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Tree diversity reduces the risk of bark beetle infestation for preferred conifer species, but increases the risk for less preferred hosts

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Abstract

1. In recent decades, European temperate forests have repeatedly suffered from severe droughts. Drought-weakened forests have often become more susceptible to pest outbreaks such as bark beetle infestations. Tree species diversity is expected to increase resistance to drought and pests, but evidence for a positive tree diversity effect on insect pest reduction is largely circumstantial.

2. Here we tested the effects of tree diversity and biogeographic origin of tree species on bark beetle infestation in a large, young tree diversity experiment, with six broadleaved and six conifer species from Europe and North America. Lower infestation risk was expected for the exotic tree species in each congeneric pair (spruce, larch and pine) and for mixtures with higher species richness and higher broadleaf proportion. Following a severe drought in summer 2018, the conifer trees were attacked by the six-toothed spruce bark beetle *Pityogenes chalcographus*. Bark beetle boreholes were recorded in winter 2018/2019 on all conifer species.

3. Norway spruce *Picea abies* and European larch *Larix decidua* were the most infested species and thus considered main hosts of the bark beetle. For these two species, probability of infestation decreased with increasing tree diversity (although this was only significant for *Larix*). In contrast, *Pinus*, which were less infested overall, were more likely to be infested in plots with high tree diversity. Exotic trees tended to be less infested, with clearest support for enemy release found at the level of infestation intensity when considering pure conifer stands. Overall, the effects of tree diversity and tree species origin were not as strong as the effect of position within the experimental site, where higher rates of infestation were observed at the edge than in the centre.

4. *Synthesis*. Increasing tree diversity may reduce the risk of bark beetle infestation for genera prone to high infestation rates (*Picea* and *Larix*), but risk for less preferred genera (*Pinus*, and to some extent the exotic tree species) may increase with tree diversity due to spillover from preferred hosts. In mixed forests, the risk of

infestation, even by relatively specialized insect pests, may be redistributed among tree species rather than reduced for all.

1 | INTRODUCTION

The diversification of forest composition is a key strategy to adapt to the challenges of climate change in temperate forests (e.g. increased susceptibility to herbivores; Bauhus et al., 2017; DeLucia et al., 2012; Millar et al., 2007). As in many diversity experiments, the right combination of tree species is on a par with the best performing monocultures or even exceeds their productivity (Forrester & Bauhus, 2016) and increases diversity across species groups (Penone et al., 2019). The specific process of herbivory has been studied intensively in grasslands (e.g. Scherber et al., 2006), but much less in forests (Abdala-Roberts et al., 2015; Jactel & Brockerhoff, 2007). The main direct mechanism through which tree diversity can affect herbivory is by attracting herbivores onto neighbouring, non-preferred species ('associational susceptibility'; Barbosa et al., 2009) or indeed by making preferred hosts less apparent, reducing infestation ('associational resistance'; Jactel & Brockerhoff, 2007). Herbivores may benefit from feeding on several, nutritionally complementary species (Bernays & Minkenberg, 1997; Unsicker et al., 2008), although more specialized herbivores rather suffer from greater plant diversity (Jactel & Brockerhoff, 2007).

Ongoing climate change is leading to global increases in the frequency and severity of drought (Buras et al., 2019; Haynes et al., 2014; IPCC, 2014). Forest ecosystems suffering from drought are more prone to herbivore attacks (Allen et al., 2010; Walther et al., 2002), especially by boring insects (Koricheva et al., 1998). Moreover, changes in forest structure and composition have increased forests' vulnerability to disturbances such as wind-throws and subsequent pest outbreaks (de Groot et al., 2019; Seidl et al., 2011). Bark beetles (Coleoptera, Curculionidae, Scolytinae) are a group of often highly specialized herbivores feeding on the phloem tissue of trees. Some bark beetle species can develop severe pest outbreaks (Lieutier et al., 2004). In Europe, the spruce bark beetles *Pityogenes chalcographus* (L.) and *Ips typographus* (L.) colonize drought-stressed or storm-damaged trees when their populations are low, and mass attack surrounding healthy trees once their population size is high (Biedermann et al., 2019; Göthlin et al., 2000; Wermelinger, 2004), which is then considered a bark beetle outbreak (Weed et al., 2015). The smaller *P. chalcographus* tends to attack trees with thinner bark, typically infesting young stands of *P. abies* or parts of the crown and branches of older trees in co-occurrence with the larger *I. typographus*, which colonizes the main stem (Schwenke, 1974; Schwerdtfeger, 1957). Owing to the large economic impact of bark beetle outbreaks, management options are being sought that reduce the susceptibility of forests to bark beetle infestations and their

consequences. Cultivating mixed-species forests might serve this purpose (Bauhus et al., 2017; Jactel et al., 2017). In addition, the use of non-native tree species, to which native bark beetle species have not yet adapted, might also reduce a forest's susceptibility to bark beetles (Bertheau, Salle, Rossi, et al., 2009).

It is hypothesized that bark beetle-infestation risk is reduced in mixed forests compared to monocultures (Klapwijk et al., 2016; Lieutier et al., 2004); however, the effect of tree species richness on bark beetle infestation has not been explicitly studied. The few existing studies focus on non-experimental settings, examining interactions between species richness and bark beetle infestation. For example, Baier et al. (2002) found that conifers in mixed stands suffered more from bark beetle infestation than monocultures, as a possible explanation they state that the taller trees in mixed stands traded growth for defence. In contrast, Ganho and Marinoni (2006) found greater bark beetle abundance on pine monocultures. Both studies did not further quantify tree diversity.

It is often expected that native tree species provide better food and reproduction resources to native insects than exotic tree species do. The specialized spruce bark beetle *P. chalcographus* might not have adapted to the introduced conifer species yet. The plant chemistry of the novel host may be unfamiliar and therefore less favoured by native herbivores (Cipollini & Peterson, 2018). Previous studies comparing native and introduced plant species found reduced herbivore loads on introduced plants (Meijer et al., 2015; Schierenbeck et al., 1994; Strong et al., 1984), which also follows from the enemy release hypothesis explaining the success of invasive species via decreased herbivore regulation (Keane & Crawley, 2002).

A number of traits are important in determining bark beetle infestation, including tree size and bark thickness (Dolph, 1984; Kozak & Yang, 1981; Stängle et al., 2016). Tall trees with thick bark offer more suitable breeding material (phloem) for bark beetles (Amman, 1972). Yet, tall trees might also be more vigorous, which results in greater tree resistance, thus impeding the occurrence of infestation (Lieutier et al., 2004). Therefore, the effect of tree size on bark beetle infestation might be nonlinear. The apparency as a driver of associational resistance and determinant for bark beetle colonization might play a role in the tree diversity context. For another group of insect pests, leaf miners, it has been shown that infestation decreased significantly with decreasing tree apparency defined as the difference in total height between focal tree and their nearest neighbouring trees (Castagneyrol et al., 2013). It is unknown whether this mechanism also applies to bark beetle infestation. Bark beetles seem to be driven by olfactory but also visual cues and thus prefer tall and more apparent trees (Campbell & Borden, 2006).

In the present study, we examined a natural outbreak of *P. chalcographus* at the IDENT tree diversity experiment in Freiburg Germany (Tobner et al., 2014; Wein et al., 2016) colonizing 6-year-old European and North American tree species. This unforeseen event made it possible to study the effects of tree diversity and tree origin on bark beetle infestation with the rigour of a controlled tree diversity experiment.

The aim of our study was to address the question how bark beetle infestation is affected by tree diversity and tree origin. Specifically, we tested the two hypotheses that (a) with increasing tree diversity, that is, tree species richness and proportion of broadleaf (i.e. non-host trees), infestation risk and density is reduced, and (b) exotic origin of trees reduces infestation risk and density. To better understand the mechanisms behind the effects of tree diversity and origin, we then explored tree size, apparency and occurrence of main host tree species in the plot as potential drivers of the observed effects. We expected taller and more apparent trees to have higher infestation risk, and that infestation risk is increased for all trees if a main host species is present in a plot.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted at the IDENT-Freiburg field site (International Diversity Experiment Network with Trees; Tobner et al., 2014; Wein et al., 2016), which is part of TreeDivNet, a global network of tree-biodiversity experiments (Verheyen et al., 2016). It is located in south-western Germany (48°01′10″N/7°49′37″E) at an elevation of about 240 m a.s.l. The climate is oceanic (Cfb following Köppen climate classification), with a mean annual temperature of 11.8°C and a mean annual precipitation of 832 mm (period from 1990 to 2018). June to November 2018 was drier than any other drought period since drought recording in 1951 in Germany (Freiburg 2018:32% less precipitation and 2.3°C higher temperature compared to international reference period 1961–1990; German Weather Service, 2018; UFZ drought monitoring, 2018). The sandy-loamy soil of the field site is a partly anthropogenically disturbed and rather shallow (40 cm) Cambisol with high gravel content. The experiment is surrounded by residential areas in about 100-m distance to the west and south of the site and a continuous deciduous forest in 100 m north-west of the site, dominated by pedunculate oak *Quercus robur* and admixed Douglas fir *Pseudotsuga menziesii* as the only conifer species.

2.2 | Experimental design

In November 2013, approximately 20,000 tree seedlings were planted in plots with seven rows and columns in a grid pattern at a distance of 45 cm (49 trees per plot; plot size 13 m^2). Around each plot, a buffer zone of 90 cm was left, that is, the outermost rows of two adjacent plots were 1.8 m apart (Figure S1). For detailed planting information, see Wein et al. (2016).

The tree species pool consists of 12 species selected according to leaf habit and continent of origin. Six species originate from North America and six from Europe, with three gymnosperm and three angiosperm species from each continent (see Tobner et al., 2014; Wein et al., 2016). Species belong to six genera, which results in congeneric pairs of a European (mentioned first) and a North American representative of similar history of species colonization (Brändle et al., 2008): *Acer platanoides* L., *A. saccharum* Marshall, *Betula pendula* Roth, *B. papyrifera* Marshall, *Quercus robur* L., *Q. rubra* L., *Larix decidua* Mill., *L. laricina* (Du Roi) K. Koch, *Picea abies* (L.) H. Karst., *P. punges* Engelm., *Pinus sylvestris* L. and *P. strobus* L. The experimental design comprises four replicated blocks with 102 plots, compromising monocultures and, two-, four- and six-species mixtures (see Wein et al., 2016 for detailed information on species compositions). Additionally, in the full design, mixtures comprising European species (with the exception of six-species mixtures) were replicated for a tree species richness × fertilization experiment with N, P and N + P addition. For this study, we included all plots containing at least one conifer species, resulting in 15 monoculture plots and 28, 24 and 5 with two, four and six tree species respectively. One replicate of six-species mixture includes all six conifer species, the other four six-species-mixture replicates consist of 50% conifer species. We included plots across all fertilizer treatments to best cover the spatial extent of the infestation pattern, even though fertilizer treatment was of no further relevance for the research questions addressed in this paper.

2.3 | Beetle detection and identification

The first boreholes were observed non-systematically in July 2018. The most probable infestation history is that trees were weakened due to the summer drought in 2018 and the bark beetle *Pityogenes chalcographus* L. outbreak started in 2018 with one or two generations. Trees died due to drought alone and also due to bark beetle infestation. Total herbivore abundance of other herbivorous insects did not change compared to previous years. A preliminary tree mortality and bark beetle inventory in November 2018 showed that broadleaved trees were not infested by *P. chalcographus*. Therefore, only the six conifer species were checked for bark beetle boreholes. A systematic inventory to assess bark beetle presence/absence was conducted in January 2019. Six trees per conifer species and plot were randomly selected. Samples thus ranged from six trees in monocultures to 36 trees in the mixture with all six gymnosperm species (N = 2,870 trees). Each tree was thoroughly searched for boreholes. Borehole search within 30-cm-high bands at 0.6 m, 1.2 m and 1.8 m stem height, to best capture possible variation of borehole density within a tree individual, took approximately 2 min per tree to decide whether the tree was infested or not. Trees with one or more boreholes were classified as infested. In case of infestation (at least one

borehole found on the stem within the three bands), the number of boreholes was counted. We consistently scanned the south-eastern side of a tree, which is where infestation was expected to occur first according to the beetles' anemotaxis resulting in a flight against the wind. Trees lower than 1.2 m or 1.8 m were checked only at one or two heights respectively. Additionally, tree status (healthy/weakened/dead) was recorded.

To identify bark beetles, adults were extracted from bore-holes on three trees per conifer species on three plots ranging from the lowest to highest diversity (10–12 bark beetle individuals per conifer species). Species identification was done in the lab-oratory using a stereomicroscope (S6E, Leica Microsystems) and identification key (Grüne, 1979). All individuals were identified as *P. chalcographus*, a small species, which can mainly be found on Norway Spruce *Picea abies*, but also rarely on other conifer spe-cies including *Larix decidua*, *Abies alba* Mill., *Pseudotsuga menziesii* (Mirbel) Franco and *Pinus* spp. (Bertheau, Salle, Roux-Morabito, et al., 2009; Schwenke, 1974). *P. chalcographus*' life cycle allows for up to three generations per year. The larval development takes approximately 5–10 weeks depending on climatic conditions (Führer & Mühlenbrock, 1983; Schwerdtfeger, 1929). For the very similar spruce bark beetle *Ips typographus*, it is known that its main dispersion range during outbreaks lies around over 500 m (Kautz et al., 2011).

2.4 | Data analyses

Analyses were conducted using a two-stage approach as suggested for the analysis of tree diversity experiments (Schmid et al., 2017). In stage-1 analysis, models contained only the predictor variables that were set by the experimental design: tree diversity, tree ori-gin, fertilization and distance to stand edge. Thus stage-1 analysis focuses on testing the original hypotheses according to the experi-mental design. In stage-2 analysis, other predictors were added to the models of stage 1, to explore their potential as drivers of bark beetle infestation and to understand if they are likely mediators (mechanisms) of the diversity and origin effects observed in stage 1. The predictors considered only in stage 2 were tree apparency, tree size, as well as proportion and presence of main host species in the plot.

Stage-1 analyses were conducted for infestation probability (proportion of infested trees) at plot level. A GLM was used with the number of trees with infestation success and number of trees with infestation failure for each plot as response variable. To ac-count for overdispersion, data were analysed using quasi-binomial models (Consul, 1990). Each plot-level analysis was performed both for the community level as well as for each genus separately, to be able to detect vastly different patterns between all three genera (for each genus the analysis was conducted on a subset of plot-level analysis). Residual spatial autocorrelation was negligible in data ag-gregated at plot level for plot- and genus analysis (Figure S2). For tree diversity, two different components were assessed, namely

tree species richness (SR) and percentage of broadleaved trees (%broadleaf) in the plot (as conifers are the potential host species for the bark beetle, this second diversity component reflects the mixing with non-host trees). Because the two components of tree diversity were negatively correlated, they were tested in separate models to avoid collinearity (Table S1) and are presented in parallel. Tree origin was included as the proportion of exotic species among the focal trees. The interaction between the two predictors of inter-est (among the design variables), tree diversity and tree origin was also included in the models. Distance to stand edge was calculated as shortest distance of each plot centre to the nearest study site edge. Fertilization was included as a four-level factor (none, N, P and N + P). In the *Pinus* model, the interaction between tree diversity and tree origin could not be included due to only very few infested trees (as only three trees of exotic *P. strobus* were infested, param-eter uncertainty was excessive when this interaction was included). To additionally check for the effects of treatments on the intensity of infestation, the mean borehole density of infested trees was cal-culated per plot and tested against the same predictors as for stage 1 models of infestation probability. Here, a linear model was used, with $\log(y + 1)$-transformed mean borehole density as the response. The relationship between infestation risk and intensity was exam-ined using a simple linear model with plot-level mean of borehole density as response and proportion of infested trees in the plot as a predictor.

In stage-2 analysis, predictors, tree size, tree apparency and presence of main hosts in the plot were assessed in separate mod-els, all built by adding the predictor to each of the models consid-ered in stage 1 for infestation probability. Tree size was measured by stem diameter at one-third height and then converted to 10-cm height above the soil for all monitored trees (diameter proved to be a good proxy of height in the IDENT-FR inventory). To better understand the effects of tree size, for each tree genus it was ex-plored how tree diameter is related to tree diversity and how bark beetle infestation at the tree level is related to tree size (Figures S6 and S7). Tree apparency was calculated only for the 5 × 5 core trees of a plot (as for the outer row of trees in a plot, no data for tree height were available). Apparency was calculated as the mean height difference between the focal tree and its eight surrounding trees, as suggested by Castagneyrol et al. (2013). We adapted the formula slightly by dividing by weighted distance between neigh-bour tree and focal tree instead of 8, as we do not have height data for all neighbour trees. Apparency was then averaged over all 5 × 5 core trees of the plot for inclusion in plot-level analyses. On the plot level, mean size and mean apparency were highly cor-related; cases with correlation <0.7 (*Picea* and *Larix* models), also a model with both predictors added was evaluated. On community level and for the non-preferred host genus *Pinus*, the effect of the availability of main hosts was tested. More specifically, four al-ternative predictors were tested: proportion of *Picea abies* (main host according to the literature) in the plot, presence of *Picea abies* in the plot, proportion of *Picea abies* and *Larix decidua* (the two species with similar and highest infestation rate in our study; main

hosts hereafter) and presence of the two main hosts. The main reason for adding these predictors was to investigate if tree diversity effects on infestation of less preferred host trees were likely to be driven by the presence of proportion of main hosts ('spillover'). To compare models in stage-2 analysis, QAIC was used (AIC adjusted for quasi-models, calculated with MuMIn; Bartoń, 2020).

3 | RESULTS

Bark beetle boreholes were found on 11.5% of the 2,870 monitored conifer trees (Figures S3 and S4). The proportion of infested trees differed among the tree genera, with 15.5% for *Picea* (infested *Picea*/ total sampled *Picea*: 154/993), 14.3% for *Larix* (125/877) and 4.7% for *Pinus* (47/992). Highest infestation rates were found for native spruce (*P. abies*, 16.8%, 138/826) and surprisingly also for native larch (*L. decidua*, 17.4%, 120/698). Native *P. sylvestris* showed a comparatively low infestation rate (5.5%; 44/803). Exotic tree species were not attacked by bark beetles in monocultures and had generally a lower infestation rate than their native congeners (*P. pungens*: 9.9%, *L. laricina*: 2.8% and *P. strobus*: 1.3%). Of all infested trees, 89% were considered dead at the time of the bark beetle survey, 10% were categorized as weakened, showing signs of stress such as dead branches or needle discolouration and loss, and only 1% were categorized as healthy trees with typically only a few boreholes.

3.1 | Bark beetle infestation probability at plot level (stage 1, community level)

At the community level, neither component of tree diversity had a significant effect on bark beetle infestation probability (Figure 1a,b; Table 1). The proportion of infested trees decreased significantly with an increasing proportion of exotic conifers among them (SR model: $p = 0.027$, but not in %broadleaf model: $p = 0.098$). The interaction between tree diversity and tree origin was not significant. Plots closer to site edges had a higher proportion of infested trees ($p < 0.001$; Table 1), while fertilization had no significant effect.

3.2 | Bark beetle infestation probability at the genus level (stage 1)

At the genus level, the effect of tree diversity was inconsistent among genera (Figure 1c–h; Table 1): the proportion of infested trees per plot decreased with increasing tree diversity for the main host genera *Picea* and *Larix*, but increased with tree diversity for overall less infested *Pinus*. For *Picea*, this decline was not significant (SR: $p = 0.090$, %broadleaf: $p = 0.078$), but for *Larix*, the proportion of infested trees decreased with increasing tree species richness ($p = 0.021$) and percentage broadleaf ($p = 0.015$). There was a tendency for positive SR effects on infestation probability if trees had exotic origin, reflected by an interaction between SR and

origin (*Picea*: $p = 0.271$, *Larix*: $p = 0.048$). In monocultures, exotic *L. laricina* were significantly less frequently infested than native *L. decidua* ($p = 0.028$ for origin). In contrast to the other genera, *Pinus* was more infested with increasing tree species richness ($p = 0.006$), but there was no significant effect of %broadleaf. Consistent with the community level, infestation probability significantly decreased with increasing distance from stand edge in each genus ($p < 0.01$ for *Picea* and *Larix*; in *Pinus*, only a non-significant trend with $p = 0.058$) and fertilization had no significant effect. The results from the three genus-specific models are consistent with the results found in the models with European species only (Table S2).
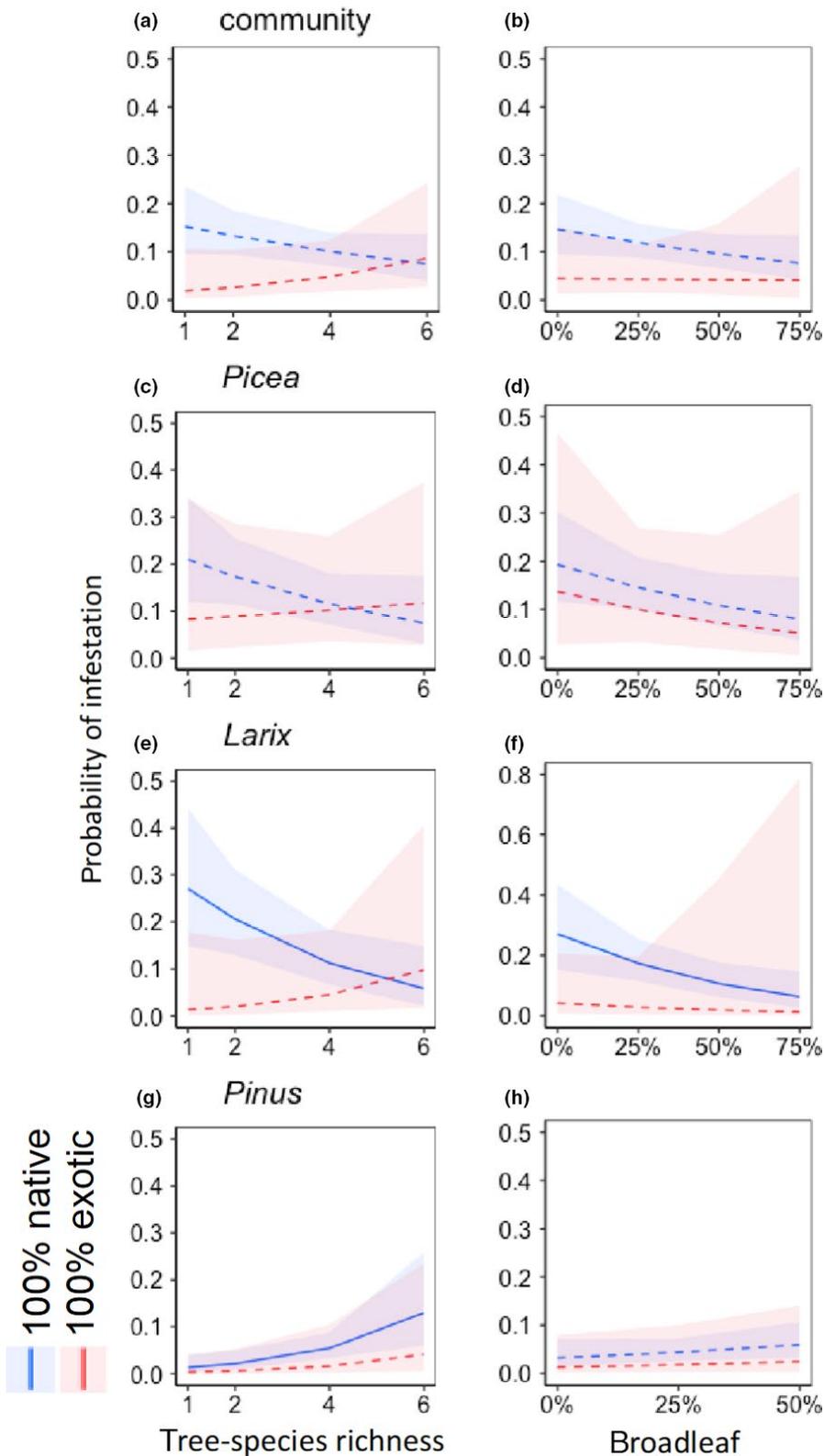
3.3 | Drivers of infestation intensity (stage 1)

There was a weak positive correlation between infestation probability and intensity at community level ($R^2 = 0.03$, $p = 0.071$) and for *Larix* ($R^2 = 0.21$, $p = 0.003$). No relationship between infestation measures was found for *Picea* ($R^2 = -0.01$, $p = 0.448$) and *Pinus* ($R^2 = -0.02$, $p = 0.468$). Infestation intensity was tested against the same predictors as infestation probability on plot level. Species richness had no effect on hole density at the community level ($p = 0.307$, Figure S5a; Table S3). There was a significant interaction between %broadleaf and proportion of exotic conifers ($p = 0.032$, Figure S5b; Table S3): hole density increased with %broadleaf for exotic conifer species, but decreased for native conifer species. Thus, only in pure conifer stands exotics had a significantly lower hole density than natives. More detailed results on infestation intensity are shown in the supplements (Figure S5; Table S3).

3.4 | Mechanistic drivers of bark beetle infestation probability (stage 2)

Adding mean tree size to the community-level model and the *Larix* model increased model performance ($\Delta QAIC = 3.8/16.1$) with positive effects of size on infestation probability (Figure 2b,d). In these models, when size was added, tree origin became non-significant (SR models; $p = 0.065$ and 0.067, respectively, Table S4). Thus, the observed lower risk for the exotic species might partly be driven by their smaller size. For *Picea*, there was a negative effect of mean size when added to the SR model, and SR became significant ($p = 0.011$, negative estimate, Figure 2a,c). For *Pinus*, there was no significant effect of mean size when added to stage 1 models. In no case did the addition of mean size reduce the significance of tree diversity predictors.

Exploring stem diameter relationships on the tree level (Figures S6 and S7) showed that *Picea* and *Pinus* trees are smaller with higher SR, whereas there is no effect in *Larix* (an overall positive effect of tree diversity on tree height is still possible due to the response of broadleaved trees). Infestation by *P. chalcographus* responded to tree size in a genus-specific and nonlinear manner: surprisingly, tree size was not a significant predictor on the tree level for *Picea* ($p = 0.981$,

FIGURE 1 Drivers of infestation probability in the community and for each conifer genus separately (stage 1): Effect plots of tree species richness (a, c, e, g) and proportion of broadleaf (b, d, f, h) at community level, genus *Picea*, *Larix* and *Pinus* on proportion of trees infested by bark beetles; note: different *y*-axis scale for (f); solid lines are significantly different from 0 ($p < 0.05$); error envelope depicts 95% confidence interval; tree origin was a continuous predictor on the plot level (proportion of exotics among focal trees), but for better readability, no lines for mixed origin are shown; raw data are shown in Figure S8

in contrast to plot level), and a hump-shaped effect of tree size was found for *Larix* and *Pinus* (both $p < 0.001$). Comparing this to data on bark thickness (well-correlated to diameter within a genus) suggests that many exotic *L. laricina* may have been below the preferred size (bark thickness) range of the bark beetle, but for the other five species, most trees were in the preferred range.

Apparency is related to tree size, and has been suggested as a mechanism of tree diversity effects (Castagneyrol et al., 2013). Mean apparency added as predictor to stage 1 models did not improve the model fit for neither *Picea*, nor *Pinus* ($p \geq 0.14$ for apparency, Table S4), but seemed a strong driver at the community level (ΔQAIC > 3, Figure 2e) and even more for *Larix* (ΔQAIC > 15, Figure 2f). In

all cases, other effects stayed qualitatively the same, showing that apparency was not a mediator of tree diversity effects in our study, but an additional driver of infestation risk. On the community level, mean size and mean apparency explained the data equally well (ΔQAIC < 0.5). For *Larix*, the model with apparency was superior to the model with size (ΔQAIC = 6.4). When including both, apparency and size, in the *Larix* models, only apparency, but not size, was significant, and tree origin, SR and their interaction remained significant.

The presence of main host species was a better predictor when not only *P. abies*, but also *L. decidua* was included (ΔQAIC = 21.5). At the community level, both the presence and proportion of main hosts were significant ($p < 0.001$, Table S5) when added to the stage 1 models (Figure 2g). In the model with presence of main hosts added, SR and the interaction between SR and origin became significant predictors, with negative estimate for SR (in natives) and positive estimate for presence of main hosts. For *Pinus*, the presence (but not proportion) of main hosts was a significant driver of infestation ($p = 0.049$, Figure 2h) when added to the model and SR was not significant anymore ($p = 0.257$). When the presence of main hosts was used as a predictor in the *Pinus* model instead of SR, it was significant ($p = 0.005$) and the model performance was improved (ΔQAIC = 3.2). This suggests that the presence of main was possibly the mediator of the positive SR effect in *Pinus*.

4 | DISCUSSION

Our experimental results show associational effects of tree species richness on bark beetle infestations. Main host species benefitted from a diverse neighbourhood, while less favoured hosts suffered from spillover infestation, but had still much lower proportion infested than main host species. Exotic conifers were attacked less frequently than native ones and never in monoculture.

A dual effect of tree species richness was observed: it was beneficial to the main host genera (*Picea* and *Larix*), indicating that these might experience associational resistance. Accordingly, Klapwijk et al. (2016) reviewed the effects of silvicultural practices and stated that in mixed forest stands *P. abies* also suffers less infestation from the bark beetle *I. typographus* and explained this with a lower host availability. As *P. chalcographus* is a herbivore with intermediate degree of specialization, associational resistance, that is, decrease in detection of focal plants in species-rich neighbourhoods, matches previous findings for other specialized herbivores (Jactel & Brockerhoff, 2007). This dilution of main hosts is a major driver for the negative effect of tree diversity on specialized forest insect pests (Jactel et al., 2021). Moreover, it fits the overall pattern that boring and sucking herbivores tend to suffer from plant diversity, while this is not necessarily the case for other guilds of herbivores (Koricheva et al., 2006). On the other hand, for the less preferred host genus *Pinus* increasing species richness had a negative effect, which can be interpreted as associational susceptibility. For *Pinus*, tree species richness effect was likely mediated via higher probability of the main host

trees in plots with high species richness, but was unaffected by the presence or absence of angiosperms. It was noticeable that in monoculture only European species were infested (mainly *P. abies*, *L. decidua* and with only one single tree *P. sylvestris*). This further indicates that less suitable hosts (which likely includes all three exotic species) experienced associational susceptibility with a greater risk of infestation in mixture. This is also described as 'spillover' effect (reviewed by Barbosa et al., 2009). Bark beetles' response to their aggregation pheromones is increased by host volatiles (Erbilgin et al., 2007). Host trees, therefore, function as a source, attracting herbivores which then also attack less preferred hosts in proximity.

Percentage of broadleaf trees as a component of tree diversity negatively affected bark beetle infestation probability for main hosts. For *Picea* and *Larix*, a higher broadleaf proportion in the community was beneficial. Furthermore, bark beetles may have difficulties detecting conifers mixed with angiosperms, both visually and olfactorily (Campbell & Borden, 2006), as they find a suitable host in mixed forests by processing positive cues, such as pheromone release, and negative cues, for example, non-host stimuli (Zhang & Schlyter, 2004). Many angiosperm volatiles are known to inhibit bark beetle attraction to their aggregation pheromones (Huber et al., 2021). A more thorough investigation of the contribution of individual broadleaf species to the observed diversity effect remains to be done. The literature on tree diversity effects on phloem-feeding bark beetles is still scarce. For seed-feeding beetles in the subfamily Scolytinae (bark beetles in the wider sense), abundance has been shown to increase with relative abundance of their hosts (Gianoli et al., 2006; Sandoval Rodríguez et al., 2017). On a larger scale, de Groot et al. (2019) have concluded that infestation of *P. abies* was lower in mixed Slovenian forests based on the amount of sanitary felling, an indicator of bark beetle outbreaks. In conclusion, despite relatively weak effects, our study is the best evidence so far that the main host trees of bark beetles profit from increased tree diversity.

Although *Pityogenes chalcographus* is often considered a specialist on *Picea abies*, all six conifer species in the experiment were infested to some degree. They can, therefore, all be considered potential hosts, but are not preferred equally. Thus, *P. chalcographus* showed only a moderate degree of specialization here. Concordantly, adult preference, as well as performance in larval development, has been found to only weakly depend on the hosts' phylogenetic relationship (Bertheau, Salle, Roux-Morabito, et al., 2009). In conclusion, the host range of this bark beetle species comprised three different genera with six species from different geographic origins and might thus be broader than traditionally thought.

Some support for the expectation of lower enemy risk on exotic trees was found at the presence/absence level. Native Norway spruce (*P. abies*) as the known main host species had a high proportion of infested trees (almost the same as the most infested species, *L. decidua*), but all other conifer species were also infested. Tree origin had a significant effect at community level (in the model with

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TABLE 1 Model summaries for tree species richness and percentage of broadleaf-models (stage 1): estimates are on the link-scale (logit); %broadleaf: percentage of broadleaf in the plot, SR: tree species richness, p.exotic: proportion of exotic conifers in the plot, edgedist: distance to stand edge; values in bold indicate significance level $p < 0.05$

Predictors	Community						Picea						Larix						Pinus					
	Proportion of infested conifers						Proportion of infested Picea						Proportion of infested Larix						Proportion of infested Pinus					
	Species richness			%Broadleaf			Species richness			%Broadleaf			Species richness			%Broadleaf			Species richness			%Broadleaf		
	est	SE	p	est	SE	p	est	SE	p	est	SE	p	est	SE	p	est	SE	p	est	SE	p	est	SE	p
(intercept)	-0.77	0.45	0.089	-1.03	0.35	**0.004**	-0.07	0.57	0.909	-0.45	0.44	0.308	0.23	0.69	0.738	-0.30	0.54	0.582	-4.52	0.93	**<0.001**	-2.91	0.56	**<0.001**
SR	-0.16	0.10	0.124				-0.24	0.140	0.090				-0.36	0.15	**0.021**				0.48	0.17	**0.006**			
p.exotic	-2.69	1.21	**0.027**	-1.30	0.78	0.098	-1.40	1.20	0.247	-0.41	0.97	0.676	-4.10	1.84	**0.028**	-2.13	1.05	**0.044**	-1.24	1.07	0.245	-0.91	0.98	0.357
Edgedist	-0.10	0.03	**<0.001**	-0.10	0.03	**<0.001**	-0.12	0.04	**0.003**	-0.12	0.04	**0.002**	-0.12	0.04	**0.004**	-0.11	0.04	**0.008**	-0.09	0.05	0.058	-0.09	0.05	0.067
Fertilizer [N]	0.08	0.40	0.842	0.17	0.40	0.677	0.08	0.49	0.866	0.23	0.49	0.635	0.005	0.62	0.994	0.19	0.61	0.756	0.60	0.73	0.408	0.18	0.71	0.807
Fertilizer [N, P]	-0.41	0.43	0.349	-0.34	0.43	0.431	-0.56	0.58	0.332	-0.50	0.58	0.391	-0.34	0.62	0.582	-0.16	0.61	0.792	0.51	0.69	0.464	0.06	0.67	0.930
Fertilizer [P]	0.24	0.37	0.519	0.31	0.37	0.410	-0.20	0.51	0.688	-0.11	0.51	0.832	0.71	0.53	0.183	0.83	0.53	0.122	1.16	0.60	0.054	0.71	0.57	0.219
SR * p.exotic	0.47	0.26	0.065				0.32	0.29	0.271				0.78	0.39	**0.048**									
%Broadleaf				-0.97	0.61	0.114				-1.35	0.76	0.078				-2.28	0.92	**0.015**				1.29	1.03	0.211
%Broadleaf * p.exotic				0.86	2.06	0.677				-0.08	2.34	0.971				0.57	4.32	0.896						
Observations	291			291			158			158			141			141			159			159		

FIGURE 2 Mechanistic drivers of infestation probability (stage 2): effect plots for (a) mean diameter for *Picea*; (b) for *Larix*; (c) tree species richness including mean diameter for *Picea*; (d) for *Larix*; (e) mean apparency for community level and (f) for *Larix*. (g) Presence of main hosts (*Picea* and *Larix*) for community level and (h) for *Pinus*; note different *y*-axis scale; solid lines are significantly different from 0; error envelope and bar depict 95% confidence interval
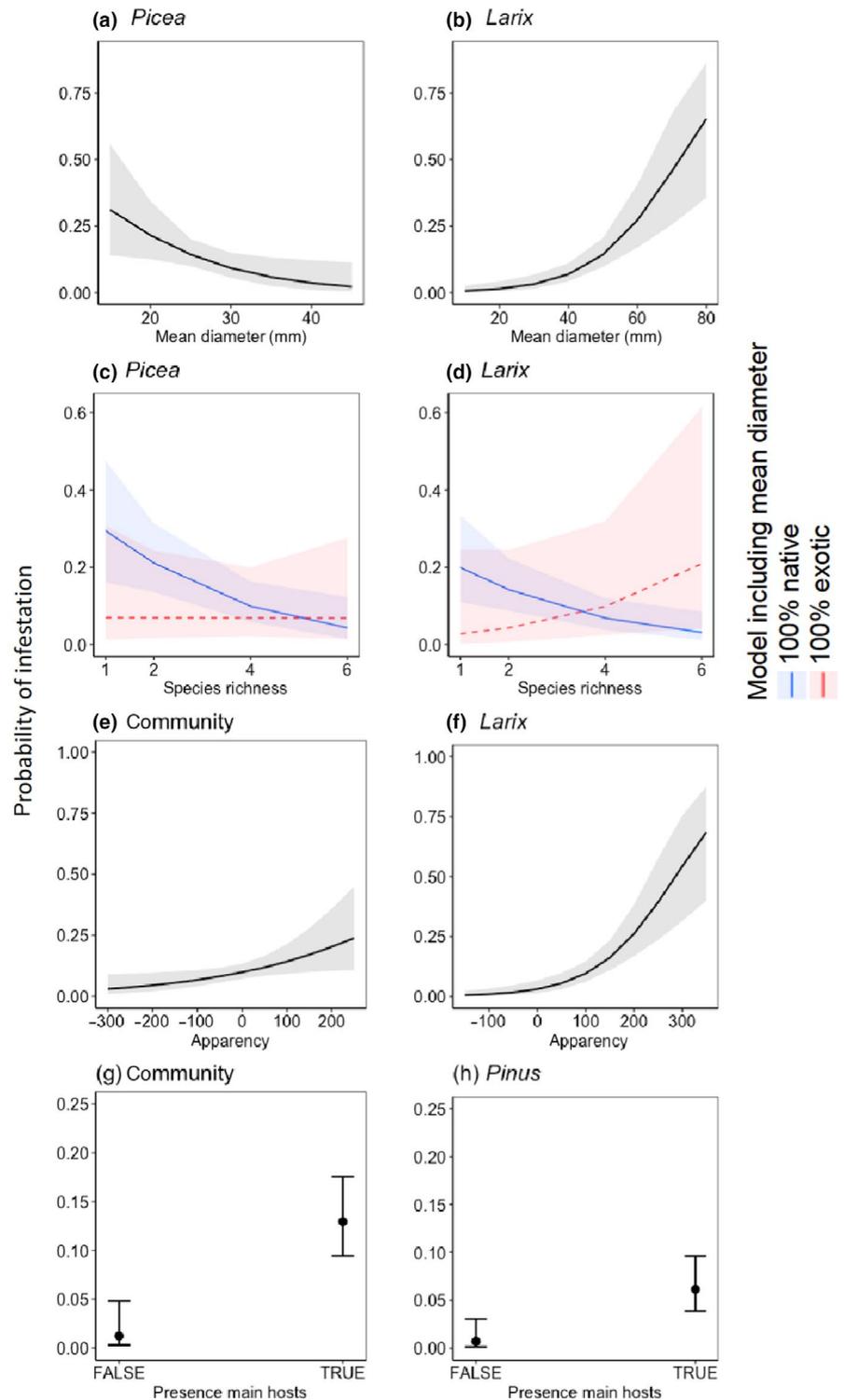
species richness), indicating that exotic conifers had a reduced infestation risk compared to native congenerics. However, the strongest origin effect was found for the genus *Larix*, where the effect may also be caused by the low growth performance of the exotic species. Given that all conifers in our site are of the same family (Pinaceae), our findings suggest that exotic plants are less likely to gain enemy release if native relatives of the plants are attacked by herbivores with flexible host ranges (Agrawal & Kotanen, 2003). The capacity of some specialized bark beetle species to expand to novel hosts

becomes even more crucial under changing climate conditions and emphasizes the need for more research in that field (Rosenberger et al., 2018).

Although lower infestation probability of exotics was equivocal, infestation intensity was higher for native trees at least when the percentage of broadleaf trees was low in the plot, providing some support for lower enemy risk on exotic plants. Lower herbivore load on exotic, or more precisely invasive plants, would be expected according to the enemy release hypothesis (Keane & Crawley, 2002).

For exotic hosts, also the secondary mass aggregation of conspecific bark beetles (Byers et al., 1988; Rudinsky, 1962) may work less efficiently because some components of the aggregation pheromone might be missing when beetles feed on novel hosts (Cale et al., 2015). Generally, for *P. chalcographus*, it has been found that adult preference and brood development are positively linked (Bertheau, Salle, Roux-Morabito, et al., 2009). The lower hole density on exotic trees may be, at least partly, explained by suboptimal brood development. It is remarkable that lower bark beetle performance on exotic trees was found repeatedly in three genera (two of them containing hosts similarly preferred in our study), so that it cannot simply be explained by exotics being outside of the phylogenetic host niche of the bark beetle.

Besides community composition, tree size could be one of the important mechanistic drivers explaining bark beetle infestation pattern. At the community level, for *Picea*, there was a negative relationship between tree size and infestation probability. The interpretation for this relationship is challenging. Taller trees might be more vigorous and thus better able to impede bark beetle infestation through resin excretion or other defences (Lieutier et al., 2004). In fact, the reduction of bark beetle infestation risk due to tree diversity became significant for *Picea* only when this negative effect of tree size was included in the model. Tree diversity and tree size were negatively correlated for conifers (but not for broadleaved species). Therefore, it might not only be associational resistance that protected *Picea* from infestation in high tree diversity environments (which was the stronger effect in our study), but also that trees stayed relatively smaller and were, therefore, less attractive for the bark beetle. At the same time, tree growth might occur at the expense of tree resistance in *P. abies*, which might further explain the lower infestation rate for trees of smaller diameter but with greater resistance (Baier et al., 2002; Herms & Mattson, 1992). Unfortunately, we could not assess tree vigour in our study. The interpretation of tree size effects at the community level is complicated by nonlinear relationships between infestation probability and size at the tree level. While tree size and infestation probability were not significantly related for *Picea*, a hump-shaped relationship was detected for individual trees of *Larix* and Pinus, indicating that there was an optimal tree size niche for *P. chalcographus*. This preference for small- to medium-sized trees by *P. chalcographus* was also found in earlier studies (Göthlin et al., 2000; Schwerdtfeger, 1929). Although this suggests that the tallest trees often escaped from or successfully defended against bark beetle attack, a positive relationship between average tree size and infestation probability was found for *Larix* and *Pinus* on the community level. This is in accordance with the expectation that bigger trees offer a thicker bark with more food resources (Amman, 1972). As many communities contained a mixture of small and large trees, it is well possible that community average size showed different effects than individual size. We believe that in communities suffering from more infestation with larger average size, this pattern was likely driven by low suitability of very small trees in combination with other tree size-related mechanisms.

Related to tree size, apparency might be another important driver of bark beetle infestation. More apparent trees might be easier to detect by bark beetles (Zhang & Schlyter, 2004). This was particularly the case for *Larix*, when a larch tree was taller than its neighbouring trees, the probability of infestation increased. This is likely the reason for the positive effect of tree size we found for *Larix* (as size and apparency were closely related for that species). Therefore, we think that more copious food resources in larger *Larix* might be less important for community-level infestation risk than apparency. Apparency was an important driver of infestation, but did not explain the diversity and origin effects we found.

Adding to this line of argumentation, edge trees are likely to be more apparent for bark beetles approaching the tree diversity experiment from outside. Consistently, our study shows, in accordance with a previous study (Göthlin et al., 2000), that trees close to the edge had a higher probability of being infested than trees in the interior of the study site. Distance to stand edge turned out to have a stronger effect on infestation probability than tree diversity and origin. Additionally, more favourable microclimatic conditions at forest edges might lead to a preference for this habitat (Kautz et al., 2013). The fact that this pattern was consistent for all genera and also on community level in our study suggests that this predictor related to habitat structure is of predominant importance to predict bark beetle infestation.

Our bark beetle mass infestation followed a drought event, as it is often the case (Negrón et al., 2009; Kelsey et al., 2014). At the IDENT-Freiburg site, drought was the primary cause of death for most trees in 2018. In total, 44% of the conifers died after the drought, of which one fourth was simultaneously infested by bark beetles. As usual, when evaluating multiple mortality factors, it is not possible to ascertain whether drought-stressed trees would have died without infestation. Although we do not know if large-scale monocultures would have a higher infestation risk, at least we could show that attack by *P. chalcographus* is a risk to multiple conifer species in mixed stands, as our experimental site becomes a high diversity stand on the hectare scale. However, the question of how the results of necessarily small-scale experiments can be extrapolated to the scales of forest stands and ecosystems is open and an area of active research.

5 | CONCLUSIONS

We conclude that there is a distinct influence of tree diversity on bark beetle infestation. Different hosts show opposing diversity effects: main host species benefited from higher tree diversity (associational resistance), whereas less preferred hosts suffered from associational susceptibility, when planted in mixtures with main hosts. All host trees benefitted from being hidden among other trees in the stand, by being small, not apparent and further away from stand edge. Three exotic tree species were also susceptible to *P. chalcographus*, although they seemed to be less optimal hosts. Our findings provide hints for tree species and species mixtures to

choose for designing drought- and pest-resistant forests and should be tested on larger operational scales to face ongoing climate change and hence more frequent summer droughts.

AUTHORS' CONTRIBUTIONS

S.B. and J.F. designed the study; J.B. designed and established the diversity experiment jointly with others; C.A.N. established and maintained the experiment; S.B. and T.F. collected the data; S.B. and J.F. performed the analysis and prepared the manuscript with contributions from T.F., P.H., C.A.N., C.F.D. and J.B.; J.F. provided guidance throughout the study. All the authors read, reviewed and approved all versions of the paper.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.bk3j9kdbr (Berthelot et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.