Windthrow-induced changes in faunistic biodiversity in alpine spruce forests

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Abstract
After the severe windthrow caused by the storm Vivian in 1990 in the Alps, political conflicts arose over the question whether clearing of the resulting gaps in the forest should be promoted and publicly subsidised. One argument against clearing was that uncleared windthrow areas would be better for the enhancement and conservation of biodiversity. In three regions in the Eastern Swiss Alps, the fauna was assessed for up to ten years after the storm in pairwise comparisons between cleared and uncleared windthrow areas and an intact managed forest control plot.

A total of 1856 species of invertebrates, reptiles, and small mammals were collected and identified. Windthrow areas yielded 35–69% more animal species than the intact forest plot. Neither the number of arthropod species collected in flight and pitfall traps, nor the number of red-listed species showed any significant differences between cleared or uncleared plots. However, extrapolation of rarefaction functions to estimate total species numbers per plot revealed that a combination of cleared and uncleared areas enhances biodiversity significantly more (by 21–26%) than a single treatment. Combining the data on the fauna recorded in both treatments with those of the surrounding forest shows that the species richness in the new mosaic of forest and gaps has increased by 100% since the storm.

During the observed period of succession following the first assessment after the storm, the species richness further increased by 17% in both treatments. Within ten years after the storm there was no sign of ecological resilience in the sense of a faunistic convergence back to the original species composition. Moreover, the fauna in the two treatments did not become more similar. Rather, it became less similar.

The best way, therefore, to enhance biodiversity after a windthrow is to do both, clear one half of the windthrow and leaving the other half uncleared.

Keywords: biodiversity, fauna, storm, windthrow, succession, conservation, ecological resilience, Switzerland

1 Introduction

In our managed alpine forests, natural disturbances such as the windthrow caused by the storm Vivian in 1990 are stochastically recurrent events. Therefore it is very likely that the fauna and flora adapt to such sudden and drastic changes in their habitats. What may appear as a disaster to a single organism or an economic disaster for foresters or forest owners, can be a chance for survival for numerous other species.

Our aim was to evaluate the gains and losses for various aspects of biodiversity after Vivian, and to compare the management effects of clearing vs. not clearing after windthrow.

We tested several hypotheses:

1. Windthrow causes an overall increase in biodiversity (intermediate disturbance theory, CONNELL 1979).

2. Species richness is greatest in uncleared windthrow (greatest structural diversity).
3. More species of conservation concern (red-listed species) profit from uncleared windthrow (many saproxylic species are endangered, SPEIGHT 1989; KÖPPEL *et al.* 1998).
4. The faunal assemblies of cleared and uncleared windthrow areas differ, so combining both treatments within an area will yield maximum biodiversity (mosaic concept, DUELLI 1992; DUELLI 1997).
5. There is a particular fauna for both cleared and uncleared windthrow areas that is independent of the regional characteristics.
6. Ecological resilience is higher in uncleared windthrow. The fauna in the intact forest is more similar to the uncleared site than to the cleared site. Furthermore, the species assembly in uncleared plots returns to its original composition faster, i.e. it becomes more similar to the intact forest plot faster than the fauna in the cleared plots.

The first four hypotheses were addressed in earlier papers (WERMELINGER *et al.* 1995; DUELLI and OBRIST 1999), mainly derived from data recorded during the first three years after the storm. They are summarised later in this paper, based on enlarged data sets.

2 Material and methods

After the severe storms in February 1990 it took about one year to find and legally safeguard monitoring plots in cleared and uncleared windthrow areas that were close enough for paired sampling (SCHÖNENBERGER this issue). This meant that in the first season after the storm there were no faunistic investigations. Three alpine regions in Eastern Switzerland were chosen, each with areas of 1–2 ha of uncleared and cleared windthrow. In Schwanden (Kt. Glarus), there was a control plot in an intact forest in addition to the two clearing treatments. In Schwanden, with experimental sites between 900 and 1100 m a.s.l., the Abieti-Fagetum contained numerous beech trees which had survived the storm. The plots in Pfäfers (Kt. St. Gallen), 1400–1500 m a.s.l., were dominated by wind-felled spruce trees. In Disentis (Kt. Grisons), at 1400–1550 m a.s.l., the spruce trees on the whole mountain slope containing the two sites had been blown down.

The faunistic investigations mainly focussed on invertebrates, but small mammals were also collected in some years with Sherman traps, and additionally in pitfall traps intended for arthropods. Pitfall trap catches also gave some indications of the development of the reptile and amphibian populations.

Insects and other arthropods were collected with three types of traps: In each of the sampling plots, three window traps (flight interception traps, 50 x 80 cm glass, DUELLI *et al.* 1999) were installed at a distance of at least 20 m to each other. In addition, five pitfall traps (funnel traps with 15 cm diameter, OBRIST and DUELLI 1996), and five yellow water pans (20 cm diam., DUELLI *et al.* 1999) were placed in each sampling plot. The traps were emptied weekly from May (depending on snow cover and accessibility) to September in the years 1991, 92, 93, 94, 96 and 2000. The data analysed by WERMELINGER *et al.* (2002) comprise a subset of the data set analysed here.

Diurnal butterflies were recorded in 1992 and 1993 with standardised transects, and molluscs in the same two years with standardised soil sampling and hand collection (RÜETSCHI 1998).

The lab-sorted material was partly identified in-house, but mostly sent to external specialists for species identification.

Data processing and statistics:
Identification lists returned from the specialists were read into a large Oracle database (Oracle Corporation, Redwood Shores, CA), which allows queries on the data to be combined in space and time.

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

Similarity between sites, treatments or single trap stations was compared with the Sörensen and Renkonen indices. It compares the relation of identical to total species numbers, but also considers the dominance of species occurring in both sites (MÜHLENBERG 1993).

Exploratory and statistical data analysis was performed with DataDesk statistical software (Data Description, Inc. Ithaca, NY). If not stated explicitly, an error probability of $p \leq 0.05$ applies to all statements about statistical significance.

3 Results

3.1 Species richness

Table 1 gives an overview of the identified taxa. A total of 268 175 individuals of 1856 species were collected in the six years of sampling. 1797 species and 240 670 individuals were collected in the yearly periods between weeks 20 and 37. All arthropods except the Rhopalocera were collected with the three trap types described above.

In general, there was no statistical difference between the species numbers in cleared and uncleared plots. While the cleared site at Disentis was more diverse, the reverse was true for Pfäfers. The species richness at the two plots at Schwanden was very similar. Only two groups had consistently more species in one of the treatments: While butterflies were more diverse on cleared plots, the molluscs had more species in the uncleared plots. The figures for molluscs in all three regions, however, show no differences between the two treatments.

In contrast to the even distribution of species numbers between the two treatments, the total number of individuals collected was clearly and consistently higher in the uncleared plots.

The faunistic gains and losses induced by the storm could only be assessed at the sites in Schwanden, where a forest control plot allows a comparison with the state of the intact forest before the storm. The molluscs are the only taxonomic group with more species in the forest than in the windthrow sites. In all the other taxa, the forest at Schwanden yielded only about 65% of the species, compared to the two treatments. The strongest avoidance of the forest interior was observed in the bees and wasps (Hymenoptera aculeata, without ants). Unfortunately, the butterflies were not assessed inside the forest.

3.2 Change over time

The black bars in Table 1 show which groups were investigated repeatedly up to the year 2000. For these taxa, the species numbers collected in 1991 and 2000 can be compared between treatments, and at the Schwanden sites with those in the intact forest (Table 2). There has been a trend for the species numbers to increase over the 10 years, by around 17% in both the cleared and the uncleared sites. The increase is mainly due to the Heteroptera (true bugs) and carabid beetles, while the species numbers of spiders, syrphids, and some saproxylic beetles have 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 only 5%. This site is in proximity to cleared and uncleared windthrow areas, so the observed increase in species numbers of carabid beetles and Heteroptera is most likely the result of immigration from surrounding windthrow sites, where these two taxa also showed the highest increase in species richness.

Table 1. Number of species collected during the six sampling seasons, separated into region, treatment (uncl.: uncleared plot; cl.: cleared plot) and taxonomic group. The lowest row gives the total number of individuals collected in thousands. Black boxes in the right column indicate included years of the respective taxonomic group. *= some locations and/or trap types only partially identified; – = not identified; + = without Formicidae.

Number of species		**all sites**			**Disentis**		**Pfäfers**		**Schwanden**			1991 1992 1993 1994 1996 2000	
Group	Subgroup	uncl.	cl.	Total	uncl.	cl.	uncl.	cl.	uncl.	cl.	forest		
Araneae	All	132	130	168	58	68	76	59	89	96	74	■■■■□□	
Opiliones	"	9	8	10	–	–	8	8	7	6	7	■□□□□□	
Pseudoscorpiones	"	3	2	3	0	0	1	1	2	2	1	□■□■□□	
Isopoda	"	3	1	3	0	0	2	0	2	1	1	■■□□□□	
Diplopoda	"	13	14	15	5	4	11	10	8	9	7	■■■□□□	*
Heteroptera	"	120	131	167	63	76	65	63	74	66	38	■■■■■■	
Coleoptera	Buprestidae	13	11	14	7	6	7	8	11	9	3	■■■■■■	
"	Carabidae	57	53	63	27	32	33	27	39	36	27	■■■■□■	
"	Cerambycidae	45	43	50	32	32	31	31	34	29	19	■■■■■■	
"	Scolytidae	34	36	41	24	24	30	28	26	26	25	■■■■■■	
"	Staphylinidae	142	148	187	82	93	94	73	83	85	66	■■□□□□	
"	Rest	339	344	459	175	205	168	146	210	202	162	■■■■■□	*
Hymenoptera	Aculeata +	246	269	317	161	214	161	134	146	133	29	■■□□□□	*
"	Formicidae	41	36	44	33	29	24	24	25	29	21	■■■■□□	*
Diptera	Syrphidae	115	114	142	65	68	91	88	82	70	52	■■■■■■	
Lepidoptera	Rhopalocera	44	53	62	19	31	20	23	31	33	–	□■■□□□	
Mollusca	Gastropoda	25	25	34	10	8	20	17	15	14	19	□■■□□□	
Vertebrata	Small mammals	12	13	15	12	9	8	7	5	11	2	□■□■■□	
"	Reptiles	1	3	3	0	1	1	1	1	3	0	■■■■■■	
Total		1394	1434	1797	773	900	851	748	890	860	553	■■■■■■	
Number of individuals (in 1000)		118	97	241	35	29	45	38	38	30	17		

In a comparison of the succession of biodiversity in the windthrow plots with that of the intact forest (Table 2), the species gain in the uncleared plot increased from 50% in 1991 to 69% in 2000, in the cleared plot from 35% to 52%. Hence, 10 years after the storm, the succession has resulted in an increase of well over 50% in total species richness.

Table 2. Comparison of species numbers at Schwanden in selected taxonomic groups, between the years 1991 and 2000. Signs indicate whether species numbers changed more than 10% and if so, increasingly (<) or decreasingly (>). The bottom line compares species numbers in the two treatments with the samples from the intact forest.

		Schwanden								
		uncleared			cleared			forest		
Order	Family	1991	10% diff	2000	1991	10% diff	2000	1991	10% diff	2000
Araneae		48	=	52	52	=	56	40	>	28
Coleoptera	Buprestidae	6	<	7	5	>	3	2	>	0
Coleoptera	Carabidae	19	<	25	19	<	26	14	<	21
Coleoptera	Cerambycidae	19	=	19	19	>	17	12	>	9
Coleoptera	Scolytidae	17	>	6	12	>	7	12	=	13
Diptera	Syrphidae	38	=	37	21	<	30	21	>	17
Heteroptera		16	<	45	19	<	33	8	<	25
Total		163	<	191	147	<	172	109	=	113
Total in comparison to forest		+ 50%		+ 69%	+ 35%		+ 52%			

3.3 Conservation concerns: more endangered species in uncleared plots?

For Switzerland, the collection of red-lists of endangered animal species (Duelli 1994) only contains a selected range of species groups. A major disadvantage is that it does not yet include the saproxylic beetles. To arrive at an approximate figure for the number of threatened species we compared our species list with the red-lists of adjacent countries, published electronically on CD-ROM (Köppel *et al.* 1998). The data set we used from the CD contains information from 132 publications (not listed separately in the references) from Austria, Germany, Italy, Liechtenstein and Switzerland.

We assigned the diverging categories of threat in these publications to the categories 1 to 3 of the existing Swiss red-lists (Duelli 1994). Table 3 gives the results for the category 1 (threatened by extinction), and the species in lower categories of threat. Clearly, there is no significant difference in the percentage of threatened species between either treatments or regions (Table 3).

Table 3. Percentage of species attributed to red-list status 1–3 (Duelli 1994; Köppel *et al.* 1998) separated into region and red-list status. 1 = endangered, 2 = vulnerable, 3 = regionally vulnerable.

	Disentis		Pfäfers		Schwanden		
Red List status	uncl.	cl.	uncl.	cl.	uncl.	cl.	forest
1	14 (2%)	15 (2%)	19 (2%)	14 (2%)	20 (2%)	14 (2%)	13 (2%)
2	16 (2%)	19 (2%)	18 (2%)	11 (1%)	16 (2%)	17 (2%)	11 (2%)
3	53 (7%)	60 (7%)	64 (8%)	62 (8%)	77 (9%)	67 (8%)	47 (8%)
All categories	83	94	101	87	113	98	71
No. species total	773	900	851	748	890	860	553

3.4 Estimated species numbers per plot (extrapolated rarefaction functions)

Although the overall species numbers collected in cleared and uncleared sites did not differ, the species composition was not the same in the two treatments. To estimate the potential gain of a combination of both treatments in a region with several windthrow sites, or within one larger windthrow gap, we estimated the total numbers of species present in cleared, uncleared, and mixed plots with extrapolating rarefaction functions (DUELLI and OBRIST 1999). Simply merging the species lists of both treatments for a region does not help because a mere doubling of the number of traps (i.e. collected individuals) within one treatment would increase the species numbers considerably.

To overcome the dependence of species richness on numbers of collected individuals, the estimated total species numbers per plot can be extrapolated to identical sample sizes with rarefaction methods (Fig. 1). All the identified catches of all groups, years, and weeks were included in these calculations. Extrapolating the rarefaction functions to 500 000 individuals, which is a very conservative estimate for the total number of individuals of all the identified groups present on one hectare, we calculated an average of 978 species in uncleared and 941 species for cleared treatments for the analysed groups (Table 4). The same calculation for the forest resulted in only 653 species.

Combining both treatments in any given site significantly increases species numbers ($F_{2,4}$ = 16.978, p = 0.0111) by an average of 23%. Maximal species numbers (1307) were achieved for Schwanden when combining both treatments and the intact forest (Table 4), which would exactly double the species richness (100% increase).

Table 4. Number of species extrapolated to 500 000 individuals, from the total of all trap catches, separated in region and treatment. Numbers were also extrapolated for the combined treatments. The last column indicates the increase in species numbers due to the combination of both treatments.

Location	Treatment	Extrapolated number of species for 500 000 individuals	% increase in species numbers
Disentis	uncleared	917	
	cleared	990	
	both treatments	1199	26%
Pfäfers	uncleared	1000	
	cleared	865	
	both treatments	1131	21%
Schwanden	uncleared	1017	
	cleared	967	
	both treatments	1209	22%
	forest	653	
	both treatments and forest	1307	100%

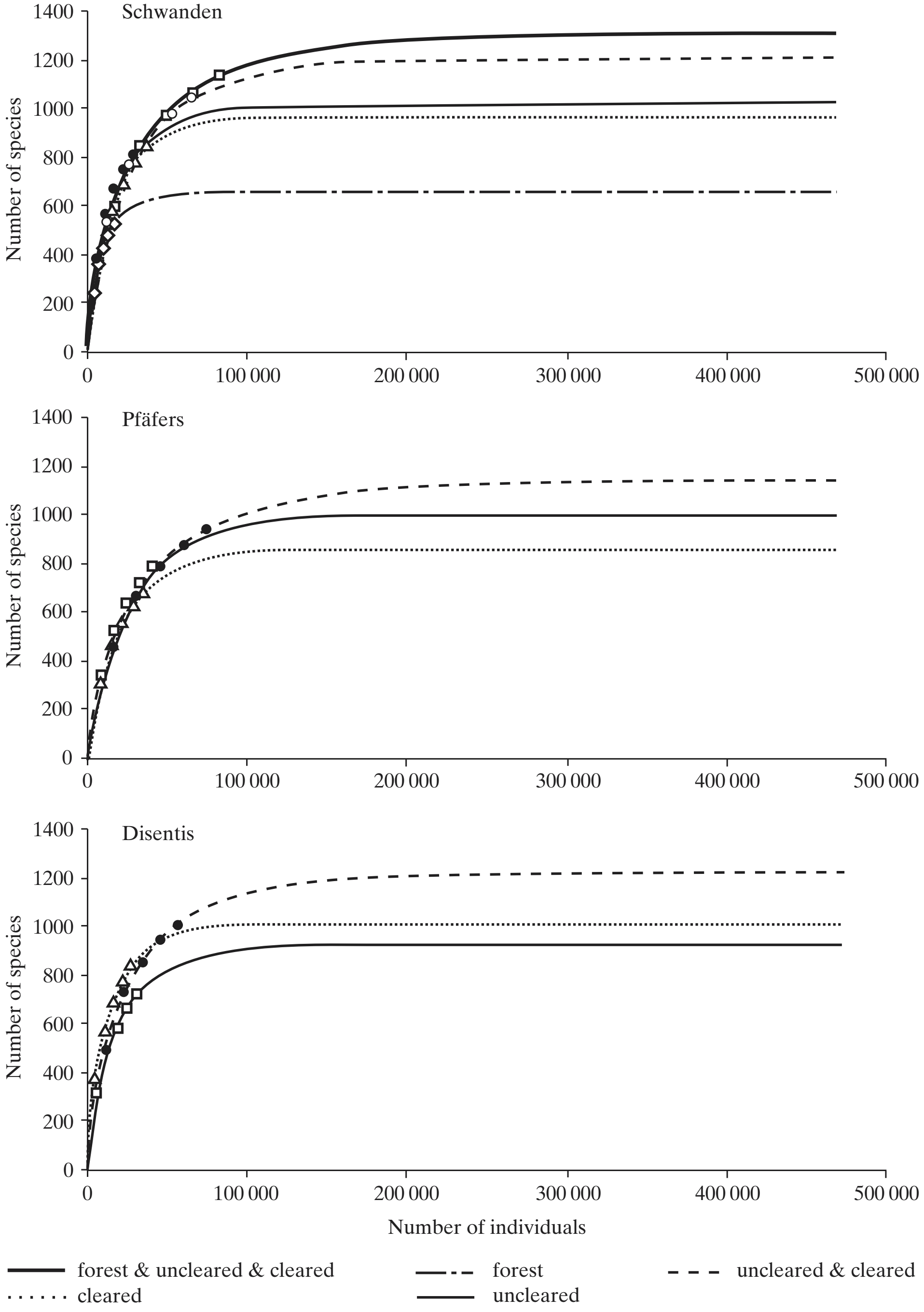

Fig. 1. Extrapolation of species numbers in all regions and treatments by rarefaction. Additionally, combinations of treatments (and the control in Schwanden) were calculated. Species numbers were extrapolated to 500 000 individuals. See also Table 4.

3.5 Does treatment (clearing or not) create a particular fauna?

For the Schwanden area, with a control plot in the intact forest, the analysis of the number of exclusive species shows prominent changes in the first years after windthrow (Fig. 2). Saproxylic Coleoptera first drastically increased in species numbers. Mainly ubiquitous species (present in two or all three habitat types) seem to have profited from the disturbance. After 1994, those species decreased in numbers, and more specialised beetles prevailed (see also WERMELINGER *et al.* this issue). In the spider community (Araneae), an initial increase of ubiquitous species was also followed by a drop. Specialist spider species seemed to decrease in numbers, except in the cleared treatment. In the Carabidae, an initially rapid change in species composition in the first years showed some phase-shift in different treatments. Towards 2000 mainly ubiquitous species rose in numbers. Finally, the Syrphidae showed a phase-shift mainly in the first two years, with a few exclusive species in the cleared site and many more in the uncleared site.

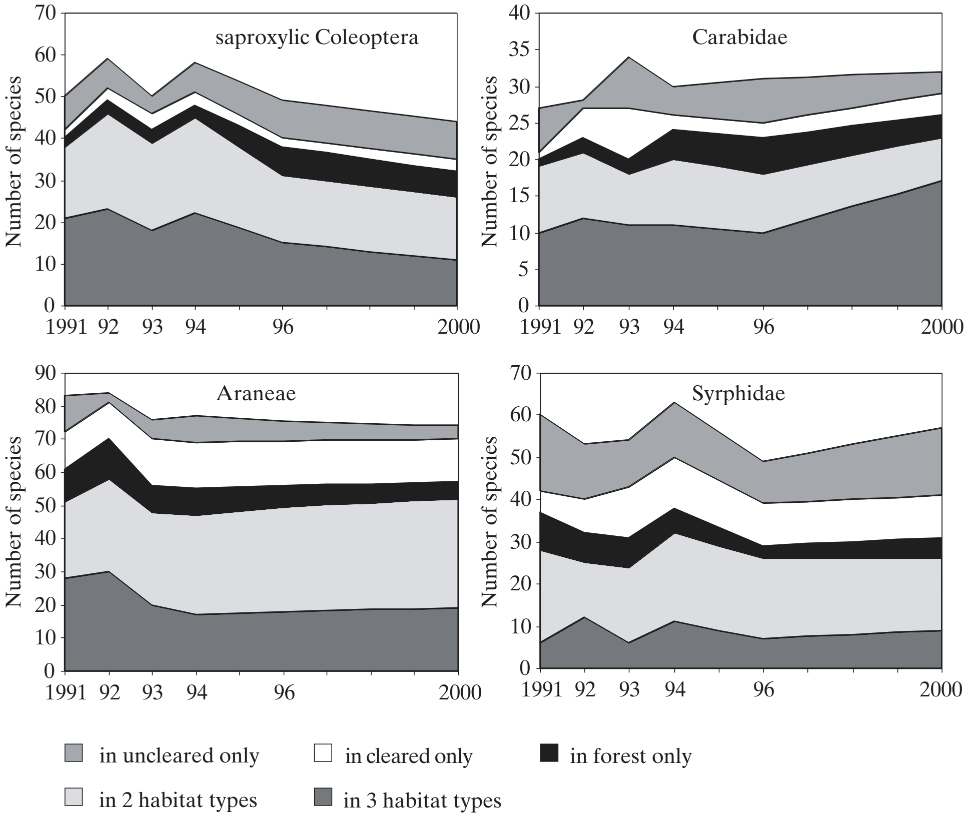

Fig. 2. Development of species numbers in four taxonomic groups at the site in Schwanden. Numbers are split up into species occurring in one treatment or the control only, in two habitat types (cleared and uncleared) or all three habitat types. Species numbers for the years 1995 and 1997 to 1999 are linear extrapolations of the adjacent years (1994, 1996, 2000, respectively).

3.6 Faunistic similarity as a function of region, treatment and distance

For the following analyses, we calculated Sörensen similarity indices between every possible pair of trap stations and statistically tested for differences with an ANOVA and regression analysis. The taxa considered in combination were the Araneae, Carabidae, saproxylic Coleoptera, and Syrphidae.

When comparing traps between Disentis and Pfäfers, significantly higher similarities were found than when comparing traps from either location with those in Schwanden ($F_{2,104} = 33.549$, $p \le 0.0001$). This does not reflect actual distances, but rather the degree of isolation brought about by the mountain chains. Following the river system, Pfäfers is closer to Disentis than to Schwanden, although in a direct line Pfäfers would be closer to Schwanden.

Within the same treatment and location, the Sörensen index decreased significantly (df = 22, t = –2.13, p = 0.0444) with increasing distance between two traps. The same was true for traps within the forest plot (df = 13, t = –2.94, p = 0.0115).

The findings in the traps in windthrow plots were most similar to those traps in the same plot, and significantly less to those in the alternative treatment ($F_{1,43} = 17.660$, p = 0.000131). They were even more dissimilar to traps in the control forest ($F_{1,93} = 113.91$, $p \le 0.0001$). In Schwanden, the forest community was more similar to the cleared treatment than to the uncleared treatment ($F_{1,34} = 8.6351$, p = 0.0059). The main reason for this was the mass occurrence of some bark beetles on the uncleared plot only.

When comparing trap locations from identical treatments and regions, the Sörensen indices were on average 0.1596 higher ($F_{1,150} = 964.1$, $p \le 0.0001$) than indices resulting from comparing trap locations from identical treatments but differing regions. The similarity between cleared and uncleared sites in different regions was only insignificantly less (0.0066) than that between traps from identical treatments in different regions. So the influence of distance (between regions) is much (24 times) greater than the influence of treatment.

Consequently, the observed slight differences in the species composition in the two treatments might be at least partly due to the effect of increased distances between the traps.

3.7 Ecological resilience after windthrow

The ecological resilience of an ecosystem indicates the time needed to return to the original state after an ecologically relevant impact (Pimm 1991). Here we measure ecological resilience by following the similarity indices during the succession after the windthrow. A high ecological resilience would manifest itself in a rapid increase in similarity (measured here as Renkonen indices) after the storm between the fauna in the intact forest and the two treatments. Similarly, we expected the species composition in the two treatments to converge over the years.

Does the fauna of windthrow forests approach that of the intact forest within the observation period? The saproxylic beetle fauna in both treatments became progressively more dissimilar to that of the forest control plot (Fig. 3). This was even more so the case with spiders. On the other hand, the carabid communities showed only slightly lower similarities with time, and the species composition of the syrphids, compared to the forest, remained very dissimilar throughout in both treatments.

How does the similarity between the species composition of cleared and uncleared windthrow evolve? We expected resilience in the form of increasing similarity between the two treatments over the years, but different trends resulted in the three regions and in different taxonomic groups. The carabid community (Fig. 4) tended to become more dissimilar in the two treatments during the first four years in Pfäfers and Disentis, and then, until 2000, remained at a lower level than 1991. The Araneae showed no consistent trend. The syrphids tended to become less similar in time, while the similarity of saproxylic Coleoptera was increasing (Fig. 4).

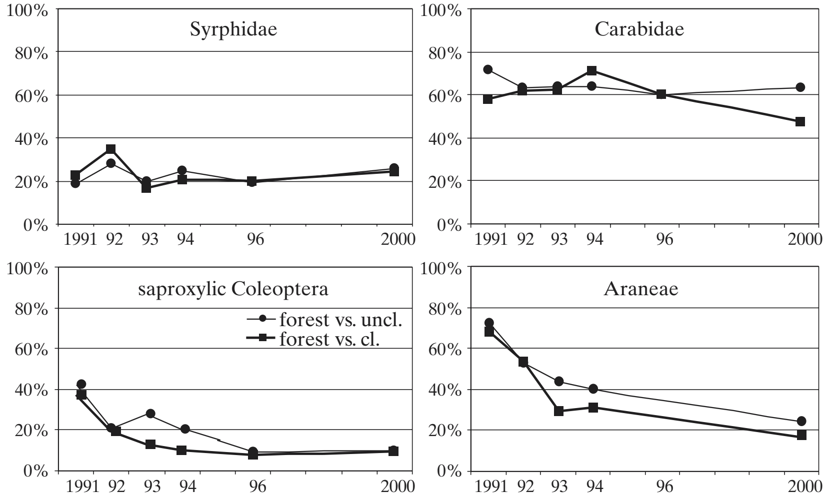

Fig. 3. Development of the similarity of the species composition in the two treatments compared to the forest in Schwanden. Renkonen indices were calculated for every sampled year for four taxonomic groups.

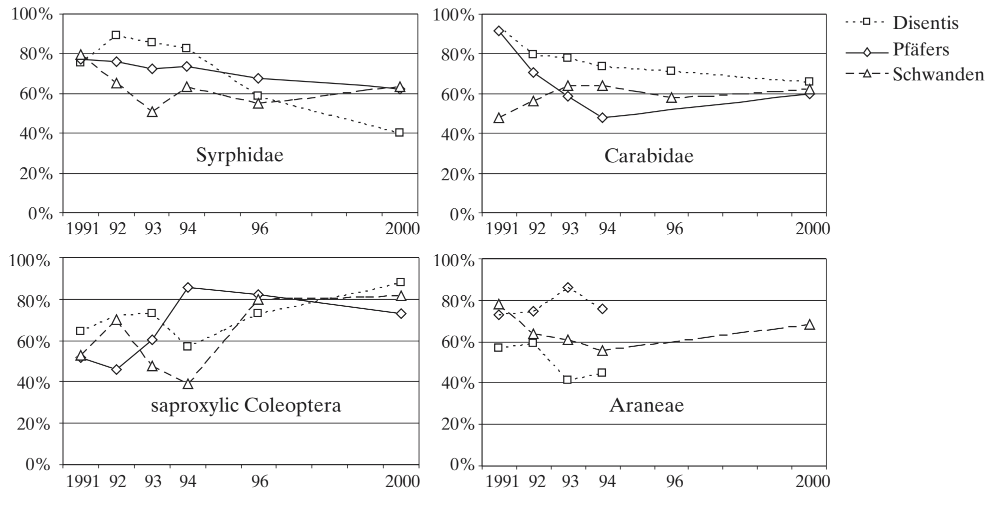

Fig. 4. Development of faunistic similarity of cleared compared to uncleared treatment. Four taxonomic groups and all three regions were considered. Renkonen indices were calculated for every sampled year. In 2000, spider data were available from Schwanden only.

4 Discussion

The faunistic project started out with the main question: What is better for biodiversity, to clear or not to clear after a windthrow? Several aspects of biodiversity have to be taken into account. Here we focused on species richness (measured per trap station or estimated per 1 hectare plot) and on species conservation (number of red-listed species). In addition, we compared the ecological resilience in the two treatments by analysing the development of similarity indices up to ten years after the storm.

Several hypotheses concerning the succession of biological diversity after the storm in 1990 were given in the introduction. They will be treated here in the light of our results and the limited literature on the subject.

1. According to the hypothesis of intermediate disturbance (CONNELL 1979), disturbances can disrupt processes of competitive exclusion, and hence increase biodiversity as long as they are not so strong and/or frequent that species are excluded.

   The hypothesis that windthrow causes an overall increase in biodiversity is well supported by our data from Schwanden, the only region with a control plot in intact forest (Table 1). Apart from bark beetles, molluscs and some arthropod groups depending on high humidity (Isopoda, Opiliones, Diplopoda), all identified animal groups showed an increase in species richness after the storm. The highest gains were observed in aculeate Hymenoptera (3–4x), buprestid beetles (3–4x), small mammals (2–5x) and the reptiles (none in the forest).

   The estimated total number of species (of all identified groups) present on one hectare of a windthrow plot was also roughly 50% higher than in the forest (Fig. 4).

   In the course of nine years succession after the first year of collecting, the species numbers further increased in the windthrow areas by more than 50%, while the species gain in the forest control plot was insignificant and presumably due to immigration from the nearby windthrow plots.

   The effect of the same storm Vivian on the fauna in windthrow in Germany has been investigated by KENTER and FUNKE (1995), KENTER *et al.* (1997), and other authors (FISCHER 1998). For epigeal arthropods, such as spiders, carabids and staphylinid beetles, these investigations found a higher species richness in windthrow areas than in the intact forest. The increase in species numbers was also in the range of 50% (KENTER *et al.* 1998).

   Similarly, the numbers for Diplopoda and Isopoda (SPELDA *et al.* 1998) only showed a slight tendency for a higher diversity in the windthrow sites, whereas the results for the molluscs in Germany also indicate a slight increase, which clearly differ from our results.

   In addition, KENTER *et al.* (1998) investigated the Chilopoda, but the results varied very much depending on the method of collecting and the locality. KRAUSS *et al.* (1998) found slightly more Collembola, Pauropoda and Symphyla in soil samples from uncleared plots than in the forest.

   LENSKI (1982), comparing clearcuts and adjacent forests in North Carolina, also found more species and individuals of carabid beetles in clearcuts than in the forest.

2. The second hypothesis claims that uncleared windthrow harbours a higher diversity of organisms because of a higher structural diversity. SPELDA *et al.* (1998) found slightly more species of soil-inhabiting arthropods and molluscs in uncleared plots, whereas KENTER *et al.* (1998), focussing on epigeal arthropods, found more species of carabids, staphylinids and spiders on cleared plots.

   On our sites, more species were found on the uncleared plot at Disentis, the reverse was true for Pfäfers, while at the Schwanden sites both the cleared and uncleared site yielded about the same number of species (Table 1). Overall, 1394 species were found on the uncleared plots, 1434 on the cleared ones. Therefore, the hypothesis of a maximum of species on the uncleared plots clearly has to be rejected. The number of specimens collected, however, was consistently higher on the uncleared plots. This was particularly true for bark beetles. The ample supply of breeding material triggered an outbreak of *Ips typographus,* leading to extensive attack on living spruce trees (WERMELINGER *et al.* this issue).

There is no doubt that the structural diversity was greater on uncleared plots, so that, other factors must have tipped the balance in favour of the cleared plots. The most likely explanation is that more sunlight reaching the ground enhances biodiversity in various ways. The quantity and diversity of flowering plants growing on the sunlit surface was much higher on the cleared plots (WOHLGEMUTH *et al.* this issue). Many insects, such as bees, wasps, bugs and syrphid flies, visit the flowers. Buprestid and cerambycid beetles also require pollen as food for reproduction. Furthermore, the cleared plots were not as completely cleared as would have been wished for a scientific experiment: Many of the uprooted tree stumps were left on the plots after the stems had been removed.

Observations in windthrow areas in the Bavarian Forest also led to different results depending on the investigated animal group. While THEOBALD-LEY and HORSTMANN (1990) found many more ant species in the cleared plots than in the uncleared plots and plantation forests, OTTE (1989) collected 14% more insect species on the uncleared plots, particularly more stenotopic forest species.

3. A strong argument against clearing windthrow areas came from advocates of species conservation, claiming that uncleared windthrow provides ideal habitats for rare and endangered species. Table 3 clearly shows that none of the red-listed categories of threat is better represented in the uncleared plots than in the cleared ones. Slightly more endangered saproxylic beetles were found on the uncleared plots, but, on the other hand, more red-listed bees were collected on the cleared plots.

4. The hypothesis that the faunal assemblies of cleared and uncleared windthrow plots differ, and thus combining both treatments within an area will yield maximum biodiversity, can be confirmed (Fig. 1). The species gain is an estimated average of 23% (Table 4).

5. From our results, there is no evidence that a particular fauna is characteristic of cleared or uncleared windthrow sites. Regional influences on the species composition are far more important than the type of treatment. There were no indicator species present in all three regions that were restricted to one of the treatments. Still, there were some differences between taxonomic groups: While more saproxylic beetles were restricted to the uncleared plot at Schwanden, more spider species were restricted to the cleared plot (Fig. 2).

6. Intuitively, one would assume that uncleared plots are more similar to the intact forest than the cleared plots. But here again, there is no evidence from our results that this is the case (Fig. 3). In fact, the fauna in both treatments is either similar (Carabidae) or dissimilar (syrphid flies) to that of the intact forest over the years, or the similarity decreases, as in spiders and saproxylic beetles.

Comparing the similarities between the species compositions of the two treatments in all three regions separately also yielded no sign of resilience (Fig. 4). Only the fauna of the saproxylic beetles shows a tendency to converge in the two treatments after some years. This is mainly due to the drastic outbreaks of a few bark beetle species on the uncleared plots in the first years after the windthrow. As soon as similarity is measured with an index which does not consider species abundances (Sörensen), the saproxylic beetles also show a decreasing similarity with time (WERMELINGER *et al.* this issue).

Quite contrary to our results, but in accordance with the initial hypothesis, OTTE (1989) in his investigation of windthrow gaps in the Bavarian Forest found much higher faunistic similarity between the uncleared plots and the forest, as compared to the cleared plots.

With birds also, the similarity between the species compositions in cleared and uncleared plots increased within a few years after the storm in the German investigations on the Vivian windthrow gaps mentioned earlier (WERTH *et al.* 1998). After the storm, many more birds were observed on the uncleared plots, particularly insectivorous birds and large predators. But with the vegetational changes during succession, the avifauna of the uncleared plots decreased and became similar to that of the cleared plots, where the species richness increased. In uncleared windthrow areas in Central Switzerland, GLUTZ VON BLOTZHEIM (2001) observed more bird species after the storm Vivian than in the kind of forest present before the storm. The highest densites of bird territories were found in the earliest successional stages of mixed stands, and the lowest inside the dense spruce forest. The numbers of occupied territories in the windthrow areas peaked 3 to 6 years after the start of the observation period. Species numbers, after a first rise following the storm, remained fairly constant or slowly increased, and reached a peak at the end of the observation period after 10 years. Only ten years after the storm, the species composition started to converge with the original forest fauna.

VÖLKL (1991) compared the fauna (reptiles, grasshoppers, bees and ants) in German forest clearings of different ages. Four to seven years after the clear-cuts, only 50% of the species composition found in old gaps were encountered in the new clearings. A continuous increase in species richness in the disturbed areas was also found in our studies. Ten years of succession were clearly not long enough to reveal the first signs of ecological resilience in the form of a faunistic recovery to the state before the storm, i.e. to the forest control plot.

5 Conclusion

A storm increases biodiversity by attracting forest species with low densities to a common habitat. It enables the reproduction, genetic exchange and build-up of local populations. The conclusion from our study and the scanty literature on the topic is that the best way to enhance biodiversity after windthrow is to both clear and not clear, clearing half of the windthrow areas and leaving the other half uncleared. In practice, with several forest gaps in an area, the best solution for biodiversity is to create pairs of gaps of similar exposition and forest type to implement both treatments. If costs are of prime concern, the choice will be to clear the most accessible or valuable half of the windthrow and leave the rest untouched. In the case of spruce stands, however, that procedure may interfere with bark beetle management strategies.

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