WINDTHROW STIMULATES ARTHROPOD BIODIVERSITY IN FORESTS

GLI SCHIANTI FORESTALI INCENTIVANO LA BIODIVERSITÀ DEGLI ARTROPODI

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Summary: After the severe windthrows caused by the storm "Vivian" in 1990 the arthropod fauna was assessed for up to ten years after the storm in three regions in the Eastern Swiss Alps. A total of 1.683 arthropod species were identified. Windthrow areas yielded 35-69% more species than the intact forest plot. Species composition but not species numbers differed between cleared and uncleared windthrow areas. Saproxylic beetles were more abundant on uncleared areas. Extrapolation of rarefaction functions revealed that a combination of cleared and uncleared areas enhances biodiversity significantly by 22% as compared to a single treatment.

Key words: Biodiversity, windthrow, succession, woody debris, saproxylic insects.

Windthrow is a natural driving force in the dynamics of forest ecosystems. It constitutes a sudden change in a habitat by affecting structures, resources and microclimate. One of the obvious effects is the ample supply of dead wood. This substrate is an indispensable prerequisite for many species of beetles, bees, wasps, ants, flies, mosquitoes and other invertebrates (SPEIGHT 1989; IRMLER *et al.* 1996; ØKLAND *et al.* 1996; SCHIEGG 2000). The newly growing vegetation in the windthrow areas is an emerging resource for a wide range of herbivorous insects. What may appear as a disaster to a single organism or to human economics, can be a chance for the survival of numerous species.

The storm Vivian in early 1990 triggered intensive research on the development of windthrow areas in Central Europe (SCHÖNENBERGER *et al.* 1995; FISCHER 1998; SCHÖNENBERGER 2002). Apart from investigations on the development of vegetation, special emphasis was put on the dynamics of invertebrates (FUNKE *et al.* 1995; KENTER *et al.* 1996; DUELLI *et al.* 2002; WERMELINGER *et al.* 2002). Between 1991 and 2000 the insect fauna was monitored in three windthrow areas in Swiss mountain spruce forests. The objectives of the investigation were to study the long-term development of the arthropod assemblages and to compare them between different clearing treatments and with the intact forest. A comprehensive overview of this study was published in more detail by DUELLI *et al.* (2002).

MATERIALS AND METHODS

Experimental setup

Three alpine regions in Eastern Switzerland were chosen, each with areas of 1-2 ha of uncleared and cleared windthrows in spruce forests. The three sites were Schwanden (Glarus, 900-1.100 m a.s.l.), Pfäfers (1.400-1.500 m), and Disentis (Grisons, 1.400-1.550 m). At the Schwanden site, there was a control plot in an adjacent intact forest in addition to the two clearing treatments.

Arthropods were collected with three types of traps: in each sampling plot three window traps (flight interception traps, 50x80 cm glass: DUELLI *et al.* 1999) were installed at a distance of at least 20 m to each other (WERMELINGER *et al.* 2002). In addition, five pitfall traps (funnel traps with 15 cm diameter: OBRIST & DUELLI 1996), and five yellow water pans (20 cm diameter: DUELLI *et al.* 1999) were placed per sampling plot. The traps were emptied weekly from May (depending on snow cover and accessibility) to September in the years 1991-1994, 1996 and 2000. Diurnal butterflies were recorded in 1992 and 1993 with standardized transects. The catches were sorted and subsequently identified by specialists to the species level.

Data analysis

Identification data were read into a large Oracle database (Oracle Corporation, Redwood Shores, CA), which allowed for any combined query on the data in space and time.

As site accessibility varied between years due to different snow thawing times, we confined our data set to weeks 20 to 37 for any time-critical analysis. Summary analyses (e.g. total species lists) comprise the full data set.

Statistical data analysis was performed with DataDesk statistical software (Data Description, Inc. Ithaca, NY). Each trap represented a replicate. If not stated explicitly, an error probability of $p \leq 0,05$ applies to all statements about statistical significance.

RESULTS

Clearing treatments

A total of 214.066 individuals in 1.683 arthropod species were collected in the six years of sampling (Table 1). In general, there was no statistical difference between the species numbers in cleared and uncleared plots. Only the butterflies (Lepidoptera, Rhopalocera) were more diverse in cleared plots than in the uncleared plots. Likewise, the percentage of threatened species did not differ between either treatment. However, species abun-

Group	Uncleared	Cleared	Total
Araneae	132	130	168
Opiliones	9	8	10
Pseudoscorpiones	3	2	3
Isopoda	3	1	3
Diplopoda	13	14	15
Heteroptera	120	131	167
Coleoptera	630	635	814
Hymenoptera: Aculeata	287	305	361
Diptera: Syrphidae	115	114	142
Lepidoptera: Rhopalocera	44	53	62
Total	1.312	1.340	1.683
Number of individuals	117.413	96.653	214.066

Table 1 - Number of arthropod species caught in three windthrow areas with cleared and uncleared plots. Species numbers of the different groups do not base on equal numbers of years.

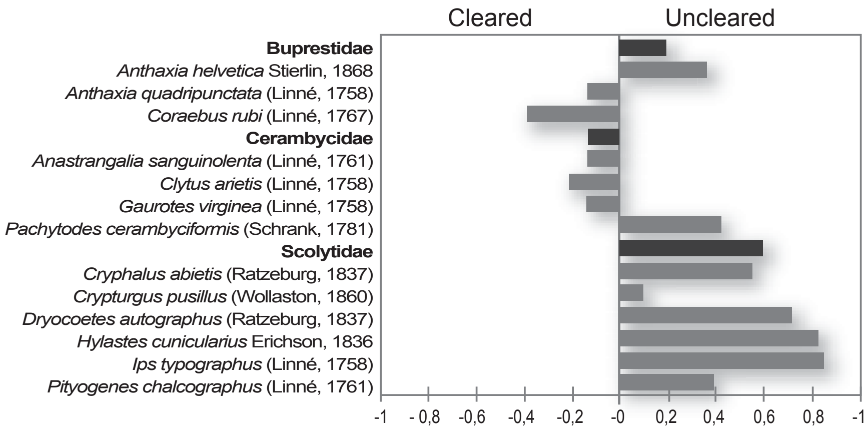

Figure 1 - Relative abundance of saproxylic beetles in cleared and uncleared windthrow areas; all sites and years combined. The value 0 represents equal abundance on both habitats, 1 means occurrence on only one habitat (see text).

Group	Cleared	Uncleared	Forest	Total
Scolytidae	15,5 %	54,7 %	29,8 %	21.846
Cerambycidae	52,7 %	45,6 %	1,7 %	3.473
Buprestidae	50,3 %	49,6 %	0,1 %	4.907
Total	25,4 %	52,8 %	21,7%	30.226

Table 2 - Relative abundance of three saproxylic beetle families at the three habitats: cleared windthrow, uncleared windthrow, and intact forest at the Schwanden site; data from six years.

dance was higher in uncleared areas. This is largely due to bark beetles: in Figure 1 the preference of the most abundant saproxylic insect species for clearing treatments is depicted as index i= (n_{ucl} - n_{cl})/N, where n_{ucl} is the number of individuals in uncleared areas, ncl the number in cleared areas, and N the total number. Scolytid beetles preferred the uncleared areas, most pronouncedly *Ips typographus* (Linné, 1758). In contrast, cerambycid beetles were generally more abundant in the cleared plots with the exception of *Pachytodes cerambyciformis* (Schrank, 1781) which was the most abundant cerambycid species. Its larvae develop in roots of a number of tree species. Within the buprestids the two *Anthaxia* Eschscholtz, 1829 species showed an opposite preference, *A. quadripunctata* (Linné, 1758) for cleared and *A. helvetica* Stierlin, 1868 for uncleared plots.

The three saproxylic groups also differed in their abundance in the intact forest at Schwanden (Table 2). Buprestid and cerambycid abundance and total species numbers were significantly higher (ANOVA $p<0,01$) in the two windthrow treatments than in the intact forest, but equally represented in both clearing treatments. The buprestid species were virtually absent in the forest (5 specimens out of 4.900 Buprestidae!). Scolytid abundance and species numbers did not differ statistically between treatments. However, they tended to reach higher numbers in the forest than in the cleared windthrow treatment. In the forest, the species richness of Cerambycidae and Buprestidae was only 20-50% of that in the uncleared areas. In total, 59 species were found in windthrow areas, whereas in the forest we caught only 32 species.

Temporal development

The temporal pattern of catches in the windthrow areas was quite differential among the saproxylic beetles (Figure 2). The scolytid fauna showed a distinct peak in the third year (1992) after the storm but declined to very low levels four years later. This pattern was mainly due to captures of *Pityogenes chalcographus* (Linné, 1791) and *I. typographus* (cf. WERMELINGER *et al.* 1999). The population build-up of species from the two other saproxylic families was delayed. Buprestid beetles reached a maximum in 1994 and thereafter decreased only slowly. Cerambycid numbers approached a maximum at the end of the observation period. The number of cerambycid and scolytid species peaked in the second year after the storm while the low number of buprestid species did not markedly change throughout the whole period under study. More results on the saproxylics may be found in WERMELINGER *et al.* (2002).

The development of arthropod species numbers was compared between treatments and with the intact forest at Schwanden (Table 3). There was a trend for an increase in species numbers within 10 years, amounting to 17% in both the cleared and the uncleared site. The increase is mainly due to the Heteroptera (true bugs) and carabid beetles, while the species numbers of spiders, syrphids, and some saproxylic beetles remained fairly constant. The bark beetles (Scolytidae), on the other hand, showed a marked decrease with time.

In the forest control plot, the increase between 1991 and 2000 was merely 5%. This site was close to windthrow areas, so

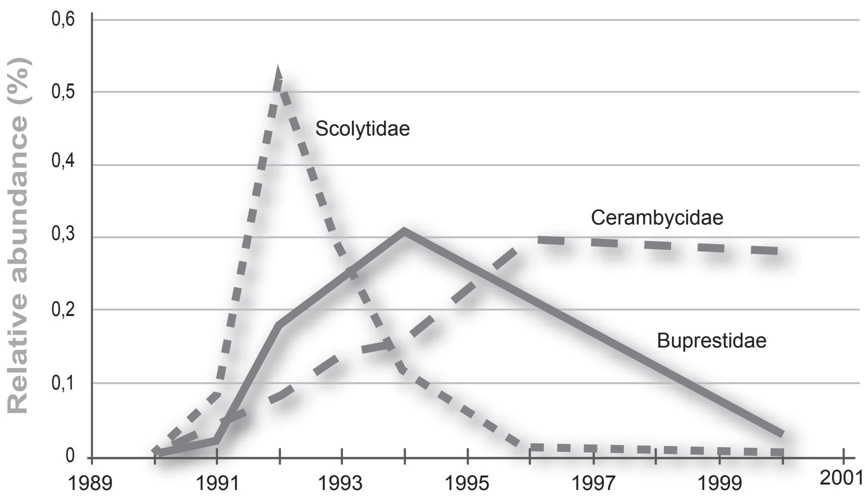

Figure 2 - Relative dynamics of three saproxylic groups of Coleoptera; all sites combined.

the increased species numbers of carabids and Heteroptera are most likely the result of immigration from surrounding windthrow sites.

Estimated species gain with treatment combinations

Although the overall species numbers collected in cleared and uncleared sites were similar, the species composition differed between the two treatments. To estimate the potential gain of a combination of both treatments and intact forest in a region we estimated the total numbers of species per plot by means of extrapolating rarefaction functions which corrects for unequal sample sizes (DUELLI *et al.* 2002). Extrapolating the functions to 500.000 individuals, we calculated 967 species in the cleared and 1.017 species in the uncleared treatment (Table 4). The forest achieved only 653 species. Combining both treatments significantly increased species numbers by 22%. This is also confirmed by the other study sites. A further increase is achieved by combining both treatments and the intact forest, which exactly doubled the species richness (100% increase).

DISCUSSION AND CONCLUSIONS

Windthrows caused an overall increase in biodiversity compared to the intact forest. Apart from bark beetles and arthropod groups depending on high humidity such as Isopoda, Opiliones, and Diplopoda, all identified groups showed an increase in species richness after the storm. The highest gains were observed in aculeate Hymenoptera and buprestid beetles. In the course of the ten-year-investigation, the species numbers increased in the windthrows by 17%, while the species gain in the forest control plot was insignificant and presumably due to immigration from nearby windthrows. Investigations in Germany on windthrows of the same storm "Vivian" also found a higher species richness in windthrows than in the intact forest (e.g. KENTER & FUNKE 1995; KENTER *et al.* 1997).

Arthropod abundance was consistently higher in the uncleared plots. However, uncleared windthrows did not harbor a higher species diversity or more endangered species than cleared ones. Though the species number was similar the assemblages of the two treatments differed from each other. While many saproxylic species were more numerous in uncleared than in cleared areas insects such as bees, wasps, bugs and syrphid flies preferred the cleared areas where amount and diversity of flowering plants growing on the disturbed surface was higher (WOHLGEMUTH *et al.* 2002). In addition, various adult cerambycids and buprestids feed on pollen or leaves and thus prefer the cleared areas while their developing larvae depend on dead wood supplied in uncleared areas.

Among the saproxylic beetles, scolytids as typical exploiters of short-lived substrates responded rapidly to the favorable conditions: their population dynamics peaked in the third year after the storm. Many buprestid and cerambycid species have longer larval development times or may also colonize older substrates. Therefore, the emergence of species in these families was delayed by several years. A short-term increase in not only the insect numbers but also the species richness of saproxylics has been found also in other windthrow studies (e.g. OTTE 1989), while in clearcuts their abundance decreased (WERNER 2002).

Many saproxylic species are endangered. Disturbances like windthrow provide new resources for them and many other arthropod groups and thus increase biodiversity. Storms stimulate population dynamics and allow weak populations to strengthen in a suitable, but ephemeral environment.

		Cleared		Uncleared		Forest	
Order	**Family**	**1991**	**2000**	**1991**	**2000**	**1991**	**2000**
Araneae		52	56	48	52	40	28
Coleoptera	Buprestidae	5	3	6	7	2	0
"	Carabidae	19	26	19	25	14	21
"	Cerambycidae	19	17	19	19	12	9
"	Scolytidae	12	7	17	6	12	13
Diptera	Syrphidae	21	30	38	37	21	17
Heteroptera		19	33	16	45	8	25
Total		147	172	163	191	109	113
Total in comparison to forest			+ 35 %	+ 52 %		+ 50 %	+ 69 %

Table 3 - Species numbers of the years 1991 and 2000 in the cleared and uncleared windthrow areas at Schwanden and comparison with the intact forest.

Treatment	Species at 500.000 individuals	Increase in species numbers (%)
Uncleared	1.017	
Cleared	967	
Both treatments	1.209	22%
Forest	653	
Both treatments and forest	1.307	100%

Table 4 - Estimated number of species in single and combined habitat types (clearing treatments and forest) at Schwanden.

Within a forest with storm-caused gaps creating a mosaic of cleared and uncleared windthrow areas can best enhance faunal biodiversity.

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