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Short-term effect of windthrow disturbance on ground beetle communities: gap and gap size effects

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Abstract

Windstorm is the main natural disturbance in temperate forests. Canopy perforation induces important ecological changes in terms of microclimate and ground microhabitats and creates patchy open areas in the forest mosaic. In managed oak-hornbeam forests storm-damaged in France in 1999, we sampled carabid beetles by pitfall and window-flight interception traps in 2001. I compared ground beetle assemblages in unlogged natural openings vs. closed forests. I studied short-term gap and gap size effects on carabid abundance, richness and assemblage composition (species and ecological groups based on habitat preference). Shortly after the disturbance, I observed a diversification of ground beetle assemblages in gaps at both air and ground levels in spite of a lower abundance in pitfall traps. The cumulative species richness for an equal sampling effort was greater in gaps (even in small ones) than in the closed forest. This richness increased with increasing gap area. Some forest species significantly declined in gaps, but none disappeared. Other forest species remained unaffected and several corticolous and arboricolous species were even favoured. Gap area did not significantly affect the forest group. Several open-land species appeared or increased in abundance in gaps. Their colonization was favoured by gap area. The assemblage composition, studied by NMDS and ANOSIM test, clearly differed between gaps (even small) and forest controls. Gaps larger than 0.3 ha were grouped according to the composition and colonization of open-land species. In uncleared gaps, the short-term community dynamics was dominated by colonization rather than local extinction processes.

Key words: Natural opening, colonisation, forest

Abbreviations: G = Gap, F = Forest control, SG = Small Gap, MG =Mid-size Gap, LG = Large Gaps

Introduction

Nature-based silviculture is a promising approach to meet the criteria for sustainable forestry. This brings natural disturbances into focus as a basic reference for forest management (Bengtsson *et al.*, 2000). In most temperate deciduous forests, wind is the main natural disturbance (Emborg *et al.*, 2000). By opening the canopy, windthrow causes a typical forest fragmentation called perforation (Forman, 1995). It results in a shifting mosaic of open early-successional patches in a forest matrix. The patch-gap analogy reverses the usual forest fragmentation perspective: opening size can be focused instead of woodlot size (Rudnicky & Hunter, 1993). Habitat patches can be considered in the light of island biogeography and landscape ecology concepts. Colonization and local extinction in habitat islands depend on patch characteristics (area, shape) and landscape. In community ecology, the relationships between disturbance, habitat heterogeneity and community dynamics is modelled by the synthetic Patch Dynamic Concept (Townsend, 1989).

Carabids have been studied in different forest openings: burnt (Holliday, 1991) or cut (Koivula, 2001) areas, but rarely in windthrow gaps (Duelli *et al.*, 2002; Kenter *et al.*, 1998). In western Europe, Lothar, the huge storm in 1999, gave us the possibility of a natural experiment. In the resulting gaps, carabid habitats were drastically disturbed in terms of ground cover, micro-sites, micro-climate and potential prey (Bouget & Duelli, 2004). In the present paper first I will assess whether and how carabid assemblages responded to the windstorm disturbance in the short term just one year and a half after the storm event. In other words, do gaps equate to habitat islands? Then, I will go on to appraise whether this response depends on gap area or not. Do changes in carabid abundance, richness and assemblage composition (species and ecological groups) depend on gap size? Patch area effects are related to the species-area relationship (Forman, 1995). A larger patch is more likely to have a greater habitat heterogeneity (habitat diversity hypothesis), a higher density of specific micro-habitats (density hypothesis) and a sharper micro-climatic contrast with the neighbouring matrix (edge effect).

The influence of gap isolation and the comparison between natural gaps and man-made openings are discussed in two other papers.

Sites, material and methods

Research area

Three lowland forests were under study: the state forests of Armainvilliers (1525 ha) and Crecy (a 1250-ha national block within a 5000-ha forest), and the Ferrieres regional forest (2890 ha) in the 'Brie' region. They are located about 50 km south-east of Paris and 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. All three are oak-hornbeam forests (*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.

Sampling design and study sites

A 50-plot sampling design was used to test the two effects quoted above. Twenty-four storm-created, unlogged gaps in 14 plots were selected within the study area. Gap perimeters and areas were mapped using the differential mode of a Global Positioning System (GPS). Gap shapes were irregular and a variable number of standing trees remained inside all the gaps. Study gaps ranged from 0.12 to 3.3 ha and were divided into three size classes: small (<0.3 ha, n_{SG}=8), medium (0.3-1 ha, n_{MG}=7) and large (> 1 ha, n_{LG}=9). To control for the environmental variation between sites (Underwood 1997), each gap was paired with an adjacent (25–50 m apart), closed-canopy control site (*n*=14).

Study group

Carabid beetles are widely recognised as potentially valuable indicators of environmental variation because they are a highly diverse taxon, can be easily sampled, and are sensitive to changes in the physical and biological environment (Lövei & Sunderland, 1996). All individuals were determined to the species level and assorted to ecological groups according to habitat preference (many references were used, especially Coulon *et al.* (2000), Desender (1986) and Turin (2000)). The nomenclature follows Freude (1976).

Sampling protocol

Ground beetles were sampled using window (for wing-dispersing species) and pitfall (for ground-dwelling species) traps. The parameter measured was the species activity-abundance but for the sake of brevity, hereafter I refer to activity-abundance as “abundance”. Pitfall traps were polyethylene beakers (85 mm in diameter x 110 mm in depth =0.55 L) half-filled with a 1:1 monopropylenglycol:water solution saturated with salt to kill and preserve the trapped arthropods. Acrylic glass covers (100 mm square) were positioned approximately 10 cm above each trap to prevent flooding by rain. Each window trap consisted of a transparent plastic pane (1 m^2) and a container below the pane. Salt water with ethanol was used for killing and preserving the beetles. A detergent was added in all the traps to reduce surface tension.

To maintain a minimum distance between traps, the number of traps per gap depended on gap size. One window and two pitfall traps were set up in forest controls and small gaps, one window and three pitfall traps in mid-size gaps, two window and four pitfall traps in large gaps. Traps were left in the field for one week prior to initial trapping, to reduce digging-in effects (Digweed *et al.,* 1995). The study focused on one sampling season during the second vegetation growth after the storm (2001). To cover the main period of carabid activity, traps were emptied and preserving fluid replenished monthly from mid April to mid October (for pitfall traps) or to late July (for window traps).

Data analysis

Pitfall and window trap datasets were kept separated. We compared the cumulative species richness between habitat classes using sample-based (and not individual-based) rarefaction calculations processed with EstimateS (Colwell & Coddington, 1994). Sample size was standardised at the least number of trap samples between habitat types. In each class, the expected number of species and standard deviation were then interpolated in the random sub-sample drawn for a larger sample (Magurran, 1988). Sampling order was randomized 100 times with replacement to eliminate sampling error and heterogeneity among the units sampled.

The other analyses were carried out using the computer package S-Plus 6.1. Linear mixed-model ANOVA (nested spatial variables as random effects: block, plot and site; fixed factors: habitat type, gap parameters, period) was used to test for differences in mean abundance and mean richness per trap of all carabids or ecological groups between forest and gap plots (Pinheiro & Bates, 2000). This model takes the configuration of the sampling design into account (e.g. the spatial pattern of traps over the research area). It is applied on ln (x+1) transformed data. Differences among means were investigated by multiple comparison tests (Sidak or Tukey post hoc tests).

As individual species abundances per trap did not comply with parametric assumptions, the non parametric pairwise Wilcoxon signed-ranks test (Legendre & Legendre, 1998) was used to compare the abundances between gaps and paired forest controls and to assess the species response to opening.

Three techniques were used to investigate assemblage composition (the first two methods include a log transformation of the data). Non metric multi-dimensional scaling (NMDS) based on the Bray-Curtis dissimilarity was used for pattern recognition in species composition (Clarke, 1993), pairwise ANOSIM procedures for testing for differences in assemblage composition amongst predefined groups (Clarke, 1993), and Indicator species analysis (IndVal) for detecting species indicative of particular habitats (Dufrêne & Legendre, 1997). The IndVal (Indicator Value) procedure is a useful method to find indicator species characterizing groups of samples. It combines a species' abundance with its frequency of occurrence in the various groups of samples. Samples were grouped using a hierarchical habitat typology derived from a hierarchical ascendant classification (UPGMA) of the Bray-Curtis similarity matrix.

Table 1. Gap and gap size effects. Mixed-model ANOVA of mean data per trap. Numbers are mean value in gaps, forest controls, small, mid-size and large gaps. N=abundance, S=richness, rel. N=relative abundance; letters indicate significant differences between means after a post-hoc Tukey or Sidak test. All F values are significant, *p*<0.01.

	All Species		Forest Species			Open-Land Species		
	N	S	N	Rel.N.	S	N	Rel.N.	S
Pitfall trap catches								
Forest	20.23	3.69	13.6	72.4	2.7	3.95	14	0.49
Gap	9.7	2.86	6.1	76.5	1.98	3.15	17.7	0.61
$F_{2,23}$	*234*	*456*	*174*	*1471*	*237*	*8*	*11.5*	*11*
Forest			13.64 *a*	72.4 *a*	2.70 *a*	3.95 *a*	14 *a*	0.49 *a*
Small gap			5.41 *b*	80.9 *a*	1.92 *a.b*	1.23 *a*	11.1 *a*	0.36 *a*
Medium gap			5.46 *b*	75.7 *a*	1.81 *b*	3.14 *a*	18.9 *a*	0.66 *a*
Large gap			7.11 *b*	74.5 *a*	2.16 *a.b*	4.39 *a*	20.7 *a*	0.74 *a*
$F_{4,21}$			*68*	*558*	*103*	*5*	*7.3*	*9*
Window trap catches								
Forest	2.31	0.91	0.28	18	0.17	0.28	27.5	0.26
Gap	5.28	2.8	0.46	15.4	0.34	1.61	35.2	1.18
$F_{2,23}$	*25*	*42*	*22*	*12*	*30*	*41*	*89*	*42*
Forest			0.28 *a*	18 *a*	0.17 *a*	0.28 *a*	27.5 *a*	0.26 *a*
Small gap			0.42 *a*	25.1 *a*	0.42 *a*	1.03 *a.b*	33.5 *a*	0.75 *a.b*
Medium gap			0.43 *a*	12.6 *a*	0.29 *a*	1.78 *b*	44 *a*	1.31 *b*
Large gap			0.50 *a*	12.5 *a*	0.33 *a*	1.81 *b*	31.1 *a*	1.33 *b*
$F_{4,21}$			*11*	*7.5*	*15*	*25*	*4.5*	*24*

Results

Sample overview

Over the seven monthly trapping sessions, the valid pitfall traps yielded 8427 individuals of 48 species. Seventeen species (35%) were represented by fewer than 5 individuals and 18 (37%) were open-land species. *Pterostichus madidus, Carabus auratus, Abax parallelepipedus, Pterostichus oblongopunctatus, Nebria brevicollis* were the dominant species. Over the four monthly sessions, the valid window traps yielded 875 individuals in 60 species. Thirty-four of these (57%) were represented by fewer than 5 individuals and 31 (52%) were open-land species. *Bembidion lunulatum, Acupalpus dubius, Bembidion dentellum, Amara similata* were the most abundant species. By adding the two data sets, the richness reached 80 species. Twenty-eight (35%) were trapped by both pitfall and window traps, 20 (25%) were only trapped by pitfall and 32 (40%) only by window traps.

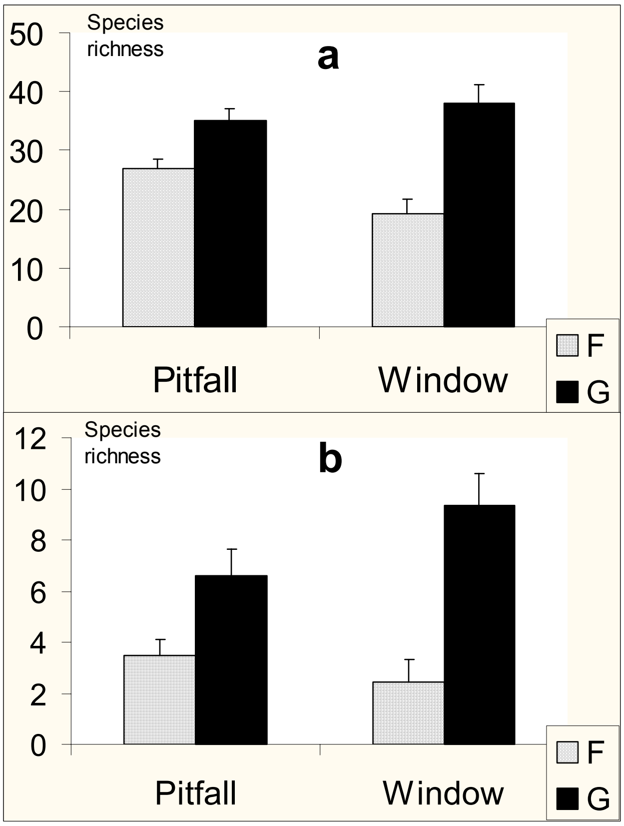

Figure 1. Sample-based rarefaction interpolation of total and open-land species richness in gaps (G) and forest controls (F) (100 sample randomisations with replacement; error bars are the corresponding standard deviations). Pitfall (n_{traps}=135), window (n_{traps}=36). (a): total species richness. (b): open-land species richness.

The two traps gave complementary insights on moving ground beetles in the air and at ground level. Window trap data seem to be very useful for studies on colonization.

Gap effect on the whole assemblage

According to the mixed-model ANOVA, significantly different numbers of individuals and species per trap were caught between closed forest and gaps, but the relationship depended on trap type. Pitfall traps caught more individuals and species of ground-dwelling carabids in forest controls whereas window traps caught more individuals and species of wing-dispersing individuals in gaps (Table 1). With standardized sampling effort, the sample-based rarefaction calculations showed that the cumulative species richness was higher in gaps than in closed forest, at both ground and air levels (Fig. 1a).

ANOSIM tests proved that gaps differed significantly in assemblage composition from closed forest at both ground and air levels (pitfall: ANOSIM statistics R=0.35, $p<0.0001$; window: R=0.42, $p<0.0001$).

Gap effect on species and ecological groups

Life history phenomena underlying the whole-assemblage response were briefly explored through the study of the colonisation of open-land species and of the persistence of forest species. At ground level, abundance and richness of forest species decreased from forest to gap, whereas the inverse trend was noticed at air level (Table 1, Table 2). Most forest species significantly declined in abundance immediately after the opening (paired Wilcoxon test, Table 2).These included *L. rufomarginatus, A. parallelepipedus, P. oblongopunctatus, P. assimilis,* and *P. madidus*. I did not observe any short-term disappearance of forest species. Some forest species, such as: *M. piceus*, *P. cristatus, A. parallelus,* were not significantly affected. Others were even favoured by the disturbance, including *D. quadrimaculatus*, *P. livens, and T. nana*.

Randomised accumulation curves showed that the ecological group of open-land species increased in abundance and richness in gaps (Fig. 1b). The abundance and richness of open-land species increased in gaps (Table 1, Table 2). Many open-land species appeared (*C. campestris, A. sexpunctatum, B. quadrimaculatum*) and others increased in abundance after the canopy opening, sometimes (*P. cupreus, P. versicolor)* but not always (*A. similata, L. pilicornis*) significantly (Wilcoxon test; Table 2). Eurytopic species with affinity to open areas also responded positively to clearing (*N. palustris, B. lunulatum). N. biguttatus,* an eurytopic species with affinity to forest environment, was negatively affected (Table 2). The IndVal method identified roughly the same characteristic species as those sorted as gap sensitive by paired Wilcoxon tests**.** At air level (Fig. 2b), IndVal detected no characteristic forest species but several gap species, which are either open-land (*C. campestris, B. lampros, A. similata)*, eurytopic (*B. lunulatum)* or even forest species living under bark (*T. nana*, *P. livens*). At ground level (Fig. 2a), indicator species were rather different. Forest indicators were more numerous: *L. rufomarginatus, P. oblongopunctatus, P. assimilis, P. madidus, N. brevicollis*. Gap species were mainly open-land species: *A. sexpunctatum, P. cupreus*, *C. campestris, P. versicolor* (Fig. 2a).

Gap area effect on the whole assemblage

Gap area affects the cumulative species richness. At a standardised sampling effort, at air and ground levels, more species were caught in large gaps (Fig. 3a). All gaps, even small ones, showed a higher species richness than the closed forest. The two ordination biplots identify patterns in species composition (Fig. 4). The overall ANOSIM test was significant for pitfall but not for window data. From pair-wise ANOSIM tests, four differences were significant in the pitfall data set ($R_{SG-LG}=0.23$*, $R_{F-LG}=0.33$*, $R_{F-MG}=0.49$*, $R_{F-SG}=0.42$**). Large and mid-sized gaps were grouped into a single cluster, but mid-size gaps were not significantly different from small gaps. All gaps, even small ones, differed from closed forest. Only one difference was significant in the window data set ($R_{SG-LG}=0.32$*).

Table 2. Direction and extent of change in mean species abundance per trap from closed forest to gap (Wilcoxon signed-rank tests between abundance in each gap and in its paired forest control; ** $p<0.01$, * $0.01<p<0.05$, NS $p>0.05$).

Species/characteristic	Pitfall traps		Window traps	
	From forest to gap (%)	*p*	From forest to gap (%)	*p*
Forest species				
Absolute abundance	- 60	**	+ 64	*
Relative abundance	+ 6	**NS**	- 16	**NS**
Species richness	- 27	**	+ 115	*
Platynus assimilis Paykull	- 79	*	- 81	**NS**
Leistus rufomarginatus Dufts.	- 95	*		
Nebria brevicollis F.	- 93	**		
Notiophilus rufipes Curtis	- 87	**		
Pterostichus oblongopunctatus F.	- 83	**		
Abax parallelepipedus Piller & Mitter.	- 54	**		
Carabus nemoralis Müller	- 50	**		
Pterostichus madidus F.	- 48	**		
Pterostichus cristatus Dufour	- 27	**NS**		
Molops piceus Panzer	- 22	**NS**		
Abax parallelus Dufts.	- 22	**NS**		
Platynus livens Gyll.	+ 34	**NS**	+ 127	*
Dromius quadrimaculatus L.			+ 342	*
Tachyta nana Gyll.			+	**
Open land species				
Absolute abundance	+ 804	**	+ 886	**
Relative abundance	+ 109	**	+ 162	**
Species richness	+ 212	**	+ 757	**
Loricera pilicornis F.	+ 46	**NS**	+	**NS**
Poecilus cupreus L.	+ 1686	**	+ 600	**
Poecilus versicolor Sturm	+ 883	**	+	*
Cicindela campestris L.	+	*	+	**
Agonum sexpunctatum L.	+	*	+	*
Amara similata Gyll.	+ 167	**NS**	+	**
Bembidion quadrimaculatum L.	+	**NS**	+	**
Acupalpus flavicollis Sturm			+	**
Stenolophus teutonus Schrank			+ 526	*
Bembidion lampros Herbst			+ 931	**
Carabus auratus L.	- 39	**		
Eurytopic species				
Notiophilus palustris Dufts.	+ 650	**		
Pterostichus strenuus Panzer	+ 267	*		
Harpalus latus L.	+ 383	**NS**		
Acupalpus dubius Schilsky			+ 20	**
Bembidion lunulatum Fourcroy			+ 161	*
Pterostichus vernalis Panzer			+	*
Notiophilus biguttatus F.	- 54	*		

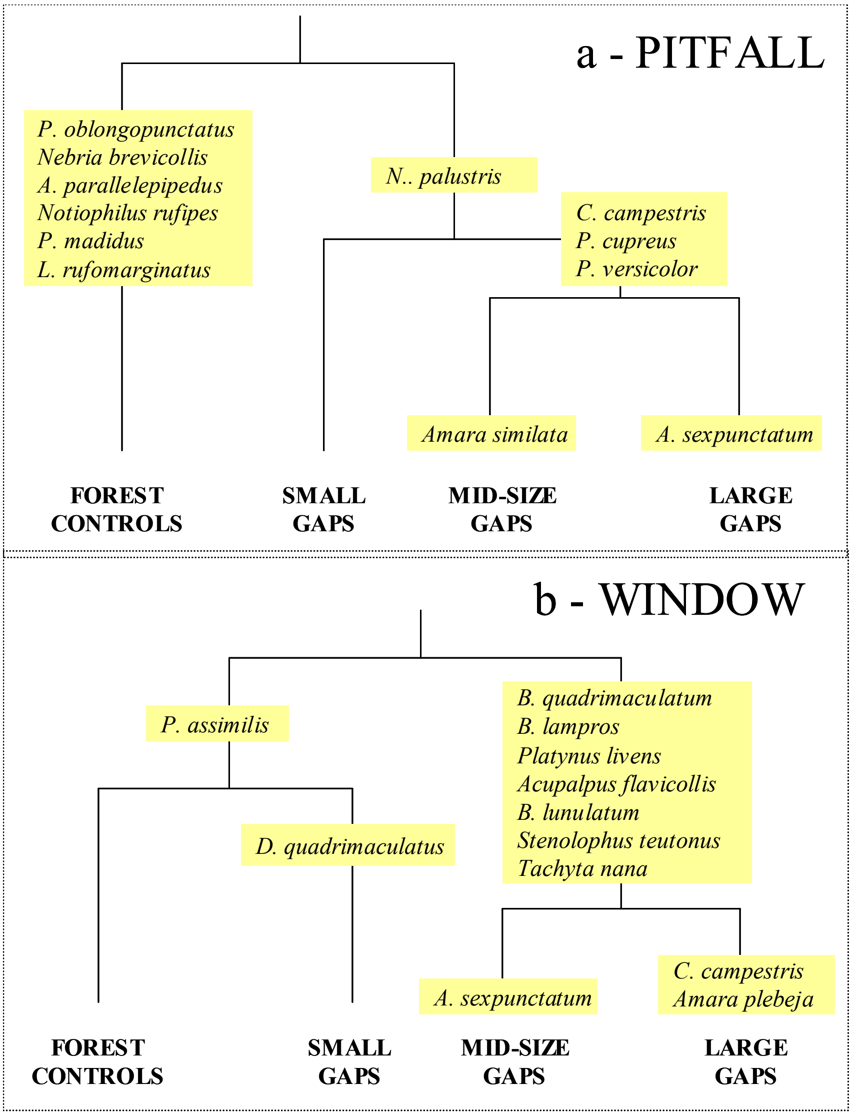

Figure 2. Characteristic species detected by the IndVal method (Dufrêne & Legendre 1997); (a): pitfall trap dataset; (b): window trap dataset. The process was based upon a hierarchical habitat typology from an ascendant classification (UPGMA) on Bray-Curtis dissimilarities. Only species with significant ($p<0.05$) and >25% Indicator Value are mentioned. When the Indicator Value of a species is significant at different levels, the species appear only at the level of its maximum Indicator Value.

Gap area effect on ecological groups

We did not observe any clear relationship between gap size class and abundance or richness of the forest species group (Table 1). No species abundance decreased in larger gaps. In contrast, data per trap indicated that richness, absolute and relative abundance of open-land species increased with gap area (even if pairwise differences in mean are not always significant; Table 1). At the ground level, more open-land species and individuals were caught in mid-size and large gaps than in small gaps and closed forest (these last two habitats being equal, Fig. 3b). At the air level, more open-land species and individuals were found in large than in small and mid-size gaps (the last two habitats being equal, Fig. 3b). Fewer open-land species and individuals were caught in forest than in gaps (whatever their area).

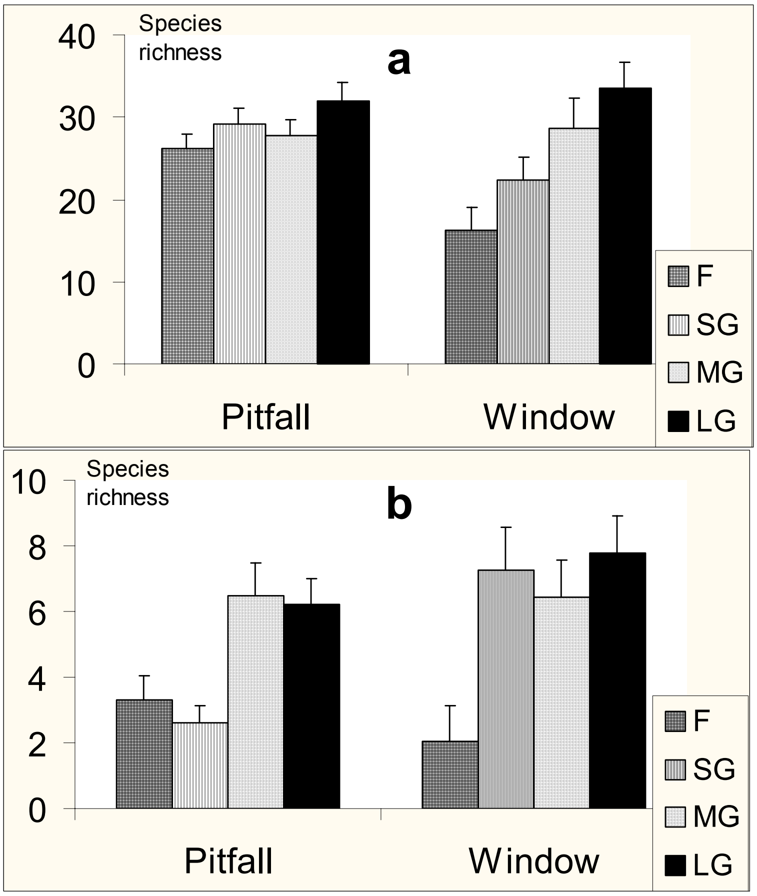

Figure 3. Sample-based rarefaction interpolation of total and open-land species richness in different gap size classes (from SG to LG) and forest controls (F) (100 sample randomisations with replacement; error bars are the corresponding standard deviations). Pitfall (n_{traps}=135), window (n_{traps}=36). (a): total species richness. (b): open-land species richness.

Discussion

Ecological determinants of windthrow gap effects are diverse. New micro-habitats (such as root plates, pits and mounds, fallen crowns) are created and some of them act as sheltering or overwintering sites. The density of grassy patches and coarse woody debris increase. The canopy opening strengthens micro-climatic contrasts and favours the development of the herb layer. Populations of xylophages and phytophages (i.e. potential prey) grow, but predation pressure by vertebrates can also grow.

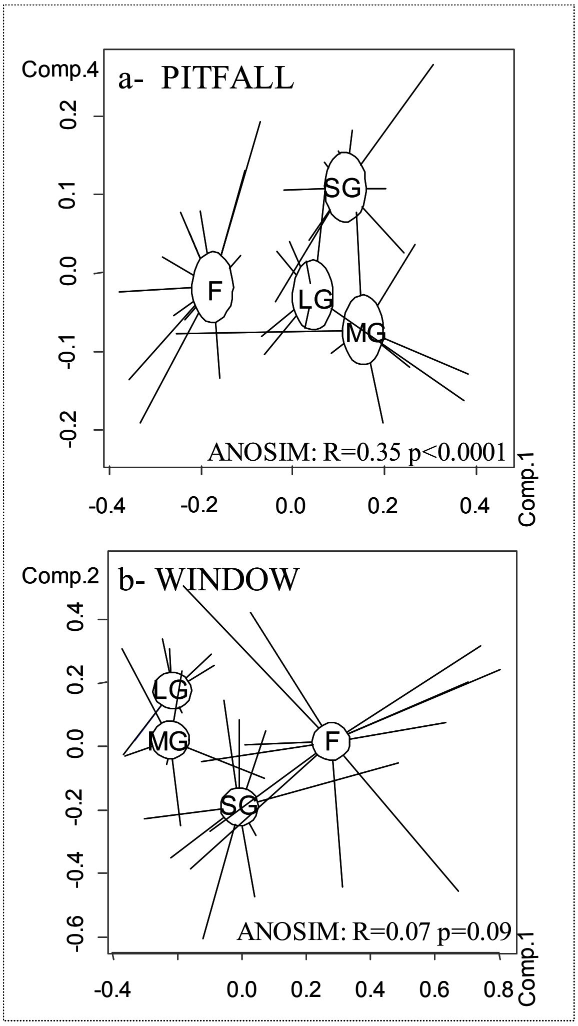

Figure 4. NMDS ordination plot of the Bray-Curtis dissimilarity matrix. The two axes with highest correlation to habitat type are represented. Stress values below 0.2 indicate a reliable representation (Clarke 1993): (a): 4dstress=0.091; (b): 4dstress= 0.138. From pair-wise ANOSIM tests (with Bonferroni correction of the significance threshold (Legendre & Legendre 1998): ** p<0.05/6=0.008; * p<0.01/6=0.002), four differences were significant in the pitfall data set (R_{SG-LG}=0.23*, R_{F-LG} =0.33*, R_{F-MG}=0.49*, R_{F-SG}=0.42) and only one in the window data set (R_{SG-LG}=0.32*). The differences in mean may be summarised in the following way ; pitfall: F(a,b), SG(b), MG(b,c), LG(c) ; window: F(a,b), SG(a), MG(a,b), LG(b).**

Gap effect: ground beetle response to opening

Shortly after the disturbance, I observed a gap effect, with the diversification of ground beetles assemblages, in spite of a lower abundance in pitfall data. A lower average catch was also observed on other natural clearings at ground level (Grechanichenko & Guseva, 2000; Saint-Germain & Mauffette, 2001; Martel *et al.*, 1991; Kenter *et al.,* 1998). In addition, species richness was higher in glades than in closed forest studied by Grechanichenko & Guseva (2000) and Duelli *et al.* (2002). In a spruce forest storm-damaged in 1990, richness was higher between 1992 and 1995 but higher in forest controls from 1996 onwards (Kenter *et al.*, 1998). However, species diversity was lower at deciduous sites disturbed by an ice storm (Saint-Germain & Mauffette, 2001) or by canopy dieback (Martel *et al.,* 1991). In clear-cuts, in addition to carabids, the phenomenon of higher abundance and richness appears to be the rule for spiders, ants and butterflies (see references in Heliola *et al.*, 2001).

The assemblage composition was altered from closed forest to gaps. Gaps are more dominated by colonisation than by local extinction processes (Walker & Chapin, 1987). Changes in forest species occur mainly at ground level, whereas changes in open-land species are more evident at air level (as colonisation occurs mainly by air dispersal).

The colonisation of gaps by open-land species

I have shown the importance of colonisation processes in gap community dynamics shortly after the opening disturbance. In spruce gaps, during the first three years after disturbance, richness and relative abundance of open-habitat species (*Bembidion lampros, Poecilus versicolor*, *Amara* sp.) grow at the expense of forest species (Kenter *et al*., 1998). After logging, gap conditions at the ground level are even more open: micro-climatic variations increase, the herb layer develops. This practice may strengthen the colonization of open-land species.

The persistence of forest species in gaps

The contrast between unlogged gap and forest was relatively low during the first years following the storm because the residual overstory and the living foliage of downed crowns formed a ground cover. This cover may enable the forest species to survive temporarily (Otte, 1989). Indeed, in the short-term, all the forest species persisted in gaps, although at a decreasing abundance. Some species remained unaffected. After regeneration felling in managed oakwoods, Richard *et al.* (2004) also distinguish unaffected or negatively affected (without disappearance) species. In clear-cuts, forest generalists show an abundance which increases with canopy openness (Koivula, 2001; Heliola *et al*., 2001), probably due to broader physiological tolerance and habitat requirements. In gaps, favoured species were arboricolous species foraging in fallen branches (*D. quadrimaculatus*), or subcorticolous species sheltering under the bark of fallen trees (*P. livens, T. nana*). The catches of forest specialists may represent remnant populations on their way to local extinction (Koivula, 2001). In Polish pine forests, Szyszko (1990) showed that the most radical changes in forest-species abundances occur three years after clear-cutting. However, in maple forests, *Synuchus impunctatus*, the dominant forest species, proved to be sensitive to the ice-storm disturbance (Saint-Germain & Mauffette, 2001). Nonetheless, Kenter *et al.* (1998) describe the revival of relative abundance of forest species four years after the storm in spruce gaps.

Gap area effect

The highest species richness was found in large gaps, in agreement with the species-area relationship predicted by patch-related concepts (Forman, 1995). Although the intensity of environmental changes is correlated with gap area, my results do not agree with the Intermediate Disturbance Hypothesis (the highest diversity in mid-size gaps). The size range covered by our study design was perhaps insufficient, and disturbance effects may not have been observed yet (delayed emigration of forest species).

Overall change in the carabid assemblages increased with gap area. Similarly, during the first years after clear-cutting, the carabid assemblages change much more in 2-ha clearcuts than in gap-felled stands (Koivula, 2001). Gap area did not affect the persistence of forest species. However, du Bus de Warnaffe (2002) showed that forest species survive in small openings (<0.5 ha) whereas they are threatened in clearings larger than 2 ha. Gap area favoured the colonisation of open-land species. Accordingly, many studies (e.g. Bauer (1989), De Vries *et al.* (1996), Magura *et al.* (2001)) reported that richness of carabid specialists of a fragmented habitat type respond positively to fragment size. Open patches in forest are perceived as habitat islands from 0.05 ha by open-land species (du Bus de Warnaffe, 2002).

Implications for forest management

Brawn *et al.* (2001) have pointed out that many bird species adapted to disturbance-mediated habitats have recently declined in North America, even more severely than old-growth species. Niemela *et al.* (1996) argue that a higher number of carabid specialists occur in early open habitats than in old-growth, and that the suitable period for these species is shorter than for closed-canopy species in the natural forestry cycle. From a conservation perspective, several gaps should be kept uncleared.

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