

# Background Insect Herbivory in Riparian Poplar Forests: the Role of Local, Landscape, and Regional Factors

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## Research

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# Abstract

## Background

Forest management and landscape structure have long been considered as the main drivers of insect herbivory in forest landscapes, but relatively little is known about how ecological factors acting at local, landscape and regional scales shape background insect herbivory under natural conditions. Here, 90 primeval and managed poplar stands were sampled in riparian forests along the rivers in the Eastern part and the Western part of North China. We measured defoliation intensity of insect herbivores within forest stands in transects at near, intermediate and far distance from the rivers. We assessed the effects of region, landscape isolation, forest management, stand position, vegetation cover, and tree size on defoliation intensity. We also explored indirect effects of region and forest management on insect herbivory via changes in stand-level tree size and vegetation cover.

## Results

Defoliation intensity increased with landscape-scale forest isolation and decreased with distance from forest stand to the river regardless of stand type. Defoliation intensity was higher in primeval stands than in managed poplar stands, but this difference only significant in the Eastern part of North China. Tree height varied among two regions and between primeval and managed stands. Defoliation intensity was strongly correlated with tree height and vegetation cover. But the effects of region and forest management on defoliation intensity were only partly explained by tree size and vegetation cover.

## Conclusions

These results indicate that background insect herbivory can be driven by ecological factors at different scales and offer an insight into the impact of man-made changes along a gradient of landscape isolation in forest ecosystems. Our findings provide a multi-scale perspective to improve potential control strategies and risk assessment of insect damage on riparian forests in real-world situations.

# Background

Forest plant communities are essential for the provision of a wide variety of natural resources and crucial ecosystem services that are of great importance to human society, and are also indispensable resources for a large number of animals and microorganisms (Gamfeldt et al. 2013; Brockerhoff et al. 2017). Among these organisms that rely on plants for survival, insect herbivores play a key role in energy flow from autotrophic plants to higher trophic levels (Schmitz 2008; Stein et al. 2010; Zhu et al. 2014). Insect herbivory can largely influence ecosystem functioning by affecting growth of plant species, modifying plant community composition, and accelerating nutrient cycling (Belovsky and Slade 2000; Hartley and Jones 2008; Bagchi et al. 2014). In forest ecosystems, once leaf consumption by insect herbivores affects tree growth, insect herbivory will influence tree regeneration and subsequent processes in nutrient fluxes, and eventually modify ecosystem structure and function (Stadler et al. 2008; Wirth et al. 2008;

Lemoine et al. 2017). Consequently, herbivory by phytophagous insects is of great importance in understanding ecological interactions (Stam et al. 2014; Zhu et al. 2014; Verçosa et al. 2019).

Previous studies have focused primarily on the eruptive insect species that impose severe damage on their host plant species, as outbreaks of these insects may cause great economic losses and widely attract policymakers' attention (De Somviele et al. 2004; Wesołowski and Rowiński 2006). Insect herbivores are ubiquitous disturbance agents that play important roles in the long-term dynamics of forest ecosystems, but only a few phytophagous insect species exhibit eruptive population dynamics and reach the outbreak level, causing massive defoliation, dieback or mortality in host trees (Björkman et al. 2011; Cavaletto et al. 2019). By contrast, most insect herbivores remain at low densities and collectively impose minor but chronic damage on host trees (Zvereva et al. 2012), which is called the background insect herbivory (background herbivory hereafter) (Kozlov et al. 2015b; Kozlov and Zvereva 2017).

However, several studies have indicated that even relatively minor herbivory may negatively impact tree growth and foliar biomass at larger spatial scales (Zvereva et al. 2012; Kozlov and Zvereva 2017), which shows the need to explore the factors affecting the levels of background herbivory at a large scale. To date, we still lack a comprehensive understanding of ecological factors driving pronounced variation in the levels of insect herbivory across multiple spatial scales, despite a long history of research. For decades, patterns of insect herbivory were attributed primarily to differences in plant secondary metabolites, but it appears to be a poor predictor of insect damage under natural, non-outbreak conditions, especially over large spatial scales (Carmona et al. 2011; Schuldt et al. 2012; Agrawal and Weber 2015). This lack of intensive study on background herbivory strongly constrains our understanding of the actual driving forces behind spatial variations in tree-herbivory interactions in real-world situations, and stimulates a research for multi-scale drivers of background herbivory among different forest stands.

Levels of insect herbivory are shaped by multiple ecological factors acting at different spatial scales. The size of a plant has been shown to affect abundance of herbivorous insects as differences in plant size can lead to variations in conspicuousness (being apparent) and in attractiveness (arousing interest) of plants for associated insects at the individual scale (Haysom and Coulson 1998; Schlinkert et al. 2015). Larger plants can produce more new leaves and consequently suffer more persistent attacks from a greater number of insect herbivores than smaller plants (Barone 2000; Castagnéryrol et al. 2013). Woody plants experience much higher leaf herbivory than non-woody plants due to higher appärencey of the latter (Turcotte et al. 2014). Within woody plants, background herbivory increases from dwarf shrubs to large trees (Kozlov et al. 2015a). As the tree increases in height, significant increase occurs in both abundance and species richness of insect herbivores (Campos et al. 2006). And such findings that insect herbivory increases with tree size may appear applicable only to broad-leaved trees (Kozlov and Zvereva 2017).

Besides tree size, landscape factors also play a key role in driving variation in the levels of insect herbivory (Wesołowski and Rowiński 2006; Castagnéryrol et al. 2019; Cavaletto et al. 2019). Landscape composition and configuration are increasingly considered as factors affecting insect herbivory, as insect herbivores tend to reach the highest densities in habitat patches where resources are concentrated

(Andersson et al. 2013; Rösch et al. 2013). And habitat fragmentation can reduce insect herbivory via direct negative effects on species richness and abundance of insect herbivores (Rossetti et al. 2017). Declines in insect herbivory can be exacerbated by habitat isolation that usually increases in fragmented landscapes and hampers insect movement between fragments (Fáveri et al. 2008; Maguire et al. 2015). Nevertheless, habitat isolation can also increase insect herbivory in small fragments through indirect positive effects due to losses of natural enemies, which are often more vulnerable to fragmentation than insect herbivores (Schüepp et al. 2014; Morante-Filho et al. 2016; Genua et al. 2017). In this context, landscape-level forest isolation is expected to influence background herbivory in forest ecosystems. Within habitat patches, effects of focal plant's neighbours on background herbivory have been frequently reported, but general patterns are hard to find (Castagneyrol et al. 2014; Kozlov et al. 2015a; Moreira et al. 2017; van Schrojenstein Lantman et al. 2018). And it well may appear that these effects on the levels of insect herbivory depend primarily on patch-scale composition of both host plant and insect communities, as well as on ecological factors at the stand level such as forest management, abiotic environment and vegetation cover (Wesołowski and Rowiński 2006; Ober and Hayes 2008; Eilers and Klein 2009; Gossner et al. 2014; Porcel et al. 2017; Stiegel et al. 2017; Castagneyrol et al. 2018).

Here, we present results of a study conducted in riparian forests, where patches of primeval poplar stand untouched by forestry operations have survived, although managed poplar plantations are widely planted for timber production and ecological restoration in Northern China, a region that experiences frequent droughts and water scarcity (Zhou et al. 2013). This study thus offers a unique opportunity to observe changes in levels of background herbivory between the "primeval" (no direct human intervention) and "managed" (man-made forests) stands and among three distances from poplar stands to the river, and to assess impacts of multiple ecological factors (e.g., forest isolation, vegetation cover and tree size). Although several studies have made great advances in understanding of certain drivers of background herbivory, interactive effects between factors at multiple scales and potential tree size-dependent effects of ecological factors on background herbivory are currently unknown (Castagneyrol et al. 2019).

In this study, we measured leaf damage caused by foliar insect herbivores in primeval and managed poplar stands at the near, intermediate and far distance from the rivers in Northern China, with the aim of identifying how the pattern of background leaf damage on riparian forests is shaped by environmental drivers acting at the local (forest management, tree size and vegetation cover), landscape (forest isolation), and regional (Eastern part and Western part of North China) scales. In particular, we hypothesised that (1) background herbivory will be higher in primeval stands than in managed stands, and (2) the difference will be larger in the Eastern part of North China and such forest management effects will be partly explained by individual tree size and vegetation cover. We further hypothesised that (3) background herbivory and tree size will vary among forest stands at different positions and that (4) background herbivory will be positively affected by forest isolation at the landscape scale. By assessing independent and interactive effects of ecological factors at multiple scales on background herbivory, our study will provide crucial information for spatial occurrence and intensity of forest defoliation, improving our understanding of the patterns that drive background herbivory in real-world situations.

## **Materials And Methods**

### **Study area and experimental design**

Table 1 Summary of study area, study sites (cities) and stand combinations. (W: the Western part of North China; E: the Eastern part of North China; P: the primeval stand; M: the managed stand)

No.	Provinces and Autonomous Regions	Study Sites (Cities)	Region	Stand Combinations
1	Xinjiang Uygur Autonomous Region	Altay	W	P + P + P
		Altay	W	M + M + M
		Altay	W	P + P + P
		Altay	W	P + P + P
		Altay	W	P + P + P
2	Gansu	Jiuquan	W	P + P + P
		Jiuquan	W	M + M + M
		Zhangye	W	P + P + P
		Zhangye	W	P + P + P
		Wuwei	W	P + P + P
3	Ningxia Hui Autonomous Region	Wuwei	W	P + P + P
		Yinchuan	W	M + M + M
		Yinchuan	W	M + M + M
		Yulin	W	M + M + M
		Yulin	W	P + P + P
4	Shaanxi	Datong	E	M + M + M
		Datong	E	M + M + M
5	Shanxi	Chifeng	E	P + P + P
		Chifeng	E	P + P + P
		Tongliao	E	M + M + M
		Tongliao	E	P + P + P
6	Inner Mongolia Autonomous Region	Langfang	E	M + M + M
		Dalian	E	M + M + M
7	Hebei	Shenyang	E	M + M + M
		Siping	E	M + M + M
8	Liaoning	Changchun	E	M + M + M
9	Jilin			

No.	Provinces and Autonomous Regions	Study Sites (Cities)	Region	Stand Combinations
10	Heilongjiang	Changchun	E	P + P + P
		Harbin	E	M + M + M
		Suihua	E	P + P + P
		Suihua	E	M + M + M

Our study was carried out in natural and planted poplar forests along the rivers in different study sites (cities with riparian poplar forests), which were located in seven provinces and three autonomous regions in Northern China (Fig. 1a; Table 1). We selected poplars from sect. Leuce Duby (Salicaceae, *Populus*) as they are one of the most important components of riparian ecosystems throughout much of the Northern Hemisphere, shaping and improving the environment of sensitive riparian habitats (Philippe and Bohlmann 2007; González et al. 2018). Due to their low cost of cultivation and rapid wood growth, poplars make up the largest fraction of intensively managed riparian forest acreage in Northern China (Lin et al. 2006; Zhou et al. 2013). Poplar forests are subject to attack from a wide variety of insect herbivores owing to their large tree size and ecological dominance in many communities (Bernhardsson and Ingvarsson 2011). Even though defoliators constitute the largest proportion of insect herbivores, only a few species are responsible for high levels of leaf damage on poplars (Kosola et al. 2001; Philippe and Bohlmann 2007). Such background leaf damage occurs continuously in natural and planted poplar forests in study area. Within all study sites, the forest landscape in riparian poplar forests is fragmented and is characterized by the presence of forest patches, interspersed with various types of grasslands. The remaining landscape is characterized by agricultural lands and urban areas.

In 2018 and 2019, we selected 15 trios of primeval (P) and managed (M) pure poplar stands in the Eastern part of North China and another 15 trios in the Western part of North China ( $N = 90$ ) (Table 1). The proportion of primeval old-growth stands was higher in the Western part, while riparian forests in the Eastern part were primarily managed stands. Therefore, the major difference in stand structure between riparian forests in Eastern and Western part was due to forest stand type, which enabled us to evaluate effects of man-made changes on the levels of background herbivory. Each of the 30 trios consists of three sampling plots ( $30 \times 30$  m) that are allocated to one of two stand combinations according to the actual situation of forest distribution (i.e. P + P + P and M + M + M; Table 1). We also explored the patterns of background herbivory in poplar forests in a transect at three different positions. Within all study sites, three sampling plots were set at (a) near distance (forest interior, 10–50 m from the river), (b) intermediate distance (forest centre, 550–600 m from the river), and (c) far distance (forest edge, 1150–1200 m from the river) from the bank of rivers, respectively (Fig. 1b). We defined three stand positions in relative instead of absolute terms because the distance from stands to rivers varied between different study sites and among different geographical regions. An important additional criterion was employed for plot selection, i.e. the distance between the centers of sampling plots was at least 600 m.

# Measurements of background herbivory and stand-level characteristics

In each of the 90 forest stands, we randomly selected five poplar trees and measured background herbivory of insect herbivores in September 2019, at the end of the defoliation activity. Four branches were randomly selected from the lower, intermediate and upper stand stratum of each tree, and four types of leaf damage (chewing, galling, leaf mining and leaf rolling) were recorded at 50 leaves per branch. Therefore, a total of 200 leaves per poplar tree were sampled in each stand. The sampling method was adapted to the stand stratum in relative instead of absolute terms because tree height varied among the different stands, thus leaves were collected using a 10 m pole pruner for the intermediate as well as upper stratum and using a pair of pruning shears for the lower stratum of all poplar stands (Wang et al. 2021).

The same well-trained operators conducted together the measurement of all sampled leaves in the laboratory. We initially distinguished leaf damage caused by different herbivore guilds (chewers, gall formers, leaf miners and rollers), but as the latter three guilds caused too small damage to allow separate analyses and each of three guilds occurred only in certain study sites, we aggregated all damage types to quantify overall background herbivory. To make the data more comparable, we used a grid of  $0.25\text{ cm}^2$  ( $0.5 \times 0.5\text{ cm}$ ) printed on a transparent plastic sheet and overlaid on selected leaves (Castagneyrol et al. 2019; Wang et al. 2021). We calculated the total percentage of leaf area affected or removed by insect herbivores divided by the number of sampled leaves (50) as the measure of defoliation intensity per branch, which is the method used most commonly to measure insect herbivory (Andrew et al. 2012).

During July 2019, two stand-level characteristics were measured to quantify stand structure of each forest stand. Within the core area of each stand, tree height of each of five selected poplar trees was recorded. As tree height and diameter at breast height are correlated in most tree species and one is often a proxy of the other, we only considered tree height as the measure of tree size, which is an important structural trait (Fang et al. 2010), critical in forest ecosystems and for above ground biomass estimate. Tree height was then averaged per forest stand. In addition, percentage of understory vegetation cover was calculated from 10 random  $1\text{ m} \times 1\text{ m}$  quadrats on a diagonal of each stand (Rahman et al. 2015).

## Landscape-scale forest isolation

We determined the main habitat types in a circular buffer of 300 m radius around each forest stand based on open-access remotely sensed images covering all study sites, which were acquired from the European "Sentinel-2A" satellite in August 2019. In order to select satellite images accurately, we collected the geographical coordinates of the center of each forest stand using a handheld GPS unit. We distinguished woodlands, grasslands and open habitats using ENVI version 5.4, and open habitats included rivers, farmlands and urban areas. Then proportions of different habitat areas in each forest landscape were quantified using ArcGIS version 10.5. By using the 300 m radius buffer, we avoided spatial overlapping between nearby buffers, which is needed to make accurate landscape-scale inferences (Wang et al. 2019). Moreover, this landscape size was large enough to include a large variation

in landscape-level forest isolation (ranging from 13.5–92.3%) and was previously found to be suitable to study tree-insect herbivores interactions in riparian poplar forests (Wang et al. 2019, 2021). Finally, we calculated the percentage of open area in buffers of 300 m radius around selected stands as a proxy for forest isolation at the landscape scale using ArcGIS version 10.5 (Castagneyrol et al. 2019).

## Statistical methods

All statistical analyses were conducted in R version 3.5.1 (R Core Team 2018). The defoliation intensity data of all leaf-feeding guilds from four branches and from five poplar trees were pooled to the stand level for statistical analyses. The effects of region, landscape isolation, forest management, stand position and vegetation cover on defoliation intensity were assessed using linear mixed-effect models (LMMs) (function “lmer” implemented in the R package lme4; Bates et al. 2015). In order to identify if the effects of these explanatory variables on background herbivory dependent on tree size, we also assessed the direct effects of environmental factors on tree height. We tested two- and three-way interactions between explanatory variables. To account for the non-independence of sampling plots within each study site, study site ID was included as a random effect. Region (Eastern or Western part of North China), forest isolation (percentage of open area in the landscape), forest type (primeval or managed stand), stand position (near, intermediate or far distance from the rivers) and vegetation cover were assigned as fixed effects. Response variables were log-transformed to improve the distribution of model residuals.

We used an information-theoretic approach to determine the best model set from global LMMs via Akaike's Information Criterion corrected for small sample size (AICc) (Grueber et al. 2011). The input variables were standardized using Gelman and Su's (2016) approach (function “standardize” implemented in the R package arm) in order to better interpret parameter estimates after model averaging. The “dredge” function in the R package MuMIn (Bartoń 2019) was used to select top-ranked models with  $\Delta\text{AICc} < 2$ . This top set of models was then averaged to generate averaged parameter estimates using the function “model.avg”. We applied full model averaging method to reduce model selection bias and appropriately determine which explanatory variables have the strongest effect on each response variable (i.e. defoliation intensity and tree height) (Grueber et al. 2011). Significant interactive effects between region and forest type (see Results) were assessed by comparing variations in response variables between the primeval and managed poplar stands for each part of North China and variations in response variables among two regions for each forest type separately. P values were based on the model-averaged estimates and SEs, and P value  $< 0.05$  was considered statistically significant (Cavaleotto et al. 2019). Furthermore, marginal  $R^2(R^2_m)$  and conditional  $R^2(R^2_c)$  were calculated to assess the proportion of variance explained by fixed effects and by both fixed and random effects (function “rsquared” implemented in the R package piecewiseSEM), and thus provide absolute values for the goodness-of-fit of best-fit models (with the minimum AICc value; Lefcheck et al. 2019).

We would also like to figure out how the region, landscape isolation, forest type, stand position, vegetation cover as well as tree height affect background herbivory. As results that tree height was strongly influenced by region and forest management (see Results) can cause issues from collinearity,

the effect of tree height and other factors on defoliation intensity was assessed in a separate linear model where we replaced explanatory variables region and forest type by tree height. We applied same information-theoretic approach for model simplification. In addition, we used structural equation modelling (SEM) to identify whether effects of region and forest management on background herbivory act directly or indirectly via changes in stand-level characteristics. R package piecewiseSEM permits the inclusion of hierarchical data by piecing multiple LMMs into one causal framework (Lefcheck 2016). We first developed an a priori hypothetical model in which defoliation intensity was only affected by vegetation cover and tree height based on theoretical and empirical evidence. We considered these two variables as endogenous predictors. Then region and forest type served as exogenous predictors that only influenced vegetation cover and tree height. We assessed the overall fit of the piecewise SEM using Shipley's test of direct separation, which determines the probability of an informative path missing from the hypothesised network (Shipley 2009; Lefcheck 2016). The model was considered rejected if  $\chi^2$ -test of Fisher's C statistic fell below the significance level ( $P < 0.05$ ), indicating that the model is inconsistent with the data. Finally, we used the standardized path coefficients ( $\beta$ ) and P values to assess the significance of individual predictors within the final model.

Table 2 Model-averaging results of the top-ranked models ( $\Delta\text{AIC}_c < 2$ ) for assessing effects of multiple environmental drivers on defoliation intensity and tree height. Marginal ( $R^2_m$ ) and conditional ( $R^2_c$ )  $R^2$  are shown for the best-fit model; parameter estimate is standardized effect size and is therefore on a comparable scale; Std. Error is unconditional SE and thus incorporates model selection uncertainty.

Response variables	$R^2_m$ ( $R^2_c$ )	Explanatory variables	Estimate	Std. Error	z-value	P-value
Defoliation intensity	0.75 (0.88)	Intercept	5.14	1.18	4.30	< 0.001
		Region	-1.20	0.60	1.97	0.029
		Forest isolation	1.73	0.01	4.40	< 0.001
		Forest type	-0.74	0.27	2.71	0.007
		Stand position	-0.22	0.08	2.87	0.004
		Vegetation cover	-1.23	0.50	2.40	0.016
		Forest type $\times$ Stand position	0.08	0.05	0.15	0.880
		Forest type $\times$ Region	-0.51	0.33	0.15	< 0.001
		Stand position $\times$ Region	-0.07	0.05	0.14	0.882
		Forest type $\times$ Stand position $\times$ Region	0.67	0.20	0.24	0.564
Mean tree height	0.66 (0.78)	Intercept	14.94	1.05	14.02	< 0.001
		Region	-3.29	1.66	1.95	0.001
		Forest type	1.59	0.74	2.11	< 0.001
		Stand position	-0.03	0.22	0.14	0.887
		Vegetation cover	-0.53	0.25	0.42	0.736
		Forest type $\times$ Stand position	5.20	2.53	2.02	0.609
		Forest type $\times$ Region	0.46	0.90	0.51	0.043
		Stand position $\times$ Region	-0.08	0.27	0.29	0.770

## Results

## **Effects of region, forest isolation, forest management, stand position and vegetation cover on defoliation intensity**

Defoliation intensity of insect herbivores varied among different poplar stands (1.0% - 7.6 % per poplar leaf) and was on average (mean  $\pm$  SE)  $3.39 \pm 0.23$  cm<sup>2</sup> per leaf (corresponding to *ca.* 7% leaf area). Defoliation intensity in the Eastern part of North China was much more than that in the Western part of North China ( $P = 0.029$ ) (Table 2). It increased with increasing forest isolation in the surrounding landscape (Estimate =  $1.73 \pm 0.01$ ;  $P < 0.001$ ) (Fig. 2), but decreased with the distance from poplar stands to rivers ( $P = 0.004$ ) (Table 2) and vegetation cover (Estimate =  $-1.23 \pm 0.50$ ;  $P = 0.016$ ) (Table 2) in both primeval and managed stands and across two regional parts of North China. There was a consistent difference between forest types, trees in the primeval stands were significantly heavier defoliated than in the managed stands whether stands were at near, intermediate, or far distance from river ( $P = 0.007$ ) (Fig. 3; Table 2). Furthermore, we only found a significant region  $\times$  forest type interaction ( $P < 0.001$ ) (Table 2) as differences between primeval and managed poplar stands were significant in the Eastern part of North China (Fig. 3). And defoliation intensity was significantly lower in the Western part than in the Eastern part of North China within primeval poplar stands (Fig. 3).

## **Effects of region, forest isolation, forest management and stand position on tree height**

When assessing the effects of environmental drivers on tree size of poplars, we found that tree height varied consistently between forest types and among two geographical regions with a significant region  $\times$  forest type interaction for tree height per stand ( $P = 0.043$ ) (Table 2), but stand position and forest isolation had no significant effects on tree height (Table 2). Tree height was on average (mean  $\pm$  SE)  $12.3 \pm 0.04$  m, and it was larger in the Eastern part than in the Western part of North China in both primeval and managed poplar stands ( $P = 0.001$ ) (Table 2). However, differences in tree height between two parts of North China were larger in primeval stands than in managed stands (Fig. 4). Mean tree height was much higher in primeval stands than in managed stands whether forest stands were at near, intermediate, or far distance from the rivers ( $P < 0.001$ ) (Table 2), but this difference was only significant in the Eastern part of North China (Fig. 4).

## **Effects of region and forest management on defoliation intensity were partly explained by tree height and vegetation cover**

When the explanatory variables region and forest management were replaced by mean tree height in a separate LMM, the variation in defoliation intensity among two geographical regions and between two forest stand types could be partly explained by tree size. The results indicated that defoliation intensity responded positively to higher forest isolation in the surrounding landscape (Estimate =  $1.34 \pm 0.01$ ;  $P < 0.001$ ) (Table 3) and poplar stands at nearer distance from river ( $P = 0.004$ ) (Table 3). We also found that defoliation intensity decreased with vegetation cover (Estimate =  $-0.99 \pm 0.56$ ;  $P = 0.009$ ) (Table 3), but increased with mean tree height (Estimate =  $0.17 \pm 0.04$ ;  $P < 0.001$ ) (Table 3), which are consistent with our results that both tree height and defoliation intensity were higher in the Eastern part of North China

and in primeval poplar stands. Additionally, tree height of poplars could explain largely but not completely effects of region and forest management on defoliation intensity as  $R^2$  of the best-fit model (with the minimum AICc value) was lower when the factors region and forest management were replaced by mean tree height ( $R^2_m = 0.71$  and  $R^2_c = 0.84$  vs.  $R^2_m = 0.75$  and  $R^2_c = 0.88$ ) (Table 2; Table 3).

**Table 3** Model-averaging results of the top-ranked models ( $\Delta\text{AICc} < 2$ ) for assessing effects of forest isolation, stand position, tree height and vegetation cover on defoliation intensity. Marginal ( $R^2_m$ ) and conditional ( $R^2_c$ )  $R^2$  are shown for the best-fit model; parameter estimate is standardized effect size; Std. Error is unconditional SE.

Response variable	$R^2_m$ ( $R^2_c$ )	Explanatory variables	Estimate	Std. Error	z-value	P-value
<b>Defoliation intensity</b>	0.71 (0.84)	Intercept	-1.20	1.10	1.08	0.279
		<b>Forest isolation</b>	<b>1.34</b>	<b>0.01</b>	<b>4.65</b>	< 0.001
		<b>Stand position</b>	<b>-0.48</b>	<b>0.16</b>	<b>2.86</b>	<b>0.004</b>
		<b>Mean tree height</b>	<b>0.17</b>	<b>0.04</b>	<b>3.98</b>	< 0.001
		<b>Vegetation cover</b>	<b>-0.99</b>	<b>0.56</b>	<b>1.76</b>	<b>0.009</b>

The results of SEM with the Fisher's C-statistic falling above the significance level ( $C = 5.93$ ;  $df = 2$ ;  $P = 0.085$ ) revealed that the effects of region and forest management on defoliation intensity were partially mediated by their effect on both vegetation cover and mean tree height (Fig. 5). From the 8 pathways present in the best model, all of them were significant and were consistent with our predictions (Fig. 5). Specifically, vegetation cover was positively related to forest stands in the Western part of North China ( $\beta = 0.44$ ;  $P < 0.001$ ) and negatively related to primeval poplar stands ( $\beta = -0.08$ ;  $P = 0.041$ ). However, mean tree height was negatively related to forest stands in the Western part of North China ( $\beta = -0.34$ ,  $P < 0.001$ ) and positively related to primeval poplar stands ( $\beta = 0.53$ ;  $P < 0.001$ ). Furthermore, background herbivory decreased with increasing vegetation cover ( $\beta = -0.34$ ;  $P < 0.001$ ) but increased with increasing tree height ( $\beta = 0.30$ ;  $P < 0.001$ ). Finally, background herbivory was lower in the Western part than in the Eastern part of North China ( $\beta = -0.33$ ;  $P < 0.001$ ) and was higher in primeval stands than in the managed poplar stands ( $\beta = 0.28$ ;  $P < 0.001$ ) (Fig. 5).

## Discussion

Our study explored the effects and potential interplay of local, landscape and regional scale factors that drive background leaf damage caused by insect herbivores in riparian poplar forests. We found a regional difference in defoliation intensity between the primeval and managed poplar stands, and further analysis revealed that such effects of forest management were only significant in the Eastern part of North China.

Although tree size did not vary with all of the environmental drivers, some (i.e., forest isolation and stand position) were important predictors of defoliation intensity. We also observed that stand-level characteristics such as vegetation cover and tree height were important factors that drive variations in background herbivory on poplars. Moreover, region and forest management effects on background herbivory mainly act indirectly through vegetation cover and tree height. Therefore, this study demonstrates that insect herbivory under natural, non-outbreak conditions is a complex ecological process that can be shaped by multiple environmental drivers acting at different spatial scales.

### **Background herbivory was much higher in the primeval than in managed poplar stands**

As primeval poplar stands experienced higher defoliation intensity of insect herbivores than managed stands whether these stands were at near, intermediate, or far distance from river in both regional parts of North China, the current differences of background herbivory had to be due to anthropogenic changes instead of climate and soil conditions. And we can rule out the direct effects of human actions, because a variety of methods and tools (e.g. chemical or biological insecticides) that are widely used for pest control in agriculture are not available or are not suitable for application in forestry (Wang et al. 2019). However, forestry operations could affect defoliation intensity of phytophagous insects in a number of indirect ways (Wesołowski and Rowiński 2006). Plant communities in the managed stands were much less diverse owing to weeding and other practices, which could hamper the occurrence and population growth of a variety of insect herbivore species (Eilers and Klein 2009). Thus, poplars in the managed part were less heavily defoliated than in the primeval part and the homogenisation of stands could be responsible for these differences (Durak and Holeksa 2015). Furthermore, large number of within-stand operations known to affect insect herbivory discussed so far could adequately account for the lower background herbivory in the managed poplar stand, but operations responsible for these differences were also possibly operating at larger spatial scales (Kozlov and Zvereva 2017; Castagneyrol et al. 2019). Habitat fragmentation caused by logging operations could directly increase mortality of dispersing insect larvae, which in turn could prevent insect herbivory to higher levels in the managed stands (Wesołowski and Rowiński 2006). However, in this study, forest management effects on defoliation intensity were only significant in the Eastern part of North China. Such pattern that we observed might be explained by the fact that differences of tree height between primeval and managed stands were larger in the Eastern part than Western part of North China, as insect herbivores coming from other forest stands are likely to arrive in the larger trees (Turcotte et al. 2014). This seems the most plausible mechanism accounting for such spatial pattern of background herbivory found in our study.

### **Effects of stand position and vegetation cover on background herbivory**

Although we observed that insect herbivores caused more background damage in poplar stands at the nearer distance from river, our findings contrast with previous work in that we found no clear effect of distance from river on the abundance and richness of defoliating insect herbivores (Wang et al. 2019). Stone and Bacon (1995) also found that consumption of foliage by insects on the trees subjected to flooding compared to the non-flooded trees was not significantly different, but these results are less

consistent for background herbivory itself. Several previous studies suggested distance from running/standing water, soil moisture and vegetation cover are always the main local factors affecting invertebrate community composition and diversity (Magagula 2003; Rahman et al. 2015). For both primeval and managed stands of riparian forests, poplar trees in riparian border can produce significantly larger leaf area, and offer food sources and shelter for more insect species (Stone and Bacon 1995). However, outbreaks of insect species occur rarely and high-level insect damage generally occur over relatively short time intervals (Kozlov and Zvereva 2017). The lower outbreak risk of local insect herbivores can be explained, at least partly, by our results that background herbivory decreased with vegetation cover. Vegetation cover can modify microclimatic conditions and provide ideal living space to promote the community establishment of natural enemies, such as carabid beetles (Rahman et al. 2015). Vegetation cover can directly change microclimates of terrestrial habitat, resulting in diverse invertebrate communities (Lavallee and Richardson 2010). This could explain that a habitat with high vegetation cover was proved to have the highest abundance and species richness of natural enemies (Magagula 2003). And a study on forest-floor invertebrate communities suggested that riparian habitats had a great influence in maintaining populations of different predator species in forest ecosystems, in part because vegetation cover in such habitats determined their habitat choices (Rykken et al. 2007). Therefore, this study demonstrated the potential of vegetation cover to prevent high levels of insect herbivory, which may be stronger than the effect of distance from river on background herbivory.

### **Effects of region and forest management on background herbivory were partly explained by stand characteristics**

First of all, we found a significant interactive effect of region and forest management on tree height as differences in tree height between forest types were more pronounced in the Eastern part of North China and differences between regions were more pronounced in the primeval stands. Obviously, given the different forest management form of riparian poplars in the Eastern and Western part of North China (Zhou et al. 2013), it is likely that the proportion of primeval old-growth stands varies dramatically between two regional parts of North China, resulting in the regional differences of tree size and more pronounced differences in tree size between forest types in the Eastern part of North China. Therefore, the large tree size of poplar trees in the primeval stands and in the Eastern part of North China could increase level of background herbivory (Barone 2000). Secondly, we observed that background herbivory strongly responded to stand-level tree size and vegetation cover. Specifically, it increased with increasing tree height but decreased with increasing vegetation cover directly. However, despite this direct effect of stand level factors on background herbivory, we also detected direct effects of region and forest management on it. Thus, the effects of region and forest management on background herbivory seemed to be primarily explained by effects of region and forest management on stand level factors. Furthermore, this study is the first to address stand characteristics-dependent effects of region and forest type on background herbivory, but our results indicate that considering such indirect effect will be critical for future studies of tree-insect herbivore interactions in riparian forests.

### **Background herbivory increased with forest isolation at the landscape scale**

Our findings revealed that landscape-scale isolation have a strong positive effect on defoliation intensity of insect herbivores in forest fragments in riparian poplar forests. Effects of habitat fragmentation on insect herbivory were generally studied in forests, and forest isolation appears to be an important variable in explaining variation in levels of insect herbivory (Kozlov and Zvereva 2017; Castagneyrol et al. 2019). This study also found the pervasive effect of landscape-scale forest isolation, significantly increasing background herbivory on poplar trees, although such findings contrast with other studies conducted in tropical forests, in which insect herbivory levels were either smaller in more fragmented forests (Ruiz-Guerra et al. 2010) or unrelated to forest fragmentation (Souza et al. 2013). Interestingly, the density of understory woody plants decreased in landscapes with higher forest isolation and this may limit the availability of plant items, “forcing” insect herbivores to concentrate on the available trees and cause more leaf damage (Morante-Filho et al. 2016; Moreira et al. 2016). Higher forest isolation also increases the mortality of large shade-tolerant trees and promote the proliferation of pioneer species, such as poplars (Laurance et al. 2006; Arroyo-Rodríguez et al. 2016), tending to be poorly defended against insect herbivores and thus cause direct consequences for background herbivory (Coley and Barone 1996). Furthermore, it is possible that the generalist, disturbance-adapted insect species could be more abundant and representative in more disturbed sites, located in more isolated landscapes (Guimarães et al. 2014), and these insect species may exert higher overall background herbivory levels. Therefore, landscape-scale variables such as forest isolation and local-scale variables such as stand characteristics need to be incorporated into a broader research framework, and any generalizations of tree-insect herbivore interactions in riparian forests have to be based on multi-scale environmental drivers.

## Conclusions

Defoliation intensity of insect herbivores is often regulated by landscape structure, but current knowledge regarding background herbivory is primarily derived from studies of local-scale interactions between trees and insect herbivores (Kozlov and Zvereva 2017). Here, we elucidated the role of factors acting at multiple spatial scales to explain background herbivory of non-outbreak insect species in riparian forests. We not only explored the effects of region, landscape isolation, forest management, and stand position on overall background leaf damage but also determined the key role of tree height and vegetation cover in driving these interactions. Forest isolation appears to affect background herbivory in a direct manner, even though it cannot be explained by simple top-down or bottom-up mechanisms. This finding can help predicting spatial patterns of forest insect defoliation according to landscape structure and can develop a multiple-scale perspective to improve risk assessment of forest background herbivory. In addition, by demonstrating that background herbivory in the primeval stands significantly exceeded that in the managed stands only in the Eastern part of North China, we unravel the importance of considering regional-scale variability of ecological factors when addressing background herbivory on riparian forests. Thus, our study provides a more profound understanding of the complex forces that drive insect herbivory under natural, non-outbreak conditions in forest ecosystems, with possible far-reaching consequences for the ecology of riparian forests in highly isolated landscapes.

# Abbreviations

AICc: Akaike's information criterion corrected for small sample size; LMM: linear mixed-effect model; R<sup>2</sup><sub>c</sub>: conditional R<sup>2</sup>; R<sup>2</sup><sub>m</sub>: marginal R<sup>2</sup>; SEM: Structural equation modeling

# Declarations

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## Authors' contributions

WB, TC, and LY designed the research; WB and LD conducted the field work; WB analyzed data and drafted the manuscript; TC and LY revised the manuscript. All authors read and approved the final manuscript.

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## Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

## 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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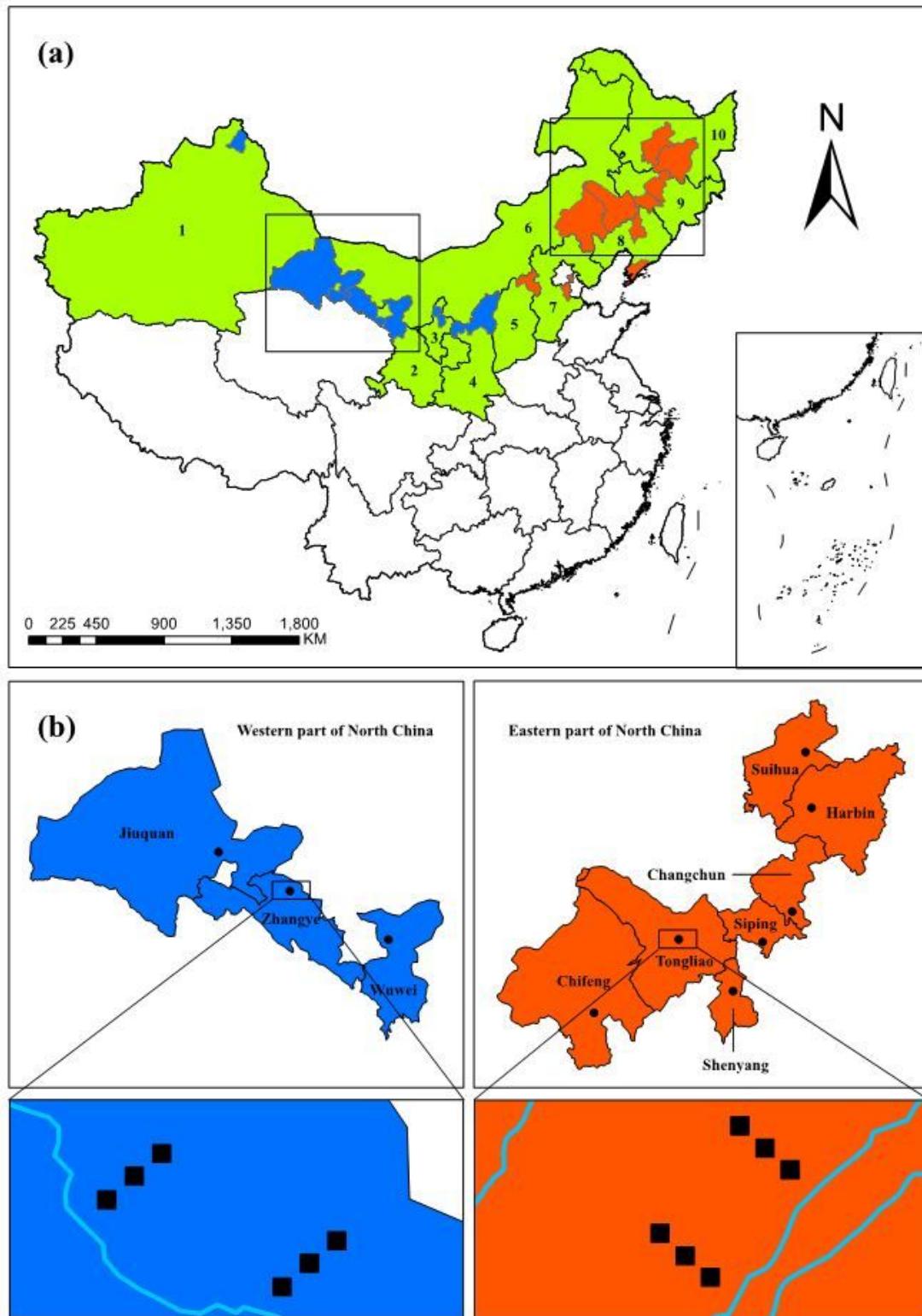
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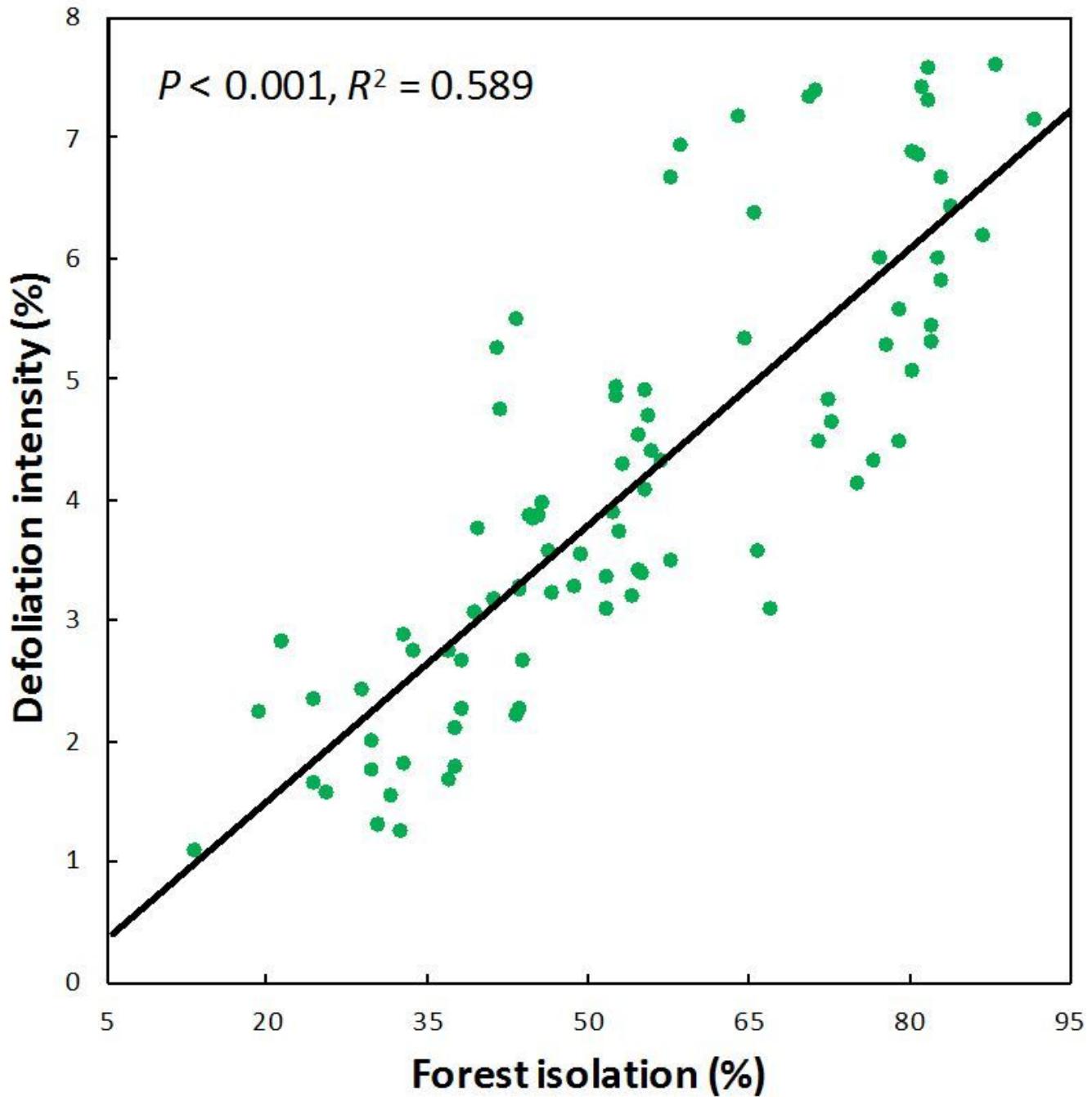
## Figures



**Figure 1**

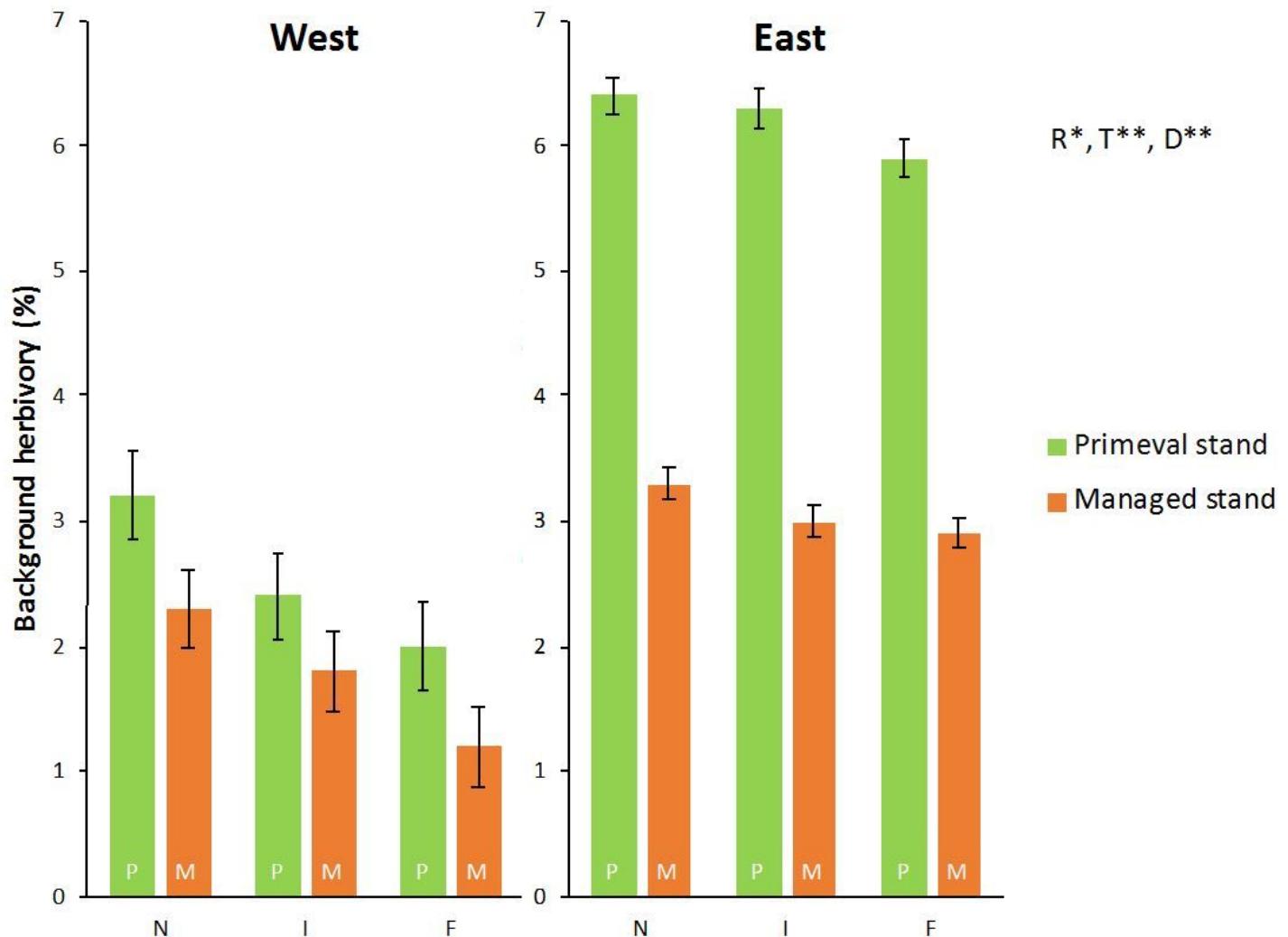
(a) Location of the study area in seven provinces and three autonomous regions in Northern China (green areas, see detailed description in Table S1); (b) Examples of study sites (cities with riparian poplar forests) showing where sampling and measurement of background herbivory were carried out as well as examples of sampling plots at three different distances from rivers in Western part (blue areas) and Eastern part (red areas) of North China, respectively. (The blue lines on the map represent rivers; filled

black circles represent study sites, and filled black squares represent sampling plots) 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.



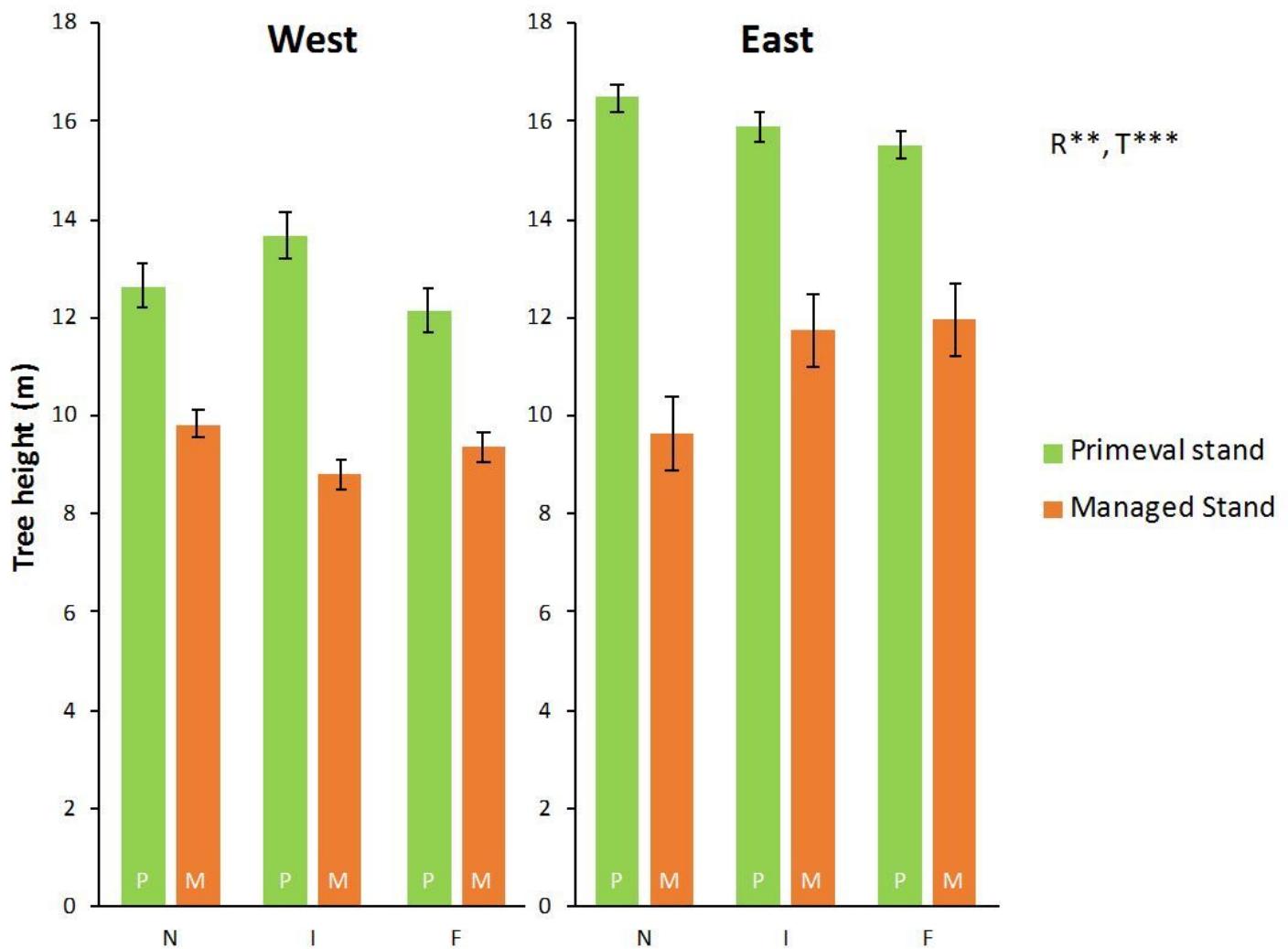
**Figure 2**

Effects of forest isolation in the surrounding landscape on background herbivory. Each point represents defoliation intensity (%, total percentage of leaf area removed or affected by insect herbivores divided by the number of leaves analyzed) per poplar forest stand.



**Figure 3**

Background herbivory in primeval (P) and managed (M) stands in the Western (W) and the Eastern (E) part of North China. Lengths of bars and error bars represent defoliation intensity averaged (mean  $\pm$  SE) between forest types at three stand positions (N, I and F: near, intermediate and far distance from rivers). Effects of region (R), forest management (T), and stand position (D) on defoliation intensity including significance level are indicated above the plot (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ).



**Figure 4**

Tree height in primeval (P) and managed (M) stands in the Western (W) and the Eastern (E) part of North China. Lengths of bars and error bars represent tree height averaged (mean  $\pm$  SE) between forest types at three stand positions (N, I and F: near, intermediate and far distance from rivers). Effects of region (R) and forest management (T) on tree height including significance level are indicated above the plot (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ).

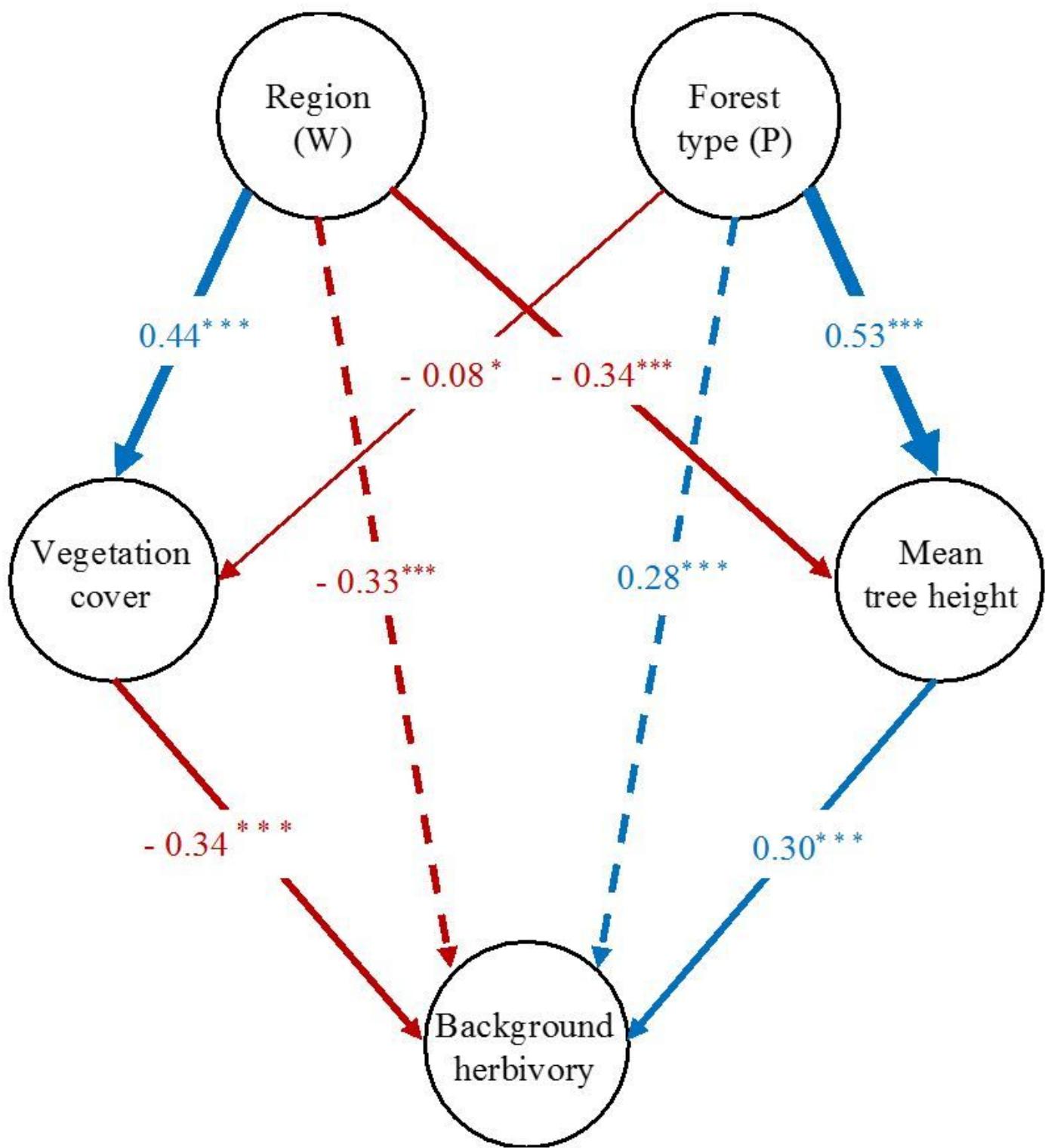


Figure 5

Structural equation models illustrating direct and indirect effects of region (W: the Western part of North China) and forest type (P: the primeval stand) on background herbivory. Standardized path coefficients are indicated near the arrows and the thickness of the arrows corresponds to the magnitude of these coefficients, and all significant coefficients are indicated with asterisks (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ). Significant positive and negative relationships between nodes are shown in blue and red,

respectively. Solid and dashed lines represent significant direct and indirect relationships among variables, respectively.