influence of multi-scale factors on RTB damage and will help in more accurate predictions of future patterns of RTB outbreaks. In addition, our research emphasizes the important role of landscape structure in mitigating RTB damage under disturbance conditions. However, it is not clear whether the influence of landscape structure on RTB dispersal will be weakened during RTB outbreak period under disturbance conditions, which will be explored in our future study.

Declarations

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Authors' contributions

Zhongyi Zhan and Youqing Luo conceived and designed research. Zhongyi Zhan conducted experiments. Zhongyi Zhan and Lixia Wang analyzed data and wrote the manuscript. All authors participated in review and revision of the manuscript.

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Availability of data and materials

The datasets analyzed in this study are available from the corresponding author on reasonable requests.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Figures

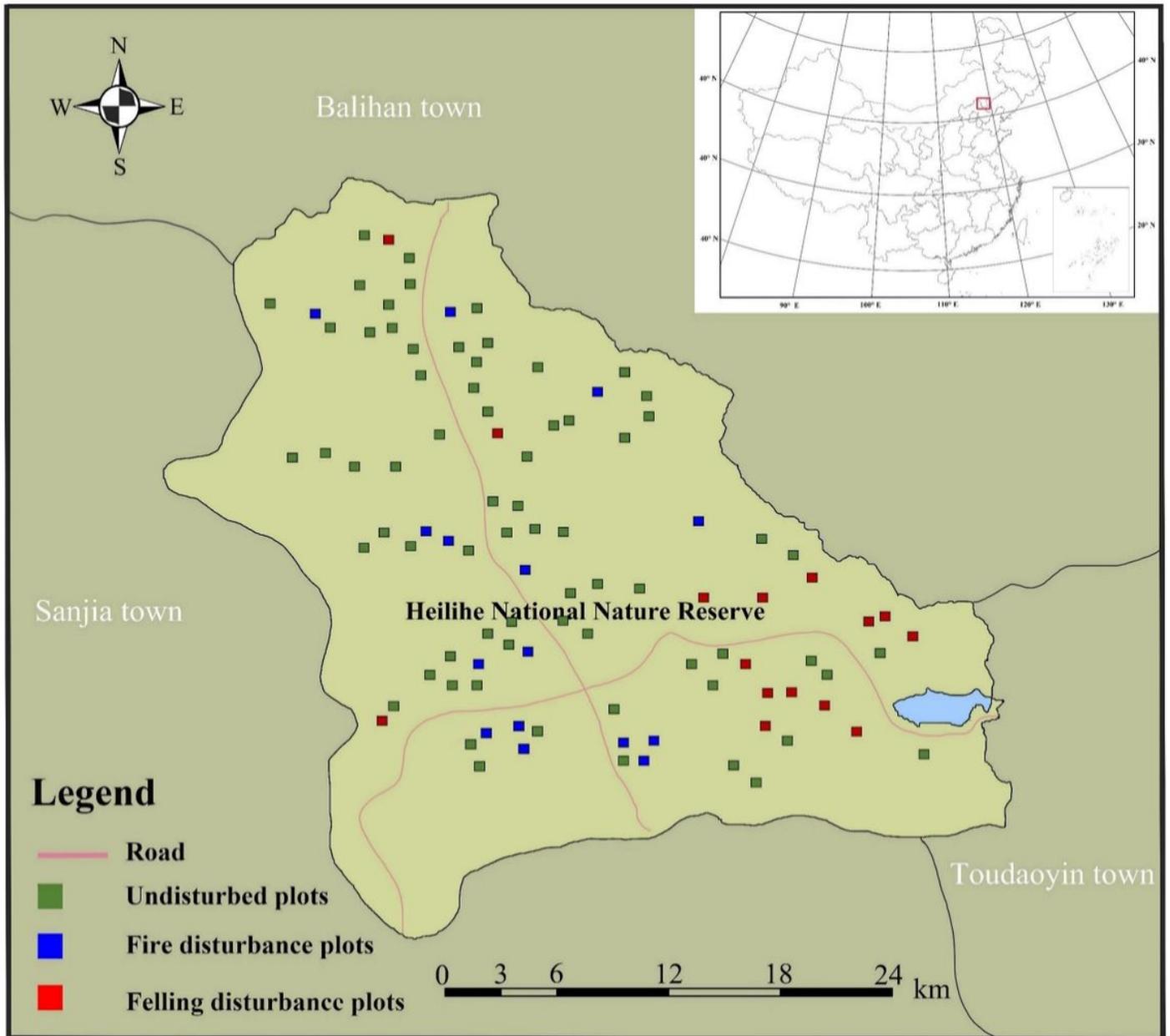


Figure 1

Distribution of sample plots in the study area.

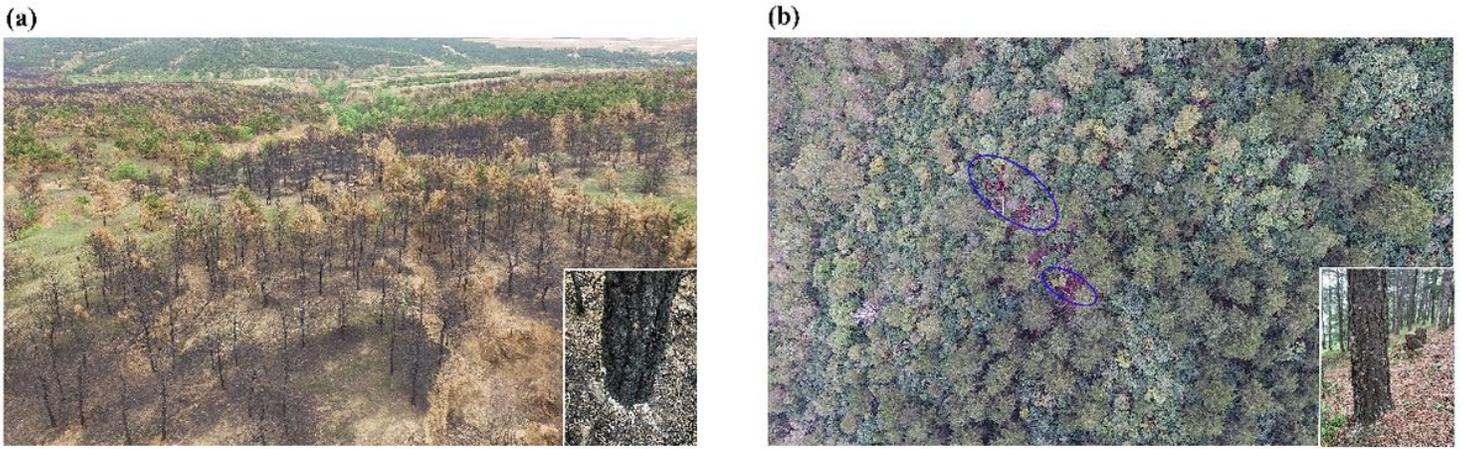


Figure 2

Sites under natural and human disturbances in the study area. (a) Forests after fire; (b) felled woods left after stolen felling.

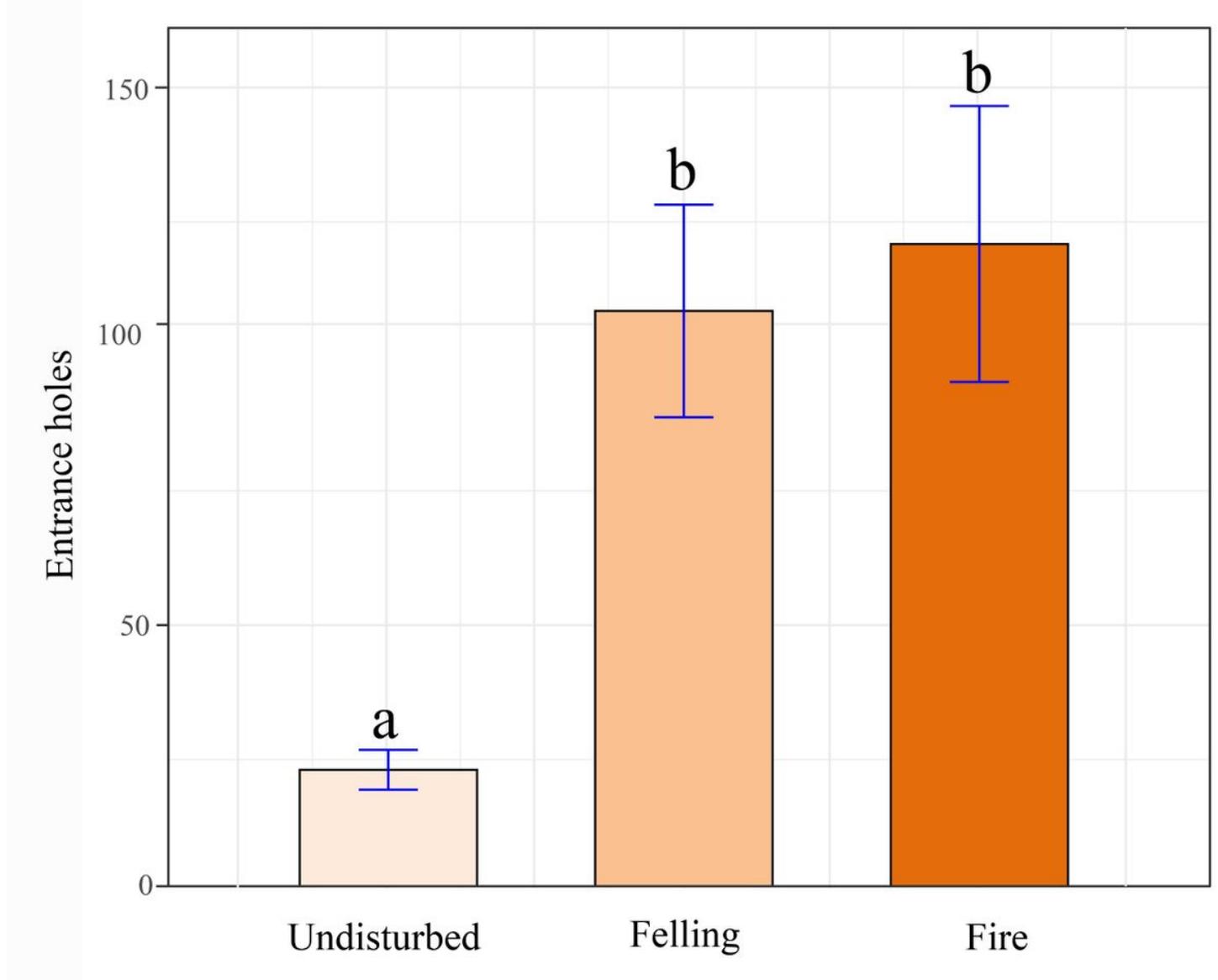


Figure 3

The mean counts of RTB entrance holes under different disturbance conditions. The error bars represent the standard error of the mean. Letters above bars indicate statistical differences between forest types according to the analysis of variance ($P < 0.05$).

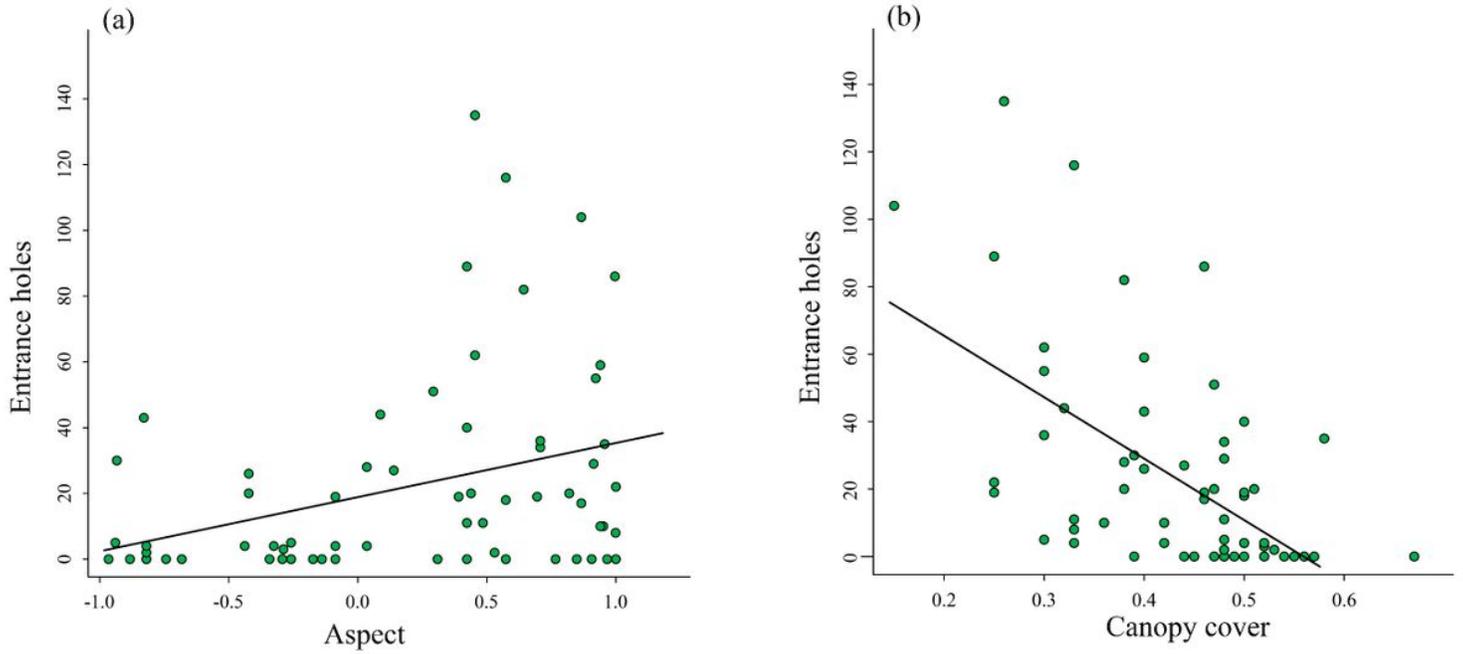


Figure 4

The responses of RTB entrance holes to (a) aspect (x-axis represents a change from northeast to southwest) and (b) canopy cover under non-disturbance condition.

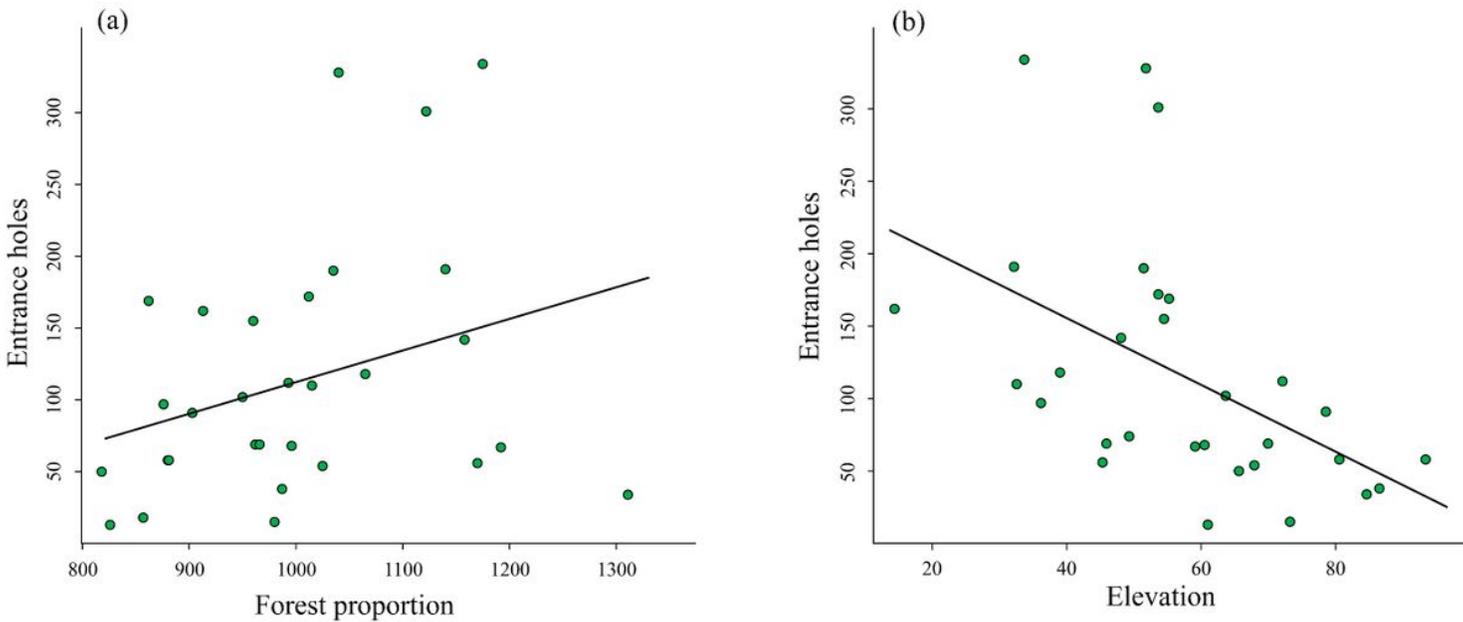


Figure 5

The responses of RTB entrance holes to (a) forest proportion and (b) elevation under disturbance condition.

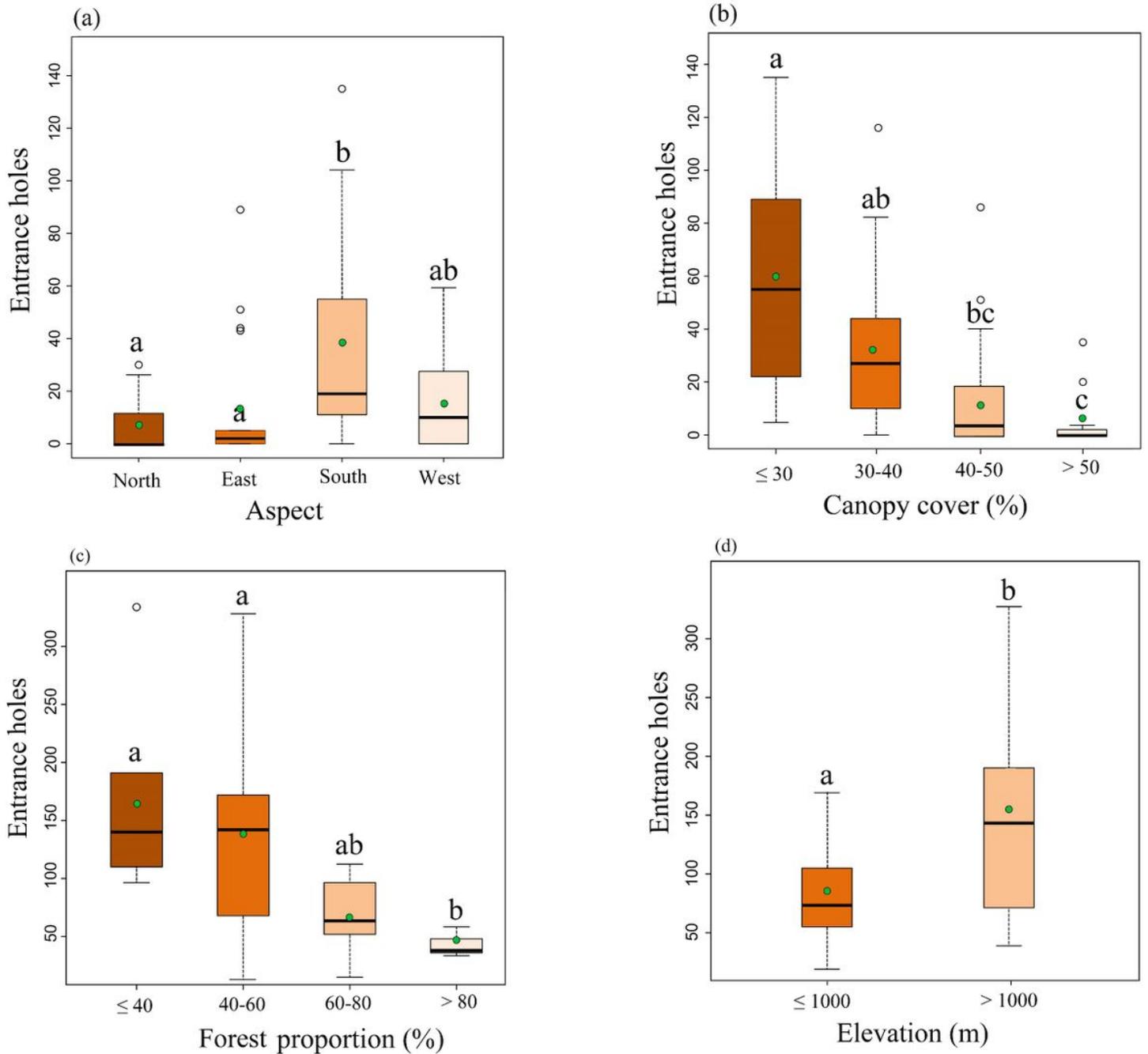


Figure 6

Boxplot of the number of RTB entrance holes for important variables under disturbance and no-disturbance conditions, which were divided according to the direction or equidistant intervals: (a) aspect, (b) canopy cover, (c) forest proportion, and (d) elevation. Green dots indicate mean values, and letters indicate significant differences between groups.

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