Forest management, site characteristics and climate change affect multiple biotic threats in riparian forests

Maarten de Groot [a,*], Silvio Schueler [b], Markus Sallmannshofer [b], Charlotte Virgillito [b,c], Gyula Kovacs [b], Thomas Cech [b], Gregor Božič [a], Rok Damjanić [a], Nikica Ogris [a], Gernot Hoch [b], Andreja Kavčič [a], András Koltay [d], Miran Lanšćak [e], Zvonimir Vujnović [e], Ivan Lukić [e], Laszlo Nagy [d], Sanja Novak Agbaba [e], Saša Orlović [f], Leopold Poljaković-Pajnik [f], Srdjan Stojnić [f], Marjana Westergren [a], Milica Zlatković [f], Martin Steinkellner [b], Erik Szamosvari [b], Katharina Lapin [b]

[a] *Slovenian Forestry Institute, Večna pot 2, 1000 Ljubljana, Slovenia*
[b] *Austrian Research Centre for Forests BFW, Seckendorff-Gudent-Weg 8, 1131 Vienna, Austria*
[c] *University of Lorraine, Faculty of Science and Technology, BP 70239, 54506 Vandoeuvre-lès-Nancy Cedex, France*
[d] *Department of Forest Protection, Forest Research Institute, University of Sopron, Hegyalja utca 18, Matrafured, Hungary*
[e] *Croatian Forest Research Institute, Cvjetno Naselje 41, 10450 Jastrebarsko, Croatia*
[f] *University of Novi Sad, Institute of Lowland Forestry and Environment (ILFE), Antona Čehova 13D, 21000 Novi Sad, Serbia*

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ABSTRACT

In a changing world, riparian forests are coming under more and more stress from biotic threats. This impacts all stages from saplings to older trees. One of the most dominant biotic threats are alien species and eruptive pest species. Sustainable silvicultural methods are required to reduce the risk of such biotic threats. We investigated the influence of climate, site, tree, and silvicultural characteristics on leaf damage by insect pests or fungal pathogens, herbaceous alien plant species, browsing, and the abundance of native tree saplings. Transects across the Danube-Mura-Drava biosphere reserve from Austria in the northwest to Serbia in the southeast, each containing 7–8 plots, were established to assess tree and site characteristics, regeneration, as well as fungal and insect leaf damage. We found that the horizontal stand structure affected insect leaf damage in different ways. Insect leaf damage was positively correlated with fungal leaf damage and tree height, and negatively correlated with intensity of forest management (from natural forests to coppice/plantations), temperature and precipitation during the vegetation season. Fungal leaf damage was negatively associated with intensity of forest management, and negatively with public ownership and tree species richness. Browsing was positively influenced by the number of saplings. The abundance of alien herbaceous plant species was negatively associated with distance to the watercourse, mean tree height, mean temperature of the vegetative period (MTVP), competition level, and the number of trees per layer, and positively associated with the DBH.

1. Introduction

Riparian forests are ecosystems that maintain a high level of biodiversity and provide numerous ecosystem services in urban and rural landscapes (González et al. 2017; Gundersen et al. 2010; Turunen et al. 2021). They provide habitats for many threatened species (Godreau et al. 1999) and ecosystem services such as pollination, pest control, filtration of pollutants, erosion control, and many more for agriculture in urban and rural areas (Riis et al. 2020). However, due to their position in the landscape, they are vulnerable to various threats (Johnson et al. 2020; Richardson et al. 2007). Over the past decades, there has been a huge decline of riparian forests, leaving many in an unfavorable or even bad state (EEA 2016). River regulation, climate change, invasive alien species, emerging pests, habitat destruction, and disconnection from the respective watercourse are the major threats contributing to this decline (EEA 2016; FAO 2020). There is therefore an urgent need to understand

the interplay of the various threats, their causes and forest management to preserve riparian forests and improve their ecosystem status.

River regulation, climate change, invasive alien species, and eruptive pests and diseases are connected and can have a cascading effect with huge impacts on forests (Jactel et al. 2019; Lehmann et al. 2020; Richardson et al. 2007). Many tree populations have declined in riparian forests because of drought, pests and diseases, and drainage activities (Rivers et al. 2019). In addition, weakened native tree species were found to be good hosts for a number of alien invasive pests and diseases (Biedermann et al. 2019; Kausrud et al. 2012; Ramsfield et al. 2016). Moreover, globalization facilitates the spread of invasive forest diseases, including ash dieback caused by the emerging fungal pathogen *Hymenoscyphus fraxineus* (T. Kowalski Baral, Queloz & Hosoya) originating from Asia. In Europe, *H. fraxineus* has caused large scale decline of populations of European ash (*Fraxinus excelsior* L.) (Thomas 2016), threatening an extinction cascade among associated species (Hultberg et al. 2020). Furthermore, acute oak decline, a complex disease caused by multiple biotic and abiotic factors including pathogenic bacteria is an increasing concern in several European countries and threatens native oak species (Haavik et al. 2015). However, forests generally show strong biotic resistance to biological invasions by alien plant species (Nunez-Mir et al. 2017 and references therein). As most invasive alien plants are light-demanding pioneer species, the dense canopy cover of forests limits the establishment of these species. In recent years, however, more and more large-scale disturbances have created large canopy gaps in forests, which have subsequently been invaded by alien plant species. Some invasive alien plant species are known to have a high negative impact due to their competitive behavior towards other plants in the herbaceous layer (Lapin et al. 2021). They may potentially have a negative impact on the reproductive success of affected riparian forests, by outcompeting saplings and restricting tree regeneration (Langmaier and Lapin 2020).

Although threats to riparian forests (i.e. river regulation and climate change) are mostly out of the control of local land and forest managers, sustainable management options may be suitable for combating biotic threats to riparian forests (Castello and Teale, 2011). Silvicultural practices are how foresters can influence forests to make them more resistant to climatic change and biotic threats. Sustainable silvicultural practices that increase resistance to insect and pathogen outbreaks have been tested in different forest ecosystems, and it has been shown that increasing tree species richness decreases leaf herbivory by insects (Jactel et al. 2017). Moreover, close-to-nature silvicultural management practices in mixed species forest stands increases resistance to bark beetle outbreaks (de Groot et al. 2019). Other ways of counteracting biotic threats are to increase structural diversity in terms of age class and vertical structure. Resistance to alien plant species can be increased by avoiding large gaps and planting tree species with a dense canopy cover, as most invasive alien species are light-demanding (Eschtruth and Battles 2009). Combining the aforementioned silvicultural practices provides sustainable forest management with an emphasis on resistance to biotic threats.

The situation in the riparian forests in Central Europe has been worsening over the past few decades (Dyderski et al. 2015; EEA EUNIS; Musche et al. 2019). The Mura-Drava-Danube catchment is a major drainage area of the rivers Mura, Drava and Danube, which drain large parts of the Eastern Alpine region and multiple countries in continental Europe. These forests have been endangered by increasing numbers of eruptive insects and pathogens like oak lace bug (*Corythucha arcuata*) and *Erysiphae alphitoides,* the causative agent of oak powdery mildew disease, fungal pathogen *H. fraxineus* and *Phytophthora* spp. (Haavik et al. 2015; Paulin et al. 2020; Thomas 2016; Zúbrik et al. 2013). Furthermore, this region has experienced several extreme heat wave events during the past decade, reducing the vitality of many trees. Foresters in the region are looking for alternative silvicultural practices or non-native species to be planted in these forests (Lapin et al. 2020).

Many studies have been conducted on the effects of climate change and biotic threats in forests (Pureswaran et al. 2018 and references therein). However, many of these studies have only focused on one of the various biotic threats, such as pathogenic fungi, insect pests, or alien plant species. In this study, we present a combined analysis of these threats based on a unique dataset of transects encompassing the riparian forests of the entire Mura-Drava-Danube biosphere reserve. We had the opportunity to measure biotic threats in different management types and across a climatic gradient, thus simulating potential increase in temperature due to climate change. The multifaceted dataset collected in the field allowed a simultaneous investigation of different threats as well as their interactions and corresponding management options in riparian forests.

The aim of this study was to quantify the effects of tree, climate, site, and silvicultural characteristics on the leaf damage caused by insect pests and pathogens and the abundance of alien herbaceous plants as well as their overall impact on forest regeneration. We studied biotic threats along a climatic gradient for one year in Central Europe. We hypothesize that 1) leaf damage due to fungal pathogens and insect pests is negatively affected by stand characteristics such as tree species richness, vertical structural diversity as well as particular site and climate conditions; 2) leaf damage due to fungal pathogens and insect pests are negatively correlated, because they are differently affected by humidity; 3) alien herbaceous plant species are positively affected by flooded forests with open canopies, which are created e.g. by diseases, pests or other natural disturbances.

2. Materials and methods

2.1. Area description

The study area is characterized by riparian forest ecosystems in Central and South-Eastern Europe. It covers 8300 km^2 along a river system spanning more than 500 km of major European rivers (15.647° to 19.448° E, 45.165° to 46.765° N). The Mura-Drava-Danube Transboundary Biosphere Reserve (BR) aims to become an international model area for sustainable regional development. It consists of spatially connected BRs in Austria, Slovenia, Hungary, Croatia, and Serbia. The core zone along the rivers represents a major ecological corridor designated as protected areas of various categories. More than one quarter of the area is covered by forests (2250 km^2); within the core zone along the rivers the forest share increases to 61%. Its forests consist mainly of oak (*Quercus* spp.), ash (*Fraxinus* spp.), poplar (*Populus* spp.), and willow (*Salix* spp.) (Sallmannshofer et al. 2021), species typical for riparian forests.

The extremely fertile plains are nowadays used for agriculture, forestry, and conservation purposes as well as recreation and tourism. The annual mean temperature ranges from 9.3 °C in the north-western part of the study area to 11.7 °C in the eastern part (Sallmannshofer et al. 2021). The gradient from the Illyrian climate in Austria and Slovenia to Pannonian conditions in the east results in a strong variation of average annual precipitation between 1000 mm in the west to less than 500 mm in the north-east (Sallmannshofer et al. 2021).

2.2. Survey protocol and data collection

We identified 47 transects (Fig. 1, top) through digital orthophoto and river analysis in QGIS (v. 2.18.16) from Bing satellite imaginary (Microsoft Bing 2019). The river polygons within the countries were divided into equally sized segments, marking the starting points of transects orthogonal to the river axis. Whenever these points did not fall into forests large enough to cover a length of 300 m, starting points were relocated to the closest position that matched those criteria. The transects continued to the boundaries of the forest complex or ended after a maximum of 600 m. Along the transects, we located 321 sampling plots in distances of 75 m from each other (Fig. 1, bottom). To include potential historic riparian forest nowadays cut-off from the river system
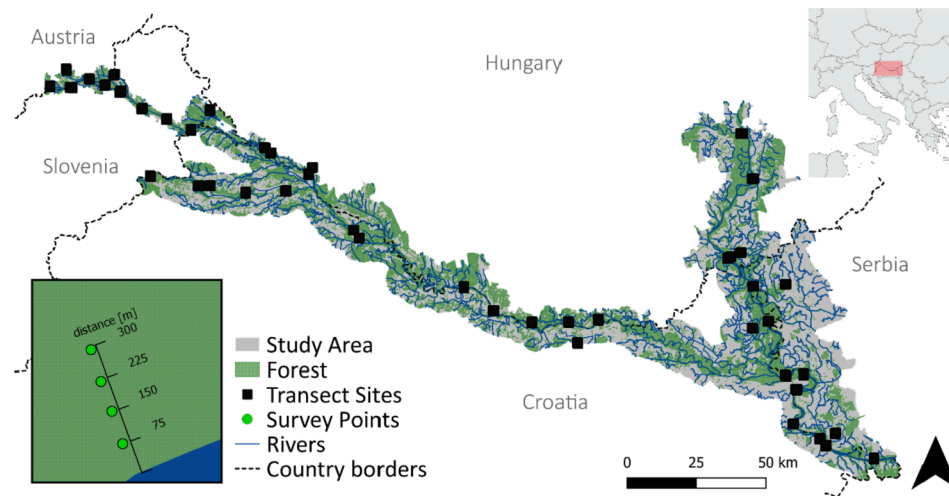
Fig. 1. Locations of the 47 sampling transects across the biosphere reserve located in southwest Europe. The insert shows the position of the transect perpendicular to the river with the survey points/plots.

and distant to rivers, we extend the transect axis even beyond the immediate riparian forest if such distant forests were available within the borders of the BR.

The data collection included various silvicultural, ecological and phytopathological assessments that were undertaken in spring and summer 2019 (see Table 1 for description of the classes). All assessments followed the transects sampling plots along the transect. The transects were 300–600 m long and 20 m wide. In total there were 321 sampling plots, at which the following assessments have been made.

2.2.1. Forest structure assessment

At each sampling plot, angle count sampling (Bitterlich 1948), a plotless method with variable sized-plots, was used to identify tree species and to measure tree height and DBH of every tree in the angle count. We counted the number of trees per layer in the vertical stand structure assigned to the occurring layers by their actual height (no theoretical straightening): overstory (>2/3 of the stand's maximum height), midstory (1/3–2/3 of the stand's maximum height), understory (<1/3 of the stand's maximum height). Tree species richness was assessed by determining the number of different tree species. The horizontal structure of the canopy was derived from the canopy closure around the angle count plot as a proxy for light availability and competition, stratified into six classes: congested, closed, broken, open, gappy, and grouped/cohorted. Tree competition was classified according to Kraft's crown classes (DeYoung 2016).

2.2.2. Forest management assessment

Forests were categorized into four classes: 'Nature-like forests' characterized by natural development processes and showing no signs of management such as tree stumps of anthropogenic; 'Uneven-aged forests'; 'Even-aged forests' consisting of forest stands of trees of a single age class; and 'Intensively managed forests' which include coppice, biomass and timber plantations. We distinguished between public and private ownership and accounted for the presence of nearby roads. Presence of forest roads was observed visually in the field during the assessments.

2.2.3. Biotic threats assessment

In the angle counts, we quantified fungus-induced leaf damage and insect-induced leaf damage on tree level. For both fungus-induced leaf damage and insect-induced leaf damage, percentage of affected leaves was estimated from the ground using binoculars. However, where necessary, a branch per tree was cut off and leaves were examined for the presence of necrotic lesions, fungal fruiting bodies, leaf mines and

other signs of leaf diseases and insect pests using hand lenses. The most relevant herbaceous invasive alien species (IAS) in riparian forests were identified prior to the fieldwork, using the CABI Horizon Scan (https://www.cabi.org/HorizonScanningTool) and the listing of IAS in riparian habitats in the Griis databases (http://www.griis.org/). Botanists and foresters used this list to identify IAS present along the transects. The abundance of IAS was determined using an adapted Braun-Blanquet approach (Moore 1962). Ungulate browsing on regeneration was evaluated by assigning browsing damage classes per individual seedling (Table 1) that was found within regenerations plots. Two regeneration plots were installed at each sampling plots with a size of 1 m^2 each for seedlings < 50 cm and 5 m^2 each for seedlings between 50 and 200 cm tall.

2.2.4. Site and climate conditions

Climate data for each transect was obtained from the HISTALP database (Auer et al. 2007). The database contains homogenized precipitation and temperature data from 192 and 131 weather stations in the broader Alpine and Dinarides region. We calculated long-term (1985–2014) mean temperature (MTVP) and total precipitation (TPVP) during the vegetation season (April-September).

Since river bodies are important for riparian forests, we characterized the effects of the river system by calculating the variable 'horizontal distance' of a certain sampling plot to the river shore. The minimal horizontal distance to the river was calculated based on the coordinates of each angle count plot. Vector data of the major river networks were received from the EU-Hydro River Network Database, Version 1.2 (EU-Hydro) (EEA 2020) for the Danube river basin. These data provide precise contour lines of river and water bodies derived from photo interpretation of image data (2011–2013) at a resolution of 2.5 m (Sallmannshofer et al. 2021).

2.3. Data analysis

When necessary, data was averaged on plot level when individual trees were measured. First the data were checked for normality, heteroscedasticity, and outliers (Zuur et al. 2010). We used a general linear model (GLM) with a Gaussian distribution to analyze the data for the damage by pests and pathogens and herbaceous alien species abundance. Browsing was analyzed with an ordinal regression. We prepared five different models with 1) insect-induced leaf damage (Hypothesis 1 and 2), 2) fungus-induced leaf damage (Hypothesis 1 and 2), 3) ungulate browsing (Hypothesis 1), 4) herbaceous alien plant abundance (Hypothesis 3). The independent variables were divided as shown in

Table 1

Variable grouping and their description by variable name, type and classes.

	Variable group	Variable name	Variable type	Variable classes / unit (when relevant)
Independent variables	Forest structure	Tree height	continuous	m
		DBH	continuous	cm
		Number of trees per layer (overstory, midstory, understory)	continuous	Number of trees
		Tree competition as per Kraft	ordinal	1 Dominant trees (D), 2 Codominant trees (C), 3 intermediate trees (I), 4 suppressed trees (S)
		Horizontal canopy structure	ordinal	congested, closed, broken, open, gappy, grouped/ cohorted
		Tree species richness	continuous	Number of tree species
	Forest management	Forest type	nominal	Nature-like forest, uneven-aged forest, even-aged forest, intensively managed forests (coppice, biomass and timber plantation)
		Ownership	dichotomous	Public, private
		Presence of forest roads	dichotomous	Present, not present
	Site and climate conditions	Mean temperature during the vegetation period (MTVP)	continuous	℃
		Total precipitation during the vegetation period (TPVP)	continuous	mm
		Distance to river	continuous	m
Dependent variables	Biotic threats	Insect induced leaf damage	continuous	Median percentage of the trees per plot
		Fungus induced leaf damage	continuous	Median percentage of the trees per plot
		Alien plant species abundance	continuous	Percentage
		Ungulate browsing	Ordinal	1: not browsed 2: leading head shoot not browsed, side shoot browsed 3: leading head shoot browsed, side

Table 1 (*continued*)

Variable group	Variable name	Variable type	Variable classes / unit (when relevant)
			shoot not browsed 4: leading head shoot and side shoot browsed
Regeneration	Regeneration abundance	continuous	Number of saplings

Table 1. For the variables which were recognized as biotic threats, fungus-induced leaf damage was included when insect-induced leaf damage, and alien plant species abundance were the dependent variables. Insect-induced leaf damage was included when fungus-induced leaf damage, and alien plant species abundance were the dependent variables. We used the median of the leaf damage of the pathogens or pests per tree measured in the plot for the pests and pathogen damage. Before analysis the damage percentage of pests and pathogens were log +1 transformed. For the browsing the total number of saplings per plot were taken into account and the class with the largest percentage was taken into account for the analysis. The models were tested for spatial autocorrelation with a Moran's I test. When the models turned out to be spatially autocorrelated, spatial filtering was applied, and Moran's eigenvector was included in the model. Model selection was performed for every biotic threat by first preparing a complete model. Then the Akaike Information Criterion (AIC) was calculated and ordered from the smallest to the largest AIC. The estimates of the parameters were averaged from all models which were 2 AIC units from the best model. The averaged models might also include non-significant independent variables, because it was important for only one of the models, but not the other which would be averaged.

Data management, statistical analysis, and visualization were performed in the program R (R Core Team 2018) using the packages "ggplot2" (Wickham 2016), "spdep," "spatialreg" (Bivand and Piras 2015), MASS (Venables and Ripley 2002) and "adespatial" (Dray et al. 2018).

3. Results

Insect-induced leaf damage in the Mura-Drava-Danube BR was 9% on average, with a minimum of 0% and maximum of 80%. Variables exhibiting a significant influence were the horizontal structure, the median of the fungus-induced leaf damage, management type, mean tree height, and TPVP (Table 2, Fig. 2). Leaf damage was significantly higher in closed horizontal structures than in broken ones. There was a strong positive correlation with fungus-induced leaf damage and mean tree height, and a negative correlation with TPVP and MTVP. There was a higher percentage of insect-induced leaf damage in coppice than in even-aged forests, while the other management types were not significant compared to even-aged forests. Ownership type and the distance to the river where not significantly associated with insect-induced leaf damage, but are still included in the averaged model.

Fungus-induced leaf damage was 6% on average, with a minimum of 0% and a maximum of 60%. The significant variables explaining this type of leaf damage were horizontal structure, insect-induced leaf damage, management type, ownership type, and tree species richness (Table 2, Fig. 3). Congested horizontal structure exhibited a significantly higher prevalence of fungus-induced leaf damage than broken horizontal structure. There was a positive correlation of fungus-induced leaf damage with the insect-induced leaf damage and a negative correlation with tree species richness. Leaf damage by fungi was more prevalent in privately owned forests than in public forests, and more prevalent in

Table 2
Models of insect- and fungus-induced leaf damage as well as abundance of herbaceous alien species in the forest and their independent variables. The table shows the respective model estimate, standard error, z value, and P value. Significant variables (P < 0.05) are in bold.

Dependent variable	Independent variables	classes	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)
insect leaf damage	(Intercept)		8.4957	3.2427	3.2581	2.6080	**0.009**
	Horizontal_structure	closed	0.5350	0.1812	0.1822	2.9370	**0.003**
		congested	−0.0508	0.2478	0.2492	0.2040	0.839
		gappy	0.0765	0.2921	0.2937	0.2600	0.795
		grouped / cohorted	−0.2034	0.2989	0.3006	0.6770	0.499
		open	0.5328	0.3007	0.3024	1.7620	0.078
	log(1 + fungi leaf damage)		0.4966	0.0690	0.0694	7.1590	**<0.001**
	Management_type	High-growing coppices / plantations	0.5517	0.2670	0.2684	2.0550	**0.040**
		Nature-like forests	−0.3427	0.2130	0.2142	1.6000	0.110
		Unevenaged forest	−0.3395	0.2055	0.2067	1.6420	0.101
	Mean Height		0.0263	0.0127	0.0127	2.0670	**0.039**
	mean temperature during the vegetation season		−0.4407	0.1831	0.1840	2.3950	**0.017**
	Ownership type-Public		0.3972	0.2186	0.2198	1.8070	0.071
	Sum of the precipitation in the vegetation season		−0.0007	0.0003	0.0003	2.2240	**0.026**
	log(1 + distance to river)		−0.0777	0.0559	0.0562	1.3820	0.167
fungal leaf damage	(Intercept)		1.5327	0.3544	0.3561	4.3040	**<0.001**
	fitted(MEbinom1)vec2		−2.1797	0.9748	0.9802	2.2240	**0.026**
	fitted(MEbinom1)vec18		2.4702	1.0003	1.0059	2.4560	**0.014**
	Horizontal_structure	closed	−0.1476	0.1544	0.1553	0.9510	0.342
		congested	0.6139	0.2106	0.2118	2.8990	**0.004**
		gappy	−0.3445	0.2573	0.2587	1.3320	0.183
		grouped / cohorted	−0.2685	0.2632	0.2647	1.0140	0.310
		open	−0.4117	0.2632	0.2647	1.5550	0.120
	log(1 + insect leaf damage)		0.3913	0.0510	0.0513	7.6310	**< 2e-16**
	Management type	High-growing coppices / plantations	−0.1849	0.2152	0.2164	0.8540	0.393
		Nature-like forests	0.2834	0.1791	0.1802	1.5730	0.116
		Unevenaged forest	0.7037	0.1743	0.1753	4.0140	**< 0.001**
	ownership_type	Public	−1.2216	0.1493	0.1502	8.1360	**<0.001**
	Tree species richness		−0.1225	0.0524	0.0527	2.3260	**0.020**
	Number of trees per layer		−0.0285	0.0222	0.0223	1.2780	0.201
	Sum of the precipitation in the vegetation season		0.0002	0.0003	0.0003	0.9240	0.355
	Mean Height		−0.0098	0.0110	0.0111	0.8830	0.377
	log(1 + distance to river)		0.0327	0.0477	0.0480	0.6830	0.495
	Median DBH		−0.0024	0.0035	0.0035	0.6820	0.495
IAS plant abundance	(Intercept)		13.1286	3.8241	3.8413	3.4180	**0.001**
	factor(Competition)2		0.1753	0.1924	0.1938	0.9050	0.366
	factor(Competition)3		0.6523	0.2586	0.2604	2.5050	**0.012**
	fitted(MEbinom1)vec6		−4.3189	1.1985	1.2056	3.5820	**< 0.001**
	fitted(MEbinom1)vec3		−4.5107	1.0905	1.0985	4.1060	**< 0.001**
	fitted(MEbinom1)vec22		3.8603	1.0553	1.0625	3.6330	**< 0.001**
	fitted(MEbinom1)vec1		5.0284	1.1873	1.1950	4.2080	**< 0.001**
	fitted(MEbinom1)vec5		3.5407	1.1505	1.1585	3.0560	**0.002**
	log(1 + distance to river)		−0.1858	0.0602	0.0607	3.0630	**0.002**
	Mean Height		−0.0318	0.0145	0.0146	2.1710	**0.030**
	Median DBH		0.0122	0.0060	0.0060	2.0240	**0.043**
	mean temperature during the vegetation season		−0.5234	0.2125	0.2134	2.4520	**0.014**
	Number of trees per layer		−0.0584	0.0268	0.0270	2.1680	**0.030**
	Sum of the precipitation in the vegetation season		−0.0005	0.0004	0.0004	1.3560	0.175
	Horizontal structure	closed	−0.2603	0.1884	0.1898	1.3710	0.170
		congested	−0.2705	0.2560	0.2579	1.0490	0.294
		gappy	0.5682	0.3000	0.3022	1.8800	0.060
		grouped / cohorted	0.7548	0.3070	0.3093	2.4400	**0.015**
		open	0.1357	0.3264	0.3289	0.4130	0.680
	Tree species richness		0.0937	0.0629	0.0633	1.4800	0.139
	Ownership type	Public	0.2229	0.2301	0.2318	0.9620	0.336
	log(1 + fungi leaf damage)		−0.0565	0.0687	0.0692	0.8160	0.414

uneven-aged continuous cover forests than in even-aged forests. Number of tree layers, total precipitation during the vegetation season, tree height, distance to the river, and DBH were not significant in the individual models but were nevertheless included in the averaged model (Table 2).

The average abundance of alien species was 18% of the ground cover and ranged from 0 to 92%. Competition, distance to the river, tree height, median DBH, MTVP, number of tree layers, and horizontal structure influenced the abundance of alien species significantly (Table 2, Fig. 4). The intermediate competition had a significantly stronger effect on the IAS abundance than competition level dominant. There was a greater abundance of alien species closer to the river course. Forests with lower and thicker trees and fewer horizontal tree layers exhibited a greater abundance of alien species. A larger abundance of alien herbaceous plant species was observed for forests with grouped horizontal structure compared to broken horizontal structure. TPVP, tree species richness, ownership type, and fungus-induced leaf damage did not affect the abundance of alien species but were nevertheless
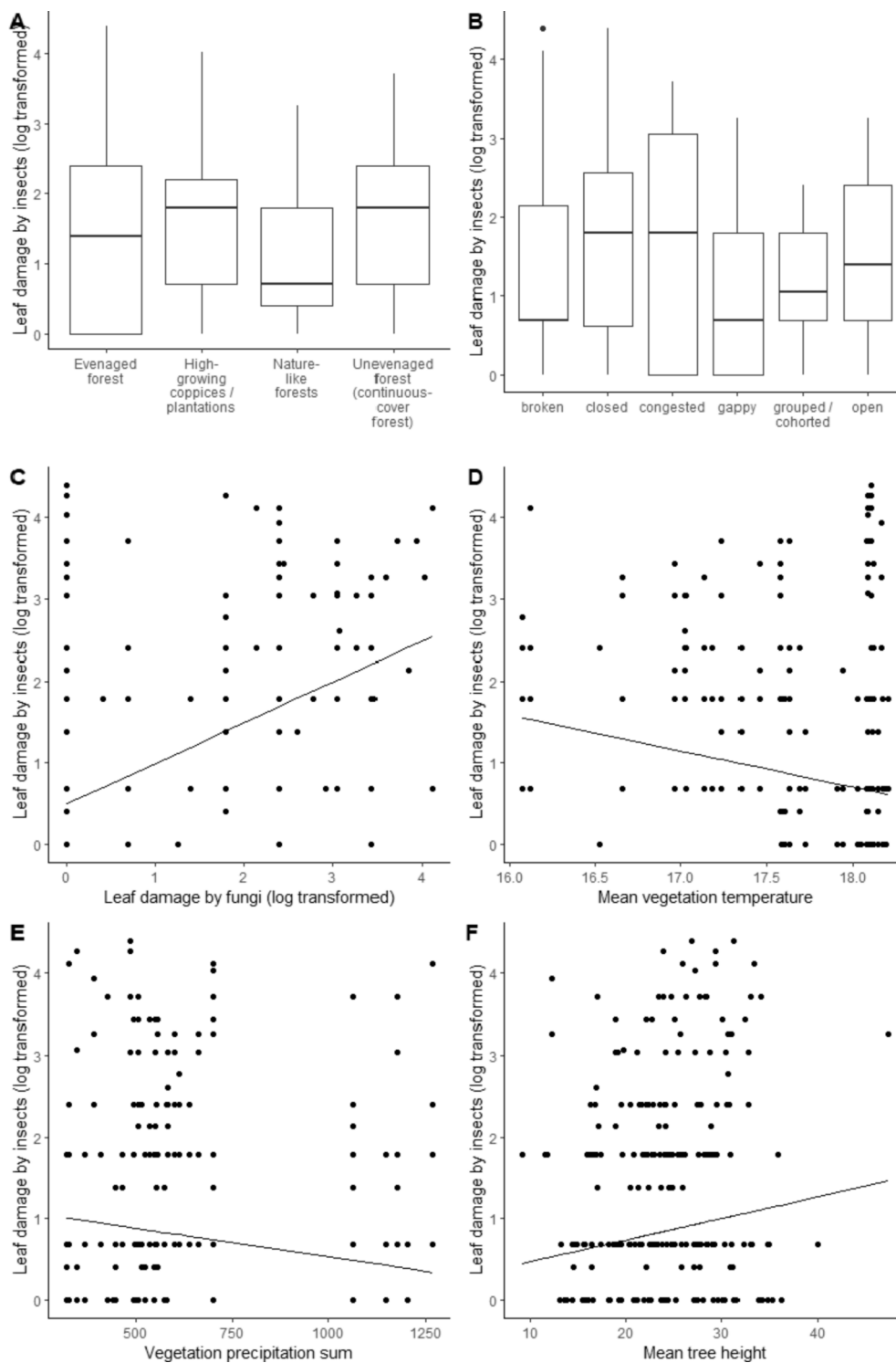
Fig. 2. Factors affecting leaf damage by insects: management type (A), horizontal canopy structure (B), fungus-induced leaf damage (C), mean vegetation temperature (D), total precipitation during the vegetation season (E), and the mean tree height.

included in the averaged model. Browsing was only significantly positively affected by the number of saplings (Table 3, Fig. 5).

4. Discussion

Biotic threats were affected in numerous ways by silvicultural practices, climatic characteristics and site characteristics (Fig. 6). Our results only partially confirmed hypothesis 1, that close-to-nature silvicultural practices focusing on increased tree species richness and structural diversity would decrease fungus- and insect-induced leaf damage. We found that increasing tree species richness results in lower fungus-induced leaf damage. However, fungus-induced leaf damage was more prevalent under uneven-aged continuous cover forests than in more intensive management types. Also, forest with closer canopy revealed both, higher fungus- and insect-induced leaf damage. In contrast to our second hypothesis, we determined a positive correlation between insect-induced and fungus-induced leaf damage.

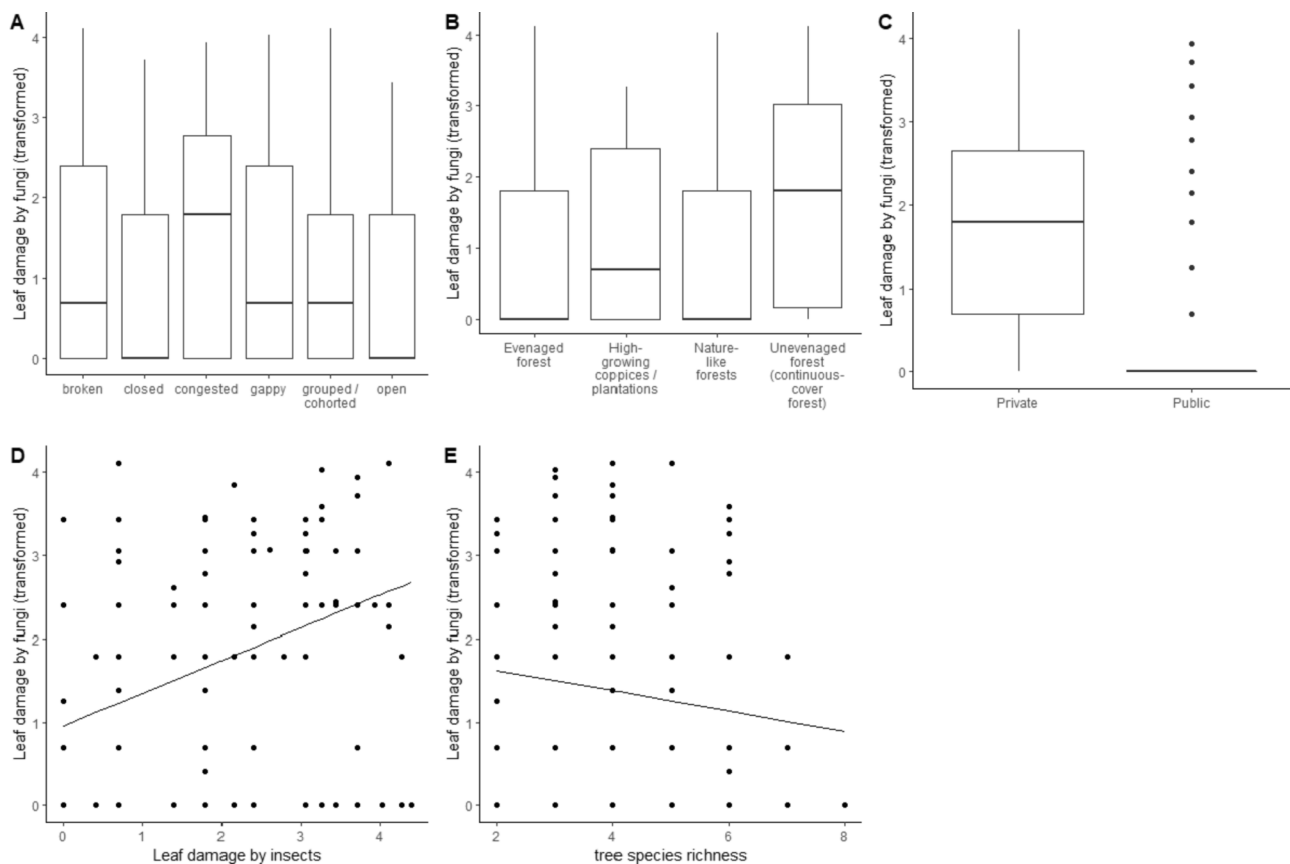In terms of IAS, we confirmed our hypothesis and showed that forests

Fig. 3. Fungus-induced leaf damage and influencing variables horizontal canopy structure (A), management type (B), ownership type (C), leaf damage by insects (D), and tree species richness (E).

with grouped and gappy horizontal structures have greater abundance of IAS than forests with closed and congested canopy cover. Despite a gradient along canopy cover types, the influence of fungus-induced leaf damage was insignificant when analyzed through this metric.

4.1. Interactions among biotic threats

Our results show a positive correlation between fungus- and insect-induced leaf damage, but no correlation with alien herbaceous plant species abundance. The positive correlation between fungus-and insect-induced leaf damage suggests facilitation between both types of de-foliators, with each decreasing the overall vitality of the tree, attracting the other damaging agent. Such facilitation has previously been shown between the hemlock woolly adelgid and the gypsy moth (Kinahan et al. 2020), although no general rule appears to be established for these types of interactions (Eberl et al. 2019). Another explanation for the positive correlation between both threats could be a more generally reduced vitality of single trees, where a limited defense makes them attractive for various biotic threats. Such a reduced vitality could potentially be connected to climate change, but the observed mean vegetation temperature and precipitation had a weak correlation with insect-induced damages and non-significant for fungus-induced damages. Another explanation for reduced vitality could be past river management in the neighboring forest areas (Belletti et al. 2020; Van Looy et al. 2017), but such effects could not be tested in our dataset. With more severe and frequent climate disturbances expected in the future, outbreak of and interactions between biotic agents are expected to have an increased impact on forests (Ramsfield et al. 2016).

The lack of correlation between leaf damaging agents and alien herbaceous plant species is interesting because there are potential direct and indirect influences of pests and diseases promoting plant invasions

in forests (Eschtruth and Battles 2009; McEwan et al. 2009), including riparian forests. Canopy disturbance, which can also be induced by pests and diseases, facilitates the presence of alien plant species (Eschtruth and Battles 2009). However, this facilitation is more commonly present in insect species detrimental to trees (Hausman et al. 2010), rather than temporary changes in canopy cover caused by fungus- and insect-induced damage (McEwan et al. 2009). Moreover, damage by insects and fungi leading to discoloration or necrosis does not directly increase opening of the canopy.

4.2. Impact of silvicultural practices

Silvicultural practices and the resulting forest structures had an effect on biotic threats. When tree species richness was higher, there was less fungus-induced leaf damage. This was not the case with insect-induced leaf damage and the presence of alien herbaceous plants, respectively, which both were unaffected by tree species richness. This confirms the results of other studies for fungus-induced leaf damage (Field et al. 2020) but is in contrast to studies in temperate forests, which found a negative correlation between insect-induced leaf damage and tree species richness (Fernandez-Conradi et al. 2018; Field et al. 2020; Guyot et al. 2019; Jactel et al. 2017; Jactel et al. 2005). Previously observed decrease in leaf damage is especially associated with the lack of resources for insects (Klapwijk et al. 2016), and for insects, with an increase of different host volatiles that makes it more difficult for insects to find respective host trees (Schiebe et al. 2011). One reason for the lack of correlation between insect damage and tree species richness could be our focus on overall leaf damages instead of species-specific damages.

The horizontal structure of the canopy influences biotic threats differently. While alien herbaceous plant species are more abundant in areas with open canopy, fungus-induced leaf damage is facilitated with
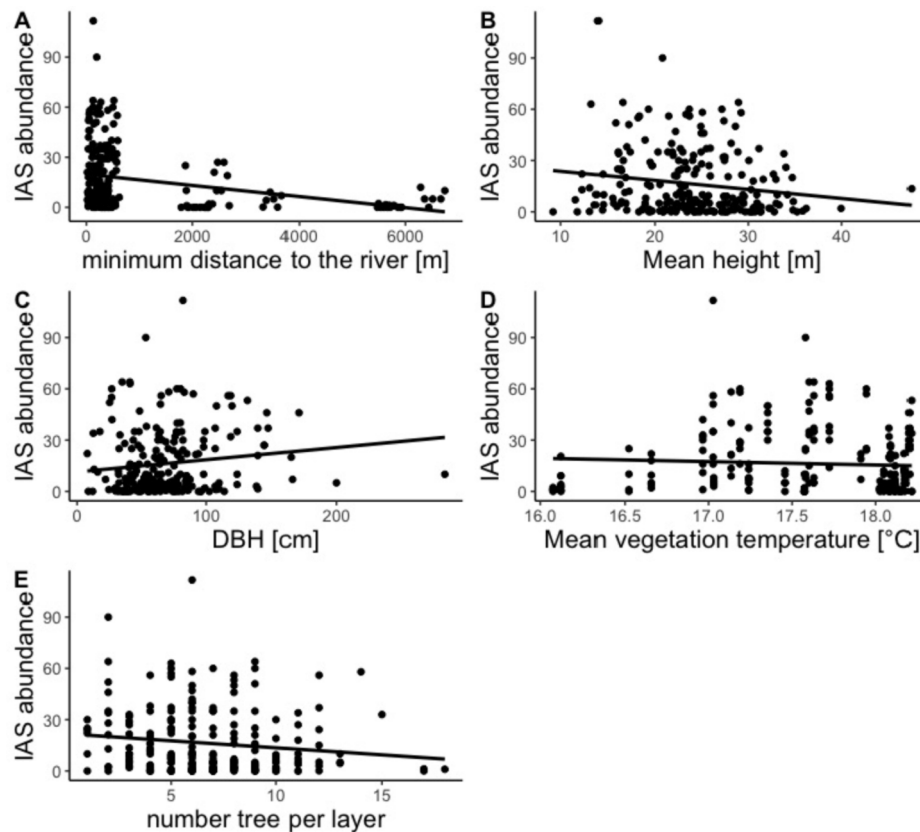
Fig. 4. Influence of distance to the river (A), mean height (B), mean DBH (C), mean temperature during the vegetation season (D), and number of tree layers (E) on the abundance of alien herbaceous species (IAS).

Table 3
Model output of the averaged model of an ordinal regression for the influence of independent variables on browsing. The table shows the respective model estimate, standard error, z value, and P value. Significant variables (P < 0.05) are in bold.

Independent variables	classes	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)
log(1 + number of native saplings)		1.012	0.222	0.224	4.522	**< 0.001**
Management type	High-growing coppices / plantations	−0.344	0.605	0.609	0.565	0.572
	Nature-like forests	0.838	0.578	0.582	1.438	0.15
	Unevenaged forest	−0.657	0.429	0.432	1.523	0.128
1|2		0.057	0.738	0.741	0.077	0.939
2|3		0.580	0.738	0.742	0.783	0.434
3|4		0.721	0.739	0.742	0.972	0.331
log(1 + distance to river)		−0.145	0.129	0.130	1.113	0.266
Median DBH		0.009	0.010	0.010	0.979	0.328
Number of_Trees per_Layer		0.038	0.059	0.060	0.636	0.525
Ownership type	Public	−0.177	0.384	0.387	0.456	0.648

closed canopy. Insect leaf damage fluctuates between the different openness of canopy. These differences between groups most likely lie in the niches they occupy (Zelnik et al. 2015). Alien herbaceous plant species are often light demanding species and therefore will flourish in disturbed habitats with large gaps (Eschtruth and Battles 2009). In contrast, fungal pathogens generally require moisture to spread and infect plants and thus they prefer closed canopy where microclimate is moist compared to the dryer one in forests with open canopies (Huber and Gillespie 1992, this study). The fluctuating abundance of insect damage over the openness gradient might reflect a combination of resource availability in closed canopy and stressed leaves in open canopy plots.

The number of trees per layer only affects alien herbaceous plants. The negative correlation between the number of trees per layer and the alien herbaceous species abundance is in concordance with the biological resistance hypothesis in invasion biology (Nunez-Mir et al. 2017).

The increase of trees per layer in turn increases competition for nutrients, light and other important factors promoting growth of alien herbaceous plant species. As already mentioned above most of the alien plant species found in the study area are restricted by light availability and higher abundance of trees per layer decreases establishment opportunities for alien plants.

Browsing by deer was expected to negatively affect sapling numbers, however, this study exhibited a positive correlation between these two variables. This suggests that the correlation between browsing by deer and sapling numbers is principally dependent on resource availability, a bottom-up influence of the number of saplings on visible browsing damage.

4.2.1. Climatic variables and site characteristics and biotic threats
Climatic variables had an impact on biotic threats. The MTVP was negatively associated with insect leaf damage. Precipitation during the
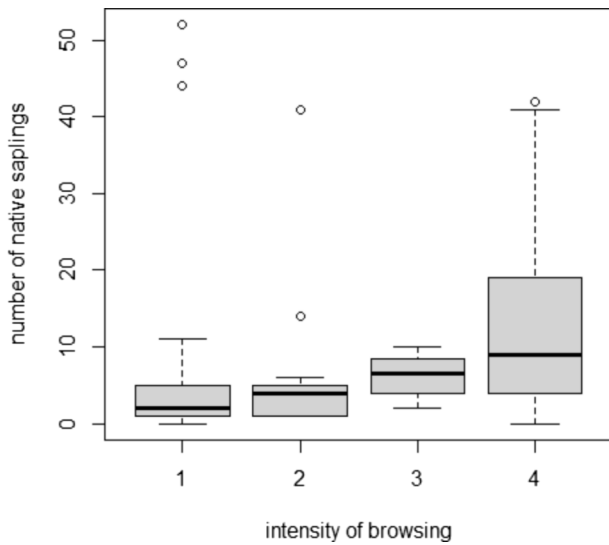
Fig. 5. Influence of the intensity of browsing on the number of native saplings. 1: not browsed, 2: leading head shoot not browsed, side shoot browsed, 3: leading head shoot browsed, side shoot not browsed, 4: leading head shoot and side shoot browsed.

vegetation season was negatively associated with insect leaf damage. It was found that intermittent water stress results in a higher abundance of sap feeding insects than constant stress (Sconiers and Eubanks 2017), which could explain the inverse correlation between higher temperatures leading to less leaf damage. The result regarding the temperature was unexpected because drier summers often brought about an increase in the fitness and outbreaks of pest insects (Dale and Frank 2017; Jactel et al. 2019; Seidl et al. 2017). A possible explanation could be that we only measured one year and that climatic variation between years also affects insect leaf damage. The negative association of the alien herbaceous plant species to temperature is intriguing. It is expected that not all alien species are consistently favored (Leishman and Gallagher 2015) or that not the same climatic factors are important for all species (Hulme 2014). Therefore, the abundance of alien plant species could be

correlated with the introduction point to the area rather than the climatic gradient sampled. In addition, results of this study showed that leaf damage by pathogenic fungi is unaffected by temperature and precipitation. This is surprising as plant diseases are influenced by environmental conditions (Agrios 2005). However, in this study, fungus-induced leaf damage was more pronounced in forests with closed canopy, where microclimate should be milder (i.e. with less severe extreme weather events, higher humidity) and thus more favorable for leaf disease development. Moreover, compared to *H. fraxineus* most other fungi causing foliar diseases of forest trees (e.g. *Colletotrichum* spp., *Erysiphae* spp.) have broader temperature requirements for growth, infection and spread (Agrios 2005). In addition, the data from this study represent climatic conditions of a single vegetation season and more research is needed to truly unravel the relationship between climatic variables and biotic threats (Desprez-Loustau et al. 2006; Hauptman et al. 2013). Distance from the river only affected alien herbaceous plant species; fewer alien plant species were found farther away from the watercourses. Rivers are important pathways for plant propagule migration, with flooding routinely transporting seeds into the forest (Richardson et al. 2007; Vogt et al. 2006). Furthermore, riparian forests are often intersected with trails that facilitate seed dispersal by wind, animals or people (Richardson et al. 2007). Since other biotic threats have different dispersal modes (Asplen 2018; Fitt et al. 1987) we did not find a negative association between distance to the river and leaf damaging fungi and insects.

4.2.2. Implication for the sustainable forest management

Our study showed that biotic threats are not reduced by one universal stand characteristic and that different biotic threats can even be promoted by opposite stand characteristics. It is therefore important that the forest manager understands these different stand characteristics and can accurately evaluate the threat in their forests. Site specific conditions can change the effect of biotic threats found across a variety of site types.

Manipulation of stand characteristics is how foresters can mitigate the impact of the biotic threats considered in this study. 1) Tree species richness can be enhanced by systematically planting different tree species per stand. 2) Horizontal closeness of the canopy structure significantly influences both fungi and insect leaf damage, but with opposing
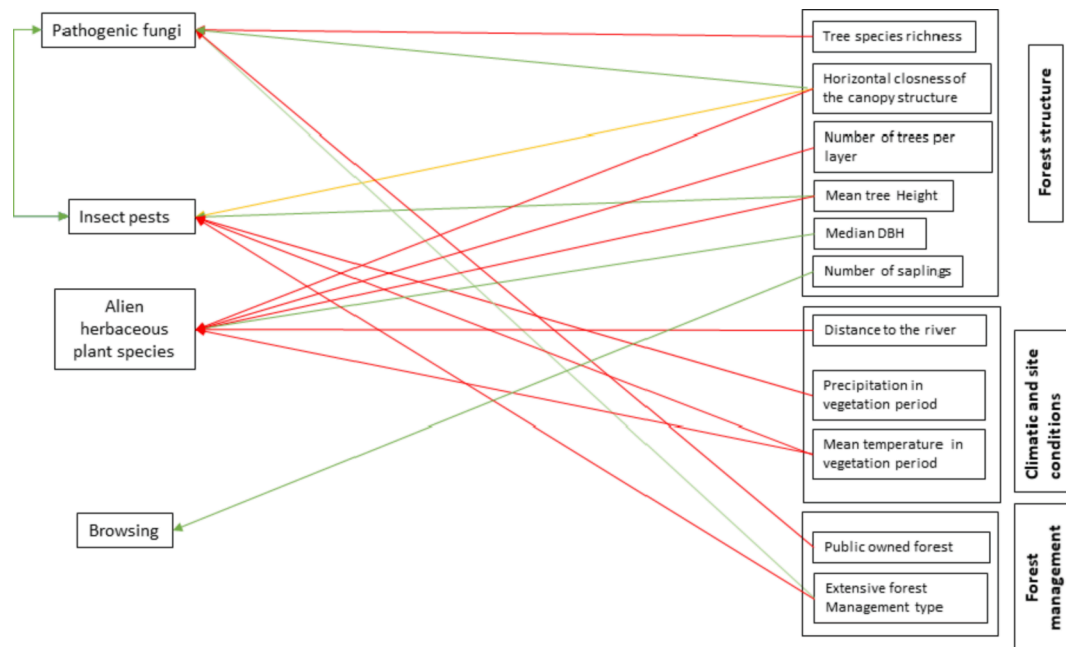

Fig. 6. Diagram of the influence of different climatic and site characteristics as well as stand characteristics and forest management variables on the biotic threats. Red arrows indicate a negative correlation, while green arrows indicate a positive correlation and the yellow arrow indicates a fluctuating association.

effects. A closed forest could be made by individual tree-based management and would be successful at resisting alien herbaceous species invasion, but not against fungus-induced leaf damage. Therefore, managing forests by planting tree species with a strong canopy cover will be insufficient, particularly in the case of softwood riparian forests, which show high levels of disturbance and are primarily composed of light-demanding pioneers. 3) The number of trees per layer would increase the level of shadiness in the forest and therefore limit the invasion of alien plant species. 4) The number of trees per layer can be increased by enhancing the natural regeneration and planting more trees. Altogether, these measures would make the forests more resistant to biotic threats, but the effectiveness depends on site-specific influences.

Interestingly, our study showed that fungi-induced leaf damage occurs more frequently, while the abundance of native saplings and insect-induced leaf damage occurs less often in nature-like and uneven-aged forests compared to even-aged or intensively managed forests like plantations. One possible explanation is that thinning increases the resistance of individual trees to biotic and abiotic stress, enabling an increase in the horizontal and vertical structural diversity as well as the resistance of individual trees (Brang et al. 2014). Another explanation is that less intensively managed forests have more humid microclimates and are therefore conductive to fungi growth. Leaf damage by insects is strongly negatively impacted by increased tree species richness and diversification of forest microclimates. Therefore, insect infestations would more likely succeed on plantations containing trees of similar age and species (Seidl et al. 2018). In any case, the intensity of the management depends on different silvicultural practices described above. Although outside the scope of this study, including forest management type reveals important variables or combinations of variables which reflected intensity of biotic threats and native sapling numbers that were not accounted for in the results.

5. Conclusions

In conclusion, our study showed the extent to which biotic threats influence and affect riparian forests, is dependent on forest stand, management, site and climatic characteristics. Regardless, forest owners and managers will need to change management practices and implement adaptive strategies to mitigate the impact biotic threats. Although globally the spread of pests and diseases is driven by climate change, many stakeholders react to environmental changes locally. Furthermore, even across the same geographic region, stakeholders can have highly diverse reactions to these changes (Deuffic et al. 2020). The outcome of this study clearly supports a recommendation that forest management measures require a threat-specific response to lower the risk of large-scale outbreaks and related threats. Furthermore, futures studies and recommendations should be species targeted rather than broadly group specific, as was the case with this study.

CRediT authorship contribution statement

Maarten de Groot: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Visualization. **Silvio Schueler:** Conceptualization, Supervision, Writing – review & editing. **Markus Sallmannshofer:** Conceptualization, Methodology, Investigation, Data curation, Writing – original draft. **Charlotte Virgillito:** Formal analysis, Writing – original draft, Visualization. **Gyula Kovacs:** Writing – original draft. **Thomas Cech:** Investigation, Supervision, Writing – review & editing. **Gregor Božič:** Investigation, Writing – review & editing. **Rok Damjanić:** Investigation, Writing – review & editing. **Nikica Ogris:** Investigation, Supervision, Writing – review & editing. **Gernot Hoch:** Investigation, Writing – review & editing. **Andreja Kavčič:** Investigation, Writing – review & editing. **András Koltay:** Investigation, Writing – review & editing. **Miran Lanšćak:** Investigation, Writing – review & editing. **Zvonimir Vujnović:** Investigation, Writing – review & editing. **Ivan Lukić:** Investigation, Writing

– review & editing. **Laszlo Nagy:** Investigation, Writing – review & editing. **Sanja Novak Agbaba:** Investigation, Writing – review & editing. **Saša Orlović:** Investigation, Writing – review & editing. **Leopold Poljakoviić-Pajnik:** Investigation, Writing – review & editing. **Srdjan Stojnić:** Investigation, Writing – review & editing. **Marjana Westergren:** Funding acquisition, Project administration, Writing – review & editing, Supervision. **Milica Zlatković:** Investigation, Writing – review & editing. **Martin Steinkellner:** Data curation, Writing – review & editing. **Erik Szamosvari:** Investigation, Writing – review & editing. **Katharina Lapin:** Conceptualization, Methodology, Writing – original draft, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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