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Saproxylic insect diversity of beech: limbs are richer than trunks

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Abstract

The ecological value of dead wood (coarse woody debris) is broadly acknowledged, but in most commercial forests in Central Europe dead wood amounts are still low. Dead trees are removed because they are thought to obstruct forest management and to be potential sources of outbreaks of pest species. Consequently, the saproxylic fauna is impoverished in many forests of Central Europe. In places where one cannot agree on leaving entire dead trees, dead limbs could be promoted instead. However, limbs are thought not to be an appropriate habitat for saproxylic insects. I tested the hypothesis that trunks of beech *Fagus sylvatica* (L.) host more saproxylic Diptera and Coleoptera than fallen dead limbs of beech by comparing observed and estimated species richness and diversity. In both insect groups, limbs hosted more species and had a higher diversity than trunks. More threatened saproxylic coleopteran species were reared from limbs than from trunks. Species overlap between trunks and limbs was 55.3% for Diptera and 82.6% for Coleoptera. Hence, a considerable proportion of saproxylic insect species would benefit if at least dead limbs were allowed to accumulate in commercial forests.

Keywords: Coleoptera; Dead wood; Dimension; Diptera; Diversity; Saproxylic

1. Introduction

The importance of dead wood (coarse woody debris) for biodiversity in forest ecosystems has repeatedly been stated (Elton, 1966; Maser and Trappe, 1984; Kirby and Drake, 1993; Kaila et al., 1994; Jonsell et al., 1998; Bowman et al., 2000). However, during the past centuries, old and dead trees have consequently been removed from most Central European forests. This greatly reduced overall biodiversity and especially the number of saproxylic insect species. Throughout Europe, this group today includes a large proportion of threatened species (Speight, 1989; Mikkola, 1991; Mawdsley and Stork, 1995; Geiser, 1998).

In the recent years, an increasing number of forest reserves has been established, where dead wood is allowed to accumulate, but amounts in commercial forests are still low (e.g. <5 m^3 ha^{-1} on average in the lowlands of Germany and Switzerland; Albrecht, 1991; Brassel and Brändli, 1999). Even fallen branches and limbs are mostly removed or burnt, at least in Switzerland (Forster et al., 1998). Actions undertaken to promote dead wood should therefore focus on commercial forests. It is often argued, though, that dead trees in commercial forests are dangerous because people might be harmed by limbs breaking

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off or by falling trunks. Additionally, dead trees are thought to obstruct forest management and to be potential sources of pest outbreaks. Where one cannot agree on leaving entire dead trees, promoting fallen branches and limbs would be an alternative way to enhance dead wood amounts. This is particularly important, as it has been shown that large distances between dead wood pieces are fatal for certain saproxylic insect species (Schiegg, 2000a). However, dead wood of larger dimensions is usually considered to be more appropriate for saproxylic insects as micro-climate is more stable than in limbs or branches (Boddy, 1983; Kolström and Lumatjärvi, 2000). As yet, no study has explicitly focused on the significance of dead wood dimensions for this group, though some authors have included dead branches or limbs in their studies (Larkin and Elbourn, 1964; Schmitt, 1992; Rauh, 1993; Hilt and Ammer, 1994; Kleinevoss et al., 1996; Haase et al., 1998). I tested the hypothesis that trunks host more saproxylic insect species than limbs by comparing observed and estimated species richness and diversity of saproxylic Diptera and Coleoptera breeding in trunks and limbs of beech *Fagus sylvatica* (L.). Beech is potentially the dominating tree species in the forests of the Swiss lowlands (Brändli, 1998). It is important to know the number and identity of the species developing in limbs relative to those breeding in trunks in order to evaluate the significance of limbs as a habitat for saproxylic insects.

2. Methods

2.1. Study area

The study was carried out in the forest reserve of Sihlwald (47°15′; 8°33′) on a NE-facing slope shaped by several small valleys 10 km south of Zurich, Switzerland. The entire forest covers 10 km^2 and is dominated by beech and spruce *Picea abies* (Karst.), followed by ash *Fraxinus excelsior* (L.) and fir *Abies alba* (Mill.). Dead wood averages 6.3 m^3 ha^{-1} of mainly beech and spruce (own unpublished data). I selected 14 study plots between 500 and 800 m asl similar to each other in terms of aspect, stand structure and age as well as tree species composition. Plot centres were at least 600 m apart to ensure independence of the collections.

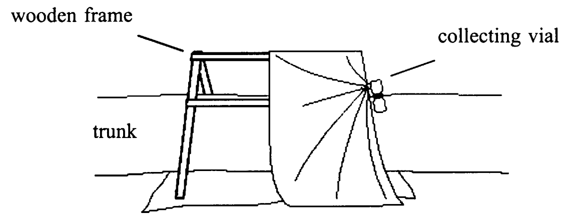

Fig. 1. A trunk eclector during installation.

2.2. Data collection

Insects were collected by a modified version of eclectors (emergence traps, Funke, 1971; Schmitt, 1992; Hilt and Ammer, 1994; Irmler et al., 1996, Kleinevoss et al., 1996; Økland, 1996; Hövemeyer, 1999), which can also be used on fallen dead wood lying on the forest floor (Schiegg et al., 1999). Due to the tent-like construction of the eclectors, pieces of dead wood could be enclosed to rear saproxylic insects (Fig. 1). Four eclectors were installed in each of the 14 plots. I defined parts of stems of fallen dead beech trees (diameter at the smaller end >20 cm; $L = 1.5$ m) as ‘trunks’. Accordingly, large beech limbs without side branches (diameter at both ends 5–10 cm; $L = 1.0-1.5$ m) lying on the forest floor were defined as ‘limbs’. Two traps per plot contained each a part of a trunk (trunk eclectors) and another two traps per plot were filled with limbs (limb eclectors), giving 28 traps of each type, 56 in total. The limbs were collected from the forest floor within 10 m around the traps. I measured the length and diameter of each piece of dead wood and calculated the surface area and volume enclosed in each trap. As stage of decay greatly influences the community composition of saproxylic insects (Derksen, 1941), only dead beech wood at a medium stage of decay was considered. Medium stage of decay was defined according to Albrecht (1991): the wood is partly softened and shows clear signs of colonization by saproxylic insects and fungi. The bark is partly lose but less than 10% of its surface is covered by moss. The collecting vials were attached and filled with a 2% formaldehyde solution at 24 April 1996, when collecting started. They were emptied monthly until 25 November 1996. All specimens of Diptera and Coleoptera were identified by various specialists to species level except for Psychodidae, Chironomidae, Cecidomyiidae, and Phoridae.

2.3. Species classification

Only saproxylic species were included in the analyses classified according to McAlpine et al. (1981), Freude et al. (1964–1983), Koch (1989–1992), Smith (1989), and on information given by the specialists responsible for the species identification. I categorised a beetle species as a potential forest pest, when it was recorded by Schwenke (1982) as having caused considerable damage to forest stands. Based on the classifications given by Koch (1989–1992), I separated the beetle species into predatory (i.e. feeding mainly on other living arthropods, see also Hammond, 1997) and non-predatory species, as well as into stenotopic, eurytopic and ubiquistic species. Stenotopic species occur only in particular habitat types, eurytopic species in several habitats similar to each other, and ubiquistic species are found in various kinds of different habitats. A beetle species was regarded as threatened, when it was recorded in the Red List of Germany (Geiser, 1998). The Swiss Red List for Coleoptera contains data of a few selected families (Brancucci, 1994; Marchi, 1994).

The dipteran species were only divided into predatory and non-predatory species, based on data given by McAlpine et al. (1981), Schwenke (1982), and Smith (1989), as ecological literature on this groups still is sparse. Species that I collected only from limbs or only from trunks were called exclusive species. The data from each trap were pooled over the year.

2.4. Dead wood volume and surface

To compare the species numbers between limbs and trunks, I checked by regression analysis whether species richness was dependent upon either dead wood surface area or dead wood volume. As there was not enough variation in these two parameters within the traps, I used the differences in surface area and volume between limb and trunk eclectors of a plot as independent variables. The dependent variable was the difference in species richness between the two trap types. I found a significant, positive relationship both for Diptera ($R^2 = 0.21$, $n = 28$, $P = 0.03$) and for Coleoptera ($R^2 = 0.17$, $n = 28$, $P = 0.04$) when volume was used as independent variable. Neither for Diptera ($R^2 = 0.04$, $n = 28$, $P = 0.31$), nor for Coleoptera ($R^2 = 0.12$, $n = 28$, $P = 0.09$) such a relationship could be established when using surface area as the independent variable. I therefore compared the assemblages on the basis of equal volumes. As dead wood volume in the trunk eclectors (mean± S.D.: 0.168 ± 0.061 m^3) was on average four times greater than in the limb eclectors (0.041 ± 0.007 m^3), I pooled the data of four randomly selected limb eclectors and chose one trunk eclector with a volume as close as possible to the summed volume of the four limb eclectors. I repeated this procedure seven times until all 28 limb eclectors and seven trunk eclectors were considered, which resulted in a total dead wood volume of 1.15 m^3 for each trap type as basis for comparisons of species numbers.

2.5. Diversity measurements

Diversity was measured with the Shannon index (Lloyd et al., 1968) and Fisher's α (Fisher et al., 1943) using the species numbers adjusted for the differences in dead wood volume. Fisher's α has a good discriminant ability, is less biased by the abundance of the commonest species compared to the Shannon index (Magurran, 1988) and can be applied even if the underlying distribution does not follow a log series (Taylor, 1978). The differences of the Shannon indices were tested using a modified t-test specially designed for this purpose (Hutcheson, 1970). After testing the Shannon index, I applied a jack-knife procedure to both indices, which improved the estimate of diversity and enabled standard errors to be calculated (Zahl, 1977; Magurran, 1988).

2.6. Estimated species richness

The insect data were fitted to a truncated lognormal distribution following the maximum likelihood method (Cohen, 1961; Magurran, 1988). Goodness of fit was tested by a χ^2-test (Magurran, 1988). The fit of any model depends on the number of species involved (Pielou, 1975), which renders it advisable to include as many species as possible. I therefore used for these procedures the complete data set not corrected for the differences in dead wood volume.

Rarefaction curves (Simberloff, 1972) usually are applied to reach a standardised estimate of the number of species collected with any given sampling effort, e.g. the number of individuals (Colwell and Coddington, 1994). However, these methods can also be used to extrapolate the number of species for a given, large number of individuals. I used the following equation described by Duelli (1997) and subsequently used by Duelli et al. (1999) and Schiegg et al. (1999) to describe the asymptotic function of the number of species per number of individuals:

$$N_s = \frac{N_s(1 - \exp(-p_1 N_i^{p_2}))}{(1 - \exp(-p_1 N_i^{p_2})}$$

where N_s is the number of species caught with a given number of traps, N_i the number of individuals caught with a given number of traps, $N_s(N_i)$ the total number of species (individuals) caught with all traps and p_1 and p_2 the function parameters.

Applying this function to a sufficiently large dataset allows to estimate the number of species that would have been obtained if more individuals had been collected (e.g. 1 million individuals), for a more detailed description see Duelli (1997). Again, the data were not adjusted to the different amounts of volume sampled.

3. Results

3.1. The species collected

A total of 426 species of saproxylic Diptera (30 095 individuals) and 228 species of saproxylic Coleoptera (4906 individuals) were collected. Table 1 gives an overview of the three most abundant species in all samples and in each ecological category.

The most abundant dipteran species in the limb samples, the ceratopogonid *Forcipomiya pseudonigra* sp. n. is a species new to science (Delécolle and Schiegg, 1999). Whereas the dipteran samples are dominated only by representatives of two families, namely *Ceratopogonidae* and *Sciaridae* (Table 1), the trunk samples of Coleoptera contained mostly specimens of *Cisidae*, *Scolytidae* and *Lymexylonidae*, and the limb samples specimens of *Staphylinidae* and *Latridiidae* (Table 1). The identity of the most abundant species differs between the trunk and limb samples in most categories, both in Diptera and in Coleoptera.

3.2. Numerical comparisons

The limbs significantly surpassed the trunks in total species richness and in the number of individuals, both in Diptera and Coleoptera (Mann–Whitney U-test, $n = 7$, $P < 0.05$). Most relationships did not change even if all trunk eclectors were considered, containing four times the dead wood volume of the limb eclectors (Table 2). Sixty beetle species sampled from trunks and 66 beetle species sampled from limbs were recorded in the Red List of Germany (all traps considered). The variance of the number of species collected was significantly larger in the limb samples than in the trunks samples of Coleoptera (F-test, $F = 1.90$, $df = 27$, $P = 0.01$), but no difference was detected in the dipteran samples ($F = 1.59$, $df = 27$, $P = 0.11$).

In Coleoptera, the limb samples yielded significantly more potential pest and predatory species than the trunk samples (Mann–Whitney U-test, $n = 7$, $P < 0.01$) also when the significance level was adjusted for the number of tests performed (significance level $P = 0.017$; Sokal and Rohlf, 1995). Also in Diptera, the limb samples contained significantly more predatory species than trunk samples (Mann–Whitney U-test, $n = 7$, $P < 0.05$). Furthermore, limbs and trunks differed with regard to the number of stenotopic, eurytopic and ubiquistic Coleoptera species (Friedman non-parametric two-way ANOVA, after Zar, 1984, $H = 17.28$, $P < 0.01$, $n = 7$; Fig. 2) which was caused by the limb samples yielding in each category more species than the trunk samples ($n = 7$, $P < 0.01$; significance level adjusted to $P = 0.017$, see above). It seems that the dominance of the limb samples was mainly due to the number of eurytopic and ubiquistic species (Fig. 2).

Significantly more species were collected exclusively from limbs than from trunks, both in Diptera and Coleoptera ($n = 7$, $P < 0.05$; Table 3). Soerensen index of similarity (Mühlenberg, 1989) was 55.3% for Diptera and 82.6% for Coleoptera.

Both in Diptera and Coleoptera higher species diversity was found in the limb than in the trunk samples (Table 4). The differences of the Shannon

Table 1
The three most abundant species and number of individuals of Diptera and Coleoptera in the trunk and limb eclector samples[a]

Trunks	Limbs
All species (Diptera)	
Bradysia fungicola (Winnertz 1967); 3463	*Forcipomyia pseudonigra* (Delécolle and Schiegg 1999); 1105
Scatopsciara calamophila Frey 1948; 1649	*Scatopsciara calamophila* Frey 1948; 964
Camptochaeta minutula (Bukowski and Lengersdorf, 1936); 1432	*Scatopsciara nacta* (Johannsen 1912); 946
Predators	
Medetera acanthura Negrobov and Thuneberg 1970; 78	*Medetera abstrusa* Thuneberg 1955; 57
Euthyneura myrtilli Macquart 1836; 58	*Oedalea austroholmgreni* Chvála 1981; 46
Tachypeza nubila (Meigen 1804); 55	*Rhamphomyia gibba* (Fallén 1916); 38
All species (Coleoptera)	
Octotemnus glabriculus (Gyllenhal 1827); 579	*Leptusa fumida* (Erichson 1839); 209
Xyleborus dispar (Fabricius 1792); 421	*Aridius nodifer* (Westwood 1839); 177
Hyleocoetus dermestoides (Linné 1761); 277	*Proteinus brachypterus* (Fabricius 1792); 122
Potential pest species	
Xyleborus dispar (Fabricius 1792); 421	*Anobium costatum* Aragona 1830; 23
Ptilinus pectinicornis (Linné 1758); 13	*Hedobia imperialis* (Linné 1767); 6
Rhagium mordax (Degeer 1775); 5	*Strangalia maculata* (Poda 1761); 6
Predators	
Rhizophagus dispar (Paykull 1800); 83	*Denticollis linearis* (Linné 1758); 67
Gabrius splendidulus (Gravenhorst 1802); 69	*Gabrius splendidulus* (Gravenhorst 1802); 30
Rhizophagus nitidulus (Fabricius 1798); 43	*Rhizophagus perforatus* Erichson 1845; 23
Stenotopic species	
Rhizophagus nitidulus (Fabricius 1798); 43	*Orchesia undulata* Kraath 1853; 33
Bolitochara mulsanti Sharp 1875; 27	*Ptenidium intermedium* Wankow 1869; 30
Liodopria serricornis (Gyllenhal 1813); 24	*Catops subfuscus* Keller 1846; 25
Eurytopic species	
Octotemnus glabriculus (Gyllenhal 1827); 579	*Leptusa fumida* (Erichson 1839); 209
Xyleborus dispar (Fabricius 1792); 421	*Aridius nodifer* (Westwood 1839); 177
Hyleocoetus dermestoides (Linné 1761); 277	*Denticollis linearis* (Linné 1758); 67
Ubiquistic species	
Proteinus brachypterus (Fabricius 1792); 50	*Proteinus brachypterus* (Fabricius 1792); 122
Anotylus sculpturatus (Gravenhorst 1860); 13	*Proteinus macropterus* (Gyllenhal 1806); 51
Epuraea biguttata (Thunberg 1784); 4	*Anotylus sculpturatus* (Gravenhorst 1860); 47

[a] Samples pooled over the year.

Table 2
Number of species and individuals collected from 1.15 m^3 both of trunks and limbs[a]

	Diptera		Coleoptera	
	Trunks	Limbs	Trunks	Limbs
Species	167 (305)	347	70 (153)	182
Individuals	3165 (14552)	15441	737 (2620)	2286

[a] The numbers within parentheses were obtained when all trunk eclectors (total volume = 4.66 m^3) are considered.

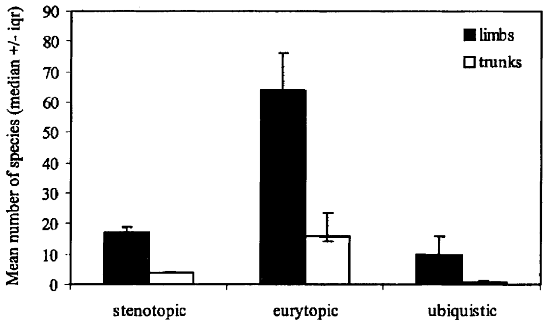

Fig. 2. Mean number of stenotopic, eurytopic and ubiquistic beetle species collected from 1.15 m^3 of trunks and limbs. Values given are medians ± interquartile ranges, $n = 7$.

Table 3
Number of species reared either from trunks or limbs, and shared between trunks and limbs (samples of 1.15 m^3)

	Trunks	Limbs	Shared
Diptera	25	205	142
Coleoptera	13	125	57

indices were significant ($t_{Diptera} = 23.67$, $t_{Coleoptera} = 4.54$, $n = 7$, $P < 0.05$ in both cases, Table 4).

3.3. Estimated species richness

The trunk data did not differ significantly from a truncated lognormal distribution in both Diptera ($\chi^2 = 5.8$, df = 8, $P > 0.20$) and Coleoptera ($\chi^2 = 11.9$, df = 7, $P > 0.10$). The limb data could not be described by any parametric model creating patterns similar to those obtained empirically, neither in Diptera nor in Coleoptera. The deviations from a truncated lognormal distribution were not large and arose only from one abundance class, the second highest in Diptera ($\chi^2 = 27.2$, df = 8, $P < 0.01$) and the lowest in Coleoptera ($\chi^2 = 19.0$, df = 7, $P < 0.01$).

The estimated species richness in Diptera was about 25% higher in the trunks and 27% higher in the limbs than the observed species richness. In Coleoptera, the estimate was 15% higher in the trunks and 18% in the limbs (Table 5). Still more species were predicted for

Table 4
Jack-knifed estimate of diversity of the trunk and limb inhabiting assemblages of Diptera and Coleoptera obtained from 1.15 m^3 of both trunks and limbs[a]

	Diptera		Coleoptera	
	Trunks	Limbs	Trunks	Limbs
Shannon	3.21 (0.13)	4.02 (0.00)	2.28 (0.60)	4.30 (0.00)
Fisher's α	37.57 (1.46)	74.95 (1.02)	18.68 (1.27)	56.83 (1.11)

[a] Standard errors are given in parentheses.

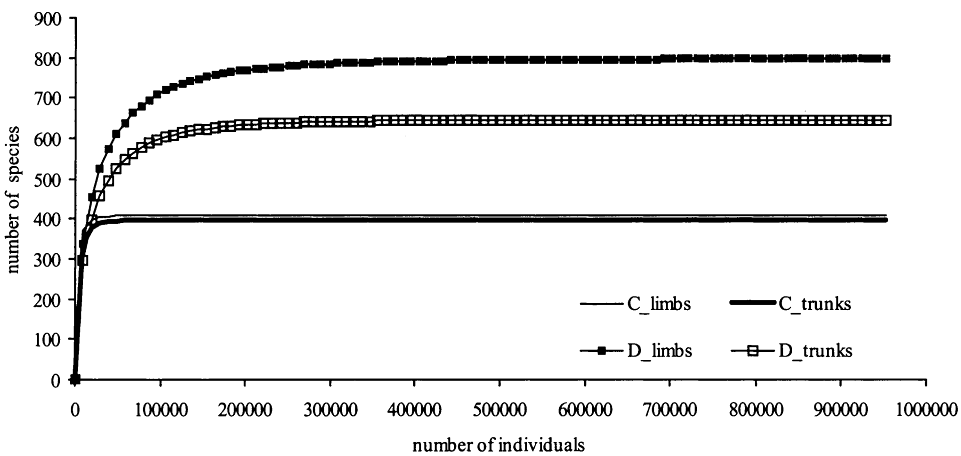

Fig. 3. Extrapolated (rarefaction) number of species against number of individuals. C = Coleoptera; D = Diptera; limbs = reared from limbs; trunks = reared from trunks.

Table 5
Observed and estimated number of species (truncated lognormal model) reared from trunk and limbs of beech[a]

Number of species	Diptera		Coleoptera	
	Trunks	Limbs	Trunks	Limbs
Observed	305	347	153	182
Estimated	406	(444)	179	(222)

[a] In parentheses: the underlying distribution deviated significantly from a truncated lognormal distribution.

limbs than for trunks, although the data have not been corrected for the different amounts of dead wood volume sampled. The number of species estimated with the rarefaction method was in Diptera 798 for limbs and 645 for trunks and in Coleoptera 408 for limbs and 396 for trunks, respectively (Fig. 3). Species accumulation with increasing numbers of individuals was slower in Diptera than in Coleoptera, indicating that the beetle species occurred in lower abundances than dipteran species.

4. Discussion

4.1. Species richness of limbs

The overall dominance of limbs in terms of species richness and diversity as found in this study is unexpected, but is partly in line with the findings of other studies conducted in similar habitats. However, as information about dead wood volume or stage of decay is usually not given, the results are difficult to compare. Schmitt (1992) collected fewer exclusive beetle species from small-sized than from large-sized dead wood of beech, and in the study of Hilt and Ammer (1994), dead wood of smaller dimensions hosted more exclusive beetle species in spruce, but the opposite was true in oaks *Quercus* sp.. It may be concluded that the significance of dead wood dimension for saproxylic insects varies among tree species.

Limbs collected from the forest floor are presumed to have a higher moisture content than trunks (Boddy, 1983), and their bark is rougher and more often covered by lichens than the bark of trunks, at least in beech (own observation). Moisture content and surface structure have been shown to enhance the abundance of wood dwelling insects (Wallace, 1953; Larkin and Elbourn, 1964; Dajoz, 1980). Furthermore, the rotting process of limbs, and therefore the colonisation by saproxylic insects, usually starts before they break off, and so a limb lying on the forest floor may also contain species occurring in the canopy.

At least in Coleoptera, the dominance of the limb assemblages was most pronounced for eurytopic and ubiquistic species. This could be caused by the fluctuating microclimate of limbs. Species confined to more narrow niches may not be able to cope with the large changes in moisture or temperature that often take place in dead wood of smaller diameters. Limbs distributed over the forest floor experience a large range of humidity or light intensity, which may be an additional reason for the species richness of the limb samples. Limbs represent a diverse habitat per unit volume and this may result in higher species diversity. This may be supported also by the larger variance in number of beetle species found in the limb than in the trunk samples. It might be surprising that species number was related to dead wood volume but not to dead wood surface area, making, therefore, dead wood volume rather than surface area the appropriate basis for numerical comparisons. However, this finding agrees with Väisänen et al. (1993), who have found that the species richness of beetles restricted to the subcortical zone of trunks was better explained by dead wood volume than surface area.

4.2. Species-abundance distribution and estimation of true species richness

The estimated number of species also was higher in limbs than in trunks, both when using species-abundance distributions and extrapolation of rarefaction curves. The use of parametric models to explain patterns of species-abundance distributions has been intensively debated (Hughes, 1986), but most authors agree on their advantages for comparative purposes (Magurran, 1988 and references therein). So far as I am aware, this is the first time that the species-abundance distributions of saproxylic insects have been described. Kaila et al. (1994) state that the species-abundance distributions of saproxylic beetles collected with window traps to resemble a log series, but do not give any data. In the present study, the pattern obtained by the trunk eclector data followed a truncated lognormal distribution, but this model did not reflect the data from the limb eclectors. Since most collections with large numbers of taxonomically related species can be described by a lognormal distribution (Sugihara, 1980), it is remarkable that the assemblages gathered from the limb eclectors behaved differently. This may indicate the existence of distinct communities breeding in limbs and trunks. On the other hand, species overlap between limbs and trunks was fairly large, mainly in beetles. So, it seems that the abundances of some species vary with substrate type rather than the identity of the species themselves.

As the limb samples deviated significantly from a truncated lognormal distribution, the estimated number of species may not be reliable. Some authors, however, believe graphic inspection to be sufficient to decide whether an empirical distribution follows a predicted pattern (Lambshead and Platt, 1985; Hughes, 1986; Colwell and Coddington, 1994). As the estimated and the observed distribution did not differ fundamentally, I considered the calculation of the estimated numbers as justified.

5. Conclusions

A considerable part of saproxylic Diptera and Coleoptera breeds in dead limbs of beech and, with its large number of species, contributes significantly to biodiversity in forests. Limbs also host a remarkedly high number of threatened species. Hence, if dead wood amounts were preserved by leaving dead limbs, a large number of saproxylic insect species could profit from the available habitat. This is, of course, only a minimum solution suitable for some saproxylic species. The main efforts must still focus on the preservation of dead wood of all varieties to ensure sufficient habitat for the large number of species dependent on dead wood.

High dead wood amounts in managed forests not only increase their value as habitat of a diverse flora and fauna, but also help bridging the gaps between forest reserves. Some saproxylic insects are thought to be only poorly mobile (Speight, 1989; Warren and Key, 1991; Nilsson and Baranowski, 1997) and have been shown to respond to the spatial arrangement of dead wood even on the scale of less than 200 m (Schiegg, 2000b). Commercial forests hosting large amounts of dead wood could serve as stepping stones between forest reserves helping to prevent habitat isolation, and possibly facilitating recolonisation of formerly lost habitats.

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