Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests

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Abstract
Storms are important disturbance factors in the development of forest ecosystems. They trigger definite changes in vegetation composition and hence also in the associated insect fauna. Three windthrow areas created by the storm Vivian in 1990 in alpine spruce forests were each subdivided into a cleared and an uncleared treatment. The abundance of the three most frequent beetle families (Scolytidae, Cerambycidae, and Buprestidae) was monitored with two different trap types during six summer periods within the first 10 years after the windthrow. The large supply of breeding substrate triggered a distinct increase in insect abundance and in the species richness of this guild (except for the number of buprestid species) over a period of approximately five years. The first group reaching peak numbers were the Scolytidae (in 1992), followed by the Buprestidae (1994) and then by the Cerambycidae (1996). *Ips typographus*, the most important bark beetle, peaked in the third season after the storm (1992). The maximum numbers of saproxylic species were trapped in June/early July. In uncleared windthrow areas beetle abundance as well as species numbers were generally higher than in cleared treatments. In the windthrow areas, cerambycid and buprestid species were 30–500 times more abundant than in an adjacent intact forest. Their species number exceeded that in the forest 2–4 times. To promote saproxylic species in general as well as endangered species of saproxylics, some parts of windthrow areas should be cleared and others left uncleared. The controversy about protecting the forest and promoting biodiversity is discussed.

Keywords: Buprestidae, Cerambycidae, Scolytidae, biodiversity, dead wood, succession, *Ips typographus,* Switzerland

1 Introduction

Extensive windthrow completely transforms a habitat and its microclimates from being a more or less closed forest to an open and sunlit environment. Structures and resources are destroyed and new ones are created. One of the most obvious changes is the sudden increase in the supply of dead wood. This substrate is a prerequisite for many species of beetles, bees, wasps, ants, flies, mosquitoes and other invertebrates (e.g. Speight 1989; Albrecht 1991; Glück and Spelda 1996; Irmler *et al.* 1996; Økland *et al.* 1996; Köhler 2000; Schiegg 2000). Dead wood may serve as a resource for feeding, breeding, or overwintering. Species depending on this substrate during some part of their life are called saproxylic (Speight 1989).

During much of the two last centuries dead wood was extensively exploited for industrial or private use. Therefore, many saproxylic species have become endangered or even extinct in certain regions (Speight 1989). Among the Coleoptera roughly a quarter of the central European species are saproxylic. Of these, in Germany almost 50% are considered endangered (Geiser 1998). For Switzerland, no comparable information exists. Uncleared windthrow areas, however, provide a habitat for saproxylic insects that have become scarce, and thus are important for nature conservation. On the other hand, windthrow areas in spruce forests are prone to potential pest outbreaks such as bark beetles (mainly *Ips typographus*).

Such an outbreak also occurred after the exceptionally violent gale disaster Vivian in 1990 (WERMELINGER *et al.* 1999). The storm Vivian triggered intensive research on the development of windthrow areas in Central Europe (LÄSSIG and SCHÖNENBERGER 1997; FISCHER 1998; FISCHER and MÖßMER 1999; SCHÖNENBERGER this issue). Apart from investigations on the development of vegetation, special emphasis was put on the dynamics of invertebrates, particularly insects (FUNKE *et al.* 1995; WERMELINGER *et al.* 1995; KENTER *et al.* 1996). Starting in 1991 the insect fauna was monitored in three windthrow areas in Swiss mountain spruce forests during the following decade. While some results on overall biodiversity are described by DUELLI *et al.* (this issue), we focus here on the dynamics of the three most abundant saproxylic beetle families, i.e. Scolytidae, Cerambycidae, Buprestidae, in cleared and uncleared windthrow areas.

2 Material and methods

2.1 Experimental setup

Three windthrow areas from the 1990 storm Vivian in subalpine spruce forests near Schwanden (canton GL), Pfäfers (SG), and Disentis (GR) were divided into two treatment plots each. Part of each area was left untreated with all wood left *in situ* (= uncleared treatment). In the other part of the area the timber was removed in 1990/91 and only the stumps remained on site (= cleared treatment). The size of the treatments ranged from 0.9 to 2.6 ha. At Schwanden, an adjacent forest stand was chosen as an additional control treatment. It was a dense stand consisting mostly of young, approx. 50-year-old spruce trees. For a more detailed description of the site characteristics see SCHÖNENBERGER (this issue).

Beetles were collected in two trap types. Window (flight intercept) traps consisted of a wooden frame with a vertical glass pane (80 x 50 cm) 1.3 m above ground (DUELLI *et al.* 1999). Three window traps were distributed across each treatment (Fig. 1), and their window orientation varied by 60° each, to avoid bias due to wind effects. The insects flying against the pane dropped into two plastic trays containing water with some traces of detergent and fungicide. The second trap type (5 per treatment) was made of yellow buckets attached to a pole 1 m above ground with an upper diameter of 20 cm containing water and detergent/fungicide. This yellow trap is especially suitable for catching those insects attracted to flowers (pollinators). Trap catches do not necessarily reflect a species' abundance but rather mirror its activity, longevity and degree of attraction to the colour yellow. The 21 window traps and 35 yellow traps were operated from May to September in 1991–1994, 1996, and in 2000. They were emptied weekly during the whole season. The samples were separated into different taxonomic groups and identified by specialists.

2.2 Data evaluation

For the present analysis the three most abundant coleopteran wood-inhabiting families, Scolytidae, Cerambycidae, and Buprestidae, were selected from the complete fauna data set (DUELLI *et al.* this issue). For each family the most efficient trap type was used for data analysis, i.e. yellow traps for Buprestidae and Cerambycidae, and window traps for Scolytidae. The start of the sampling period varied considerably from year to year reflecting the accessibility of the study sites during the spring thaw. Only catches during the weeks 20–37 (mid May to mid September) were considered (except for phenology and *Ips*-dynamics using all available data, Figs. 3, 7), so as to ensure the data sets were equivalent for all years under study.

Differences between treatments were tested by analyses of variance (DataDesk, Data Description Inc.). Each trap represents a replicate. The number of sampled species is not independent of the number of collected insects (cf. HUBALEK 2000), i.e. the more insects are collected, the greater is the likelihood of collecting "all" species. Calculating diversity indices is one way to compare species richness from unequal sample sizes. The Shannon-Weaver (H') index was used to assess community diversity across the years (SOUTHWOOD 1978; for a discussion of diversity indices see HUBALEK 2000). Sørensen's coefficients C of similarity were calculated (SOUTHWOOD 1978) to compare the faunal composition of the two clearing treatments.

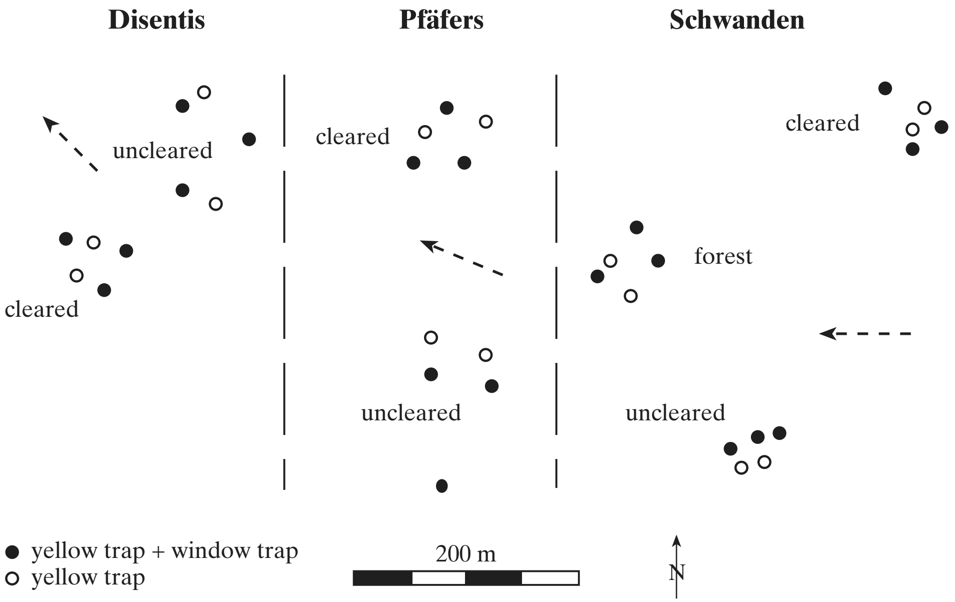

Fig. 1. Design of trap positions in the three experimental sites in Disentis, Pfäfers, and Schwanden. Open circles = yellow trap only, filled circles = window and yellow trap; dashed arrow indicates direction of slope.

3 Results

The storm Vivian occurred in February 1990. Thus, the season 1990 is considered the *first* year after the storm, since it was the first activity period when the insects had to face a changed environment. Correspondingly, year 1991 is equivalent to the *second* year after the storm, and so on.

3.1 Development of abundance and species number

The individuals of the three beetle families analysed in this study constituted the vast majority of the saproxylic Coleoptera. In total some 68 000 individuals were considered in this analysis, belonging to 11 different buprestid species, 37 cerambycid species, and 38 scolytid species (Table 1).

Table 1. List of collected species and corresponding trap catches at three experimental sites with two windthrow treatments each (uncleared, cleared). The Schwanden site includes an additional control treatment in an intact forest.

Species	Disentis		Pfäfers		Schwanden			Total
	uncl.	cleared	uncl.	cleared	uncl.	cleared	forest	
Scolytidae								
Cryphalus abietis	99	82	1660	584	319	261	765	3770
Cryphalus intermedius			4	14				18
Cryphalus piceae			31	45	2		2	80
Cryphalus saltuarius	4	2	27	6				39
Crypturgus cinereus					1			1
Crypturgus hispidulus	6		22	3	28	15	3	77
Crypturgus pusillus	32	7	228	65	3219	223	32	3806
Dendroctonus micans	5	2	3	2	6	1		19
Dryocoetes alni			8					8
Dryocoetes autographus	271	82	569	200	2346	275	680	4423
Dryocoetes hectographus	14	4	64	17	22	3	67	191
Ernoporicus fagi				1	12	3		16
Ernoporus tiliae				1				1
Hylastes ater							7	7
Hylastes attenuatus		2						2
Hylastes cunicularius	277	437	567	299	283	198	2905	4966
Hylastes opacus						1		1
Hylurgops glabratus	4	4	4			1	12	25
Hylurgops palliatus	12	10	35	5	313	21	842	1238
Ips amitinus	22	22	4	1	69	20	1	139
Ips cembrae				1				1
Ips typographus	62	86	2449	153	1203	137	48	4138
Leperisinus fraxini	1		1		4	11	1	18
Orthotomicus laricis	34	11	65		187	4		301
Phthorophloeus spinulosus	22	17	60	61	14	9	5	188
Pityogenes bidentatus				1				1
Pityogenes bistridentatus				1				1
Pityogenes chalcographus	580	454	5548	454	3411	1993	74	12 514
Pityogenes conjunctus	14	31	124	37	38	62	19	325
Pityophthorus pityographus	128	126	369	165	164	90	30	1072
Polygraphus poligraphus	39	6	109	21	3	2	5	185
Taphrorychus bicolor			24	32			3	59
Tomicus minor			1					1
Xyleborus dispar	28	44			37	11	6	126
Xyleborus germanus		2			1			3
Xylechinus pilosus	4	1	7	11	1	1	246	271
Xyloterus domesticus					4		7	11
Xyloterus lineatus	86	41	1419	78	269	39	749	2681
Cerambycidae								
Acmaeops collaris			1					1
Acmaeops septentrionis	4		3					7
Agapanthia cardui					8	10		18
Agapanthia villosoviridescens					6	16		22
Alosterna tabacicolor	81	50	11	11	10	3	30	196
Anastrangalia dubia	10	6	20	8		3		47
Anastrangalia sanguinolenta	3	9	9	11	78	98	1	209
Brachyta interrogationis	9	14						23
Callidium aeneum	3	1						4

Table 1 continued.

Species	Disentis		Pfäfers		Schwanden			Total
	uncl.	cleared	uncl.	cleared	uncl.	cleared	forest	
Clytus arietis	4	2	25	20	114	38		203
Clytus lama	3		12	23	4	6		48
Cortodera femorata	1							1
Corymbia maculicornis		4		1				5
Corymbia rubra		1		1	13	43		58
Evodinus clathratus	4	7	23	2	2	2		40
Gaurotes virginea	341	288	308	641	314	528	4	2424
Judolia sexmaculata	43	57						100
Leptura inexspectata					1	1		2
Leptura maculata				2	24	20		46
Lepturalia nigripes	1							1
Molorchus minor	14	9	15	15	15	10		78
Monochamus sutor					3		1	4
Oberea oculata	1							1
Oberea pupillata	2							2
Obrium brunneum							1	1
Oxymirus cursor	8	8		1	4	11	1	33
Pachyta lamed			1					1
Pachyta quadrimaculata	1	12	2	3	2			20
Pachytodes cerambyciformis	585	1058	137	97	927	959	4	3767
Phytoecia cylindrica	1		4	2				7
Pidonia lurida	2		2		6	6	6	22
Rhagium bifasciatum	8	4	2	2	13	33	3	65
Rhagium inquisitor	1	1	1			1		4
Rhagium mordax	4		2	1	9	14		30
Stenurella melanura	3	15	6	6	26	29	1	86
Tetropium castaneum	4	3	4	3	3		8	25
Tetropium fuscum		1						1
Buprestidae								
Agrilus cyanescens				1				1
Agrilus laticornis					1	3	4	8
Agrilus sulcicollis	1							1
Agrilus viridis			1	1	36	16		54
Anthaxia godeti			27	11	2			40
Anthaxia helvetica	1177	992	723	995	1046	1868	1	6802
Anthaxia quadripunctata	1736	443	5454	3105	1319	538		12 595
Anthaxia similis	5	5	8	2	2	4		26
Chrysobothris affinis					1			1
Chrysobothris chrysostigma					1			1
Coraebus rubi		22			27	38		87
Total of 86 species	5804	4485	20 203	7223	15 973	7679	6574	67 941

The temporal pattern of catches in the windthrow areas was quite heterogeneous (Fig. 2). The scolytid fauna showed a distinct peak in the third year (1992) after the windthrow but declined to very low levels four years later. This pattern was mainly due to captures of *Pityogenes chalcographus* and *I. typographus* (cf. section 3.4 and WERMELINGER *et al.* 1999). The population build-up of species from the two other saproxylic families was slower.

Buprestid beetles reached a maximum in 1994 and thereafter decreased only slowly. Cerambycid numbers increased during the whole period of observation. The most abundant species were *Anthaxia quadripunctata* and *A. helvetica* (Buprestidae) and *Pachytodes (Judolia) cerambyciformis* (Cerambycidae).

Increases in buprestid and cerambycid abundance were not paralleled by increases in the number of different species (Fig. 2). The number of cerambycid species peaked in the second year after the storm, which is similar to the pattern for the scolytid species. Diversity in both groups thereafter declined for some years, but a decade after the storm it was tending to rise again. The low number of buprestid species did not markedly change throughout the whole period under study.

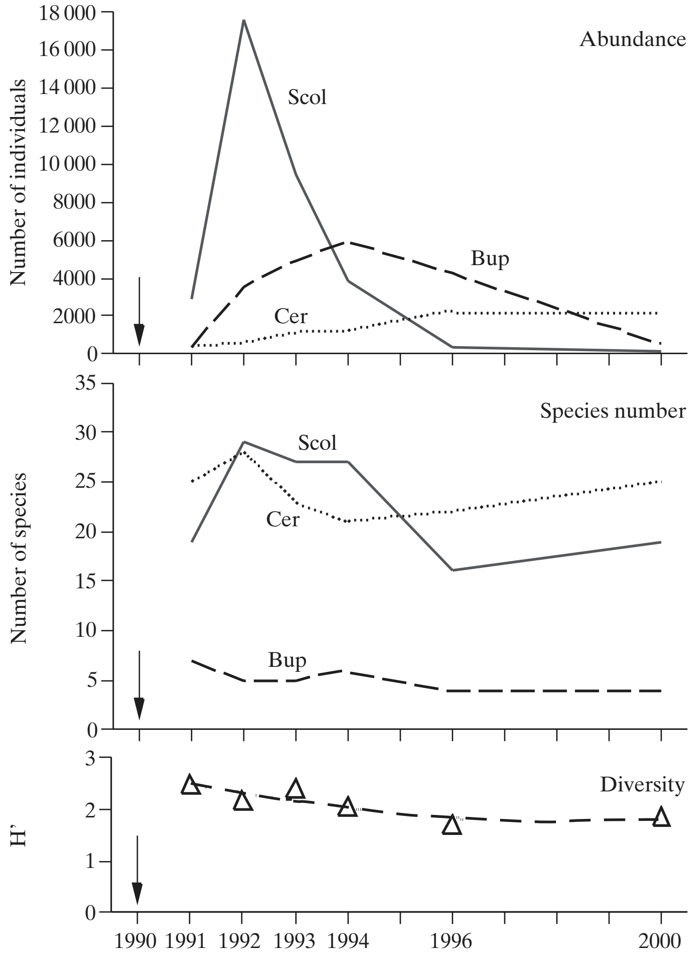

Fig. 2. Development of abundance, species number, and diversity (Shannon-Weaver index H', including trendline) of Scolytidae (Scol), Cerambycidae (Cer), and Buprestidae (Bup) for ten years after the storm in three windthrow areas combined; arrow indicates year of windthrow.

The Shannon-Weaver index (H') calculated over all saproxylics was highest in the second year (Fig. 2). Thereafter it declined but was starting to rise again at the end of the observation period. The somewhat lower value in 1992 is due to the two dominating scolytids, *I. typographus* and *P. chalcographus,* depressing the evenness and therefore also the Shannon index. The patterns of H' for the individual families were similar to overall H' except that no increase in diversity was noted for buprestids at the end of the observation period.

3.2 Phenology and succession

A rough overview of the saproxylic families' flight activity is illustrated in Figure 3 to identify optimal sampling periods. Data from 1993 were selected because it had a long sampling period and high frequency of species and individuals. The phenologies of the three taxa show different patterns. The number of scolytid beetles species was highest in May and June. The peak number of the cerambycid species was delayed and more species were present during much of the season. Maximum species numbers were found in June and July. The dominant species emerged primarily in June/July *(Gaurotes virginea)* and July/August *(P. cerambyciformis)*. The flight patterns of the buprestid species were similar to those of the cerambycids, but the period of increased species richness lasted approximately one month longer. The two dominating buprestids, i.e. the closely related species *A. helvetica* and *A. quadripunctata,* showed distinct differences in their emergence times: *A. helvetica* peaked in late May/early June, while *A. quadripunctata* emerged from July up to late August.

A succession of saproxylic taxa is visible over the entire ten-year sampling period (Table 2). The order is from the pioneering Scolytidae to the Cerambycidae, with the Buprestidae in the middle (see also Fig. 2). No bark beetle species had elevated populations longer than 1994. In addition, the high-population periods of the scolytids were shorter than those of the two other taxa.

The cerambycid species generally benefited later from the plentiful resources. An exception is *Molorchus minor,* a small species colonising newly dead conifers. It was noticeable during the first five years after the windthrow. The buprestid *Agrilus viridis* also peaked in 1992. Two cerambycid species showed population peaks quite late after the windthrow (*P. cerambyciformis* in 1996 and *Judolia sexmaculata* in 2000).

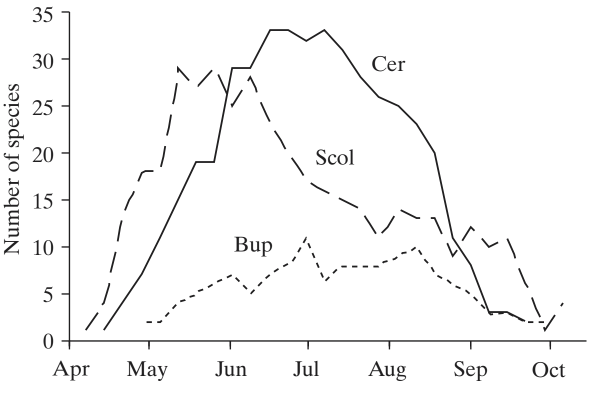

Fig. 3. Seasonal dynamics of saproxylic species number (Scol = Scolytidae, Cer = Cerambycidae, Bup = Buprestidae) in 1993 based on all windthrow areas.

Table 2. Succession of the most abundant saproxylic beetle species after the windthrow. Each bar represents the period in which ≥90 % of all individuals belonging to the respective species were caught. Dots represent abundance maxima.

	1991	1992	1993	1994	1996	2000
Scolytidae						
Ips typographus	▬	●	▬			
Cryphalus abietis	▬	●	▬			
Xyloterus lineatus	▬	●	▬			
Pityogenes conjunctus	▬	●	▬	▬		
Pityogenes chalcographus		●	▬			
Hylurgops palliatus		●	▬			
Hylastes cunicularius		●	▬	▬		
Pityophthorus pityographus		●	▬	▬		
Dryocoetes autographus		▬	●	▬		
Crypturgus pusillus			●	▬		
Buprestidae						
Agrilus viridis	▬	●	▬			
Anthaxia helvetica		▬	●	▬	▬	
Anthaxia quadripunctata		▬	▬	●	▬	
Anthaxia godeti			●	▬	▬	▬
Coraebus rubi				▬	●	
Cerambycidae						
Molorchus minor	▬	●	▬	▬		
Stenurella melanura	▬	▬	▬	▬	▬	●
Gaurotes virginea		▬	●	▬	▬	▬
Clytus arietis		▬	●	▬	▬	▬
Alosterna tabacicolor		▬	▬	▬	▬	●
Anastrangalia sanguinolenta			▬	▬	▬	●
Pachytodes cerambyciformis				▬	●	▬
Judolia sexmaculata					▬	●

3.3 Effects of clearing treatments

The effect of the windthrow clearing treatments on the saproxylic beetles is shown in Figure 4. The lines, representing the number of individuals, indicate higher abundance in uncleared windthrow areas in all study sites. In general, the differences between the treatments were most obvious in the third season (1992) after the storm, brought about mainly by the increased number of bark beetles in uncleared areas (cf. Fig. 2). Figure 4 also shows a conspicuous difference between the Disentis site and the other sites. Considerably fewer saproxylic beetles were caught at Disentis than at Pfäfers or Schwanden.

In general, uncleared areas not only had larger numbers of individuals but also more species (dark columns). This is statistically significant only for scolytids (all years, ANOVA $p < 0.01$). However, these differences were observed only during the first half of the decade. Ten years after the storm neither the numbers of species nor those of individuals differed between clearing treatments. However, the species composition remained different. This is illustrated by the coefficient of similarity (Fig. 5). A value of 1 for Sørensen's coefficient means complete matching of the species composition in both treatments. After clearing in 1990/91, the coefficient increased for approx. two years and thereafter decreased again. After 1996 the three study sites showed different behaviour: the clearing treatments at Pfäfers and Schwanden shared fewer species in 2000 than in 1996, while at Disentis the two treatments seemed to converge. However, this last value is based on only a few species.

Windthrow areas and an adjacent standing forest were compared at the Schwanden site (Fig. 6). Buprestid and cerambycid abundance and total species numbers (for ANOVA *mean* number of species per trap) were significantly higher ($p < 0.01$) on the two windthrow treatments than in the intact forest, but equally represented in both windthrow clearing treatments. The thermo- and heliophilic buprestid species especially were virtually absent in the forest (5 specimens out of 4900 Buprestidae). Scolytid abundance and species numbers did not differ statistically (ANOVA $p > 0.05$) between treatments. They reached similar numbers in the forest as well as in the windthrow treatments. However, two species, *Cryphalus abietis* and *Hylastes cunicularius* (cf. Table 1), were clearly more abundant in the forest. The latter, a potential forest pest (cf. section 3.4), was ten times more abundant in the forest than in the uncleared windthrow and made up 45% of all scolytid beetles in the forest. In the forest, the species richness of Cerambycidae and Buprestidae was only 20–50% of that on the uncleared areas. An execption to this rule was *Alosterna tabacicolor* (Cer.), which was more abundant in the forest. In total, 59 species were found in windthrow areas, whereas in the forest we caught only 32 species. These differences between the windthrow areas and the forest were still evident after one decade.

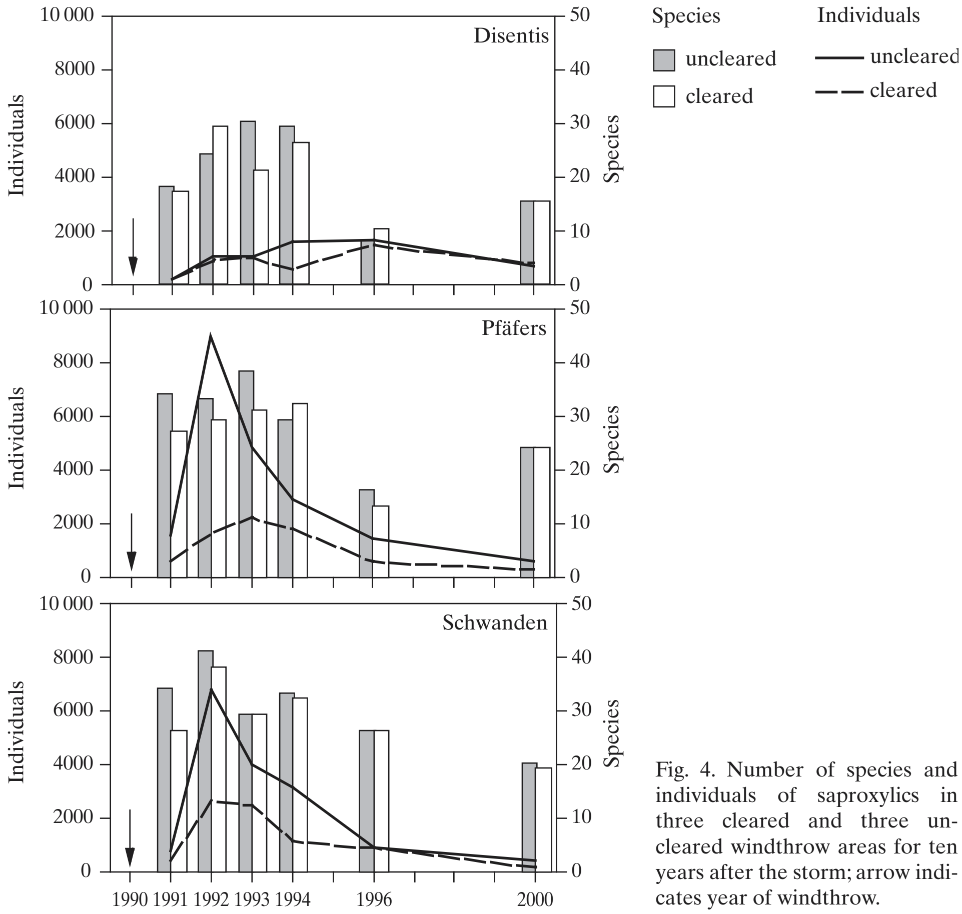

Fig. 4. Number of species and individuals of saproxylics in three cleared and three uncleared windthrow areas for ten years after the storm; arrow indicates year of windthrow.

The key species in the windthrow areas were the scolytids *P. chalcographus*, *Crypturgus pusillus* (preferring uncleared areas) and *Orthotomicus laricis,* the buprestids *A. helvetica* and *A. quadripunctata,* and the cerambycids *P. cerambyciformis* and *G. virginea* (cf. Table 1). In fact, all the buprestids greatly preferred the windthrow habitats. Typical forest species were *H. cunicularius* and *Xylechinus pilosus.*

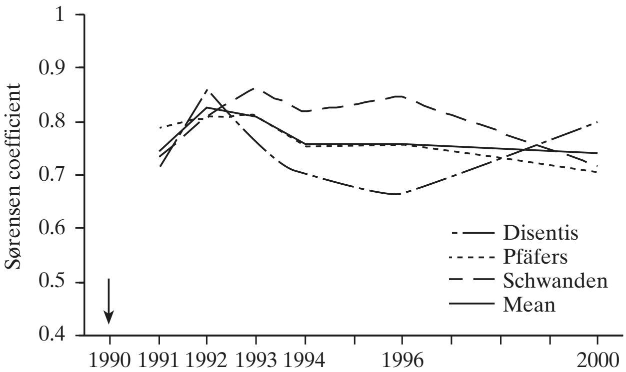

Fig. 5. Coefficient of similarity (Sørensen) for saproxylic beetle assemblages in cleared and uncleared windthrow areas for ten years after the storm (three study sites and mean); arrow indicates year of windthrow.

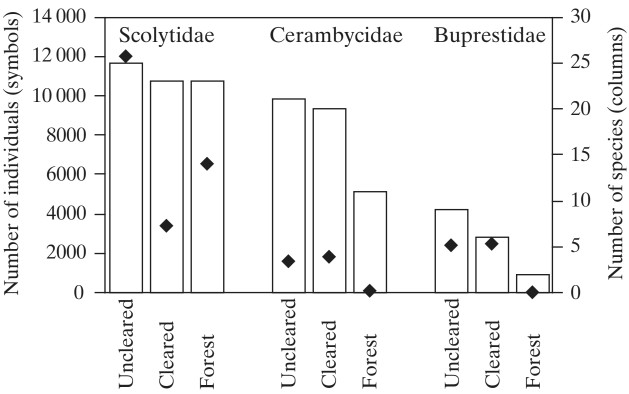

Fig. 6. Total number of individuals (symbols) and species (columns) in a cleared and an uncleared windthrow area, as well as in the intact forest; data from Schwanden 1991–2000.

3.4 Potential forest pests

Special attention was paid to the dynamics of the European spruce bark beetle *I. typographus.* The development of its abundance after the windthrow is depicted in Figure 7 for the study site at Schwanden. There was a rapid increase in beetle numbers on the uncleared windthrow areas, and their abundance peaked in the third season after the storm. The peak was followed by a sudden drop one year later. This behaviour differs from that on cleared areas where the abundance remained at a low level with only slightly higher numbers at the delayed peak in 1993. In the intact forest *I. typographus* was present in only very small numbers. Populations in both clearing treatments and the forest remained at this low level for the rest of the investigation period. At Pfäfers the population dynamics of this species revealed a similar pattern. Peak numbers in the uncleared area in 1992 were almost 50 times those in the cleared area. Population breakdown was somewhat retarded compared to Schwanden. At Disentis, however, there were moderate numbers of *I. typographus* throughout all the years and in both treatments.

Another well-known forest species is the small six-spined spruce engraver beetle *P. chalcographus.* This phloem feeder was the most abundant bark beetle species in the windthrow areas (cf. Table 1, see also WERMELINGER *et al.* 1999). Like *I. typographus* it peaked in 1992 but was not so much restricted to uncleared areas as the former, but it was almost absent from the forest.

A third harmful bark beetle, i.e. *H. cunicularius,* peaked in 1992 and thereafter steadily declined. It is striking that *H. cunicularius* was much more abundant in the standing forest than on either windthrow treatment (cf. Table 1).

The population trends for *Xyloterus (Trypodendron) lineatus,* a species that damages the sapwood, were very similar. Its populations also peaked three years after the storm and they were most abundant in the forest habitat and least abundant in cleared areas.

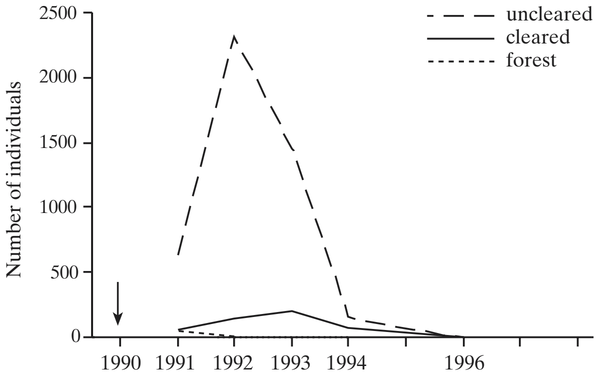

Fig. 7. Abundance of the European spruce bark beetle *(Ips typographus)* in a cleared and an uncleared windthrow area, as well as in the intact forest at the Schwanden site for the first years after the storm; arrow indicates year of windthrow.

4 Discussion

4.1 Multiseasonal dynamics of the saproxylic fauna

Disturbances play a major role in the natural development of forest ecosystems (ATTIWILL 1994). In comparison to an intact forest, open windthrow areas represent new environmental conditions and resources for flora and fauna. Flowering plants provide insects with nectar and pollen, the leaves of the pioneer vegetation serve as a food supply to folivores, and disturbed soils, dead bark and wood are substrates for the oviposition and larval development of many species. Saproxylic beetles are pioneers in colonising dead wood, prior to Diptera (flies and mosquitoes) and Hymenoptera (mainly parasitoids, KOPF and FUNKE 1998b). While the larvae depend on dead wood, adults, at least some groups, depend on flowers. The enhanced availability of these resources as a result of the windthrow was reflected by the sudden increase in beetle abundance.

The response of the various taxonomic groups was not uniform. There was a shift in relative abundance from Scolytidae to Buprestidae to Cerambycidae during this 10-year survey. Scolytids as typical exploiters of short-lived substrates responded rapidly to the favourable conditions. They have short developmental times, some species are even bivoltine, and feed exclusively on bark or wood, even as adults. They therefore do not depend on new vegetation. Some well-known outbreak species, such as *I. typographus* or *P. chalcographus,* took advantage of the short period of optimal bark quality: their population dynamics peaked in the third year after the blow-down. For disturbances other than wind, a similar temporal pattern was found for scolytids on clearcuts, while on burnt areas only few individuals were present (WERNER 2002). Both the abundance and the species richness of bark beetles increased during the first five years. This was accompanied by a pronounced change in species composition (WERMELINGER *et al.* 1999).

Many buprestid and cerambycid species have longer larval developmental times, often requiring several years. In addition, they do not rely solely on newly dead trees but may also colonise older substrates. Therefore, the emergence of species in these families was delayed several years and was more distributed across the seasons. The buprestid species reached their maximum numbers five years after Vivian. The cerambycids continued to increase over the whole observation period. Buprestid species number did not show any temporal trend, but the number of cerambycid species seemed to be higher for a longer time. Unfortunately, there are no data on the initial situation, i.e. the first year (1990) after the storm. However, a short-term increase in not only the insect numbers but also the species richness of saproxylics has been also found in other windthrow studies (e.g. OTTE 1989), while on clearcuts their abundance decreased (WERNER 2002). Diversity, expressed as the Shannon index, was high at the beginning and dropped after five years to a lower level. At one site (Pfäfers), it increased again towards the end.

The highest number of species was found in June/early July. If resources do not allow sampling throughout the whole season, then an optimal period for sampling these taxa in a survey should include these two months. This is valid at least for spruce forests between 900 and 1600 m a.s.l.

4.2 Effects of habitat type

The increase in individual and species numbers mentioned above is more pronounced in uncleared windthrow areas than in cleared ones. Therefore, more species occurred in higher numbers in uncleared areas. This was especially true for the first three years of the investigation, but thereafter both individual and species numbers converged in cleared and uncleared areas. However, the species composition was different as indicated by the coefficients of similarity. Saproxylic faunal similarity started at approx. 75% in 1991 (when the timber harvest was completed) and increased during the next 2–3 years (treatments became more similar to each other) and then generally declined again approaching the original values. A possible explanation for the increase in similarity at the beginning is that some species reaching high numbers in 1992/93 "flooded" the adjacent treatments, thereby overriding the contribution of habitat-specific elements to the coefficient. As abundances tended back to "normal", the treatments showed again a more incongruent species set. Regarding the 2000 increase in similarity at Disentis (Fig. 5), it needs to be pointed out that the species bringing about the differences between the treatments were mostly single catches. In addition, at this site the two treatments were immediately adjacent to each other, while at Pfäfers and Schwanden they were separated by a forest stand of approx. 100–200 m width (cf. Fig. 1). Note that the somewhat different findings of DUELLI *et al.* (this issue; Fig. 4) are mostly due to the use of a different index (Renkonen) that also includes abundance.

At Schwanden, both clearing treatments showed distinctly higher numbers of individuals and species compared to the standing forest. In the latter, only very few cerambycids and buprestids of a limited species range were found. The adults of these groups prefer warmer habitats to dense forests. The scolytids tended to prefer the uncleared area and the forest to the cleared area. Clearcut areas seem to be different from windthrows since the three taxa were found to be more abundant in the forest than on clearcut areas except for scolytids in the first year (WERNER 2002).

As far as endangered species are concerned, 16 species listed in the red lists of Germany (GEISER 1998) were found. Fifteen of them were found in uncleared areas, 10 in cleared ones, and only one species in the forest. In Switzerland, the cerambycid *Pachyta lamed* from the uncleared area at Pfäfers is protected by law. This indicates the importance of windthrow areas for conserving endangered saproxylics.

The question of whether clearing or leaving windthrow areas contributes more to biodiversity is difficult to answer. In our investigation more saproxylic species were found in uncleared areas than in cleared ones (Table 3). However, from this Table it also becomes evident that it is more beneficial to this guild to apply both treatments in parallel in a given region, thus providing a mosaic of cleared and uncleared patches and forest. This approach conforms with the biology of many cerambycids and buprestids in which the adults feed on flowers or leaves and thus prefer open habitats rich in pioneer vegetation, and the larvae develop in dead wood which is more likely to be present in uncleared windthrow areas. There is also higher biodiversity of other taxa in landscapes with both cleared and uncleared areas (DUELLI and OBRIST 1999; DUELLI *et al*. this issue).

Table 3. Total number of species caught in windthrow areas with different clearing treatments and with both treatments combined at three different sites (all years pooled).

	Uncleared	Cleared	Both
Scolytidae			
Disentis	22	22	24
Pfäfers	26	26	31
Schwanden	25	23	27
All sites	31	33	37
Cerambycidae			
Disentis	26	20	29
Pfäfers	20	19	24
Schwanden	21	20	23
All sites	34	28	36
Buprestidae			
Disentis	4	4	5
Pfäfers	5	6	6
Schwanden	9	6	9
All sites	10	8	11
Total	75	69	84

It is obvious that a windthrow does not "create" additional insect species. Specialised saproxylics that normally live in a managed forest habitat poor in dead wood can maintain only very low densities (and therefore are unlikely to be caught in traps). These may migrate into newly created habitats with ample resources such as windthrow areas, where they can readily multiply. The opposite effect is evident at the Disentis site: this large windthrow area was not surrounded by intact forests and it is where the lowest numbers of individuals and species were found. Of course, this relatively low biodiversity may also be due to its high elevation.

Many saproxylic species are endangered. Disturbances like windthrow provide an opportunity for mate finding and reproduction and therefore allow weak populations to strengthen in a suitable, but ephemeral environment.

4.3 Forest protection

The European spruce bark beetle *I. typographus* is by far the most important forest pest in Switzerland. It is specialised in infesting newly dead or weakened spruce trees. After Vivian, the largest mass outbreak of the 20th century occurred in Switzerland due to the ample supply of suitable breeding material and favourable weather conditions (ENGESSER *et al.* 1998; WERMELINGER *et al.* 1999). The infestation of the fallen timber in the windthrow areas was limited to 2–3 years (Fig. 7, see also KOPF and FUNKE 1998a) with severalfold larger populations in the uncleared areas than in the cleared ones. Most *I. typographus* were attracted to the plentiful breeding substrates and only a few were caught in the forest during this time. After the fallen timber had become unsuitable for breeding, the beetles started to infest the adjacent forest edges about two years after the storm (FORSTER 1993; SCHRÖTER *et al.* 1998) and eventually spread into the nearby stands. There, single wind-felled trees were often the unnoticed origin of infestation spots. Despite the huge numbers of *P. chalcographus* found in this study, this species did not pose a threat to standing spruce trees. The dynamics of potential forest pests is confirmed by other investigations in similar experimental setups (KOPF and FUNKE 1998a; SCHRÖTER *et al.* 1998).

Obviously, *H. cunicularius* also profited from the windthrow. This bark beetle develops in spruce stumps and, as an adult, completes its maturation and regeneration feeding in the bark of young spruce or pine plants. It can therefore cause substantial damage in spruce plantations. It seemed to prefer the forest conditions in our study, although the resources for its maturation feeding on young conifers and for oviposition in trunks would be better in windthrow areas. Possibly, uprooted spruce trunks do not represent ideal oviposition sites. However, this species can develop in at least slanting trunks (LUITJES 1976). The results of our study support the recommendation not to plant young trees within the first two years after clear cutting or windthrow. This recommendation also holds for the large pine weevil (*Hylobius abietis,* Curculionidae) with a similar biology to *H. cunicularius.* These weevils were caught in pitfall traps between 1991 and 1994. They were most abundant in the second year (1991) after the storm, and thereafter they decreased markedly. The results of the trap catches were confirmed by a survey of maturation feeding on planted trees in the field (cf. WERMELINGER *et al.* 1995).

5 Conclusions

Windthrow triggers a dynamic succession of insects that initiate the decomposition of bark and wood. In the case of spruce forests, large-scale windthrow almost inevitably leads to extensive outbreaks of *I. typographus* bark beetles and hence to further tree losses, but such disturbances also supply new resources for many rare insect species. Sensible promotion of the saproxylic fauna does not exclude timber harvest. Biodiversity can be best enhanced by creating a mosaic of harvested areas (where economically feasible) rich in herbs, of untouched areas rich in dead wood, and of intact forests. This procedure may be in conflict with efficient bark beetle management. However, after extensive storm damage in mountain forests it is often impossible, due to limited manpower and resources, to clear all the windthrow areas before the spruce bark is too dry for colonisation by the spruce bark beetle. Often the proceeds from selling the timber do not cover the harvest costs. Therefore, it is a reasonable strategy after large-scale windthrow in mountain forests to leave the timber in the windthrow areas for the benefit of saproxylics, and to concentrate on sanitation felling of the newly attacked living spruce trees.

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6 References

ALBRECHT, L., 1991: Die Bedeutung des toten Holzes im Wald. Forstwiss. Cent.bl. 110: 106–113.

ATTIWILL, P.M., 1994: The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manage. 63: 247–300.

DUELLI, P.; OBRIST, M.K., 1999: Räumen oder belassen? Die Entwicklung der faunistischen Biodiversität auf Windwurfflächen im schweizerischen Alpenraum. Verh. Ges. Ökol. 29: 193–199.

DUELLI, P.; OBRIST, M.K.; SCHMATZ, D.R., 1999: Biodiversity evaluation in agricultural landscapes: above-ground insects. Agric. Ecosyst. Environ. 74: 33–64.

DUELLI, P.; OBRIST, M.K.; WERMELINGER, B., 2002: Windthrow-induced changes in faunistic biodiversity in alpine spruce forests. For. Snow Landsc. Res. 77, 1/2: 117–131.

ENGESSER, R.; FORSTER, B.; MEIER, F.; ODERMATT, O., 1998: Forstschutzsituation 1997 in der Schweiz. Allg. Forst Z. Waldwirtsch. Umweltvorsorge 53, 7: 375–377.

FISCHER, A., 1998: Die Entwicklung von Wald-Biozönosen nach Sturmwurf. Landsberg, ecomed. 427 pp.

FISCHER, A.; MÖßMER, R., 1999: Forschung in Sturmwurf-Ökosystemen Mitteleuropas. Forstl. Forsch.ber. Münch. 176: 144 pp.

FORSTER, B., 1993: Entwicklung der Borkenkäfersituation in den Schweizer Sturmschadengebieten. Schweiz. Z. Forstwes. 144: 767–776.

FUNKE, W.; KENTER, B.; BAUMANN, K.; SCHWARZ, E.; BELLMANN, H.; KRAUS, J.; WERTH, H., 1995: Sukzession der Lebensgemeinschaften von Windwurfflächen (bei Langenau, Bad Waldsee und Bebenhausen) – Untersuchungen an Arthropodenzönosen. Veröffentlichungen Projekt «Angewandte Ökologie» 12: 24–25.

GEISER, R., 1998: Rote Liste der Käfer (Coleoptera). In: BINOT, M.; BLESS, R.; BOYE, P.; GRUTTKE, H.; PRETSCHER, P. (eds) Rote Liste gefährdeter Tiere Deutschlands. Vol. 55. Schr.reihe Landsch.pflege Nat.schutz 168–230.

GLÜCK, E.; SPELDA, J., 1996: Sukzession der Destruentencoenosen von Sturmwurfflächen. Veröffentlichungen Projekt «Angewandte Ökologie» 16: 367–377.

HUBALEK, Z., 2000: Measures of species diversity in ecology: an evaluation. Folia Zoologica 49: 241–260.

IRMLER, U.; HELLER, K.; WARNING, J., 1996: Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). Pedobiologia 40: 134–148.

KENTER, B.; BAUMANN, K.; BELLMANN, H.; WERTH, H.; FUNKE, W., 1996: Tiergesellschaften auf Windwurfflächen in Süddeutschland – Untersuchungen an Arthropoden- und Avizönosen. Veröffentlichungen Projekt «Angewandte Ökologie» 16: 357–366.

KÖHLER, F., 2000: Totholzkäfer in Naturwaldzellen des nördlichen Rheinlands. LÖBF-Schr.reihe Landesanst. Ökol. Bodenordn. Forsten Nordrh.-Westfal. 18: 352 pp.

KOPF, A.; FUNKE, W., 1998a: Borkenkäfer und Borkenkäferfeinde. In: FISCHER, A. (ed) Die Entwicklung von Wald-Biozönosen nach Sturmwurf. Landsberg, ecomed. 315–320.

KOPF, A.; FUNKE, W., 1998b: Xylobionte Arthropoden. In: FISCHER, A. (ed) Die Entwicklung von Wald-Biozönosen nach Sturmwurf. Landsberg, ecomed. 282–291.

LÄSSIG, R.; SCHÖNENBERGER, W., 1997: Was passiert, wenn man die Natur sich selber überlässt? Ergebnisse der Sukzessionsforschung auf Windwurfflächen. Laufener Seminarbeitr. 1/97: 67–74.

LUITJES, J., 1976: Die Entwicklung von Insekten im Sturmholz von 1972/73 in den Niederlanden. Z. Pflanzenkrankh. Pflanzenschutz 83: 87–95.

ØKLAND, B.; BAKKE, A.; HÅGVAR, S.; KVAMME, T., 1996: What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodivers. Conserv. 5: 75–100.

OTTE, J., 1989: Ökologische Untersuchungen zur Bedeutung von Windwurfflächen für die Insektenfauna (Teil I). Waldhygiene 17: 193–247.

SCHIEGG, K., 2000: Effects of dead wood volume and connectivity on saproxylic insect species diversity. Ecoscience 7: 290–298.

SCHÖNENBERGER, W., 2002: Windthrow research after the 1990 storm Vivian in Switzerland: objectives, study sites, and projects. For. Snow Landsc. Res. 77, 1/2: 9–16.

SCHRÖTER, H.; BECKER, T.; SCHELSHORN, H., 1998: Die Bedeutung der Sturmwurfflächen als "Borkenkäferquellen" für umliegende Wirtschaftswälder. In: FISCHER, A. (ed) Die Entwicklung von Wald-Biozönosen nach Sturmwurf. Landsberg, ecomed. 292–314.

SOUTHWOOD, T.R.E., 1978: Ecological Methods. London, Chapman and Hall. 524 pp.

SPEIGHT, M.C.D., 1989: Saproxylic invertebrates and their conservation. Strasbourg, Council of Europe. 82 pp.

WERMELINGER, B.; DUELLI, P.; OBRIST, M.; ODERMATT, O.; SEIFERT, M., 1995: Die Entwicklung der Fauna auf Windwurfflächen mit und ohne Holzräumung. Schweiz. Z. Forstwes. 146: 913–928.

WERMELINGER, B.; OBRIST, M.K.; DUELLI, P.; FORSTER, B., 1999: Development of the bark beetle (Scolytidae) fauna in windthrow areas in Switzerland. Mitt. Schweiz. Entomol. Ges. 72: 209–220.

WERNER, R.A., 2002: Effect of ecosystem disturbance on diversity of bark and wood-boring beetles (Coleoptera: Scolytidae, Buprestidae, Cerambycidae) in white spruce *(Picea glauca* [Moench] Voss) ecosystems of Alaska. USDA For. Serv. PNW-RP 546. 15 pp.

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