Contrasting responses of saproxylic insects to focal habitat resources: the example of longhorn beetles and hoverflies in Belgian deciduous forests

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Abstract

Although both saproxylic longhorn beetles and hoverflies benefit from the presence of woody substrates for reproduction, they differ in their requirements for floral resources and for microbiotopes of overmature and senescent trees. This led us to expect contrasting responses between the two species groups in relation to these essential resources. We examined this prediction in 22 mature oak- and beech-dominated stands of southern Belgium by relating their species assemblages to local vegetation structure and composition, altitude and landscape composition. Stands were organised in pairs as a function of their overall dead wood supply. Free-hanging window traps, stump emergence traps and Malaise traps produced 30 longhorn beetle species (1637 individuals) and 106 hoverfly species (3020 individuals). Paired-comparisons controlling for annual variation in captures showed that, unlike saproxylic hoverflies, stands with dead wood hosted more species and individuals of longhorn beetles. Accordingly, the two species groups were found to be independent on ordination axes, responding to different sets of environmental conditions. While stands dominated by oaks with a high snag volume were highly favoured by longhorn beetles, saproxylic and threatened syrphids were limited to open-stands with large trees and a well-developed, species rich herb layer providing the floral resources required for their reproduction. Our results suggest that, when defining criteria to identify or restore important habitats for saproxylic insect conservation, variables related to different aspects of dead wood supply should not be the only criteria taken into account.

Introduction

The study of factors underlying variability in the diversity of saproxylic organisms, those that depend upon woody substrates or upon the presence of other saproxylics for at least part of their life cycle (Speight 1989), has received growing attention during the last decades in the field of ecology, conservation biology, and forest management (Samuelsson et al. 1994; Grove 2002). This mainly stems from the findings that, besides representing a significant part of forest biodiversity (Siitonen

2001), these species are functionally important to forest ecosystems. Wood-dependent organisms play critical roles during the processes of woody debris decomposition and nutrient cycling through multitrophic interactions (Edmonds and Eglitis 1989; Harmon et al. 1994); they influence forest structure and composition (Harmon et al. 1986; Kuuluvainen 2002). Their availability affects forest bird communities, notably by limiting the population size of numerous species of woodpeckers, important cavity providers for secondary cavity-nesters (Martin and Eadie 1999; Bednarz et al. 2004). Some saproxylic organisms have narrow micro-habitat requirements and poor dispersal capacities (Siitonen 2001; Grove 2002). This makes them a group of species particularly susceptible to habitat loss and fragmentation and, as a result, extinction-prone. Accordingly, Speight (1989) estimated some 40% of Europe's saproxylic invertebrates to be already on the verge of extinction over much of their range while the majority of the remainder would be in decline. Due to their specificity for substrate and microclimatic conditions characterising mature timber habitat, saproxylic communities have been suggested as useful bio-indicators of forest quality, and as tools in the process of identifying important forests for nature conservation (Speight 1989; Good and Speight 1996).

As a general pattern, saproxylic insects respond to different aspects of dead wood availability, such as total amount (Økland et al. 1996; Martikainen et al. 2000), quality (Irmler et al. 1996; Schiegg 2001; Hövemeyer and Schauermann 2003; Similä et al. 2003) or spatial distribution (Schiegg 2000). Among them, longhorn beetles (Coleoptera, Cerambycidae) and hoverflies (Diptera, Syrphidae) share similar broad ecological requirements. They all rely upon diverse wooden micro-habitats for reproduction (Jeniš 2001; Speight et al. 2003a). At the tree level however, while the saproxylic beetles mainly select freshly dead woody habitats for oviposition, saproxylic hoverflies also colonise microhabitats of overmature and senescent trees (Bense 1995; Speight and Good 2003). Trunk cavities, rot-holes, insect workings, sap runs and woody surfaces under loose bark are key biotopes for saproxylic syrphids (Speight et al. 2003b). Among the 100 European saproxylic Syrphidae species with terrestrial larval activity, 66% have larvae only found on overmature/senescent trees, against 9% with larvae only living in woody debris (Speight et al. 2004). The remaining 25% of the species select microhabitats associated with both old trees and dead wood. On the other hand, most adult Syrphidae are obligate flower visitors, depending on both pollen and nectar of actinomorphic plants (e.g., Apiaceae, Asteraceae, Ranunculaceae, Rosaceae) to develop their reproductive organs and sustain their costly flight behaviour, respectively (Ellis and Ellis-Adam 1993; Branquart and Hemptinne 2000). By contrast, as many as 60% of the European saproxylic longhorn beetle species are reported as not visiting flowers (Jeniš 2001). Among potential benefits, flower resources affect fitness-related traits of individuals like fecundity, longevity and dispersal success (Stürken 1964; Haslett 1989; Hanks et al. 1998; Millar et al. 2003). Flowers are also used as mating sites by an array of longhorn beetle and hoverfly species (Villiers 1978; Vockeroth and Thompson 1981; Gilbert 1986; Barbalat 2002). Such difference in preferences for larval microhabitats and floral resources between the two species groups is expected to influence their response to habitat changes and, more specifically, to dead wood and overmature tree supplies.

In this paper, we aim to clarify environmental factors that explain species diversity and abundance of saproxylic longhorn beetles and hoverflies, including threatened ones, among mature beech *Fagus sylvatica* and oak *Quercus* spp.-dominated forest stands of southern Belgium. Among potential determinants we relate saproxylic diversity to local vegetation structure and composition, altitude and landscape composition. Particular attention is paid to the effects of dead wood and old tree availability, two limiting resources in modern forest landscapes, as well as to flower supply on community and species responses. Our study sites are located amongst those deciduous forest habitats with the largest amount of coarse woody debris that are still available in Belgium, with a total stand volume up to 150 m^3 ha^{-1}. This paper contributes to current attempts to improve predictions of insect distributions by linking focal habitat resources with species biology (Dennis et al. 2003; Dennis 2004; Shreeve et al. 2004).

Material and methods

Study area and site selection

The field study was conducted in the southern part of Belgium from 2002 to 2003. A total of 22 mature deciduous forest stands were selected, distributed over four natural regions (Figure 1). Dominant tree species (oak/beech) and the availability of woody debris were the main criteria of site selection. Sites were organised by pairs (11 pairs), with paired stands showing similar plant composition, soil properties and abiotic factors (elevation, rainfall, temperature) but with contrasting management histories. Accordingly, paired stands were thereafter classified as having a high (>25 m^3 of dead wood per ha) or a low (<25 m^3) amount of coarse woody debris. They were located 2–10 km apart from each other.

Insect data

We used various kinds of traps to sample the insect composition of the different study sites. In the 11 sites with a high amount of dead wood, insect traps were situated where woody debris was most abundant. In each stand, 8 flight-window traps (W) were placed and numbered along 2×100 m perpendicular transects crossing each other in their middle, with the traps number 1, 2, 3, 4 in the north-south direction, and the traps 5, 6, 7, 8 in the west-east direction. Traps 1–2, 3–4 and 5–6, 7–8 were suspended on a metal wire between trees 25 m apart, leaving the transect junction (between

Figure 1. Location of the study sites (circles).

traps 2–3 and 6–7) free of window traps. Flight-window traps consisted of two perpendicular intercepting 40 × 60 cm transparent plastic panels, with a funnel leading to a container below the panels filled with water, salt and detergent. Traps were covered with a transparent 80 × 80 cm plastic roof to minimise funnel obstruction with plant debris and to divert rainfall. To optimise the capture of insects that have contrasting flight behaviour and host preferences, we also used 2 Malaise (M) and 3 stump-emergence (E) traps. Malaise tents (with a second one only in 2003) were located some 30 m apart near the centre of the plot in a sunny place, with ethylene–glycol in the container to preserve the insects. They were protected from wild boars *Sus scrofa* by a robust metal fence stretched on wooden posts. In 2003, together with the second Malaise trap, we placed 1 IPM Intercept Panel Trap (PS), made of black cardboard panels, where the sampling transects crossed. Sampling covered the period from March to October 2002–2003. Traps were emptied once a month, and regular visits were made in May–June to minimise the risks of trap funnel obstruction at times of maximum insect activity.

We extracted data on the propensity of adult longhorn beetles to visit flowers from Jeniš (2001) and Bense (1995). Following Speight et al. (2004) criteria on microhabitat preferences of European Syrphidae, we classified the collected hoverfly species as saproxylic when their larvae exclusively live on overmature/senescent trees, on dead trees, or both. We estimated the number and abundance of threatened longhorn and hoverfly species in our study plots according to national red lists from Germany (Schmidl and Bussler 2003; von der Dunk et al. 2003), assuming these checklists to provide conservative information on insect species status in Belgian forests.

Site characteristics

We were interested in relating insect data to factors assumed to have direct measurable effects on saproxylic assemblages (vegetation structure and composition, floral resources, dead wood supply and quality, altitude). Patch occupancy was also studied in relation to the surrounding landscape composition, and in particular to the extent of exotic conifer plantations. This variable, a good indicator of the level of habitat continuity and connectivity over time (conifer plantations were absent from Belgian forest landscapes in the 18th century; see Ferraris' historical maps), was assumed to have long-lasting effects on the saproxylic population processes at the landscape level and, therefore, population persistence in the deciduous forest remnants (Mazerolle and Villard 1999). Habitat description procedures followed pan-European recommendations for data collection in forest reserves (Hochbichler et al. 2000). Schematically, the sampling design was a collection of circular plots of different sizes and locations on a grid network of 50 × 50 m, according to the habitat features to be measured (Fayt et al. 2003).

In each stand, we used five nested sample plots of 0.05 ha and 0.1 ha, with one located at the crossing of the insect sampling transects and the others 50 m apart in the cardinal directions, centred on the perimeter flight-window traps (1, 4, 5, and 8). In the 0.05 ha plots, we measured the volume of fallen branches with a diameter between 5 and 9 cm. We quantified the volume of standing living and dead trees with a girth at breast height between 16 and 125 cm. We also estimated the volume of logs with a diameter at the smallest end between 10 and 40 cm. Larger living trees, snags, logs and fallen branches as well as stump volume and the number of tree species were measured in the 0.1 ha plots. The volume of living and freshly dead trees was estimated from yield volume tables (Dagnelie et al. 1999), based on girth and height measurements. We applied the measurements guidelines developed by Harmon and Sexton (1996) to evaluate the volume of remaining woody debris. The volume of broken snags and stumps was calculated using a formula for a frustum of a cone: $V = H (A_b + (A_b A_t)^{0.5} + A_t)/3$, where H is the height, and A_b, A_t are respectively the areas of the base and top. We used Newton's formula to evaluate log volume: $V = L (A_b + 4 A_m + A_t)/6$, where L is the length, and A_b, A_m, and A_t are respectively the areas of the base, middle and end of the trunk. Fallen branch volume was derived from Huber's formula: $V = (\pi \times d^2/4) \times L$, where d is the middle diameter and L the length of the branch. Modified after Hunter (1990), four decay classes were used to describe the stage of wood decomposition of the different categories of woody debris. The first stage included snags, logs,

Table 1. List of measured explanatory variables, their description, mean values (± SE) and test values from paired-sample *t*-tests used to compare stands with high (*n* = 11) and low (*n* = 11) amount of coarse woody debris (cwd).

Variable	Explanation	Unit	High cwd Mean ± SE	Low cwd Mean ± SE	*t*	*p*-value
Alt (115–600)	Altitude	m	408.082 ± 40.945	374.091 ± 37.006	2.645	0.025
Dec2000 (59.30–1042.60)	Amount of deciduous forests in 2000 m-radius	ha	363.418 ± 91.715	304.836 ± 69.401	2.253	0.048
Con2000 (19.80–1025.30)	Amount of coniferous forests in 2000 m-radius	ha	452.436 ± 90.094	494.427 ± 111.255	−0.374	0.716
Mix2000 (0.60–313.30)	Amount of mixed forests in 2000 m-radius	ha	102.191 ± 35.990	60.064 ± 17.273	0.442	0.668
Ope2000 (16.20–758)	Amount of open land in 2000 m-radius	ha	310.896 ± 50.168	341.209 ± 75.586	0.388	0.706
Cov_grd (0.5–5)	Bare soil cover	Class[a]	3.318 ± 0.478	2.318 ± 0.569	1.305	0.221
Cov_her (1–5)	Herbaceous plant cover	Class[a]	2.818 ± 0.400	3.182 ± 0.553	−0.231	0.822
Cov_flr (0–1.256)	Sum of flowering plant covers	%	0.277 ± 0.137	0.334 ± 0.139	−0.392	0.703
Cov_2 (0–3)	<2 m tree cover	Class[a]	0.955 ± 0.327	0.682 ± 0.194	0.599	0.563
Cov_2_8 (0–3)	2–8 m tree cover	Class[a]	0.773 ± 0.246	0.773 ± 0.255	0.070	0.946
Cov_8_15 (0–4)	8–15 m tree cover	Class[a]	1.591 ± 0.420	1.000 ± 0.224	1.109	0.293
Cov_15 (0.5–5)	>15 m tree cover	Class[a]	4.045 ± 0.429	4.091 ± 0.392	−0.400	0.698
Sp_herb (2–42)	No. of herbaceous plant species		13.091 ± 3.576	12.182 ± 3.405	0.567	0.583
Sp_tree (1–9)	No. of tree species		4.545 ± 0.578	4.818 ± 0.807	0.071	0.945
Bracan (0–774)	Amount of dead branches in canopy[b]	No. ha^{-1}	235.636 ± 73.832	280.545 ± 87.516	−0.165	0.872
Cwd_sna (0–47.52)	Snag volume	m^3 ha^{-1}	28.396 ± 4.352	2.622 ± 0.869	5.597	< 0.001
Cwd_log (0–33.36)	Log volume	m^3 ha^{-1}	11.570 ± 3.999	0.978 ± 0.455	2.702	0.022
Cwd_lbr (0.72–73.40)	Volume of fallen large[c] dead branches	m^3 ha^{-1}	10.400 ± 6.359	4.158 ± 1.673	1.898	0.087
Cwd_sbr (0.38–6.67)	Volume of fallen small[d] dead branches	m^3 ha^{-1}	2.807 ± 0.461	1.752 ± 0.292	1.925	0.083
Cwd_grd (1.82–108.12)	Fallen dead wood volume[e]	m^3 ha^{-1}	24.777 ± 9.125	6.888 ± 1.955	3.014	0.013
Cwd_stu (0.29–4.51)	Stump volume	m^3 ha^{-1}	2.135 ± 0.420	2.085 ± 0.184	−0.389	0.706
Cwd_tot (3.97–150.88)	Total dead wood volume[f]	m^3 ha^{-1}	55.309 ± 10.349	11.595 ± 2.190	7.541	< 0.001
Cwd1_tot (0–25.31)	Dead wood volume in decay class 1[f]	m^3 ha^{-1}	10.134 ± 3.130	0.888 ± 0.331	3.384	0.007
Cwd2_tot (0.65–76.36)	Dead wood volume in decay class 2[f]	m^3 ha^{-1}	22.717 ± 6.387	5.631 ± 15.760	3.306	0.008
Cwd3_tot (0.79–45.50)	Dead wood volume in decay class 3[f]	m^3 ha^{-1}	15.884 ± 4.289	3.049 ± 0.796	3.666	0.004
Cwd4_tot (0.57–24.27)	Dead wood volume in decay class 4[f]	m^3 ha^{-1}	6.527 ± 1.932	2.076 ± 0.478	2.814	0.018
Tree_a40 (4–114)	Amount of living trees with dbh[g] ≥40 cm	No. ha^{-1}	49.818 ± 8.720	53.273 ± 7.813	−0.121	0.906
Tree_b40 (36–1004)	Amount of living trees with 5 cm ≤ dbh < 40 cm	No. ha^{-1}	424.727 ± 89.063	309.818 ± 64.713	1.188	0.263
Tree40 (0.02–0.64)	Availability of living trees with dbh ≥40 cm[h]		0.171 ± 0.055	0.200 ± 0.055	−0.503	0.626
Girt_a40 (136–267)	Mean girth of living trees with dbh ≥40 cm[i]	cm	178.939 ± 10.838	173.363 ± 10.150	0.558	0.589
SG40 (1202–20358)	Summed girth of standing trees with dbh ≥40 cm[i]	cm ha^{-1}	9005.000 ± 1630.524	10381.273 ± 1006.366	−1.377	0.199
SG60 (0–10494)	Summed girth of standing trees with dbh ≥60 cm[i]	cm ha^{-1}	4268.727 ± 1144.518	4154.1818 ± 1015.178	0.417	0.686
SG80 (0–6034)	Summed girth of standing trees with dbh ≥80 cm[i]	cm ha^{-1}	1282.727 ± 545.178	1268.909 ± 396.766	−0.120	0.907
G (18.26–35.64)	Basal area of living trees	m^2 ha^{-1}	25.043 ± 1.447	25.903 ± 1.200	−0.423	0.681
G40 (1.46–29.76)	Basal area of living trees with dbh ≥40 cm	m^2 ha^{-1}	13.879 ± 2.694	15.110 ± 1.717	−1.331	0.213

Table 1. (Continued).

Variable	Explanation	Unit	High cwd Mean ± SE	Low cwd Mean ± SE	t	p-value
Gr_Fag (0–100)	Beech relative basal area	%	46.727 ± 12.404	48.473 ± 11.942	−0.865	0.407
Gr_Que (0–94.25)	Oak relative basal area	%	43.582 ± 10.885	44.214 ± 11.383	0.024	0.982

[a] 0=0, 1 = 1–5, 2 = 5–25, 3 = 25–50, 4 = 50–75, and 5≥75%.
[b] With a base diameter > 5 cm.
[c] With a diameter ≥10 cm.
[d] With 5 cm ≤ diameter < 10 cm.
[e] Cwd_log + Cwd_lbr + Cwd_sbr.
[f] Cwd_sna + Cwd_log + Cwd_lbr + Cwd_sbr + Cwd_stu.
[g] Diameter at breast height = 1.3 m above ground level.
[h] Tree_a40/(Tree_a40 + Tree_b40).
[i] Measured at breast height.
Variables were transformed for normality (log + 1 for counts, arcsin-square root for percentages and proportions). Significant p-values in bold, without Bonferroni correction.
Minimum–Maximum values are given between arrows.

branches and stumps with hard wood and intact bark cover and the second the substrates with bark partly loose. Wooden microhabitats in the third and fourth classes lacked bark, but with a friable wood texture in the last stage, leading to visible changes in their original shape.

We conducted a plant inventory and evaluated the bare soil, herb and tree layer covers in a 0.05 ha plot delimited from the centre of the 0.8 ha plot containing the insect traps. An index of floral resources was built for each site by summing the respective cover of plants known to produce accessible amounts of pollen and nectar, among which were *Crataegus laevigata* (Poir.) DC., *Crataegus monogyna* Jacq., *Frangula alnus* Mill., *Prunus avium* L., *Prunus spinosa* L., *Sorbus aucuparia* L., *Anemone nemorosa* L., *Angelica sylvestris* L., *Filipendula ulmaria* (L.) Maxim., *Hedera helix* L., *Hypericum pulchrum* L., *Potentilla reptans* sp., *Potentilla sterilis* (L.) Garcke, *Ranunculus ficaria* L., *Ranunculus repens* L., *Rubus idaeus* L., *Valeriana dioica* L., *Rosa* sp., *Rubus* sp., and *Taraxacum* sp.

We finally looked at landscape composition by calculating from satellite imagery and field mapping the amount of deciduous/coniferous/mixed forests and open fields (clear-cut, pasture, peatland, meadow) in a 1256 ha plot (2000 m radius) from the insect transect junction.

Overall, 37 variables were included as potential explanatory factors in the analyses (Table 1). The different measurements were carried out from 2002 to 2004.

Statistical analyses

All the analyses were carried out by use of SAS Enterprise (version 2.0), except for ordination techniques which were conducted with CANOCO 4.0 for Windows (ter Braak and Smilauer 1998). Default settings of the gradient analyses methods included species scores divided by standard deviation, species data transformation and centring. Counts were $\log_{10}(x + 1)$ and percentages and proportions arcsin-square root transformed to normalize their distributions, if necessary.

We first conducted a validation test of our sampling scheme stratified by dead wood supply (high/low) using discriminant analyses. This allowed us to identify the set of variables among the 37

included in the analyses that best explained the criteria applied when selecting the study sites. The importance of dead wood variables in separating sites classified as either with either high or low amount of coarse woody debris was additionally tested by comparing the mean values of the different variables between pair stands using paired-sample t-tests, followed by a sequential Bonferroni correction ($\alpha = 0.05$) to control for the error rate from multiple comparisons of means (Rice 1989).

The sampling efficiency of insect communities in our study sites was assessed by drawing individual species accumulation curves in relation to the sampling effort applied over the study period (8 Window (2002) + 8 Window (2003) and 1 Malaise (2002) + 2 Malaise (2003) traps). This procedure combines the average number of species per sampling unit, and variation in species composition among them, into the cumulative number of species. The shape of the curve is a good indicator of sampling efficiency, with the slope approaching the asymptote as the sample estimate becomes closer to the true community value. For each site, sampling efficiency was estimated by calculating the ratio a/N, where a is the number of species that were sampled only once, and N the number of sampling units (traps). This index expresses the slope of the curve when the whole community is inventoried, that is, the number of new species that, on average, would be expected to be gained if adding one more insect trap (Lauga and Joachim 1987). With a ratio $a/N = 0.1$ for example, we would need 10 more traps to gain a new species.

The effect of dead wood supply on insect distribution was first tested by comparing species numbers and abundances between paired stands (1,1), with high or low amount of dead wood (1,2) and with year as a confounding factor (1,2). Analysis of variance was performed according to a split plot design, with dead wood as a main plot factor and year as a subplot factor. Deadwood and year were considered as fixed effects, while pair and deadwood × pair effects were included as random factors in the model.

A principal component analysis (PCA) was then conducted to describe the general structure of the species pool, based on their abundance estimates in relation to each other and the environmental data (indirect gradient analysis). Besides clarifying relationships between variables, this linear technique is particularly useful for inferring the relative importance of environmental variables correlated with main trends of species and abundance estimates. The number of dimensions of the ordination space to be retained for the ordination analysis was defined so that the proportion of the explained variation reached cumulatively two-thirds of the total variance of the data set. Both species numbers and abundances were represented on the biplot, given their similar contributions to the first two axes. We then performed partial Redundancy Analyses (pRDA), a direct gradient analysis, in order to calculate the proportion of variation of our biological data set (species richness and abundance) that is explained by a set of independent environmental variables once the effect of spatial structure (here, the region) was taken into account. Following this partially constrained procedure, information that could be explained by the regional effect was first extracted and then the explanatory variables were used to account for the residual variation. Only individual variables that explained a significant part ($\alpha = 0.05$) of the relationship were included in the model. They were identified by a manual forward selection procedure. We made two ordinations, with and without non-saproxylic Syrphid data. The significance of the models was tested by Monte Carlo permutation tests (999 permutations under full model).

Finally, since species are most likely to have a unimodal species response curve in relation to environmental gradients (i.e. species are non linearly related to each other, with bell-shaped curves along the gradients), we also performed a Canonical Correspondence Analysis (CCA) on species abundance profiles to detect possible species-environmental relationships (ter Braak 1988). As with the partial RDA, we decomposed species variance into non-spatial environmental, spatial environmental, spatial non-environmental and undetermined components by removing the effect of spatial structure (region). In order to force the ordination to test the working hypothesis (effects of dead wood, flower supply and old trees), we limited the analyses to a subset of explanatory factors expected to positively affect the distribution of saproxylic insects: vegetation cover (VG), the amount of dead wood (DW), and the availability of old trees (OT). The variables associated with vegetation cover were the availability of floral resources (Cov_flr) and tree species (Sp_tree), with dead wood the

Table 2. Results of Stepwise Discriminant Analysis showing the sets of environmental variables best explaining the criteria used for site selection.

Criteria	Value	Step no.	Variables entered	Partial R^{2a}	Model R^{2b}	F-value	p-value
Dead wood	High/Low	1	Cwd_tot	0.722	0.722	51.83	**<0.001**
		2	Cwd_lbr	0.366	0.823	10.94	**0.004**
		3	Cov_2	0.114	0.844	2.32	0.145

[a]Proportion (%) of variance explained by the variables entered in the model.
[b]Total proportion (%) of variance explained by the model.
Significant effects ($p < 0.05$) are in bold. See Table 1 for explanation of acronyms.

volume of standing (Cwd_sna) and fallen trees (Cwd_log), and with old trees the mean girth (Girt_a40) and summed girth (SG80) of large trees.

Following du Bus de Warnaffe and Dufrêne (2004), we decomposed the total variation of our insect species/sites files as:

$$A = A \cap (B_1|B_2 \cap B_3) + A \cap (B_2 \cap B_3|B_1) + A$$
$$\cap (B_2|B_1 \cap B_3) + A \cap (B_1 \cap B_3|B_2) + A$$
$$\cap (B_3|B_1 \cap B_2) + A \cap (B_1 \cap B_2|B_3) + A \cap (B_1$$
$$\cap B_2 \cap B_3) + A|(B_1 + B_2 + B_3)$$

where A is the total variance of the species assemblages, B_1 = VG, B_2 = DW, B_3 = OT, (B1|B2∩B3) is the variation explained by VG independently of the variation explained by the interaction between DW and OT (shared by both), ($B_2 \cap B_3|B_1$) the variation explained the interaction between DW and OT independently of VG and so on, ($B_1 \cap B_2 \cap B_3$) the variation explained by the interaction between the three factors VG, DW and OT, and A|($B_1 + B_2 + B_3$) the variation not explained by B_1, B_2, B_3 and their interactions. Thus, the amount of species variance (A) solely explained by one factor (here VG) was obtained from: A∩(VG|DW∩OT) + A∩(VG∩DW|OT) + A∩(VG∩OT|DW) + A∩(VG∩DW∩OT). The amount of unexplained variation was deduced from the above equation. Those different components were calculated by performing series of CCA with variation partitioning.

Results

Sampling scheme

On average, stands classified with either a high or a low amount of dead wood mostly differed in terms of their dead wood supply among the four decay classes, together with the altitude and the extent of native deciduous forests in the surrounding landscape (Table 1). After a Bonferroni correction, only the total amount of woody debris and snag volume were significant at the 0.05 level. Accordingly, discriminant analyses revealed that, among the different environmental variables, the total volume of coarse woody debris best separated the two stand categories ($p < 0.001$) (Table 2).

Sample sizes and sampling efficiency

Catches yielded altogether 30 longhorn beetle (Cerambycidae) species (1637 individuals) and 106 hoverfly (Syrphidae) species (3020 individuals, Table 1 and Appendix 1). Among the longhorn beetles, 19 species were flower visitors. Overall, 27 species of Syrphidae were saproxylic, among which 20 were known to colonise both old and dead trees and seven had larvae exclusively associated with microhabitats of overmature trees. None of the species were dead wood specialists. According to German Red Lists of Cerambycidae and Syrphidae, we found six longhorn beetle and 11 hoverfly species listed as threatened (Appendix 1).

In most study sites, the number of longhorn beetle species collected with window traps (W) approached the true community value, as suggested by the different species accumulation curves tending towards the asymptote (Figure 2). Accordingly, 67% (14/21) of the sites had an a/N value well below 0.5 (i.e., sites that would require more than two additional traps to collect a new species). In only one site would the addition of one trap allow the capture of more than one new species ($a/N = 1.50$). Likewise, 3 Malaise traps (M) allowed an effective sampling of local cerambycid communities, since 40% (8/20) of the
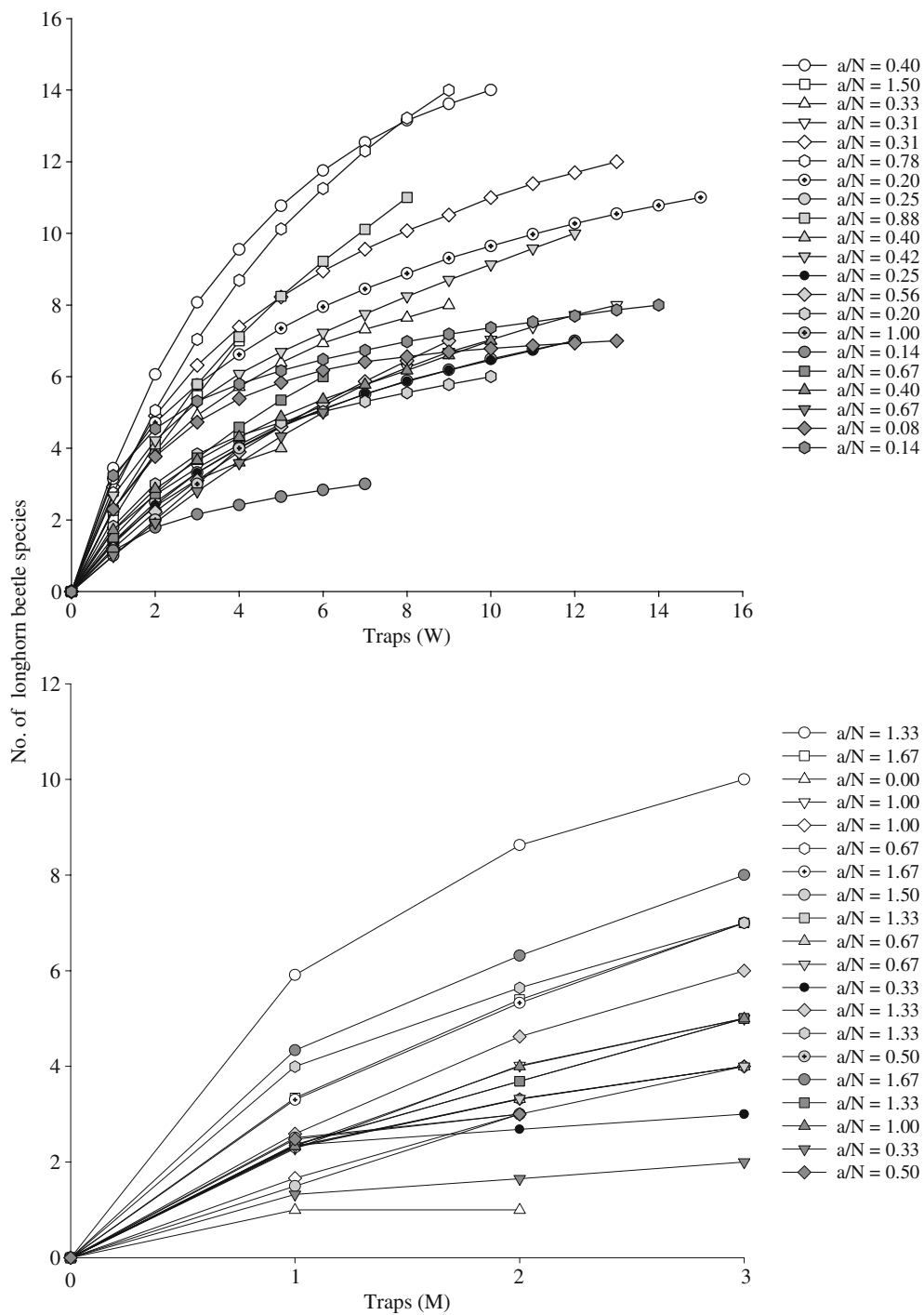
Figure 2. Cumulative number of longhorn beetle species as a function of the sampling effort (number of window (W) and Malaise (M) traps). Data are cumulated for 2002–2003. *a/N* gives the number of new species that, on average, would be expected to be gained with an additional trap (see text).
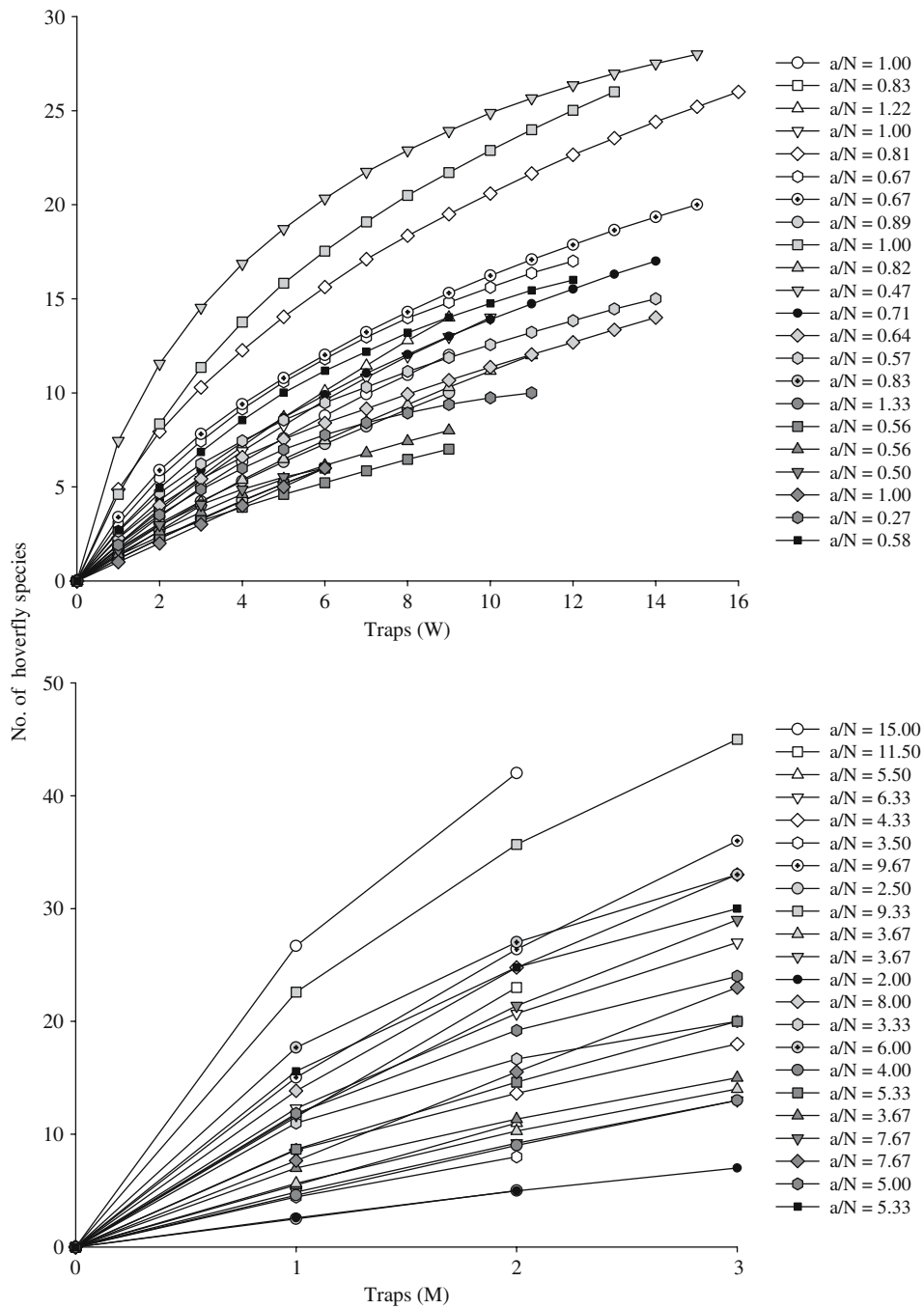
Figure 3. Cumulative number of hoverfly species in relation to trapping effort (Window and Malaise traps), with data cumulated for 2002–2003. a/N is an indicator of sampling efficiency (see text).

sites would need more than one Malaise trap to collect an additional new species ($a/N < 1$), and less than two new species would be found if one trap was added to the remaining 60% of sites ($1 \leq a/N < 2$).

Species accumulation curves revealed that 16 out of the 22 sites (73%) would require more than one additional window trap to collect a new hoverfly species ($a/N < 1$) (Figure 3). Using Malaise traps, between two and 15 new hoverfly

Table 3. Results of mixed-model ANOVA assessing differences in longhorn beetle and hoverfly species richness and abundance between stands (11 pairs) with high and low amount of coarse woody debris (cwd, 2002–2003).

Variable	Explanation	n	High cwd Mean ± SE	Low cwd Mean ± SE	Source of variation	Error df	F-value	p-value
S_Cer	No. of longhorn beetle species	30	10.636 ± 0.754	9.000 ± 1.036	Deadwood	12.889	4.358	0.057
					Year	29.173	0.032	0.859
					Deadwood* Year	29.173	0.515	0.479
S_Cer_rl	No. of red-listed longhorn beetle species[a]	6	1.375 ± 0.263	1.143 ± 0.143	Deadwood	2.186	2.329	0.256
					Year	61.620	0.156	0.694
					Deadwood * Year	61.620	7.636	**0.008**
S_Syr_s	No. of saproxylic hoverfly species[b]	27	8.636 ± 1.130	6.273 ± 0.832	Deadwood	45.366	2.447	0.125
					Year	51.032	10.363	**0.002**
					Deadwood * Year	51.032	1.703	0.198
S_Syr_ow	No. of hoverfly species with larvae on both overmature trees and dead wood[c]	20	6.727 ± 0.854	4.818 ± 0.796	Deadwood	115.142	2.387	0.125
					Year	33.898	2.397	0.131
					Deadwood * Year	33.989	5.385	**0.026**
S_Syr_o	No. of hoverfly species with larvae only on overmature trees[d]	7	1.909 ± 0.368	1.455 ± 0.207	Deadwood	6.641	1.127	0.325
					Year	58.619	28.005	**< 0.001**
					Deadwood * Year	58.619	1.120	0.294
S_Syr_ns	No. of non-saproxylic hoverfly species	79	27.364 ± 2.787	18.545 ± 1.580	Deadwood	0.866	13.140	0.201
					Year	7.838	18.265	**0.003**
					Deadwood * Year	7.838	0.650	0.444
S_Syr_rl	No. of red-listed hoverfly species[a]	11	3.000 ± 0.258	1.875 ± 0.398	Deadwood	36.978	3.476	0.070
					Year	48.303	10.393	**0.002**
					Deadwood * Year	48.303	0.000	1.000
A_Cer	No. of individual longhorn beetles	1637	93.545 ± 28.550	55.273 ± 19.570	Deadwood	17.461	3.208	0.091
					Year	7.994	1.938	0.201
					Deadwood * Year	7.994	0.143	0.715
A_Cer_rl	No. of individual red-listed longhorn beetles[a]	31	2.750 ± 1.473	1.286 ± 0.286	Deadwood	2.221	0.764	0.466
					Year	32.389	1.011	0.322
					Deadwood * Year	32.389	3.458	0.072
A_Syr_s	No. of individual saproxylic hoverflies[e]	747	35.091 ± 7.667	32.818 ± 13.589	Deadwood	25.589	0.925	0.345
					Year	30.781	9.682	**0.004**
					Deadwood * Year	30.781	0.912	0.347
A_Syr_ow	No. of individual hoverflies with larvae on both overmature trees and dead wood[c]	634	30.364 ± 7.605	27.273 ± 12.950	Deadwood	0.294	0.943	0.691
					Year	3.354	5.330	0.095
					Deadwood * Year	3.354	1.693	0.275
A_Syr_o	No. of individual hoverflies with larvae only on overmature trees[d]	113	4.727 ± 1.207	5.546 ± 1.498	Deadwood	67.457	0.096	0.758
					Year	43.378	42.499	**< 0.001**
					Deadwood * Year	43.378	0.097	0.756

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Table 3. (Continued).

Variable	Explanation	n	High cwd Mean ± SE	Low cwd Mean ± SE	Source of variation	Error df	F-value	p-value
A_Syr_ns	No. of individual non-saproxylic hoverflies	2273	142.636 ± 30.673	64.000 ± 12.527	Deadwood	32.625	10.044	0.003
					Year	12.717	30.594	< 0.001
					Deadwood * Year	12.717	4.673	0.050
A_Syr_rl[a]	No. of individual red-listed hoverflies[a]	136	7.800 ± 2.328	7.250 ± 2.234	Deadwood	0.323	0.533	0.729
					Year	25.643	17.197	< 0.001
					Deadwood * Year	25.643	0.003	0.953

[a]From German Red-Lists.
[b]S_Syr_ow + S_Syr_o.
[c]Includes species with larvae living in trunk cavities, rot-holes, insect workings, sap runs, under loose bark and on snags, logs, stumps and rotting tree roots.
[d]Includes species with larvae living in trunk cavities, rot-holes, insect workings, sap runs and under loose bark.
[e]A_Syr_ow + A_Syr_o.
Deadwood, year and their interaction were entered into the model as fixed effects and pair and deadwood × pair as random effects. Variables were log-transformed + 1 for normality, if necessary. Sample sizes (n) and mean values (±SE) are added, with significant effects (p < 0.05) in bold.

species were expected to be found following the addition of a fourth Malaise trap, although less than five new species would be found in nine (41%) ($a/N < 5$) of the 22 sites. When only considering saproxylic hoverflies, an additional Malaise trap would only produce three or less new species ($a/N \leq 3$) in 75% of the sites.

Insect numbers and dead wood

The results of the mixed effect model (Table 3) indicated a positive (but not quite significant) impact of dead wood supply (high/low) on species diversity and abundance of longhorn beetles. Moreover, difference in dead wood explained variation in the number of Red List cerambycid species, depending on the year (a significant year x deadwood interaction). Looking at the hoverfly species data set, the number of saproxylic species with larvae living on both overmature trees and dead wood was positively affected by the amount of dead wood, although the relationship varied between years. The overall number of hoverfly species, whether saproxylic or not, and the richness in Red List species varied significantly between years, independently of the dead wood supply. A similar trend holds for individual numbers, although only the non-saproxylic hoverflies were significantly more abundant in stands with dead wood, in addition to yearly variation in numbers.

Relationships between variables and variance partitioning

The eigenvalues for the first two axes of the PCA ordination were 0.462 and 0.182 respectively, explaining cumulatively 46.2% and 64.4% of the variation in the total dataset. The first ordination axis contrasted stands embedded in deciduous forest landscapes, – with a high amount of dead wood, a well-developed and species-rich herb layer with abundant floral resources, – to stands surrounded by conifer plantations with a high basal area, bare soil and lacking woody debris (Figure 4a). The second axis polarised stands with large trees (beech-dominated) and a high volume of fallen large branches to multi-layered oak-dominated stands with a high snag supply.

Figure 4. PCA-ordination of the biological and environmental descriptors plotted in the plane determined by the first two principal axes, with (a) and without (b) non-saproxylic hoverfly data. The dependent variables are shown in italic; the significant explanatory variables identified by pRDA (forward selection subroutine) after controlling spatial structuring of the data (Region) are framed. See Tables 1 and 3 for explanation of acronyms.

Once the non-saproxylic Syrphidae were removed from the data set, retaining only with saproxylic and threatened species assemblages, the first two ordination axes had eigenvalues of 0.491 and 0.200 respectively. They cumulatively explained 69.2% of the variance. Here, the axes contrasted stands with similar ecological conditions, but the second axis was more strongly

correlated with oak and beech relative basal areas (Figure 4b).

PCA ordination indicated positive associations between cerambycid species diversity and snag volume. Among stands, those dominated by oak trees with a high snag volume were particularly favourable to cerambycid species diversity, including threatened species, while the extent of deciduous tree cover in the surrounding landscape had a clear positive impact on local abundances. By contrast, saproxylic and threatened syrphids were clearly avoiding closed shady stands with extensive bare soil cover, embedded in a coniferous landscape. Instead, they favoured stands with a well-developed and species rich herb layer providing pollen and nectar, together with the presence of large trees.

The partial RDA analyses revealed that the total explained variance of the biological data, including both species and individual numbers, was 47.2%. Of this, 35.4% was explained by a linear combination of four non-spatial environmental variables, namely, in order of selection, the basal area, the total volume of dead wood with hard wood and bark partly loose, the volume of fallen large branches, and altitude (Figure 4a). Spatial structuring of the data not attributable to the environmental variables accounted for 9.4% of the total variance, indicating that no fundamental spatial structuring process has been missed. The remaining 2.4% was explained by the interaction between the biological data, the environment and spatial structuring (regional effect). Without the non-saproxylic Syrphidae data, a similar proportion of the biological data was explained (52.6%). However, 40.4% of it was then explained by a different combination of ecological factors, including in order of selection, the numbers of herbaceous plant and tree species, the amount of deciduous forest in the surrounding landscape, the altitude, and the extent of herbaceous plant cover (Figure 4b). Spatial structuring of the data not attributable to the environmental variables accounted for 4.9% of the total variance; 7.3% was explained by the interaction between the biological data, the environment and spatial structuring. The species-environmental relationships described by the two models were non-random ($p < 0.01$).

Overall, the CCA indicated that 35.2% and 34.9% of the longhorn beetle and hoverfly species

data were explained by the combined effects of the selected 'Vegetation', 'Dead Wood' and 'Old Tree' variables and their interactions, respectively (Figure 5). Vegetation variables (Cov_flr and Sp_tree) explained ≥30% of the variation for two longhorn beetle species (*Gramnoptera ruficornis*, *Tetrops praeusta*) and nine hoverfly species (*Dasysyrphus hilaris*, *D. nigricornis*, *Eristalis nemorum*, *Ferdinandea cuprea*, *Merodon equestris*, *Temnostoma apiforme*, *T. bombylans*, *Xylota abiens*, *X. segnis*). All the species were flower visitors (Appendix 1). The dead wood variables (Cwd_sna and Cwd_log) explained ≥30% of the variation for three longhorn beetle species (*Anoplodera sexguttata*, *Pachytodes cerambyformis*, *Rhagium sycophanta*) and four hoverfly species (*Baccha elongata*, *Chrysogaster coemiteriorum*, *Cheilosia lenis*, *Pipiza bimaculata*). None of those Syrphid species were dependent on dead woody substrates. The combination of old tree variables (Girt_a40 and SG80) explained > 30% of the

Figure 5. Part of variation of (a) longhorn beetle and (b) hoverfly species abundance explained by selected vegetation (VG), dead wood (DW) and old tree (OT) variables and their interactions.

variation for four longhorn beetle species (*Anoplodera sexguttata*, *Leptura aethiops*, *Pachytodes cerambyformis*, *Rhagium sycophanta*) and four hoverfly species (*Brachypalpus valgus*, *Paragus haemorrhous*, *Platycheirus peltatus*, *Pipizella viduata*). Only *B. valgus* was associated with microhabitats of overmature trees (Appendix 1).

Discussion

Although both saproxylic longhorn beetles and hoverflies benefit from the presence of wooden substrates for reproduction, they differ in their requirements for floral resources and for microbiotopes of overmature and senescent trees. In this study, 63% of the longhorn beetle species collected were flower visitors, but they all depended on dead parts of branches, stems, stumps or roots to oviposit (Jeniš 2001). By contrast, most, if not all, the syrphids rely on both pollen and nectar to sustain foraging and egg production (Branquart and Hemptinne 2000), but none of those captured were specifically associated with dead wood microhabitats. Instead, 74% of the assemblage inventoried were species that occur on both woody debris and old trees and 26% species that only reproduce on overmature trees. This led us to expect contrasting responses between the two species groups in relation to dead wood and overmature tree availability in mature deciduous forest habitats differing in floral resources.

The study of general relationships between the insects and their environment revealed that 42% of the between-species variance was explained by a linear combination of five environmental variables. Stand openness and its effects on floral resources, tree dimensions and the volume of dead wood still retaining some bark cover were key determinants of local longhorn and hoverfly species diversity in the woodlands of southern Belgium. Once the non-saproxylic hoverfly species were removed from the analyses, however, the variance of the saproxylic and threatened insect data was explained by ecological variables that used to characterise European native temperate forests (Bengtsson et al. 2000): an abundant and species rich herb layer, numerous tree species, and a continuous deciduous forest cover over the landscape. Altitude also explained part of the variance, most probably because the majority of
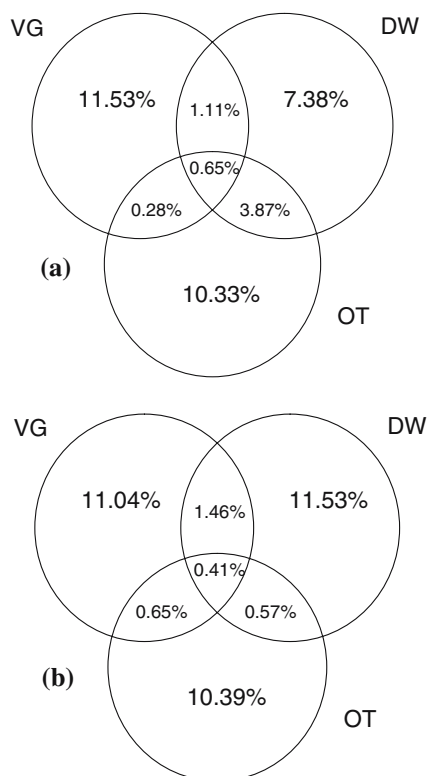
the deciduous stands with high dead wood supply are nowadays located on the least productive lands of Belgium (Table 1). But importantly, the two saproxylic species groups were clearly independent on the ordination axes, despite a lack of differences in their species abundance profiles in relation to vegetation, dead wood and old tree variables, presumably due to the presence of numerous rare species. This result demonstrates contrasting responses between the two groups for the measured environmental conditions.

The finding that paired stands, classified as a function of their dead wood supply (high/low), differed in their number of cerambycid species and, to a lesser extent, individuals (Table 3), with higher mean values in richer stands, indicates a positive impact of local tree mortality on longhorn beetle individual and population responses. The importance of dead wood supply *per se* in explaining such differences was supported by the results of the discriminant analyses. Among the 37 environmental variables that were included in the model, the pair stands were best separated by their total volume of woody debris. As shown on the PCA ordination biplot, oak-dominated stands with a high snag volume were particularly favourable to cerambycid diversity, including threatened species. In Belgium, of the 63 species of longhorn beetles associated with beech and oak forests, 32 are considered to live in both habitats and 27 to occur preferentially on oak trees (Muylaert 1990; Bense 1995).

Contrary to longhorn beetles, we found high numbers of saproxylic and threatened hoverfly species and individuals in stands with an open structure and large trees, providing ecological conditions for a well-developed and species rich herb layer, sources of pollen and nectar. They clearly avoided closed shady stands with extensive bare soil cover, embedded in a coniferous landscape. This is what would have been expected if, as predicted from a resource-based model of habitat exploitation, most of the saproxylic hoverfly species collected had larvae associated with overmature and dead tree microhabitats, in addition to obligate pollen and nectar requirements prior to oviposition. The importance of large trees for the development of microhabitats that benefit saproxylic syrphids is supported by Dufour (2003), who found the production of live tree microhabitats in our study plots to be a function of tree diameter, with the number of trunk cavities and rot holes increasing exponentially on trees with a diameter at breast height above 80 cm. Surprisingly, the abundance of non-saproxylic species was higher in stands with dead wood. Most probably, those stands also contained unmeasured habitat resources and conditions that are important for the non-saproxylic community, such as abundant aphid populations or aquatic microhabitats (Dusek and Laska 1986; Speight et al. 2004).

In this study, despite geographically representative sampling among structurally complex habitats, we only captured 48% of the cerambycid species expected to be found in Belgian beech and oak forests, and 46% of the saproxylic Belgian hoverfly species. In Belgian forests, focal habitat resources such as dead wood and overmature trees have undergone general and dramatic reduction in their availability over the past centuries (Lemaire 2001; Branquart et al. 2005), reinforcing the long-lasting effects of landscape transformation and fragmentation on local community composition. In our study stands, most of the dead wood available originated from storm events in the early 90s. Based on the latest forest inventories, Branquart et al. (2005) found the number of large trees (with diameter at breast height > 90 cm) in our study region to be largely deficient compared to the situation in temperate natural forests. Oaks with large trunk diameter were especially scarce. Loss of the microhabitat continuity can be especially serious for saproxylic insect species with limited dispersal capabilities, such as those associated with the stable microhabitats of overmature trees (Nilsson and Baranowski 1997), or species that depend on temporary conditions of wood decay (Speight 1989). Speight (2002) showed that 80% or more of the Atlantic Region *Fagus* and *Quercus* forest-associated syrphid species occurring in Belgium are present, for all *Fagus* and *Quercus* microhabitat categories except overmature trees. Looking at the saproxylic species in particular, nearly half of them are categorised as being under threat (data from Verlinden and Decleer 1987). It is thus likely that the present-day communities we sampled were historically impoverished already at the start of the study, with just a few relict populations having survived in a handful of localities over the landscape. A consequence of this could be a progressive mismatch between dead

wood and old tree variables and species distribution.

Alternatively, such low proportions may also partly be a normal result of low sampling effectiveness, especially when collecting rare and threatened species (Martikainen and Kouki 2003). Among syrphids for example, saproxylic species like *Sphegina clunipes* and *S. elegans* or *Xylota segnis* and *X. sylvarum* were mostly captured using stump emergence traps, suggesting limited movement propensity for some of the species. Among longhorn beetles, standardised direct searching in May-June 2004 produced three new species in one of the eight stands with the highest dead wood availability, among which one was a new species (*Stenurella nigra*) for the project. Low trap numbers may also result from high between-year variation in individual numbers, as noticed for hoverflies (Table 3). This may be owing to sampling effects associated with small population size (Owen 1981; Gilbert and Owen 1990). On the other hand, capture rate is a function of the movement patterns of individuals between their foraging, mating and oviposition habitat patches. The presence outside the study plots of focal habitats such as abundant flower resources at forest edges will influence the distribution patterns of insects (Warren and Key 1991; Barbalat 2002), and so their probability of being trapped. In order to optimise sampling efficiency however, we located our Malaise traps (the most effective sampling device we used for longhorn beetles and hoverflies – Appendix 1) in the few canopy openings of our sample plots. Also, results from species accumulation curves suggest that, overall, our sampling effort allowed a representative sampling of the studied communities. Importantly, most of the saproxylic insect species collected had a highly patchy distribution, with 43% of the longhorn beetle species and 44% of the saproxylic hoverfly species occurring in three out of the 22 stands inventoried, or 70% and 75% of the species among eight stands, respectively. Thus, our results support the idea that a large part of the species collected have residual and highly localised populations. We call for urgent restoration efforts over Belgian forest landscapes, starting from those very few forest patches that still possess a diverse fauna of saproxylics.

Implications for insect conservation

The results of this study allow us to propose stand-level management guidelines for the maintenance and restoration of saproxylic longhorn beetle and hoverfly fauna (Figure 6). They are based on the finding that, despite shared larval requirements for wooden substrates, the two saproxylic species groups respond differently to the availability of focal resources such as flowers, overmature trees and woody debris. We suggest however that both communities could benefit from the thinning and retention of large diameter trees, since it would promote the simultaneous production of both overmature and dead tree microhabitats and general light conditions necessary for floral development (Warren and Key 1991; Härdtle et al. 2003). The ecological changes would thus resemble those found in wind throw gaps, a transient vegetation stage of naturally dynamic forest habitats particularly attractive for saproxylic insects (Bouget and
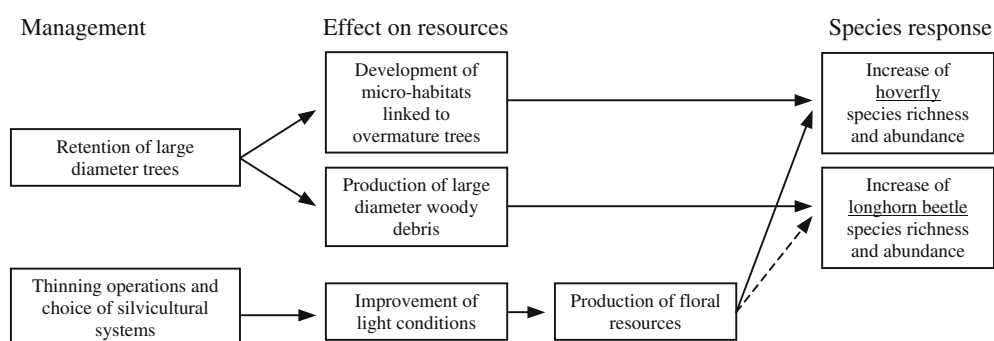

Figure 6. Proposed stand-level management methods to improve the habitat carrying capacity for both longhorn beetle and hoverfly species diversity.

Duelli 2004), besides the development of new niches provided by the old living trees. Among silvicultural systems, we see shelterwood and group-felling as most appropriate in promoting such conditions, combining the presence of mature trees with the opening of the canopy that allows the development of a dense understorey and ground flora (Fuller and Peterken 1995). The maintenance and production of large-diameter living and dead trees is a function of harvesting standards: adopting extended rotations and green tree retention will favour production and restoration of key woody microhabitats for the saproxylic insects (Franklin et al. 1997; Grove 2002). Flower resources, a vital element for most of those insects, will greatly benefit from ecologically-sound management of forest gaps, margins and rides (Warren and Key 1991; Bouget and Duelli 2004). In line with Barbalat (2002), we consider oak trees to be highly favourable to saproxylic insect conservation, knowing their natural needs for stand openness and light. Moreover, maturing oaks naturally produce large dead branches in the lower part of their canopy, providing living conditions for the insects, even under traditional management regime. Recent distribution data from the Netherlands have shown how improvement of forest quality, in terms of forest cover, stand openness and amount of large and dead trees, can have a rapid and positive impact on numerous saproxylic hoverflies (Reemer 2005).

At the landscape scale however, we also suggest that the quality of the matrix should be taken into account in the process of identifying stands with a high potential for the saproxylic insect conservation. We found that the amount of deciduous forest in the surrounding landscape positively explained a significant part of the saproxylic and threatened species variance in the studied deciduous remnants. This suggests that landscape composition and connectivity are crucial for species distribution and local population persistence (Didham et al. 1996, 1998; Mazerolle and Villard 1999). In support of this finding, and despite the extensive ecological corridors they represent, Speight (2000) showed that recent conifer plantations only facilitate movement of generalist hoverfly species through the European landscape.

Appendix 1. List of species, their abundance by trap type, larval foraging macrohabitat (overmature trees vs. coarse woody debris)[a], adult propensity to visit flowers for foraging or mate searching[b] and status[c].

Species	Sample size					Larval macrohabitat			Flower visitor	Red-listed
	E	M	PS	W	Total	omt–cwd	omt	cwd		
Cerambycidae										
Alosterna tabacicolor	0	13	0	20	33			×	×	
Anoplodera sexguttata	0	4	0	6	10			×	×	×
Brachyleptura maculicornis	0	2	0	28	30			×	×	
Clytus arietis	0	18	0	9	27			×	×	
Cortodera humeralis	1	0	1	0	2			×	×	×
Corymbia rubra	0	1	0	33	34			×	×	
Eupogonocherus hispidulus	1	6	0	5	12			×		
Gramnoptera ruficornis	0	8	0	2	10			×	×	
Leiopus nebulosus	0	3	0	8	11			×		
Leptura aethiops	0	3	0	17	20			×	×	
Leptura aurulenta	0	2	0	0	2			×	×	×
Leptura maculata	0	20	0	208	228			×	×	

Appendix 1. (Continued).

Species	E	M	PS	W	Total	omt–cwd	omt	cwd	Flower visitor	Red-listed
Leptura quadrifasciata	0	3	0	22	25			×	×	
Obrium brunneum	0	0	1	0	1			×	×	
Obrium cantharinum	0	0	0	1	1			×		×
Oxymirus cursor	1	7	1	18	27			×		
Pachytodes cerambyformis	0	10	0	40	50			×	×	
Phymatodes testaceus	0	0	0	1	1			×		
Plagionotus arcuatus	0	0	0	2	2			×		
Prionus coriarius	1	0	0	7	8			×		
Pyrrhidium sanguineum	0	0	1	16	17			×		
Rhagium bifasciatum	6	103	1	47	157			×	×	
Rhagium mordax	22	187	1	117	327			×	×	
Rhagium sycophanta	0	1	0	0	1			×	×	×
Saperda scalaris	0	1	0	3	4			×		
Stenostola ferrea	0	3	0	12	15			×		×
Stenurella melanura	1	27	0	544	572			×	×	
Stictoleptura scutellata	0	0	0	5	5			×	×	
Tetropium castaneum	0	0	0	4	4			×		
Tetrops praeusta	0	0	0	1	1			×	×	
Syrphidae										
Baccha elongata	0	18	0	3	21				×	
Blera fallax	0	7	0	0	7	×			×	
Brachypalpus laphriformis	0	20	0	0	20		×		×	
Brachypalpoides lentus	1	0	0	1	2	×			×	
Brachypalpus valgus	0	2	0	0	2		×		×	
Brachyopa vittata	0	0	0	2	2	×			×	
Caliprobola speciosa	34	41	0	1	76	×			×	×
Chalcosyrphus nemorum	0	17	0	1	18	×			×	
Chalcosyrphus piger	0	1	0	0	1	×			×	
Cheilosia lenis	0	1	0	0	1				×	
Cheilosia pagana	0	2	0	3	5				×	
Cheilosia scutellata	0	2	0	0	2				×	
Cheilosia variabilis	0	1	0	0	1				×	
Chrysotoxum arcuatum	0	53	0	1	54				×	
Chrysotoxum bicinctum	0	81	0	0	81				×	
Chrysogaster coemiteriorum	0	1	0	4	5				×	×
Chrysogaster rondanii	0	0	0	7	7				×	
Criorhina asilica	0	3	0	0	3	×			×	
Criorhina berberina	7	24	0	1	32	×			×	
Criorhina floccosa	5	22	1	0	28	×			×	×
Criorhina pachymera	0	1	0	0	1	×			×	×
Dasysyrphus albostriatus	0	2	0	0	2				×	
Dasysyrphus hilaris	0	6	0	2	8				×	
Dasysyrphus lunulatus	0	2	0	4	6				×	
Dasysyrphus nigricornis	0	5	0	28	33				×	
Dasysyrphus venustus	0	56	2	110	168				×	
Didea fasciata	0	1	0	0	1				×	
Didea intermedia	0	1	0	0	1				×	
Episyrphus auricollis	0	5	0	0	5				×	
Episyrphus balteatus	0	268	0	115	383				×	
Episyrphus cinctellus	1	98	0	13	112				×	
Epistrophe diaphana	0	2	0	0	2				×	
Epistrophe eligans	0	10	0	1	11				×	
Epistrophe euchroma	0	2	0	1	3				×	
Epistrophe grossulariae	0	3	0	0	3				×	
Epistrophe nitidicollis	0	7	0	2	9				×	

Appendix 1. (Continued).

Species	Sample size					Larval macrohabitat			Flower visitor	Red-listed
	E	M	PS	W	Total	omt–cwd	omt	cwd		
Eristalis lineata	0	2	0	21	23				×	
Eristalis nemorum	0	0	0	4	4				×	
Eristalis pertinax	0	29	1	175	205				×	
Eristalis piceus	0	0	0	16	16				×	
Eristalis rupium	0	1	0	0	1				×	
Eristalis tenax	0	2	0	142	144				×	
Eupeodes corollae	0	29	1	20	50				×	
Eupeodes lapponicus	0	7	0	5	12				×	
Eupeodes latifasciatus	0	6	0	2	8				×	
Eupeodes luniger	0	3	0	1	4				×	
Ferdinandea cuprea	0	24	0	0	24	×			×	
Ferdinandea ruficornis	0	2	0	0	2		×		×	
Helophilus pendulus	0	47	0	13	60				×	
Helophilus trivittatus	0	0	0	14	14				×	
Leucozona lucorum	0	1	0	0	1				×	
Melangyna cincta	1	42	2	9	54				×	
Melangyna lasiophthalma	0	7	0	15	22				×	
Melanostoma mellinum	0	47	0	16	63				×	
Melanostoma scalare	0	132	1	70	203				×	
Merodon equestris	0	1	0	0	1				×	×
Myathropa florea	8	53	1	7	69		×		×	
Neoascia podagrica	0	0	0	1	1				×	
Orthonevra geniculata	0	0	0	2	2				×	×
Orthonevra intermedia	0	2	0	0	2				×	
Paragus haemorrhous	0	2	0	0	2				×	
Parasyrphus lineolus	0	6	0	1	7				×	
Parasyrphus macularis	0	1	0	1	2				×	
Parasyrphus malinellus	0	13	0	1	14				×	
Parasyrphus punctulatus	0	10	0	7	17				×	
Pipiza bimaculata	0	1	0	0	1				×	
Pipiza fenestrata	0	3	0	0	3				×	
Pipiza lugubris	0	1	0	0	1				×	
Pipiza luteitarsis	0	1	0	0	1				×	
Pipiza quadrimaculata	0	5	0	0	5				×	
Pipizella viduata	0	2	0	0	2				×	
Pipizella virens	0	2	0	0	2				×	
Platycheirus albimanus	0	60	0	21	81				×	
Platycheirus angustatus	0	8	0	0	8				×	
Platycheirus clypeatus	0	12	0	1	13				×	
Platycheirus parmatus	0	1	0	0	1				×	
Platycheirus peltatus	0	3	0	0	3				×	
Platycheirus scutatus	0	1	0	1	2				×	
Platycheirus tarsalis	0	1	0	1	2				×	×
Pyrophaena rosarum	0	1	0	0	1				×	
Rhingia campestris	0	9	0	4	13				×	
Scaeva pyrastri	0	0	0	2	2				×	
Scaeva selenitica	0	3	0	0	3				×	
Sericomyia lappona	0	11	0	17	28				×	
Sericomyia silentis	0	69	0	42	111				×	
Sphegina clavata	0	0	0	3	3		×		×	
Sphegina clunipes	17	0	0	3	20	×			×	
Sphegina elegans	15	0	0	1	16		×		×	
Sphaerophoria fatarum	0	0	0	1	1				×	
Sphaerophoria scripta	0	20	0	10	30				×	
Syrphus ribesii	1	24	0	7	32				×	

Appendix 1. (Continued).

Species	Sample size					Larval macrohabitat			Flower visitor	Red-listed
	E	M	PS	W	Total	omt–cwd	omt	cwd		
Syrphus vitripennis	0	16	0	4	20				×	
Temnostoma apiforme	1	3	0	0	4	×			×	×
Temnostoma bombylans	0	23	0	0	23	×			×	
Temnostoma vespiforme	0	13	0	2	15	×			×	
Trichopsomyia flavitarsis	0	1	0	0	1				×	
Volucella bombylans	0	3	0	4	7				×	
Volucella inflata	0	1	0	0	1		×		×	×
Volucella pellucens	0	3	0	27	30				×	
Xanthandrus comtus	0	4	0	0	4				×	
Xanthogramma laetum	0	8	0	1	9				×	
Xylota abiens	0	8	0	0	8	×			×	×
Xylota jakutorum	0	5	0	4	9	×			×	
Xylota meigeniana	1	5	0	2	8	×			×	×
Xylota segnis	97	48	0	82	227	×			×	
Xylota sylvarum	96	29	0	1	126	×			×	

[a]According to Speight et al. (2004).
[b]According to Jeniš (2001).
[c]From German Red-Lists.
See text for trap details. E = Emergence trap, M = Malaise trap, PS = flight window trap, W = window trap; omt-cwd = overmature trees and coarse woody debris, omt = overmature trees, cwd = coarse woody debris.

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