1   **Impact of windthrow and salvage-logging on taxonomic and functional**

2   **diversity of forest arthropods**

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23   **Abstract**

24   Windthrow is recognized as the most important driver in European forest dynamics

25   and its importance is likely to increase with climate change. Typically, windthrown

26   timber is salvaged for economic and phytosanitary reasons. This markedly affects the

27   natural development of the disturbed areas, in particular by removing important dead

28   wood resources. For a sustainable and ecologically sound management of

29   disturbance effects, more knowledge is needed on the impact of windthrow and

30   salvage logging on animal species communities.

31   We monitored various arthropod taxa (spiders and insects) two and five years after

32   the storm Lothar in 1999 in salvaged and unsalvaged windthrows as well as in

33   adjacent intact forests. Basing on a comprehensive data set with 1276 species and

34   228 718 individuals, species diversity, abundance and community composition were

35   compared. Species richness and abundance of most taxonomic and functional

36   groups (pollinators, saproxylics and predators) in the windthrow habitats clearly

37   differed from those in the intact forests. On average, twice as many species were

38   present in windthrows as in the forest. Windthrows also supported more red-listed

39   beetles (mainly saproxylics) than the intact forest and more habitat indicator species

40   (mainly Heteroptera and Aculeata) were found in windthrow areas.

41   No difference in species diversity was found between salvaged and unsalvaged

42   windthrows. However, similarity analyses showed that the communities of certain

43   taxonomic and functional groups differed between the two salvaging treatments. A

44   combination of unsalvaged and salvaged windthrows in intact forests increased local

45   species richness approximately 2.5 times relative to that in the forests alone.

46   Therefore after large-scale windthrows, a mosaic of salvaged and unsalvaged

47   windthrow patches fosters high forest biodiversity levels.

48

49   Keywords: disturbance, insects, saproxylic beetles, similarity, species richness,

50   timber harvest

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1. Introduction

Disturbances rapidly alter the state of an ecosystem, creating landscape heterogeneity and distinctly impacting the system's trajectory (Turner 2010). Windthrow is a typical abiotic disturbance that stochastically recurs at various spatial and temporal scales (Thom *et al.* 2013). In Europe, windstorms are the prime natural disturbance agent in forests, followed by fire and biotic agents (Schelhaas *et al.* 2003). The large-scale windthrows caused by the devastating winter gales Vivian and Wiebke (1990), Lothar (1999), Gudrun (2005) and Kyrill (2007) in Central and Northern Europe led to extensive discussions about the ecological and economic consequences of harvesting the fallen timber, i.e. of salvage logging. Windthrow in forests affects timber resources, the protective function of mountain forests and the silvicultural planning of forest managers.

1.1 Ecological consequences of windthrow

Large windthrows bring about drastic changes in a forest. The formerly closed-canopy habitat abruptly becomes open landscape. The loss of the dominant tree canopy leads to more sun exposure and favors herbaceous ground vegetation (Wohlgemuth *et al.* 2002). This dynamically developing habitat with multifaceted structures provides food and shelter for a great variety of organisms. Recent research has highlighted the ecological significance of windthrow as a natural component in the dynamics of forest ecosystems and as an important driver for biodiversity (Duelli *et al.* 2002; Bouget & Duelli 2004; Gandhi *et al.* 2009). An obvious consequence of windthrow is that it creates ample supply of dead wood. This substrate is increasingly valued as an essential habitat for threatened saproxylic species, and has been singled out as an indicator for the sustainable stewardship of

78   forests by the European Environment Agency (EEA 2010). However, the lack of dead

79   wood is still a limiting factor for many saproxylic taxa in most managed European

80   forests. Primeval forests with large quantities of dead wood in various dimensions

81   and decay classes support a specific fauna of saproxylic species (Müller *et al.* 2005;

82   Gossner *et al.* 2013). In intensively managed forests, a number of saproxylic beetle

83   species are threatened and are thus red-listed (e.g. Nieto & Alexander 2010). The

84   substrates that are most lacking are large-diameter logs in medium to late

85   decomposition stages (Brin *et al.* 2011; Gossner *et al.* 2013; Seibold *et al.* 2015).

86   While the development of arthropod communities after wildfire has been in the

87   focus of a considerable number of studies (e.g. Boulanger & Sirois 2007; Moretti *et*

88   *al.* 2010; Cobb *et al.* 2011; Elia *et al.* 2012), less research has been devoted to the

89   short- and long-term responses of arthropod communities to windthrow (Bouget &

90   Duelli 2004). Most investigations to date have concentrated on the short-term

91   reactions of specific insects, e.g. the dynamics of detrimental bark beetles in

92   coniferous forests (e.g. Bouget & Noblecourt 2005; Komonen, Schroeder & Weslien

93   2011; Wermelinger *et al.* 2013; Stadelmann *et al.* 2014) or other saproxylic beetles

94   (Kopf & Funke 1998; Wermelinger *et al.* 2002; Bouget 2005; Gandhi *et al.* 2009).

95   Others have compared unlogged windthrows with intact forest (Otte 1989; Kenter &

96   Funke 1995; Bouget 2005; Grimbacher & Stork 2009). Most studies were carried out

97   in coniferous forests.

98

99   *1.2 Salvaging effects*

100   Only limited data are available on the effects of salvage logging on the insect

101   fauna. Usually, windthrows are salvaged for economic as well as for phytosanitary

102   reasons. Apart from eliminating important resources for saproxylic species, salvage

103   logging also alters surface structure, soil, microclimatic and vegetational conditions in

104   the logged areas. While some findings on specific taxa in spruce forests have been

105   published (Otte 1989; Kenter *et al.* 1998; Duelli *et al.* 2002; Thorn *et al.* 2014), no

106   results are available to date based on consistent data sets across multiple taxonomic

107   and functional groups of arthropods or for non-coniferous forests.

108   With climate change, large-scale storms are likely to become more frequent and/or

109   more severe (Fuhrer *et al.* 2006; Usbeck *et al.* 2010). Thus, forest managers will be

110   faced more often with making a decision about salvage-logging windthrows, taking

111   into consideration both economic and ecological aspects. Moreover, the pressure to

112   salvage windthrown timber will increase because with promoting non-fossil fuels the

113   damaged and low-quality timber and slash is now increasingly exploited as energy

114   wood. Therefore, comprehensive knowledge is needed particularly on the effect of

115   salvage-logging on biodiversity. However, studies in windthrows are not easily-

116   planned experiments with sufficient replicates in space and time, and the abiotic and

117   biotic properties often differ even between windthrows that were caused by the same

118   storm.

119

120   *1.3 Goal of this study*

121   This article focuses on the effects of windthrow per se, as well as of salvage

122   logging, on arthropod α- and β-diversity by comparing the composition of various

123   taxonomic and functional arthropod groups. We used three case studies from

124   different forest types, each with salvaged windthrows, unsalvaged windthrows and

125   intact stands and from two sampling years. Specifically, we applied generalized linear

126   mixed models to evaluate the effects of these three treatments on species richness,

127   abundance and diversity of six taxonomic and three trophic groups. Moreover, we

128   calculated Bray-Curtis similarities to compare community compositions and used

129   IndVal analyses to identify indicator species for the treatments.

130

131

132   **2. Materials and methods**

133   *2.1 Study sites and treatments*

134   Studying ecological effects of natural disturbances such as severe storms have to

135   rely on real situations that often do not meet all statistical requirements of specifically

136   designed experiments and thus have case-study character. Hence, the windthrow

137   areas caused by the devastating storm "Lothar" on 26 December 1999 had to meet

138   the following minimal requirements: complete tree blowdown, similar elevation,

139   nearby control forest, salvaged and unsalvaged plots available, and contracted

140   agreement that these plots remain unchanged for long-term research for at least two

141   decades. Three locations could be selected on the Central Plateau of Switzerland

142   (Table 1): Sarmenstorf (Canton Aargau) with a beech (*Fagus sylvatica* L.) forest,

143   Messen (Canton Solothurn) with a spruce (*Picea abies* [L.] Karst.) forest and

144   Habsburg (Canton Aargau) with a mixed forest. The mixed forest was approx. half

145   coniferous (mainly spruce with some *Pinus sylvestris* L., *Larix decidua* Mill. and *Abies*

146   *alba* Mill.) and half broad-leaved (mainly beech with some *Acer pseudoplatanus* L.).

147   At each location, we selected a triplet of treatments, i.e. an unsalvaged windthrow, a

148   salvage-logged windthrow, and an intact control forest. In the unsalvaged plots, no

149   timber harvesting or regeneration planting was carried out. In the salvage-logged

150   windthrow plots, the timber was harvested, but the stumps and small branches were

151   left on site and some regeneration planting was done. The intact forest plots

152   unaffected by windthrow served as control treatment. In each location, the three

153 treatment plots were close to each other (a few 100 m, one control forest 3 km) to

154 keep site conditions and stand structures as similar as possible. In each treatment

155 plot, dead wood was classified as either CWD (coarse woody debris) or FWD (fine

156 woody debris). CWD has a mean diameter >10 cm and included upright snags and

157 stumps, while FWD is between 1 and 10 cm diameter. The volume was estimated

158 with the fixed-area-plot sampling method (Harmon & Sexton 1996).

159 The arthropod communities in these study sites have been monitored since 2001.

160 Here we present the results of the sampling campaigns two and five years after the

161 windstorm.

162

163 Table 1. Characteristics of the investigated sites and treatment plots (salvaged and unsalvaged
164 windthrow and adjacent intact forest). CWD= coarse woody debris (ø > 10 cm), FWD= fine
165 woody debris (ø = 1-10 cm). The climate data are means from the years 2000 to 2004.

166

	Sarmenstorf			Habsburg			Messen		
Location	WGS84: 8°15'17" / 47°19'13" CH1903: 661800 / 241100			WGS84: 8°12'20" / 47°28'22" CH1903: 657600 / 258000			WGS84: 7°27'52" / 47°5'23" CH1903: 601800 / 215100		
Altitude (a.s.l.)	600 m			450 m			550 m		
Slope	10 % NE			5 % SE			0%		
Mean annual temperature	10.1°C			9.3°C			9.7°C		
Mean annual precipitation	1066 mm			1195 mm			1148 mm		
Forest type	Beech (Fagus sylvatica)			Mixed (50 % conifers, 50 % broadleaves)			Spruce (Picea abies)		
Forest development stage	young timber (31-40 cm dbh)			medium timber (41-50 cm dbh)			pole wood (12-30 cm dbh)		
Windthrow area unsalvaged	2.3 ha			30 ha			3.5 ha		
salvaged	5 ha			13 ha			1.2 ha		
	Forest	Unsalvaged	Salvaged	Forest	Unsalvaged	Salvaged	Forest	Unsalvaged	Salvaged
Dead wood (m³/ha) CWD	24.5	295.9	52.1	14.3	563.3	70.1	24.5	222.8	38.7
FWD	12.1	28.7	96.9	8.4	80.1	8.9	12.0	52.0	10.8
Total	36.7	324.6	148.9	22.7	643.4	79.0	36.5	274.8	49.5

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169 *2.2 Insect sampling design*

170 In each treatment plot, three flight interception traps were set up approximately

171 100 m apart from each other, and five pitfall traps were distributed in the same way

172 according to a design used in other similar studies (Müller & Brandl 2009; Stenbacka

173   *et al.* 2010). The flight interception trap consisted of a wooden frame supporting a

174   yellow plastic funnel (43 cm in diameter) with two acrylic glass panes (50 x 43 cm

175   each) mounted crosswise on top of the funnel (Duelli *et al.* 1999). The funnels were

176   closed with a rubber stopper and filled with water spiked with 0.5 % Rocima GT

177   (Acima, Buchs, Switzerland) as a bactericide and detergent. The pitfall trap consisted

178   of a plastic funnel (15 cm in diameter) screwed to a bottle filled with an aqueous 4 %

179   formaldehyde solution (Duelli *et al.* 1999). It was placed in a plastic tube buried in the

180   soil and protected from rainfall with a transparent plastic roof.

181   A total of 27 flight traps and 45 pitfall traps were operated from mid-March to the

182   end of September in both 2001 and 2004. Every week, the arthropod catches were

183   collected and the traps serviced. In the laboratory, the arthropods were stored in

184   70 % alcohol and subsequently identified by taxa specialists. Nomenclature follows

185   the Fauna Europaea database (de Jong *et al.* 2014).

186

187   *2.3 Data analysis*

188   In the analysis, the sampling period was restricted to the period from 20 March to

189   27 September to have comparable catching periods in both years. For each species,

190   the catches were pooled per year and trap. Analyses were made for six taxonomic

191   groups, i.e. Araneae, Coleoptera (56 families), Aculeata (without Formicidae),

192   Syrphidae, Heteroptera and Neuropterida (Raphidioptera, Neuroptera, Megaloptera),

193   and for three functional groups (guilds), i.e. pollinators (Apoidea, Syrphidae),

194   saproxylic beetles (Buprestidae, Cerambycidae, Lucanidae, saproxylic genera of

195   Elateridae) and predators (Araneae, Carabidae, Neuropterida, predatory families of

196   Heteroptera) (cf. Table A.1 in the online Appendix). The red-listed species (Table

197   A.2) were selected according to combined Central European lists, largely relying on

198   the Red Lists from Switzerland's neighboring country Germany (Köppel *et al.* 1998).

199   All statistical analyses of the effects of treatment and forest type were performed

200   using R-software v.3.3.2 (R Core Team 2016). Each doublet of flight interception trap

201   and the nearby pitfall trap represented a sampling unit (i.e. 27 sampling units), except

202   for the epigeic Araneae where each of the 45 pitfall traps was a sampling unit. We

203   treated the sampling unit as random effect, thus accounting for over-dispersion by

204   using trap-level random effects (Jamil *et al.* 2013). To test for effects on insect

205   abundance, we used GLMER with Poisson distribution and then applied post-hoc

206   tests with nonparametric methods using function mctp (R package nparcomp) with

207   type Tukey and applying Fisher transformation method. If species richness or

208   Simpson diversity data were not normally distributed (Shapiro test) we processed

209   them like the abundance data. If data proved normally distributed, they were

210   analyzed with LMER (R package lme4). In these cases we did post-hoc tests using

211   Tukey contrasts of function glht (R package multcomp).

212   Similarities of the arthropod communities in and between treatments were

213   calculated using the Bray-Curtis similarity index (Bray & Curtis 1957), computed as

214   1 - D, where D is the dissimilarity index between species communities. Community

215   similarities were calculated in each treatment (intact forest 'F', unsalvaged windthrow

216   'U' and salvaged windthrow 'S') and between pairs of treatments (U-S, U-F and S-F).

217   For these between-treatment comparisons, all possible combinations of trap pairs of

218   the treatment pairs were considered in order to minimize within-treatment variability.

219   Species characteristic for treatment (i.e. intact forest, unsalvaged and salvaged

220   windthrow) were identified using indicator value analysis (IndVal) (Dufrêne &

221   Legendre 1997). We followed the method described by De Cáceres *et al.* (2010),

222   which involves testing the association of the species with single treatments and all

223   their combinations. The significance of association (P<0.05) was obtained using a

224   randomization procedure (999 permutations) and Holm's correction for multiple tests.

225   All significant indicator species with a sensitivity value <0.25 were removed to

226   discard those that are too rare, i.e. that occur in less than 25 % of sampling plots, as

227   suggested by De Cáceres *et al*. (2012).

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229

230   **3. Results**

231   *3.1 Effects on species richness, abundance and diversity*

232   From the two sampling years, a total of 1 276 species (2001: 997 sp.; 2004: 995

233   sp.) with 228 718 individuals (2001: 104 798 ind.; 2004: 123 920 ind.) were identified

234   (Table A.1). The three treatments, i.e. forest, salvaged and unsalvaged windthrow,

235   were found to have a very profound impact on both species richness and abundance

236   (Table 2). Species richness and abundance of all taxonomic and functional groups

237   significantly differed between treatments. While almost all differences between the

238   salvaging treatments were insignificant (irrespective of forest type; Table A.3), the

239   arthropod diversity in intact forest in most cases clearly differed from those in

240   windthrow areas (both salvaged and unsalvaged).

241   The species richness of all taxa followed the same pattern: Considerably more

242   species were found in the windthrow areas (Fig. 1A). This was most pronounced for

243   bees and wasps (Aculeata) and true bugs (Heteroptera). Their number of species

244   found in the open windthrow plots was almost four times higher than that in the

245   forest. Only 99 of the 331 aculeate species occurred in the forest. As an exception,

246   the number of spider (Araneae) species tended to differ also between the two

247   salvaging treatments (cf. Table A.3).

248

249

250 Table 2. Significances and contrasts of LMER/GLMER analyses of species richness, abundance and

251 Simpson diversity of arthropod taxonomic and functional groups as affected by treatment

252 (salvaged and unsalvaged windthrow, intact forest) and forest type (conifer, beech, mixed

253 forest). Significance levels: ***= p<0.001, **= p<0.01, *= p<0.05; the arrows indicate higher

254 (up) or lower (down) values of the second argument compared to the first one (example:

255 'Forest–Unsalvaged ↗' = value for 'unsalvaged windthrow' is higher than for 'intact forest').

	Treatment effects				Forest type effects			
Species number	Treatment	Forest-Unsalv.	Forest-Salvaged	Unsalv.-Salvaged	Forest Type	Beech-Mixed	Beech-Spruce	Mixed-Spruce
Total taxa	***	*** ↗	*** ↗	ns	**	ns	ns	ns
Araneae	***	*** ↗	*** ↗	ns	***	ns	** ↗	ns
Coleoptera	***	*** ↗	*** ↗	ns	**	ns	ns	ns
Aculeata	***	*** ↗	*** ↗	ns	*	ns	ns	ns
Syrphidae	***	*** ↗	*** ↗	ns	***	ns	ns	ns
Heteroptera	***	*** ↗	*** ↗	ns	***	ns	ns	ns
Neuropteroidea	**	*** ↗	*** ↗	ns	ns	ns	ns	* ↘
Pollinators	***	*** ↗	*** ↗	ns	*	ns	ns	ns
Saprox. Coleopt.	***	*** ↗	*** ↗	ns	***	ns	* ↗	ns
Predators	***	*** ↗	*** ↗	ns	ns	ns	ns	ns
RL Coleoptera	**	ns	** ↗	ns	ns	ns	ns	ns
Abundance								
Total taxa	***	** ↗	ns	ns	***	ns	ns	ns
Araneae	***	*** ↗	*** ↗	ns	***	* ↘	ns	ns
Coleoptera	***	ns	ns	ns	***	** ↗	** ↗	ns
Aculeata	***	*** ↗	*** ↗	ns	***	ns	ns	ns
Syrphidae	***	*** ↗	*** ↗	ns	***	ns	ns	ns
Heteroptera	***	*** ↗	*** ↗	ns	ns	ns	ns	ns
Neuropteroidea	***	*** ↗	*** ↗	ns	ns	ns	ns	ns
Pollinators	***	*** ↗	*** ↗	* ↘	***	ns	ns	ns
Saprox. Coleopt.	***	*** ↗	*** ↗	ns	***	* ↗	* ↗	ns
Predators	***	ns	ns	ns	***	*** ↘	** ↘	ns
RL Coleoptera	***	ns	ns	ns	ns	ns	ns	ns
Simpson index								
Total taxa	*	ns	ns	* ↗	***	* ↘	* ↘	ns
Araneae	***	*** ↘	ns	** ↗	***	** ↗	*** ↗	ns
Coleoptera	***	ns	** ↗	ns	***	ns	ns	ns
Aculeata	***	*** ↘	*** ↘	ns	ns	ns	ns	ns
Syrphidae	***	*** ↘	*** ↘	ns	ns	ns	ns	ns
Heteroptera	***	*** ↗	** ↗	ns	ns	ns	ns	ns
Neuropteroidea	ns	** ↗	* ↗	ns	ns	ns	ns	ns
Pollinators	***	*** ↘	*** ↘	ns	ns	ns	ns	ns
Saprox. Coleopt.	*	ns	* ↗	* ↗	ns	ns	ns	ns
Predators	*	ns	ns	* ↗	***	ns	** ↗	ns
RL Coleoptera	ns	ns	ns	ns	ns	ns	ns	ns

256

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A) Species richness

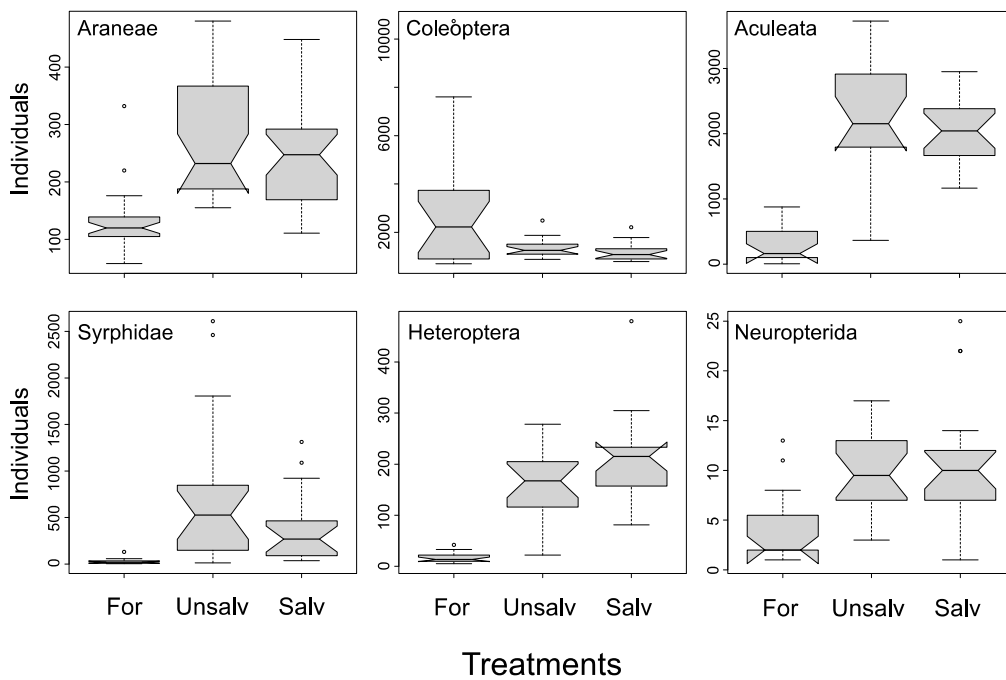
B) Abundance

258
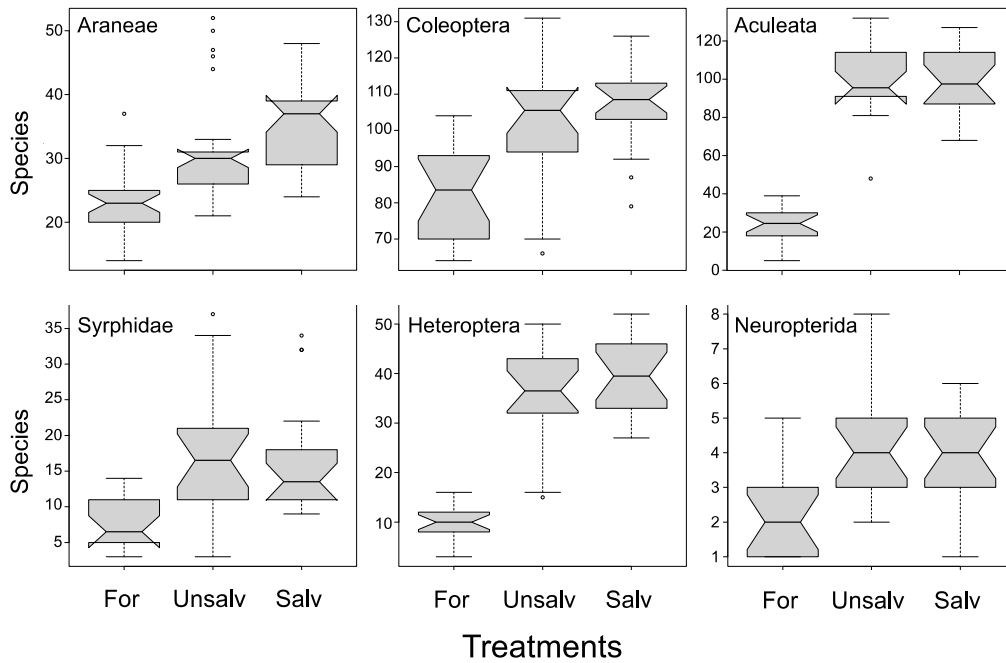
259 Figure 1: Species richness (A) and abundance (B) of arthropod taxonomic groups in intact forest (For),

260   unsalvaged (Unsalv) and salvaged (Salv) windthrow plots (treatments). Box = interquartile

261   range; whiskers = maximum interquartile-range x 1.5, dots = extreme values. Non-

262   overlapping notches of two boxes are strong evidence of a significant difference between the

263   two medians. Note that notches may exceed interquartile ranges.

264   (1.5-column figure)

265

266   The abundance of the taxonomic groups roughly followed the pattern of the

267   species richness (Fig. 1B). Except for the Coleoptera, all taxa were distinctly more

268   abundant in the windthrow areas. Among the Aculeata, the honey bee *Apis mellifera*

269   L. was clearly the most abundant species, but only 3 % of them were caught in the

270   intact forest. Hover flies and true bugs were also almost completely absent in the

271   forest (cf. Table A.1). The abundance of the Coleoptera differed from the other taxa

272   in that this group was more abundant in the intact forest (Fig. 1B). This is largely due

273   to the Carabidae and particularly to the Scolytinae that reached extremely high

274   numbers in the forest (Table A.1). The predominant carabid species was *Abax*

275   *parallelepipedus* (Piller and Mitterpacher) in all treatment and forest types. Within the

276   Scolytinae, the overwhelming majority (72 %) belonged to one single species, i.e.

277   *Xylosandrus germanus* (Blandford), an ambrosia beetle that was accidentally

278   introduced to Europe in the 1950s. This beetle was roughly 10 times more abundant

279   in the forest than in both salvaging treatments. Other coleopteran taxa, in particular

280   Buprestidae and Cerambycidae (cf. saproxylic Coleoptera in Fig. 2A and Table A.1),

281   clearly preferred the windthrows. Less than 1 % of the buprestid beetles were

282   captured in the forest.

283   The Simpson-diversity of most taxa differed between forest and windthrows but in

284   a rather inconsistent way (Table 2). Astonishingly, overall diversity of all arthropods

285   (total taxa) differed between the salvaging treatments, but did not between forest and

286   windthrows.

287   The pattern seen at the taxonomic level was also repeated at the level of

288   functional diversity (Fig. 2A). Species richness and abundance were both greater in

289   the windthrow areas than in the forest. This was particularly true for the pollinators

290   and saproxylic beetles. The higher abundance of predators in windthrows was not

291   statistically significant (Table 2). In contrast to all other taxonomic or functional

292   groups, pollinator abundance not only differed between forest and windthrow but also

293   between the salvaging treatments with more individuals found on unsalvaged plots.

294   The predatory carabids were more abundant on salvaged windthrows (Table A.1).

295   The number of red-listed Coleoptera tended to be higher in the windthrow habitats

296   than in the intact forest (Fig. 2B, Table 2). Among the beetles with red-list status, two

297   species were classified RE (regionally extinct) (cf. Table A.2), although they were

298   present in Switzerland. This is due to the fact that the conservation status compiled

299   for the invertebrate fauna of neighboring Germany obviously not fully matches the

300   Swiss situation. However, in Switzerland, these two species are endangered as well.

301   Arthropod species and abundance were affected by forest type to a much lesser

302   extent than by treatments (Table 2). The spruce forest supported more species of

303   spiders (Araneae) and saproxylics than the beech forest while the beech forest

304   showed a lower abundance of Coleoptera, in particular saproxylics, than the other

305   forest types. On the other hand, predators were clearly most abundant in the beech

306   forest. There were very few differences between forest types in the response to

307   timber salvaging (Table A.3).

308   Species richness and abundance in the two sampling years only differed, in an

309   inconsistent way, for a few specific taxonomic groups and not at all for the functional

310   groups (data not shown). The two sampling years are too close to reveal temporal

311   trends in the arthropod diversity.

312

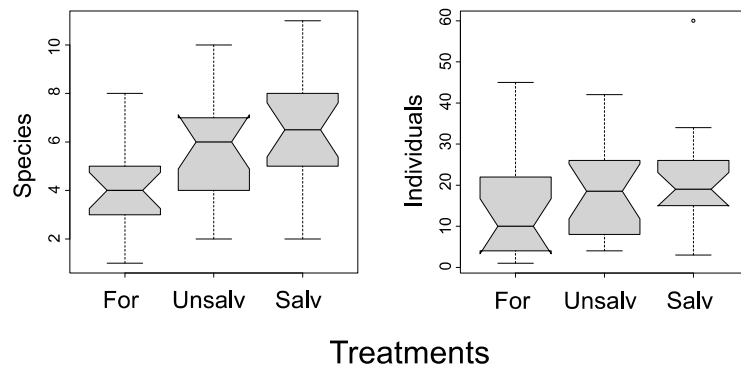## A) Functional groups
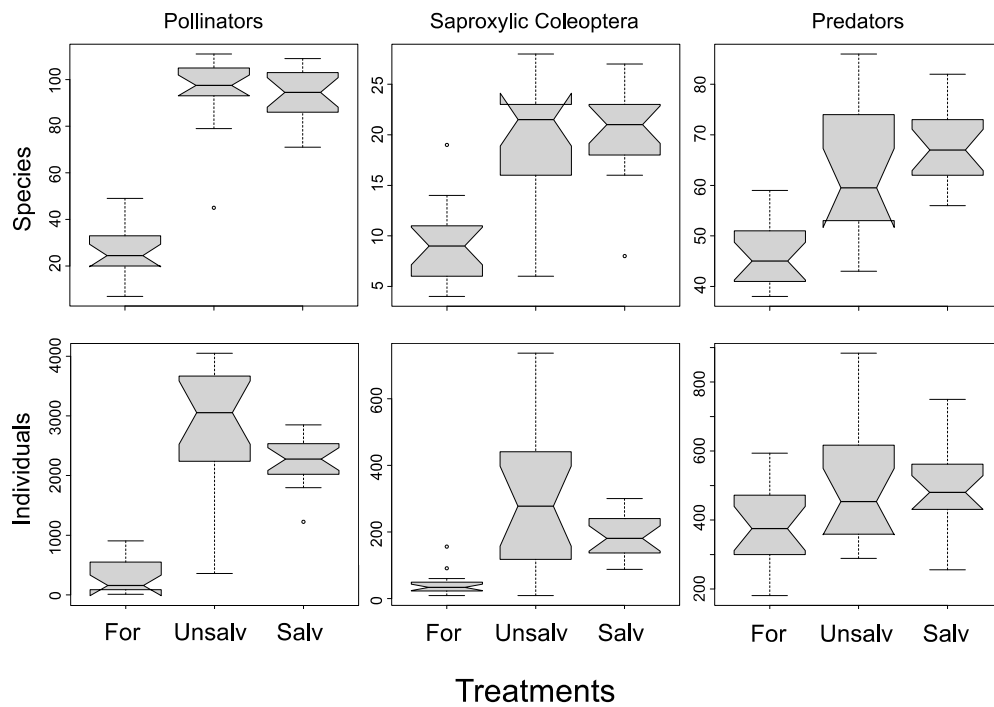
B) Red-listed Coleoptera

Figure 2: Species richness and abundance of A) functional arthropod groups and of B) red-listed beetles in intact forest (For), unsalvaged (Unsalv) and salvaged (Salv) windthrow plots (treatments) (for boxplot interpretation, see Fig. 1).

(1.5-column figure)

3.2 Community composition

As shown above, the two salvaging treatments mostly harbored a very similar species richness (Figs 1, 2). To evaluate whether they differed in the composition of

322   their communities, Bray-Curtis similarity indices were calculated. In Fig. 3, similarities

323   of the functional groups are depicted for each forest type separately, while those of

324   the taxonomic groups are given in Fig. A.1. The first three boxes in each graph, i.e.

325   those for forest, unsalvaged and salvaged windthrow, indicate the similarities of the

326   communities among the traps within a given treatment plot (within-treatment

327   similarity). Ideally, their index would equal 1 since the traps are situated in the same

328   treatment plot. In general, the within-treatment similarities were comparable in all

329   treatments with their medians ranging from 0.6 to 0.8 (Fig. 3). For the pollinators in

330   the spruce forest and for the saproxylic beetles in the mixed forest, the variation of

331   some within-treatment similarities was quite large.

332   Of more interest are the similarities of different treatments, particularly those

333   between unsalvaged and salvaged areas. Across all forest types, the similarities of

334   these two treatments (category U-S in Figs. 3, A.1) were often lower than those

335   within a given treatment. This was particularly true at the taxonomic level (Total taxa,

336   Araneae, Coleoptera) and for predators. The above pattern was not evident in the

337   pollinators and in groups with large similarity variation, such as Neuropterida or red-

338   listed Coleoptera. Expectedly, the species composition in windthrows and intact
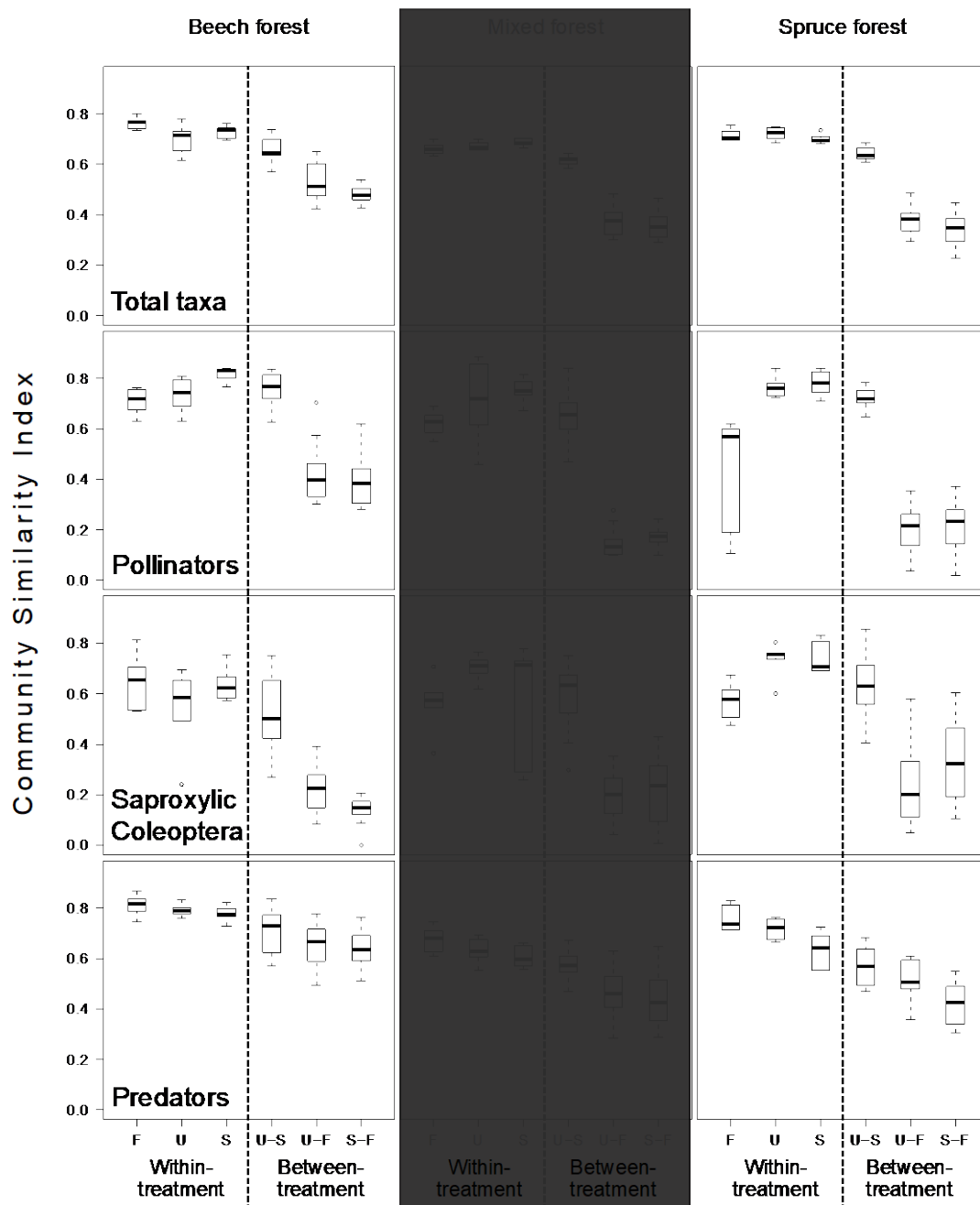
339   forest (U-F, S-F) differed most.

Figure 3: Bray-Curtis similarity indices of species communities for total captured species and functional groups within intact forest (F), unsalvaged (U) and salvaged (S) windthrows (treatments; left columns) and between pairs of those treatments (right columns) for three forest types.

(2-column figure)

For a visual summary of treatment and forest type effects, the total taxonomic composition is depicted in a Venn-diagram (Fig. 4). It shows that the number of

349   species shared between multiple treatments was similar in all forest types, and that

350   the intact forests supported the fewest species and the least exclusive ones. In each

351   forest type, roughly a quarter of all species was found in all treatment plots, and only

352   59 % of the windthrow species were shared by the two salvaging treatments in every

353   forest type. Relative to the species richness in the intact forest, an unsalvaged

354   windthrow plot increased the regional species richness roughly 2 times, and an

355   additional plot with timber salvaging approximately 2.5 times.

356   Note that these Venn-diagrams emphasize shared presences and absences while

357   similarities (Fig. 3) rely on shared presences and include abundances. This is why

358   the patterns of these two figures do have the same patterns but do not fully match.
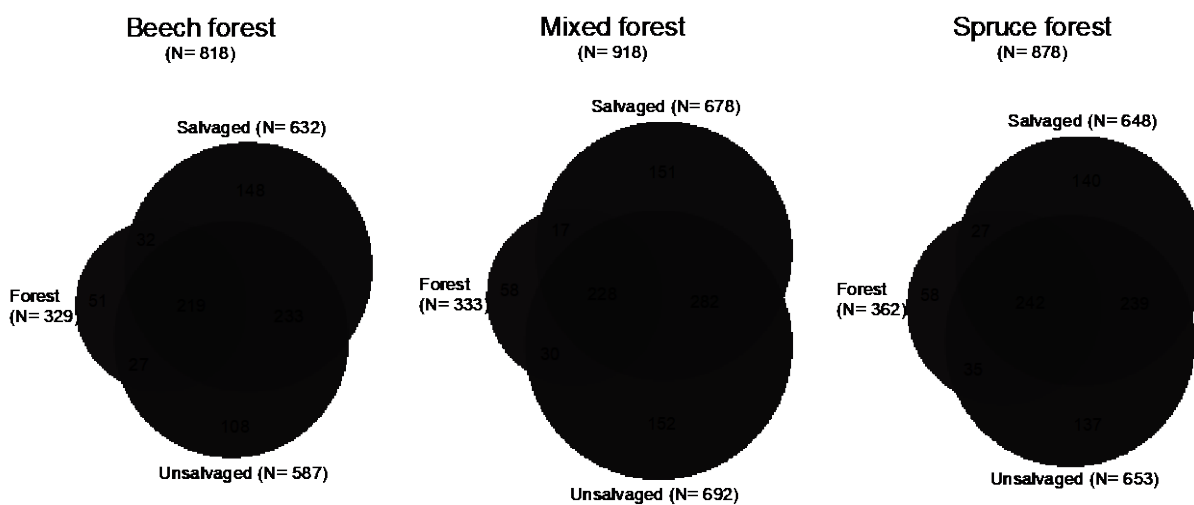
359

360

361

362   Figure 4: Diagrams of total shared species of salvaged and unsalvaged windthrows and intact forests.

363   Total species numbers (N) for forest type and treatment plot are given in parentheses.

364   (1.5-column figure)

365

366   *3.3 Indicator species*

367   Table 3 lists the species found to be characteristic of specific treatments. All

368   indicators of 'forest' belonged to the Coleoptera: two predators of bark beetles

369   (*Rhizophagus dispar, Salpingus ruficollis*), and two xylophagous species (*Alosterna*

370   *tabacicolor, Trypodendron domesticum*). They were 10-20 times more abundant in

371   the forest than in either salvaging treatment. Only one species, the crabronid wasp

372   *Spilomena beata,* was indicative for the unsalvaged treatments. Carabid beetles

373   turned out to be quite forest-type specific. Five out of seven carabid indicator species

374   were indicative of a particular forest type (data not shown).

375   Many species were typical of open windthrow habitats in general, regardless of

376   whether salvaged or not (Table 3), and most of them belong to the Aculeata. Some of

377   the most abundant aculeate species with, on average, at least 99 % of the individuals

378   found in the windthrow habitats were *Hylaeus confusus, Lasioglossum laticeps,*

379   *Trypoxilon minus* and *Polistes dominula*.

380

381

382 Table 3. Indicator species of either intact forest, salvaged or unsalvaged windthrow, or windthrows in

383 general (salvaged and unsalvaged) (p<0.05).

Taxon	Family	Species	Treatment	IndVal index
Coleoptera	Cerambycidae	*Alosterna tabacicolor* (De Geer)	Forest	0.929
Coleoptera	Curculionidae	*Trypodendron domesticum* (L.)	Forest	0.974
Coleoptera	Monotomidae	*Rhizophagus dispar* (Paykull)	Forest	0.765
Coleoptera	Salpingidae	*Salpingus ruficollis* (L.)	Forest	0.943
Aculeata	Crabronidae	*Spilomena beata* Bluthgen	Unsalvaged Windthrow	0.716
Coleoptera	Buprestidae	*Anthaxia salicis* (F.)	Salvaged Windthrow	0.745
Hemiptera	Lygaeidae	*Cymus melanocephalus* Fieber	Salvaged Windthrow	0.662
Araneae	Linyphiidae	*Neriene clathrata* (Sundevall)	Windthrows	0.651
Araneae	Lycosidae	*Trochosa terricola* Thorell	Windthrows	0.892
Coleoptera	Cerambycidae	*Clytus arietis* (L.)	Windthrows	0.981
Coleoptera	Cerambycidae	*Rutpela maculata* (Poda)	Windthrows	0.976
Coleoptera	Cetoniidae	*Cetonia aurata* (L.)	Windthrows	0.955
Coleoptera	Erotylidae	*Tritoma bipustulata* F.	Windthrows	0.775
Heteroptera	Anthocoridae	*Orius minutus* (L.)	Windthrows	0.98
Heteroptera	Lygaeidae	*Trapezonotus dispar* Stål	Windthrows	0.894
Heteroptera	Miridae	*Dicyphus errans* (Wolff)	Windthrows	0.865
Heteroptera	Pentatomidae	*Dolycoris baccarum* (L.)	Windthrows	0.973
Heteroptera	Pentatomidae	*Palomena prasina* (L.)	Windthrows	0.967
Heteroptera	Rhopalidae	*Rhopalus subrufus* (Gmelin)	Windthrows	0.816
Heteroptera	Scutelleridae	*Eurygaster testudinaria* (Geoffroy)	Windthrows	0.707
Aculeata	Apidae	*Andrena flavipes* Panzer	Windthrows	0.895
Aculeata	Apidae	*Andrena fulva* (Muller)	Windthrows	0.972
Aculeata	Apidae	*Andrena minutula* (Kirby)	Windthrows	0.961
Aculeata	Apidae	*Andrena vaga* Panzer	Windthrows	0.943
Aculeata	Apidae	*Chelostoma distinctum* (Stoeckhert)	Windthrows	0.833
Aculeata	Apidae	*Hylaeus communis* Nylander	Windthrows	0.969
Aculeata	Apidae	*Hylaeus confusus* Nylander	Windthrows	0.978
Aculeata	Apidae	*Lasioglossum laticeps* (Schenk)	Windthrows	0.997
Aculeata	Apidae	*Lasioglossum morio* (F.)	Windthrows	0.965
Aculeata	Apidae	*Lasioglossum pauxillum* (Schenk)	Windthrows	0.953
Aculeata	Apidae	*Nomada fabriciana* (L.)	Windthrows	0.894
Aculeata	Apidae	*Osmia rufa* (L.)	Windthrows	0.889
Aculeata	Apidae	*Sphecodes ephippius* (L.)	Windthrows	0.943
Aculeata	Apidae	*Sphecodes geofrellus* Kirby	Windthrows	0.972
Aculeata	Pompilidae	*Arachnospila spissa* (Schioedte)	Windthrows	0.863
Aculeata	Pompilidae	*Priocnemis coriacea* Dahlbohm	Windthrows	0.825
Aculeata	Pompilidae	*Priocnemis perturbator* (Harris)	Windthrows	0.96
Aculeata	Sphecidae	*Pemphredon inornata* Say	Windthrows	0.97
Aculeata	Sphecidae	*Trypoxylon figulus* (L.)	Windthrows	0.937
Aculeata	Sphecidae	*Trypoxylon minus* Beaumont	Windthrows	0.982
Aculeata	Vespidae	*Ancistrocerus nigricornis* (Curtis)	Windthrows	0.948
Aculeata	Vespidae	*Polistes dominula* (Christ)	Windthrows	1

384

385

4. Discussion

386

387   In this study, emphasis was put on the effect of windthrow and timber salvaging on

388   arthropod diversity as compared to intact forest. We also included different forest

389   types but did not compare their insect assemblages since this obviously depends on

390   tree composition. We rather compared the response of various biodiversity metrics

391   (species richness, abundance, and communities) to windthrow and to salvaging

392   treatments within each forest type.

393

394   *4.1 Windthrow effects*

395   A windthrow in a forest changes the habitat abruptly and drastically. The hitherto

396   closed habitat develops into a temporarily open environment with different

397   microclimatic conditions and with an ample supply of dead wood and ground

398   vegetation (Wohlgemuth *et al.* 2002). As a consequence, arthropod species richness

399   and abundance were found to significantly differ between intact forest and open

400   windthrow areas in all forest types. In windthrow plots, species richness and

401   abundance of virtually all taxonomic and functional arthropod groups exceeded those

402   in the intact forest (Fig. 1). This was most evident in the pollen- and nectar-feeding

403   Aculeata and the plant-sap-sucking Heteroptera, which took advantage from the lush

404   herbaceous vegetation in the open habitats. The pollinator guild (Apoidea and

405   Syrphidae) benefited from the abundant pollen supply from flowering plants on

406   windthrows (Fig. 2A). One of the main effects of windthrow per se obviously is a

407   pronounced rise in the supply of dead wood. Accordingly, the saproxylic beetles

408   markedly increased in species richness and abundance in the windthrow areas.

409   While positive effects of windthrows on arthropod diversity have previously been

410   demonstrated for particular taxa or forest types (Otte 1989; Duelli *et al.* 2002), our

411   results indicate that this pattern applies to different arthropod taxa and forest types as

412   well.

413   The bark beetles (Scolytinae) deviated from this general pattern in that they were

414   significantly more abundant in the closed forest than in the windthrow habitats, a

415   behavior that has already been shown previously (Otte 1989; Wermelinger *et al.*

416   2007). This may be due to microclimatic preferences, as well as to the fact that bark

417   beetles rely solely on bark or wood as a feeding and breeding substrate and not on

418   pollen or prey.

419   Species diversity also clearly changed after the storm. This was not only true for

420   the non-saproxylic Coleoptera, but also for total species diversity. Forest species and

421   open-land species overlap in the windthrow habitats, which generally results not only

422   in higher species richness but also in different species compositions.

423

424   *4.2 Salvaging effects*

425   Timber salvaging interferes with the natural development of a windthrow area as

426   the bulk of the dead wood is removed and the soil impacted by harvesting machinery.

427   In contrast to the unambiguous effects of windthrow in our study, timber salvaging

428   had almost no effect on species richness and abundance and only a minor positive

429   effect on diversity. In contrast to an earlier study in subalpine spruce forests

430   (Wermelinger *et al.* 2002), the higher supply of dead wood in unsalvaged windthrows

431   did not significantly affect the species richness and abundance of saproxylic beetles

432   (Fig. 2A). This can be explained by the high volume of dead wood (more than

433   50 m^3/ha) still remaining on the sites after they had been cleared (Table 1). This

434   seems to be generally the case for salvaged windthrow areas in Switzerland

435   (Priewasser *et al.* 2013), unlike the situation reported from a Nordic investigation,

436   where after a clear-cut only 10 m^3/ha dead wood were left on the ground (Stenbacka

437   *et al.* 2010). The reason for this may be that the mono-axial spruce trees are more

438   easily harvested as entire trees than broadleaf trees, which often have many large

439   branches ruptured by the storm and harvesting (cf. dead wood of different forest

440   types in Table 1).

441   A qualitative difference between salvaged and unsalvaged windthrows is that

442   timber harvesting removes large-sized logs and branches. This has an important

443   impact on those saproxylic insects that depend on large logs providing a constant

444   environment over a long time (Brin *et al.* 2011). A distinct shift in saproxylic species

445   composition has been found to occur in the first decade after windthrow

446   (Wermelinger *et al.* 2002). Thus, the effects of timber salvaging on species

447   developing in large-sized logs will increase with later successional stages.

448   Timber salvaging affected in particular the composition of the species

449   assemblages of certain taxa. In all forest types, the two salvaging treatments

450   consistently shared far less than two thirds of the total species (Fig. 4). The effects of

451   timber salvaging on species community composition (similarity of the two salvaging

452   treatments) were most pronounced in saproxylic beetles in the beech forest (Fig. 3).

453   This means that even if timber harvesting seems to have little impact on arthropod

454   species richness, it still attracts other species to this habitat, which is why species

455   communities differ from those in unsalvaged windthrows. This was also the case with

456   saproxylic insects in one of the few studies on salvaging effects in a North-American

457   mixed forest (Gandhi *et al.* 2009).

458   In all three forest types, i.e. beech, mixed and spruce forest, species richness of

459   windthrows differed from that of the intact forests. Moreover, the salvaging

460   treatments brought about further differences in species assemblages. These results

461   largely confirm those of an earlier study in subalpine spruce forests (Duelli *et al.*

462 2002; Wermelinger *et al.* 2002). Thus, the effects of windthrow and salvaging on

463 arthropod communities appear to be similar in various forest types and elevations.

464

465 *4.3 Red-listed species and indicator species*

466   Species richness and abundance of the red-listed Coleoptera followed the trends

467 of the other Coleoptera, with higher numbers in the windthrow gaps. More than half

468 of the red-listed species were saproxylics, which benefited from the windthrown

469 timber.

470   Only a few indicator species were found for single treatment types. Of these, most

471 were forest indicators and belonged to Coleoptera. Many species, mostly

472 Heteroptera and Aculeata, were indicative for the open habitats, i.e. salvaged and

473 unsalvaged windthrows. These results are quite robust, because the indicator

474 species were calculated including all forests and thus do not depend on forest type.

475

476 **5. Conclusions**

477   Storms are natural events in forest dynamics and significantly increase biodiversity

478 in forest ecosystems (Duelli *et al.* 2002; Bouget & Duelli 2004). We have shown that

479 most arthropod taxa increase in species richness and abundance after windthrow,

480 and that their species composition distinctly changes in the newly created habitats in

481 various forest types. Salvage-logging removes an important resource for saproxylic

482 species, but also creates new micro-habitats. Accordingly, the arthropod species

483 assemblages in salvaged and unsalvaged windthrow areas were found to differ.

484 Timber harvesting in parts of the windthrow gaps (with other gaps remaining

485 unsalvaged) is thus not detrimental per se, and even increases β-diversity, at least in

486 the first few years after the event. If in the salvaged areas substantial amounts of

487   slash are left, such as stumps and branches, saproxylic species can benefit even

488   more (Fossestol & Sverdrup-Thygeson 2009; Hjältén, Stenbacka & Andersson 2010).

489   Leaving dead wood in windthrows is increasingly being compromised by the use of

490   slash for energy wood. Our findings suggest that partial salvaging accounts for both

491   economic and ecological aspects. On a regional scale, leaving some windthrow plots

492   untouched provides a basis for promoting biodiversity not only for arthropods, but

493   also for other organisms (e.g. Thorn *et al.* 2016). In salvage-logged windthrows, part

494   of the slash may be retained (cf. Lassauce *et al.* 2012). Having a small-scale network

495   of salvage-logged and unsalvaged windthrows within intact forests provides an

496   excellent basis for sustainably managing forests and promoting biodiversity at the

497   landscape scale.

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514   Supplementary data associated with this article can be found, in the online version, at

515   http://xxxx

516

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672

673 Table A.1 Total number of species and individuals collected in two sampling years in three forest types with three treatment types, i.e. intact
674 forest, unsalvaged and salvaged windthrow plots, as well as taxa allocation to functional groups (x in parentheses means part of this
675 taxon).
676

	Sarmenstorf (beech)			Habsburg (mixed)			Messen (spruce)			Totals	Functional groups		
Taxonomic groups	Intact forest	Unsalvaged windthrow	Salvaged windthrow	Intact forest	Unsalvaged windthrow	Salvaged windthrow	Intact forest	Unsalvaged windthrow	Salvaged windthrow	All treatments	Polli-nators	Sapro-xylics	Preda-tors
Species number													
Araneae	50	70	83	47	78	101	67	88	93	173			x
Coleoptera	157	207	220	185	266	251	182	233	222	470			
Carabidae	39	46	47	30	46	49	31	46	42	89			x
Scolytinae	21	18	25	29	37	28	24	23	22	48			
Buprestidae	0	10	10	2	11	10	6	12	11	14		x	
Cerambycidae	14	19	19	18	28	21	17	24	21	48		x	
Elateridae	15	21	19	15	23	19	17	21	20	35		(x)	
Lucanidae	0	1	2	0	2	2	0	0	0	2		x	
Other Coleopt.	68	92	98	91	119	122	87	107	106	234			
Aculeata*	58	189	205	56	218	203	58	192	180	331	(x)		
Syrphidae	27	35	38	19	37	33	25	59	59	98	x		
Heteroptera	41	86	88	30	93	92	36	90	101	175			(x)
Neuropterida	9	12	14	7	14	14	7	8	10	29			x
Total	342	599	648	344	706	694	375	670	665	1 276			
Abundance													
Araneae	1 228	3 265	3 186	1 058	2 140	2 286	1 626	2 908	1 879	19 576			
Coleoptera	5 461	6 994	7 654	29 805	9 421	6 582	18 119	8 078	6 901	99 015			
Carabidae	2 063	1 574	1 502	1 089	767	1 087	1 069	916	984	11 051			
Scolytinae	1 743	2 458	2 269	24 536	3 130	1 281	11 747	1 661	566	49 391			
Buprestidae	0	23	200	1	352	494	17	846	339	2 272			
Cerambycidae	159	362	476	144	2 132	757	277	1 429	615	6 351			
Lucanidae	0	51	66	0	3	59	0	0	0	179			
Elateridae	247	236	497	277	332	548	433	412	327	3 309			
Other Coleopt.	1 249	2 290	2 644	3 758	2 705	2 356	4 576	2 814	4 070	26 462			
Aculeata*	3 430	12 244	13 413	766	15 665	13 412	700	13 093	10 112	82 835			
Syrphidae	308	2 353	1 592	73	2 307	895	114	7 987	4 312	19 941			
Heteroptera	154	878	1 108	74	779	955	83	1 209	1 668	6 908			
Neuropterida	17	54	67	31	67	73	17	53	64	443			
Total	10 598	25 788	27 020	31 807	30 379	24 203	20 659	33 328	24 936	228 718			

677

Table A.2   Red-listed beetles (with ≥ 3 individuals) caught in intact forests and in salvaged and unsalvaged windthrows. RL status is according to the regional IUCN categories: RE= Regionally Extinct, EN= Endangered, VU= Vulnerable).

		RL status	Intact forest	Unsalv. windthrow	Salvaged windthrow	Total
Pubinus tomentosus (Müller)	Aphodiidae	RE	7	9	15	31
Amara proxima Putzeys	Carabidae	RE	1	2		3
Scymnus femoralis (Gyll.)	Coccinellidae	EN	1	5	12	18
Triplax lepida (Faldermann)	Erotylidae	EN	2	5	2	9
Melandrya dubia (Schaller)	Melandryidae	EN	1	1	1	3
Ischnomera cinerascens (Pandelle)	Oedemeridae	EN			3	3
Tropideres albirostris (Schaller)	Anthribidae	VU		3		3
Anthaxia salicis (F.)	Buprestidae	VU			22	22
Anthaxia morio (F.)	Buprestidae	VU		3		3
Abax carinatus (Duftschmid)	Carabidae	VU	25	4	1	30
Amara nitida Sturm	Carabidae	VU		17	7	24
Carabus intricatus L.	Carabidae	VU	11		1	12
Cerambyx scopolii Fuessly	Cerambycidae	VU		3	1	4
Cortodera femorata (F.)	Cerambycidae	VU	10			10
Rhagium sycophanta (Schrank)	Cerambycidae	VU	1	13	23	37
Tillus elongatus (L.)	Cleridae	VU	2		2	4
Trichodes alvearius (F.)	Cleridae	VU		95	29	124
Halyzia sedecimguttata (L.)	Coccinellidae	VU	17	5	2	24
Globicornis nigripes (F.)	Dermestidae	VU		3	2	5
Ampedus erythrogonus (Muller)	Elateridae	VU	1	3	3	7
Ampedus glycereus (Herbst)	Elateridae	VU	15	62	132	209
Hylis cariniceps (Reitter)	Eucnemidae	VU	25	21	9	55
Corticaria longicornis (Herbst)	Latridiidae	VU	3	1	3	7
Lymexylon navale (L.)	Lymexylidae	VU	2	23	18	43
Mycetophagus multipunctatus Hellwig	Mycetophagidae	VU	2	1		3
Platypus cylindrus (F.)	Platypodidae	VU	1	2		3
Ontophagus illyricus (Scopoli)	Scarabaeidae	VU	1	4	3	8
Onthophagus taurus (Schreber)	Scarabaeidae	VU		2	5	7
Tropinota hirta (Poda)	Scarabaeidae	VU			9	9
Cryphalus piceae (Ratzeburg)	Scolytinae	VU	50	25	29	104
Hylesinus wachtli Reitter	Scolytinae	VU	83	8	22	113
Lymantor coryli (Perris)	Scolytinae	VU	3			3
		# species:	22	25	25	32
		# individuals:	264	320	356	940

Table A.3   Significances and contrasts of LMER/GLMER analyses of species richness, abundance and Simpson diversity of arthropod taxonomic and functional groups in salvaged and unsalvaged windthrows in different forest types. Significance levels: **= p<0.01, *= p<0.05; arrows indicate a positive effect of salvaging.

|	Effect of salvaging		
Species number	Beech	Mixed	Spruce
Total taxa	ns	ns	ns
Araneae	* ↗	ns	ns
Coleoptera	ns	ns	ns
Aculeata	ns	ns	ns
Syrphidae	ns	ns	ns
Heteroptera	ns	ns	ns
Neuropterida	ns	ns	ns
Pollinators	ns	ns	ns
Saproxylic Coleoptera	ns	ns	ns
Predators	ns	ns	ns
Red-listed Coleoptera	ns	ns	ns
Abundance			
Total taxa	ns	ns	* ↗
Araneae	ns	ns	* ↗
Coleoptera	ns	* ↗	ns
Aculeata	ns	ns	ns
Syrphidae	ns	ns	ns
Heteroptera	ns	ns	ns
Neuropterida	ns	ns	ns
Pollinators	ns	ns	ns
Saproxylic Coleoptera	ns	ns	ns
Predators	ns	ns	ns
Red-listed Coleoptera	ns	ns	ns
Simpson index			
Total taxa	ns	ns	* ↗
Araneae	* ↗	* ↗	ns
Coleoptera	ns	ns	ns
Aculeata	ns	* ↗	ns
Syrphidae	ns	ns	ns
Heteroptera	ns	ns	ns
Neuropterida	ns	ns	ns
Pollinators	ns	ns	ns
Saproxylic Coleoptera	ns	ns	** ↗
Predators	ns	ns	ns
Red-listed Coleoptera	ns	ns	ns
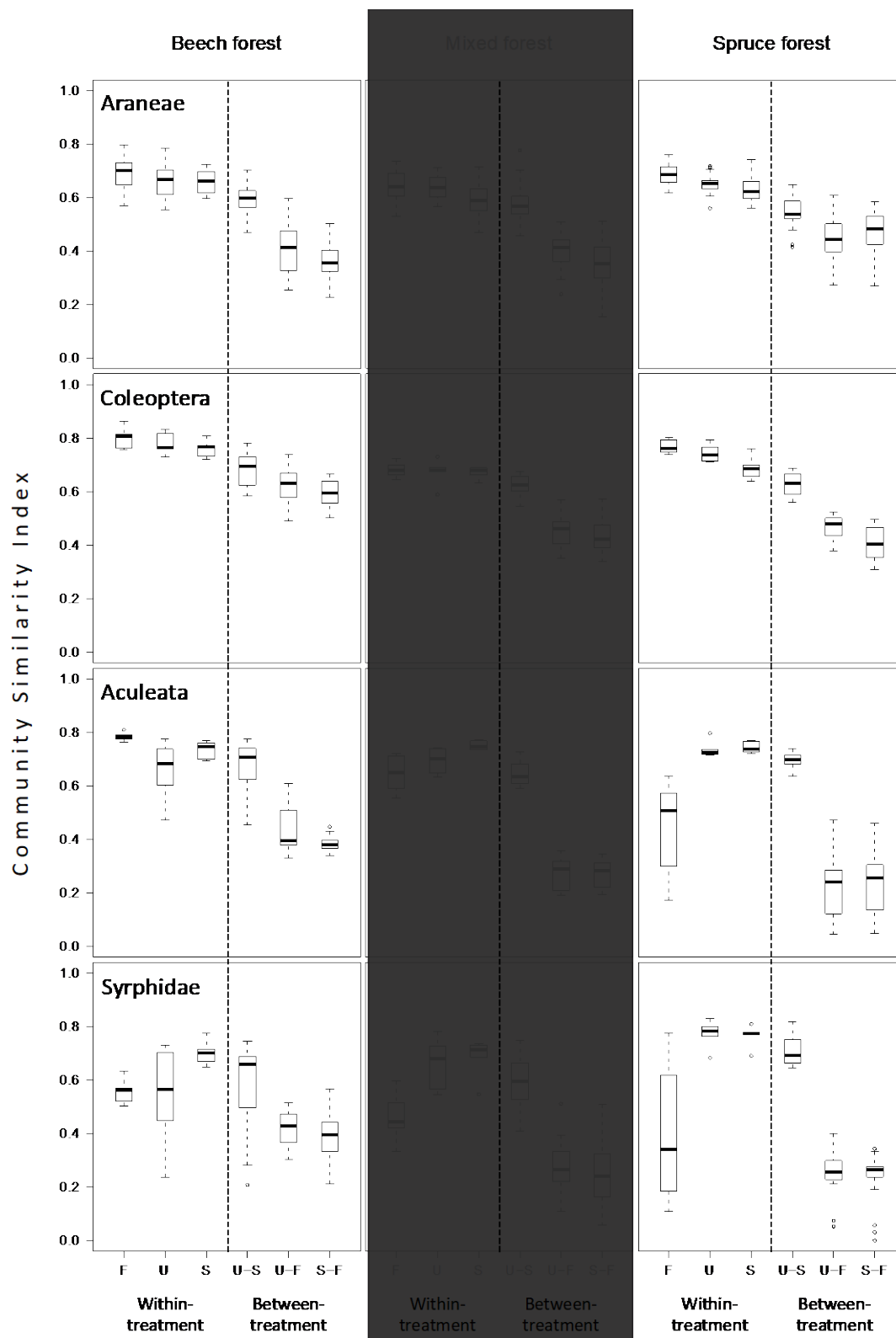
Fig. A.1 cont'd.
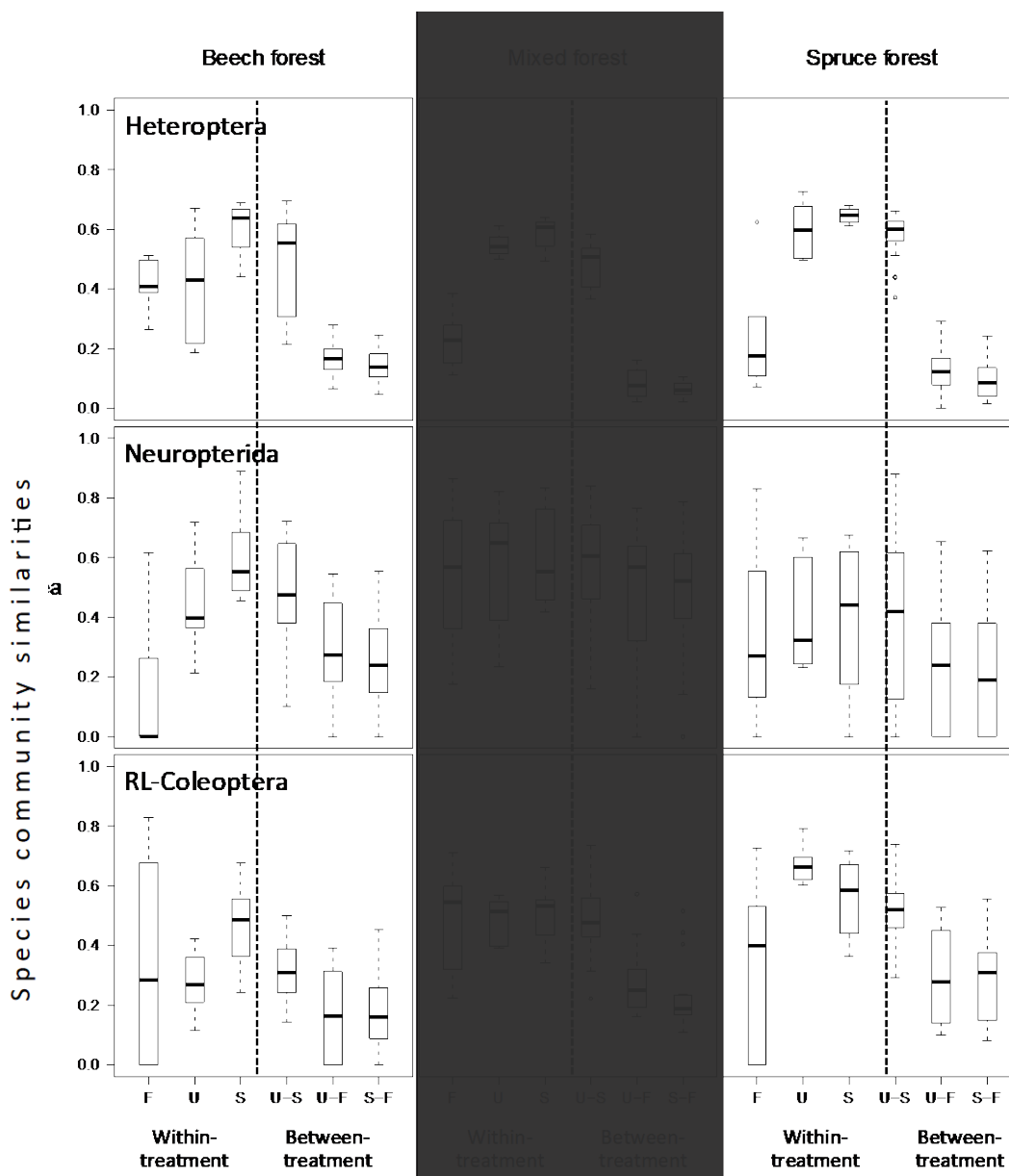
Fig. A.1   Bray-Curtis similarity indices of species communities of arthropod taxa and red-listed (RL) beetles in intact forest (F), unsalvaged (U) and salvaged (S) windthrows (treatments; left columns) and of pairs of those treatments (right columns) for each of the three forest types investigated.