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Landscape-Level And Stand-Level Factors Play Diverse Roles During Different Periods of *Dendroctonus Valens* Invasion In North China

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Abstract

In recent years, the red turpentine beetle (RTB), an invasive pest species, has caused extensive pine mortality in North China. Although some studies have theoretically clarified the interference mechanism of multi-level factors with the development of RTB damage, knowledge about this mechanism from the empirical research is still limited. The aim of this study was to determine whether the primary factors influencing RTB occurrence change during different periods of RTB invasion. Stand-level variables of sample plots were obtained through field investigation and the forest resource survey data including forest stand characteristics, topographic characteristics, and soil properties. Remote sensing classified images were to develop the characteristic variables related to landscape composition and configuration around the sample plots at multiple scales. Generalized linear models (GLMs) and generalized linear mixed models (GLMMs) were used to explore the relative importance of stand-level and landscape-level variables in explaining the severity of RTB damage. Result showed that two stand-level factors, aspect and canopy density, were the best predictors of damage in the early stage of RTB invasion. The landscape-level factor, the proportion of Chinese pine (*Pinus tabuliformis*) patches, was the main predictor of damage in the middle stage of RTB invasion. The most effective spatial scale at which RTB responded to landscape pattern was 250 m. With the increasing severity of RTB damage, the factors driving RTB invasion have shifted from the stand-level to the landscape-level. This calls for an urgent consideration of multi-scale processes to address the changing disturbance regimes in ecosystem management.

Key Message

- *Dendroctonus valens* is an invasive pest species caused extensive pine mortality in North China
- No study verified the impact of multi-level factors on bark beetle damage at different stages of outbreak.
- The stand-level factors (canopy density and aspect) had more influence on RTB occurrence in the early stage
- The landscape-level factor (host availability) was a more important predictor in the middle stage of RTB outbreak
- Forestry management of RTB outbreak should depend on knowledge combined from multiple spatial scales, from the stand scale to the landscape scale

Introduction

Red turpentine beetle (RTB), *Dendroctonus valens* (Coleoptera: Curculionidae: Scolytinae), an invasive pest introduced from North America, is an important natural disturbance agent of forest ecosystems across a wide range of landscapes in China (Qiu, 2013; Sun et al., 2012; Yan et al., 2005). In 1998, RTB invaded Shanxi Province for the first time. In the following years, RTB spread rapidly from Shanxi Province to the adjacent provinces, causing the mortality of a large amount of Chinese pine (*Pinus*

tabuliformis) trees and developing potential threats to healthy pine forests in North China (Cheng et al., 2015; Yan et al., 2005). In forest ecosystems, the outbreak of bark beetles has significant ecological effects on forest succession, fuel dynamics, nitrogen and carbon cycling, as well as substantial socioeconomic impacts (Abbott et al., 2009; Kurz et al., 2008). Considering the wide host range and spatial distribution of RTB, many geographic areas are at risk of being invaded, such as Eurasia, which has abundant suitable pine hosts (Erbilgin et al., 2007).

During the incipient stage of an outbreak, weakened or diseased pines are more likely to be selected by bark beetles (Raffa et al., 2008). Once they reach high population levels due to warm climatic conditions and availability of hosts, selective pressure declines as higher densities facilitate successful attack on more vigorous trees (Boone et al., 2011; Jones et al., 2019). In the process of the bark beetle populations from endemic to epidemic, stand- and landscape-level factors can influence the amount and distribution of tree mortality caused by bark beetles, leading to beetle-killed forest stands across the landscape (Gilbert et al., 2005; Ogris & Jurc, 2010; Raffa et al., 2008; Seidl et al., 2015; Thom et al., 2013). Understanding the multi-scale factors that are associated with increased severity of RTB outbreak is critical to predict future patterns of forest structure, function and composition, and socioeconomic impacts. However, the multi-scale factors driving RTB damage have rarely been studied.

Stand-level characteristics can directly or indirectly impact bark beetles and the vitality of their hosts, thereby influencing the stand susceptibility to bark beetles. Previous studies explored the effects of forest stand characteristics (Ml et al., 2012; Netherer & Nopp-Mayr, 2005; Pasztor et al., 2014), topographical characteristics, (Akkuzu et al., 2009; Mezei et al., 2014; Walter & Platt, 2013), and soil properties (Dutilleul et al., 2000; Simard et al., 2012) on bark beetle damage. Since the observation of the selective behavior of bark beetles at the stand scale is limited for understanding the outbreak, an examination of beetle interactions at a landscape scale would be necessary (Nelson et al., 2006; Robertson et al., 2008). Landscape composition (i.e., the proportion and diversity of the cover types) and configuration (i.e., the spatial arrangement of the cover types such as the shape and connectivity of patches of a given category) can affect the spread of insect defoliator outbreaks (Balzan et al., 2016; Dominik et al., 2018). This is particularly true for bark beetles, which interact with their tree hosts across multiple spatial scales (Raffa et al., 2008).

Boone et al. (2011) have highlighted the need for additional attention to research on the different phases of forest pest outbreaks. Landscape- and stand-level factors may have different effects on the potential locations of beetle attack during different periods of outbreaks. For example, stand-level factors may be important to explain the onset of local eruptions, while landscape-level factors are possibly more important once a regional outbreak has begun (Raffa et al., 2008; Simard et al., 2012). However, the mechanistic underpinnings whether stand- and landscape-level factors play different roles in different stages of bark beetle outbreak are scarce. As far as we know, no suitable data in the published studies can be utilized to explore the impact of landscape-level factors on bark beetle attack in the initial stage of an infestation, as the tree mortality has been massive and continuous at the landscape scale (Seidl et al.,

2015; Simard et al., 2012). The aim of this study was to close this gap, which distinguished the initial conditions leading to an outbreak and the factors facilitating the spread.

In recent years, along the distribution of pine forests, RTB has spread to Inner Mongolia and Liaoning Province of China (Tao et al., 2019). Here we carried out the experiments in the Heilihe area of Inner Mongolia and the Dahebei area of Liaoning Province. Due to the different introduction times, the degree of RTB damage was different between these two areas (Fig. 1). The purpose of this study was to identify key stand- and landscape-level factors influencing RTB invasion in different stages. We hypothesized that: (1) stand-level factors would be more important in the initial stage of RTB invasion; and (2) the role of landscape-level factors would be more vital in the middle stage of RTB invasion. In addition, we explored the optimal scale to predict RTB occurrence at three spatial scales (250, 500, and 1000 m). In addition, we explored the optimal scale to predict RTB occurrence at three spatial scales (250, 500, and 1000 m). Such result would enable us to work at the most effective spatial scale (Jackson & Fahrig, 2012).

Material And Methods

Study areas

This study was conducted in two areas: the Heilihe town of Inner Mongolia and the Dahebei town of Liaoning Province (Fig. 1). Due to the different introduction times of RTB from Shanxi Province to the above two regions, the initial occurrence times of RTB in the Dahebei area and Heilihe area were 2014 and 2017, respectively. According to the unmanned aerial vehicle (UAV) data of these two areas and the four grading criteria proposed by White et al. (2005), the Heilihe area was determined to be in the early stage of RTB outbreak with 1%-5% trees having a red crown, while the Dahebei area was in the middle stage of RTB outbreak with 5%-20% of trees showing a red crown.

The Heilihe town covers approximately 531 km^2, rising from 750 m to 1200 m above sea level. The mean annual precipitation and temperature of this area are 470 mm and 6 °C, respectively (Heilihe Forestry Station). The Dahebei town covers an area of 176 km^2 and its elevation ranges from 428 to 1018 m above sea level. Similarly, the mean annual precipitation and temperature of this area are 450.9 mm and 8.6 °C, respectively (China Meteorological Data Service Center, 2021). The two areas are dominated by Chinese pine pure forests. Besides, larch (*Larix principis-rupprechtii*) (not a host tree of RTB) and some broad-leaved tree species also grow in the study areas. The remaining landscapes are characterized as grasslands, agricultural lands, and urban areas.

Stand selection and field sampling

Area in the early stage of RTB invasion

Once forest stands are attacked by RTB, indicators such as pitch tubes and boring materials can be used to inspect whether the trees have been infected. In early August of 2018 and 2019, 79 sample plots (30 m

× 30 m), in which the trees showed a continuum of damage degree caused by RTB, were randomly selected in the study area (Fig. 2). The sample plots were located at least 500 m from each other to reduce spatial autocorrelation of landscape elements. The coordinates of these sample plots were recorded using a GPS receiver (Garmin eTrex 309x, Beijing, China) with a precision of < 3 m. In each sample plot, we recorded the diameter at breast height (DBH), species name, and status (infected or uninfected) for each tree with a DBH > 8 cm. We used the canopy projection method to calculate canopy closure (Bunnell & Vales, 2011). Mineral soil (20 cm depth) was collected and composited at the center and four corners of the sample plots. Then, soil organic matter and total nitrogen contents were calculated by the potassium dichromate oxidation and Kjeldahl methods, respectively (Bao & Jiang, 2013). As for topographical characteristics, we recorded the elevation, slope, and aspect for each sample plot. In the subsequent data processing, we transformed the aspect to a south-west-ness index to express the stand environment in sun exposure or dryness (Beers et al., 1966). We recorded the number of RTB entrance holes in the sample plots to represent the damage degree, which was used as the response variable in model construction statistics.

Area in the middle stage of RTB outbreak

In September 2018, we observed that all of the stands in the Dahebei research area were suffered large-scale RTB outbreak through field investigation. The damage in the middle stage of RTB outbreak can be directly detected using UAV images. Therefore, we used the DJI Inspire 2 drone (DJI, Shenzhen, China) to collect RGB images of the whole stand. We obtained 24 synthetic UAV images, each covering more than 20 hectares. We delineated 32 (30 m × 30 m) sample plots (Fig. 2) on UAV images and the distance between the sample plots was more than 500 m as mentioned earlier.

The mean DBH and canopy density of the sample plots were obtained from the National Forest Resources Intelligent Management Platform (2021) and corresponding UAV images. We used digital elevation model (DEM) (Aster GDEM 30 m resolution, 2021) to obtain the elevation, aspect, and slope data of the sample plots. We counted the numbers of damaged Chinese pines (yellow, red, and grey crowns in UAV images) in these sample plots to represent different degrees of RTB damage and took them as the response variable for areas in the middle stage of RTB outbreak.

The plots showing different stages of RTB outbreak were selected from areas without external interferences, such as fire and pest management that can promote or inhibit the occurrence of bark beetles (Agne et al., 2016; Mezei et al., 2017). The variables related to the stand characteristics, topographical characteristics, and soil properties of sample plots were treated as stand-level variables (Mezei et al., 2014). In addition, through remote sensing imagery of Gaofen-2 (China Centre for Resources Satellite Data and Application, 2020) and field investigation, the forest coverage of the buffer with a radius of 1000 m around the sample plots ranges from 10% to 75% to ensure a reasonable distribution of the landscape-level variables (Wang et al., 2019).

Landscape-level variables

We selected the landscape metrics that are most likely to affect the bark beetle outbreak according to the previous studies (Bone et al., 2013; Simard et al., 2012; Wang et al., 2019). We measured landscape composition using the proportion of Chinese pines (PLAND) and Shannon's diversity index (SHDI) calculated from all land cover types. We used mean shape index (SHAPE_MN) and cohesion index (COHESION) to quantify landscape configuration.

Landscape-level variables were quantified in the area around each sample plot at three radii (250, 500, and 1000 m) based on high-resolution remote sensing imagery, which were acquired from the Gaofen-2 satellite covering all study areas in September 2017 and June 2018. Land cover types were classified into five categories: Chinese pines, larches, broad-leaved trees, grasslands, farmlands, and residence communities. Additional details such as the classification method and map of the remote sensing images are available in Supporting Information (Fig S1, Table S1)

Model selection

Prior to model selection, we measured multicollinearity among all variables, and COHESION and soil organic matter were removed (see methods in Supplementary S2). The final set of variables is listed in Table 1. Next, to evaluate the response of RTB outbreak to stand- and landscape-level variables, we constructed generalized linear mixed models (GLMMs) for the area in the early stage of RTB outbreak and generalized linear models (GLMs) for the area in the middle stage of RTB outbreak. The year was used as random effect. Since overdispersion was observed in our data, we used a negative binomial error distribution that would provide better parameter estimates than the Poisson distribution (Militino, 2010).

Models were ranked based on corrected Akaike's information criterion (AICc) adjusted for small-sized samples (Krasnov et al., 2019). We selected the top model set with a ΔAICc (i.e., AICc - $AICc_{min}$) < 2, which is considered as effective. Model averaging was performed to produce Akaike weights (ω) and model-averaged partial regression coefficients for each variable. The relative importance value of each variable was quantified by the sum of the Akaike weights for each model in which the variable appeared. To approximate a normal distribution and enhance model stability, variables were log(x+1)-transformed as needed prior to model fitting (Schmiedel et al., 2015). Finally, we calculated the R^2 of the best model (with the minimum AICc value) to observe the goodness of fit.

Variables found to be the most important in the early and middle stages of RTB outbreak (aspect, canopy density, and PLAND) were grouped if they were in the same direction (for aspect) or at equidistant intervals (for canopy density and PLAND), and a nonparametric Kruskal–Wallis test with post hoc was conducted for each variable. While the model located the variables that significantly affected RTB outbreak, the purpose of this analysis was to elucidate which groups of variables differed from the others, and to help forest managers effectively monitor and control RTB outbreak. All statistical analyses were performed in the R statistical programming environment (R Core Team, 2020) including the packages arm (Gelman, 2008), lme4 (Krasnov et al., 2019), MuMIn (Bartoń, 2019; Lukacs et al., 2009), piecewiseSEM (Nakagawa et al., 2017), and glmmTMB (Brooks et al., 2017).

Table 1 List of explanatory variables used in model analysis of areas in different stages of RTB invasion

Variable category	Variable	Scale of measurement	Data source		Variable description
			Area in the early stage of RTB outbreak	Area in the middle stage of RTB outbreak	
Stand-level factors	DBH (cm)	Stand	FI	NFRD	Stand mean DBH
	Canopy density (%)	Stand	FI	NFRD	Degree of canopy closure
	Slope (°)	Stand	FI	DEM 30 m	Relief slope
	Aspect (°)	Stand	FI	DEM 30 m	Stand orientation
	Elevation (m)	Stand	FI	DEM 30 m	Stand elevation
	Total N (g/kg)	Stand	LM	—	Total nitrogen of soil
Landscape-level factors	SHAPE_MN	Landscape	FC	FC	Shape complexity of host patches
	PLAND	Landscape	FC	FC	Connectivity of host patches
	SHDI	Landscape	FC	FC	Diversity of landscape types

FI, field investigation; NFRD, national forest resource; LM, laboratory measurement; FC, forest classification; — means there is no data.

Results

Relative importance of variables in different invasion stages

Area in the early stage of RTB outbreak

The average number of RTB entrance holes in each plot was 20.82 (SE = 3.83). The aspect was the primary driving factor (P = 0.008; Table 2) affecting the RTB occurrence at both the stand and landscape scales with its relative importance approaching 1 (Fig. 3). The number of RTB entrance holes slowly increased from the northeast to southwest stands (Fig. 4a). Moreover, canopy density (relative importance = 0.96; P = 0.031) significantly influenced RTB occurrence (Table 2; Fig. 3). The number of RTB entrance holes decreased with the increase of canopy density (Fig. 4b). The landscape-level factor

SHAPE_MN (shape complexity of host patches) also played a role as its relative importance reached 0.69 (Fig. 3). Moreover, the relative importance of DBH and elevation was also close to 0.5 (Table 2), but these three indicators were not statistically significant in the models. In general, stand-level factors exerted more influence on RTB outbreak in the early stage.

Area in the middle stage of RTB outbreak

The average number of damaged trees of the 32 plots in the middle stage of RTB outbreak was 12.69 (SE = 2.64). The connectivity of Chinese pine patches (PLAND, P = 0.009; Table 2) significantly affected RTB damage among all the variables with its relative importance approaching 1 (Fig. 3). The exponentially positive correlation between RTB damage and PLAND indicated that with the increasing host patches, stands were more vulnerable to RTB outbreak (Fig. 4c). The remaining variables showed no significant effects on RTB occurrence, with the relative importance values around 0.15. Compared with the stand-level factors, the landscape-level factors were more predominant in the middle stage of RTB outbreak.

The optimal spatial scales for the two invasion stages at which RTB damage best responded to the independent variables were both defined at 250 m, which had an optimal AICc value (Table 2; the results for 500 m and 1000 m are shown in Table S2 and S3).

Table 2 Summary results of the model averaging procedure assessing effects of stand- and landscape-level factors on RTB damage (scale = 250 m).

	Estimate	Std. Error	z-value	P-value	AICc	R^2
Early invasion stage					624.6	0.20 (0.23)
Intercept	5.89	12.12	0.48	0.630		
DBH	-2.68	1.55	1.70	0.089		
Slope	1.49	1.01	1.45	0.148		
Aspect	0.94	0.36	2.61	0.009**		
Canopy density	-10.53	4.82	2.15	0.031*		
Elevation	-6.09	4.09	1.47	0.142		
Total N	7.07	7.00	0.99	0.321		
SHAPE_MN	34.49	20.20	1.69	0.092		
PLAND	-1.40	1.09	1.26	0.207		
SHDI	-13.86	7.09	1.92	0.054		
Middle invasion stage					223.8	0.26
Intercept	-2.65	4.64	0.55	0.581		
DBH	0.75	2.10	0.34	0.733		
Slope	0.47	1.00	0.45	0.651		
Aspect	0.18	0.26	0.67	0.502		
Canopy density	-1.31	5.73	0.22	0.826		
Elevation	-1.11	5.02	0.21	0.832		
SHAPE_MN	7.37	6.60	1.18	0.239		
PLAND	2.96	1.10	2.59	0.009**		
SHDI	-6.08	9.85	0.59	0.554		

P-values were calculated based on averaged parameter estimates using the top ranked models. * means significance at the 0.05 level and ** means significance at the 0.01 level. The model's R^2 in the early invasion stage represented marginal R^2 (conditional R^2).

Nonparametric test of important variables

Based on the results obtained from modeling, we divided significant variables into four groups (Fig. 5a, b, and c). 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.

5a). The number of RTB entrance holes was significantly higher in the stands with canopy density less than 30% than those with canopy density more than 40% (Fig. 5b). The number of damaged trees with a proportion of Chinese pines larger than 0.4 was significantly higher than those with a proportion of Chinese pines smaller than 0.4 (< 0.2 and 0.2-0.4).

Discussion

Performance of landscape-level and stand-level factors in different stages of RTB outbreak

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 is to explore the role of large-scale factors and small-scale factors in forest susceptibility assessment in different stages of RTB invasion. The results obtained supported our hypothesis that the stand-level factors were more important to predict damage in the early stage of RTB outbreak and the landscape-level factors performed better in predicting damage in the middle stage of RTB outbreak. This is also in line with the conjectures gained from other studies on the spruce bark beetle and the mountain pine beetle, in which the researchers failed to prove their hypotheses due to data constraints (Raffa et al., 2008; Seidl et al., 2015; Simard et al., 2012).

The diverse roles of stand-level and landsacpe-level factors play in the early and middle stages of RTB outbreak may be influenced by the population dynamics of this beetle. The interaction between the attack ability of bark beetles and tree defense determines the success rate of bark beetle colonization and then subsequent reproduction is contingent on the presence of weakened host trees such as burned or felled trees (Raffa et al., 2008; Raffa & Berryman, 1983). Under endemic conditions, stand-scale attributes, such as tree vigor, size, and canopy density, determine the outcome of bark beetle damage. However, the existence of environment conditions favored by bark beetles, such as drought and wind disturbance, enables a large-scale attack of host trees by bark beetles regardless of their ages or sizes (Raffa et al., 2008). The transition from local- to large-scale outbreak might be influenced by landscape-level factors.

Stand-level factors

Many studies have revealed a strong positive correlation between DBH and bark beetles' feeding and oviposition (Akkuzu et al., 2009; Amman, 1972; Ml et al., 2012). However, consistent with Lausch et al. (2011), DBH showed no significant influence on bark beetle preferences in our analysis. In the field investigation, we also found RTB-damaged Chinese pine trees with both large and small DBH values. Moreover, pines are less vulnerable to RTB attack in mature stands because of their stronger resistance. Netherer and Nopp-Mayr (2005) and Pasztor et al. (2014) have shown that stands with low canopy closure may suffer bark beetle attacks at a higher probability, because the relatively high temperature within stands of low canopy closure is more attractive to bark beetles. Our research also

confirmed this result, RTB preferred to invade the forest stand with a low canopy density, which was an important predictive variable in the early stage of RTB outbreak.

Previous studies (Lausch et al., 2011; Logan & Powell, 2001; Mezei et al., 2014) have shown that elevation plays an important role in the early stage of bark beetle occurrence, because the low temperature accompanying high-altitude stands could slow down the development of larvae, thus reducing the generation number of bark beetles. However, in the subsequent phases, elevation plays a minor role because the long-term damage leads to the lack of host resources in low-altitude areas. The range of activities of bark beetles gradually shifts to high-altitude areas (Gregory et al., 2017). In our analysis, elevation exhibited no significant effect on RTB outbreak in neither stage, which may possibly be attributed to the relatively small range of elevations in our study areas. Similar to the results from Simard et al. (2012), slope and aspect had no effect on RTB damage during the outbreak period. However, we found that aspect was the most important predictor of the model in the early stage of RTB outbreak (Fig. 3) and south-facing stands showed a higher degree of RTB damage compared to stands facing other directions. The susceptibility of south-facing stands may increase because higher levels of solar radiation may reduce tree vitality and enhance beetle survival (Coops et al., 2006). Slope had a weak impact on RTB damage in the early stage of the outbreak, most likely due to the uneven distribution of the field sampling data. There were fewer sampling points on the steep slope due to topographic limits, which also highlighted the importance of sampling in field experiments.

Soil total nitrogen also has a good predictive effect on spruce beetle damage during the outbreak period (Simard et al., 2012). Unfortunately, we failed to obtain soil data for the area in the middle stage of RTB outbreak. Nevertheless, we speculated that the soil properties may have little effect on RTB occurrence because the two study areas were dominated by the same soil type; this speculation was also supported by the model fitting results from areas in the early stage of RTB invasion. In addition, the effect of soil properties on bark beetles only indirectly affects the preference of bark beetles by influencing the growth of vegetation (Reynolds & Holsten, 1994). Better predictors should focus on the growth of trees or the factors that affect the population dynamics of bark beetles.

Landscape-level factors

Most of the studies have explored the impact of landscape-level factors on bark beetle damage in the initial and outbreak stages but ignored the middle stage prior to the outbreak (Bone et al., 2013; Seidl et al., 2015; Simard et al., 2012). Our research closed this gap and discovered that landscape-level factors could play a role in the middle stage of RTB outbreak. Walter and Platt (2013) used multi-temporal satellite images to monitor the red attack stage of mountain pine beetle. They revealed that the availability of host trees has an important impact on epidemic spread. Bone et al. (2013) showed that contiguous forests experienced greater tree mortality caused by mountain pine beetles when their populations reached epidemic levels. The outbreak curve of the *Ips typographus* population is closely related to the connectivity of host patches, which is a key driver of the observed area (Seidl et al., 2015). Although the connectivity of Chinese pine patches (COHESION) was excluded from our analysis, it has a

high positive correlation with the proportion of Chinese pines (PLAND; Fig S2 and S3). These findings are consistent with our results that the proportion of host patches significantly affected the damage degree in the middle stage of RTB outbreak.

The variable SHAPE_MN didn't show a significant effect on RTB damage in the early stage. However, we revealed through our field survey that RTB preferred trees located at forest edges that are exposed to solar radiation. This edge effect may explain the importance of the shape complexity of host patches (Kautz et al., 2013). Hansen et al. (2016) reported that the spruce bark beetle outbreak was smaller in extent and duration in the landscape with the mixed forest of white spruce and beetle-resistant black spruce compared with homogeneous stands of white spruce. This finding contrasts with our study in which we showed that the Shannon's diversity index describing landscape composition had no significant effect on the damage degree of RTB outbreak in the two study areas. The reason may be that the main host tree species in our study areas is *P. tabuliformis*, while other types of ground objects, such as broad-leaved trees and cultivated lands, distributing in the periphery of host stands don't affect the transmission of RTB in forest stands. This also indicates the necessity to conduct additional experiments to explore the impact of tree diversity on RTB outbreak (Castagneyrol et al., 2013).

The most effective spatial scale at which bark beetles respond to landscape pattern is primarily driven by their dispersal ability (Jones et al., 2019). Simard et al. (2012) found that 500 m was the most effective measure among four landscape scales during the outbreak period of bark beetles, which is different from that obtained from our study (250 m). This also indicated that the damage severity of bark beetles gradually developed from the middle stage of occurrence to the outbreak period at the landscape scale. With the aggravation of damage, the effective landscape scale of bark beetles may be more than 500 m, leading to a wider range of host trees to be damaged. The ability to predict landscape scale effects will enable more effective landscape research and help landscape managers carry out pest control practices at an appropriate scale.

In conclusion, we revealed that the stand-level factors (canopy density and aspect) had more influence on RTB occurrence in the early stage, while the landscape-level factor (host availability) was a more important predictor in the middle stage of RTB outbreak. This is well in line with the findings of the disturbance regimes of other beetles (Raffa et al., 2008; Seidl et al., 2015; Simard et al., 2012). In particular, we found that the landscape-level indicators could play a role in the middle stage of RTB occurrence before the final outbreak, which also highlighted the limitation of stand-scale managements, such as the application of traps and pharmacotherapy, during the population growth period of RTB. Forestry management of RTB outbreak should depend on knowledge combined from multiple spatial scales, from the stand scale to the landscape scale. In addition, our research also demonstrated that the UAV-based remote sensing technique has some advantages in the epidemiological study of RTB, which can replace the traditional field survey that is time-consuming and labor-intensive (Zhan et al., 2020).

Declarations

Authors' contribution

Zhongyi Zhan conceived and designed research. Zhongyi Zhan and Haonan Li conducted experiments. Zhongyi Zhan analyzed data and wrote the manuscript. All authors participated in review and revision of the manuscript.

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Figures

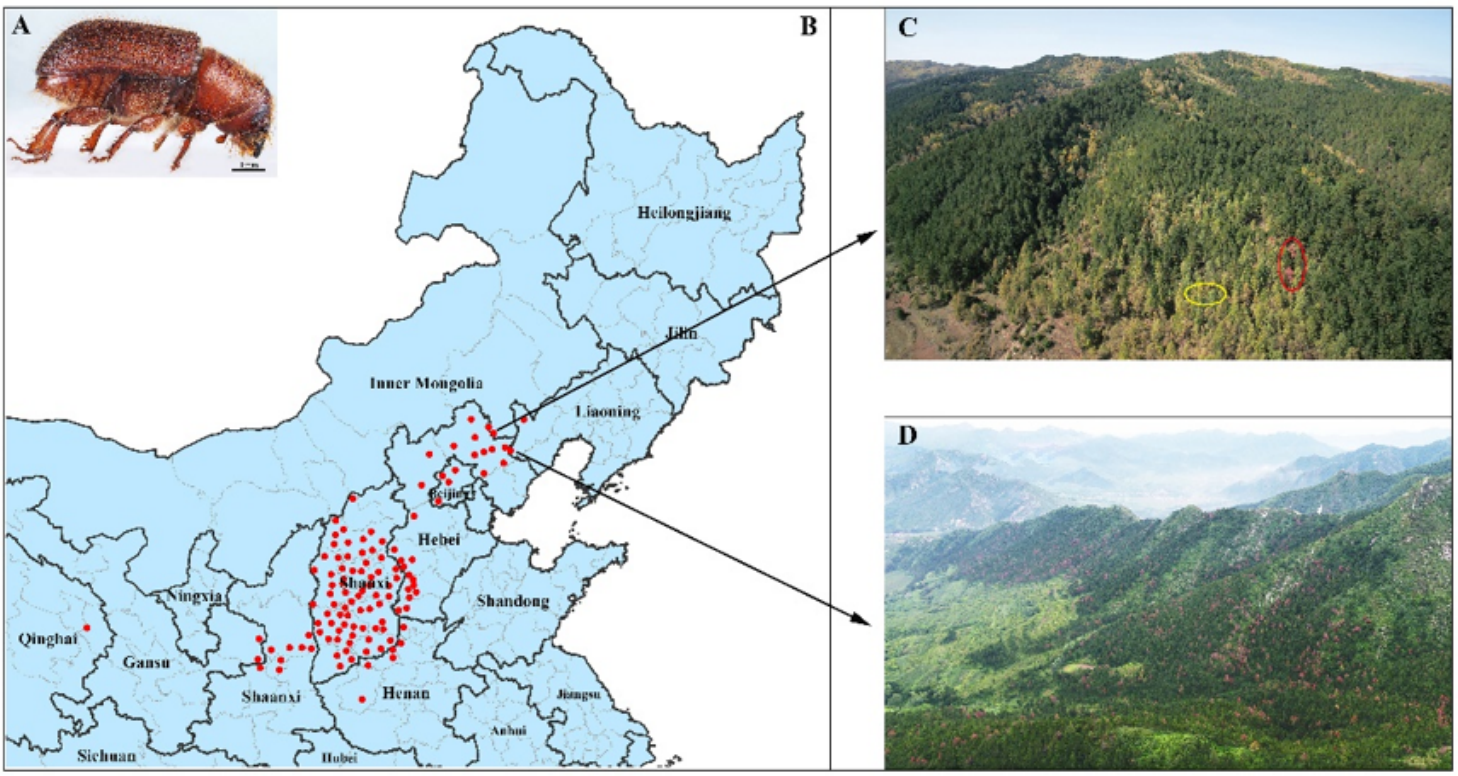

Figure 1

The forests in the early and middle stages of RTB invasion. a Adult RTB. b Areas in North China that have been invaded by RTB. Red dots indicate individual RTB invaded areas at the city level. c The Helihe area that is in the early stage of RTB invasion. The yellow trees (in the yellow circle) are discolored larch (in autumn), which are not caused by RTB invasion. The two Chinese pines with a red crown (in the red circle) are the result of RTB attack. d The Dahebei area that is in the middle stage of RTB outbreak. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

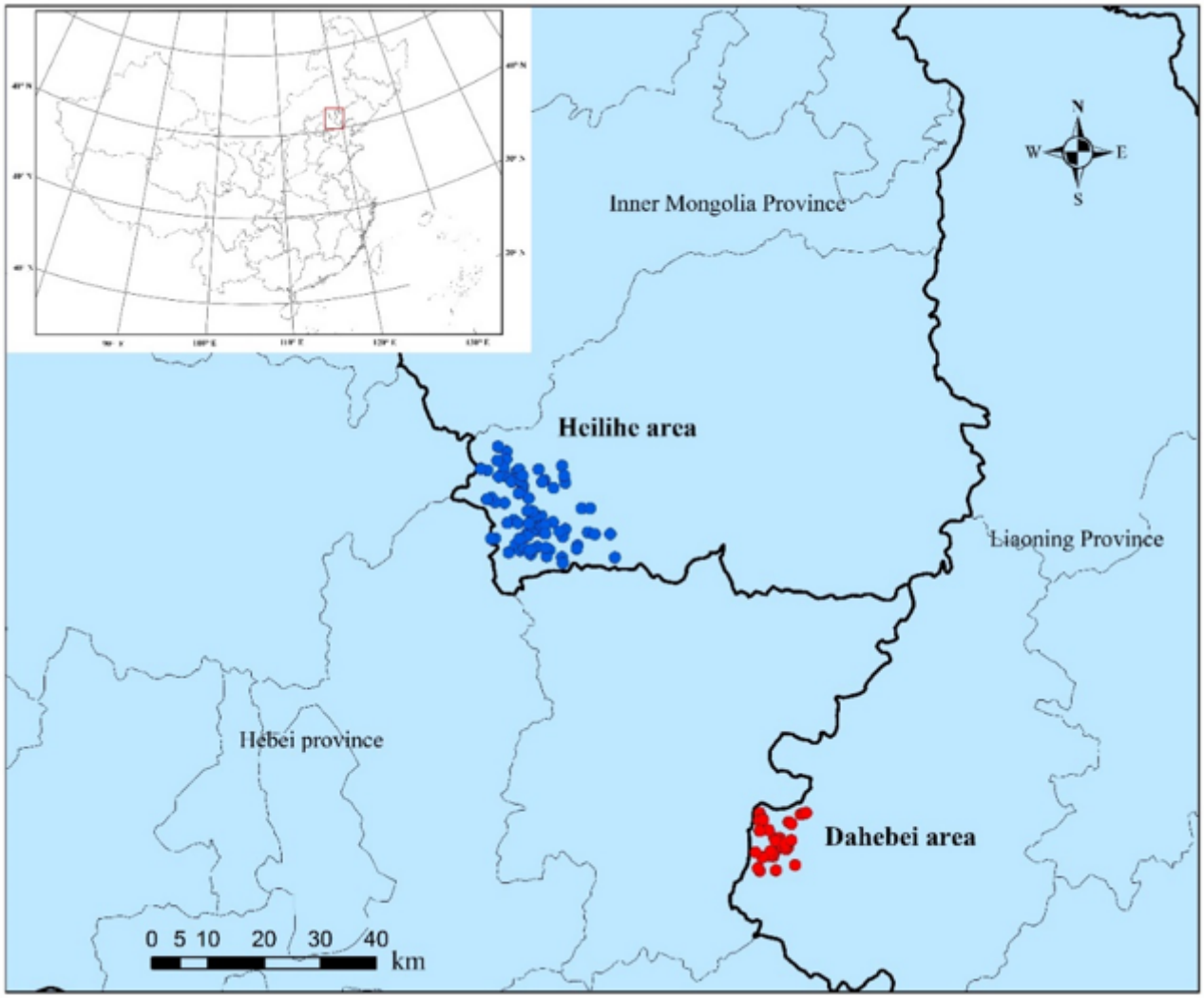

Figure 2

Location of the 79 sample plots (blue dots) in the Heilie area and 32 sample plots (blue dots) in the Dahebei area. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

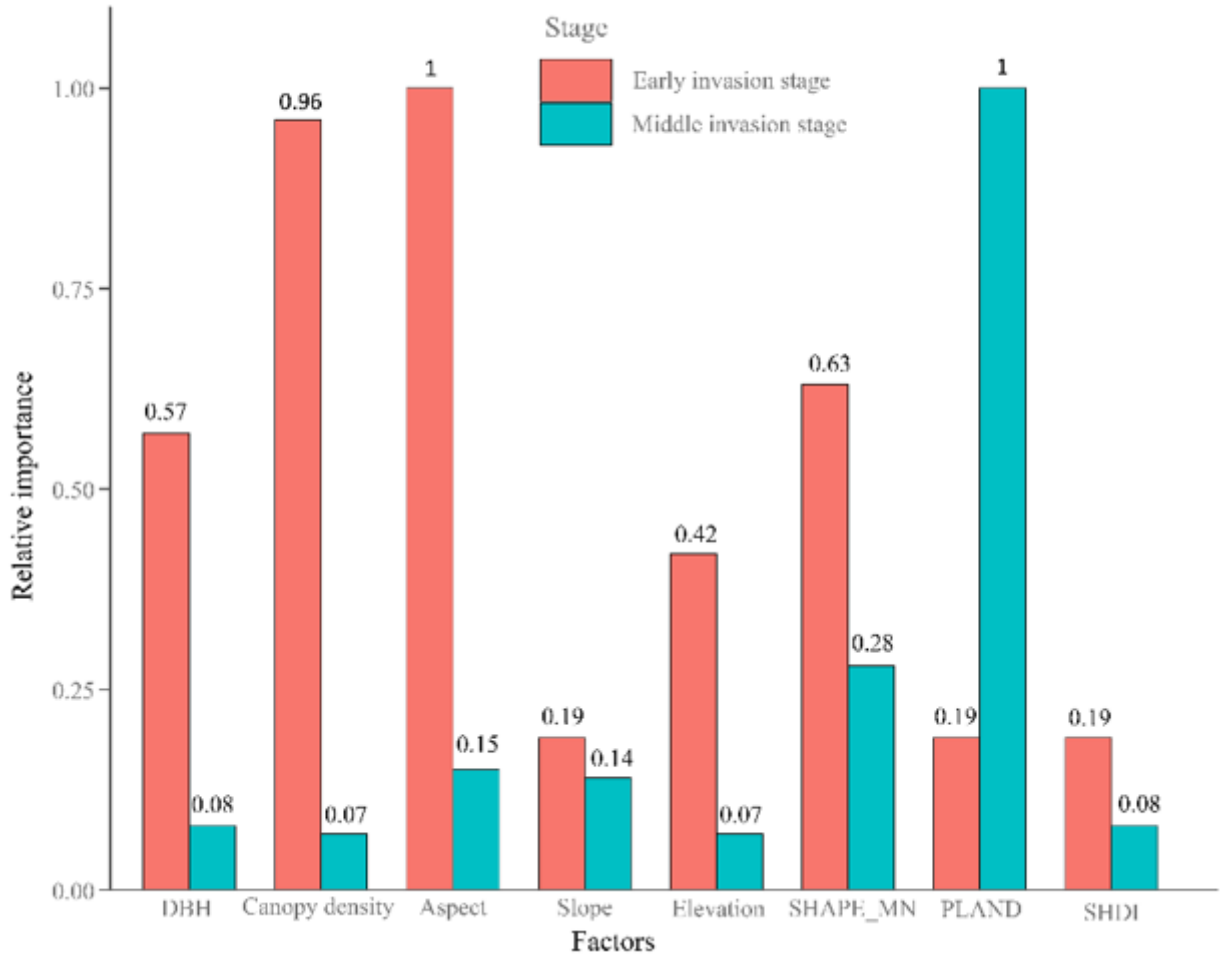

Figure 3

Relative importance of landscape- and stand-level factors in different stages of RTB outbreak. The relative importance is the sum of the Akaike weights associated with each variable in the models in the top model set.

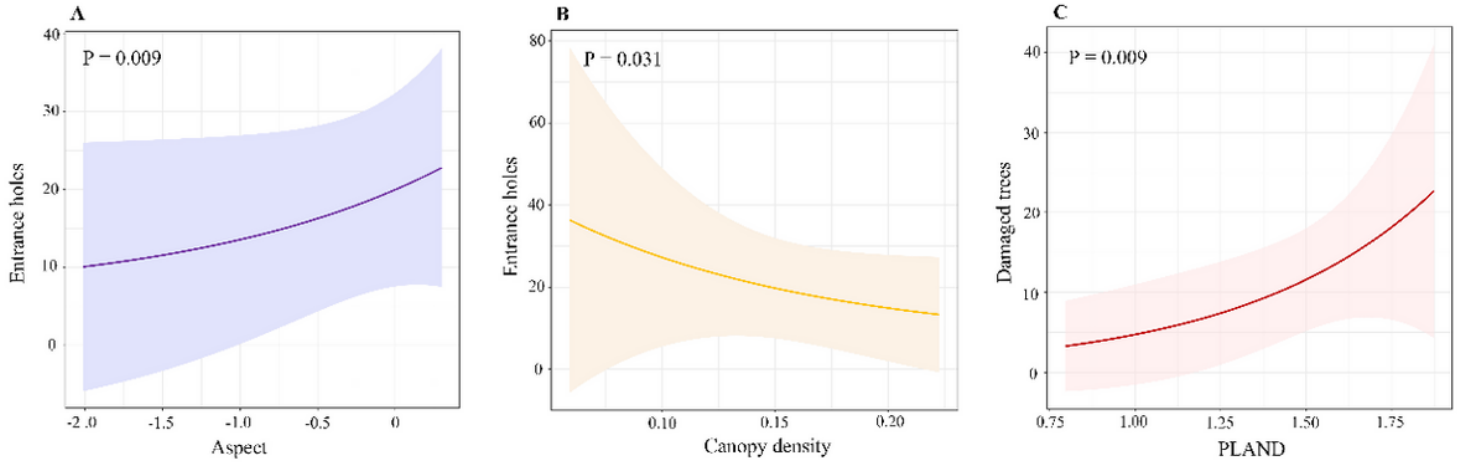

Figure 4

Model-averaged predictions and standard errors showing the response of to RTB damage to a Aspect (x-axis means the change from northeast to southwest), b Canopy density and c PLAND. P value was the parameter estimation based on model average and SEs (see Table 2)

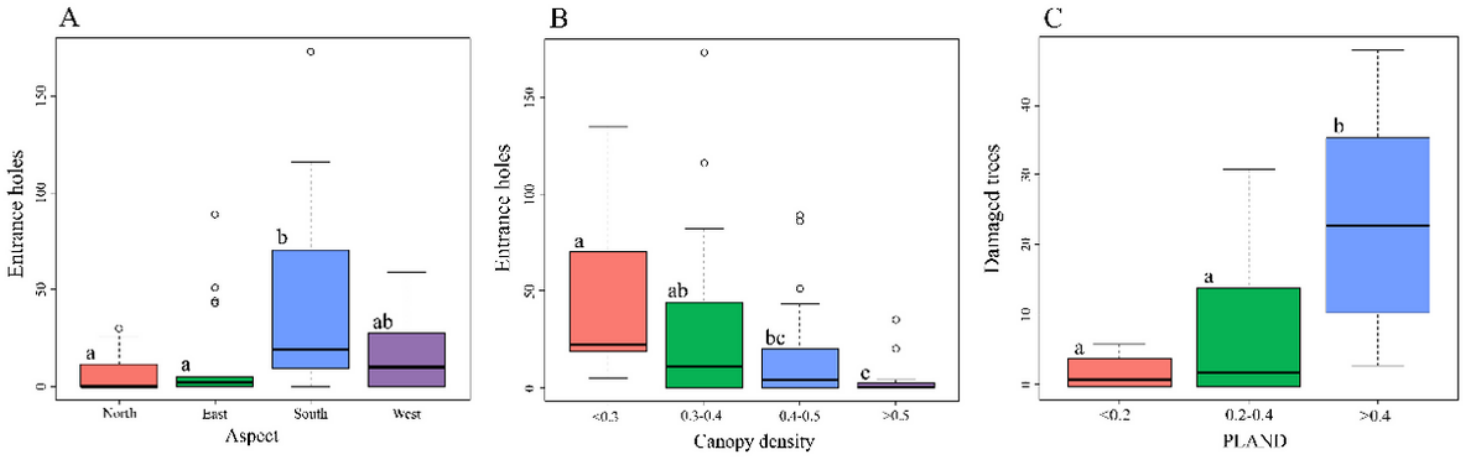

Figure 5

The numbers of RTB entrance holes and damaged trees as important variables. a Aspect (df = 15, 17, 15, and 23, from left to right). b Canopy density (df = 7, 21, 33, and 15, from left to right). c PLAND (df = 4, 17, and 11, from left to right).

Supplementary Files

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