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Short-term development of ambrosia and bark beetle assemblages following a windstorm in French broadleaved temperate forests

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Abstract: In most temperate deciduous forests, windstorm is the main source of dead wood. However, the effects of this natural disturbance on ambrosia and bark beetle communities are poorly known. In managed oak-hornbeam forests storm-damaged in France in 1999, we sampled ambrosia (and second bark beetles) by ethanol-baited window-flight traps in 2001. By comparing uncleared gaps, undisturbed closed-canopy controls and seedling-sapling stands, we investigated the short-term effects of gap formation, gap size and surrounding landscape to provide a snapshot of scolytid response. Contrary to expectations, neither the abundance nor the richness of ambrosia beetle species was significantly higher in gaps than in undisturbed stands. Few responses in abundance at the species level and only a slight difference in assemblage composition were detected between gaps and closed-canopy controls. Gaps were more dissimilar from seedling-sapling stands, than from closed-canopy controls. More scolytid individuals and species were caught in gaps than in seedling-sapling stands. Mean local and cumulative richness peaked in mid-size gaps. Only mid-size gaps differed from closed-canopy controls in terms of species composition. We identified generalist gap species (*Xyleborus saxesenii*, *X. cryptographus*), but also species significantly more abundant in mid-size gaps (*Platypus cylindrus*, *Xyloterus signatus*). The faunistic peculiarity of mid-size gaps seemed to be partly related to a bias in oak density among gap size classes. Few landscape effects were observed. Only the scolytids on the whole and *X. dispar* were slightly favoured by an increasing density in fellings at the 78 ha scale. We did not find any correlation between scolytid abundance and the surrounding closed-forest percentage area. We confirmed that temperate, deciduous, managed stands did not come under threat by ambrosia and bark beetle pests after the 1999 windstorm. Nonetheless, our data stressed the current expansion in Western Europe of two invasive species, *X. peregrinus* and especially *X. germanus*, now the predominant scolytid in the three oak forests studied.

Key words: dead wood retention, forest management, natural disturbance, pest risk, windthrow gaps

1 Introduction

In most temperate deciduous forests, windthrow is the main source of dead wood (Wohlgemuth et al., 2002). In Switzerland for instance, about two-third of all unplanned felling is caused by storm winds, and only 13% by insect calamities (Wohlgemuth et al., 2002). The catastrophic avalanches of 1999 in Switzerland only felled 160 000 m^3 of timber compared to 12.5 million m^3 of timber thrown by the storm ‘Lothar’ in 1999. Similarly, in Finnish pine and spruce forests, dead wood from windstorms represents up to 40–56% of total dead wood (Sippola et al., 1998).

The high, concentrated dead wood volumes in windthrow gaps may be attractive for some scolytids. Most of the studies to date have focused on short-term effects in conifer windstorm gaps, on pine (Lundquist, 1995) and especially on spruce (Ravn, 1985; Forster, 1993; Nicolai, 1996; Weslien and Schröter, 1997; Kopf and Funke, 1998; Lindelöw and Schroeder, 1998; Wermelinger et al., 1999; Göthlin et al., 2000), more often affected by windthrow and more sensitive to pest outbreaks. Gap effects remain poorly understood in temperate deciduous forests (Bouget and Duelli, 2004).

The forests of northern France were severely damaged by the storm ‘Lothar’ on the 26th of December 1999. All over France, the strong winds of up to 170 km/h, blew down about 170 million m^3 of timber, i.e. three times the national annual harvest. In the Seine-et-Marne department, 5% of the forests were destroyed, and 90% of the damaged stands were deciduous. In the Brie forests, Lothar felled 900 000 m^3 of hardwood timber including 410 000 m^3 of oak (Caroulle, 2002).

This severe storm created exceptionally good natural experimental conditions. In the resulting gaps, ambrosia and bark beetle habitat was drastically disturbed in terms of micro-climate and volume of breeding substrate (Bouget and Duelli, 2004).

From a faunal conservation point of view, it would be interesting to know how naturally created gaps are colonized by, ambrosia and bark beetles. From a forest management point of view, the suitability of dead wood concentrated in gaps as breeding material for potential pests would also be of interest. Since the 'perforation' (as defined by Forman, 1995) of closed canopy forest by windthrow creates open patches rich in dead wood, gaps can be considered in the light of island biogeography and landscape ecology concepts. Colonization and local extinction in habitat patches depend on patch characteristics (area) and surrounding landscape (isolation).

In the present paper, we used scolytid samples (especially ambrosia beetles) to address the following questions:

- First, were ambrosia and bark beetle assemblages actually affected in gaps compared to closed-forest controls in the short term, only 1.5 years after the storm event? Pioneer xylophagous beetles may have benefited from the high volume of sun-exposed fresh dead wood observed in the gaps.
- Second, was the response affected by the local microenvironment or by spatial parameters such as gap size and isolation? From patch-occupancy models, the abundance of gap species might be related to patch isolation, i.e. the density of source patches (such as fellings cut before 1999) in the surrounding landscape (Didham, 1997). What is more, changes in environmental parameters relevant to scolytids may increase with gap area. A larger patch is more likely to have a higher volume of dead wood (resource concentration hypothesis; Tews et al., 2004), and by sampling effect, a higher heterogeneity of the dead wood (habitat diversity hypothesis; Tews et al., 2004). The dead wood should also be more sun exposed (edge effect; Didham, 1997).
- Third, we compared assemblages in natural gaps and man-made openings. Can fellings really be sources for ambrosia and bark beetle colonization of gaps in the landscape?
- Due to the use of ethanol-baited traps, the conclusions are valid only for ambrosia beetles that have been possible to sample accurately.

1.1 Management concerns

The question as to whether the retention of dead wood poses any threat to commercial forestry has been a controversial issue between foresters and conservationists in the recent past. There are generally no major threats to the health of neighbouring broadleaved trees such as the ones posed by bark beetles to spruce and pine (for *Xyloterus* attacks in beech forests see Henin et al., 2003). However, despite a low level of risk to the stands, *Platypus* or *Xyloterus* beetle population growth can contribute to depreciation in the value of the timber. Final, diversification in ambrosia and bark beetle communities may increase the number of competing pests, thus reducing the risk of outbreak.

Another publication will analyse the complete saproxylic beetle dataset (Bouget, unpublished data).

2 Materials and Methods

2.1 Research area

Our study area is situated in the 'Brie' region in Northern France, about 50 km southeast of Paris (fig. 1). Our sample plots were located within three lowland forests: the state-owned forests of Armainvilliers (1525 ha), Crecy (a 1250 ha national block within a 5000 ha forest), and the regional forest of Ferrieres (2890 ha). These neighbouring forests formed one forest block before fragmentation during the middle ages. They are currently being managed as coppice with standards under conversion to high forest and were severely storm-damaged in December 1999. We focused on oak-hornbeam site type (*Quercus petraea*, *Q. robur* and *Carpinus betulus*), with aspen (*Populus tremula*), birch (*Betula* sp.) and lime (*Tilia cordata*). Stand type in the study sites was controlled to avoid significant differences in structure, composition and soil.

2.2 Sampling design and study sites

We used a 50-site sampling design, composed of 24 gaps, 14 closed-canopy control sites and 12 man-made openings. Among a total of 80 gaps inventoried before the study, 24 storm-created, uncleared gaps were selected in 14 plots within the study area. A control area was established in the undisturbed part of each plot. Each gap was thus paired with an adjacent (25–50 m distant), closed-canopy control site ($n = 14$), so that two or three gaps may share the same control site. Twelve seedling-sapling stands (four seeding cuts and eight sapling stands) were sampled near the gaps. These fellings were larger (5 ha on average) and slightly older (1–15-year old) than the natural gaps.

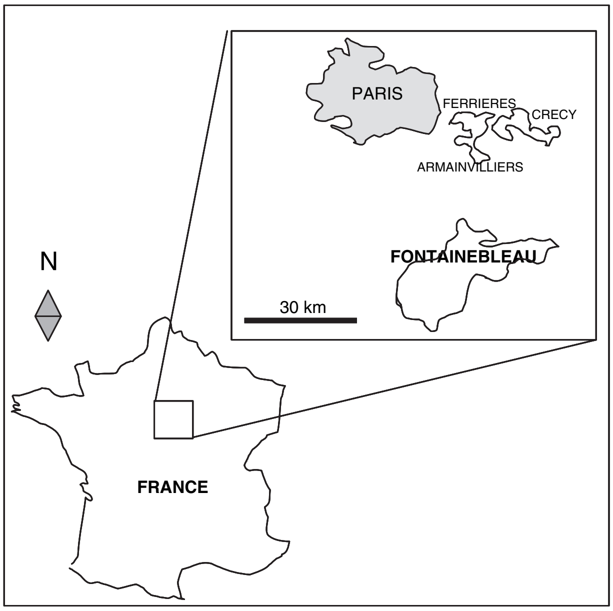

Fig. 1. *Map of study area*

The 24 gaps to be surveyed were selected according to size and isolation in order to balance the sampling design. Gap location, perimeter and area were mapped using the differential mode of a Global Positioning System (GPS). Study gaps were 0.78 ± 0.85 ha on average and ranged from 0.12 to 3.3 ha. They were divided into three size classes: small (<0.3 ha, $n_{\mathrm{SG}} = 8$), medium (0.3–1 ha, $n_{\mathrm{MG}} = 7$) and large (>1 ha, $n_{\mathrm{LG}} = 9$).

Using aerial photographs and the GIS ArcView (Data Image, France)$^{\mathrm{TM}}$, the landscape was mapped at three spatial scales within a landscape disk centred on each gap: 200 m (12 ha), 500 m (78 ha), 1000 m (314 ha). In the surrounding 78 ha landscape, felling areas covered 4.0 ± 5.3 ha on average. An amount of 12 and 314 ha scales for surrounding landscapes were also used in data analysis and were not correlated to gap size class. The distance to the closest felling was also measured; it was 337.0 ± 200.3 m on average.

2.3 Sampling protocol

We used window-flight traps baited with ethanol to sample ambrosia and bark beetles (Markalas and Kalapanida, 1997). Due to the use of ethanol-baited traps rather than passive window traps, the conclusions are valid mostly for ambrosia beetles. The window trap consisted of a transparent plastic pane (1 m^2) and a container below the pane. Salt water with detergent and ethanol was used to attract, kill and preserve the insects. The trap was hung on a natural support so that the lower margin of the pane was 1 m above the ground. To maintain a minimum distance between traps, the number of traps per gap depended on gap size. One window trap was set up in forest controls, open stands and in small and mid-size gaps; two window traps in large gaps.

The sampling was carried out during the second vegetation growth after the storm (2001). Traps were emptied and preserving fluid replenished monthly from mid-April to mid-August for one sampling season. This period covered most of the flight period for ambrosia and bark beetles.

2.4 Species included in the study

This article covers Coleoptera Scolytidae, mainly ambrosia beetles (and second bark beetles), the other saproxylic beetles being analysed in a separate paper. Scolytids are early colonizers of fresh dead wood (pioneer xylophagous). They actually include the phloeophagous taxa, which feed on inner bark, and ‘ambrosia beetles’ (*Xyleborus* and *Platypus*) which feed on fungi inside their galleries. Ambrosia and bark beetles tunnel through the inner bark and cambium and initiate the decaying process, thereby creating a valuable substrate which evolves over many decades (Bakke and Kvamme, 1993). Several pioneer bark beetles can be regarded as key species in the sense that many parasitoids, predators and saprophagous insects are dependant on their intervention (Weslien, 1992). Some species are potential pests. Approximately 140 species of scolytids have been recorded in France. In temperate broadleaved forests, ambrosia and bark beetles are one of the most species- and specimen-rich groups among the xylophagous beetles.

2.5 Habitat variables

We studied the effect of the following environmental variables on saproxylic beetles: (i) habitat type (gap, closed-canopy control, seedling-sapling); (ii) gap size, obtained by the digitalization of gap borders using a GPS, and considered to be a categorical variable in three classes rather a continuous variable to match the area of classical forest management units (see above); (iii) landscape context, mapped using aerial photographs and a GIS, and considered as six quantitative variables [the area of fellings or closed-canopy stands at three spatial scales: 200 m (12 ha), 500 m (78 ha), 1000 m (314 ha)]; (iv) micro-environment (*Quercus*, *Populus* or *Tilia* density within a 2 m radius around traps).

2.6 Data analysis

Pairwise anosim tests based on the Bray-Curtis dissimilarity were used to check for differences in assemblage composition amongst predefined groups with 10 000 spatially constrained permutations (after a log transformation of abundances; Clarke, 1993).

Among-site comparisons of similarity matrices were investigated using Mantel and partial Mantel approaches (Legendre and Legendre, 1998). A Mantel test was first computed to measure the correlation between a matrix of geographic distance and a matrix of similarity in beetle species composition among the 50 sampled sites. A partial Mantel test was performed to measure the correlation between tree species composition around traps (*Corylus*, *Quercus*, *Tilia*, *Betula*, *Populus*, *Carpinus*, *Salix*, *Castanea and Sorbus*) and beetle composition similarity matrices after controlling for the effect of a primary co-matrix of geographic distance among sites. The Mantel *r*-value was tested for significance by 999 permutations.

We compared the cumulative species richness between habitat classes (small, mid-size and large gaps, forest controls) using sample-based (and not individual-based) rarefaction calculations (Colwell and Coddington, 1994). In each class, the expected number of species and the standard deviation were then interpolated at a standardized sample size, namely the least number of trap samples between habitat classes (Magurran, 1988). Sampling order was randomized 100 times with replacement.

Linear mixed-models were used to test the effect of environmental variables upon the (ln + 1) transformed richness or abundance per trap of all ambrosia and bark beetles and species (>40 individuals). Nested spatial variables were classified as random effects (Pinheiro and Bates D. M., 2000): block (five blocks, i.e. sub-forest area limited by roads, were sampled among available blocks), plot (14) and site (38). These models took the configuration of the sampling design into account (e.g. the spatial pattern of traps over the research area). Differences among means were investigated by Tukey *post hoc* tests.

Four series of models analysed the effect of: (i) habitat type, (ii) gap size (three classes), (iii) landscape (six variables) and (iv) microenvironment (three variables). In each model, we ran as many successive separate regressions as explanatory variables treated. The significance of the fixed-effect coefficient was based on an *F*-test and adjusted with a Bonferroni correction.

In all models, the trapping period was introduced as a covariate in order to avoid pseudo replication. In models (ii), the oak density in a 12 m^2 disk around the traps was introduced as a primary covariate because of its correlation to gap size class ($F_{2,139} = 14.6$, $P < 0.001$). Similarly, gap size was introduced as a covariate in models (iv). There was no significant correlation between gap size class and other environmental variables, such as felling area in the surrounding landscape (Felling200 $F_{3,34} = 0.3^{\mathrm{ns}}$; Felling500 $F_{3,34} = 0.4^{\mathrm{ns}}$; Felling1000 $F_{3,34} = 0.6^{\mathrm{ns}}$) or local density of other tree species. Even though there was no significant correlation between gap isolation and environmental variables (local tree species density, size class), gap size class was used as a primary covariate in models (iii).

Since species abundance per trap hardly complied with parametric assumptions, and since gaps and forest controls were paired, the non-parametric pairwise Wilcoxon signed-ranks test (Legendre and Legendre, 1998) was used to compare the abundances between gaps and controls and to assess the species response to opening the canopy. Species represented by less than five individuals were not tested.

Except for rarefaction (processed with EstimateS; Colwell and Coddington, 1994), analyses were conducted using the package S-Plus 6.1.

3 Results

3.1 Sample overview

During the four monthly trapping sessions, a total of 24 116 ambrosia and bark beetle individuals belonging to 28 species were caught (table 1). Five species were represented by, fewer than five individuals and five others by only one individual. Some of these rarely caught species were linked with conifers (*P. chalcographus*, *H. cunicularius*, *P. pityographus*, *D. autographus*) or with herbs or bushes (*T. varipes* on Euphorbiaceae, *P. rhododactylus* on Genistae). A sufficient abundance for individual testing (more than 40 individuals) was found for only 12 species. The assemblages were dominated by three *Xyleborus* species: *X. germanus* (45%), *X. saxesenii* (30%) and *X. dispar* (20%), present in all the plots and representing 95% of all the ambrosia and bark beetle individuals.

3.2 Spatial autocorrelation and faunistic similarity

The Bray-Curtis dissimilarity matrix between sites was not correlated with the metric distance matrix Mantel ($r = 0.045$, $P = 0.08$). What is more, we observed only a slight block effect, while using a permutation test constrained by the habitat type (correction of spatial autocorrelation between sites which belong to the same habitat type; ANOSIM $r = 0.21$, $P = 0.05$).

3.3 Differentiation of saproxylic fauna in gaps and closed-canopy forest controls

In spite of the large volume of fresh dead wood in the gaps sampled (personal observation), the mean number of ambrosia and bark beetle individuals per trap was no higher there than in closed-forest controls (fig. 2a).

Despite the lack of a global positive response, Wilcoxon tests identified three response groups among the 16 species represented by more than five individuals. Three species were negatively affected in gaps (table 2). *Dryocoetes villosus*, *Scolytus carpini* and *Ernoporicus fagi* were absent from gaps and

Table 1. *Abundance of bark beetle species in gaps, forest controls and seedling-sapling stands*

	Cumulative abundance	Seedling-sapling stands	Gaps (Mean ± SD)	Forest controls	ANOVA ($F_{2,22}$)
X. germanus (Blandford, 1894)	10729	22.27a ± 26.59	43.58a,b ± 65.84	65.52b ± 107.93	7.60**
X. saxeseniii (Ratzeburg, 1837)	7154	21.36a ± 47.33	37.65b ± 45.40	15.67a ± 20.67	13.42**
X. dispar (Fabricius, 1792)	4716	8.51b ± 12.71	22.59a ± 30.33	20.83a ± 22.81	9.29**
X. peregrinus (Eggers, 1944)	374	4.04a ± 9.93	1.12b ± 3.40	0.61b ± 1.47	3.79*
P. cylindrus (Fabricius, 1792)	306	0.24 ± 0.96	1.80 ± 5.44	0.72 ± 1.77	3.17^{ns}
X. monographus (Fabricius, 1792)	145	0.07 ± 0.25	0.94 ± 4.52	0.15 ± 0.40	2.26^{ns}
T. asperatus (Gyllenhal, 1813)	140		0.97 ± 6.96	0.04 ± 0.19	0.74^{ns}
Leperisinus fraxini (Panzer, 1779)	103	0.89 ± 5.51	0.23 ± 0.78	0.56 ± 2.06	0.56^{ns}
E. caucasicus (Lindemann, 1876)	95	0.17 ± 0.78	0.46 ± 1.28	0.41 ± 1.40	0.35^{ns}
X. signatus (Fabricius, 1787)	86		0.34 ± 0.72	0.70 ± 1.85	4.68*
X. cryptographus (Ratzeburg, 1837)	70		0.49 ± 2.49	0.02 ± 0.13	1.73^{ns}
Taphrorychus villifrons (Dufour, 1843)	52	0.29 ± 0.79	0.20 ± 0.91	0.18 ± 0.51	0.61^{ns}
X. domesticus (Linné, 1758)	40		0.11 ± 0.45	0.44 ± 1.43	
S. intricatus (Ratzeburg, 1837)	37	0.38 ± 1.47	0.09 ± 0.46	0.13 ± 0.43	
E. fagi (Fabricius, 1798)	28	0.17 ± 0.58		0.37 ± 1.29	
X. dryographus (Ratzeburg, 1837)	11		0.07 ± 0.31	0.02 ± 0.13	
S. carpini (Ratzeburg, 1837)	6			0.11 ± 0.69	
D. villosus (Fabricius, 1792)	5	0.04 ± 0.21		0.06 ± 0.23	
E. tiliae (Panzer, 1793)	4		0.02 ± 0.14	0.02 ± 0.13	
P. pityographus (Ratzeburg, 1837)	3		0.01 ± 0.12		
S. rugulosus (Müller, 1818)	3		0.01 ± 0.12	0.02 ± 0.13	
D. autographus (Ratzeburg, 1837)	2			0.04 ± 0.19	
Pteleobius vittatus (Fabricius, 1787)	2	0.02 ± 0.15		0.02 ± 0.13	
H. cunicularius (Erichson, 1836)	1	0.02 ± 0.15			
Phloeophtorus rhododactylus (Marsham, 1802)	1			0.02 ± 0.13	
P. chalcographus (Linné, 1761)	1		0.01 ± 0.08		
S. multistriatus (Marsham, 1802)	1	0.02 ± 0.15			
Thamnurgus varipes (Eichhoff, 1878)	1	0.02 ± 0.15			

Mixed-model ANOVA of mean abundance per trap.
*$0.01 < P < 0.05$
**$P < 0.01$
^{ns}Non significant. Different letters indicate significant differences between means after a *post hoc* Tukey test, $P = 0.01$.
Only species caught in more than 40 individuals were tested.

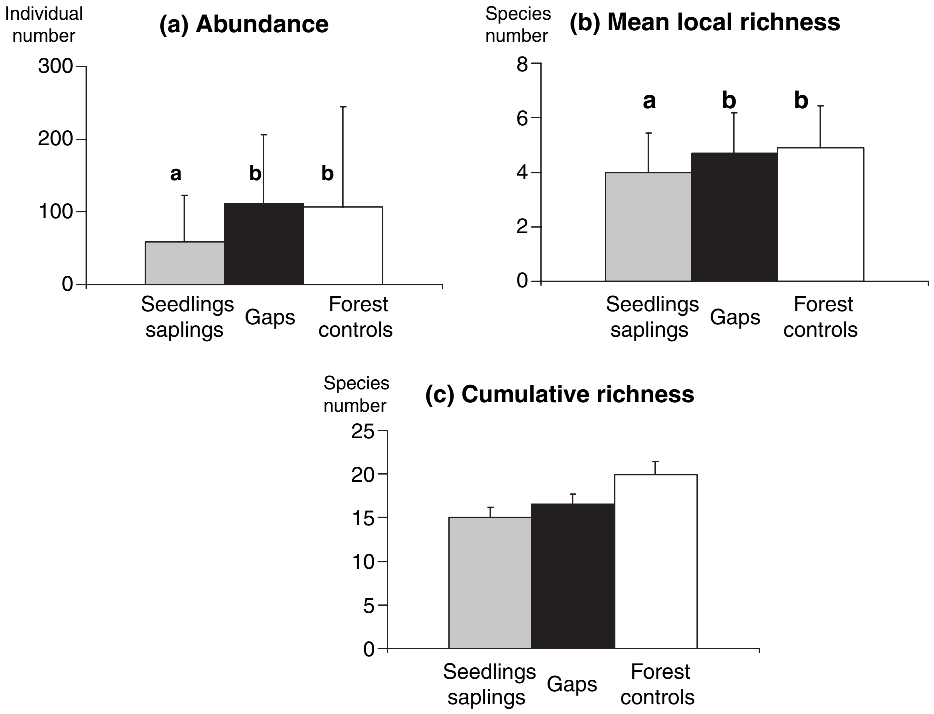

Fig. 2. *Comparison of abundance and richness of bark beetles in gaps, closed-canopy controls and seedling-sapling stands. (a) Mean abundance per trap, compared in the habitats with an* ANOVA *F-test ($F_{2,22} = 10.10$, $P = 0.0008$); letters indicate significant differences between means after a post hoc Tukey test ($P = 0.01$). (b) Mean richness per trap, compared with an* ANOVA *F-test ($F_{2,22} = 4.25$, $P = 0.03$); letters indicate significant differences between means after a post hoc Tukey test ($P = 0.01$). (c) Sample-based rarefaction interpolation of cumulative species richness, at a standardized number of 45 traps (100 sample randomizations with replacement); Error bars are the corresponding standard deviations*

Table 2. *Difference per trap in mean abundance of bark beetle species between closed forest and paired gap*

Response type	Taxa	From forest to gaps (%)	Wilcoxon test Z, P
Disfavoured in gaps	*D. villosus*	–	-2.81^{**}
	E. fagi	–	-3.26^{**}
	S. carpini	–	-1.98^{*}
	X. domesticus	−75	-1.31^{ns}
	Leperisinus fraxini	−60	-0.63^{ns}
	X. signatus	−50	-1.50^{ns}
	X. germanus	−30	0.14^{ns}
	S. intricatus	−20	-0.49^{ns}
	X. dispar	+8	0.07^{ns}
	Taphrorychus villifrons	+10	-0.29^{ns}
	E. caucasicus	+12	0.57^{ns}
	X. peregrinus	+80	0.40^{ns}
Favoured in gaps	*X. saxeseniii*	+140	2.52^{**}
	P. cylindrus	+150	2.60^{**}
	X. dryographus	+280	1.57^{ns}
	X. monographus	+530	1.68^{ns}
	T. asperatus	+2500	1.59^{ns}
	X. cryptographus	+2500	2.65^{**}

Wilcoxon signed-rank tests between abundance in each gap and in its paired forest control.
$^{*}0.01 < P < 0.05$.
$^{**}P < 0.01$.
$^{ns}P > 0.05$.
Only species caught in more than five individuals were tested.

significantly more abundant in forest controls, but the abundance in forest controls of the first two species was low (five and six individuals, respectively). Three species were favoured in gaps and benefited from dead trees: *X. cryptographus*, *P. cylindrus*, *X. saxesenii*. In gaps compared with controls, the regression of *X. domesticus*, *L. fraxini* and *X. signatus*, and the rise in abundance of *X. dryographus*, *X. monographus* (+500%), *T. asperatus* (+2500%) were not significant.

The ANOSIM tests showed that assemblage composition differed slightly in gaps compared to closed forest ($r = 0.16$, $P < 0.04$, 10 000 spatially-constrained permutations). The Bray-Curtis dissimilarity between gaps and closed forest reached 24%.

With a standardized sampling effort ($n = 45$ traps, 100 randomizations), the rarefied cumulative species richness was 20% lower in gaps than in adjacent closed stands (fig. 2c). At a local scale, mean species richness was no different in gaps and in closed stands (fig. 2b).

3.4 Spatial effects: influence of gap size

From pair-wise ANOSIM tests, only mid-size gaps differed from closed-canopy controls in terms of scolytid species composition ($r_{\text{MG-TF}} = 0.52$, $P < 0.001$). The largest Bray-Curtis dissimilarity occurred between these two habitat types (22%). The dissimilarity between small or large gaps and closed forest was only about 12% and therefore not significant ($r_{\text{LG-F}} = 0.04$, $P < 0.45$; $r_{\text{SG-F}} = 0.14$, $P < 0.79$). Among gaps, mid-size gaps were distinct from large ones ($r_{\text{LG-MG}} = 0.50$, $P = 0.006$, dissimilarity = 20%),

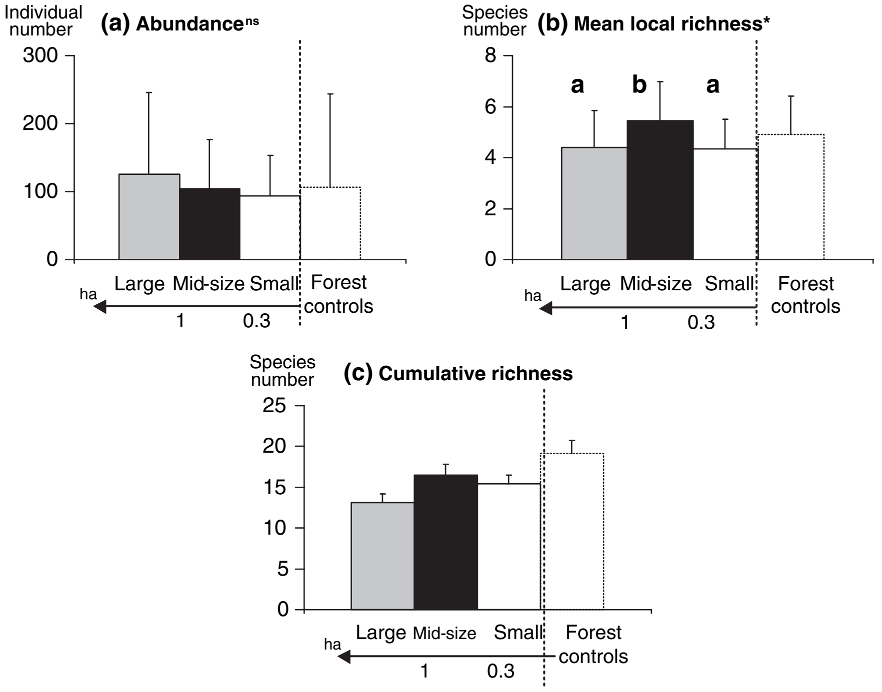

Fig. 3. *Comparison of abundance and richness of bark beetles in the three gap size classes. (a) Mean abundance per trap, compared in the size classes with an* ANOVA *F-test ($F_{2,8} = 0.12$, $P = 0.89^{ns}$); letters indicate significant differences between means after a post hoc Tukey test ($P = 0.01$). (b) Mean richness per trap, compared with an* ANOVA *F-test ($F_{2,8} = 5.63$*, $P = 0.03$); letters indicate significant differences between means after a post hoc Tukey test ($P = 0.01$). (c) Sample-based rarefaction interpolation of cumulative species richness, at a standardized number of 36 traps (100 sample randomizations with replacement). Error bars are the corresponding standard deviations. Values in closed-canopy controls are introduced as a reference*

but not from small ones ($r_{\text{SG-MG}} = 0.20$, $P < 0.28$, dissimilarity = 20%). Small and large gaps were not different ($r_{\text{LG-SG}} = 0.02$, $P = 0.48$, dissimilarity = 13%).

The abundance of ambrosia and bark beetles did not significantly increase with gap size (fig. 3a). From table 3, ANOVA and Tukey tests detected few differences in species abundances among gap size classes. A significantly greater number of individuals of *P. cylindrus* and *X. signatus* were observed in mid-size than in large gaps. The abundance of *X. monographus* and *X. peregrinus* also peaked in mid-size gaps but not significantly. The gap species *X. saxesenii* and *X. cryptographus* did not increase with gap area, and were consequently considered to be generalist gap species. We did not measure any decrease with increasing gap area for any species.

The standardized cumulative species richness peaked in mid-size gaps and was slightly higher than in small gaps and 25% greater than in large gaps (fig. 3c). Mean local richness was significantly higher in mid-size than in large and small gaps (fig. 3b).

Table 3. *Abundance of bark beetle species in gap size classes*

	Large gaps	Mid-size gaps (Mean ± SD)	Small gaps	ANOVA ($F_{2,8}$)
E. caucasicus	0.67 ± 1.57	0.44 ± 1.24	0.11 ± 0.40	2.57^{ns}
Leperisinus fraxini	0.21 ± 0.57	0.26 ± 0.95	0.25 ± 0.87	0.99^{ns}
Taphrorychus villifrons	0.11 ± 0.44	0.51 ± 1.53		2.95^{ns}
Trypophloeus asperatus		3.19 ± 12.46	0.03 ± 0.17	0.96^{ns}
X. cryptographus	0.13 ± 0.33	0.09 ± 0.29	1.58 ± 4.81	1.13^{ns}
X. dispar	27.81 ± 40.50	19.93 ± 19.69	16.64 ± 15.52	0.43^{ns}
X. germanus	57.52 ± 85.71	25.67 ± 30.83	40.58 ± 50.59	2.59^{ns}
X. monographus	0.38 ± 1.13	2.26 ± 7.9	0.36 ± 1.22	1.34^{ns}
X. peregrinus	0.67 ± 1.50	2.63 ± 5.71	0.11 ± 0.52	3.98^{ns}
X. saxeseniii	37.17 ± 46.50	50.46 ± 53.11	23.19 ± 25.93	1.34^{ns}
P. cylindrus	0.41a ± 1.21	4.30b ± 8.82	1.25a.b ± 3.40	6.68*
X. signatus	0.10a ± 0.30	0.56b ± 0.98	0.50a.b ± 0.78	5.27*

Mixed-model ANOVA of mean abundance per trap (±SD) in small (area < 0.3 ha), mid-size (0.3 < area < 1 ha) and large gaps (area > 1 ha).

*0.01 < P < 0.05.

^{ns}Non significant; letters indicate significant differences between means after a *post hoc* Tukey test (P < 0.01).

Table 4. *Species response to landscape and micro-environmental variables*

	Taxa	Environmental variable	Response
Landscape effects	All scolytids	Felling1000	+**
	X. dispar	Felling500	+**
Micro-environmental effects	*X. cryptographus*	*Populus*	+*
	X. germanus	*Tilia*	+**
	P. cylindrus	*Quercus*	+**

Two series of ANOVA based on linear mixed models tested the effect of environmental variables upon the mean beetle abundance per trap: (i) landscape models with four variables tested (distance to the closest felling or felling area within a 200 m (*Felling200*), 500 m (*Felling500*) and 1000 m radius (*Felling1000*); significance after a Bonferroni correction: *$P < 0.01$ ($=0.05/6$),**$0.01 < P < 0.05$), (ii) micro-environment models, with 3 variables (*Quercus*, *Populus* or *Tilia* density within a 2 m-radius around traps; *$P < 0.015$ ($=0.05/3$), **$0.015 < P < 0.05$).

3.5 Spatial effects: influence of landscape context

Few correlations were observed between scolytid abundance in gaps and the surface area of fellings compared to closed-canopy stands in the surrounding landscape (table 4). Among nearly significant responses, the scolytids as a whole and *X. dispar* in particular, were favoured by an increase in felling area at the 500 m scale. No species significantly responded to the variation in the area of closed-canopy stands at any of the three spatial scales.

3.6 Influence of local context

The correlation between tree species composition around the traps and scolytid composition similarity matrices was significant after controlling for the effect of geographic distance (partial Mantel test $r = 0.31$, $P = 0.003$). At the species level, the density of oak wood seemed to favour *Platypus cylindrus* at the 12 m^2 scale (table 4). *Xyleborus cryptographus* was correlated to aspen and *X. germanus* to lime local density.

3.7 Differentiation of saproxylic fauna in gaps and man-made openings

Twice as many scolytid individuals were caught in gaps than in fellings or sapling stands (fig. 2). Moreover, the ANOSIM test showed that scolytid species composition was clearly distinct in gaps and in seedling-sapling stands ($r = 0.48$, $P = 0.002$). Seedling-sapling stands were less similar to closed-canopy controls (Bray-Curtis dissimilarity = 43%) than to gaps (Bray-Curtis dissimilarity = 33%).

Xyleborus dispar and *X. saxesenii* were more abundant in gaps than in seedling-sapling stands. Conversely, *X. peregrinus* was more abundant in seedling-sapling stands than in gaps (table 1).

The standardized cumulative richness ($n = 35$ traps) was only 10% higher in gaps than in seedling-sapling stands (fig. 2c). At a local scale, mean saproxylic richness was higher in gaps than in man-made openings (fig. 2b).

4 Discussion

Due to the use of ethanol-baited traps, the conclusions are valid mostly for ambrosia beetles. The global sampling scolytids in broadleaved forest habitats would require either passive window traps or traps baited with host material.

4.1 Geographic variation

We did not observe a strong geographic differentiation in scolytid fauna throughout the study area. Despite this result, we systematically took the spatial pattern of sampling design into account in the analysis procedures. Conversely, Duelli et al. (2002) showed that the influence of distance between the three study areas on similarity between samples was 24 times greater than the influence of habitat type (uncleared or cleared gap, forest control) for all the insects studied. In their results, the Sörensen index decreased significantly with increasing distance between two traps, within the same treatment and location.

4.2 Gap effect

Contrary to expectations, in our data the abundance of ambrosia and bark beetles was not significantly higher in gaps than in undisturbed stands, even though the release rate of ethanol baits was probably higher in open sun-exposed trap positions than in closed forest. As Wermelinger et al. (2002) had already shown in Swiss spruce gaps, bark beetles did not show a significant global response but rather contrasting response reactions at the species level. The relatively monophagous species *P. cylindrus* benefited from oak windthrow (even if this increase was not as important as in England after the storm in 1987; Winter, 1993), *X. cryptographus* from aspen dead wood and *X. saxesenii* from diverse deciduous dead wood. Even if their host tree was quite abundant in gaps, the increase in the monophagous species *Ernoporus tiliae* (lime, +14%), *E. caucasicus* (lime, +12%), *Trypophloeus asperatus* (aspen, +2500%) and *X. monographus* (oak, +530%) was not significant. The species composition of the trees surrounding the traps largely determined the local structure of the ambrosia and bark beetle communities. The abundance of two gap species, *P. cylindrus* and *X. cryptographus*, correlated with local host tree density (volumes in a 2 m-circle around the traps), respectively oak and aspen.

Canopy closure is considered to be a key factor in dead wood micro-habitats (Bouget and Duelli, 2004). Sun-exposed dead wood in gaps may be the most attractive (host compounds more volatilized) or may provide a more suitable microclimate for many pioneer bark beetles (*Ips typographus* in Schroeder et al., 1999; *Taphrorychus bicolor* in Harz and Topp, 1999; *Pityogenes chalcographus* in Göthlin et al., 2000). Nevertheless, not all bark beetle species respond positively to openings. *Ernoporicus fagi*, which lives on dead branches in living hornbeam trees, was negatively affected in gaps. Similarly, Peltonen et al. (1997) and Wermelinger et al. (2002) showed that *Cryphalus saltuarius* and *Xylechinus pilosus* prefer dense, shady stands to openings, as well as *Hylastes cunicularius* and *Hylurgops glabratus* in boreal forests (Sippola et al., 2002). In our study, *X. germanus*, known to be more common in shady logs (Zach et al., 2001), suffered from a 30% decrease in gaps compared with closed-canopy controls though the figure was not significant (table 2).

Overall, we did not observe any increase in species richness for ambrosia and bark beetles in gaps. Few species responses and only a slight difference in assemblage composition were detected. The slight faunistic difference between controls and gaps may be due to the configuration of our sampling design. The closed-canopy control sites, paired with gaps, may have been influenced by close, scattered blowdowns. Ambrosia beetles, and peculiarly *Xyleborus* species, are known to be strongly attracted to ethanol (Markalas and Kalapanida, 1997) and to have high flight dispersal abilities. As a consequence, baited traps located in controls may have trapped many individuals dispersing between gaps. If studying windstorm effects were not so dependent on a stochastic event, a BACI study (before-after sampling) would be helpful to compare gaps and undisturbed plots!

Gaps were more clearly distinct from seedling-sapling stands (Bray-Curtis dissimilarity = 33%) than from closed-canopy controls (Bray-Curtis dissimilarity = 24%). The differences in volume and diversity of dead wood between gaps and fellings (where dead wood is only made up of stumps, harvesting residues and dead branches on seed trees; personal observation) seemed to have a significant impact on scolytid assemblages. Harvesting residues (Sippola et al., 2002) and high stumps (Schroeder et al., 1999) may enable some bark beetle species to develop in cut areas, mostly in the short term. In our sampling design, seedling-sapling stands were older than windthrow gaps. Only one species, *X. peregrinus*, was favoured in fellings compared with gaps and closed-canopy controls. More scolytid individuals and species were caught in gaps than in seedling-sapling stands, probably thanks to a greater supply of fresh sun-exposed dead wood in gaps. Moreover, since the disturbance was more recent in gaps, and since early dynamics are dominated by active colonization, mobile individuals were more easily caught by flight interception traps in gaps.

The dominance of samples by three polyphagous *Xyleborus* species was perhaps strengthened by their sensitivity to ethanol-baited traps. Bussler and Muller (2004) also found such a dominant configuration in German oakwoods, where *X. dispar* and *X. germanus* represented 80% of trapped individuals.

4.3 Pest risks

Temperate, deciduous managed forests are rarely threatened, by insect pests after windthrow (Winter, 1993), and standing trees adjacent to gaps are under little risk of attack. Our results confirmed this trend, since ambrosia and bark beetle abundance remained at low levels. Similarly, from the National Monitoring Network of the DSF (Forest Health Department) (Nageleisen, 2002), only one third of uprooted or broken oak trees were colonized over more than half of their surface by pioneer ambrosia beetles (*Xyloterus*, *Xyleborus and Platypus*) in 2001. Neither the DSF data nor ours described any drastic increase in *Platypus* and *Xyloterus*. Flot et al. (2000) did mention some slight damage on oak blowdowns due to *X. signatus* in Eastern France in 2000. This species did not exhibit any difference in abundance between gaps and controls in our samples (table 2). Similarly, in spite of a strong increase in percentage, *P. cylindrus* exhibited absolute abundance levels that were too low to cause outbreaks.

Key factors promoting a bark beetle outbreak include not only the abundance of suitable breeding material, but also a high initial beetle population in damaged areas, an occurrence of storms in winter or autumn, and warm and dry weather during the 2 years following the storm (Forster, 1993; Abgrall, 2001). These climatic conditions not only favour beetle population dynamics (larval development, flight intensity; Wermelinger et al., 1999), but they also further weaken trees through physiological stress (Bakke, 1992). The role of kairomones (volatiles such as alcohols, terpenes, aldehydes emitted from wood) and aggregation pheromones released, by beetles has been discussed by Schlyter and Birgersson (1999). Fermenting tree sap is also a source of attraction. Autumn or winter windstorms usually have more severe effects in central and Western Europe. The low desiccation rate during these seasons only slightly decreases the attraction of the trunks, which may be colonized by bark beetles leaving their over-wintering sites during spring flights (Abgrall, 2001). Downed logs may remain attractive to bark beetles from 1 to 3 years after falling, depending on the survival level, tree species, weather, altitude and latitude (e.g. Wermelinger, 2002 for spruce).

In our study, all the conditions were not combined to promote an outbreak. On the contrary, the winter storm was followed by rainy weather in 2000 and 2001. Moreover, many uprooted trees still had life-supporting root contact and were possibly less desiccated by the sun. According to the DSF, 75% of the uprooted deciduous trees were still alive in the summer 2001 (Nageleisen, 2002).

At the species level, our data confirmed the current expansion of *X. peregrinus* and *X. germanus* in Western Europe (Henin and Versteirt, 2004). These two polyphagous species were caught in Eastern France for the first time in 1960 and 1984, respectively (Schott, 1994; Schott and Callot, 1994). Both were quite abundant in our samples, *X. germanus* dominating the communities with about 45% of the individuals. Similarly, *X. germanus* is now the predominant scolytid in several Belgian beech forests (Gregoire et al., 2001; Henin and Versteirt, 2004), and in oak forests in Western Germany (Haase et al., 1998). The *X. germanus* is relatively indifferent to resource parameters [log size (Zach et al., 2001), and tree species (Henin and Versteirt, 2004)]. Moreover, interspecific competition seems to have little influence on *X. germanus* populations in beech, oak and spruce (Henin and Versteirt, 2004). It is therefore a very competitive species with regard to native scolytids.

Accidentally introduced into Europe from East Asia about 50 years ago (Heidenreich, 1964), *X. germanus* is a secondary pest, only attacking physiologically weakened trees (Maksymov, 1987). Even if it does not currently appear to be a major threat in Western Europe, the economic impact of this invasive species is likely to increase in the region (Henin and Versteirt, 2004), as it was recently observed on vineyards (Boll et al., 2004; Flot et al., 2000) had already reported attacks on recently planted broadleaved saplings (mountain maple in Switzerland and oak in Eastern France) by *X. germanus* (as well as *X. dispar*). Apart from economic considerations, the invasion of *X. germanus* in Western-European forests could become a problem from a conservation point of view, due to its deleterious effects on indigenous biocenoses.

4.4 Gap size effect

Since gap area is related to many environmental parameters (sun exposure, dead wood volume, diversity in dead wood types…), a gap size effect may reflect changes in habitat quantity, habitat quality and habitat heterogeneity. We did not find any previous publication to serve as a comparative reference in our study.

In our data, gap area slightly contributed to short-term changes in species composition and species richness after the windstorm. The richness and abundance of ambrosia and bark beetles were not different in gaps and in closed-canopy controls. The resource concentration hypothesis was subsequently refuted: we did not measure any rise in the number of individuals or species with an increase in gap area.

The highest cumulative richness was detected in mid-size gaps. This pattern seemed to corroborate the Intermediate Disturbance Hypothesis (IDH) on spatial scale (with an analogy between opening size and forest disturbance intensity; Petraitis et al., 1989). What is more, only mid-size gaps differed from closed-canopy controls in terms of scolytid species composition. Mid-size gaps were distinct from large but not from small gaps. Since mid-size gaps did not contain more individuals than the other classes, a sampling bias due to abundance was refuted. However, in our sampling design, traps located in mid-size gaps were surrounded by, a higher local oak density (18%) than in the small and large gaps (13 and 3%). In composition and cumulative richness analyses, local oak density was not controlled for. We therefore cannot infer that these results complied with the IDH.

Nevertheless, mean local richness also peaked in mid-size gaps, after controlling for the local oak density. Moreover, among responses at the species level, we identified generalist gap species (*X. saxesenii*, *X. cryptographus*), but also species significantly more abundant in mid-size gaps (*P. cylindrus*, *X. signatus*). The faunistic peculiarity of mid-size gaps did not therefore seem to be related to oak density only.

4.5 Landscape effects

The spatial arrangement of landscape elements is known to influence the distribution and abundance of bark beetles across complex mosaics of ecosystems (Coulson et al., 1999). In our data, few significant relationships between individual species and the surrounding landscape were observed. Only the scolytids on the whole and *X. dispar* were slightly favoured by an increasing density in fellings at the 78 ha scale. In a global study on saproxylic beetles, Okland et al. (1996) also found that several bark beetles responded, negatively however, to the percentage area of clearcuts at a large scale (400 ha): *Crypturgus subrugosus*, *C. hispidulus*, *H. cunicularius*. In agreement with our results, Okland et al. (1996) did not find any correlation between scolytid abundance and the surrounding closed-forest percentage area.

Large spatial scales may influence bark beetles, which are known to move large distances during their life cycle. Well adapted to seeking breeding substrata which are both ephemeral and unpredictable in space, colonizers of fresh dead wood such as bark beetles are generally good dispersers and may travel over several or sometimes dozens of kilometres (Nilssen, 1984; Forsse and Solbreck, 1985; Jactel and Gaillard, 1991; Duelli et al., 1997; Byers, 2000). Moreover, wind-aided dispersal is likely to be important for a part of the population (Forsse and Solbreck, 1985).

The weakness of landscape effects may be partly due to the choice of landscape variables. Indeed, we showed that fellings do not serve as habitat targets for many gap scolytids, so they probably did not act as significant sources of gap ambrosia and bark beetles.

4.6 Implications for forest management

Our results confirmed that temperate, deciduous, managed stands did not come under threat by ambrosia beetle pests after the 1999 windstorm. Ambrosia and bark beetle assemblage was not more abundant, nor was it more diverse in gaps than in undisturbed stands. Nonetheless, the study of saproxylic assemblages (including predator species) showed that uncleared gaps enhanced the gamma diversity in the forest, because of their richness and faunistic dissimilarity with other open stands and closed-canopy controls (Bouget, unpublished data). Therefore, the diversity and abundance of zoophagous saproxylic species would benefit from the maintenance of some unsalvaged gaps.

Uncleared gaps generally contribute to the continuous and diverse supply of downed logs, which ensures the survival of high populations of natural enemies and competitors. From Martikainen et al. (1999) and Similä et al. (2002), we know that competitors, predators and parasites are quite efficient at controlling and maintaining primary scolytid species at non-epidemic levels in naturally disturbed forests. Wermelinger (2002) stressed that timber retention may ensure a source of natural enemies and competitors. Fallen timber should therefore not be removed from gaps, but left lying to enhance populations of antagonists to develop. Schlyter and Lundgren (1993) reported that pest infestation risk was not higher near forest reserves than in adjacent managed stands.

In deciduous stands, windthrow gaps were not susceptible to ambrosia beetle outbreaks. When the retention of dead wood for saproxylic conservation purposes is proposed, the risk of ambrosia beetle outbreaks cannot be raised as a counter argument.

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