Diversity and conservation of saproxylic beetles in 42 European tree species: an experimental approach using early successional stages of branches

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ABSTRACT. 1. Tree species diversity is important to maintain saproxylic beetle diversity in managed forests. Yet, knowledge about the conservational importance of single tree species and implications for forest management and conservation practices are lacking.

2. We exposed freshly cut branch-bundles of 42 tree species, representing tree species native and non-native to Europe, under sun-exposed and shaded conditions for 1 year. Afterwards, communities of saproxylic beetles were reared ex situ for 2 years. We tested for the impact of tree species and sun exposure on alpha-, beta-, and gamma-diversity as well as composition of saproxylic beetle communities. Furthermore, the number of colonised tree species by each saproxylic beetle species was determined.

3. Tree species had a lower impact on saproxylic beetle communities compared to sun exposure. The diversity of saproxylic beetles varied strongly among tree species, with highest alpha- and gamma-diversity found in *Quercus petraea*. Red-listed saproxylic beetle species occurred ubiquitously among tree species. We found distinct differences in the community composition of broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood.

4. Our study enhances the understanding of the importance of previously understudied and non-native tree species for the diversity of saproxylic beetles. To improve conservation practices for saproxylic beetles and especially red-listed species, we suggest a stronger incorporation of tree species diversity and sun exposure of into forest management strategies, including the enrichment of deadwood from native and with a specific focus on locally rare or silviculturally less important tree species.

Key words. Deadwood, deadwood enrichment, decay, forest management, host specificity.

Introduction

Human impacts have modified forest ecosystems worldwide (Newbold *et al.*, 2015). Intensive logging, altered disturbance regimes, and changes in forest structure have resulted in massive declines of ecological key elements, particularly in Europe (Lindenmayer *et al.*, 2008; Lindenmayer *et al.*, 2012; Thorn *et al.*, 2020). For centuries, dead and moribund trees have been extracted, as they were considered to be a waste of resources and to serve as a hatchery of forest pathogens (Cotta, 1865; Grove, 2002). Moreover, forest management practices have decreased the diversity of native tree species, for instance, by the establishment of coniferous tree plantations (Schelhaas *et al.*, 2003) and the parallel introduction of various non-native tree species (Richardson & Rejmánek, 2011; Savill, 2015).

Deadwood plays an important role in nutrient cycles in addition to providing multiple ecosystem functions, including carbon storage (Butchart *et al.*, 2010; Lindenmayer *et al.*, 2014). In

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Europe, approximately one-quarter of all forest-dwelling species depend on deadwood (Siitonen, 2001). These saproxylic species are highly sensitive to changes in deadwood abundance and diversity (Ulyshen & Hanula, 2009; Seibold *et al.*, 2016), and many saproxylic species have therefore suffered following deadwood removal as a result of forest management (Speight, 1989; Seibold *et al.*, 2015b). Yet, 20–30% of all European saproxylic beetle species are red-listed (Seibold *et al.*, 2015b; Cálix *et al.*, 2018).

Habitat suitability for saproxylic beetles is determined by multiple extrinsic and intrinsic factors (reviewed in the study by Seibold *et al.*, 2015a; Müller *et al.*, 2020). Besides the amount of deadwood, most important are the deadwood type (e.g. stump/log/branch), the position (laying/standing) (Ulyshen & Hanula, 2009), the diameter (Buse *et al.*, 2008; Kostanjsek *et al.*, 2018), the decay stage (Parisi *et al.*, 2018), local stand characteristics (Müller *et al.*, 2015b), and particular microclimate related to sun exposure (Müller *et al.*, 2015a; Thorn *et al.*, 2016; Müller *et al.*, 2020). Another substantial factor for saproxylic beetles is the identity of their respective host tree species (Bouget *et al.*, 2014; Müller *et al.*, 2020; Vogel *et al.*, 2020). Saproxylic beetle species can be largely polyphagous, colonising a variety of different tree species, up to monophagous species, which are restricted to a single host tree species (Milberg *et al.*, 2014; Toivanen & Kotiaho, 2010), while a clear distinction between broadleaved and coniferous tree species exists (Vogel *et al.*, 2020). The host specificity of saproxylic beetles extenuates over the course of the decay process and seems to be higher in species directly feeding on deadwood compared to predatory species (Wende *et al.*, 2017). Yet, investigations of the host tree specificity of saproxylic beetles have mostly been based on occasional observations or field surveys (e.g. Palm, 1959; Hellrigl, 1978; Bense, 1995; Klausnitzer *et al.*, 2015), whereas experimental approaches (e.g. rearing or exclusion studies) under standardised conditions are scarce and regularly involve only a small subset of available tree species (e.g. Lindhe & Lindelöw, 2004; Brin *et al.*, 2011; Müller *et al.*, 2015b; Andringa *et al.*, 2019), limiting generalised statements regarding host tree specificity. Moreover, several approaches tried to examine the conservational importance of single tree species for saproxylic beetles (Jonsell *et al.*, 1998; Müller *et al.*, 2015b; Andringa *et al.*, 2019). In Europe, common oak (*Quercus robur*) is regarded as the most species-rich tree species, in addition to hosting the highest diversity of red-listed saproxylic beetles (Irmler *et al.*, 1996; Brändle & Brandl, 2001). Comprehensive recommendations about tree species and the combinations thereof that effectively support the highest diversities of saproxylic beetles are provided in the studies by Vogel *et al.* (2020), Gossner *et al.* (2016), and Andringa *et al.* (2019), in which 6, 13, and 20 tree species are compared. Those studies identified high diversities of saproxylic beetles, particularly in relation to hornbeam (*Carpinus betulus*), poplar (*Populus* sp.), and Norway spruce (*Picea abies*) as well as combinations of these tree species, including those of broadleaved and coniferous tree species.

Within the past two decades, there has been increasing recognition of the importance of deadwood for conservation (reviewed in the study by Vítková *et al.*, 2018). Conservation strategies have thus been developed by incorporating an active enrichment of deadwood during logging operations, but their focus is the amount of deadwood from regionally dominant tree species, such as European beech (*Fagus sylvatica*), whereas other aspects of deadwood quality have been largely neglected. Furthermore, single tree species, such as *P. abies* and oak (*Quercus sp.*), are commonly excluded from deadwood enrichment, whether by policy or for reasons of forest protection (Brown *et al.*, 2015; Alexander, 2016; Gößwein *et al.*, 2017). Consequently, both silviculturally unimportant and rare tree species, such as hawthorn (*Crataegus* sp.) and checker tree (*Sorbus torminalis*), have been largely ignored. Furthermore, little is known about the importance of tree species non-native to Central Europe for saproxylic beetles, such as Douglas fir (*Pseudotsuga menziesii*) and sweet chestnut (*Castanea sativa*), although the increased cultivation and introduction of these trees have been discussed with respect to climate change and other purposes (Bolte *et al.*, 2009; Richardson & Rejmánek, 2011; Schmid *et al.*, 2014).

Here, we expanded the list of tree species experimentally sampled for saproxylic beetles, by investigating 42 different broadleaved and coniferous tree species. These tree species represent >50% of all native tree species distributed in Central Europe and also include the most important non-native tree species of silvicultural interest, covering essential parts of taxonomic and phylogenetic diversity as well as proportions of forest cover (San-Miguel-Ayanz *et al.*, 2016; Rivers *et al.*, 2019). In our study, freshly cut branch-bundles were exposed for one season under two different conditions of sun exposure and their communities of saproxylic beetles afterwards reared ex situ. We quantified the impact of tree species and sun exposure on alpha-, beta-, and gamma-diversity as well as community composition of saproxylic beetles. Furthermore, the number of colonised host tree species for each species of saproxylic beetles was determined and compared between different larval feeding types.

Materials and methods

Study area and experimental design

Our study was conducted near the city of Bad Windsheim in north-western Bavaria, Germany (49°32' N 10°23' E) (Fig. 1). In this area, the mean annual temperatures obtain around 9.2 °C and the mean annual precipitation 595 mm (Agrarmeteorologie, 2020). Forest stands in the study area are mainly composed by sessile oak (*Quercus petraea*) with lower percentages of *F. sylvatica*, Scots pine (*Pinus sylvestris*), and *P. abies* as well as a high variety of around 60 other tree species. Beside high-stem forests, the study area is partly managed as coppice with standards, thus promoting sun-exposed forest structures and *Q. petraea*. Overall, there are an estimated 500 species of saproxylic beetles in the study area (Bussler *et al.*, 2018).

The study was initiated in March 2017 by assembling 252 freshly cut branch-bundles from 42 different tree species on three plots. Each plot was divided into a sun-exposed subplot on a freshly logged area and a shaded subplot within the forest
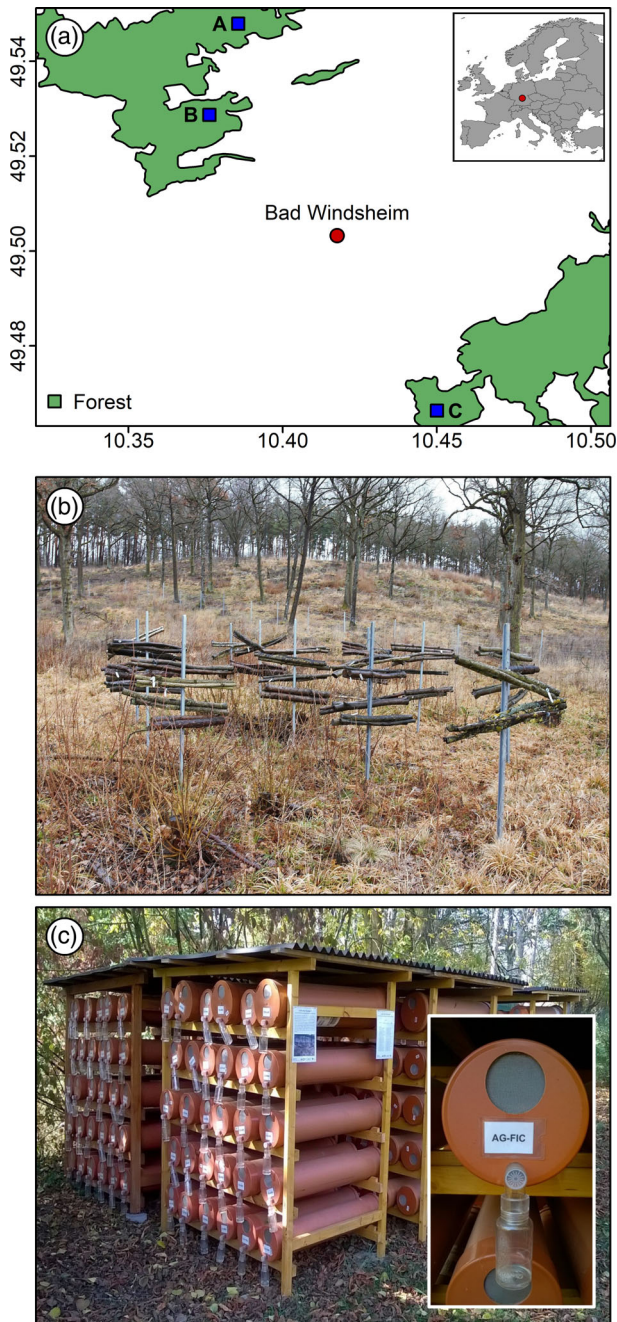
stand to capture the range of microclimate conditions (Fig. 1a). The distance between subplots was less than 100 m. The tree species were determined by Sebastian Vogel and Sven Finnberg according to Jäger *et al.* (2017). Tree species included 33 that are native to Central Europe: silver fir (*Abies alba*), field maple (*Acer campestre*), Norway maple (*Acer platanoides*), sycamore maple (*Acer pseudoplatanus*), black alder (*Alnus glutinosa*), grey alder (*Alnus incana*), birch (*Betula pendula*), *C. betulus*, common hazel (*Corylus avellana*), common hawthorn (*Crataegus monogyna*), *F. sylvatica*, alder buckthorn (*Frangula alnus*), European ash (*Fraxinus excelsior*), common juniper (*Juniperus communis*), European larch (*Larix decidua*), apple (*Malus domestica*), *P. abies*, *P. sylvestris*, aspen (*Populus tremula*), wild cherry (*Prunus avium*), hackberry (*Prunus padus*), blackthorn (*Prunus spinosa*), European wild pear (*Pyrus pyraster*), *Q. petraea*, goat willow (*Salix caprea*), black elder (*Sambucus nigra*), rowan (*Sorbus aucuparia*), service tree (*Sorbus domestica*), *S. torminalis*, yew (*Taxus baccata*), small-leaved lime (*Tilia cordata*), fluttering elm (*Ulmus laevis*), and field elm (*Ulmus minor*), and 9 tree species non-native to Central Europe: grand fir (*Abies grandis*), Weymouth pine (*Pinus strobus*), *P. menziesii*, northern red oak (*Quercus rubra*), and black locust (*Robinia pseudoacacia*) from North America. Also included were four species native to Southern Europe: *C. sativa*, common walnut (*Juglans regia*), black pine (*Pinus nigra*), and Turkey oak (*Quercus cerris*). On each subplot, a branch-bundle of every tree species was established, consisting of three branches each with a length of 100.6 (± 3.5) cm and a diameter of 4.9 (± 0.9) cm. Branch-bundles of four different tree species were randomly combined and then suspended from a metal pile, where they were left from March 2017 to February 2018 (Fig. 1b).

Between March 2018 and September 2019, beetles from the branch-bundles were reared in plastic tubes with trapping bottles attached (Fig. 1c). They were trapped with ethanol and identified by Heinz Bussler to the species level according to Freude *et al.* (1963-1984). The classification of beetles as saproxylic was based on the approach of Schmidl and Bussler (2004). Red List Categories were retrieved from the Bavarian Red List (StMUGV, 2005) and information on the larval feeding type of individual species (detrivorous, mycetophagous, xylophagous, zoophagous) from the study by Seibold *et al.* (2015b).

Data analysis

All analyses were performed using R 3.6.2 (R Development Core Team, 2019). To quantify the relative impact of tree species and sun exposure on beta-diversity of saproxylic beetles, we applied a regularised discriminant analysis (RDA; Friedman, 1989). For the RDA, we generated distance matrices by the function 'dist' (package 'proxy'; Meyer & Buchta, 2019), in detail a cophenetic distance based on the phylogenetic tree of European flora provided by Durka and Michalski (2012) as a proxy of distances between different tree species as well as a spatial distance between subplots based on the distance-based Morans's

Fig. 1. The study area and experimental design. The study was conducted (a) near the city of Bad Windsheim in north-western Bavaria (Germany), at three different sites (A–C). Each site consisted of two subplots: sun-exposed on a freshly logged area and shaded by the forest stand. The forest classification was based on Corine land cover data (version 20b2). (b) On each subplot, a branch-bundle of every tree species was established. Branch-bundles from four tree species were randomly combined and suspended from metal piles from March 2017 to February 2018. (c) Saproxylic beetles from branch-bundles were reared in plastic tubes with attached trapping bottles from March 2018 until September 2019. [Color figure can be viewed at wileyonlinelibrary.com]

eigenvector map (Dray *et al.*, 2006). Distances in species composition of saproxylic beetles were calculated based on Hellinger transformed species data. Within the RDA, sun exposure (sun-exposed/shaded) was used as a factor. The RDA was followed by a subsequent analysis of variance by the function 'ANOVA' (package 'vegan'; Oksanen *et al.*, 2019).

The alpha-diversity of tree species was ranked by applying a generalised linear mixed-effects model with a Poisson error distribution (package 'lme4'; Bates *et al.*, 2015). In addition to the tree species, the model included the branch volume as a predictor to control for variations in branch diameter and resource amount (Müller *et al.*, 2015a) as well as the plot identity as a random effect to account for replicated measurements at the plot level (for model equations see Supporting Information S2). Differences in species diversity between broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood were quantified via a separate generalised linear mixed-effects model using the branch volume as an additional predictor and the plot identity and tree species as random effects (Supporting Information S2).

The observed gamma-diversity of the tree species was ranked based on the total number of observed and red-listed saproxylic beetle species per tree species. The estimated gamma-diversity between tree species, broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood was determined by estimating the species richness (sensu Gotelli & Colwell, 2001) using sample-based rarefaction-extrapolation curves (package 'iNEXT'; Chao *et al.*, 2014; Hsieh *et al.*, 2016).

Differences in communities were visualised by nonmetric multidimensional scaling (NMDS; package 'vegan'; Oksanen *et al.*, 2019). The distance to the NMDS centroid of broadleaved and coniferous tree species served as a measure of uniqueness for each host tree species in terms of saproxylic beetle communities (Villéger *et al.*, 2010). To compare communities between broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood, we applied a permutational analysis of variance using distance matrices with branch volume as an additional predictor by the function 'adonis2' (package 'vegan'; Oksanen *et al.*, 2019). The plot identity was used as strata to constrain permutations.

The number of colonised tree species between different larval feeding types was compared by using a generalised linear model (package 'stats'; R Development Core Team, 2019) and a linear inference procedure with simultaneous adjustment of *p*-values by means of the function 'glht' (package 'mulltcomp'; Hothorn *et al.*, 2008).

Results

Overall, 112 species of saproxylic beetles with a total of 30542 individuals were reared, including 20 red-listed species (for a detailed list of the recorded species see Supporting Information S1). This species number corresponds to ~20% of all saproxylic beetles recorded in the study area. The recorded species belonged to 23 different families, with highest abundances and species numbers attributed to

Table 1. Effects of tree species, sun exposure, and spatial distribution on the beta-diversity of saproxylic beetle communities. Results based on a regularised discriminant analysis (RDA).

Predictor	Df	Variance	*F*-value	*P*-value
Tree species	41	$2.88\,e^{-01}$	2.77	0.001
Sun exposure	1	$9.38\,e^{-03}$	3.70	0.001
Spatial distribution	1	$4.38\,e^{-03}$	1.73	0.012
Residual	208	$5.27\,e^{-01}$		

Curculionidae (26235 individuals/28 species, including Scolytinae), Cerambycidae (2068/28), and Buprestidae (1285/9).

Tree species had a lower impact on saproxylic beetle communities compared to sun exposure (Table 1). The highest alpha-diversity occurred among saproxylic beetles reared from *Q. petraea*, *Q. cerris* as well as *Q. rubra*, and the lowest alpha-diversity among communities of saproxylic beetles was reared from *J. communis*, *U. laevis*, and *T. baccata* (Fig. 2a; Supporting Information S3). The alpha-diversities of tree species correlated positively with the observed gamma-diversity (adjusted $R^2 = 0.85$, $P < 0.001$) (Supporting Information S6a). Between broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood the alpha-diversity of saproxylic beetles was similar (Supporting Information S4).

Among broadleaved tree species, the highest observed gamma-diversity of saproxylic beetles was found in *Q. cerris*/*Q. petraea* (26 species), *M. domestica* (23), and *R. pseudoacacia* (18) as well as among coniferous tree species in *P. nigra* (22), *P. abies* (21), and *P. menziesii*/*P. strobus* (19) (Fig. 2b; Supporting Information S1). The lowest observed gamma-diversity was found in association with *F. excelsior*/*P.tremula*/*P. spinosa* (7), *F. alnus* (6), and *U. laevis* (3) as well as *A. alba* (8), *J. communis* (5), and *T. baccata* (3). Only *Q. rubra* (16) as a non-native tree species had a lower observed gamma-diversity than included native species from the same genus (*Q. petraea*). Species numbers were higher among saproxylic beetle communities reared from non-native *P. nigra*, *P. strobus*, and *A. grandis* (10) than from native *P. sylvestris* (18) and *A. alba*. Even non-native tree species such as *P. menziesii* and *R. pseudoacacia* had a higher observed gamma-diversity than several native tree species. Among red-listed species, the highest species numbers were found in *Q. cerris* (5), *M. domestica*/*T. cordata* (4), and *A. grandis*/*A. glutinosa*/*C. betulus*/*Q. petraea*/*S. aucuparia*/*S. caprea* (3) (Fig. 2b). For all tree species, the number of red-listed saproxylic beetle species increased as the total number of observed species increased (adjusted $R^2 = 0.18$, $P = 0.003$) (Supporting Information S6b). The estimated and observed gamma-diversity slightly differed (Fig. 2b,c), with the highest estimated gamma-diversity among saproxylic beetle communities reared from *Q. petraea*, *P. abies*, and *R. pseudoacacia*, and the lowest estimated gamma-diversity among those from *J. communis*, *U. laevis*, and *T. baccata*. The estimated gamma-diversity of saproxylic beetles was higher in broadleaved and native tree species compared to coniferous and non-native tree species, while no differences were found between sun-exposed and shaded deadwood (Supporting Information S5).
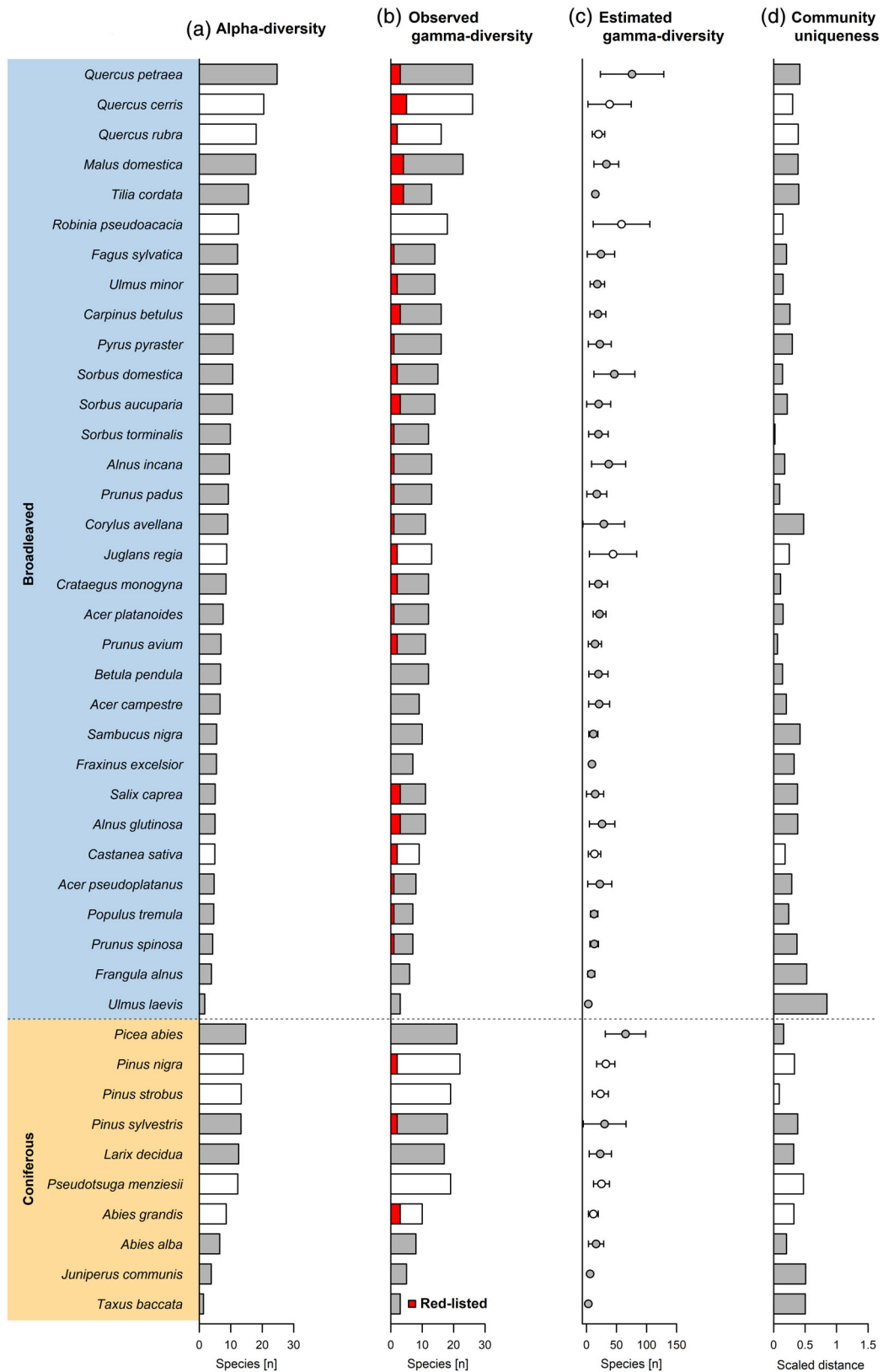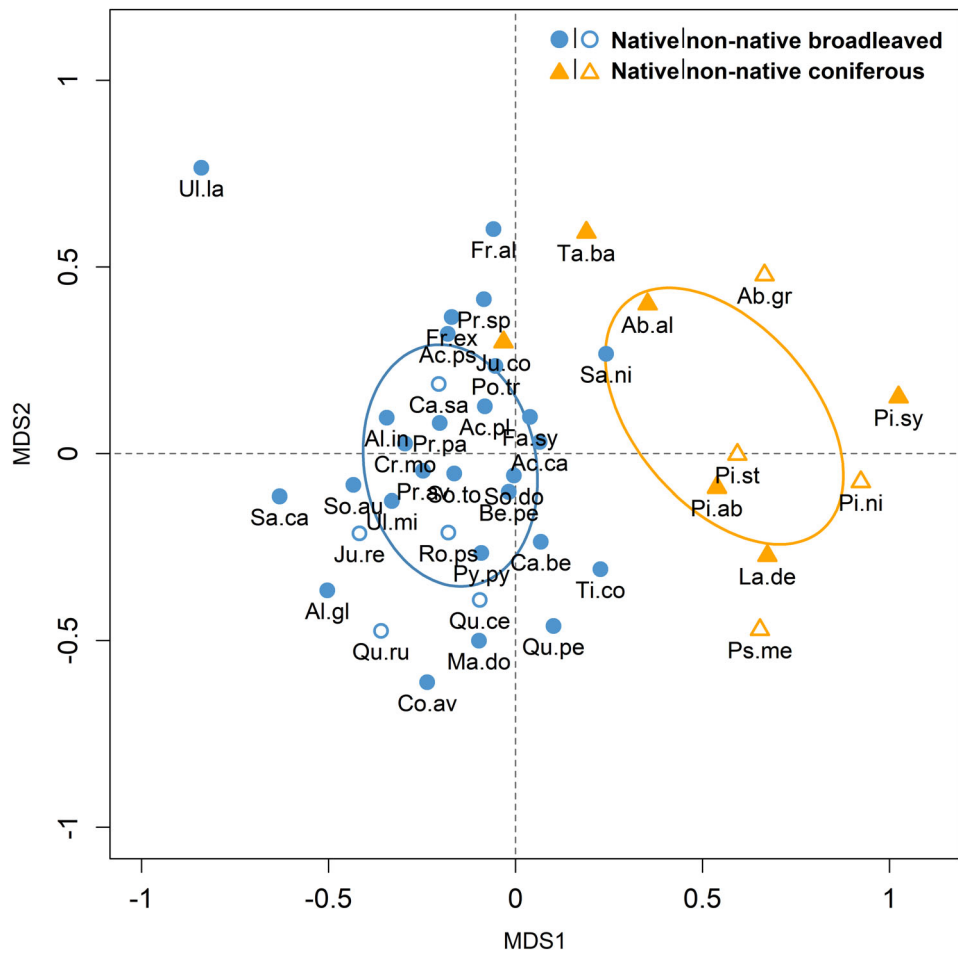
Fig. 2. Legend on next page.

Fig. 3. Nonmetric multidimensional scaling of saproxylic beetle communities found in different tree species: Ab.al = *Abies alba*, Ab.gr = *Abies grandis*, Ac.ca = *Acer campestre*, Ac.pl = *Acer platanoides*, Ac.ps = *Acer pseudoplatanus*, Al.gl = *Alnus glutinosa*, Al.in = *Alnus incana*, Be.pe = *Betula pendula*, Ca.be = *Carpinus betulus*, Ca.sa = *Castanea sativa*, Co.av = *Corylus avellana*, Cr.mo = *Crataegus monogyna*, Fa.sy = *Fagus sylvatica*, Fr.al = *Frangula alnus*, Fr.ex = *Fraxinus excelsior*, Ju.co = *Juniperus communis*, Ju.re = *Juglans regia*, La.de = *Larix decidua*, Ma.do = *Malus domestica*, Pi.ab = *Picea abies*, Pi.ni = *Pinus nigra*, Pi.st = *Pinus strobus*, Pi.sy = *Pinus sylvestris*, Po.tr = *Populus tremula*, Pr.av = *Prunus avium*, Pr.pa = *Prunus padus*, Pr.sp = *Prunus spinosa*, Ps.me = *Pseudotsuga menziesii*, Py.py = *Pyrus pyraster*, Qu.ce = *Quercus cerris*, Qu.pe = *Quercus petraea*, Qu.ru = *Quercus rubra*, Ro.ps = *Robinia pseudoacacia*, Sa.ca = *Salix caprea*, Sa.ni = *Sambucus nigra*, So.au = *Sorbus aucuparia*, So.do = *Sorbus domestica*, So.to = *Sorbus torminalis*, Ta.ba = *Taxus baccata*, Ti.co = *Tilia cordata*, Ul.la = *Ulmus laevis*, Ul.mi = *Ulmus minor*. [Color figure can be viewed at wileyonlinelibrary.com]

Communities of saproxylic beetles in broadleaved and coniferous tree species were distinctly different (Fig. 3; Supporting Information S7). The most unique community compositions for broadleaved and coniferous tree species were those occurring in association with *U. laevis*, *F. alnus*, and *J. communis* (Fig. 2d). Communities of saproxylic beetles also differed between native and non-native tree species as well as between sun-exposed and shaded deadwood (Supporting Information S7).

In our study, 36 saproxylic beetle species were exclusively found in a single tree species (Supporting Information S1). Overall, saproxylic beetle species colonised a mean of 4.91 host tree species, with the highest number colonised by *Litargus connexus* (41 tree species). Red-listed saproxylic beetle species colonised a mean of 2.95 host tree species (Supporting Information S1) but did not necessarily have a higher host tree specificity, although the number of colonised tree species increased with the

FIG 2. (a) Alpha-diversity estimated by a generalised linear mixed-effects model with species richness as response and tree species as well as branch volume as predictors, (b) observed gamma-diversity and number of red-listed species, (c) estimated gamma-diversity, and (d) uniqueness of the saproxylic beetle communities among tree species, measured as mean distance to the NMDS centroid of all broadleaved respective coniferous tree species. Native tree species are represented by grey bars, non-native tree species by white bars. [Color figure can be viewed at wileyonlinelibrary.com]

increasing abundance of single species of saproxylic beetles (adjusted R^2 = 0.34, P < 0.001) (Supporting Information S8). We detected no differences in the number of colonised host tree species between different larval feeding types (Supporting Information S9).

Discussion

Even if the tree species was of less importance compared to sun exposure, it had a significant impact on communities of saproxylic beetles. In our study, a few dominant tree species hosted the majority of saproxylic beetle diversity, but tree species with a comparatively medium or low overall diversity were of high importance for red-listed beetle species as well. Non-native tree species revealed a lower estimated gamma-diversity of saproxylic beetles compared to native tree species. Community composition largely differed between broadleaved and coniferous tree species, native and non-native tree species as well as sun-exposed and shaded deadwood. Moreover, our results provide the first insights into the host tree specificity of single saproxylic beetle species, by comparing a large number of tree species within one experimental approach.

Impact of sun exposure

Sun exposure revealed a higher relative impact on beta-diversity of saproxylic beetle communities than tree species, whereby no differences in alpha-diversity and estimated gamma-diversity were found (Supporting Information S4 and S5c). Nonetheless, community composition of saproxylic beetles varied distinctly between sun-exposed and shaded deadwood. Hence, our findings are partially in line to other studies of saproxylic beetles in branches, such as by Vogel *et al.* (2020) or Hardersen *et al*. (2020). The study of Vogel et al. (2020) revealed a higher impact of tree species on the beta-diversity of saproxylic beetle in branches but of sun exposure in logs.

Similar to the non-significant (but marginal) trend in our study, the alpha-diversity in Vogel et al. (2020) was higher in shaded compared to sun-exposed branches. The lower alpha-diversity of saproxylic beetles in sun-exposed branches was possibly caused by a reduced buffering towards extreme microclimatic conditions (i.e. heat and drought) in comparison to logs, challenging the survival and successful larval development of saproxylic beetles.

Ranking of tree species

The alpha- and observed gamma-diversity of host tree species varied distinctly between different tree species (Fig. 2a,b) but were positively correlated to each other (Supporting Information S6a). Overall, the highest alpha-, observed, and estimated gamma-diversity occurred in *Q. petraea* (Figs. 2 and 3), confirming the high importance of this tree species for saproxylic beetles (Irmler *et al.*, 1996; Brändle & Brandl, 2001). At least for the early decay stage, our finding is in line with other studies based on branches (Jonsell *et al*., 2007; Vogel *et al*., 2020), whereas in studies of logs the diversity in *Quercus* sp. was lower than in *C. betulus* or *P. tremula*, probably due to the faster decay rate of these tree species compared to Quercus sp. (Gossner et al., 2016), having an adverse effect in branches. The 38 saproxylic beetle species and particular 7 red-listed species recorded in *Q. petraea*, *Q. cerris*, and *Q. rubra* (33% of 112 species; 35% of 20 red-listed species) corresponded to the almost 30% of all red-listed species colonising *Q. robur* in Sweden (Jonsell *et al.*, 1998). Nevertheless, the importance of *Quercus* sp. for saproxylic beetles is also related to other features, such as the age and diameter of the tree species as well as the probability for containing microhabitats (Paillet *et al.*, 2019), none of which were considered in our study. Hence, the relevance of *Quercus* sp. for saproxylic beetles might reflect the dominance of this tree genus in the study area, as it would then generate the highest amount and diversity of deadwood. A preference of saproxylic beetles for the dominant tree species was also reported by Brändle and Brandl (2001) and by Bussler *et al*. (2011) based on databases of host tree species and their associated saproxylic beetles. Yet, this assumption was not applicable to the high diversity in *M. domestica*, as this tree species is artificially planted in the study area and its closest relative, the European crab apple (*Malus sylvestris*), is only marginally available. The high diversity of saproxylic beetles in *Pinus* sp., *P. abies*, *P. menziesii*, and *L. decidua* was unexpected as well (Fig. 2a–c) because these coniferous tree species are naturally rare in the study area or have been planted in small numbers. Saint-Germain *et al.* (2007) noted that coniferous tree species in early decay stages host higher species numbers of saproxylic beetles than broadleaved tree species, whose diversity typically increases during middle or later decay stages. Thus, the high alpha- and observed gamma-diversity found in coniferous tree species may have been due to the early decay stages of the branches included in our study. By contrast, the diversity of saproxylic beetles found in *F. sylvatica* was lower than expected, although this tree species has been reported to host a diversity of saproxylic beetles that is roughly as high as in *Quercus* sp. (Walentowski *et al.*, 2014).

The tree species with the lowest alpha-diversity in our study were also those with the lowest observed and estimated gamma-diversity: *J. communis*, *U. laevis*, and *T. baccata* (Fig. 2a–c). This pattern was somewhat surprising, given that *U. minor*, for instance, had a distinctly higher diversity than *U. laevis*, and the diversity of most of the other coniferous tree species was distinctly higher than that of *J. communis* and *T. baccata*. For all three tree species, the reduced diversity may reflect their different defence mechanisms. In several tree species, primary and secondary metabolites, such as oils, waxes, resins, tannins, terpenes, and polyphenols, have been shown to prevent wood colonisation by saproxylic insects (Pearce, 1996; Erbilgin, 2018; Noll *et al.*, 2016). *U. laevis* contains higher amounts of terpenes than *U. minor* and is therefore more resistant against elm bark beetle (*Scolytus scolytus*) and elm dieback (Martin *et al.*, 2004; Pajares *et al.*, 2004). In the case of *J. communis*, resin can act as an impediment, and nearly all parts of *T. baccata* contain toxic taxanes. The distinct heartwood of *J. communis* and *T. baccata* may also confer a higher general resistance against decomposers, since its concentrations of

metabolites are often higher and more toxic than those of sapwood (Kahl *et al*., 2017; Moll *et al*., 2018). Moreover, the degradation of defence mechanisms can allow a reduced host tree specificity of saproxylic beetles with increasing deadwood decomposition (Wende *et al*., 2017). Accordingly, beetle species of early succession, such as analysed in our study, will have a higher host tree specificity than beetle species of later decay stages (Parisi *et al*., 2018).

The number of red-listed species marginally increased with the increasing number of saproxylic species (Supporting Information S6b), and some of the highest numbers of red-listed species were found in tree species with an overall high diversity (Fig. 2b). Yet, numerous red-listed species were hosted by tree species with only a low or medium alpha- and gamma-diversity, including *A. glutinosa*, *C. betulus*, *S. caprea*, *S. domestica*, and *T. cordata* (Fig. 2b; Supporting Information S1). Together with the overall diversity of saproxylic beetles, this finding illustrates the importance of rare or silviculturally less important tree species for the diversity of saproxylic beetles (see also Gossner *et al*., 2016; Andringa *et al*., 2019; Vogel *et al*., 2020). Moreover, broadleaved tree species hosted most of the red-listed saproxylic beetles, in contrast to only three coniferous tree species (*P. nigra*, *P. sylvestris*, and *A. grandis*). In addition to the smaller number of coniferous tree species in the study area, this result may reflect the generally higher extinction risk of saproxylic beetles colonising broadleaved rather than coniferous tree species (Seibold *et al*., 2015b).

Non-native tree species

In our study, the alpha-diversity between native and non-native tree species was similar, whereas the estimated gamma-diversity was lower in non-native tree species and the community composition varied significantly (Supporting Information S4, S5b, and S7). Hence, our results are partially in line to those of other studies (Müller *et al*., 2015b; Ulyshen et al. 2018), whereby the importance of non-native tree species is still under debate with mixed scientific evidence. In the studies of Müller *et al*. (2015b) and Ulyshen et al. (2018), the species diversity associated with *P. menziesii* was significantly lower than that determined from native coniferous trees. Although in the studies of Bertheau *et al*. (2009) and Della Rocca *et al*. (2016), which included *P. menziesii* and *R. pseudoacacia*, there were no differences in the species diversity of native versus non-native tree species. Andringa *et al*. (2019) also observed comparably high species numbers in non-native *Larix kaempferi* and *Populus x canadensis*.

For red-listed beetle species, six of the nine non-native tree species were also accepted as host tree species. The three exceptions were *P. strobus*, *P. menziesii*, and *R. pseudoacacia*. Those tree species as well as *A. grandis* and *Q. rubra* were introduced into Central Europe from North America within the last 200 years (Schmid *et al*., 2014; San-Miguel-Ayanz *et al*., 2016), but adaption to novel tree species by saproxylic beetle specialists within this short time is unlikely (Goßner *et al*., 2009; Oleksa & Klejdysz, 2017). Generally, it is assumed that non-native tree species host more saproxylic beetle

generalists than specialists (Ulyshen et al. 2018). Nevertheless, the presence of native congeneric tree species increases this process of adaptation (Pearse & Hipp, 2009; Branco *et al*., 2015), which would explain our finding of the relatively high species numbers of red-listed species in *A. grandis* and *Q. rubra* and the absence of red-listed species in *P. menziesii* and *R. pseudoacacia*, which have no European relatives. Additionally, the adaptation to non-native tree species might be promoted by a low geographical separation or an overlapping distribution of host trees and saproxylic beetle species, as is the case for *C. sativa*, *J. regia*, *P. nigra*, and *Q. cerris* from Southern Europe.

Determinants of host tree specificity

In our study, communities of saproxylic beetles distinctly differed between coniferous and broadleaved tree species but also within both groups of tree species (Fig. 3; Supporting Information S7). This finding could indicate that factors beyond tree chemical defence mechanism determine saproxylic beetle communities. A possible explanation might be that the anatomical and physicochemical properties of deadwood strongly differ between broadleaved and coniferous tree species (Wilson & White, 1986; Meerts, 2002; Weedon *et al*., 2009), which can explain their frequently distinct communities of saproxylic taxa (Purahong *et al*., 2018). Analyses of wood-inhabiting fungi and bacteria using molecular data and a small set of wood properties demonstrated the importance of physicochemical properties (pH, density, extractives, lignin content, and water content) in determining community composition (Moll *et al*., 2018; Purahong *et al*., 2018). Additionally, the phylogenetic relatedness of the tree species might also play a role in determining saproxylic beetle communities, as wood properties seem to be more similar in closely related than in distantly related tree species (Thorn *et al*., 2015; Purahong *et al*., 2018). This might further explain the differences between broadleaved and coniferous tree species as well as the differences between *J. communis*/*T. baccata* (Cupressaceae/Taxaceae) and most other coniferous tree species (Pinaceae). Nevertheless, evidence supporting these assumptions should be the target of future studies including a larger number of tree species and information about their physicochemical/anatomical properties.

Implications for management

Our study highlights the importance of previously understudied tree species and tree species that may become prospectively important due to climate change. Recent strategies on deadwood enrichment focus mainly on the amount of deadwood, whereas tree species diversity is of relatively low priority. Nonetheless, our study demonstrates the essential contribution of various tree species in maintaining saproxylic beetle diversity. Although branches represent only one type of deadwood, they are the most common type during active deadwood enrichment and can thus be considered as representative. Based on our results, we generally suggest a stronger incorporation of tree species diversity into conservation efforts targeting saproxylic beetles, by considering

the entirety of local tree species. This can be realised by the creation of sun-exposed forest structures and forest gaps in mainly closed forests, which are beneficial for the sun-preferring tree species (e.g. *S. caprea*, *S. nigra*, *J. communis*) and also beneficial for a variety of forest-dwelling arthropod species (Thorn *et al.*, 2016). Softwood and tree species of low economic value, for example *B. pendula* and *P. tremula*, should be allowed to undergo natural senescence and decay without intervention by forest management, as these short-living species provide a high diversity of ecological niches in deadwood and in early successional stages as well as following forest disturbances (Swanson *et al.*, 2011; Thorn *et al.*, 2020). Moreover, we recommend the promotion of naturally rare tree species to increase the local tree species diversity, while non-native tree species are rather unfavourable.

Authors contributions

Sebastian Vogel, Sven Finnberg, and Jörg Müller designed the experiment. Sebastian Vogel, Heinz Bussler, Sven Finnberg, and Elisa Stengel established the study and collected data. Sebastian Vogel, Jörg Müller, and Simon Thorn analysed and interpreted the data. Sebastian Vogel led the writing of the manuscript with substantial input from all co-authors. All authors gave their final approval for the publication of the manuscript.

Acknowledgement

Conflict of Interest

The authors have no conflict of interest to declare.

Data availability statement

The data that support the findings of this study are openly available in Dryad

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Corrections added on 27 March 2021, after first online publication date: In original version of this article, the non-native Prunus serotina was incorrectly interchanged with the native Prunus padus, and nine individuals of saproxylic beetles were incorrectly removed from the data when splitting beetles in saproxylic and non-saproxylic species. The correct tree species is Prunus serotina, and results refer to a total of 113 species of saproxylic beetles and 30,550 individuals. The Supporting Information files have been amended to reflect this in the online version of the article.

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