Effects of management on ambrosia beetles and their antagonists in European beech forests

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Abstract

Land-use intensification has been shown to negatively affect biodiversity and ecosystem functioning. Because higher trophic levels are expected to suffer most strongly from intensification, negative consequences for ecosystem services, such as biological pest control by natural enemies, are likely. In European beech forests ambrosia beetles are common secondary pests of freshly cut wood and stored timber, but they may also infest living trees that are highly stressed.

We examined whether forest management intensity, ranging from unmanaged beech forests to non-natural conifer plantations, affects the abundance, attack rate, and breeding success of ambrosia beetles across three regions of Germany. We applied pheromone trapping to estimate the abundance of ambrosia beetles and exposed experimental beech logs to measure infestation rates and breeding success.

In general, we found decreasing abundance and attack probability by ambrosia beetles with increasing management intensity, which is most likely related to the availability of suitable breeding substrate. However, the abundance of the invasive species *Xylosandrus germanus* increased with increasing management intensity in one region, where high management intensity was represented by pine forests; the drier and warmer conditions in this forest type most likely increased population densities. Breeding success of *Trypodendron domesticum* increased with increasing management intensity, suggesting less effective pest control by natural antagonists, in particular by specialised parasitoids, at high management intensities.

We conclude that the availability of breeding substrate, in combination with microclimate and antagonist effectiveness, shape ambrosia beetle populations in Central European forests. Forest management strategies should thus reduce the availability of breeding substrate in production forests, in particular where microclimatic conditions are favourable for beetle reproduction (i.e. warm, moist). Moreover, unmanaged forest patches should be maintained to promote parasitoid abundance and thus to mitigate negative effects of climate change, such as increasing drought stress of trees.
Keywords: ambrosia beetles; bark beetles; Biodiversity Exploratories; forest management practice; land-use intensity; parasitoid; pest control; pest species
1 Introduction

Land use has frequently been shown to negatively affect organismic diversity and is considered a main driver of current biodiversity loss (Sala et al., 2000). Negative consequences of a loss in biodiversity due to increasing land use for ecosystem functions and services are likely, but they are less well studied, in particular in forests. At the global scale, forests provide many ecosystem services that are of high economic, as well as ecological and recreational, value. Among these services, provision of timber for various purposes (provisioning service) and pest control (regulating service) ensure the sustainable economic value of forests and are relevant in many forest ecosystems (Millennium Ecosystem Assessment, 2005).

While effects of land use on potential pest species are well studied in agricultural systems (Chaplin-Kramer et al., 2011), responses of potential pest species to forest management are less clear. It is clear that forest management can significantly affect potential pest species and therefore forest health (Jactel et al., 2009). However, no or little effect of forest management on pest abundance and damage has been observed in non-outbreak situations, e.g. for the spruce bark beetle Ips typographus (Linnaeus, 1758) in Poland (Hilszczanski et al., 2007). On the one hand, higher trophic levels, i.e. predators and parasitoids, are expected to suffer the most from management intensification because they build up small populations and are thus more vulnerable to local extinctions (Didham et al., 1998). On the other hand, predator and parasitoid diversity are often positively associated with increased herbivore suppression (e.g. Snyder et al., 2006). Therefore, increased forest management activity may increase pest species abundance as a result of less effective control by natural enemies. However, results of previous studies on the response of natural enemies and predation or parasitisation rates have been inconsistent. While Martikainen et al. (1999) observed a higher abundance of antagonists with a higher abundance of bark beetles in boreal forests, Hilszczanski et al. (2007) did not find differences in the abundance of natural enemies of the economically important spruce bark beetle I. typographus between managed and
unmanaged forests in Poland. Similarly, Gossner et al. (2014b) did not find differences in parasitoid abundance of herbivores between unmanaged and differently managed beech forests.

Effects of forest management on pest species and their antagonists might also be mediated by changes in forest structure. In boreal forests, for example, the abundance of bark beetles was found to be most strongly (and positively) correlated with the amount of recent dead wood (Martikainen et al., 1999). Parasitoid assemblages were found to depend on a high diversity of dead wood habitats (Hilszczanski et al., 2005). A higher abundance of bark beetle predators of the genus *Thanasimus* appeared to be favoured by forest gaps and thus by decreased canopy cover (Hilszczanski et al., 2007). Top-down control of forest pests may exert an even greater influence on insect herbivores than resource availability (Vidal and Murphy, 2018). There is at least some indication that management changes can affect the relative importance of bottom-up and top-down effects (Klapwijk et al., 2016). More detailed knowledge on the consequences of forest management for potential forest pest species and their interaction with other organisms is urgently needed, not least because the sustainable provision of wood will be increasingly challenged by growing risks to forest health under climate change (Kausrud et al., 2012).

European beech forests (*Fagus sylvatica* L.) would naturally dominate Central European landscapes (Zerbe, 2002). Beech is infested by relatively few herbivore species (Brändle and Brandl, 2001), and large-scale outbreaks are rare. Nevertheless, a few species are economically relevant, in particular because they decrease wood quality (Grégoire et al., 2015). Among the bark beetles, ambrosia beetles are an example of such destructive species; they infest freshly harvested wood and thus reduce timber quality (Vega and Hofstetter, 2015). Regarding *Trypodendron domesticum* (Linnaeus, 1758) in particular, infestations of weakened trees, in combination with European beech bark disease (EBBD), and of apparently healthy, but in fact highly stressed, trees have been reported during the last 15 to 20 years, and this fundamentally new type of damage poses a threat to the beech-dominated ecosystems of Central Europe (Petercord, 2006). If and how forest management affects the abundance and attack rate of ambrosia beetles associated with beech and
The interactions of these beetles with their natural enemies is largely unknown. The aim of the present study was to determine the relationship between forest management intensity, the abundance and attack rate of ambrosia beetles, i.e. native *T. domesticum*, native *Xyleborus* spp. and the invasive pest *Xylosandrus germanus* (Blandford, 1894) (Hulcr *et al.*, 2017), and their control by natural antagonists.

Specifically, we hypothesised that increasing management intensity results in (1) increased abundance and attack rates of ambrosia beetles and (2) less effective biological control of ambrosia beetles by natural antagonists. Further, we hypothesised that (3) management effects on beetles and their natural enemies are mediated by management-induced structural alterations such as vertical stand layering, tree diversity, the amount of suitable breeding substrate in the surroundings, regeneration density, and canopy openness.

2 Materials and Methods

2.1 Study area and sites

The study was conducted in three regions in Germany (http://www.biodiversity-exploratories.de; Fischer *et al.*, 2010): Schorfheide-Chorin in the north-east, the Hainich region in the centre and the Schwäbische Alb in the south-west (Fischer *et al.* 2010) (henceforth: Schorfheide, Hainich, Alb). In our study 50 experimental forest plots (EP), each 100 m x 100 m in area, were selected in each of the three regions using a stratified random design (Fischer *et al.* 2010). The forests covered the regional range of main forest types, comprising unmanaged (abandoned for the last 20–70 years) and managed uneven-aged (only Hainich) and even-aged stands (including different developmental stages) dominated by European beech (*F. sylvatica*). Additionally, even-aged oak forests (*Quercus petraea* Mattuschka Liebl.; only Schorfheide) and managed coniferous forests, dominated by either Norway spruce (*Picea abies* (L.) H. Karst.; Alb, Hainich) or Scots pine (*Pinus sylvestris* L.; Schorfheide), were included. The number of plots of each forest type sampled in each region is given in Table S1-1 (Supplement S1). In 2011 a selection of plots in Hainich were resampled.
2.2 Forest management intensity

To quantify management intensity of the studied forests, we used the quantitative forest management intensity index (ForMI) proposed by Kahl and Bauhus (2014). This index comprises three indicators: (1) the proportion of wood volume removed by harvesting; (2) the proportion of non-native tree species of the total standing, recently harvested and dead wood volume; and (3) the proportion of dead wood volume that originated from harvesting activities. The index is scaled continuously from 0 (no management) to 3 (very intensive management).

2.3 Large-scale beetle sampling using pheromones

2.3.1 Pheromone trapping

We focused on the group of ambrosia beetles because they are important in Central Europe and can be monitored using traps baited with pheromone or ethanol (Lieutier et al., 2007; Bussler et al., 2011). Preliminary studies in two managed and two unmanaged stands conducted in 2009 showed that, among the individuals caught by pheromone and ethanol baited traps, 63–77% (mean ± 1 SE = 67 ± 3) of the individuals belong to the tribes Xyloterini and Xyleborini (genera Anisandrus, Trypodendron and Xylosandrus).

To estimate the abundance of ambrosia beetles and their antagonists, we used modified bottle-traps protected from rain by a roof and baited with lineatin and ethanol (Supplement S2). In late February 2010, two traps were installed at a distance of 2 m at one randomly selected corner of each 1 ha experimental plot in all three regions (total 150 plots). The traps were set up so they faced the main wind direction, one to the north and one to the east. In 2011, 34 traps were reinstalled in the Hainich region in late February to test for consistency of management effects between years. The traps were emptied every one to two weeks during the main flight period, until about July, and every four weeks afterwards until flight activity dropped to a low level, no later than the end of
September. All catches were preserved in 70% ethanol. The protocol of species identification is
given in Supplement S3.

2.3.2 Target pest species

Previous analyses showed that, among species in the genus *Trypodendron*, high abundances of the
hardwood-associated species *T. domesticum* and the softwood-associated species *Trypodendron lineatum* (Olivier, 1795) occurred at the sample sites, with the latter preferring conifers. Among the
ambrosia beetles of the tribe Xyleborini, the native *Anisandrus dispar* (Fabricius, 1792) and the
invasive (since the 1950s; Groschke, 1952; Kirkendall and Faccoli, 2010) *X. germanus* occurred in
large numbers. We thus focused on the hardwood-associated species *T. domesticum, A. dispar* and
*X. germanus* in this study (for details see Supplement S3).

2.3.3 Ambrosia beetle natural enemies

Antagonists of bark and ambrosia beetles from many different taxonomic orders and families are
known (Kenis *et al.*, 2004; Wegensteiner *et al.*, 2015). Here, we focused on predatory beetles and
parasitoids (Hymenoptera: Apocrita) (Wegensteiner *et al.*, 2015) (for details see Supplement S3).

2.4 Experimental analysis of attack rates and interactions with natural enemies

For analysing the attack rate of ambrosia beetles, beech logs were exposed in two experiments: the
*Ambrosia Beetle Experiment* (*AmbroBEx*) and the *Biodiversity Exploratories Longterm Deadwood Experiment* (*BELongDead*) (Supplement S2, Gossner *et al.*, 2016; Kahl *et al.*, 2017).

Briefly, in *AmbroBEx*, logs of two different sizes, i.e. 100 cm long and 20 cm in diameter (‘large’
logs) and 60 cm long and 30 cm in diameter (‘small logs’), were exposed in the Hainich region
between mid-February and mid-March 2010. In each of 30 forest plots, we also used three beech
logs 4 m long and 23–46 cm in diameter from the *BELongDead* experiment. We classified entrance
holes by whether they were from *T. domesticum* or *X. germanus* (Supplement S2).
2.5 Breeding success of *T. domesticum*

Breeding-system ecleectors were installed on AmbroBEx and BELongDead logs with entrance holes to *T. domesticum* galleries suitable for eclector installation, i.e. not pointing directly towards the ground, to collect all emerging individuals of *T. domesticum* and its antagonists (Fig. S2-1 C and D in Supplement 2). We quantified breeding success of *T. domesticum* as the number of emerged progeny and assessed mortality by using information from the literature on the number of bark beetle eggs or larvae consumed by an individual predator (for details see Supplement S3).

2.6 Management-dependent changes in forest structure parameters

We assessed potential covariates at three different scales: individual log, subplot and plot.

*Log-based covariates:* We assessed the bark-free area on all logs (AmbroBEx, BELongDead) because damaged bark increases dehydration. For AmbroBEx logs, we additionally recorded the bark texture using four categories, from smooth to rough, to consider the general suitability for gallery starting points.

*Subplot-based covariates:* Within a 50-m circle around each trap we assessed the following three variables: (1) breeding resource availability, measured as the amount of dead wood in a stage suitable for ambrosia beetles, i.e. fresh dead wood, using five categories: 1 = no dead wood, 2 = \( \leq 3 \) m\(^3\) ha\(^{-1}\), 3 = \( 3 < x \leq 6 \) m\(^3\) ha\(^{-1}\), 4 = \( 6 < x \leq 10 \) m\(^3\) ha\(^{-1}\), and 5 = \( > 10 \) m\(^3\) ha\(^{-1}\); (2) canopy closure, an indicator for microclimatic conditions due to warming of dead wood logs by sunlight, was assessed as the estimated proportion of the sky covered by vegetation when looking straight up from the traps’ location at 1 m above the ground; (3) the density of vegetation, such as seedlings and young trees, projecting within 3–5 m of the direct flight corridor to the traps was recorded using three categories; ‘open’, ‘medium’ and ‘dense’.

*Plot-based covariates:* We considered (1) the main tree type, i.e. coniferous or broad-leaved forest, and (2) the forest structure, i.e. even-aged, uneven-aged or unmanaged, as classified in the forest.
inventory (Hessenmöller et al., 2011). We additionally assessed (3) the Shannon-diversity of the tree layer assessed within a 20 m x 20 m core area (Boch et al., 2013).

2.7 Data analyses

For statistical analyses we used generalized linear models (GLM) and generalized linear mixed effects models (GLMM) in R version 3.1.2 (R Core Team, 2014). For count data we used the “glmmadmb” function from the R package glmmADMB (Fournier et al., 2012; Skaug et al., 2015), and for binomial data (attack rates, breeding success) we used the “glm” and “glmer” functions from the package lme4 (Bates et al., 2015). When building the full models based on count data, we first checked for overdispersion by calculating the ratio of the sum of squared Pearson residuals (SSQ residuals) to the residual degrees of freedom and by comparing the Poisson error distribution with the negative-binomial error distribution using a likelihood ratio test (lmtest package; Zeileis and Hothorn, 2002). A model without overdispersion has a ratio close to or greater than one. When the likelihood ratio test showed a significant difference, a negative-binomial model was used. Any remaining overdispersion was accounted for by including observation-level random effects (Jamil et al., 2013). When the frequency plot of the data suggested zero-inflation, we compared models with and without the built-in correction for zero-inflation with the “glmmadmb” function. To find the minimal adequate model and determine a given term’s p-value, we applied manual backward selection by performing single-term deletion with the “drop1” function. A term was considered significant when its Chi^2-statistic p-value was <0.05. The term furthest from this criterion was excluded in the next step.

For categorial variables, we performed a post-hoc Tukey test with the “glht” function from the multcomp package (Hothorn et al., 2008) to identify significant pairwise differences. Details on the different models can be found in Supplement S4.

3 Results
3.1 Abundance of ambrosia beetles and their antagonists

In total 83% of the individuals caught in the pheromone traps were ambrosia beetles and <1% were potential natural enemies. *Trypodendron domesticum*, *T. lineatum*, *X. germanus* and *A. dispar* were by far the most abundant species (Supplement S5). The overall abundance of ambrosia beetles decreased with increasing management intensity, but only in Hainich and Schorfheide (quasipoisson GLM: ForMI × region: $F_{2,144} = 16.417$, $p<0.001$). No effect was observed in Alb.

The abundance of antagonists increased with increasing management intensity, with only a weak interaction with region, reflecting the stronger effect in Schorfheide compared with in the other regions (quasipoisson GLM: ForMI × region: $F_{2,144} = 2.9889$, $p=0.054$, Figure S5-1).

The abundance of *T. domesticum* (model 1) varied between regions in 2010 and was highest in Hainich and lowest in Schorfheide (Tukey *post-hoc* test: $p<0.001$ for all pairwise tests). It consistently decreased with increasing management intensity (Fig. 1, Table 1a). More individuals were found in categories with larger amounts of dead wood (Table 1a; Tukey *post-hoc* test: $p<0.05$ for Cat. 3 & 4 > Cat. 1) and the number of antagonists was positively related to the number of *T. domesticum* individuals. No other covariates were significant.

The abundance of *X. germanus* (model 2) showed contrasting responses to management intensity in the different regions (significant interaction between ForMI and region; Fig. 1, Table 1a): while abundance decreased with increasing management intensity in Hainich, it increased in Schorfheide. In Alb, abundance was generally low. Regarding covariates, abundance showed a hump-shaped relationship in response to dead wood amount, with the highest values corresponding to plots with moderate dead wood amounts. Abundance was higher in plots dominated by broad-leaved trees than in plots dominated by conifers (Main tree type; Table 1a).

The results for *A. dispar* (model 3) were similar to those for *X. germanus*, with abundance being positively affected by management intensity in Hainich and negatively affected in Schorfheide (Fig. 1, Table 1a). Abundance in Alb was generally low, with abundance of *A. dispar* being higher in plots dominated by broad-leaved trees than in plots dominated by conifers (Main
While the number of antagonists was positively related to the number of X. germanus individuals, it was negatively related to the number of A. dispar individuals. Regarding antagonists, only the abundances of Rhizophagus depressus and Thanasimus formicarius were affected by management intensity, but responses depended on the region (significant interaction between ForMI and region; Table 1b). The abundance of R. depressus increased with increasing management intensity in all regions, but the slope of this relationship increased from Alb to Hainich to Schorfheide (data not shown). For T. formicarius increasing abundance with increasing management intensity was found only in Schorfheide; no effect was found in the other regions. With respect to the covariates, dead wood negatively affected the two Rhizophagus species, the density of the regeneration negatively affected all antagonist species, and the abundance of R. depressus and of T. formicarus was higher in coniferous compared with in broad-leaved forests.

In Hainich, where trapping was performed in two years, results from 2011 were consistent with those from 2010 (Supplement S6). The phenology of the ambrosia beetles is shown in Supplement S7.
Figure 1: Response of bark beetle abundance (A: *Trypodendron domesticum*, B: *Xylosandrus germanus*, C: *Anisandrus dispar*) to forest management intensity in the three study regions in Germany, based on pheromone trap samples from the year 2010. Regression lines are predictions from GLMMs (for model details see Table 1).
Table 1: Effects of forest management intensity (ForMI), its interaction with region, and covariates assessed at different spatial scales on the abundance of ambrosia beetles (a) and their antagonists (b). Note that the apocrit *Perniphora robusta* was too rare to be analysed. Results of the abundance model based on a negative binomial GLMM, minimal models, and the terms dropped during the optimisation test by backward selection (based on the p-value of a likelihood-ratio test) are shown.

Df = degrees of freedom; L = statistic value; p = significance level; ED = effect direction, ↑/↓ = positive/negative, ∩ = hump-shaped; DO = order in which the terms were dropped from the model.

FS = *Fagus sylvatica*, CO = conifers.

### (a) Species abundance

<table>
<thead>
<tr>
<th>Species abundance</th>
<th><em>Trypodendron domesticum</em></th>
<th><em>Xylosandrus germanus</em></th>
<th><em>Anisandrus dispar</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Df</td>
<td>L</td>
<td>p</td>
</tr>
<tr>
<td>ForMI</td>
<td>1</td>
<td>45.84</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Region</td>
<td>2</td>
<td>15.06</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>ForMI × Region</td>
<td>2</td>
<td>0.24</td>
<td>0.890</td>
</tr>
<tr>
<td>Abundance antagonists</td>
<td>1</td>
<td>9.68</td>
<td>0.002</td>
</tr>
<tr>
<td>Dead wood</td>
<td>4</td>
<td>13.12</td>
<td>0.011</td>
</tr>
<tr>
<td>Canopy closure</td>
<td>1</td>
<td>1.72</td>
<td>0.190</td>
</tr>
<tr>
<td>Density of regeneration</td>
<td>2</td>
<td>3.96</td>
<td>0.140</td>
</tr>
<tr>
<td>Tree diversity</td>
<td>1</td>
<td>1.70</td>
<td>0.190</td>
</tr>
<tr>
<td>Main tree type</td>
<td>1</td>
<td>1.52</td>
<td>0.220</td>
</tr>
</tbody>
</table>

Random factor

<table>
<thead>
<tr>
<th>Species abundance</th>
<th><em>Rhizophagus bipustulatus</em></th>
<th><em>Rhizophagus depressus</em></th>
<th><em>Thanasimus formicarius</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Df</td>
<td>L</td>
<td>p</td>
</tr>
<tr>
<td>ForMI</td>
<td>1</td>
<td>0.274</td>
<td>0.600</td>
</tr>
<tr>
<td>Region</td>
<td>2</td>
<td>11.772</td>
<td>0.003</td>
</tr>
<tr>
<td>ForMI × Region</td>
<td>2</td>
<td>1.096</td>
<td>0.570</td>
</tr>
<tr>
<td>Abundance <em>T. domesticum</em></td>
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<td>21.858</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Dead wood</td>
<td>4</td>
<td>10.874</td>
<td>0.030</td>
</tr>
<tr>
<td>Canopy closure</td>
<td>1</td>
<td>0.976</td>
<td>0.320</td>
</tr>
<tr>
<td>Density of regeneration</td>
<td>2</td>
<td>15.952</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Tree diversity</td>
<td>1</td>
<td>5.436</td>
<td>0.020</td>
</tr>
</tbody>
</table>
3.2 Attack rates

Results on attack rates (per log) are given here; results for attack density (per m²) were consistent with these findings and are given in Supplement S8. For the AmbroBEx-logs, 27 of the 50 large logs (54%) and 39 of the 50 small logs (78%) were attacked by *T. domesticum*. The probability that an AmbroBEx-log will be attacked by *T. domesticum* was determined with respect to management intensity only; it dropped from about 52% in unmanaged forests to about 10% in forests with the highest management intensities (Fig. 2, Table 2). Regarding the BELongDead-logs, 71 (80%) were attacked by *T. domesticum*.
Figure 2: Probability that an AmbroBEx-log will be attacked by (A) Trypodendron domesticum or (B) Xylosandrus germanus. The regression line shows the predictions from a logistic generalised linear model (for model details see Table 2).
Table 2: Effects of forest management intensity (ForMI), its interaction with region, and covariates assessed at different spatial scales on the attack rate of ambrosia beetles on experimentally exposed logs. We used a binomial GLM to assess probability. Minimal models and the terms dropped during the optimisation test by backward selection (based on the p-value of a likelihood ratio test) are given. Df = degrees of freedom; L = statistic value; p = significance level; ED = effect direction, only given for continuous terms; ↑/↓ = positive/negative correlation with attack rate; DO = order in which the terms were dropped from the model.

<table>
<thead>
<tr>
<th></th>
<th>Model 4</th>
<th></th>
<th>Model 6</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Trypodendron domesticum</td>
<td></td>
<td>Xylosandrus germanus</td>
<td></td>
</tr>
<tr>
<td>Abundance in traps</td>
<td>1</td>
<td>2.725</td>
<td>0.099</td>
<td>(7)</td>
</tr>
<tr>
<td>ForMI</td>
<td>1</td>
<td>6.336</td>
<td>0.012</td>
<td>↓</td>
</tr>
<tr>
<td>Dead wood</td>
<td>4</td>
<td>7.561</td>
<td>0.11</td>
<td>(6)</td>
</tr>
<tr>
<td>Canopy closure</td>
<td>1</td>
<td>0.144</td>
<td>0.70</td>
<td>(3)</td>
</tr>
<tr>
<td>Tree diversity</td>
<td>§</td>
<td>§</td>
<td>§</td>
<td>§</td>
</tr>
<tr>
<td>Density of regeneration</td>
<td>2</td>
<td>0.471</td>
<td>0.79</td>
<td>(1)</td>
</tr>
<tr>
<td>Main tree type</td>
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<td>1.142</td>
<td>0.29</td>
<td>(5)</td>
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<tr>
<td>Bark free area</td>
<td>1</td>
<td>1.599</td>
<td>0.21</td>
<td>(8)</td>
</tr>
<tr>
<td>Bark texture</td>
<td>3</td>
<td>2.157</td>
<td>0.54</td>
<td>(4)</td>
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<tr>
<td>Beetle diversity</td>
<td>1</td>
<td>0.305</td>
<td>0.58</td>
<td>(2)</td>
</tr>
<tr>
<td>Log class</td>
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<td>NA§</td>
<td>NA§</td>
<td>NA§</td>
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<tr>
<td>Random factor</td>
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<td>none (binomial GLM)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

§ this factor had the highest p-value in single linear models and was therefore excluded prior to analyses to avoid overfitting

§ only the 100 cm x 20 cm logs were included in this model

A probability model for X. germanus showed a decrease in attack probability with increasing management intensity (Fig. 2, Table 2). As the abundance of X. germanus was highly correlated with the attack probability and with ForMI in Hainich, attack probability was only significant when abundance was excluded from the model. Other covariates had no significant effect on attack rate. With respect to the BELongDeadlogs, 83 (92%) were attacked by Xyloborini.

3.3 Breeding success
A total of 230 breeding systems of *T. domesticum* were sampled (Supplement S9 & S10). The main period of emergence in 2011 was from February to April, when 97.2% of the sampled *T. domesticum* emerged from the breeding systems (total N=750; Fig S7-2 in Supplement 7). On average only 3.39 ± 0.45 (range: 0–35) individuals emerged per breeding system. Regarding emerging antagonists, a total of 95 predatory beetles (mean ± 1 SE: 0.34 ± 0.12; range: 0–21) and 104 parasitoids (mean ± 1 SE: 0.46 ± 0.15; range: 0–20) were caught.

The number of antagonists that emerged was negatively affected by management intensity (Df=1, 221; L=6.174; p=0.015). The main antagonist observed, *Perniphora robusta*, exclusively emerged from breeding systems in unmanaged plots. The number of emerged antagonists was higher in breeding systems where the eclector was installed later (20 weeks after the gallery was discovered; Df=1,221; L=5.354; p=0.021). Mortality of *T. domesticum*, measured as the ratio of consumed to emerged beetles, was significantly negatively affected by management intensity (Figure 3; Df=1,166; L=264.84; p<0.001).
Figure 3: Mortality rate of *Trypodendron domesticum* as a function of management intensity. The dotted regression line shows the predictions from a binomial generalised linear mixed effects model. N=169 breeding system eclectors in 18 plots.
Discussion

Our large-scale study on ambrosia beetles in Central European forests revealed significant effects of management intensity on their overall abundance, attack probability and density, and breeding success. The pheromone traps were very effective in catching ambrosia beetles and the aggregation pheromone Lineatin also clearly attracted several antagonist species, supporting results from previous studies (Kenis et al., 2004). The insects are attracted from the area near the traps, and it can thus be assumed that more sampled individuals reflects more individuals in the surrounding area (Grégoire et al., 2001).

4.1 Effects of management intensity on abundance and attack probability of pest species

Increasing management intensity consistently decreased abundance and attack probability of *T. domesticum* across all regions and years, suggesting a general relationship between these variables. This is in contrast to our expectation that beetle abundance, and thus the probability that a log will be attacked, rises with increasing management intensity, owing to greater availability of fresh dead wood at higher management intensities because of more frequent harvesting operations (Schlyter and Lundgren, 1993). In our study, however, the availability of dead wood suitable for ambrosia beetles decreased with increasing management intensity (Fig. S11-1 in Supplement 11), and this unexpected relationship is the most likely explanation for our finding. This interpretation is supported by the observed positive effect of dead wood availability on the abundance and attack density of *T. domesticum*. Other studies have provided inconsistent results. Martikainen *et al.* (1996), for example, did not find a difference in overall bark beetle abundance between less intensively managed Russian and intensively managed Finnish Karelia. However, in line with our results they observed a difference in species composition, with a lower abundance of the broad-leaf specialist *Trypodendron signatum* in the less intensively managed forests.
The negative relationship between management intensity and abundance in our study might have been strengthened by the fact that *T. domesticum* prefers broad-leaved trees for breeding (Byers, 1992). However, the lack of a significant contrast between broad-leaved and coniferous forests suggests that a difference in available breeding substrate related to management intensity is the key driver. In the unmanaged forests studied here, management ceased relatively recently (20-70 years ago) and thus available dead wood is still dominated by early decay stages; it can be expected that dead wood amount will further increase with time, but mostly because of an increase of later decay stages, resulting in a more even distribution of dead wood decay stages (Morrissey et al., 2014; Larrieu et al., 2019). Consequently, suitable breeding substrate and thus abundance of *T. domesticum* is not expected to increase substantially with time.

Regarding Xyleborini, the response to management intensity was less consistent across the regions in our study. The response was weak overall for the native species *A. dispar*, which preferentially attacks a wide range of broad-leaved trees and rarely attacks conifers (Lieutier et al., 2007). For the invasive species *X. germanus*, which primarily attacks hardwood trees and has a wide range of host species (Weber and McPherson, 1983), the relationship differed between Hainich (negative) and Schorfheide (positive). The generally wider host range of Xyleborini compared to that of *Trypodendron* might explain the weak relationship between *A. dispar* abundance and management intensity, in that a change in tree species composition along the management intensity gradient might be less important. However, Xyleborini prefer broad-leaved trees over conifers as hosts (Lieutier et al., 2007), and therefore the dominating tree type of a stand (broad-leaved vs. coniferous) might be more important than management intensity itself, as indicated by a significant effect of the main tree species in our models. The contrasting pattern in the invasive species *X. germanus* is surprising and might be explained by different effects of the two conifer species studied in the two regions, spruce in Hainich and pine in Schorfheide. Pine forests are much more open than spruce or beech forests, and the microclimate might thus be favourable for the development of *X. germanus*. This species has been shown to be able to attack
apparently healthy, but in fact highly stressed, trees (Ranger et al., 2015) and thus might become an increasing threat under climate change. The reason for this attraction may be that stressed trees emit ethanol, and Xyleborini (Anisandrus, Xyleborus, Xylosandrus) beetles have fungal symbionts that need ethanol within the wood to grow and outcompete other fungi (Ranger et al., 2018).

4.2 Effects of management intensity on antagonists and pest control

With increasing abundance of T. domesticum and X. germanus in the pheromone traps, the abundance of their natural enemies also increased. This positive relationship might be explained by bottom-up effects: higher habitat availability (suitable dead wood) leads to higher prey density, which in turn supports a larger number of predators and parasitoids. It could, however, also be explained by a common response of pests and antagonists to management intensity or by a combination of both factors. As predators have lower population densities than their prey, they might be more sensitive to changes that accompany shifts in management intensity, such as changes in the abundance of alternative prey for the obligate (T. formicarius) and facultative (Rhizophagus-species) bark beetle predators. Nuorteva (1956), for instance, suggested that natural forests harbour larger populations of predators and parasitoids because of the high abundance of secondary bark beetles as alternative prey. For T. domesticum, this positive prey–predator relationship could be explained mainly by the behaviour of R. bipustulatus, which did not respond to differences in management intensity. This suggests a bottom-up effect of T. domesticum abundance on R. bipustulatus abundance. For X. germanus, a common response to management intensity is more likely because it, as well as its predators R. depressus and T. formicarius, was strongly positively affected by higher management intensity in Schorfheide. However, a contrasting response of prey and predator was observed in Hainich, indicating that mechanisms might vary among regions. In contrast, A. dispar abundance was negatively related to antagonist abundance, suggesting that top-down forces are more important for this bark beetle species.
Although the abundances of *T. domesticum* and its antagonists were positively affected by increasing management intensity at the forest stand scale, the number of emerging *T. domesticum* progeny was not affected by management intensity. In contrast, mortality by natural enemies was negatively affected by increasing management intensity at the breeding system scale. This suggests less effective top-down control of *T. domesticum* with increasing management intensity. Our method for assessing mortality, by using data on predators’ consumption rates from the literature, might have underestimated the overall mortality of the beetles. Dissecting the wood logs at the end of the experiment might have resulted in more accurate information on mortality, by making it possible to analyse pupal cocoons to quantify parasitism, to count cephalic capsules as a measure of consumed larvae and thus predation, and to quantify additional mortality factors, such as density-related intra-specific competition, entomopathogenic fungi, nematodes and mites, and climatic factors (e.g. excessive moisture). Although we assume that the method used in this study yielded reasonable estimates of the relative mortality rates between breeding systems, this needs further investigations.

The most important antagonist was the parasitoid *P. robusta*, which is more strongly specialised on *Trypodendron* species than the predators caught by pheromone traps (Wegensteiner et al., 2015). It showed overall low densities in managed forests, and we did not observe it attacking any of the individuals breeding in the experimental logs (Table S6-2; no individual emerged from breeding systems in managed forests). In general, parasitoids need to feed on nectar and pollen in order to reconstitute their egg load (Raffa et al., 2015). However, Führer (1975) suggested that female imagines of *P. robusta* can survive in managed forests without food sources, owing to a potential independence of imaginal nutrient uptake. In any case, our results indicate that potential food resources (e.g. honeydew of the common aphid *Phyllaphis fagi*) are sufficiently available in the managed beech forests studied here (Gossner et al., 2014a) and that other unknown factors, e.g. those related to differences in stand structure and limited connectivity among forest patches (Raffa et al., 2015), restrict the occurrence of *P. robusta* almost entirely to unmanaged forests.
5 Conclusions

The conclusions and generalisations that can be drawn from our findings are limited because there are many interacting variables at our forest sites. We tried to control for this in our models, but some factors could not be disentangled. For instance, it is not clear whether the different tree species composition or the warmer climate caused the positive management effects on the abundance of X. germanus in one region. Future experiments should be designed to control for these different factors, e.g. by applying different harvest intensities to even-aged timber-stage beech forests and by simultaneously controlling the amount of dead wood in a stage suitable for breeding. Nevertheless, some general conclusions can be derived from our study.

Our large-scale study on the effects of management intensity on ambrosia beetles demonstrates that different mechanisms are prominent for different species and at different scales. For T. domesticum, greater availability of suitable breeding substrate at the forest stand scale, e.g. after wind throws, seems to promote higher population densities and attack rates. This might lead to a greater risk of pest outbreaks in managed forests where pest control is reduced at the breeding system scale owing to a lack of specialised parasitoids and reduced beetle predator populations because of reduced host diversity. Our results are less conclusive for Xyleborus species, as no analyses of breeding success were conducted. The analyses of abundances and attack rates, however, suggest that top-down control is important in A. dispar, while region-specific factors seem to drive the abundance of X. germanus.

In Central Europe, broad-leaved tree species are already showing signs of increasing drought effects due to climate change. Moreover, there have been a few examples of outbreaks of T. domesticum and Xyleborini species after wind throws in managed forests following warm and dry years with increasingly stressed trees, resulting in the attack of apparently healthy trees (Kühnhölz et al., 2001). Whether climate change will lead to increased damage of trees, in particular in managed forests, by the studied ambrosia beetles should be evaluated in the coming years.
Authors’ Contributions

MMG and WWW developed the idea of the experiment. KF and MMG conducted and organised the field and lab work, performed the analyses and wrote the first draft. MMG and WWW finalised the manuscript.

Acknowledgements

We are grateful to Eric Anton, Boris Büche, Thomas Wagner and Frank Köhler for species identification; Kaspar Kremer, Ellen Sperr and the management team in the Hainich region for their assistance with field work; Jürgen Bauhus, Tiemo Kahl and Steffen Boch for providing data; Josef Dvorak and Mark Telfer for providing the images of the beetles; two anonymous reviewers for their valuable comments and suggestions; and Melissa Dawes for linguistic editing. We thank the managers of the three Biodiversity Exploratories, Kirsten Reichel-Jung, Swen Renner, Katrin Hartwich, Sonja Gockel, Kerstin Wiesner and Martin Gorke, for their work in maintaining the plot and project infrastructure; Christiane Fischer and Simone Pfeiffer for giving support through the central office; Michael Owonibi for managing the central database; and Markus Fischer, Eduard Linsenmair, Dominik Hessenmüller, Jens Nieschulze, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. This work was funded by the DFG Priority Program 1374 “Infrastructure-Biodiversity-Exploratories” (grant DFG-WE 3081/21-1). MMG obtained funding from the Swiss National Science Foundation (grant 310030E-173542/1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen and Brandenburg (according to § 72 BbgNatSchG).
Data availability

After an embargo period, all data will be made publicly available at https://www.bexis.uni-jena.de/PublicData/PublicData.aspx. (IDs: 24106).
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# Supplementary Material

**Effects of management on ambrosia beetles and their antagonists in European beech forests**

Martin M. Gossner, Konstantin Falck, Wolfgang W. Weisser

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Supplement S1 Details on study sites

The study was conducted within the framework of the long-term and large-scale Biodiversity Exploratories project, a multi-disciplinary research network for functional biodiversity research located in three regions across Germany (http://www.biodiversity-exploratories.de; Fischer et al. 2010). The three regions differ in climatic conditions and forest history. With an annual precipitation of about 520–580 mm, Schorfheide-Chorin is one of the driest parts of Germany. Most of the region is covered by forests of Scots pine (Pinus sylvestris; 39%), European beech (Fagus sylvatica; 12%), and sessile oak (Quercus petraea; 9%). Hainich-Dün is one of the largest continuous forest areas in Germany and is dominated by broad-leaved trees; conifers, in particular Norway spruce (Picea abies), comprise only 12% of the forest. The Schwäbische Alb is a highly fragmented, mixed forest landscape dominated by Fagus sylvatica (46%) and Picea abies (24%).

Table S1-1: Overview of the number of plots sampled in each region (total 149 plots), separated by forest management type and developmental stage. Small experimental logs were exposed in Hainich-Dün only (total 50 plots) and large experimental logs were exposed on a selection of plots in all three regions (total 30 plots), given in brackets.

<table>
<thead>
<tr>
<th>Region</th>
<th>Schwäbische Alb* 2010</th>
<th>Hainich-Dün** 2010</th>
<th>Hainich-Dün** 2011</th>
<th>Schorfheide-Chorin 2010</th>
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<tr>
<td></td>
<td>N</td>
<td>ForMI±SE</td>
<td>N</td>
<td>ForMI±SE</td>
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<td>5</td>
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<td>(0.35±0.18)</td>
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<td>Beech uneven-aged</td>
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<td></td>
<td></td>
<td>13</td>
<td>1.02±0.07</td>
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<td></td>
<td></td>
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<td>(3)</td>
<td>(1.04±0.17)</td>
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<tr>
<td>Beech age class</td>
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<td>1.81±0.04</td>
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<td>(1)</td>
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<td></td>
<td>4</td>
<td>1.06±0.11</td>
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<tr>
<td>Oak age class</td>
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<tr>
<td>Timber</td>
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<tr>
<td>Conifer age class***</td>
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<tr>
<td>Pole wood</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Timber</td>
<td>12</td>
<td>2.11±0.08</td>
<td>4</td>
<td>1.9±0.22</td>
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<tr>
<td></td>
<td>(3)</td>
<td>(2.14±0.17)</td>
<td>(3)</td>
<td>(1.79±0.26)</td>
</tr>
<tr>
<td></td>
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<tr>
<td>Total</td>
<td>49</td>
<td>1.48±0.10</td>
<td>50</td>
<td>0.96±0.08</td>
</tr>
</tbody>
</table>

* pheromone trap installation not possible in one even-aged managed beech plot
** small experimental logs were exposed in all 50 plots during 2010 and 2011
*** Norway spruce (Picea abies) plots were studied in Schwäbische Alb and Hainich-Dün and Scots pine (Pinus sylvestris) plots were studied in Schorfheide-Chorin

ForMI: Forest Management Intensity according to Kahl & Bauhus (2014)
Figure S2-1: A) Schematic illustration of the bottle trap; B) bottle trap in the field with catches in the collecting jar; C and D) installed eclectors in the field; E) schematic illustration of one eclector.
S2.1 Sampling of beetles and antagonists

To estimate the abundance of ambrosia beetles and their antagonists we used modified bottle traps that were protected from the rain by a roof and baited with lineatin and ethanol (see Grégoire et al. 2001; Supplement Fig. S2-1 A-B). The traps were baited with half a lineatin stick (Contech Enterprises, 7572 Progress Way, Delta, B.C. Canada, V4G 1E9) and with 100 ml of a mixture of 96% ethanol (99 parts) denatured with one part petroleum ether. The latter was exposed in a jar that was connected to the trap by a tube with a mesh that prevented insects from entering. The collecting jar was filled with 100 ml of 70% ethanol to preserve the catches. The combination of lineatin and ethanol has been suggested as suitable for representative sampling of ambrosia beetles (Trypodendron, Xyleborini) and their antagonists (Grégoire et al. 2001; Bader 2004).

S2.2 Details of attack rate study

In AmbroBEx, logs of two different sizes, i.e. 100 cm long and 20 cm in diameter (‘large logs’) and 60 cm long and 30 cm in diameter (‘small logs’), were exposed in the Hainich-Dün region between mid-February and mid-March 2010. One log of each size class was exposed close to the pheromone trap on each of 50 plots and the cut surface was coated with liquid wax to prevent the wood from drying too fast. Logs came from canopy branches cut during harvesting activities in one stand of Langula forest in November 2009. All logs were stored as 3-m-long logs at the forest site before being transferred to the forest plots. Size classes and harvesting time were selected based on the results of a preliminary study in 2009 in which a range of differently sized logs from two harvesting times were exposed. Decision criteria were attractiveness to ambrosia beetles and manageability of logs, as they needed to be carried manually a distance of up to 3 km to the forest plots.

Additionally, we used beech logs from the BELongDead experiment, which focuses on management effects on dead wood decomposition of 13 different tree species (for details see Gossner et al. 2016). All logs were harvested in the Hainich-Dün region in winter 2008/2009. On
each of 30 plots (Schwäbische Alb: 9, Hainich-Dün: 12, Schorfheide-Chorin: 9) three beech logs 4 m long and 23–46 cm in diameter, located 100 m apart within each plot, were studied.

We used both the AmbroBEx-logs and the BELongDead-logs to monitor attack rates of particular pest species. We classified two different types of entrance holes: (1) galleries with large entrance holes, about 1.2 mm in diameter, with perpendicular tunnels and wooden frass, corresponding to *Trypodendron domesticum*; and (2) galleries with smaller entrance holes, about 0.8 mm in diameter, with wooden frass, corresponding to *Xylosandrus germanus*. AmbroBEx-logs were checked every time pheromone traps were emptied, and BELongDead-logs were checked on a randomly marked 1 m section on the upper half of the log at the end of May/beginning of June 2010 and at the beginning of September 2010 in all three regions and in the Hainich-Dün additionally in August 2011 and May 2012. The position of entrance holes and the causal species were recorded, and holes were marked with coloured drawing pins to avoid double-counting during the next inspection.

To verify our entrance hole assignment to certain species, we took samples of a few individuals from the entrance holes from logs in Hainich-Dün.

**S2.3 Details on breeding-system eclectors**

For eclector installation we used both AmbroBEx-logs and BELongDead-logs. Eclectors on AmbroBEx-logs were installed in two groups: the first group was installed four weeks after we discovered the gallery, and the second group was installed after about a 20-week interval. Eclectors on BELongDead-logs were all installed at the beginning of August 2010. Galleries that looked inhabited, detected by fresh frass outside, a cleaned-out entry, a beetle in the entry, or a lid of clotted frass on the entry, were preferred for sampling.

Over each entrance hole a small metal tube (1 cm in diameter) was fixed 1 cm deep into the wood and a collecting jar, with a hole covered by gauze to allow for air circulation, was attached to the metal tube connected by a flexible plastic tube.
The eclectors were checked for catches each time the plot was visited. Catches were preserved in 70% ethanol and determined by taxonomic experts. The integrity of the eclectors was checked each time they were visited. Eclectors could be disabled by improper attachment to the metal tube, resulting from sunlight exposure or raccoon activity, resulting in fallen off eclectors and destroyed or missing components. We restored disabled eclectors, but loose metal tubes were not reattached and sampling of the gallery was terminated. Eclectors with one damaging incident during early spring, the main emergence period, or more than one incident in the remaining sampling time were excluded from the analyses.
Supplement S3 Studied species and attraction of species to different components of bark beetle pheromone traps

S3.1 Identification procedure

All samples were sorted by students to the order or suborder level, or to a lower taxonomic level after identification training (see below).

Students separated the beetles in the samples into *T. domesticum*, other *Trypodendron* spp., and other beetles, which were then identified to the species level by a specialist. Other beetles were identified to the species level by a specialist (Eric Anton, Jena). Students also separated Hymenoptera from the samples, and they were then further identified by specialists (Eric Anton with the help of other specialists). Antagonists were identified with information from the literature.

Almost all beetles, but only one species of Apocrita (*Perniphora robusta* Ruschka, 1923), could be classified to the species level. Thus, we analysed the abundance of Apocrita antagonists based on species-level data and by including all individuals sampled from families with known antagonists as potential antagonists, i.e. Bethylidae, Braconidae, Eulophidae, Eupelmidae, Eurytomidae, Pteromalidae, Torymidae and Trichogammatidae. The taxonomy follows the current Fauna Europaea nomenclature (de Jong *et al.* 2014; Alonso-Zarazaga 2015; Audisio 2015; Mitroiu 2015; van Achterberg 2015). Of the beetle species, we included the most abundant antagonists, i.e. *Thanasimus formicarius* (Linnaeus, 1758), a well-known generalist predator of bark beetles; *Rhizophagus bipustulatus* (Fabricius, 1792), the dominant antagonist we extracted from *T. domesticum* breeding systems; and *Rhizophagus depressus* (Fabricius, 1793), a proven antagonist of *T. domesticum*.

We tested the reliability of the classification of our target species by conducting an experiment on the attraction of potential antagonists to the aggregation pheromone lineatin and to ethanol (see below). In doing so we demonstrated that *Perniphora robusta*, among Apocrita, *Rhizophagus* species and *Thanasimus formicarius* are attracted to lineatin.
S3.2 Studied bark beetles

Genus *Trypodendron*

Within this group we selected the most abundant species in beech forests of the three regions as target species, based on the results of a preliminary study using traps baited with pheromone and ethanol. Within the genus *Trypodendron*, high abundances of the hardwood-associated species *Trypodendron domesticum* (Linnaeus, 1758) and the softwood-associated species *T. lineatum* (Olivier, 1795) occurred at the sample sites, with the latter species preferring conifers. Two other species, *T. signatum* (Fabricius, 1787) and *T. leave* (Eggers, 1939), occurred at low densities. Hence, we focused on *T. domesticum*.

*Trypodendron domesticum* (Linnaeus, 1758)

The European hardwood or broad-leaved ambrosia beetle *Trypodendron domesticum* is a secondary pest of fresh dead wood of broad-leaved trees, such as European beech (*Fagus sylvatica* L.), oak (*Quercus* spp. L.), and birch (*Betula* spp. L.) (Byers 1992). It has economic importance as a technical pest, as the females excavate galleries about 10 cm deep into the wood and introduce the ambrosia fungus *Ambrosiella ferruginea* (Sauvard 2007) into their tunnels for nourishment (Batra 1963), which causes dark staining (Engels *et al.* 2010). Thus, a beetle attack severely reduces the value of the wood.

For host finding, *T. domesticum* uses primary and secondary cues. Primary signals are ethanol emitted by the metabolism of microorganisms, which indicates stress of a dying tree (Graham 1968; Moeck 1970), and the colour and shape of the tree (Kerck 1978). Conifer volatiles act as a repellent (Klimetzek, Vité & Mori 1980; Byers 1992). The secondary signal is the genus-specific aggregation pheromone lineatin produced by the females (Klimetzek & Vité 1981), which attracts both sexes (Kerck 1978; Klimetzek & Vité 1981). When males are present, the amount of lineatin produced by the females is reduced (Nijholt 1970; Nijholt 1973; Klimetzek *et al.* 1981). Swarming starts in February when the temperature rises above 9.5°C (Petercord 2006). Flight
activity shows two or more peaks until end of June when it levels off (Gaubicher, De Proft & Grégoire 2003; Petercord 2006). The life cycle of *T. domesticum* is presumably similar to that of *T. lineatum*, with a six- to eight-week larval development from egg deposition to hatching (Parini & Petercord 2006). Imaginal diapause lasts three to four months and is regulated by low temperature (Paiva & Vité 1982).

*Tryptodendron domesticum* has a staggered development, with offspring beetles and young larvae present in the galleries (Eichhorn & Graf 1974). There might occasionally be a second generation, but usually *T. domesticum* is considered to be univoltine in Central Europe. The brood is nursed by both parent beetles until pupation (Gaubicher, De Proft & Grégoire 2003). Most of the offspring overwinter inside the galleries (Eichhorn & Graf 1974), and some overwinter in the soil or leaf litter (Parini & Petercord 2006).

Tribe Xyleborini

Among the ambrosia beetles of the tribe Xyleborini, we caught the native *Anisandrus dispar* (Fabricius, 1792) and the invasive (since the 1950s; Groschke 1952; Kirkendall & Faccoli 2010) *Xylosandrus germanus* (Blandford, 1894) in large numbers. The related species *Xyleborinus saxesenii* (Ratzeburg, 1837), *Xyleborus monographus* (Fabricius, 1792) and *Xyleborus dryographus* (Ratzeburg, 1837), the alien *Cyclorhipidion bodoanus* (Reitter, 1913) (since the 1960's; Kirkendall & Faccoli 2010), and the invasive (since the 1980s; Kirkendall & Faccoli 2010) *Xyleborinus alni* (Niijima, 1909), occurred locally and in relatively small numbers. Hence, we focused on the native species *Anisandrus dispar* and the invasive species *Xylosandrus germanus*.

*Xylosandrus germanus* (Blandford, 1894)

The alnus ambrosia beetle, or black stem borer, *Xylosandrus germanus* is an invasive pest (Groschke 1953) that primarily attacks hardwoods (Koch 1989-1992) but has a wide range of host species (Weber & McPherson 1983b). It has been reported that it favours roots and branches in
moist conditions (Hoffmann 1941; Kaneko, Tamaki & Takagi 1965) of both living and dead trees. The females excavate the galleries a few centimetres deep into the sapwood; the galleries consist of an entrance tunnel, a main chamber and larval tunnels where the ambrosia fungus *Ambrosiella hartigii* (Sauvard 2007) is cultivated as nourishment for the adults and larvae (Biedermann, Klepzig & Taborsky 2009). The females are attracted to the hosts by stress-related tree volatiles like ethanol, methanol and conophthorin (Klimetzek *et al.* 1986; Dodds & Miller 2010; Ranger *et al.* 2010), with ethanol being the strongest attractant (Ranger *et al.* 2010; VanDerLaan & Ginzel 2013). Swarming and subsequent attacks start at 20°C maximum daily temperature (Reding *et al.* 2013).

Two generations are produced a year and overwintering takes place in the galleries (Weber & McPherson 1983a). Males are flightless and serve for mating within the nest, resulting in up to 97% sibling-matings (Keller *et al.* 2011) and an average sex ratio of 10 females to 1 male (Weber & McPherson 1983a).

*Anisandrus dispar* (Fabricius, 1792)

The biology of pear blight beetle *Anisandrus dispar* is similar to that of *Xylosandrus germanus*. *Anisandrus dispar* is reported to be univoltine (Mani, Remund & Schwaller 1992) and is extremely polyphagous (Sauvard 2007), with a preference for broad-leaved tree species (Lieutier *et al.* 2007). Like *T. domesticum*, *Anisandrus dispar* is repelled by monoterpenes and verbenones from conifer trees. French and Roeper (2009) report a sex ratio of two-times to eight-times more females than males. Mating takes place in the maternal gallery during maturation, mainly between siblings (Sauvard 2007). The mated females disperse alone to find new breeding sites, where they bore their galleries and leave the wingless males behind. The larvae feed on the mycelium of the cultivated ambrosia fungus *Ambrosiella hartigii* (Sauvard 2007) and need ambrosia for pupation. Ambrosia production might be partly induced by a secretory product (French & Roeper 1972).

**S3.3 Bark beetle antagonists**
Coleoptera

*Rhizophagidae: Rhizophagus bipustulatus* (Fabricius, 1792), *R. depressus* (Fabricius, 1793), *R. dispers* (Paykull, 1800), *R. nitidulus* (Fabricius, 1798) and *R. parvulus* (Paykull, 1800).

Many of the root-eating beetles from the genus *Rhizophagus* are facultative predators. They prey on various xylophagous insects, mostly bark beetle and their excrements, but also feed on hyphae of fungi (Koch 1989-1992). They are attracted by both their prey’s pheromones and host-volatile ethanol (Byers 1992), and they are able to detect and colonise a high proportion of bark beetle broods (van Averbeke & Grégoire 1995). In consumption experiments a single *R. ferrugineus* consumed 79 eggs of a *Hylastes* species (Hanson 1937), and one larva of *R. depressus* consumed 14 prey larvae during its development period (Herard & Mercadier 1996) (see also Kenis, Wermelinger & Grégoire 2004). Schroeder (1996) reported a reduction of *Tomicus piniperda* offspring by 41% when reared in a cage with *R. depressus* compared with numbers observed when it was reared alone. We used 14 larvae as the consumption rate for *Rhizophagus* in our study.

Cleridae: *Thanasimus formicarius* (L. 1758)

*Thanasimus formicarius* occurs in conifer and in mixed conifer–broad-leaved forests, forest edges and gardens (Koch 1989-1992). Species of the genus *Thanasimus* are the most efficient coleopteran predator of bark beetles (Wegensteiner, Wermelinger & Herrmann 2015). Experimental studies have shown that *T. formicarius* can reduce the size of *Tomicus piniperda* (Linnaeus, 1758) broods by 81% (Schroeder 1996) and those of *Ips typographus* (Linnaeus, 1758) by 18%. Both adults and larvae prey on bark beetles (Person 1940; Gauss 1954; Reeve, Ayres & Jr. 1995; Hui & Bakke 2012). The consumption rate of adults can greatly exceed the consumption rate of larval bark beetles by larval clerids (Reeve, Ayres & Jr. 1995; Aukema & Raffa 2002). *Thanasimus formicarius* consumes approximately 50 (44–57) prey larvae during its larval development (Mills 1985; Dippel *et al.* 1997). It is estimated that they kill between 57 and 627 prey larvae per 1000 cm² (Kenis, Wermelinger & Grégoire 2004). *Thanasimus formicarius* is described as a generalist. Gauss (1954) lists more than 20 species of bark beetle as prey for *T.*
formicarius. They respond to prey pheromones and host-tree volatiles and are able to discriminate between different prey species (Bakke & Kvamme 1981; Tømmeras 1985). They feed on alighting bark beetles and oviposit in bark crevices near bark beetle entrance holes (Aukema & Raffa 2002).

Thanasimus formicarius is active very early in the season (Stephen & Dahlsten 1976; Herard & Mercadier 1996; Lawson, Furuta & Katagiri 1997). In Central Europe, oviposition begins in early April and continues until late August (Gauss 1954). Thanasimus species are highly fecund, producing 100–300 eggs per female (Thatcher & Pickard 1966; Dippel et al. 1997). Following hatching, larvae enter bark beetle galleries and forage on immature stages. The larval period of T. formicarius lasts 30–60 days (Person 1940). Once mature, the majority of larvae bore out of the bark, crawl down to the base of the tree, and pupate in bark near the ground or in the soil, although some larvae pupate in the outer bark near their development site. The majority of the population emerges in the summer of the same year, while the remaining individuals (5–20% for T. formicarius) overwinter as prepupae in the bark and emerge the following spring or even later (Person 1940; Reeve 1997). Adult T. formicarius live for 4–10 months and the entire life cycle takes one year (Gauss 1954), or two years in Scandinavia (Schroeder 1999). We used 47 larvae as the consumption rate for Thansimus formicarius in our study.

Hymenoptera

Pteromalidae: Perniphora robusta Ruschka 1923

Most of the bark beetle parasitoids belong to the family Pteromalidae (Wermelinger 2002), and Perniphora robusta is a proven ectoparasitic parasitoid of Trypodendron spp. (Eichhorn & Graf 1974; Führer 1975).

Führer (1975) found that female imagines are able to mature some eggs without eating and that offering honeydew doubled their lifespan and significantly increased the number of mature eggs produced. Führer (1975) concluded that this potential independence of imaginal uptake of nutrients
ensures survival in managed forests without food sources. One source of honeydew is the common aphid *Phyllaphis fagi*, found in beech forests.

*Perniphora robusta* has a univoltine lifecycle with a synchronised development linked especially to *T. lineatum* (Eichhorn & Graf 1974). The adults emerge and search for hosts in late May when the host larvae are in their middle to late stages. In late June larvae of *P. robusta* are completely developed and go into dormancy until late March of the following year to pupate in early May. Parasitisation of *T. domesticum* broods is almost complete when the female parasitoid enters the gallery in the appropriate time window.
S3.4 Experiment: Attraction of species to different components of bark beetle pheromone traps

Table S3-1: List of species sampled during an experiment on the attraction of potential antagonists to the aggregation pheromone lineatin and to ethanol. We conducted a comparison of pheromone traps treated with (1) lineatin and ethanol, (2) only ethanol and (3) water, to disentangle the attraction of insects to one of the attractants.

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<th>Control trap ethanol‡</th>
<th>Control trap water‡</th>
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**Elateridae**

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**Erotylidae**

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**Eucnemidae**

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**Histeridae**

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**Hydrophilidae**

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**Lampyridae**

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**Latridiidae**
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†: twin-trap
‡: single trap
Supplement S4 Details on the statistical models used

S4.1 Abundance-based model

To analyse the drivers of the abundance of ambrosia beetle (*T. domesticum*, *X. germanus*, and *A. dispar*) and their antagonists (*R. bipustulatus*, *R. depressus*, *T. formicarius*) we used data from 2010 and included forest management intensity (ForMI) and its interaction with region as main predictors. As covariates, the abundance of antagonists (response: bark beetle abundance), the abundance of *T. domesticum* (response: bark beetle antagonists), and variables assessed at the plot and subplot-scales (see main article) were used. The between-year stability of effects was analysed by fitting an additional model for the Hainich-Dün region with data for 2010 and 2011 (see Supplement S6). Negative-binomial GLMMs were used for analysing abundance of *T. domesticum* (model 1) and abundance of *Xylosandrus germanus* (model 2), with region as random factor, and abundance of *Anisandrus dispar* (model 3), with region and observation as random factors, fitted as:

~ region × ForMI + abundance of antagonists + canopy closure + dead wood + tree diversity + main tree type + density of regeneration + (1 | region) [+ (1 | observation); only for *Anisandrus dispar*]

S4.2 Attack-based model

The attack of logs was analysed separately for *T. domesticum* and *Xylosandrus germanus*. For the analysis of *T. domesticum* attacks on the AmbroBEx-logs, we pooled the data from both 2010 and 2011 by summing up the attacks on each log. In 2012, decay of most logs reached a decomposition stage in which they become unattractive for *Trypodendron*. Thus, we omitted the very few attacks from this year from the analyses. *Xylosandrus germanus* attacks were analyzed for 2010 only, as they occurred almost exclusively in that year. We fitted three models with attacks as the response variable and ForMI as the main predictor, along with the abundance of the respective species and total beetle Shannon-diversity from the pheromone traps, and plot, subplot and log-level measurements were included as covariates. To account for differences in the sampled area, we included the log surface area as an offset in the count models, which resulted in attack densities. We
used a binomial GLMM to model the attack probability of *T. domesticum* (model 4; no random factor because only the 100 cm x 20 cm log was used) and *Xylosandrus germanus* (model 6; plot as random factor), with log infested or not infested as the response variable. We used negative-binomial GLMMs to model the abundance of *T. domesticum* (model 5; plot as random factor) and *Xylosandrus germanus* (model 7; plot as random factor):

\[
\text{~ ForMI + bark beetle species abundance + beetle diversity + canopy closure + dead wood + main tree type + density of regeneration + bark texture + bark free area + log class + (1 | plot)}
\]

Owing to the high proportion of attacked BELongDead-logs, the models for attack rate did not converge. For the analyses of the attack density for *T. domesticum* and *Xylosandrus germanus* we used the data from 2010 from all three regions. The number of entrance holes was used as the response variable, ForMI and its interaction with region were used as the main predictor variables, and plot, subplot and log-level measurements were included as covariates. Plot within region was included as a nested random factor. Negative-binomial GLMMs were used for *T. domesticum* (model 8) and *Xylosandrus germanus* (model 9):

\[
\text{~ ForMI × region + bark beetle species abundance + canopy closure + dead wood + main tree type + tree diversity + bark free area + (1 | region/plot)}
\]

### S4.3 Breeding success

To analyse the effects of management on breeding success of *T. domesticum*, we first tested the emerged progeny and all emerged antagonists in two separate models. ForMI was included as the main predictor variable, along with subplot and log-level covariates. We included only data from AmbroBEx-logs because the time between gallery creation and eclector installation was only known for these logs. We used the following negative-binomial GLMMs, with plot as random factor (model 10):

\[
\text{T. domesticum progeny ~ ForMI + canopy coverage + date of gallery creation + time between gallery creation and eclector installation + (1 | plot)}
\]
Secondly, we tested the mortality of *T. domesticum* and thus breeding success by using information from the literature on the number of bark beetle eggs or larvae consumed by one predator (*Thanasimum*: 47, *Rhizophagus*: 14) or parasitoid (1) (see Supplement S2). Here we combined AmbroBEx-logs and BELongDead-logs but included only eclectors where at least one individual of either *T. domesticum* or antagonists emerged. The final data set consisted of 169 eclectors. In this binomial GLMM we included *T. domesticum* mortality as the response variable, management intensity as the predictor, and log as a random factor (model 11):

ebind (*T. domesticum* consumed, *T. domesticum* emerged) ~ ForMI + (1 | log)
Supplement S5 Overview of species caught by pheromone traps

In total, 83% of the individuals caught in the pheromone traps were ambrosia beetles and <1% were potential natural enemies (Table S5-1). Among ambrosia beetles, *T. domesticum* was most abundant in the pheromone traps in 2010 and 2011, with a total of 467,001 sampled individuals (83.3% of that genus); 80,118 individuals (14.3%) of the non-target softwood-associated species *T. lineatum* were caught, and *T. signatum* and *T. laeve* contributed 11,653 (2.1%) and 1,899 (0.3%) individuals, respectively. For Xyleborini, two species were represented with almost equal abundance: *Xylosandrus germanus* with 49,522 (45.7%) and *Anisandrus dispar* with 48,505 (44.7%) individuals. With 10,221 (9.4%) individuals, *Xyleborus saxeseni* was much less abundant, and from *Xyleborus monographus*, *Xyleborus dryographus*, *Xyleborus alni*, and *Cyclorhipidion bodoanus* only 195 (0.2%) individuals were sampled in total (for details on the abundance of sampled Coleoptera and Apocrita see Tables S5-1 to S5-3).
### Table S5-1: Overview of the number of plots, organised by forest management type, and the average abundance (mean ± SE) per plot of target species, i.e. *Trypodendron* spp. and Xyleborini, and their most abundant possible antagonists from pheromone traps.

<table>
<thead>
<tr>
<th></th>
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<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Beech</td>
<td>Beech</td>
<td>Spruce</td>
</tr>
<tr>
<td>Management type</td>
<td>Unmanaged</td>
<td>Even-aged</td>
<td>Even-aged</td>
</tr>
<tr>
<td>N</td>
<td>5</td>
<td>32</td>
<td>12</td>
</tr>
</tbody>
</table>

#### Coleoptera – target pest species

<table>
<thead>
<tr>
<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Trypodendron domesticum</em> (L. 1758)</td>
<td>1202.8±385.8</td>
<td>6413.2±727.9</td>
<td>1447.7±334.6</td>
</tr>
<tr>
<td><em>Trypodendron leave</em> Eggers 1939</td>
<td>17.4±10.3</td>
<td>5.2±0.9/0.0</td>
<td>0.2±0.2/0.0</td>
</tr>
<tr>
<td><em>Trypodendron lineatum</em> (Oliv. 1795)</td>
<td>1407.8±564.1</td>
<td>32.9±4.3/11.1</td>
<td>33±8.8</td>
</tr>
<tr>
<td><em>Trypodendron signatum</em> (F. 1787)</td>
<td>36.8±11.2</td>
<td>102.4±17.3/84.3</td>
<td>69.2±16</td>
</tr>
<tr>
<td><em>Anisandrus dispar</em> (F. 1792)</td>
<td>36.8±13</td>
<td>45.4±17.3</td>
<td>693±112.6</td>
</tr>
<tr>
<td><em>Xylosandrus germanus</em> (Blandf. 1894)</td>
<td>2±1.1</td>
<td>334.5±116.6/965.7±220.7</td>
<td>182.7±42.8</td>
</tr>
<tr>
<td><em>Xyleborinus saxesenii</em> (Ratz. 1837)</td>
<td>1±0.3</td>
<td>17.7±8.9/5.5</td>
<td>92.5±18.3</td>
</tr>
<tr>
<td>Xyleborini spp.</td>
<td>0±0</td>
<td>0±0</td>
<td>1.7±1.3</td>
</tr>
</tbody>
</table>

#### Coleoptera – antagonists

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td><em>Rhizophagus depressus</em> (F. 1792)</td>
<td>7.2±4.2</td>
<td>2.1±0.3/1.2±0.5</td>
<td>4.2±1/4.3±1.5</td>
</tr>
<tr>
<td><em>Thanasimus formicarius</em> (L. 1758)</td>
<td>14.6±5.3</td>
<td>4.9±1.2/4.3±1.6</td>
<td>33.2±9.4/24.9±3.6</td>
</tr>
<tr>
<td><em>Rhizophagus bipustulatus</em> (F. 1792)</td>
<td>5±1.7</td>
<td>12.6±4.6</td>
<td>3±1.3/3±0.8</td>
</tr>
</tbody>
</table>

**Note:** The table includes data on the number of plots managed in different ways and the average abundance of target species and their antagonists. The table is organized by region and year, with management types ranging from unmanaged to uneven-aged and even-aged. The data are presented as mean ± standard error (SE).
<table>
<thead>
<tr>
<th>Apocrita antagonists</th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Perniphora robusta</em></td>
<td>2√</td>
<td>8</td>
<td>0√</td>
<td>17/52</td>
<td>7/15</td>
<td>16/17</td>
</tr>
</tbody>
</table>

-15.2±4.5  2.6±0.9  6±2.2  2.5±0.9
Table S5-2: Complete list of Coleoptera species and their abundances from pheromone traps, separated by management type and main tree type. Species are grouped by family and presented in alphabetical order.

<table>
<thead>
<tr>
<th></th>
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<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Beech</td>
<td>Spruce</td>
<td>Beech</td>
</tr>
<tr>
<td>Main tree</td>
<td>Unmanaged</td>
<td>Even-aged</td>
<td>Unmanaged</td>
</tr>
<tr>
<td>N</td>
<td>5</td>
<td>32</td>
<td>12</td>
</tr>
</tbody>
</table>

**Aderidae**

*Anidorus nigrinus* (Germ., 1831)

|          | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 1 | 2 |

*Euglenes pygmaeus* (DeGeer, 1774)

|          | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 1/0 | 0 | 1 | 0 | 3 |

**Anobiidae**

*Anobium costatum* Arrag., 1830

|          | 4 | 25 | 0 | 44/26 | 29/10 | 12/12 | 1/0 | 35 | 10 | 3 | 3 |

*Anobium fulvicorne* Sturm, 1837

|          | 0 | 0 | 0 | 1/1 | 0/0 | 0/0 | 0/0 | 0 | 0 | 4 | 0 |

*Anobium nitidum F.*, 1792

|          | 0 | 0 | 0 | 0/0 | 0/0 | 1/0 | 0/0 | 0 | 0 | 0 | 0 |

*Dorcata dresdensis* Hbst., 1792

|          | 0 | 2 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 0 |

*Dorcatoma robusta* Strand, 1938

|          | 0 | 0 | 0 | 0/0 | 0/0 | 0/1 | 0/0 | 2 | 1 | 0 | 0 |

*Dorcatoma substriata* Hummel, 1829

|          | 0 | 1 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 0 |

*Dryophillus pusillus* (Gyll., 1808)

|          | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 1/0 | 0 | 0 | 0 | 0 |

*Ernobius abietinus* (Gyll., 1808)

|          | 1 | 0 | 1 | 0/0 | 0/0 | 0/0 | 1/0 | 0 | 0 | 0 | 0 |

*Ernobius abietis* (F., 1792)

|          | 0 | 1 | 3 | 0/0 | 0/0 | 0/0 | 2/0 | 0 | 0 | 0 | 0 |

*Ernobius longicornis* (Sturm, 1837)

|          | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 1 |

*Ernobius mollis* (L., 1758)

|          | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/1 | 0 | 0 | 0 | 0 |

*Hedobia imperialis* (L., 1767)

|          | 0 | 3 | 0 | 0/1 | 1/2 | 1/1 | 1/0 | 0 | 0 | 1 | 0 |

*Ptilinus pectinicornis* (L., 1758)

|          | 0 | 20 | 1 | 16/1 | 3/3 | 10/5 | 3/2 | 0 | 4 | 0 | 0 |

*Ptinus coarcticollis* Sturm., 1837

|          | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 6 |

*Ptinus fur* (L., 1758)

<p>|          | 0 | 1 | 0 | 1/2 | 0/0 | 0/3 | 0/0 | 0 | 1 | 0 | 0 |
|--------------|-------------------------|-------------------------|--------------------------|
|              | Beech Spruce Beech Beech Beech Spruce Beech Oak Pine | Beech Spruce Beech Beech Beech Spruce Beech Oak Pine | Beech Spruce Beech Beech Beech Spruce Beech Oak Pine |
| N            | 5 32 12 13/6 13/9 20/15 4/4 6 15 7 22 | | |
| <strong>Pitius rufipes</strong> Ol., 1790 | 0 0 0 0 0 0 0 0 0 0 33 0 | | |
| <strong>Pitius subpilosus</strong> Sturm, 1837 | 0 0 0 0 0 0 0 0 0 0 0 1 | | |
| <strong>Xestobium plumbeum</strong> (Ill., 1801) | 0 3 0 3/3 1/4 4/3 0/0 18 20 1 7 | | |
| <strong>Xestobium rufovillosum</strong> (DeGeer, 1774) | 0 0 0 0 0 0 0 0 0 0 1 0 | | |
| <strong>Anthicidae</strong> | | | |
| <strong>Notoxus monoceros</strong> (L., 1761) | 0 0 0 0 0 0 0 0 0 0 0 0 | | |
| <strong>Anthribidae</strong> | | | |
| <strong>Anthribus abinus</strong> (L., 1758) | 1 5 0 4/1 2/2 8/11 1/0 5 29 3 26 | | |
| <strong>Brachytarsus nebulosus</strong> (Forst., 1771) | 0 0 0 0 0 0 0 0 0 0 14 | | |
| <strong>Choragus sheppardi</strong> Kirby, 1818 | 0 0 0 1/0 1/0 0/0 0/0 0 0 0 0 | | |
| <strong>Dissoleucas niveirostris</strong> (F., 1798) | 0 0 0 0/1 0/0 0/0 0/0 1 1 0 1 | | |
| <strong>Attelabidae</strong> | | | |
| <strong>Apoderus coryli</strong> (L., 1758) | 0 0 0 0 0 0 1/0 0/0 0 0 0 0 | | |
| <strong>Byctiscus betulae</strong> (L., 1758) | 0 0 0 0 0 0 0/0 0 0 0 0 | | |
| <strong>Caenorhines aqueatus</strong> (L., 1767) | 0 0 0 0 0 0 0 0 0 0 0 1 | | |
| <strong>Deporaus betulae</strong> (L., 1758) | 0 0 0 0 0 0 0/0 0 0 0 0 | | |
| <strong>Deporaus tristis</strong> (F., 1794) | 0 0 0 0 0 0 0 0 0 0 0 0 | | |
| <strong>Lasiorhynchites olivaceus</strong> (Gyll., 1833) | 0 0 0 0 0 0 0 0 0 0 0 0 | | |
| <strong>Biphyllidae</strong> | | | |
| <strong>Diplocoelus fagi</strong> Guer., 1844 | 1 17 3 37/7 4/0 9/6 0/1 9 12 4 11 | | |</p>
<table>
<thead>
<tr>
<th><strong>Brachypteridae</strong></th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>Management type</td>
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<td>Beech Beech Spruce</td>
<td>Beech Beech Spruce</td>
</tr>
<tr>
<td></td>
<td>Unmanaged Even-Aged</td>
<td>Unmanaged Even-Aged</td>
<td>Unmanaged Even-Aged</td>
</tr>
<tr>
<td>N</td>
<td>5 32 12 13/6 13/9 20/15</td>
<td>4/4 6 15 7 22</td>
<td></td>
</tr>
</tbody>
</table>

**Brychiidae**

- *Brachypterus urticae* (F., 1792)
  - 0 2 1 0/0 0/0 0/0 0/0 0 2 1 2
- *Heterhelus scutellaris* (Heer, 1841)
  - 0 0 0 0/0 0/0 0/0 0/0 0 0 1 0

**Brentidae**

- *Eutrichapion viciae* (Payk., 1800)
  - 0 0 0 0/0 0/0 0/0 0/0 0 0 0 1
- *Ischnopterapion virens* (Hbst., 1797)
  - 0 3 0 0/0 1/0 0/0 0/1 0 0 0 0
- *Oxystoma cerdo* (Gerst., 1854)
  - 0 0 0 0/0 0/0 0/0 0/0 0 0 0 1
- *Oxystoma craccae* (L., 1767)
  - 0 0 0 0/0 0/0 0/0 0/0 0 0 0 1
- *Oxystoma ochropus* (Germ., 1818)
  - 0 0 0 0/0 0/0 0/0 0/0 0 0 0 0
- *Perapion curtirostre* (Germ., 1817)
  - 0 0 0 0/0 0/0 0/0 0/0 0 0 0 1
- *Protapion apricans* (Hbst., 1797)
  - 0 0 0 0/0 0/0 1/0 0/0 0 0 0 0
- *Protapion fulvipes* (Fourcr., 1785)
  - 0 0 0 0/0 1/0 0/0 0/0 3 0 0 2

**Byrrhidae**

- *Byrrhus pilula* (L., 1758)
  - 0 0 0 0/0 0/0 1/0 0/0 0 0 0 0
- *Byturus ochraceus* (Scriba, 1790)
  - 0 0 0 0/0 0/0 0/0 1/0 0 0 0 0
- *Byturus tomentosus* (DeGeer, 1774)
  - 0 3 40 1/0 0/0 16/1 1/2 0 11 7 9

**Cantharidae**

- *Cantharis decipiens* Baudi, 1871
  - 0 1 0 0/0 3/1 4/2 0/0 0 0 0 0
- *Cantharis fusca* L., 1758
  - 0 1 0 0/0 0/0 0/0 0/0 0 0 0 0
- *Cantharis nigricans* (Müll., 1776)
  - 0 0 0 0/0 1/1 4/0 0/1 1 5 7 3
- *Cantharis pellucida* F., 1792
  - 0 0 0 0/0 0/6 0/5 0/2 0 2 0 2
- *Malthinus facialis* Thom., 1864
  - 0 0 0 0/0 0/0 1/1 0/0 0 0 0 0
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<tr>
<td>Region (Year)</td>
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<td>Beech</td>
</tr>
<tr>
<td>N</td>
<td>5</td>
<td>32</td>
<td>12</td>
</tr>
<tr>
<td>Malthinus fasciatus (Ol., 1790)</td>
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<td>Malthinus frontalis (Marsh., 1802)</td>
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<tr>
<td>Malthinus punctatus (Fourcr., 1785)</td>
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<tr>
<td>Malthinus spec.</td>
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<tr>
<td>Malthodes crassicornis (Mäckl., 1846)</td>
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<tr>
<td>Malthodes lobatus Kiesw., 1852</td>
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<td>Malthodes marginatus (Latr., 1806)</td>
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<td>Malthodes spathifer Kiesw., 1852</td>
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<tr>
<td>Malthodes spec. Kiesenwetter, 1852</td>
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<td>1</td>
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<td>Metacantharis eleypeata (Ill., 1798)</td>
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<td>Metacantharis discoidea (Ahr., 1812)</td>
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<tr>
<td>Podabrus alpinus (Payk., 1798)</td>
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<td>Podistra rufotestacea (Letzner 1845)</td>
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<td>Rhagonycha fulva (Scop., 1763)</td>
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<td>Rhagonycha lignosa (Müll., 1764)</td>
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<td>Rhagonycha limbata Thoms., 1864</td>
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<td>Rhagonycha translucida (Kryn., 1832)</td>
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<td>Agonum fuliginosum (Panz., 1809)</td>
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<td>Amara communis (Panz., 1797)</td>
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<tr>
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</tr>
<tr>
<td></td>
<td>Beech</td>
<td>Spruce</td>
<td>Beech</td>
</tr>
<tr>
<td>Main tree</td>
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<tr>
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<td>Beech</td>
<td>Spruce</td>
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<tr>
<td></td>
<td>5</td>
<td>32</td>
<td>12</td>
</tr>
</tbody>
</table>

1. *Amara convexior* Steph., 1828  
2. *Amara curta* Dej., 1828  
3. *Amara familiaris* (Duft., 1812)  
4. *Amara montivaga* Sturm, 1825  
5. *Amara ovata* (F., 1792)  
6. *Amara plebeja* (Gyll., 1810)  
7. *Amara ovata* (F., 1792)  
8. *Anisodactylus binotatus* (F., 1787)  
9. *Anthracus consputus* (Duft., 1812)  
10. *Asaphidion curtum* (Heyd., 1870)  
11. *Asaphidion flavipes* (L., 1761)  
12. *Bembidion deletum* Serv., 1821  
13. *Bembidion gattula* (F., 1792)  
14. *Bembidion lampros* (Hbst., 1784)  
15. *Bembidion lunulatum* (Fourcr., 1785)  
16. *Bembidion quadrimaculatum* (L., 1761)  
17. *Calathus cinctus* (Motsch., 1850)  
18. *Dromius agilis* (F., 1787)  
19. *Harpalus distinguendus* (Duft., 1812)  
20. *Harpalus griseus* (Panz., 1797)  
21. *Harpalus laeipes* Zett., 1828  
22. *Harpalus latus* (L., 1758)
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**Neosirocalus floralis** (Payk., 1792) 0 0 0 0/0 1/0 0/0 1/1 0 0 0 0

**Orthotomicus laricis** (F., 1792) 0 0 0 0/0 0/0 0/0 0/1 0 0 0 0 1

**Phthorophloeus spinulosus** Rey, 1883 0 0 0 0/0 0/0 0/0 0/1 0 0 0 0 0

**Phyllobius arborator** (Hbst., 1797) 0 0 2 0/0 0/0 0/0 1/0 0 0 0 2

**Phyllobius argentatus** (L., 1758) 1 2 0 4/8 4/18 3/3 0/0 2 3 2 0 0

**Phyllobius betulinus** (Bechst. Scharf., 1805) 0 0 0 0/0 0/0 0/0 0/1 0 0 0 0 0

**Phyllobius calcaratus** (F., 1792) 0 0 0 0/0 0/0 0/0 0/1 0 0 0 0 0

**Phyllobius macalicornis** Germ., 1824 0 0 0 0/0 0/0 0/0 0/0 0 0 0 0 0

**Phyllobius oblongus** (L., 1758) 0 3 0 0/0 0/0 1/3 0/0 0 0 0 0 0

**Pityogenes bidentatus** (Hbst., 1783) 0 0 0 0/0 0/0 0/0 0/1 0 0 1 38

**Pityogenes chalcographus** (L., 1761) 56 13 12 0/0 0/0 1/1 2/9 0 0 0 2

**Pityogenes trepanatus** (Nördl., 1848) 0 0 0 0/0 0/0 0/0 0/0 0 0 0 3

**Pityophthorus lichtensteini** (Ratz., 1837) 0 0 0 0/0 0/0 0/0 0/2 0 0 0 21

**Pityophthorus pityographus** (Ratz., 1837) 2 3 1 0/0 0/0 0/0 1/0 0 0 0 0 3

**Platypus cylindrus** (F., 1792) 0 0 0 0/0 0/0 0/0 0/0 1 1 1 0

**Polydrusus impar** Goz., 1882 0 1 2 0/0 0/1 0/1 0/0 0 0 0 0 0

**Polydrusus mollis** (Ström, 1768) 0 0 0 0/0 1/0 0/0 0/0 0 0 0 0 0

**Polydrusus pallidus** Gyll., 1834 2 0 1 0/0 0/0 0/0 0/0 0 0 0 0 0

**Polydrusus pilosus** Gredl., 1866 0 0 0 0/0 0/0 0/0 1/0 0 0 0 0 0

**Polydrusus pterygomalis** Boh., 1840 2 6 0 6/0 2/1 1/5 0/2 0 0 0 0 0

**Polydrusus sericeus** (Schall., 1783) 0 0 0 2/0 0/0 1/2 0/0 0 0 0 0 0
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<td>Trypholoeus rybinski Rtt., 1894</td>
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<td>Xyleborus alni Niijima, 1909</td>
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<td>Antisandrus dispar (F., 1792)</td>
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### Leiodidae

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Aphodius sticticus (Panz., 1798) | 4 | 12 | 4 | 3/4 | 10/6 | 11/7 | 4 | 26 | 48 | 18 | 18 |
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**Serica brunnea** (L., 1758)  
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**Scirtidae**

*Cyphon hilaris* Nyh., 1944  
0 0 0 0 0 0 0 0 0 1 0 0

*Cyphon laevispinus* Tourn., 1868  
0 0 0 0 0 0 0 0 1 3 1 0

*Cyphon ochraceus* Steph., 1830  
0 0 0 0 0 0 0 0 1 0 0 0

*Cyphon padi* (L., 1758)  
0 0 0 0 0 0 0 0 3 0 2 0

*Cyphon palustris* Thoms., 1855  
0 0 0 0 0 0 0 0 1 0 0 0

*Cyphon pubescens* (F., 1792)  
0 0 0 0 0 0 0 0 0 1 0 0

*Cyphon variabilis* (Thunb., 1787)  
0 0 0 0 0 0 0 0 0 0 1 0

*Microcara testacea* (L., 1767)  
0 0 0 0 0 0 1 0 0 0 0 0

*Prionocyphon serricornis* (Müll., 1821)  
0 0 1 0 0 0 0 0 0 0 0 0

**Scraptiidae**

*Anaspis flava* (L., 1758)  
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*Anaspis frontalis* (L., 1758)  
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<td><em>Anaspis ruficollis</em> (F., 1792)</td>
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**Stenichnus scutellaris** (Müll.Kunze, 1822)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 0/1 | 0/0 | 1 | 12 | 1 | 24 |

**Silphidae**

**Dendroxena quadrimaculata** (Scop., 1772)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 1 | 1 | 3 | 0 |

**Nicrophorus vespilloides** (Hbst., 1783)

|                | 0 | 1 | 0 | 0/0 | 1/0 | 1/0 | 0/0 | 0 | 0 | 0 | 0 |

**Oiceoptoma thoracica** (L., 1758)

|                | 0 | 0 | 2/0 | 0/0 | 1/1 | 0/2 | 0/0 | 0 | 0 | 0 | 0 |

**Phosphaga atrata** (L., 1758)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 1/0 | 0/0 | 0 | 0 | 0 | 0 |

**Thanatophilus sinusatus** (F., 1775)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 1/0 | 0/0 | 0 | 0 | 1 | 0 |

**Silvanidae**

**Ahasverus advena** (Waltl, 1834)

|                | 0 | 0 | 1 | 0/0 | 0/1 | 2/0 | 0/1 | 1 | 0 | 1 | 1 |

**Silvanoprus fagi** (Guer., 1844)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 1 | 0 | 0 |

**Silvanus bidentatus** (F., 1792)

|                | 0 | 3 | 10 | 6/1 | 2/1 | 2/0 | 0/1 | 1 | 6 | 6 | 11 |

**Silvanus unidentatus** (F., 1792)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 1 | 0 | 1 |

**Uleiota planata** (L., 1761)

|                | 0 | 0 | 0 | 1/0 | 0/0 | 2/0 | 1/0 | 1 | 2 | 2 | 1 |

**Sphindidae**

**Aspidiphorus orbiculatus** (Gyll., 1808)

|                | 0 | 0 | 1 | 0/0 | 0/0 | 0/1 | 0/0 | 0 | 2 | 0 | 2 |

**Sphindus dubius** (Gyll., 1808)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 1 | 0 | 0 |

**Staphylinidae**

**Acrotona muscorum** (Bris., 1860)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 1/0 | 0/0 | 0 | 0 | 0 | 1 |

**Acrotona parvula** (Mannh., 1831)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 2 | 0 | 0 |

**Acrotona pygmaea** (Grav., 1802)

|                | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 1 |
|-----------------------|------------------------|-------------------------|---------------------------|
|                       | Beech | Spruce | Beech | Beech | Beech | Spruce | Beech | Spruce | Beech | Oak | Pine |
| Management type       | Unmanage | Even-Aged | Unmanage | Even-Aged | Unmanage | Even-Aged | Unmanage | Even | Unmanage | Even-Aged | Even-Aged |
| N                     | 5      | 32      | 12     | 13/6       | 13/9     | 20/15       | 4/4     | 6      | 15    | 7    | 22   |
| Acrontona sylvicola (Kr., 1856) | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 1 0 1 |
| Acrulia inflata (Gyll., 1813) | 0 1 2 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Agaricohara latissima (Steph., 1832) | 1 1 1 2/2 | 3/2 | 16/6 | 5/4 | 0 0 0 0 |
| Aelobia scapularis (Sahlb., 1831) | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aelohara albolillosa Bernh., 1901 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aelohara bipustulata (L., 1761) | 0 1 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aelohara brevipennis Grav., 1806 | 0 0 0 1/0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aelohara laevigata Gyll., 1810 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aelohara lanuginosa Grav., 1802 | 0 0 1 0 | 0 0 1/0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aelohara rugicorns Grav., 1802 | 0 0 0 0 | 0 0 1/0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aelohara sparsa Heer, 1839 | 3 29 17 28/2 | 43/26 | 58/56 | 29/15 | 4 6 8 19 |
| Aelohara spissicornis Er., 1839 | 0 2 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aelohara stichai Likovsky, 1965 | 0 0 0 3/3 | 1/3 | 12/5 | 1/8 | 0 0 0 0 |
| Aeluonota rafotestatea (Kr., 1856) | 0 3 0 0 | 0 0 2/1 | 1/1 | 0/1 | 0 0 0 1 |
| Aloxonota gregaria (Er., 1839) | 0 6 1 6/3 | 1/2 | 7/3 | 3/0 | 1 1 1 2 |
| Aloxonota insecta (Thoms., 1856) | 0 0 0 1/0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aloxonota planifrons (Wtrh., 1864) | 0 0 0 0 | 0 0 0 0 | 0 1/0 | 0 0 0 0 | 0 0 0 0 |
| Aloxonota analis (Grav., 1802) | 1 7 0 1/0 | 1/2 | 4/9 | 3/5 | 1 3 2 1 |
| Aloxonota cavarifrons (Mannh., 1830) | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 | 0 0 0 0 |
| Aloxonota decipiens (Shp., 1869) | 0 0 0 3/0 | 2/0 | 5/0 | 0/0 | 0 0 0 0 |
| Aloxonota nigrofusca (Steph., 1832) | 0 0 0 0 | 0 0 1/1 | 1/0 | 0 0 0 0 | 0 0 0 0 |
|--------------|------------------------|-------------------------|--------------------------|
|              | Beech | Spruce | Beech | Beech | Beech | Spruce | Beech | Oak | Pine |
| Management type | Unmanaged | Even-Aged | Unmanaged | Even-Aged | Unmanaged | Even-Aged | Unmanaged | Even-Aged | Unmanaged | Even-Aged | Even-Aged |
| N            | 5 | 32 | 12 | 13/6 | 13/9 | 20/15 | 4/4 | 6 | 15 | 7 | 22 |
| Amphichroum canaliculatum (Er., 1840) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Anomognathus cuspidatus (Er., 1839) | 0 | 11 | 3 | 0 | 2/1 | 2/6 | 0 | 0 | 3 | 0 | 3 |
| Anotylus clypeonitens (Pand., 1867) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Anotylus hamatus (Fairm., Lab., 1856) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Anotylus ineccatus (Grav., 1806) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Anotylus inustus (Grav., 1806) | 0 | 0 | 0 | 0 | 0 | 0 | 1/0 | 0 | 0 | 0 | 0 |
| Anotylus mutator (Lohse, 1963) | 1 | 0 | 1 | 1/5 | 4/5 | 7/4 | 0 | 0 | 0 | 0 | 0 |
| Anotylus mutator/sculpturatus | 2 | 4 | 3 | 0/5 | 0/8 | 0/6 | 0/3 | 0 | 0 | 2 | 0 |
| Anotylus rugosus (F., 1775) | 0 | 2 | 0 | 0 | 0 | 0 | 3/0 | 0/0 | 0 | 3 | 3 |
| Anotylus saulcyi (Pand., 1867) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Anotylus sculpturatus (Grav., 1806) | 0 | 2 | 1 | 1/0 | 0/4 | 0/2 | 0 | 0 | 0 | 0 | 2 |
| Anotylus spec. Thoms., 1859 | 0 | 0 | 0 | 0 | 0 | 0/3 | 0/3 | 0/0 | 0 | 0 | 0 |
| Anotylus tetracarinatus (Block, 1799) | 0 | 1 | 0 | 1/1 | 0/0 | 1/0 | 1/0 | 1 | 5 | 4 | 3 |
| Anthobiom atrocephalum (Gyll., 1827) | 0 | 0 | 0 | 0 | 0 | 0 | 0/0 | 0 | 0 | 1 | 2 |
| Anthobiom melanocephalum (Ill., 1794) | 0 | 0 | 0 | 0 | 0 | 0/0 | 3/0 | 0/0 | 0 | 0 | 0 |
| Anthobiom unicolor (Marsh., 1802) | 0 | 0 | 0 | 0 | 0/0 | 0 | 0/0 | 0 | 0 | 0 | 2 |
| Anthophagus angusticollis (Mannh., 1830) | 1 | 10 | 1 | 7/4 | 9/13 | 11/21 | 0/1 | 0 | 0 | 0 | 0 |
| Atheta aegra (Heer, 1841) | 0 | 0 | 0 | 1/0 | 2/1 | 2/0 | 0/0 | 0 | 0 | 0 | 0 |
| Atheta aeneipennis Thoms., 1856 | 0 | 3 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 0 |
| Atheta amicula (Steph., 1832) | 0 | 0 | 0 | 0/0 | 0/0 | 0/1 | 0/0 | 0 | 0 | 0 | 0 |
| Atheta aquatilis (Thoms., 1867) | 1 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 0 |
|-------------------------------|-------------------------|--------------------------|---------------------------|
| Main tree                     |                         |                          |                           |
| Management type               | Beech       | Spruce   | Beech       | Beech       | Spruce   | Beech       | Oak   | Pine   | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged | Unmanaged | Even Aged |
| Atheta atramentaria (Gyll., 1810) | 0          | 0         | 0          | 0          | 0         | 0          | 0         | 0         | 0         |
| Atheta borella Brundin, 1948 | 0          | 0         | 0          | 0          | 0         | 0          | 0         | 0         | 0         | 3         | 0         | 0         |
| Atheta castanoptera (Mannh., 1831) | 0          | 0         | 1          | 0          | 0         | 0          | 0         | 0         | 0         | 0         | 0         | 0         |
| Atheta cauta (Er., 1837)      | 0          | 0         | 0          | 1          | 0         | 0          | 0         | 0         | 0         | 0         | 0         | 0         |
| Atheta celata (Er., 1837)     | 0          | 0         | 0          | 0          | 0         | 0          | 0         | 0         | 0         | 2         | 0         | 0         |
| Atheta corvina (Thoms., 1856) | 0          | 0         | 0          | 0          | 0         | 0          | 0         | 0         | 0         | 0         | 1         | 0         |
| Atheta crassicornis (F., 1792) | 3          | 5         | 0          | 2          | 6         | 7          | 3         | 15        | 1         | 0         | 1         | 1         |
| Atheta debilis (Er., 1837)    | 0          | 0         | 0          | 0          | 0         | 0          | 0         | 0         | 0         | 0         | 1         | 0         |
| Atheta elongatula (Grav., 1802) | 0         | 5         | 4          | 0          | 2         | 0          | 0         | 0         | 0         | 1         | 0         | 0         |
| Atheta fungi (Grav., 1806)    | 2          | 2         | 4          | 6         | 3         | 2         | 4         | 2         | 3         | 1         | 7         | 1         |
| Atheta fungicola (Thoms., 1852) | 0         | 1         | 0          | 0          | 1         | 0          | 0         | 0         | 0         | 0         | 1         | 0         |
| Atheta gagatina (Baudi, 1848) | 0          | 0         | 0          | 0          | 1         | 0          | 0         | 0         | 0         | 0         | 0         | 0         |
| Atheta griepi Scheerp., 1951  | 0          | 0         | 0          | 0          | 0         | 0          | 0         | 0         | 0         | 1         | 0         | 0         |
| Atheta hansseni Strand, 1943  | 0          | 0         | 0          | 0          | 0         | 0          | 4         | 0         | 0         | 0         | 0         | 0         |
| Atheta harwoodi Will., 1930   | 0          | 2         | 0          | 0         | 0         | 0          | 0         | 0         | 0         | 0         | 2         | 0         |
| Atheta hypnorum (Kiesw., 1850) | 0          | 0         | 1          | 0          | 0         | 0          | 0         | 0         | 0         | 0         | 0         | 0         |
| Atheta indubia (Shp., 1869)   | 0          | 1         | 0          | 0         | 0         | 0          | 0         | 0         | 0         | 0         | 0         | 0         |
| Atheta inquinula (Grav., 1802) | 0          | 0         | 0          | 0          | 1         | 0          | 0         | 0         | 0         | 1         | 0         | 0         |
| Atheta kochi Roub., 1937      | 0          | 0         | 0          | 0          | 0         | 0          | 2         | 0         | 0         | 0         | 0         | 0         |
| Atheta laevana (Muls.Rey, 1852) | 0         | 0         | 1          | 1         | 0         | 0          | 2         | 0         | 0         | 0         | 0         | 0         |
| Atheta laticollis (Steph., 1832) | 0         | 0         | 0          | 0          | 0         | 0          | 0         | 0         | 0         | 0         | 1         | 0         |
|---------------|-------------------------|-------------------------|--------------------------|
|               | Beech | Spruce | Beech | Beech | Beech | Spruce | Beech | Oak | Pine |
| Management type | Unmanaged | Even-Aged | Unmanaged | Even-Aged | Uneven-Aged | Even-Aged | Unmanaged | Even-Aged | Even-Aged | Unmanaged |
| N             | 5     | 32     | 12     | 13/6   | 13/9   | 20/15   | 4/4   | 6    | 15   | 7    | 22    |
| *Atheta longicornis* (Grav., 1802) | 0 | 0 | 0 | 0/1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Atheta marcida* (Er., 1837) | 0 | 0 | 0 | 0/0 | 0 | 0/1 | 0 | 2 | 0 | 1 |
| *Atheta monticola* (Thoms., 1852) | 0 | 0 | 0 | 1/0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Atheta myrmecobia* (Kr., 1856) | 0 | 0 | 0 | 0 | 0 | 0/1 | 0 | 0 | 0 | 0 | 0 |
| *Atheta negligens* (Muls.Rey, 1873) | 0 | 0 | 1 | 0 | 0 | 0/1 | 0 | 0 | 0 | 0 | 0 |
| *Atheta nigricornis* (Thoms., 1852) | 12 | 174 | 66 | 173/54 | 60/46 | 121/152 | 10/22 | 4 | 8 | 5 | 12 |
| *Atheta oblita* (Er., 1839) | 0 | 0 | 0 | 0 | 0 | 0/1 | 0 | 0 | 0 | 0 | 0 |
| *Atheta orbata* (Er., 1837) | 0 | 0 | 0 | 2/0 | 0 | 1/0 | 0/1 | 2 | 0 | 0 | 4 |
| *Atheta pallidicorpus* (Thoms., 1856) | 0 | 0 | 1 | 0 | 0 | 1/0 | 1 | 0 | 1 | 0 | 0 |
| *Atheta palustris* (Kiesw., 1844) | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 |
| *Atheta parca* (Muls.Rey, 1873) | 0 | 0 | 0 | 0 | 0 | 0/0 | 0 | 0 | 0 | 0 | 0 |
| *Atheta picipes* (Thoms., 1856) | 0 | 4 | 5 | 2/0 | 0 | 1/0 | 1 | 0 | 0 | 0 | 0 |
| *Atheta pittionii* Scheerp., 1950 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Atheta ravilla* (Er., 1839) | 0 | 0 | 0 | 0 | 0 | 0/0 | 0 | 0 | 0 | 0 | 0 |
| *Atheta sequanica* (Bris., 1859) | 0 | 0 | 0 | 0 | 0 | 0/0 | 0 | 0 | 0 | 0 | 0 |
| *Atheta sodalis* (Er., 1837) | 0 | 2 | 1 | 0/0 | 0 | 1/0 | 0/1 | 0 | 4 | 0 | 2 |
| *Atheta subtilis* (Scriba, 1866) | 0 | 2 | 1 | 0/0 | 0 | 1/0 | 0/1 | 0 | 0 | 0 | 0 |
| *Atheta triangulum* (Kr., 1856) | 0 | 1 | 0 | 0/3 | 3/3 | 0/3 | 0 | 0 | 0 | 0 | 0 |
| *Atheta volans* (Scriba, 1859) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Atrecus affinis* (Payk., 1789) | 0 | 2 | 1 | 0 | 0 | 1/0 | 0 | 0 | 0 | 0 | 0 |
|--------------|------------------------|-------------------------|--------------------------|
| Main tree    | Beech                  | Spruce                  | Beech                    | Beech | Spruce |
|              | Beech                  | Even-Aged               | Beech                    | Even-Aged |
|              | Unmanaged              | Uneven-Aged            | Unmanaged               | Uneven-Aged |
|              |                        |                        |                          |          |
|              |                        |                        |                          |          |
|              |                        |                        |                          |          |
| N            | 5                      | 12                     | 13/6                     | 13/9    |
|              | 6                      | 15                     | 15                       | 7       |
|              | 22                     |                        |                          |          |
| Autalia rivularis (Grav., 1802) | 0 | 1 | 0 | 0/0 | 0/0 | 1/0 | 0/0 | 1 | 0 | 0 | 0 |
| Batrisodes adnexus (Hampe, 1863) | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 3 |
| Bibloplectus ambiguus (Reichb., 1816) | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 1 | 0 | 0 |
| Bibloplectus tenebrosus (Rtt., 1880) | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 1 | 1 | 1 | 0 |
| Bibloporus bicolor (Denny, 1825) | 34 | 50 | 35 | 6/13 | 5/2 | 10/10 | 10/11 | 1 | 6 | 3 | 7 |
| Bibloporus minatus Raffr., 1914 | 0 | 0 | 0 | 4/3 | 0/3 | 3/1 | 3/4 | 8 | 27 | 12 | 24 |
| Bibloporus spec. Thom., 1859 | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 0 |
| Bisnius fimbriatius (Grav., 1802) | 6 | 5 | 2 | 4/0 | 1/1 | 3/3 | 2/2 | 3 | 2 | 3 | 2 |
| Bisnius pseudoparcaus (Brunne, 1976) | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 0 |
| Bolitobius castaneus (Steph., 1832) | 0 | 0 | 0 | 2/1 | 0/0 | 1/0 | 0/0 | 0 | 0 | 0 | 0 |
| Bolitobius cingulata (Mannh., 1830) | 0 | 0 | 0 | 0/0 | 0/0 | 0/1 | 0/0 | 0 | 0 | 0 | 0 |
| Bolitochara lucida (Grav., 1802) | 0 | 0 | 0 | 2/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 0 |
| Bolitochara muscula Shp., 1875 | 0 | 0 | 0 | 1/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 0 |
| Bolitochara obliqua Er., 1837 | 2 | 4 | 1 | 4/1 | 0/0 | 1/0 | 0/0 | 0 | 1 | 0 | 0 |
| Brachygluta simia (Aube, 1833) | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 0 |
| Bryophacis crassicornis (Maekl., 1847) | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 0 | 0 | 0 | 1 |
| Bryoporus cernus (Grav., 1806) | 0 | 0 | 0 | 0/0 | 1/0 | 0/0 | 0/0 | 0 | 0 | 0 | 1 |
| Bythinus burrellii Denny, 1825 | 2 | 3 | 6 | 0/0 | 2/0 | 1/3 | 0/1 | 0 | 0 | 0 | 0 |
| Callicerus obscurus Grav., 1802 | 0 | 0 | 0 | 0/0 | 1/0 | 0/0 | 1/0 | 0 | 0 | 0 | 0 |
| Callicerus rigidicornis (Er., 1839) | 0 | 0 | 0 | 0/0 | 0/0 | 0/1 | 0/0 | 0 | 0 | 0 | 0 |
| Carpelinus corticinus (Grav., 1806) | 0 | 7 | 0 | 0/0 | 0/0 | 0/0 | 0/0 | 1 | 2 | 1 | 0 |
|--------------|------------------------|-------------------------|--------------------------|
| Main tree    | Beech                  | Spruce                  | Beech                   |
|              | Unmanaged Even-aged    | Unmanaged Even-aged     | Unmanaged Even-aged     |
| Management type |                   |                         |                         |
| N            | 5                      | 32                      | 12                      |
|              | 13/6                   | 13/9                    | 20/15                   |
|              | 4/4                    | 6                       | 15                      |
|              | 7                      | 22                      |                          |
| *Carpelimus gracilis* (Mannh., 1830) | 0 0 0 0 0/0 0/1 2/0 0 0 0 0 |
| *Carpelimus impressus* (Boisd.Lacord., 1835) | 0 0 0 0/0 0/0 0/0 0/0 1 0 0 0 |
| *Carphacis striatus* (Ol., 1794) | 0 0 0 0/0 0/1 0/0 0/0 0 0 0 0 |
| *Coprophilus striatulus* (F., 1792) | 2 0 0/1 7/8 3/6 0/3 0 2 0 1 |
| *Coryphium angusticolle* Steph., 1834 | 0 0 1/0 0/0 0/0 0/0 0 0 0 0 |
| *Cypha longicornis* (Payk., 1800) | 0 0 0 0/0 1/0 0/2 0/0 0 1 0 1 |
| *Cypha semenulum* (Er., 1839) | 0 0 0 0/0 0/0 0/0 0/0 0 0 0 0 |
| *Cypea curtula* (Er., 1837) | 0 0 0 1/0 0/0 2/0 0/1 0 0 0 0 |
| *Dadobia immersa* (Er., 1837) | 1 3 8 0/0 1/0 1/0 2/0 1 1 1 7 |
| *Dinaraea aequata* (Er., 1837) | 2 0 1/0 0/0 0/1 2/0 0/1 0 0 0 0 |
| *Dinaraea angustula* (Gyll., 1810) | 0 0 0 0/0 1/0 1/0 0/0 0 0 1 0 |
| *Dinaraea linearis* (Grav., 1802) | 2 0 0/0 0/0 0/1 0/0 0 0 1 0 |
| *Dropephylla linearis* (Zetterst., 1828) | 1 2 1 0/0 0/0 0/0 0/0 0 0 0 0 |
| *Enalodroma hepatica* (Er., 1839) | 0 0 0 0/0 0/0 0/0 0/0 1 0 0 1 |
| *Euplectus bescidicus* Rtt., 1881 | 0 1 0/0 0/0 0/1 0/1 1 0 2 0 0 |
| *Euplectus bruneus* (Grimm., 1841) | 0 0 2 1/0 0/0 1/1 0/0 0 1 0 0 |
| *Euplectus decipiens* Raffr., 1910 | 0 2 1 1/0 0/0 0/0 0/0 0 0 0 0 |
| *Euplectus faveolus* Guillb., 1888 | 0 1 2 3/1 1/2 0/2 4/3 1 0 0 0 |
| *Euplectus infirmus* Raffr., 1910 | 0 0 0 0/0 0/0 0/0 0/0 0 0 0 2 |
| *Euplectus karstenii* (Reichb., 1816) | 0 1 0 0/0 0/0 0/0 0/0 0 0 0 0 |
| *Euplectus nanus* (Reichb., 1816) | 0 0 0 0/0 0/2 0/0 0/0 0 0 0 0 |
|--------------|------------------------|-------------------------|--------------------------|
|              | Beech | Spruce | Beech | Beech | Beech | Spruce | Beech | Oak | Pine |
| Management type | Unmanaged | Even-Aged | Even-Aged | Unmanaged | Even-Aged | Even-Aged | Unmanaged | Even-Aged | Even-Aged |
| N | 5 32 12 13/6 13/9 20/15 4/4 6 15 7 22 |
| Euplectus punctatus Muls., 1861 | 0 0 0 | 0/1 | 0/0 | 0/1 | 0/1 | 1 | 0 0 0 |
| Euplectus signatus (Reichb., 1816) | 0 0 0 | 1/0 | 0/0 | 0/0 | 0/0 | 0 5 2 0 |
| Euryusa castanoptera Kr., 1856 | 15 57 16 25/29 2/4 10/9 | 6/2 | 3 73 29 28 |
| Euryusa optabilis Heer, 1839 | 0 0 0 | 0/0 | 0/0 | 0 0 0 2 |
| Eusphalerum abdominale (Grav., 1806) | 0 0 0 | 0/0 | 0/0 | 0 0 0 |
| Eusphalerum atrum (Heer, 1838) | 0 0 0 | 0 0 0 0 0 0 |
| Eusphalerum limbatum (Er., 1840) | 1 7 1 0/0 2/1 3/3 0/0 0 0 0 0 |
| Eusphalerum longipenne (Er., 1839) | 0 0 0 | 0/0 | 0/0 | 0/0 0 0 0 |
| Eusphalerum luteum (Marsh., 1802) | 0 1 0 0/1 1/1 1/6 0/1 0 0 0 0 |
| Eusphalerum minutum (F., 1792) | 0 0 0 | 0/0 | 0/0 | 0 0 0 0 |
| Eusphalerum rectangulum (Fauv., 1869) | 0 0 0 | 0/0 | 0/0 | 0 0 0 0 |
| Eusphalerum semicoeleopratum (Panz., 1795) | 1 3 1 5/1 2/1 20/8 1/0 0 0 0 0 |
| Eusphalerum signatum (Märk., 1857) | 0 0 0 | 1/0 | 0/0 | 0 0 0 0 |
| Eusphalerum sorbi (Gyll., 1810) | 1 8 2 0/1 2/1 3/3 0/0 0 0 0 0 |
| Eusphalerum stramineum (Kr., 1857) | 0 0 0 | 0 0 0 0 0 0 |
| Eusphalerum tenenbaumi (Bernh., 1932) | 0 2 0 0/0 0/0 0/1 0/0 0 0 0 0 |
| Gabrius appendiculatus Sharp, 1910 | 0 10 6 0/1 0/1 0 0 0 1 1 0 1 |
| Gabrius astutoides (Strand, 1946) | 0 0 1 | 0 0 0 0 0 0 0 |
| Gabrius breviventer (Sperk, 1835) | 0 3 4 0/0 0 0 0/0 2 4 1 0 |
| Gabrius femoralis (Hochh., 1851) | 0 2 0 0/0 0/0 0/0 0 0 0 0 |
| Gabrius spec. Steph., 1829 | 0 3 0 0/0 0/0 0/0 0 0 0 0 |

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<tr>
<td>Main tree</td>
<td>Beech</td>
<td>Spruce</td>
<td>Beech</td>
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<tr>
<td>Management type</td>
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<td>Even-Aged</td>
<td>Unmanaged</td>
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<td>12</td>
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<td>5</td>
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<tr>
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<td><em>Gyrohypnus fracticornis</em> (Müll., 1776)</td>
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<td>0</td>
</tr>
<tr>
<td><em>Gyrophaena fasciata</em> (Marsh., 1802)</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Gyrophaena gentilis</em> Er., 1839</td>
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<td>3/2 4/1 4/1</td>
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**Tachinus laticollis** Grav., 1802
1 1 3 1/0 0/0 0/1 2/0 1 0 0 1

**Tachinus lignorum** (L., 1758)
0 0 1 0/0 0/0 0/0 0/0 0 0 0 0

**Tachinus pallipes** Grav., 1806
1 2 8 0/0 0/0 0/1 1/6 0 0 0 1

**Tachinus rufipes** (L., 1758)
1 7 5 1/0 1/0 1/0 0/0 0 0 2 1

**Tachinus signatus** Grav., 1802
0 0 0 0/0 0/0 0/1 0/0 0 0 0 0

**Tachinus subterraneus** (L., 1758)
0 1 0 0/0 0/0 0/0 0/1 0 0 0 0

**Tachyporus chrysomelinus** (L., 1758)
0 1 0 0/0 0/0 0/1 0/0 0 1 1 0

**Tachyporus dispar** (Payk., 1789)
1 0 0 0/0 0/0 0/1 2/0 0/0 0 1 1 0

**Tachyporus hypnorum** (F., 1775)
0 1 1 1/0 2/0 1/2 0/1 1 11 3 4

**Tachyporus nitidulus** (F., 1781)
0 0 0 0/0 1/1 1/0 0/0 0 0 0 0

**Tachyporus obtusus** (L., 1767)
2 0 0 0/0 0/0 2/2 0/0 0 1 0 0

**Tachyporus pulchellus** Mannh., 1841
0 0 0 0/0 0/0 0/0 0/0 1 0 2 0

**Tachyporus solutus** Er., 1839
0 0 1 0/0 0/0 0/0 0/0 0 1 0 0

**Tasgius morsitans** (Rossi, 1790)
0 0 0 0/0 0/0 0/0 0/0 0 0 1 0

**Thamiaraea cinnamomea** (Grav., 1802)
0 0 0 1/0 0/0 0/0 0/0 0 0 0 0

**Tinotus morion** (Grav., 1802)
0 0 0 0/0 0/0 1/0 0/0 0 0 0 1

**Trichophya pilicornis** (Gyll., 1810)
0 0 0 1/0 0/0 0/0 0/0 0 0 0 0

**Trichium brevicolle** (Reichb., 1816)
1 0 2 0/0 1/0 0/1 0/0 0 1 1 1

**Tychus niger** (Payk., 1800)
0 0 1 0/0 0/1 0/0 1/1 0 0 0 0

**Tyrus mucronatus** (Panz., 1803)
0 0 0 0/0 0/0 0/0 0/0 0 4 1 22

**Velleius dilatatus** (F., 1787)
0 0 0 0/0 0/0 0/0 0/0 1 0 2 0
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Species Count:

- **Xantholinus linearis** (Ol., 1795): 0 0 0 0/0 0/0 0/0 0/0 0 0 1 0
- **Xantholinus longiventris** Heer, 1839: 0 1 0 0/0 0/0 0/0 0/0 3 2 2 4
- **Xylostiba bosnica** (Bernh., 1902): 0 0 1 0/0 0/0 0/0 0/1 0 0 0 1
- **Xylostiba monilicornis** (Gyll., 1810): 1 0 0 5/1 1/3 1/0 0/1 0 0 0 0
- **Zyras cognatus** (Märk., 1842): 0 1 0 0/0 0/0 0/0 0/1 0 0 0 1
- **Zyras haworthi** (Steph., 1832): 0 1 0 0/0 0/0 0/0 0/0 0 0 0 0
- **Zyras humeralis** (Grav., 1802): 0 1 0 0/0 0/0 0/0 0/0 0 0 0 0
- **Zyras lugens** (Grav., 1802): 0 1 0 0/0 0/0 0/0 0/0 1 0 1 1

**Tenebionidae**

- **Bolitophagus reticulatus** (L., 1767): 0 0 0 2/4 0/2 4/11 0/3 2 8 0 12
- **Corticeus unicolor** (Pill. Mitt., 1783): 0 0 0 1/0 1/0 0/0 1/0 0 0 0 1
- **Lagria hirta** (L., 1758): 0 1 0 1/0 0/0 0/0 0/0 0 1 0 6
- **Mycetochara linearis** (Ill., 1794): 0 0 0 0/0 2/0 2/1 0/0 1 0 0 0
- **Scaphidema metallicum** (F., 1792): 0 0 0 0/0 0/0 0/1 0/0 0 0 0 0

**Tetramomidae**

- **Tetratoma ancora** F., 1790: 0 2 1 32/26 4/3 8/4 0/0 0 0 0 0

**Throscidae**

- **Aulonothroscus brevicollis** Bonv., 1859: 0 2 0 2/0 0/0 1/0 0/2 1 0 0 9
- **Trixagus carinifrons** Bonv., 1859: 0 3 5 8/2 42/7 8/3 31/48 0 5 1 70
- **Trixagus dermestoides** (L., 1767): 0 0 2 1/0 1/2 2/1 15/6 4 8 2 31
- **Trixagus meybohmi** Leseigneur, 2005: 0 0 0 0/0 0/3 0/0 0/0 0 0 0 0
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<td><em>Nemosoma elongatum</em> (L., 1761)</td>
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**Table S5-3**: Complete list of Apocrita species and their abundances from pheromone traps, separated by management type and main tree type. Species are grouped by family and presented in alphabetical order.

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<tr>
<td>N</td>
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<td>32</td>
<td>12</td>
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**Andrenidae**

- *Andrena bicornis*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0/0
  - Schorfheide-Chorin (2010): 0/0

- *Andrena haemorrhoa*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0/0
  - Schorfheide-Chorin (2010): 0/1

- *Andrena helvola*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0/3
  - Schorfheide-Chorin (2010): 0/0

- *Andrena helvola/variens*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0/0
  - Schorfheide-Chorin (2010): 0/0

- *Andrena minutula*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0/1

- *Andrena nitidiuscula*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0/0
  - Schorfheide-Chorin (2010): 0/0

- *Andrena ruficrus*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0/0
  - Schorfheide-Chorin (2010): 0/0

- *Andrena spec.*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0/0
  - Schorfheide-Chorin (2010): 0/0

**Aphelinidae**

- *Aphelinidae spec.*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0/1

- *Aphelinus spec.*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

- *Encarsia spec.*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

- *Eretmocerus mundus*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

- *Eretmocerus spec.*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

**Apidae**

- *Bombus pratorum*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

- *Bombus spec.*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0/1

- *Bethylidae*

- *Cephalonomia formiciformis*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

- *Cephalonomia tarsalis/hammi*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

- *Earinus gloriatorius/elator*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

- *Alysiinae spec.*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0/2

- *Braconidae spec.*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

**Braconidae**

- *Cephalonomia formiciformis*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

- *Cephalonomia tarsalis/hammi*
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  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

**Braconidae spec.**

- *Braconidae spec.*
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  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

**Chelonius spec.**

- *Chelonius spec.*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0

**Earias lophiorum/declivis**

- *Earias lophiorum/declivis*
  - Schwäbische-Alb (2010): 0
  - Hainich-Dün (2010/2011): 0
  - Schorfheide-Chorin (2010): 0
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- **Monelata solida**: 2 0 0 1/5 6/12 2/1 0/0 0/0 3 3 1 0
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- *Aphelopus melaleucus* | 0    | 0     | 0      | 1/0  | 3/0  | 1/2   | 0/0  | 1    | 1   | 0    | 0    |
- *Aphelopus serratus* | 0    | 0     | 0      | 0/0  | 1/0  | 0/1   | 0/0  | 0    | 0   | 0    | 0    |

**Encyrtidae**
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**Eucoilidae**
- *Glauraspis microptera* | 0    | 0     | 0      | 0/0  | 1/0  | 7/0   | 1/0  | 0    | 0   | 0    | 0    |
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**Torymidae**
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Supplement S6: Temporal variability of abundance patterns

To test for annual variation in forest management effects, we sampled a subset of 35 plots in the Hainich-Dün region with pheromone traps in 2011. We found no interaction effect between year and management intensity (Table S6-1), which suggests that observed effects are independent from sampling year.

Table S6-1: Effects of year and its interaction with forest management intensity (ForMI) and other covariates assessed at different spatial scales on the abundance of ambrosia beetles. Negative binomial GLMMs were performed; minimal models and the terms dropped during the optimisation test by backward selection on the negative binomial GLMM, based on the p-value of a likelihood-ratio test, are shown. Df = degrees of freedom; L = statistic value; p = significance level; ED = effect direction for continuous terms: ↑/↓ = positive/negative correlation with abundance and results of Tukey contrasts (function glht) for factors; DO = order in which the terms were dropped from the model.

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<tr>
<th>Species Abundance</th>
<th>Trypodendron domesticum</th>
<th>Xylosandrus germanus</th>
<th>Anisandrus dispar</th>
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<tr>
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<td>Df L p ED DO</td>
<td>Df L p ED DO</td>
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<td>1 3.228 0.072 ↓</td>
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<td>ForMI * Year</td>
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<td>4 11.634 0.020 5↓</td>
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<td>1 0.012 0.912</td>
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<td>1 0.029 0.002 spruce&lt;beech</td>
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<td>Latitude</td>
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<td>1 2.308 0.129</td>
<td>1 1.084 0.298 (6)</td>
<td>32.810 &lt;0.001 ↓</td>
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Random factor      | Plot                    | Plot                          | Plot   |
Supplement 7: Phenology of *Trypodendron domesticum* and studied Xyleborini

**Figure S7-1**: Mean abundance of *Xylosandrus germanus* and *Anisandrus dispar* sampled by pheromone traps (N=50) and attack density (per m²) of AmbroBEx-logs (N=50) by Xyleborini in chronological sequence. The total numbers found in the Hainich-Dün region in 2010 are shown.

**Figure S7-2**: Mean abundance of *Trypodendron domesticum* sampled by pheromone traps (N=50), attack density (per m²) of AmbroBEx-logs (N=50) by *T. domesticum*, and emerged *T. domesticum* sampled by eclectors (number varies). The mean numbers found in the Hainich-Dün region in 2010 are shown.
Supplement S8: Results on attack density

For the AmbroBEx-logs, the attack density of *Trypodendron domesticum* was $54.0 \pm 14.3$ entrance holes per m$^2$ in the large logs (median: 1.4, range: 0–393.3) and $0.8 \pm 0.3$ entrance holes per m$^2$ in the small logs (median: 0, range 0–12). The attack density of large logs (small logs were excluded from further analysis) was not affected by management intensity. It was higher when the bark was structured to some degree and when there was a moderate level of dead wood in the surrounding area (hump-shaped relationship) (Table 3).

Distinguishing between entrance holes from *Xylosandrus germanus* and *Anisandrus dispar* turned out to be difficult in the field, but a comparison of flight phenology of the species with the occurrence of attacks on AmbroBEx-logs revealed congruence between the number of *Xyleborus* attacks and *Xyleborus germanus* abundance; we thus assumed that all attacks were carried out by this species (Fig. S7-1 in Supplement 7). Attack densities on the large AmbroBEx-logs ranged from 0 to 759.2 entrance holes per m$^2$ (mean ± SE: 144.8 ± 29.3, median: 41.1), with no attacks observed on 8 logs (16%). For the small AmbroBEx-logs, attack densities ranged from 0 to 713.6 entrance holes per m$^2$ (mean ± SE: 92.5 ± 23.5, median: 23.2), with no attacks observed on 12 logs (24%).

For the BELongDead-logs, attack density was $40.8 \pm 5.5$ entrance holes per m$^2$ (median: 17.5, range 0–240). Attack density was only affected by region, with lower hole densities found in the Schorfheide-Chorin region than in the other two regions.

Because BELongDead-logs were checked only twice, a comparison with flight phenology was not possible. Therefore, we defined one model to predict Xyleborini attacks and used the abundance of both *Xylosandrus germanus* and *Anisandrus dispar* as predictors. The Xyleborini attack densities in 2010 ranged from 0 to 940.5 entrance holes per m$^2$ (mean ± SE: 108.2 ± 17.7, median: 51.4), and 7 of the 89 logs (8%) did not have entrance holes. Forest management intensity (ForMI) did not have a significant effect on attack density (Table S8). Region influenced attack density, with the highest densities occurring in Schorfheide-Chorin.
In Hainich-Dün and Schorfheide-Chorin, attack densities increased with increasing abundance of *Xylosandrus germanus*, whereas in Schwäbische Alb this relationship was strongly negative. The abundance of *Anisandrus dispar* did not influence attack density. Logs in broad-leaved forests were attacked more frequently than those in coniferous forests, and the presence of a closed canopy reduced attack density. Other covariates did not have a significant effect on attack density.
### Table S8: Effects of forest management intensity (ForMI), its interaction with region, and covariates assessed at different spatial scales on the attack density of ambrosia beetles on experimentally exposed logs. We used a negative-binomial GLM for abundance model 5 and a negative-binomial GLMM for abundance models 7–9. Minimal models and the terms dropped during the optimisation test by backward selection (based on the p-value of a likelihood ratio test) are given. Df = degrees of freedom; L = statistic value; p = significance level; ED = effect direction (only given for continuous terms) where ↑/↓ = positive/negative correlation with attack density and ∩ = hump-shaped relationship; DO = order in which the terms were dropped from the model.

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<td>Trypodendron domesticum</td>
<td>Xylosandrus germanus</td>
<td>Trypodendron domesticum</td>
<td>Xyleborini</td>
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<tr>
<td>Df</td>
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<td>p</td>
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<td>DO</td>
<td>Df</td>
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<tr>
<td>Abundance in traps</td>
<td>1</td>
<td>1.666</td>
<td>0.20</td>
<td>(4)</td>
<td>1</td>
<td>23.554</td>
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<tr>
<td></td>
<td>1</td>
<td>1.888</td>
<td>0.17</td>
<td>(4)</td>
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</tr>
<tr>
<td>ForMI</td>
<td>1</td>
<td>4.910</td>
<td>0.027</td>
<td>↓</td>
<td>1</td>
<td>1.972</td>
</tr>
<tr>
<td>Region</td>
<td>NA*</td>
<td></td>
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<td>13.162</td>
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<td>ForMI x Region</td>
<td>NA*</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>5.308</td>
</tr>
<tr>
<td>Dead wood</td>
<td>4</td>
<td>2.848</td>
<td>0.58</td>
<td>∩</td>
<td>4</td>
<td>4.788</td>
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<td>Canopy closure</td>
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<td>0.040</td>
<td>0.84</td>
<td>(2)</td>
<td>1</td>
<td>0.506</td>
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<tr>
<td>Tree diversity</td>
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<td></td>
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<td>0.250</td>
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<td>Density of regeneration</td>
<td>2</td>
<td>0.248</td>
<td>0.88</td>
<td>(1)</td>
<td>2</td>
<td>0.968</td>
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<td>Main tree type</td>
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<td>1.180</td>
<td>0.28</td>
<td>(6)</td>
<td>1</td>
<td>1.868</td>
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<td>0.366</td>
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<td>Bark free area</td>
<td>1</td>
<td>0.562</td>
<td>0.45</td>
<td>(3)</td>
<td>1</td>
<td>1.114</td>
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<td></td>
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<td>1.256</td>
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<tr>
<td>Bark texture</td>
<td>3</td>
<td>10.252</td>
<td>0.016</td>
<td>(7)</td>
<td>3</td>
<td>5.850</td>
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<tr>
<td>Beetle diversity</td>
<td>1</td>
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<td>0.12</td>
<td>(5)</td>
<td>1</td>
<td>0.018</td>
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<tr>
<td>Log class</td>
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</tr>
</tbody>
</table>

†: Xylosandrus germanus
‡: Anisandrus dispar
* AmbroBEx-logs were only exposed in the Hainich-Dün region, single level, or omitted based on expected relevancy
§ this factor showed the highest p-value in single linear models and was therefore excluded prior to analyses to avoid overfitting
§ only the 100 cm x 20 cm logs were included in this model
‡: single factors were not tested because of a significant interaction
§ this variable was not assessed in BELongDead
+ only one log class was studied in BELongDead
Supplement S9: Results of breeding success of *Trypodendron domesticum*

The 230 breeding systems of *T. domesticum* were sampled (on a total of 17 AmbroBEx-logs (small logs: 6; large logs: 11) on 17 plots (for 3D-models of galleries based on CT-scans, see Figs. S8-1 & S8-2). Two of the eclectors were damaged by raccoons and four breeding systems were connected to other galleries (see Fig. S8-2), these systems were excluded from the analyses, resulting in a total of 224 breeding systems (small logs: 14; large logs: 210). The number of sampled breeding systems per log was 2.5 ± 0.7 (mean ± SE) and 19.5 ± 5.6, respectively. The distribution of the 17 sampled logs was slightly shifted towards lower intensity plots, with a mean (±SE) ForMI of 0.78 ± 0.14 (range 0–1.80), compared with the distribution of all 100 logs (mean ± SE: 0.96 ± 0.08; range 0–2.25). On the BELongDead-logs another 83 eclectors were installed and showed no damage.

The number of emerged *T. domesticum* and antagonists varied greatly among breeding systems, with many eclectors showing no or few catches and some eclectors showing many catches. From all emerged *T. domesticum* (mean ± SE: 3.39 ± 0.45; range: 0–35) we subtracted 156 individuals, two per gallery but no more than were present, that were considered to be parent beetles, leaving the presumed progeny. The number of *T. domesticum* progeny emerging per breeding system was affected neither by management intensity nor by canopy cover and did not differ between the two time periods after attack discovery when the eclectors were installed (all variables were dropped during backward selection). Of the tested covariates, only the date when the gallery was first discovered, i.e. time of infestation, affected the number of *T. domesticum* progeny, with more progeny occurring in galleries that were established earlier (Df=1,221; L=16.290; p<0.001).

The parasitoid *Perniphora robusta* is more strongly specialised on *Trypodendron* species than the predators caught by pheromone traps (Wegensteiner, Wermelinger & Herrmann 2015). This suggests that, at the breeding system scale, the control of *T. domesticum* by antagonists decreases with increasing management intensity, with its most
important antagonist showing overall low densities in managed forests (Table S6-2; no individual emerged from breeding systems in managed forests). In general, parasitoids need to feed on nectar and pollen in order to reconstitute their egg load (Raffa, Grégoire & Staffan Lindgren 2015). However, Führer (1975) suggested that female imagines of *P. robusta* can survive in managed forests without food sources, owing to a potential independence of imaginal nutrient uptake. In any case, our results indicate that potential food resources (e.g. honeydew of the common aphid *Phyllaphis fagi*) are sufficiently available in the studied managed beech forest (Gossner *et al.* 2014) and that other unknown factors, e.g. related to differences in stand structure and limited connectivity among forest patches (Raffa, Grégoire & Staffan Lindgren 2015), restrict the occurrence of *P. robusta* almost entirely to unmanaged forests.
Supplement S10: Examples of *Trypodendron domesticum* galleries based on Computer Tomography

**Figure S10-1**: 3D-model of a 100 cm x 20 cm log from the Hainich region; A–C show transparent bark and galleries of *T. domesticum* and others; A) sampled galleries (the red bulky part at the surface shows the hole remaining after the metal tube was removed), B) galleries with larval chambers (excluding sampled galleries), C) incomplete galleries and galleries of other species, D) outer appearance of log.
Figure S10-2: Characteristic shapes of galleries with one (A), two (B), and three (C) adult galleries, all with larval chambers; galleries in red were sampled with eclectors and galleries in green were not sampled. The red bulky part at the surface shows the hole remaining after the metal tube was removed. (D) The 3D reconstruction of the galleries reveals connections between the galleries, with possible exchange of insects. No individuals were sampled from the eclector attached to the red gallery on the right side; the individuals probably escaped through the green gallery.
Supplement S11: Relationship between management intensity and dead wood

The availability of fresh dead wood suitable for ambrosia beetles decreased with management intensity (Fig. S11-1).

**Figure S11-1:** Amount of dead wood as a function of management intensity. The amount of dead wood in a suitable stage for ambrosia beetles was measured in five categories: 1 = no dead wood, 2 = \( \leq 3 \) m\(^3\) ha\(^{-1}\), 3 = \( 3 < x \leq 6 \) m\(^3\) ha\(^{-1}\), 4 = \( 6 < x \leq 10 \) m\(^3\) ha\(^{-1}\), and 5 = \( > 10 \) m\(^3\) ha\(^{-1}\).
S12 References


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VanDerLaan, N.R. & Ginzel, M.D. (2013) The capacity of conophthorin to enhance the attraction of two Xylosandrus species (Coleoptera: Curculionidae: Scolytinae) to ethanol and the efficacy of verbenone as a deterrent. Agricultural and Forest Entomology, 15, 391-397.

