The use of sentinel logs to assess host shifts in early beetle colonisers of deadwood under climate-and forestry-induced tree species substitutions

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The use of sentinel logs to assess host shifts in early beetle colonisers of deadwood under climate- and forestry-induced tree species substitutions

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Abstract. 1. Global change scenarios project drastic modifications in tree species range and an increase in exotic tree plantations. Subsequent tree species substitutions may alter habitat conditions for biodiversity.

2. We measured substitutability between tree species for early deadwood colonisers, through a sentinel log approach, i.e. through the experimental exposure of paired down deadwood (DDW) pieces to native beetles in native stands. We compared two native/substitute tree species pairs: one conifer pair composed of a rapidly expanding exotic species (Douglas fir) and a declining native species (silver fir), and one deciduous pair composed of two native species, one expanding (sessile oak) and one retreating (beech) at the regional scale.

3. The effects of expanding exotic and native trees on beetle communities were not in line with expectations.

4. Species assemblages in Douglas fir DDW were indistinguishable from those in native silver fir DDW and did not contain fewer species. Assemblages were not more generalist on average in substitutes than in substituted trees: we did not note any decrease in species richness of functional groups to the detriment of specialist species.

5. Moreover, species richness and abundance were higher in substitute oak than in native beech DDW, confirming that species from the regional pool were able to colonise oak, even though it is a minor tree species at the regional level.

6. Large-scale monitoring schemes including multi-taxon, multi-year and multiple native/substitute pairs would further our knowledge of the generic effects of tree species substitution on biodiversity and ecosystem functioning.

Key words. Beech, climate change, Douglas fir, exotic plantations, functional trait, oak, saproxylic beetles, Silver fir.

Introduction

Climate change is expected to greatly affect species distributions in the near future (Thuiller *et al*., 2005). Throughout Europe, some native tree species are likely to lose climatically favourable areas, and ecoclimatic modelling predicts shrinking distribution areas for some tree species in French forests (Badeau *et al*., 2010). Climate change scenarios project drastic reductions in

the range of several common species such as European beech (*Fagus sylvatica*) and silver fir (*Abies alba*), especially at lower altitudes (Badeau *et al*., 2010). Over the last 20 years, silver fir (Gillmann *et al*., 2014) and beech forests (Chira *et al*., 2003) have already experienced successive dieback episodes in Western and Central Europe.

Meanwhile during the last decades, partly in response to the challenges associated with climate change, forest managers throughout the world have increasingly been planting exotic tree species in their search for commercial tree species that are better adapted to future climatic conditions (Canadell & Raupach 2008). As examples, Douglas fir (*Pseudotsuga menziesii*) and

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Atlas cedar (Cedrus atlantica) have increasingly been promoted in western European forestry in place of native conifers (Schmid *et al.*, 2014) because of their resistance to drought, their yield and their wood quality.

These changes in native tree species' ranges due to both the influence of climate change and the forestry-induced expansion of exotic tree species are likely to alter habitat conditions for forest biodiversity (Felton *et al.*, 2013), example through the tree species composition of dead wood available for saproxylic biodiversity (Ulyshen *et al.*, 2018). The composition of dead wood in terms of host tree species is a fundamental dimension of food suitability and resource availability for saproxylic taxa (e.g. Bouget *et al.*, 2013; Müller *et al.*, 2015). However, host tree specificity among saproxylic species is not so narrow: for instance, 75% of French saproxylic beetle species for which data are readily available, are not specific to a single host species but are known to use at least two tree species (Bouget *et al.*, 2019)!

There is an emerging body of literature on the response patterns of wood-associated organisms to tree species substitution, including phytophagous (eg Brändle *et al.*, 2008) or xylophagous insects (e.g. Zumr, 1992, Bertheau *et al.*, 2009) and more rarely, fungi (Gange *et al.*, 2011; Heilmann-Clausen & Læssøe, 2012). The colonisation of exotic tree deadwood by native xylophagous insects remains poorly known and available studies have given contrasted results (see review by Ulyshen *et al.*, 2018). Several ecological mechanisms inherent to the new host trees (regional abundance, presence of congeneric native trees, time elapsed since introduction) or to the insects themselves (host tree diversity), may be involved in the occupancy of exotic trees by native insects (Gossner *et al.*, 2009). Colonisation of new host trees concerns both local shifts in species associated to the substituted tree species, and the contribution of the regional pool of species. Several ecological hypotheses have been invoked to explain the community assembly of native insect species found on new host trees. Some concepts focus mostly on herbivores and living trees, and cannot be extended to deadwood eaters. For instance, the Biotic Resistance Hypothesis stipulates that introduced tree species recognised as a food source by native herbivores are less well defended than native trees due to a lack of coevolution (Lombardero *et al.*, 2012); introduced species are therefore more easily colonised by native herbivores than are native substrates. Conversely, other concepts relevantly apply to dead wood substrates. On the one hand, the ecological concept of "escape in space from enemies" (Brin & Bouget, 2018) stems from the idea that wood-dwelling insects and their natural enemies exhibit contrasting colonisation abilities when the resource is highly aggregated in space and time. Even though wood-feeding beetles are more demanding in terms of host tree species than zoophagous beetles, they may benefit from decreased predation pressure in new resource patches, which are more slowly colonised by predator species. On the other hand, biotic homogenisation may occur; this refers to the occupancy of exotic substrates by widespread generalist species to the detriment of native specialist biotas in changing, especially human-altered, environments (McKinney & Lockwood, 1999; Smart *et al.*, 2006). The direct and indirect consequences of tree species substitutions on biodiversity are of interest not only in terms of conservation strategies for endangered species (Mori *et al.*, 2017), in particular saproxylic species, but also in terms of ecosystem functioning (e.g. deadwood decomposition or biotic regulation of pathogens and pests).

In an experiment in natural conditions, we measured the substitutability between two tree species (one substitute and one substituted) for early deadwood colonisers using a 'sentinel log' method, i.e. through the experimental exposure of paired down deadwood (DDW) pieces to native beetles in native stands. Our 'sentinel log' approach was symmetrically derived from the 'sentinel plant' method, which is increasingly advocated as a strategy to identify potential plant pests in a particular region before they are introduced (Mansfield *et al.*, 2019).

Herein, we document the early colonisation of freshly cut deadwood by saproxylic beetles, which is likely to precondition the deadwood for further succession by other invertebrates and fungi (Stokland *et al.*, 2012). Saproxylic beetle assemblages are composed of interacting guilds, including mainly xylophagous wood-borers, consumers of wood-decaying fungi and predators (Bouget *et al.*, 2019). Assemblage dissimilarity between tree species is assumed to be particularly significant for pioneer xylophagous species, known to be more closely associated to tree species or tree genus than other feeding guilds (Dajoz, 2000). The colonisation of an introduced tree species substrate through insects from the regional species pool breeding on the substituted tree species could therefore be partial. We hypothesised that species richness for early deadwood colonisers would be lower in DDW from the substitute tree species than in DDW from the substituted tree species. According to the ecological hypotheses mentioned above, we also expected contrasts in species assemblage composition in the DDW between the substitute and the substituted tree species, to the detriment of specialist or zoophagous species and in favour of generalist species in the substitute tree deadwood.

Materials and methods

Experimental design

To focus on the effects of wood quality and discard potential effects of local deadwood quantity and diversity on insect diversity associated with native and non-native trees, we used emergence traps to collect insects directly from woody substrates organised in a paired design. Two pairs of tree species (one substitute and one substituted) were compared to reveal distinct patterns of tree species substitution. The conifer pair was composed of an exotic species, Douglas fir (*Pseudotsuga menziesii*), which is being increasingly planted as a substitute for a native species, silver fir (*Abies alba*), currently decreasing in surface area, mainly at low elevations. The deciduous pair included a native species expanding in range due to its low sensitivity to climate change, sessile oak (*Quercus petraea*), as a substitute for European beech (*Fagus sylvatica*), a native species whose range is shrinking (Badeau *et al.*, 2010). Fresh woodfrom these four tree species was sawn off trees felled during winter 2015–2016. Two diameter classes were collected: 1-m-long small branches (2.5–7.5 cm in diameter; $n = 400$) and 1-m-long logs (7.5–12.5 cm in diameter; $n = 160$), making 100 branches

and 40 logs for each tree species. The 'Sentinel logs', bundles made up of this artificially created Down Deadwood (DDW), were exposed to colonisation by native beetles from March to October 2016 in two different regions depending on the tree species: (i) for the Douglas fir/silver fir pair – in the Pays de Sault (Eastern Pyrenees, 1000 m asl, $n = 10$ plots) and Baronnies (Central Pyrenees, 800–1200 m asl, $n = 10$ plots), and (ii) for the sessile oak/beech pair – in the Eawy forest (Normandy, 200 m asl, $n = 10$ plots) and Baronnies (Central Pyrenees, 800–1200 m asl, $n = 10$ plots) (see map in Fig. 1). The plots were selected in stands dominated by the native substituted tree species (in a 300 m-radius buffer zone) and surrounded by forests where the substituted tree species is very common at the landscape scale (3000 ha). The substitute tree species was absent from the experimental stand and the 300 m-radius buffer zone, and rare at the landscape scale. This sampling design simulated a change in tree species dominance and avoided situations where the substitute tree species was already quite common. The plots

were set up in mature stands (i.e. more than 100 years old) and recently harvested or windthrown areas (<2 years) were excluded. The minimum distance between plots was 300 m and they were located more than 30 m from the forest edge. Each plot was divided into two subplots, 5 m far away from each other. In each subplot, one bundle with one log and two (or three) branches of the substitute tree species and one bundle with one log and two (or three) branches of the substituted tree species were placed 50 cm apart on the ground, in an area deprived of bushy vegetation. Overall, the experimental design was balanced in terms of diameter class and tree species replicates.

Sampling early wood colonisers

The experimental DDW was collected at the end of the active flying season for insects (October) and immediately put into
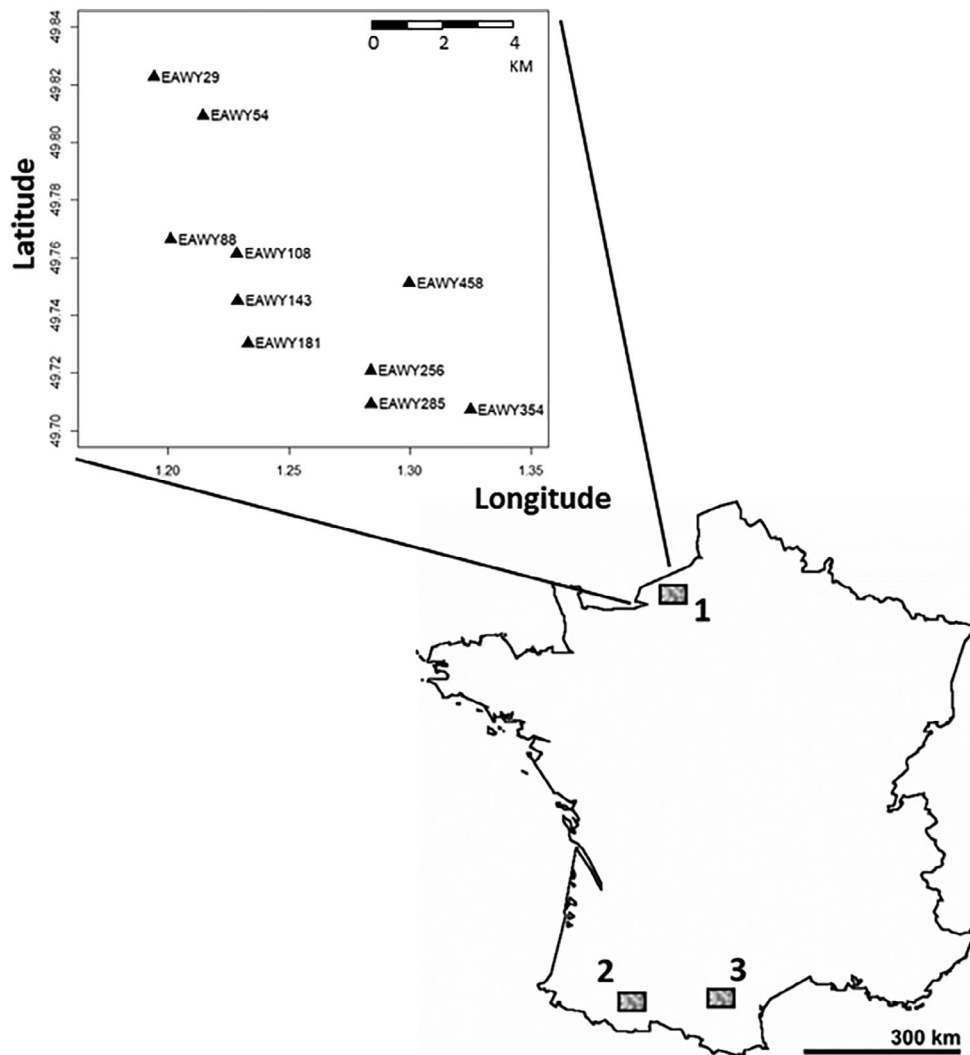
Figure 1. Map of the distribution of study sites: (1) Eawy forest, (2) Baronnies forests, (3) Pays de Sault, and zoom in on the spatial design of 10 plots in the Eawy fores

emergence bags. We used one bag per plot, per tree species and per log type, which meant that each bag contained either two deadwood logs or five deadwood branches according to their diameter class. The 160 emergence bags were left under natural forest conditions and monitored. Their collectors were regularly emptied to sample the emerging beetles over 18 months starting in April 2017, since most beetle colonisers have a 1-year development cycle. The beetles were identified at the species level whenever possible; 20 taxa were identified at the genus level only.

Beetle species traits. We selected two crucial ecological traits related to the ecological requirements of each species: (i) feeding habit and (ii) host tree preference. The trait values were extracted from the ecological information stored in the French database on saproxylic beetle ecology (Bouget et al., 2019; Table A2). Two feeding guilds, wood-eating species (including both xylophagous and saproxylophagous beetles) and lignicolous zoophagous species, were assessed. The response of the mycophagous beetle guild, poorly represented in our current data, was not analysed. Host tree preference was encoded by an index value as follows: (i) oligophagous species associated with a few deciduous tree species at most, or oak specialists; (ii) species associated with deciduous trees in general; (ii) polyphagous generalists associated with both coniferous and decidous trees; (iv) species associated with conifers in general; and (5) oligophagous species associated with a few conifers at most, or fir specialists.

Data analysis

All analyses were performed in R, version 3.5.1 (R Core Team 2018). The beetle data from the emergence bags were merged for each diameter class and each tree species.

To describe beetle assemblage structure, we computed community-weighted means (CWM) and functional dispersion (FDis) for host tree preference values (dbFD function, FD package, Laliberté & Legendre, 2010). CWM is defined as the mean of trait values weighted by the relative abundance of each species bearing each value. FDis is defined as the mean distance of a given individual species to the weighted centroid of all the species in the assemblage and is unaffected by species richness (Laliberté & Legendre, 2010). An increase in CWM of the host tree preference trait corresponds to a more generalist species assemblage in deciduous case studies (i.e. polyphagous on average), but to a more specialist species assemblage in coniferous plots (fir specialists). In coniferous and deciduous case studies, an increase in trait FDis indicates a more generalist species assemblage.

To determine whether and how univariate assemblage metrics were influenced by tree species, we computed either linear or generalised linear mixed models. We investigated the following response variables: mean values per trap of CWM or FDis for host tree preference, number of individuals and species for all species and feeding guilds, and the abundance ratio of wood-eating/zoophagous. The error structure of the generalised linear mixed-effects models was adjusted to better fit the data. To do

Table 1. Variations in saproxylic beetle assemblage metrics related to tree species [error structure: Linear[N], lognormal[LN] or generalised linear (Poisson[P], negative binomial[NB]) mixed-effects models].

[m] = m Mean values per bag; ± = standard error, ***$P < 0.001$, ** $P < 0.01$, * $0.01 < P < 0.05$, [ns] $P > 0.05$.

	Deciduous				Conifer			
	Error structure	Retreating substituted tree species (beech)	Expanding substitute tree species (sessile oak)	Estimate [sd] and P-value	Error structure	Retreating substituted tree species (silver fir)	Exotic substitute tree species (douglas fir)	Estimate [sd] and P-value
Number of individuals[m]	NB	11.1 ± 2.42	32.15 ± 6.49	−0.96 [0.28]***	NB	4 ± 1.19	3.5 ± 2.62	0.39 [0.36][ns]
Number of species[m]	NB	2.65 ± 0.28	3.93 ± 0.36	−0.39 [0.12]**	NB	1.38 ± 0.17	1.08 ± 0.16	0.24 [0.21][ns]
Cumulative number of species		14.79 [11–18]	19.74 [16–23]			11.27 [9–14]	15.48 [12–19]	
CWM host preference[m]	LN	2.73 ± 0.04	2.88 ± 0.03	−0.54 [0.16][ns]	N	3.26 ± 0.09	3.10 ± 0.08	−0.08 [1.18][ns]
FDis host preference[m]	N	0.38 ± 0.08	0.22 ± 0.05	3.60 [2.48][ns]	N	0.34 ± 0.07	0.2 ± 0.05	−0.60 [1.27][ns]
Abundance of zoophagous beetles[m]	NB	1.53 ± 0.34	2.15 ± 0.38	−0.34 [0.27][ns]	NB	1.4 ± 0.5	0.53 ± 0.2	0.24 [0.22][ns]
Species richness of zoophagous beetles[m]	P	0.73 ± 0.13	1.15 ± 0.15	−0.46 [0.23][ns]	P	0.5 ± 0.11	0.43 ± 0.14	0.16 [0.33][ns]
Abundance of wood-eating beetles[m]	NB	8.35 ± 2.27	28.58 ± 6.4	−1.15 [0.35]**	NB	2.43 ± 1.12	2.65 ± 2.67	0.36 [0.52][ns]
Species richness of wood-eating beetles[m]	P	0.93 ± 0.09	1.55 ± 0.18	−0.52 [0.20]*	P	0.7 ± 0.15	0.38 ± 0.1	0.48 [0.30][ns]
Abundance ratio wood-eating/zoophagous[m]	LN	5.14 ± 1.33	15.44 ± 4.45	−0.66 [0.24]**	LN	1.85 ± 0.88	2.65 ± 1.95	0.14 [0.18][ns]

so, glmms were fitted for the negative binomial family, the log-normal family (i.e. log-transformed response), the Poisson family (glmer.nb, glmer, lmer, lme4 functions, R-package), with region and plot as nested random effects accounting for the spatial configuration of the sampling design, and with diameter class as a secondary covariate accounting for the differences between branches and logs.

A species accumulation function (*rich* R-package) computed rarefaction curves and returned the bootstrap estimate of cumulative species richness for each tree species, for a standard interpolated number of sampled sites ($n = 20$ samples for coniferous tree species; $n = 30$ samples for deciduous tree species, 1000 random permutations), as well as its statistical envelope (lower and upper bounds of the estimate corresponding to the quantile values at a *P*-value = 5%).

To determine whether the species composition of the saproxylic beetle assemblages was influenced by tree species, we performed PERMANOVA analyses (Anderson & Walsh, 2013) based on a Bray-Curtis distance, with 999 permutations constrained by study region (vegan package). We used the R function *nestedbetasor* (*vegan* package) to partition the Sorensen dissimilarity index into: (i) the Simpson dissimilarity index, describing spatial turnover (where some species are replaced by others as a consequence of environmental sorting or spatial and historical constraints), and (ii) the nestedness-resultant dissimilarity (where the species from samples with lower species richness are subsets of the species in richer samples, reflecting a non-random process of species loss) (Baselga, 2012).

To investigate the preferences of individual beetle species for tree species, we used indicator species analysis (*multipatt* function, *indicspecies* package, De Cáceres & Legendre, 2009) based on the indicator value index (IndVal) to combine the exclusivity and fidelity of species within a group of sites. Low-frequency (occupied sites <10%) and low-abundance species (<10 individuals in total) were discarded. We therefore included only seven beetle species for the beech-oak pair and six species for the silver fir-Douglas fir pair in the analysed table. Permutation tests ($n = 9999$) assessed the statistical significance of the indicator-species values.

Results

Overall, the experimental DDW was successfully colonised during the experiment, since only a few emergence bags (7% of the log bags and 18% of the branch bags) did not provide any beetles during the 18-month period. The proportion of empty bags (i.e. without any emerging beetles) depended on tree species: 20% for Douglas fir, 14% for silver fir, 9% for beech and 8% for sessile oak. Tree species did not significantly affect the mean number of empty bags per plot (see
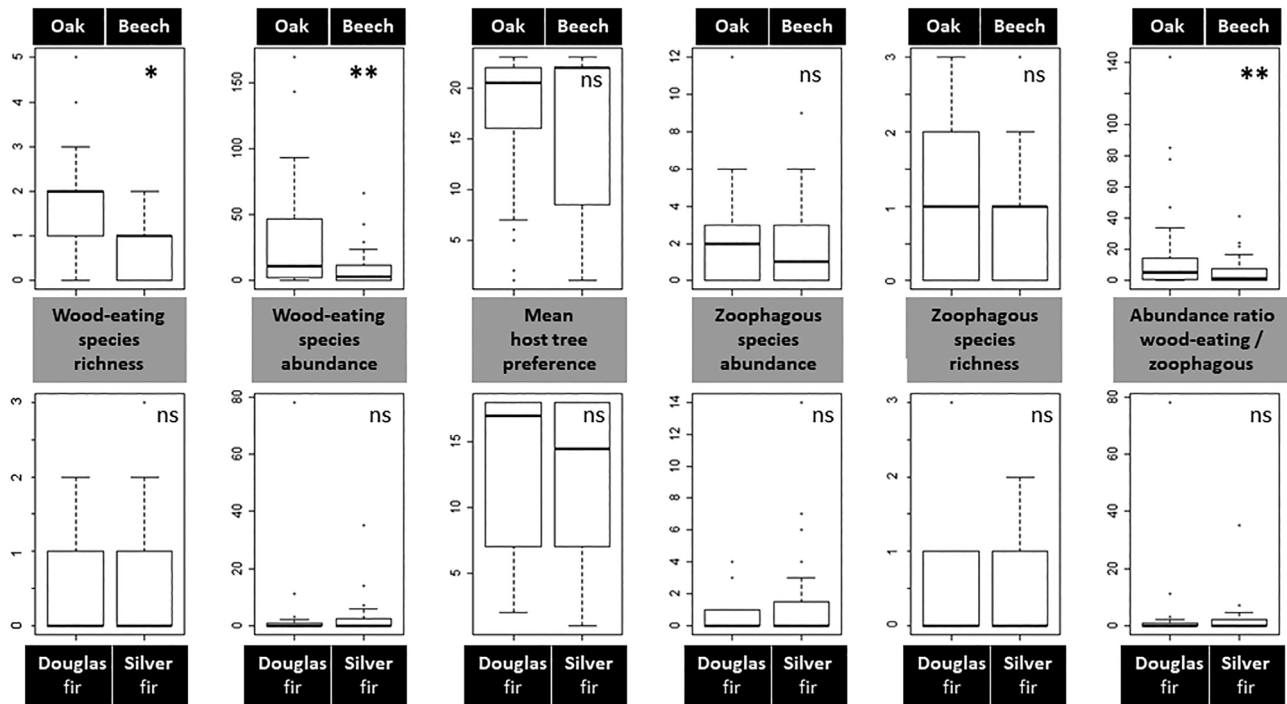
Figure 2. Effect of tree species on saproxylic beetle assemblage metrics (mean host tree preference, mean abundance and species richness for all species and feeding guilds, abundance ratio of wood-eating/zoophagous beetles) in paired comparisons (substitute vs substituted, deciduous above, conifer below) using linear or generalised linear mixed models. An increase in CWM of the host tree preference trait (mean host tree preference) corresponds to a more generalist species assemblage in deciduous case studies (i.e. polyphagous on average), but to a more specialist species assemblage in coniferous plots (fir specialists). See table 1 for error structure and detailed statistical results for each response variable, *** $P < 0.001$; ** $0.001 < P < 0.01$, * $0.01 < P < 0.05$, ns $P > 0.05$

Table A1. The whole sampling design provided 1885 saproxylic beetle individuals in 53 taxa (including 24 singletons, see Table A2).

Mean numbers of saproxylic beetle individuals and species per bag were similar for both conifers, but significantly higher for oak than for beech (Table 1). The cumulative number of species was on average more than 30% higher in the DDW of the substitute tree species than in the substituted tree species, for both coniferous and deciduous species pairs (Table 1), even though bootstrap confidence intervals slightly overlapped in each pair.

PERMANOVA analyses of differences in species composition showed a slightly significant contrast between beech and sessile oak ($P = 0.01$, 1000 replications), but a non-significant assemblage dissimilarity between Douglas fir and silver fir ($P = 0.07$, 1000 replications). In the beech-oak case study, the contribution of nestedness to total dissimilarity was very low (2.8%), while spatial turnover processes were dominant (97.2%).

Paired comparisons of assemblage metrics between tree species revealed not very many significant differences. No difference in the CWM or FDis of the host preference trait was measured between substituted and substitute tree species, either for broadleaves or for conifers (Table 1). For the deciduous species, more wood-eating beetle species and individuals were caught on average per bag from oak than from beech deadwood (Table 1; Fig. 2); mean abundance ratio (wood-eating/zoophagous) was significantly higher in oak than in beech deadwood (Fig. 2). In the coniferous context, a similar number of wood-eating individuals and species emerged from silver fir and from Douglas fir deadwood (Fig. 2). Mean numbers of zoophagous beetles and mean abundance ratio [wood-eating/ zoophagous] were also similar for both Douglas and Silver fir (Table 1; Fig. 2).

From mixed models focusing on univariate assemblage metrics, only consistent results across the two study regions were retained. It should however be noted that some regional discrepancies occurred when comparing substituted and substitute tree species. The contrast was actually stronger in Eawy than in Baronnies site for broadleaves, and in Sault than in Baronnies site for conifers (Table A3).

From the IndVal analysis conducted on a small number of selected species, one species was significantly characteristic of beech deadwood (*Cartodere nodifer*, Latridiidae, $P < 0.05$); another one was associated to silver fir deadwood (*Pissodes piceae*, Curculionidae, $P < 0.05$); and two species were specific to oak deadwood (*Xylosandrus germanus*, Curculionidae, and *Rhizophagus bipustulatus*, Monotomidae). Finally, only two nationally listed rare species were detected in our dataset: *Kyklioacalles pyrenaeus* (Curculionidae), caught in both silver and Douglas fir deadwood, and *Laemophloeus kraussi* (Laemophloeidae), which emerged from beech wood.

Discussion

The success of our emergence experiment in data provision compared with other published studies (e.g. Nittérus et al. 2004; Della Rocca *et al.*, 2016) should be noted. Overall, though we focused on small-diameter classes and early decay stages, we measured only a slight response of saproxylic species to tree substitution. We did not observe sharply distinct wood-dwelling beetle assemblages in the fresh deadwood from the substitute tree species compared with the native substituted tree species. Moreover, the highest dissimilarity level we observed was between the two deciduous native species, not between the exotic and native coniferous species.

In the conifer case study (native vs exotic), deadwood from the exotic Douglas fir did not provide fewer species on average per deadwood piece. On the contrary, Douglas fir deadwood held more total species over the sampling design, in line with the Biotic Resistance Hypothesis suggested for herbivores (Lombardero *et al.*, 2012). Overall species composition was not distinct and not nested between exotic Douglas fir and native Silver fir. Indeed, species assemblages in Douglas fir deadwood did not contain a smaller number of species. About 50% of the taxa collected from Douglas fir substrates were listed for Silver fir deadwood in the French database on saproxylic beetle ecology (Bouget *et al.*, 2019). It is noteworthy that Douglas fir is listed as a potential host tree species for only 12 out of the 260 conifer-preferring xylophagous beetle species in the French database on saproxylic beetle ecology (Bouget *et al.*, 2019). Overall, improved knowledge of the niche breadth of wood-associated insects would be informative.

Mean values and dispersion of quantitative traits were not lower in Douglas fir than in silver fir deadwood, which means that assemblages were not more generalist on average in substitute than in substituted trees. In other words, no sign of biotic homogenisation of fresh-deadwood beetle coloniser assemblages was detected on Douglas-fir. Müller *et al.* (2015), but also Roques *et al.* (2006), insisted on the lack of specialist species among the species colonising Douglas fir; they represented only a small generalist subset of the assemblage collected from native spruce. In the available literature, the reported ecological impacts of Douglas fir plantations on biodiversity are diverse and often inconsistent (Tschopp *et al.*, 2015); in general, the impacts are considered less severe than those of other exotic tree species (Schmid *et al.*, 2014). In line with our results, a previous study found that the number of species in arthropod communities on Douglas fir was similar to the one on native conifer species (Schmid *et al.*, 2014). Another study restricted to scolytids colonising experimentally exposed deadwood found no difference in species richness among native conifers [namely Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Silver fir and Douglas fir] (Bertheau *et al.*, 2009). In the European study by Branco *et al.* (2015), Douglas fir was the exotic species that recruited the greatest number of native insects. Contrary to our results, Müller *et al.* (2015) clearly demonstrated that saproxylic beetles avoided experimental logs of exotic Douglas fir DDW in Germany, in accordance with another German study of saproxylic canopy arthropods (Gossner & Ammer, 2006). It should be pointed out that their set of experimental logs included mainly large deadwood pieces, 20–60 cm in diameter, which makes their design clearly different from ours. Knowing that contrasts in bark thickness between Silver and Douglas fir mainly occur in large-diameter logs, sampling gaps may contribute to the observed discrepancies in beetle response.

Tree-associated insects would appear to colonise new woody resources, such as the exotic deadwood in our study, more easily and more quickly than do their natural enemies ("escape in space from enemies", Brin & Bouget, 2018). Such a shift in arthropod communities is nevertheless still controversial, since Hartley *et al*. (2010) found lower herbivore abundance but more predator species on a recently introduced exotic tree species compared to the native species. In our results, at odds with the "escape" hypothesis, indigenous predators used the exotic DDW as foraging habitat, so that zoophagous species richness and abundance, and relative number of zoophagous individuals compared to xylophagous prey, were equal in Douglas fir DDW and in silver fir DDW. Consequently, no decrease in potential pest regulation by natural enemies was observed in exotic DDW compared with the native DDW.

Factors other than a lack of natural enemies can facilitate or constrain establishment success of indigenous insects on a new host such as Douglas fir in Europe (Neuvonen & Niemela, 1981). The probability of exotic trees being colonised by native insects increases with (i) the presence of congeneric native trees in the area of introduction or the close phylogenetic proximity with native tree species (Connor *et al*., 1980); (ii) the abundance and geographical extent of forests planted with exotic trees (Branco *et al*., 2015); and (iii) the time elapsed since introduction (Brändle *et al*., 2008). Although Douglas fir has no congeners in Europe, it was first introduced to France from North America more than 175 years ago and it has been planted on a large scale in European forests for 50 years (Schmid *et al*., 2014).

So far studies comparing the colonisation of exotic and native trees by native insects have given contrasting results (Ulyshen *et al*., 2018), partly due to differences in substrate features (size, decay) involved in the comparisons. Newly introduced conifers are often more colonised than native species but opposite conclusions have been reported as well, both in temperate and Mediterranean forests (Evans, 1987; Fraser & Lawton, 2008; see also Lachat *et al*., 2007 in tropical forests). In European Nordic countries, among the 80 insect species observed reproducing on the introduced lodgepole pine (*Pinus contorta*, Engelmark *et al*., 2001), the majority use native Scots pine as their main host. Some pine-associated species are missing on lodgepole pine, partly due to different bark structure. Contrary to expectations, most of the insect species that have colonised the suboptimal lodgepole pine hosts are Scots pine specialists rather than generalists (with regard to host selectivity; Lindelöw & Björkman, 2001). Historical factors seem to play a crucial role in the recruitment of specialist insects (Dalin & Björkman, 2008). Buse *et al*. (2010) and Degomez and Wagner (2001) also found far lower numbers of saproxylic beetles or arthropods on two non-native trees (*Pinus brutia* in Israel and *Robinia pseudoacacia* in Arizona, respectively), both of which had been introduced into the study region approximately 100 years before. Similarly, Eucalyptus, introduced into southern Europe in the middle of the 19th century, can only be utilised by a relatively small number of insect species with generalist host preferences, as shown in a study in Spain (Lombardero *et al*., 2012). On the other hand, Della Rocca *et al*. (2016) observed no differences in saproxylic species composition among exotic (*Robinia pseudoacacia*, present in Italy for approximately

400 years) and native trees (such as *Quercus robur* and *Populus alba*).

One may also consider the consequences of tree species substitutions on biodiversity in terms of ecosystem functioning. Fresh deadwood mainly attracts early colonisers, which are likely to precondition the deadwood for further succession by fungi and other invertebrates (Stokland *et al*., 2012). For our experimental data, xylophagous species richness and abundance was equal in Douglas fir and silver fir DDW. Despite this stable xylophagous beetle abundance, we cannot definitely exclude a decrease in initial decomposition ability in exotic DDW. Preliminary data on the fungus communities of our experimental logs suggest that Douglas fir hosts lower species richness and distinct species assemblages compared with Silver fir. Given these contrasting responses for two crucial groups in the wood decomposition process, the overall decomposition of exotic DDW should be further investigated. A decomposition experiment by Ulyshen *et al*. (2018) in the United Sates suggests that termites did not contribute as significantly to the decomposition of non-native wood species as they did for native wood species. Nonetheless, Fierro *et al*. (2017) assert that the ecosystem services provided by saproxylic beetles are as functional in exotic pine plantations as in native forests.

In our deciduous case study (native expanding vs native retreating), we found a slight but significant dissimilarity in saproxylic species assemblage composition between the two communities associated to the tree species: beech, currently dominant but retreating, and sessile oak, locally minor but potentially expanding at the regional level. Assemblage composition is known to be dissimilar in oak and beech substrates (Kappes & Topp, 2004). In our study, the beech-oak contrast was stronger in the mountainous Baronnies site than in the lowland Normandy site, even though the occurrence of oak and beech is more sharply spatially segregated in highland contexts. The dissimilarity pattern was mainly due to species turnover and not to nestedness, which means that beech specialists could be losers in case of tree substitution. It should be noted, however, that all the species collected in our samples from deciduous tree substrates had previously been recorded at the national level on both oak and beech deadwood in the French database on saproxylic beetle ecology (Bouget *et al*. 2019). Bearing this in mind, the between-species dissimilarity patterns we observed may involve distinct biotic interactions on oak or beech substrates, or they may reflect stochastic colonisation processes at a fine-grained scale (Brin & Bouget, 2018). They may also sometimes relate to indirect colonisation processes mediated by deadwood-associated microhabitats, such as wood-decaying fungi, which occur more frequently on native beech substrates. Our logs and branches were actually colonised by local fungi and partly covered by fungus mats at bagging at the end of the experimental colonisation period (1 year). The beech logs and branches probably hosted more fungi than did the oak deadwood and were consequently more attractive to fungicolous beetles, such as *Cartodere nodifer* (Latridiidae), a fungus feeder characteristic of beech deadwood from our IndVal results. Our results did not show any biotic homogenisation, nor did we find any decrease in decomposition ability or in pest biotic regulation ability at the assemblage level. The xylophagous functional

groups even seemed more abundant and more diverse in the substitute tree species. Along the same lines, species richness and abundance were higher in DDW from the substitute tree species, in accordance with the exceptionally high species richness of associated specialist insect herbivore species observed on oaks (Brändle & Brandl, 2001). Previous faunistic comparisons of various tree species have revealed that oak hosts richer communities than does beech (Bouget *et al.*, 2019); this is also true for fresh logging residues (Lassauce *et al.*, 2012). Our results suggest that species from the regional pool were able to colonise sessile oak deadwood, even when oak is a minor tree species at the local, or forest, level. Oak specialists may have adapted to colonising scattered oak trees in natural lowland beech-oak forests; from Müller *et al.* (2015), the choice of host trees by local saproxylic beetle communities is not driven by regional resource availability. Given the oak-beech dissimilarity, our findings are not in line with a shift of beech-associated species to oak substrates.

Large sampling schemes should be designed to explore the response of assemblages and individual species to tree substitution and to detect ecosystem function implications and potential loser species among native host-tree specialists. Comprehensive systems should involve (i) the monitoring of sentinel logs and (ii) insect window-flight trapping in exotic forest plantations. They should have a multi-taxon scope, and at least monitor both insect and fungus colonisation. Contrasting colonisation of exotic substrates by insects and fungi has indeed already been demonstrated (Lombardero *et al.*, 2012; Schmid *et al.*, 2014; Ulyshen *et al.*, 2018) and even observed in our context in a companion study comparing Douglas and silver fir (unpublished results). A thorough multi-taxon approach would help to determine whether non-native deadwood does indeed provide valuable habitats from a conservation perspective (Ulyshen *et al.*, 2018). Deadwood monitoring should also encompass a large range of DDW diameters and positions (shaded vs sunny, ground-lying vs standing, etc.) and extend over a long time period (at both the colonisation and emergence steps) to address the effects of tree species substitution on saproxylic species depending on large-diameter, deadwood-associated microhabitats whose occurrence increases with decaying time, and/or rotten logs (Kostanjsek *et al.*, 2018) and should include species with a multi-year development stage. Since we here observed significant between-site discrepancies, the whole experimental design should include many sampling sites. The monitoring should also extend to other native/substitute pairs, including many expanding exotic tree species.

Conflict of interest

The authors have no known conflicts of interest associated with the publication of this study. The authors certify that there are no disputes over the ownership of the data presented in the paper. All contributions have been attributed appropriately, via coauthorship or acknowledgement, as appropriate to the situation.

Data availability statement

Data available on request from the authors

References

Anderson, M.J. & Walsh, D.C. (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecological Monographs*, **83**, 557–574.

Badeau, V., Dupouey, J.L., Cluzeau, C., Drapier, J. & Le Bas, C. (2010) Climate change and the biogeography of French tree species: first results and perspectives. *Forests, Carbon cycle and Climate Change* (ed. by D. Loustau), pp. p. 231–252. Quae, Paris.

Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, **21**, 1223–1232.

Bertheau, C., Salle, A., Rossi, J., Bankhead-Dronnet, S., Pineau, X., Roux-Morabito, G. & Lieutier, F. (2009) Colonisation of native and exotic conifers by indigenous bark beetles (Coleoptera: Scolytinae) in France. *Forest Ecology and Management*, **258**, 1619–1628.

Bouget, C., Brustel, H., Noblecourt, T. & Zagatti, P. (2019) *Les coléoptères saproxyliques de France – Catalogue écologique illustré, Éditions MNHN*, Vol. **738**. collection Patrimoines Naturels.

Bouget, C., Larrieu, L., Parmain, G. & Nusillard, B. (2013) In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation*, **22**, 2111–2130.

Branco, M., Brockerhoff, E.G., Castagneyrol, B., Orazio, C. & Jactel, H. (2015) Host range expansion of native insects to exotic trees increases with area of introduction and the presence of congeneric native trees. *Journal of Applied Ecology*, **52**, 69–77.

Brändle, M., Kühn, I., Klotz, S., Belle, C. & Brandl, R. (2008) Species richness of herbivores on exotic host plants increases with time since introduction of the host. *Diversity and Distributions*, **14**, 905–912.

Brändle, M. & Brandl, R. (2001) Species richness of insects and mites on trees: expanding Southwood. *Journal of Animal Ecology*, **70**, 491–504.

Brin, A. & Bouget, C. (2018) Biotic interactions between saproxylic insect species. *Saproxylic Insects: Diversity, Ecology and*

Conservation. Zoological Monographs(ed. by M. Ulyshen), Vol. **1**, pp. p. 471–514. Springer, Cham.

Buse, J., Levanony, T., Timm, A., Dayan, T. & Assmann, T. (2010) Saproxylic beetle assemblages in the Mediterranean region: impact of forest management on richness and structure. *Forest Ecology and Management*, **259**, 1376–1384.

Canadell, J.G. & Raupach, M.R. (2008) Managing forests for climate change mitigation. *Science*, **320**, 1456–1457.

Chira, D., Dănescu, F., Roşu, C., Chira, F., Mihalciuc, V., Surdu, A. & Nicolescu, V.-N. (2003) Some recent issues regarding the European beech decline in Romania. *Annals of Forest Research*, **46**, 167–176.

Connor, E., Faeth, S., Simberloff, D. & Opler, P. (1980) Taxonomic isolation and the accumulation of herbivorous insects – a comparison of introduced and native trees. *Ecological Entomology*, **5**, 205–211.

Dajoz, R. (2000) *Insects and Forests: The Role and Diversity of Insects in the Forest Environment*, Vol. **668**. Intercept Lavoisier Publishing, Paris.

Dalin, P. & Björkman, C. (2008) Native insects colonizing introduced tree species—patterns and potential risks. *Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems*(ed. by T. D. Paine), pp. 63–77. Springer, Dordrecht.

De Cáceres, M. & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*, **90**, 3566–3574.

Degomez, T. & Wagner, M.R. (2001) Arthropod diversity of exotic vs. native Robinia species in Northern Arizona. *Agricultural and Forest Entomology*, **3**, 19–27.

Della Rocca, F., Stefanelli, S. & Bogliani, G. (2016) *Robinia pseudoacacia* as a surrogate for native tree species for saproxylic beetles inhabiting the riparian mixed forests of northern Italy. *Agricultural and Forest Entomology*, **18**(3), 250–259.

Engelmark, O., Sjöberg, K., Andersson, B., Rosvall, O., Ågren, G.I., Baker, W.L., Barklund, P., Björkman, C., Despain, D.G., Elfving, B., Ennos, R.A., Karlman, M., Knecht, M.F., Knight, D.H., Ledgard, N.J., Lindelöw, Å., Nilsson, C., Peterken, G.F., Sörlin, S. & Sykes, M.T. (2001) Ecological effects and management aspects of an exotic tree species; the case of Lodgepole pine in Sweden. *Forest Ecology and Management*, **141**, 3–13.

Evans, H. (1987) Sitka spruce insects: past, present and future. *Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences*, **93**, 157–167.

Felton, A., Boberg, J., Björkman, C. & Widenfalk, O. (2013) Identifying and managing the ecological risks of using introduced tree species in Sweden's production forestry. *Forest Ecology and Management*, **307**(1), 165–177.

Fierro, A., Grez, A., Vergara, P.M., Ramírez-Hernández, A. & Micó, E. (2017) How does the replacement of native forest by exotic forest plantations affect the diversity, abundance and trophic structure of saproxylic beetle assemblages? *Forest Ecology and Management*, **405**, 246–256.

Fraser, S.M. & Lawton, J.H. (2008) Host range expansion by British moths onto introduced conifers. *Ecological Entomology*, **19**, 127–137.

Gange, A.C., Gange, E.G., Mohammed, A.B. & Boddy, L. (2011) Host shifts in fungi caused by climate change? *Fungal Ecology*, **4**, 184–190.

Gillmann, M., Cailleret, M., Boivin, T., Nageleisen, L.-M. & Davi, H. (2014) Individual vulnerability factors of Silver fir (*Abies alba* Mill.) to parasitism by two contrasting biotic agents: mistletoe (*Viscum album* L. ssp. abietis) and bark beetles (Coleoptera: Curculionidae Scolytinae) during a decline process. *Annals of Forest Science*, **71**(6), 659–673.

Gossner, M. & Ammer, U. (2006) The effects of Douglas-fir on tree-specific arthropod communities in mixed species stands with European beech and Norway spruce. *European Journal of Forest Research*, **125**, 221–235.

Gossner, M.M., Chao, A., Bailey, R.I. & Prinzing, A. (2009) Native fauna on exotic trees: phylogenetic conservatism and geographic contingency in two lineages of phytophages on two lineages of trees. *The American Naturalist*, **173**, 599–614.

Hartley, M.K., Rogers, W.E. & Siemann, E. (2010) Comparisons of arthropod assemblages on an invasive and native trees: abundance, diversity and damage. *Arthropod Plant Interactions*, **4**, 237–245.

Heilmann-Clausen, J. & Læssøe, T. (2012) On species richness estimates, climate change and host shifts in wood-inhabiting fungi. *Fungal Ecology*, **5**(5), 641–646.

Kappes, H. & Topp, W. (2004) Emergence of Coleoptera from deadwood in a managed broadleaved forest in central Europe. *Biodiversity and Conservation*, **13**, 1905–1924.

Kostanjsek, F., Sebek, P., Baranova, B., Seric Jelaska, L., Riedl, V. & Cizek, L. (2018) Size matters! Habitat preferences of the wrinkled bark beetle, *Rhysodes sulcatus*, the relict species of European primeval forests. *Insect Conservation and Diversity*, **11**, 545–553.

Lachat, T., Peveling, R., Attignon, S., Goergen, G., Sinsin, B. & Nagel, P. (2007) Saproxylic beetle assemblages on native and exotic snags in a West African tropical forest. *African Entomology*, **15**, 13–24.

Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.

Lassauce, A., Lieutier, F. & Bouget, C. (2012) Woodfuel harvesting and biodiversity conservation in temperate forests. Effects of logging residue characteristics on saproxylic beetle assemblages. *Biological Conservation*, **147**(1), 204–212.

Lindelöw, Å. & Björkman, C. (2001) Insects on lodgepole pine in Sweden — current knowledge and potential risks. *Forest Ecology and Management*, **141**(1–2), 107–116.

Lombardero, M.J., Alonso-Rodríguez, M. & Roca-Posada, E.P. (2012) Tree insects and pathogens display opposite tendencies to attack native vs. non-native pines. *Forest Ecology and Management*, **281**, 121–129.

Mansfield, S., McNeill, M.R., Aalders, L.T., Bell, N.L., Kean, J.M., Barratt, B.I.P., Boyd-Wilson, K. & Teulon, D.A.J. (2019) The value of sentinel plants for risk assessment and surveillance to support biosecurity. *NeoBiota*, **48**, 1–24.

McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, **14**(11), 450–453.

Mori, A.S., Lertzman, K.P. & Gustafsson, L. (2017) Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *Journal of Applied Ecology*, **54**, 12–27.

Müller, J., Wende, B., Strob, C., Eugster, M., Gallenberger, I., Floren, A., Steffan-Dewenter, I., Linsenmair, K.E., Weisser, W.W., & Gossner, M.M. (2015) Forest management and regional tree composition drive the host preference of saproxylic beetle communities. *Journal of Applied Ecology*, **52**, 753–762.

Neuvonen, S. & Niemela, P. (1981) Species richness of Macrolepidoptera on Finnish deciduous trees and shrubs. *Oecologia*, **51**, 364–370.

Nittérus, K., Gunnarsson, B. & Axelsson, E. (2004) Insects reared from logging residue on clear-cuts. *Entomologica Fennica*, **15**, 53–61.

R Core Team. (2018) R: A Language and Environment for Statistical Computing, v3.5.1., Vienna, Austria. Available at: https://www.R-project.org/.

Roques, A., Auger-Rozenberg, M.A. & Boivin, S. (2006) A lack of native congeners may limit colonization of introduced conifers by indigenous insects in Europe. *Canadian Journal in Forest Research*, **36**, 299–313.

Schmid, M., Pautasso, M. & Holdenrieder, O. (2014) Ecological consequences of Douglas fir (*Pseudotsuga menziesii*) cultivation in Europe. *European Journal of Forest Research*, **133**(1), 13–29.

Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C. & Firbank, L.G. (2006) Biotic homogenization and changes in

species diversity across human-modified ecosystems. *Proceedings of the Royal Society of London Series B Biological Sciences*, **273** (1601), 2659–2665.

Stokland, J.N., Siitonen, J. & Jonsson, B.G. (2012) *Biodiversity in Dead-Wood*. Cambridge University Press, Cambridge.

Thuillier, W., Lavorel, S., Araujo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*, **102**(23), 8245–8250.

Tschopp, T., Holderegger, R. & Bollmann, K. (2015) Auswirkungen der Douglasie auf die Waldbiodiversität. *Schweizerische Zeitschrift für Forstwesen*, **166**(1), 9–15.

Ulyshen, M.D., Pawson, S.M., Branco, M.P., Van Horn, S.J., Hoebeke, E.R. & Gossner, M.M. (2018) Chapter 23: utilization of non-native wood by saproxylic insects. *Saproxylic Insects: Diversity, Ecology and Conservation. Zoological Monographs*(ed. by M. Ulyshen), Vol. **1**, pp. p. 797–834. Springer, Cham.

Zumr, V. (1992) Attractiveness of introduced conifers to xylophagous beetles and their acceptance. *Journal of Applied Entomology*, **113**, 233–238.

APPENDIX

Table A1. Number of empty emergence bags per plot (*n* = 40 plots) across the sampling design for four paired tree species. Possible values for the empty bags are 0, 1 or 2. Variations in empty bag metrics related to tree species (*P*-value based on likelihood ratio tests comparing null models and generalised (Poisson) linear mixed models): conifer-douglas fir mean = 0.80 ± se0.15, silver fir mean = 0.55± se0.15 (pval = 0.33 ns); deciduous-beech mean = 0.35 ± se0.13, oak mean = 0.30± se0.12 (pvam = 0.78 ns).

Tree species group	Tree species	Region	Plot	Nb of empty bags
deciduous	oak	baronnies1	1BARHE	0
deciduous	oak	baronnies1	1HECHE	0
deciduous	oak	baronnies1	2BARHE	0
deciduous	oak	baronnies1	2HECHE	1
deciduous	oak	baronnies1	3BARHE	0
deciduous	oak	baronnies1	3HECHE	0
deciduous	oak	baronnies1	4BARHE	0
deciduous	oak	baronnies1	4HECHE	2
deciduous	oak	baronnies1	5HECHE	0
deciduous	oak	baronnies1	6HECHE	1
deciduous	oak	normandie	108EAWY	0
deciduous	oak	normandie	143EAWY	0
deciduous	oak	normandie	181EAWY	1
deciduous	oak	normandie	256EAWY	0
deciduous	oak	normandie	285EAWY	0
deciduous	oak	normandie	29EAWY	0
deciduous	oak	normandie	354EAWY	0
deciduous	oak	normandie	458EAWY	0
deciduous	oak	normandie	54EAWY	0
deciduous	oak	normandie	88EAWY	1
conifer	douglas	baronnies2	1BANSA	2
conifer	douglas	baronnies2	1BARSA	2
conifer	douglas	baronnies2	1HECSA	1
conifer	douglas	baronnies2	2BANSA	1
conifer	douglas	baronnies2	2HECSA	1
conifer	douglas	baronnies2	3BANSA	1
conifer	douglas	baronnies2	3HECSA	0
conifer	douglas	baronnies2	4HECSA	2
conifer	douglas	baronnies2	5HECSA	1
conifer	douglas	baronnies2	6HECSA	0
conifer	douglas	sault	10COM	1
conifer	douglas	sault	1COM	1
conifer	douglas	sault	2COM	0
conifer	douglas	sault	3COM	0
conifer	douglas	sault	4COM	0
conifer	douglas	sault	5COM	1
conifer	douglas	sault	6COM	1
conifer	douglas	sault	7COM	0
conifer	douglas	sault	8COM	0
conifer	douglas	sault	9COM	1
deciduous	beech	baronnies1	1BARHE	0
deciduous	beech	baronnies1	1HECHE	0
deciduous	beech	baronnies1	2BARHE	0
deciduous	beech	baronnies1	2HECHE	0
deciduous	beech	baronnies1	3BARHE	0
deciduous	beech	baronnies1	3HECHE	0
deciduous	beech	baronnies1	4BARHE	0
deciduous	beech	baronnies1	4HECHE	2
deciduous	beech	baronnies1	5HECHE	1
deciduous	beech	baronnies1	6HECHE	1

(continued)

Table A1. (continued)

Tree species group	Tree species	Region	Plot	Nb of empty bags
deciduous	beech	normandie	108EAWY	0
deciduous	beech	normandie	143EAWY	1
deciduous	beech	normandie	181EAWY	0
deciduous	beech	normandie	256EAWY	1
deciduous	beech	normandie	285EAWY	0
deciduous	beech	normandie	29EAWY	0
deciduous	beech	normandie	354EAWY	1
deciduous	beech	normandie	458EAWY	0
deciduous	beech	normandie	54EAWY	0
deciduous	beech	normandie	88EAWY	0
conifer	silver fir	baronnies2	1BANSA	1
conifer	silver fir	baronnies2	1BARSA	1
conifer	silver fir	baronnies2	1HECSA	0
conifer	silver fir	baronnies2	2BANSA	2
conifer	silver fir	baronnies2	2HECSA	0
conifer	silver fir	baronnies2	3BANSA	0
conifer	silver fir	baronnies2	3HECSA	1
conifer	silver fir	baronnies2	4HECSA	1
conifer	silver fir	baronnies2	5HECSA	1
conifer	silver fir	baronnies2	6HECSA	1
conifer	silver fir	sault	10COM	0
conifer	silver fir	sault	1COM	0
conifer	silver fir	sault	2COM	2
conifer	silver fir	sault	3COM	1
conifer	silver fir	sault	4COM	0
conifer	silver fir	sault	5COM	0
conifer	silver fir	sault	6COM	0
conifer	silver fir	sault	7COM	0
conifer	silver fir	sault	8COM	0
conifer	silver fir	sault	9COM	0

Table A2. List of species and related ecological traits: host tree preference, feeding guild (Myc = Mycetophagous, Xyl = Xylophagous, Sxy = Saproxylophagous, Zoo = zoophagous), rarity group, ab.decid (cumulative number of individuals in deciduous deadwood), ab.conif (cumulative number of individuals in conifer deadwood). Host tree preference was encoded with an index value: 1 (oligophagous or oak specialists associated with a few deciduous tree species at most), 2 (associated with deciduous tree species in general), 3 (polyphagous generalists associated to both conifer and decidous tree species), 4 (associated with conifer tree species in general), and 5 (oligophagous or fir specialists associated with a few conifer tree species at most).

Species	Family	Dataset	Host tree preference	Feeding guild	Rarity group	ab. oak	ab. beech	ab. douglas	ab. abies
Acalles micros Dieckmann, 1982	CURCULIONIDAE	deciduous	2	Xyl	common	3	2	0	0
Acalles misellus Boheman, 1844	CURCULIONIDAE	deciduous	3	Xyl	common	1	0	0	0
Anaspis maculata Geoffroy in Fourcroy, 1785	SCRAPTIIDAE	conifer	2	Sxy	common	0	0	0	1
Anisandrus dispar (Fabricius, 1792)	CURCULIONIDAE	deciduous	3	Xyl	common	49	14	0	0
Arthrolips fasciata (Erichson, 1842)	CORYLOPHIDAE	deciduous,conifer	2	Sap	common	2	0	1	1
Atomaria sp.	CRYPTOPHAGIDAE	deciduous	3	Myc	common	0	0	0	0
Aulonothroscus brevicollis (Bonvouloir, 1859)	THROSCIDAE	deciduous	2	Sxy	common	1	0	0	0
Bryaxis curtisii (Leach, 1817)	STAPHYLINIDAE	deciduous	3	Zoo	common	1	0	0	0
Cartodere nodifer (Westwood, 1839)	LATRIDIIDAE	deciduous, conifer	2	Myc	common	0	4	2	1
Cerylon fagi C. Brisout de Barneville, 1867	CERYLONIDAE	deciduous	2	Myc	common	2	0	0	0
Cerylon histeroides (Fabricius, 1792)	CERYLONIDAE	deciduous	3	Myc	common	0	1	0	0
Corticarina sp.	LATRIDIIDAE	conifer	3	Myc	common	0	0	0	0
Cryphalus asperatus (Gyllenhal, 1813)	CURCULIONIDAE	conifer	4	Xyl	common	0	0	4	50
Cryptolestes duplicatus (Waltl, 1839)	LAEMOPHLOEIDAE	deciduous	2	Zoo	common	3	0	0	0
Cryptophagus sp.	CRYPTOPHAGIDAE	deciduous, conifer	3	Myc	common	0	0	0	0
Dacne bipustulata (Thunberg, 1781)	EROTYLIDAE	deciduous	3	Myc	common	0	1	0	0
Dasytes croceipes Kiesenwetter, 1866	DASYTIDAE	conifer	3	Zoo	common	0	0	0	1
Diplocoelus fagi Guérin-Méneville, 1838	BIPHYLLIDAE	deciduous	1	Myc	common	9	16	0	0
Dryocoetes autographus (Ratzeburg, 1837)	CURCULIONIDAE	conifer	4	Xyl	common	0	0	89	11
Epurea sp.	NITIDULIDAE	deciduous	3	Zoo	common	0	0	0	0
Eulagius filicornis (Reitter, 1887)	MYCETOPHAGIDAE	deciduous	1	Myc	common	1	0	0	0
Hylastes angustatus (Herbst, 1793)	CURCULIONIDAE	conifer	4	Xyl	common	0	0	1	0
Hylesinus varius (Fabricius, 1775)	CURCULIONIDAE	conifer	2	Xyl	common	0	0	1	0
Kyklioacalles pyrenaeus (Boheman, 1844)	CURCULIONIDAE	conifer	3	Xyl	rare	0	0	4	2
Laemophloeus kraussi Ganglbauer, 1897	LAEMOPHLOEIDAE	deciduous	2	Zoo	rare	0	3	0	0
Leiodes flavicornis (Brisout de Barneville, 1884)	LEIODIDAE	conifer	2	Myc	common	0	0	1	0
Leiopus nebulosus (Linnaeus, 1758)	CERAMBYCIDAE	deciduous	2	Xyl	common	1	0	0	0
Lissodema lituratum (A. Costa, 1847)	SALPINGIDAE	conifer	2	Zoo	common	0	0	1	0

(continued)

Table A2. (continued)

Species	Family	Dataset	Host tree preference	Feeding guild	Rarity group	ab. oak	ab. beech	ab. douglas	ab. abies
Litargus connexus (Geoffroy, 1785)	MYCETOPHAGIDAE	deciduous	3	Myc	common	1	0	0	0
Palaeoacalles navieresi (Boheman, 1837)	CURCULIONIDAE	conifer	1	Xyl	common	0	0	0	8
Pissodes piceae (Illiger, 1807)	CURCULIONIDAE	conifer	5	Xyl	common	0	0	0	20
Pityokteines curvidens (Germar, 1824)	CURCULIONIDAE	conifer	5	Xyl	common	0	0	0	3
Placonotus testaceus (Fabricius, 1787)	LAEMOPHLOEIDAE	conifer	3	Zoo	common	0	0	0	7
Ptilinus fuscus Geoffroy in Fourcroy, 1785	PTINIDAE	deciduous	2	Sxy	common	1	0	0	0
Ptinomorphus imperialis (Linnaeus, 1767)	PTINIDAE	deciduous	2	Sxy	common	0	2	0	0
Pyrrhidium sanguineum (Linnaeus, 1758)	CERAMBYCIDAE	deciduous	2	Xyl	common	3	0	0	0
Rhizophagus bipustulatus (Fabricius, 1792)	MONOTOMIDAE	deciduous,conifer	3	Zoo	common	25	7	9	34
Rhizophagus dispar (Paykull, 1800)	MONOTOMIDAE	conifer	3	Zoo	common	0	0	4	7
Rhizophagus nitidulus (Fabricius, 1798)	MONOTOMIDAE	deciduous	3	Zoo	common	3	2	0	0
Rhyncolus ater (Linnaeus, 1758)	CURCULIONIDAE	conifer	4	Sxy	common	0	0	3	0
Salpingus planirostris (Fabricius, 1787)	SALPINGIDAE	deciduous	2	Zoo	common	1	0	0	0
Salpingus ruficollis (Linnaeus, 1760)	SALPINGIDAE	deciduous	3	Zoo	common	1	0	0	0
Scaphidium quadrimaculatum Olivier, 1790	STAPHYLINIDAE	conifer	3	Myc	common	0	0	1	0
Scolytus intricatus (Ratzeburg, 1837)	CURCULIONIDAE	deciduous	2	Xyl	common	5	0	0	0
Stenichnus scutellaris (P.W.J. Müller & Kunze, 1822)	STAPHYLINIDAE	conifer	2	Zoo	common	0	0	1	0
Tachyporus sp.	STAPHYLINIDAE	conifer	3	Zoo	common	0	0	0	0
Trachodes hispidus (Linnaeus, 1758)	CURCULIONIDAE	deciduous	3	Xyl	common	0	1	0	0
Trotomma pubescens Kiesenwetter, 1851	SCRAPTIIDAE	conifer	3	Sxy	common	0	0	1	0
Trypodendron signatum (Fabricius, 1792)	CURCULIONIDAE	deciduous	2	Xyl	common	5	2	0	0
Uleiota planatus (Linnaeus, 1760)	SILVANIDAE	conifer	3	Zoo	common	0	0	1	0
Xyleborinus saxesenii (Ratzeburg, 1837)	CURCULIONIDAE	deciduous,conifer	3	Xyl	common	159	69	7	2
Xyleborus monographus (Fabricius, 1792)	CURCULIONIDAE	deciduous	1	Xyl	common	4	1	0	0
Xylosandrus germanus (Blandford, 1894)	CURCULIONIDAE	deciduous	3	Xyl	common	913	245	0	0

Table A3. Variations in saproxylic beetle assemblage metrics related to tree species and study site (error structure: linear or generalised linear mixed-effects models). [m] = Mean values per bag; ± = standard error; ***$P < 0.001$, **$0.001 < P < 0.01$; *$0.01 < P < 0.05$; [ns] $P > 0.05$.

| | Deciduous | | | | | | Conifer | | | | | |
| | Eawy | | | Baronnies | | | Sault | | | Baronnies | | |
	Retreating substituted tree species (beech)	Expanding substitute tree species (sessile oak)		Retreating substituted tree species (beech)	Expanding substitute tree species (sessile oak)		Retreating substituted tree species (silver fir)	Exotic substitute tree species (douglas fir)		Retreating substituted tree species (silver fir)	Exotic substitute tree species (douglas fir)	
Number of individuals[m]	13.45 ± 3.99	49.05 ± 10.70	***	8.75 ± 2.13	15.25 ± 3.78	**	5.85 ± 1.92	1.90 ± 0.41	*	2.15 ± 0.58	5.10 ± 3.78	ns
Number of species[m]	2.55 ± 0.43	4.30 ± 0.56	**	2.75 ± 0.47	3.55 ± 0.61	*	1.70 ± 0.3	1.45 ± 0.26	ns	1.05 ± 0.26	0.70 ± 0.25	ns
CWM host preference[m]	2.70 ± 0.10	3.00 ± 0.12	ns	2.86 ± 0.08	2.89 ± 0.07	ns	3.09 ± 0.18	2.89 ± 0.13	ns	3.33 ± 0.11	3.50 ± 0.11	ns
FDis host preference[m]	0.42 ± 0.10	0.25 ± 0.05	ns	0.36 ± 0.06	0.21 ± 0.04	ns	0.35 ± 0.05	0.19 ± 0.04	ns	0.33 ± 0.04	0.22 ± 0.06	ns
Abundance of zoophagous beetles[m]	1.55 ± 0.54	2.15 ± 0.42	ns	1.50 ± 0.33	2.15 ± 0.61	ns	1.85 ± 0.75	0.90 ± 0.28	ns	0.95 ± 0.39	0.15 ± 0.08	ns
Species richness of zoophagous beetles[m]	0.50 ± 0.15	1.20 ± 0.22	ns	0.95 ± 0.19	1.10 ± 0.21	ns	0.50 ± 0.15	0.70 ± 0.2	ns	0.50 ± 0.13	0.15 ± 0.08	ns
Abundance of wood-eating beetles[m]	10.75 ± 3.71	45.50 ± 10.49	***	6.05 ± 1.86	11.75 ± 3.31	***	3.85 ± 1.76	0.70 ± 0.2	*	1.05 ± 0.39	4.80 ± 3.79	ns
Species richness of wood-eating beetles[m]	1.05 ± 0.15	1.85 ± 0.27	*	0.85 ± 0.16	1.35 ± 0.27	*	1.05 ± 0.25	0.50 ± 0.13	ns	0.40 ± 0.13	0.40 ± 0.15	ns
Abundance ratio wood-eating/zoophagous[m]	7.44 ± 2.41	34.18 ± 10.29	**	4.17 ± 1.63	5.38 ± 1.82	ns	2.94 ± 1.81	0.55 ± 0.19	*	0.95 ± 0.39	4.75 ± 3.80	ns