

1                   Windstorm effects on herbaceous vegetation in temperate forest  
2                   ecosystems: changes in plant functional diversity and species trait values  
3                   along a disturbance severity gradient

4  
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18  
19                   CC conceived the ideas; JS designed methodology and sampling design; JS, EC and JZ collected the data; GB  
20                   analysed the data; CC led the writing of the manuscript. All authors contributed critically to the drafts and gave  
21                   final approval for publication.

22  
23                   Abstract

24

25 Catastrophic wind disturbance affects not only forest structure and regeneration, but also functional and  
26 compositional dynamics of the herbaceous layer. However, the issue of changes in functional diversity  
27 and functional trait values of the understory layer in response to wind disturbance has not been  
28 addressed so far. This study aims at investigating the patterns of variations in functional diversity, trait  
29 values and species richness of herbaceous species following wind disturbance.

30 The study was carried out in the Piska Forest, a woodland complex in northern Poland, which was  
31 almost completely destroyed by a windstorm in 2002 and part of which was successively set aside to  
32 study the effects of natural disturbance on forest ecosystems. Vegetation surveys were conducted at  
33 112 sample plots between 2014 and 2015. Four forest habitat types were identified and individually  
34 examined. The degree of disturbance severity was assessed as percentage of dead trees on all trees per  
35 surface unit. A set of twelve functional traits was assigned to the recorded species.

36 Three functional diversity metrics (richness, evenness and divergence) were calculated based on the  
37 selected functional traits. We assessed the relationship between each of such metric and disturbance  
38 severity for each habitat type. The relationship between species richness and disturbance severity was  
39 also determined. We then estimated the relative importance of habitat type and disturbance severity on  
40 both functional diversity and species richness. Lastly, we examined the response of functional trait  
41 values to both disturbance severity and habitat type.

42 Our results showed that wind disturbance effects on functional diversity are not univocal and that they  
43 strongly depend on habitat type. In fact, while in coniferous stands disturbance determined a decrease  
44 of functional divergence and left functional richness unaltered, in mixed-coniferous habitats it  
45 enhanced functional richness and did not affect functional divergence. In mixed-deciduous habitats,  
46 both functional richness and divergence decreased. In swamp habitats no major changes in functional  
47 diversity were observed. Changes in functional evenness were not significant. At the same time,

48 disturbance significantly enhanced species richness in all forest habitats, but the coniferous one. It was  
49 not possible to clearly disentangle the relative contribution of disturbance and habitat type, since the  
50 two are strictly correlated. Out of the tested functional traits, only SLA, seed releasing height and share  
51 of stress-tolerant species exhibited significant response along the tested disturbance gradient. Most of  
52 the other traits reacted only to variations in the habitat type.

53

54 **Key words:** natural disturbance/ temperate forest ecosystems/ functional richness/ functional  
55 divergence/ habitat type/ life traits

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57

## 58 Introduction

59

60 Complexity has its costs. Forests, as complex-structured, multi-layered ecosystems, are those  
61 which undergo the most dramatic changes following catastrophic natural events. Windstorms represent  
62 the more frequent natural disturbance in the forests of the temperate belt (Nagel, Svoboda, & Diaci,  
63 2006; Papaik & Canham, 2006; Fischer, Marshall, & Camp, 2013) and their frequency is expected to  
64 increase as a consequence of the ongoing climate changes (Dale et al., 2001; Goldenberg et al. 2001;  
65 Gregow et al., 2017).

66 Although generally perceived as negative phenomena by society and policy makers, windstorms  
67 play a pivotal ecological role. Several studies (Zielonka & Malcher, 2009; Dobrowolska, 2015; Wild et  
68 al., 2014; Kulakowski et al., 2017, 2019; Szwagrzyk et al., 2017; Meigs & Keeton, 2018) have  
69 highlighted that catastrophic windstorms, far from representing a threat to forest ecosystem integrity  
70 and functioning, actually make up an integral component of this ecosystem and trigger important forest

71 dynamics. Due to the considerable changes they generate in the overall structure of forest stands, and  
72 consequently, in micro-environmental conditions, windstorms represent stimulators of forest  
73 regeneration (Long et al., 1998; Panayotov et al., 2011; Bolte et al., 2014; Dobrowolska, 2015),  
74 enhance diversification of forest stands in terms of age, height and structure (Dobrowolska, 2015) and  
75 provide a chance for shade-intolerant and early-successional species to take advantage of the canopy  
76 opening created by tree falling (Bormann & Likens 1979; Peterson & Pickett, 1995). Most importantly,  
77 wind disturbance, as other types of natural disturbances, creates and maintains forest spatial  
78 heterogeneity (Seidl et al, 2014, Meigs et al., 2017; Kulakowski et al., 2019). Because of the beneficial  
79 effects of wind disturbance on forest ecosystems, an increasing tendency to simulate wind disturbance  
80 in forest management practices and forest ecosystem modelling has been established during the last  
81 decades (Cooper-Ellis et al., 1999; Crow & Perera, 2004; Drever et al., 2005; Rammig et al., 2007;  
82 Seidl et al., 2014).

83         So far, most studies about the impact of windstorms on forest ecosystems eaddressed the  
84 structural and compositional changes they produce in the tree layer and on forest regeneration (Peterson  
85 & Pickett, 1991, 1995; Wolf et al., 2004; Bolte et al., 2014; Dobrowolska, 2015; Meigs et al., 2017;  
86 Rossi et al., 2017; Szwagrzyk et al., 2017; Meigs & Keeton, 2018), and at a lesser extent, on their  
87 effects on soils (Schaeztl et al., 1989; Munthe et al., 2007; Šamonil et al., 2010) and insect  
88 communities (Bouget & Duelli, 2004).

89         Far less is known about post-disturbance effects on the herbaceous layer. Yet, this is the layer  
90 which hosts most of forest biodiversity (Gilliam and Roberts, 2003a; Whigham, 2004; Gilliam 2007,  
91 2014) and provide the setting for most vegetation dynamics, ultimately affecting all forest  
92 compartments. Indeed, while overstory influences herbaceous species dynamics by determining light  
93 availability (Gilliam 2007, 2014) and driving soil fertility (Muller 2003, Neufeld and Young 2003),  
94 understory species can in turn affect forest structure by enhancing or interfering with tree species

95 regeneration (George & Bazzaz 1999a, b, 2003; Nilsson & Wardle, 2005; Royo & Carson 2006). Since  
96 herbaceous layer diversity, composition and biomass are strongly correlated to changes in forest  
97 structure (Tonteri et al., 2016; Mestre et al., 2017; Bugno-Pogoda et al., 2021; Chelli et al., 2021) we  
98 may expect it to undergo major dynamics following wind disturbance, at both compositional and  
99 functional level. (

100         Yet, research on the effects of wind disturbance on the herbaceous layer has focused just on  
101 changes in species taxonomical diversity. Cooper-Ellis et al. (1999) observed an increase of understory  
102 species richness after a simulated hurricane in broad-leaved forests of Northeastern USA. A significant  
103 increase in species richness following windstorm events was reported also by Ulanova (2000) and  
104 Palmer et al. (2000) In their review on the effect of natural disturbance on forest ecosystems of the  
105 temperate and boreal belt, Thom & Seidl (2015) showed that all tested indicators of biological diversity  
106 were positively affected by them. Meanwhile, other aspects of post-disturbance forest dynamics are  
107 still waiting to be elucidated. One of these is the effect of windstorm disturbance on functional  
108 diversity and on the share and distribution of specific life-traits in the understory. Since plants exert  
109 multiple functions (resource acquisition, space occupation, reproduction and dispersal, resprouting after  
110 disturbance) in both the above- and belowground compartments, addressing diversity merely as a  
111 variation of taxonomic units may lead to overlook fundamental forest dynamics. In particular, plant  
112 functions regarding the belowground compartment are usually neglected, despite they are key for  
113 understory species persistence (Klimesova et al., 2018. Campetella et al., 2020). Functional diversity  
114 and life trait analyses address just such multifunctionality and help us foresee how assemblages of  
115 species sharing similar functional features will react to changes in abiotic and biotic factors.

116         In fact, it is not only individual species that experience disappearance and replacement, the two  
117 elemental phases of vegetation dynamics. Although compositional changes within ground vegetation  
118 can potentially occur without involving significant changes in functional relationships (if the relative

119 share of individual functional units remain constant after disturbance), dominance relationships among  
120 functional units are likely to be subverted by the sudden change in environmental conditions (e.g.  
121 canopy cover, light availability, exposure to wind) following windstorm events. The examination of  
122 how functional assemblages are shuffled and redistributed following catastrophic disturbance events  
123 can give us a much more sensible information about how the environment is responding to them.

124 This study proposes to investigate the long-lasting effects of windstorm disturbance on  
125 functional diversity of the herbaceous layer. The Szast Reserve, within the Piska Forest, a lowland  
126 forest complex in northern Poland, provided an ideal site for studying understory specie dynamics  
127 following catastrophic natural disturbance, having been set aside after a powerful windstorm destroyed  
128 most of the forest stands. The study was conducted 13 years after the windstorm event, when the forest  
129 ecosystem was already in an advanced stage of recovery.

130 We examined changes in different functional diversity metrics and in mean values of response  
131 traits across areas characterized by different degrees of disturbance severity and habitat types. The  
132 analyses of these changes were conducted separately for each different forest habitat. In fact, forest  
133 ecosystem response to wind disturbance is expected to be influenced by stand species composition and  
134 structure (Cooper-Ellis et al., 1999; Baker et al., 2002) and, overall, by habitat type (Peterson and  
135 Rebertus 1997; Baker et al., 2002; Ilisson et al. 2005; Anyomi et al, 2017). Examining the impact of  
136 windstorm on forest diversity patterns without considering the potential effect of habitat type would  
137 lead to an oversimplification and to the loss of precious ecological information.

138 Specifically, we hypothesize that:

- 139 1) Functional diversity of the herbaceous layer will generally increase along with the disturbance  
140 severity gradient, since we expect new guilds of species, typical of open areas, to enter the com-  
141 munity following the stand disruption;

- 142 2) Functional diversity and species richness will be strongly correlated, since each species newly  
143 arriving in a plant community likely represents a new different set of functional traits;
- 144 3) Habitat type will exhibit a deciding influence on the relationship between severity gradient and  
145 functional diversity patterns;
- 146 4) Clonal traits and SLA will decrease along the severity gradient, while Canopy Height, Releas-  
147 ing Height, Seed Mass, as well as share of Ruderals, Annual/Biennials and Anemochoric  
148 species will increase.

149

## 150 Material and methods

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### 152 *Study site*

153

154 The Szast P.F. (Szast P. F., 53°33'33"N, 21°49'47"E), within the Puszcza Pinska forest complex,  
155 covers approximately 460 ha and lies on a flat terrain, with elevation ranging from 150 to 180 m a.s.l  
156 (Fig 1). The mean annual temperature is 6.9°C and the sum of annual precipitation is 613 mm.

157 The forest communities prevailing in the study area are Scots pine forest on well-drained sandy  
158 soils, *Leucobryo-Pinetum* (coniferous type — C) and mixed Scots pine–pedunculate oak forest, *Pino-*  
159 *Quercetum* (mixed coniferous type — MC). In more fertile and wet habitats, riparian forest, *Fraxino-*  
160 *Alnetum* (mixed deciduous type — MD) and swamp forests (S) *Carici elongatae-Alnetum* occur.

161 In 2002 a violent windstorm destroyed approximately 30,000 ha of the Piska Forest. As a result,  
162 large-scale salvage logging was conducted, with more than 3 million cubic meters extracted in the  
163 following 2 years (Rykowski, 2012), but an area of approximately 460 ha of the disturbed forest was  
164 set aside in 2003 as a “reference site” for studying the natural regeneration processes of forest

165 ecosystems after catastrophic wind disturbance (Dobrowolska, 2015; Rykowski, 2012; Szwagrzyk et  
166 al., 2017).

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168

### 169 *Data collection*

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171 In order to get an objective estimate of the range and spatial distribution of the disturbance  
172 severity in our study area, we established a network of 112 circular sample plots located at the nodes of  
173 a regular grid covering the whole forest area of the Szast reserve. The plots were spaced at 200 m, had  
174 a size of 100 m<sup>2</sup> and their centers marked with pieces of plastic pipe. At each plot, living and dead trees  
175 were measured and mapped within an area of 500 m<sup>2</sup>, which provided a clear picture of tree mortality  
176 following the windstorm. The plots were nested in the middle of the 500m<sup>2</sup> plots for tree stand  
177 measurements. The severity of disturbance was calculated for each plot as the percentage of broken or  
178 uprooted trees divided by the number of both living and dead trees together (Szwagrzyk et al. 2017).  
179 Field work was carried out in 2014 and 2015, 12–13 years after the disturbance event.

180 All vascular plant species present within the 100 m<sup>2</sup> plots were recorded, and their cover was  
181 assessed as percentage. Based on the forest habitat maps provided by the Bureau of Forest Management  
182 and Geodesy, available online in the Polish National Forests Database,  
183 (<https://www.bdl.lasy.gov.pl/portal/en>), four habitat types were distinguished in our study area:  
184 coniferous (C), mixed coniferous (MC), mixed deciduous (MD) and swamp (S) habitat types. These  
185 habitat types can be considered as lying along a gradient going from the poorest one, i.e. coniferous  
186 type, to the richest one, i.e. swamp type.



187 We selected 11 response functional traits (Tab.1), which were tested for the herbaceous  
 188 vascular species recorded in the sampling, tree species being excluded from the analyses. These traits  
 189 were selected based on their significance from the point of view of the plant adaptation to a post-  
 190 disturbance scenario. Clonal traits such as persistence of clonal connections, bud bank size and lateral  
 191 spread provide crucial information about plant adaptation to an environment where resources are  
 192 heterogeneously distributed, while Clonal Index synthetizes the clonal predisposition of species. Plant  
 193 longevity and CSR strategies provide a tool to assess the stage of vegetation succession in disturbed  
 194 sites and the dynamics which can be expected to take place, while dispersion mode give us information  
 195 about how new species and guilds can enter the community. Finally, SLA, Seed Mass, Canopy Height  
 196 and Releasing Height provide elemental information about plant ability to compete for resources,  
 197 dispersal abilities and chances to successfully reproduce.

198 Data about canopy height were taken from Szafer (1969) and Rutkowski (1998) while data  
 199 about all other functional traits were taken from TRY, LEDA and COP-LA (Klimesova et al., 2017)  
 200 databases (Table1). Data about CSR strategy were integrated from Grime et al. (2007). Continuous trait  
 201 values were averaged for each species. Categorical traits were selected based on the geographic origin  
 202 of the data and the affinity of environmental conditions and vegetation to the ones of our study site (we  
 203 chose only records from Europe, possibly from Central Europe), as well as on the authority of the data  
 204 sources.

205

206

207 Table 1. Summary of the selected plant functional traits.

Plant trait	Description	Data range	Data source
Canopy height	Maximum height of the photosynthetic part of a plant	cm	Szafer (1969), Rutkowski (1998)

Releasing height	Height of seed releasing	cm	LEDA Database
Seed mass	Oven-dry mass of an average seed of a species (Cornelissen et al. 2003).	mg	TRY Database
Specific leaf area (SLA)	One sided area of a fresh leaf divided by its oven-dry mass.	mm <sup>2</sup> *mg <sup>-1</sup>	TRY Database
Total bud bank size	Number of buds on plant organs.	Number of buds	Klimešová et al. (2017).
Lateral spread	Horizontal extension of clonal organs	m	Klimešová et al. (2017).
Persistence of clonal connections	Lifespan of the physical connection between mother and daughter shoots.	years	Klimešová et al. (2017).
Clonal index	An aggregate measure of the ability of a species to spread clonally (Klimešová et al. 2017).	Categories: 0 – 6	Klimešová et al. (2017).
Plant longevity	Plant life span	Categories: Annual/biennial – perennial	TRY Database
CSR strategy	Life strategies	Categories: C, S, R, CR, CS, CSR	TRY Database, Grime (2007)
Seed dispersal mode	Modes of seed dispersal in space	Categories: Anemochorical, Zoochorical, Hydrochorical	TRY Database

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209

## 210 Statistical analyses

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212 In order to test for differences in abundance-weighted trait values in plant communities under  
213 different disturbance levels, we calculated Community-level Weighted Means (CWMs) per plot for  
214 each functional trait using the R package “FD” (Laliberté, Legendre, & Shipley, 2014). CWMs were  
215 derived by averaging trait values in the community weighted by the relative abundance of taxa bearing  
216 each value in the plot (Lavorel et al., 2008). For nominal functional traits, CWM were calculated  
217 considering the relative abundance of each individual class (Tordoni et al. 2019).

218 Furthermore, a distance-based framework to compute multidimensional functional diversity  
219 (FD) indices was applied: specifically, the functional trait matrix was combined with the species  
220 composition matrix to calculate, at the plot level, the following statistics: 1) Functional Richness, 2)  
221 Functional Evenness and 3) Functional Divergence (for the description of these three indices see  
222 Villéger et al. 2008).

223 Quantitative and nominal functional traits (as CWM), species diversity and functional diversity  
224 indices were analyzed using generalized linear models (GLMs, McCullagh & Nelder 1989).  
225 Disturbance level (quantitative), Habitat (factor with 4 levels) and the interaction term Disturbance x  
226 Habitat were used as linear predictors in each model. Normal error distribution was selected as a fitting  
227 parameter in GLM for quantitative functional traits and for Functional diversity indices, Binomial error  
228 distribution for binary functional traits and, finally, Poisson error distribution was used to model  
229 Species Richness (count data). The adequacy of the selected error distributions in GLM as well the  
230 occurrence of a linear relationships between responses and predictors were checked and tested on  
231 model residuals once the model was performed.

232 Significance of each predictor in the linear predictor was tested using the F-statistic for Normal  
233 models and using the X2statistic for Poisson and binomial models. As a measure of “goodness of fit”  
234 for each GLM, the adjusted  $D^2$  ( $D^2_{adj}$ ) was calculated (Bacaro et al., 2008).

235 Both species composition and functional composition at the plot level were analyzed via  
236 Redundancy Analysis (RDA). For species composition, an RDA on the Hellinger-transformed plant  
237 species abundances constrained by all the predictors (Coordinates, Disturbance and Habitat type) was  
238 performed. Quantitative predictors were standardized (mean 0, 1 standard deviation) before running the  
239 analysis. A similar RDA analysis was performed using the CWM functional matrix instead of the  
240 species composition data, and using the same predictors. RDA analyses and significant tests (for  
241 constrained axes and environmental predictors) were performed using the “rda”, “anova.cca” and  
242 “permustats” functions within the “vegan” v.2.5-7 package (Oksanen et al., 2020).

243 Finally, using a variation partitioning approach (Borcard et al., 1992; Legendre, 2008), we  
244 partitioned the variation in each response matrix (composition and functional) that could be explained  
245 by habitat as well as ~~by the plot location (space)~~ and from the disturbance level. The outputs obtained  
246 allowed us to distinguish the proportion of total variation explained by the (a) pure effect of habitat,  
247 (b) pure effect of disturbance, (c) partial shared effects of the two set of factors, (d) total shared effect  
248 of all the variables considered along with unexplained variation. The partitioning was based on the  
249 adjusted  $R^2$  statistic as recommended by Peres-Neto et al. (2006).

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251

## 252 Results

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254 GLMs showed that the response of the tested metrics of functional diversity strongly varied  
255 depending on habitat type.

256 The disturbance effect on Functional Richness was found to be highly significant. Functional  
257 Richness increased with increasing disturbance for mixed-coniferous stands, while it decreased for

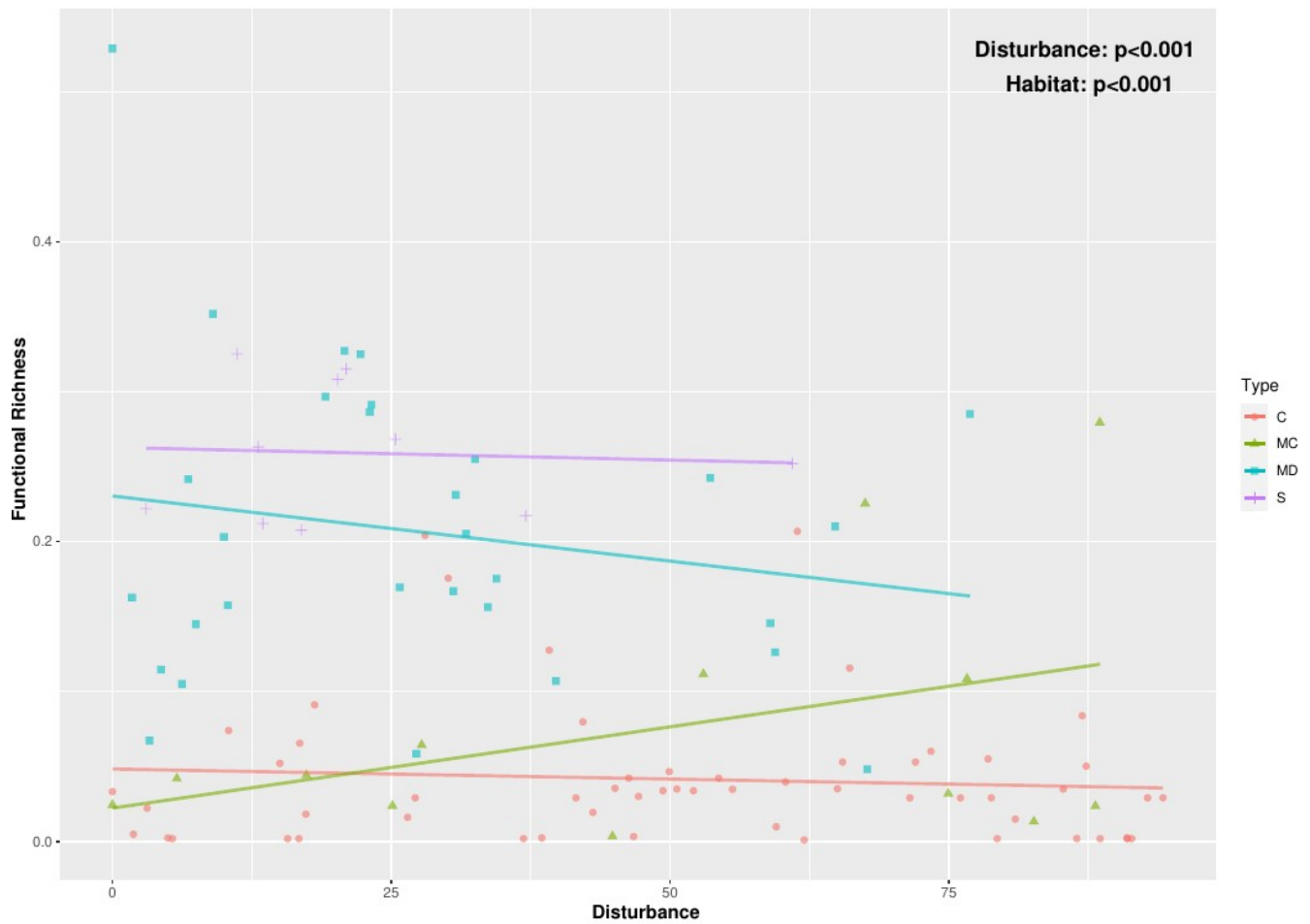
258 mixed-deciduous stand and remained substantially unaffected by disturbance gradient for coniferous  
259 and swamp stands (Fig.1a, Supplementary Material). The habitat effect was also significant, while the  
260 interaction term Disturbance x Habitat was not (Supplementary Material).

261 Functional Evenness exhibited no significant response to disturbance (graph not shown) and  
262 only the interaction term Disturbance x Habitat was significant (Supplementary Material).

263 Functional Divergence exhibited strongly significant correlation to disturbance, decreasing with  
264 the latter for coniferous and mixed-deciduous habitat types, while remaining unaffected in the case of  
265 mixed-coniferous and swamp types (Fig 1b, Supplementary Material). As for Functional Richness, the  
266 habitat effect was also significant, while the interaction term Disturbance x Habitat was not  
267 (Supplementary Material).

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269 a)



271 b)

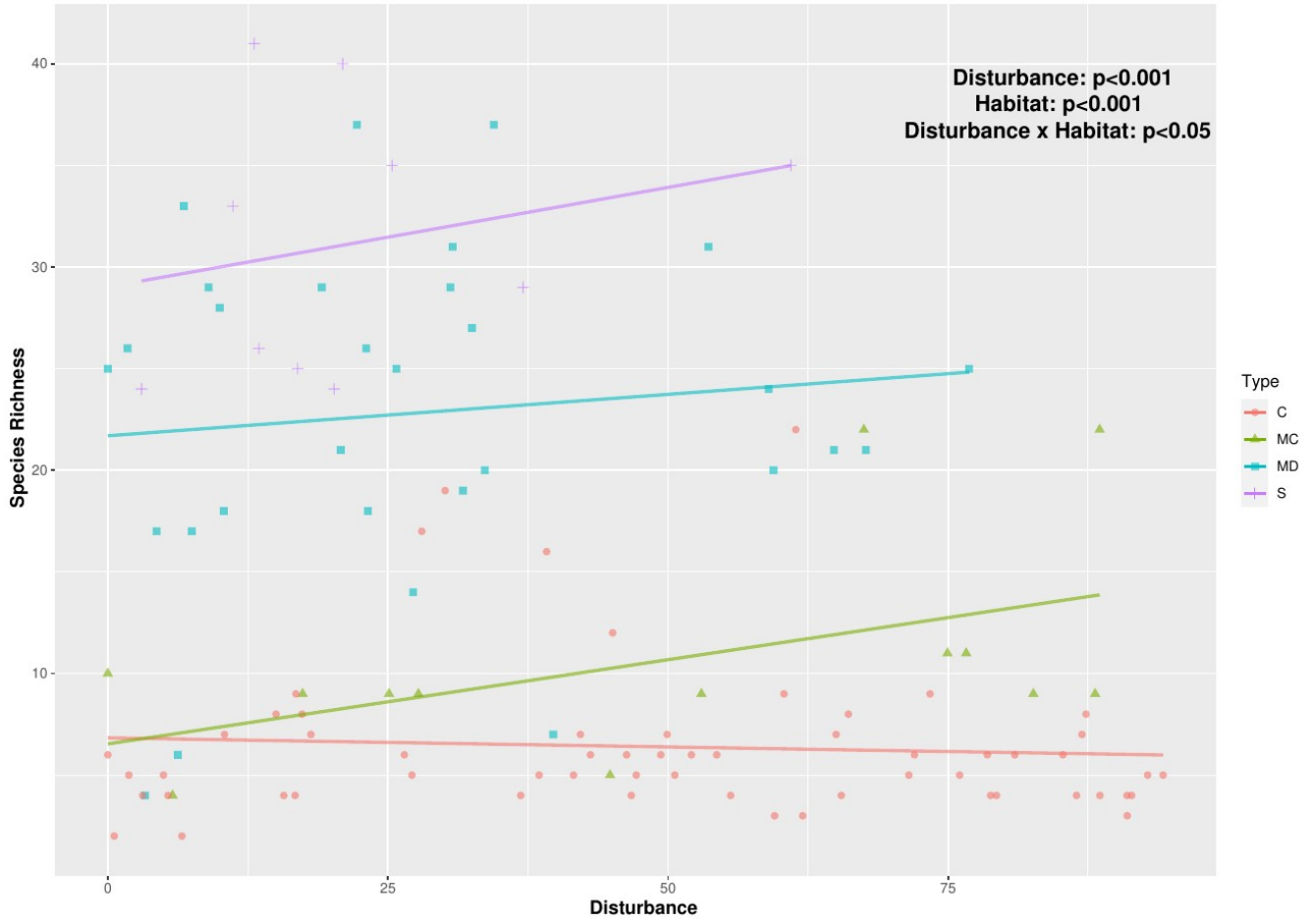
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273 Fig.1. GLM models showing variation along with disturbance gradient of: a) functional  
 274 divergence. The graph for functional evenness was not shown since the model was not significant (see Table 2).

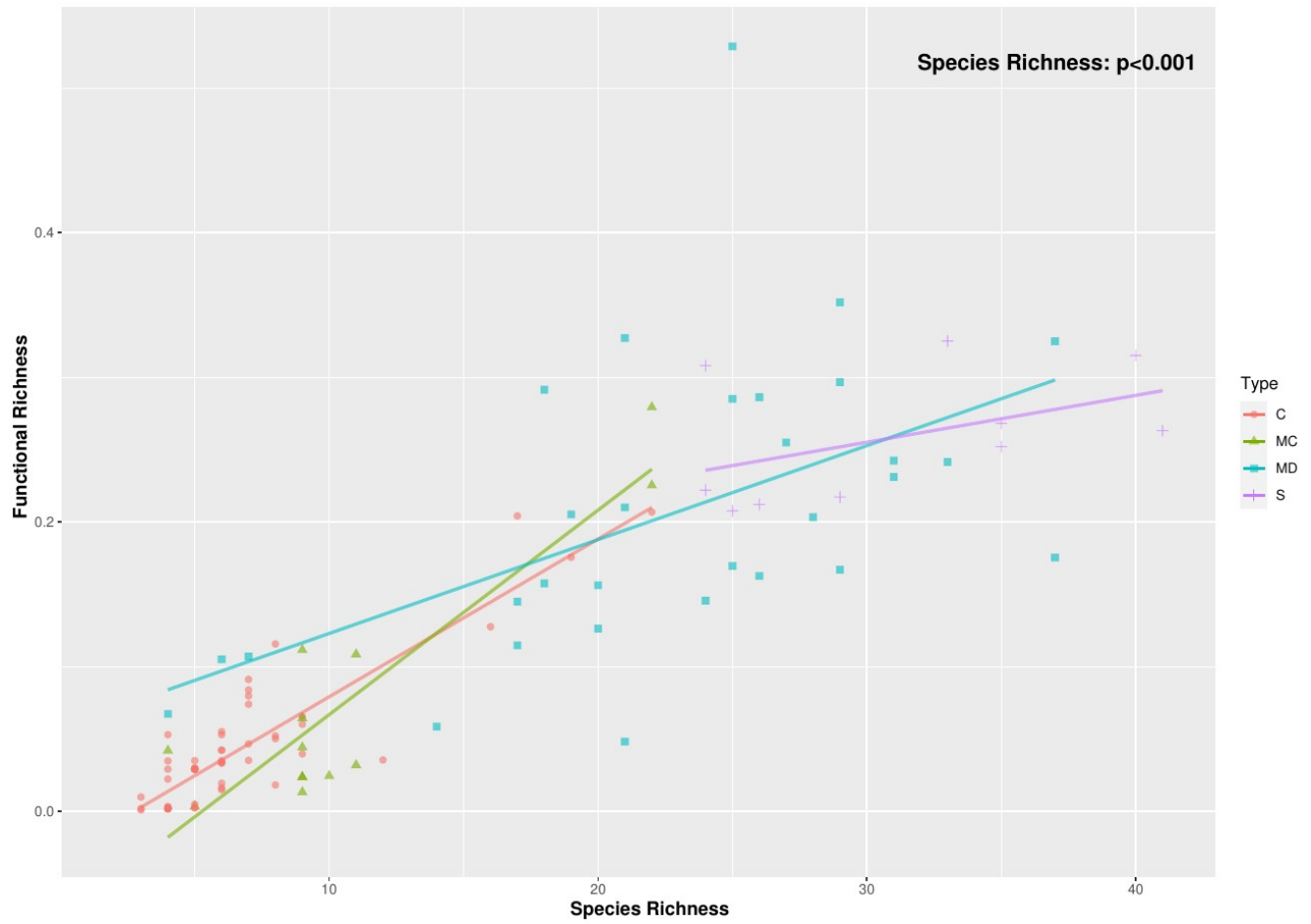
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276 a)

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279 b)



281 Fig.2. GLM models of variation of a) species richness along with disturbance severity and b) of functional  
 282 diversity along with species richness.

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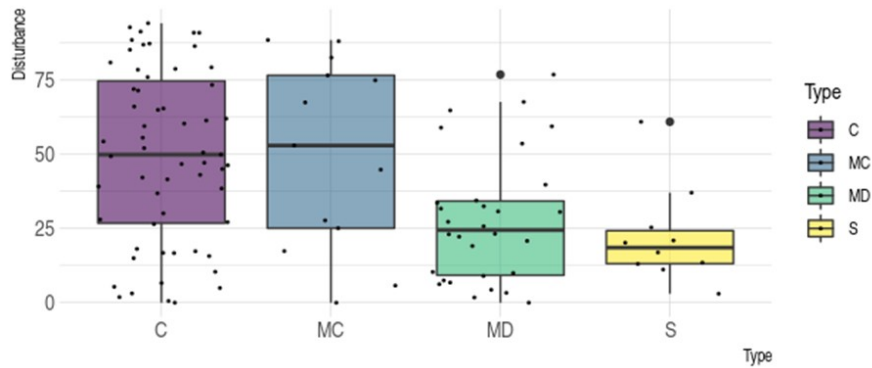
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288           Species richness increased with increasing disturbance for all forest types except for coniferous  
289 stands, the strongest increase being observed for mixed-coniferous and swamp habitat types (Fig.2a,  
290 Supplementary Material). Overall, 166 species were recorded in the survey, with the highest number in  
291 the mixed-deciduous type (Supplementary Material).

292           Functional richness in turn increased with increasing species richness for all habitat types, with  
293 the strongest relationships shown for mixed-coniferous and coniferous stands (Fig.2b). Both species  
294 richness and functional richness were higher in swamp stands, following in mixed-deciduous, mixed-  
295 coniferous and coniferous stands (Fig.1 and Fig.2).

296           Disturbance severity was strongly correlated with the habitat type/fertility, being the highest in  
297 coniferous and mixed-coniferous stands and the lowest in swamp forests (Fig. 3).

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300 Fig.3. Relationship between disturbance gradient and habitat type/fertility. C= coniferous; MC= mixed-  
 301 coniferous; MD= mixed-deciduous=; S= swamp.

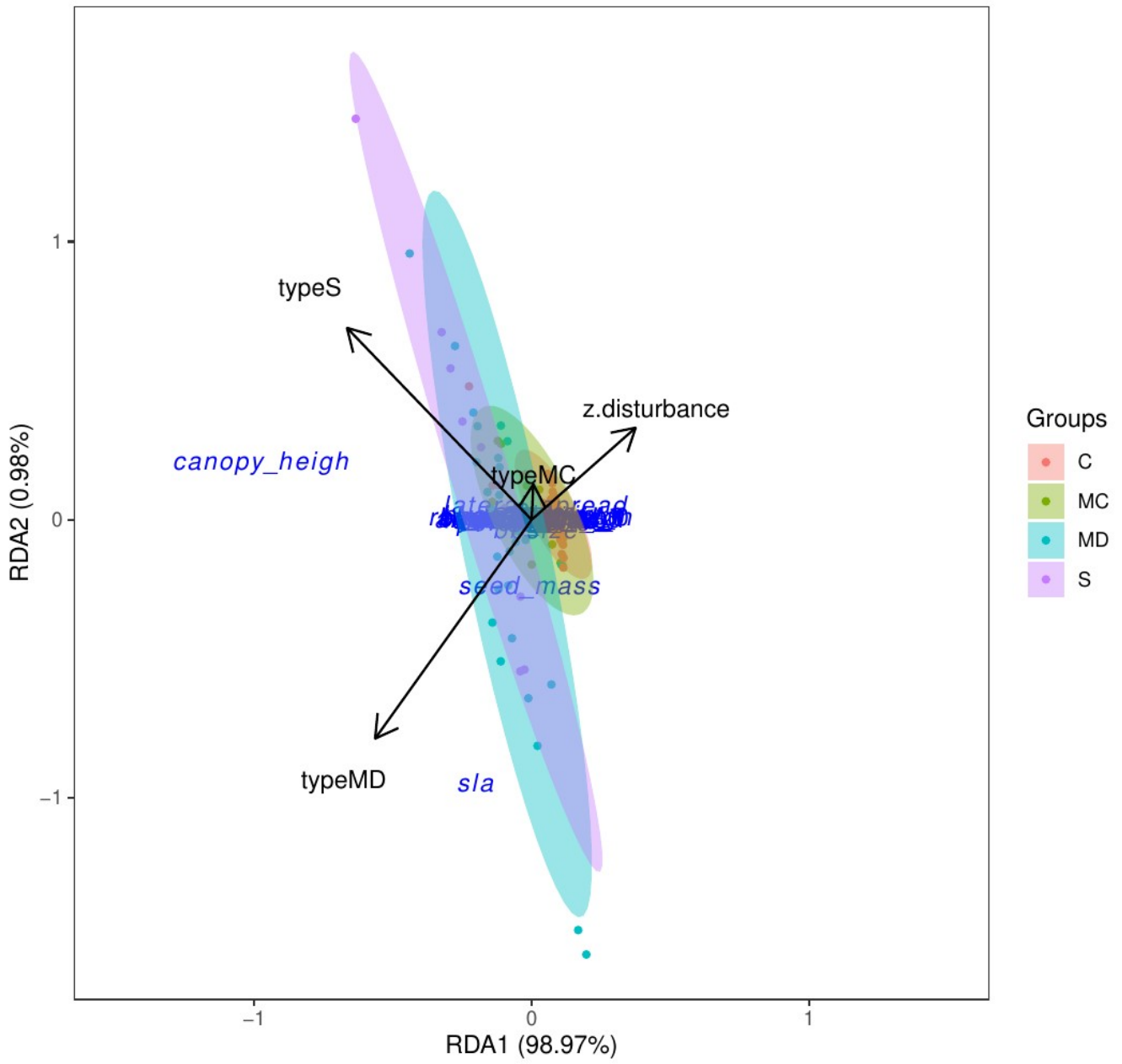
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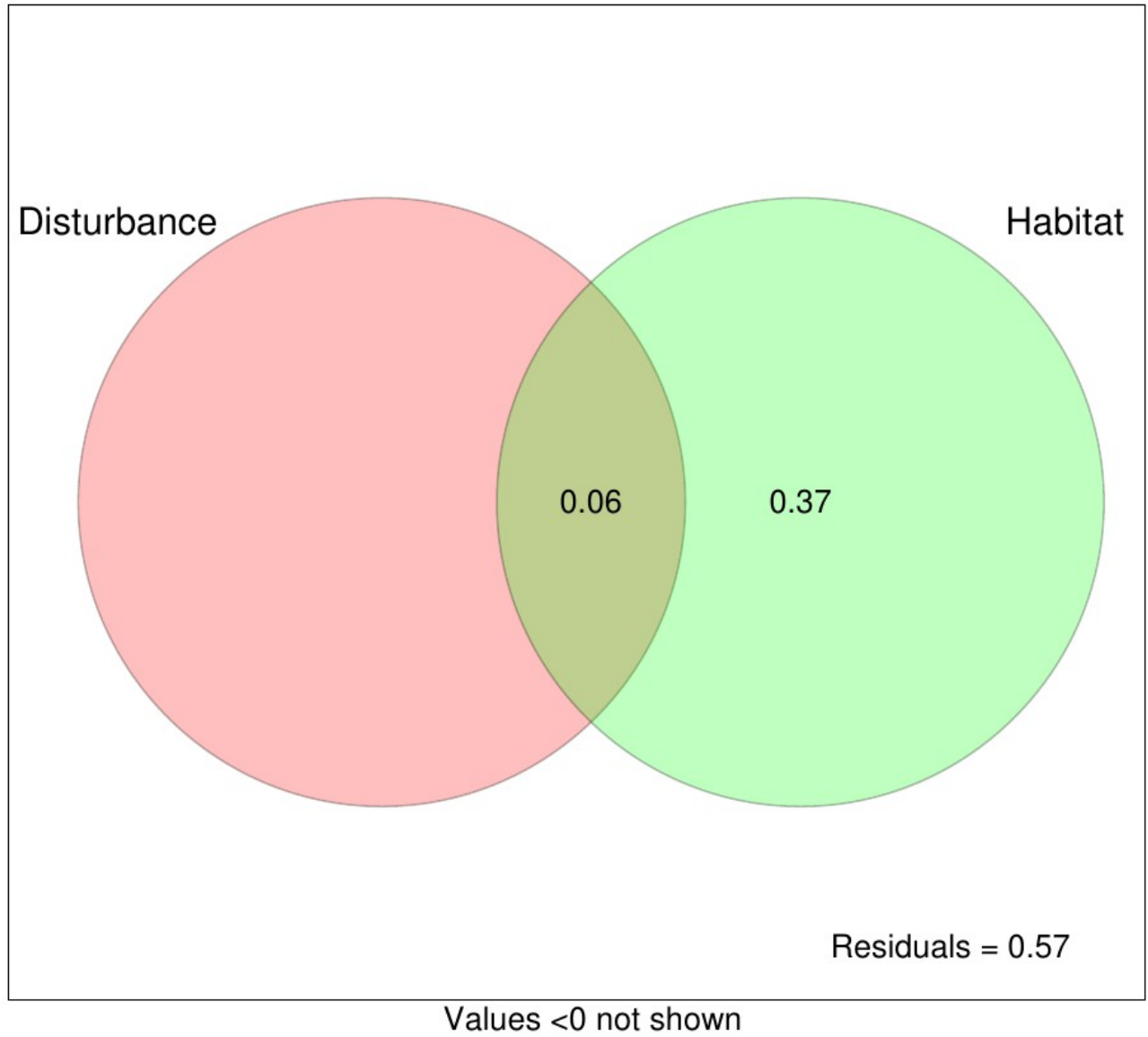
304 In the RDA based on functional diversity data (Fig.4a), RDA axes explained 44% of the total  
 305 variation, but only the first axis was significant (Tab 3). All the predictors were significant in the  
 306 ordination. The main predictor of functional diversity was habitat type, followed by disturbance degree  
 307 (Table 4). Out of all functional traits, only SLA and Canopy Height were shown to significantly vary  
 308 according to the tested explicative variables (Fig.4a). However, Variation Partitioning showed that only  
 309 habitat type significantly explains variation in functional diversity (Fig. 4b).

310 a)

311



313 b)



315 Fig.4. a) RDA of functional diversity; b) Functional Variation Partitioning

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317

318 Table 3. RDA axes summary.

319

% Exp	% Cum Exp	% Exp	% Cum	Significa
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	Variance	Variance	Variance/Total	Exp Variance/ Total	Significance
Rda1	0.989	0.989	0.444	0.444	<b>0.001***</b>
Rda2	0.001	0.999	0.004	0.448	0.825 <sup>NS</sup>
Rda3	<0.001	0.999	<0.001	0.448	1.000 <sup>NS</sup>
Rda4	<0.001	1.000	<0.001	0.449	1.000 <sup>NS</sup>
Total		R <sup>2</sup> =0.448			<b>0.001***</b>

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322 Table 4. RDA summary of explanatory variable significance.

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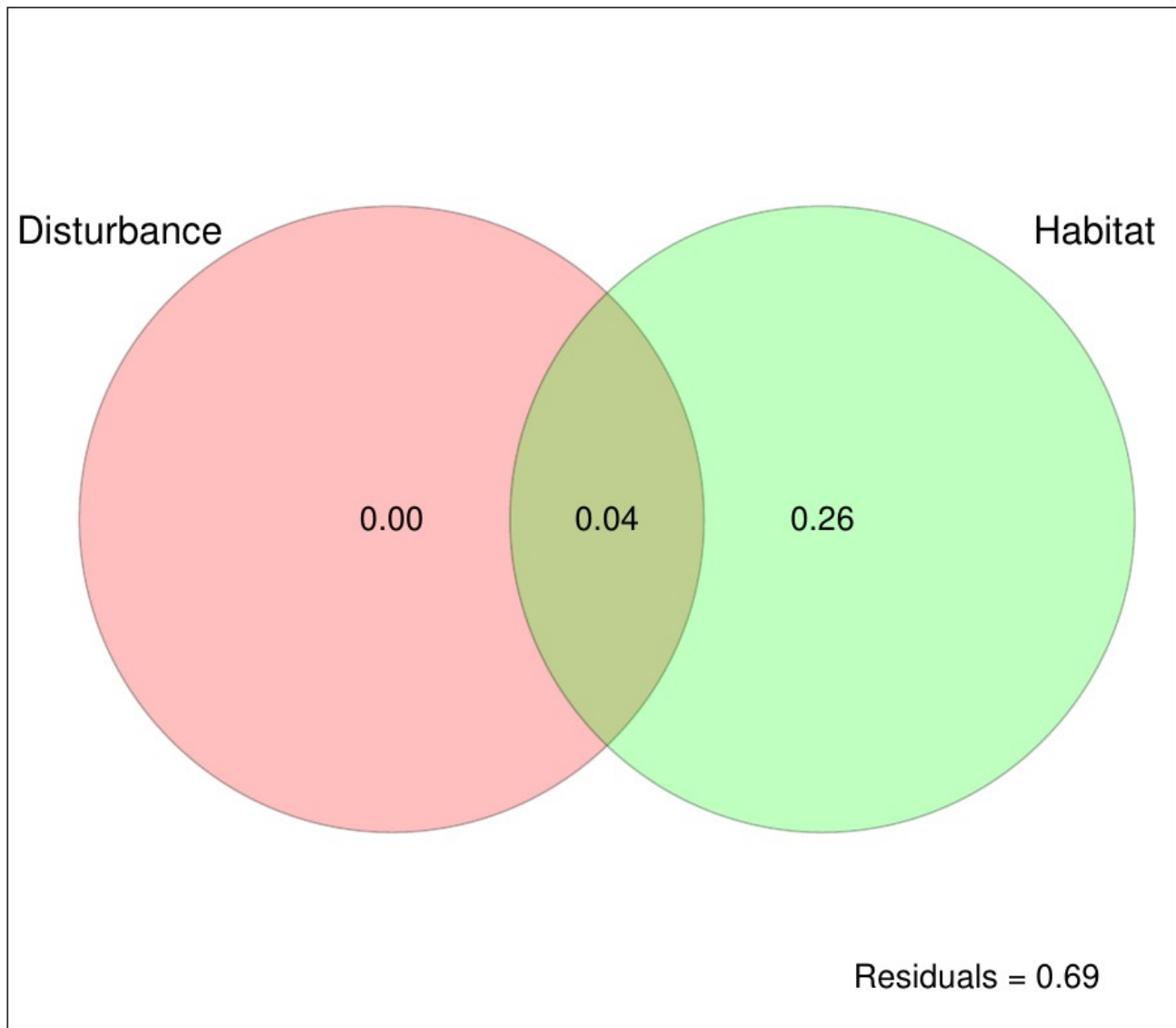
Variable	df	F	Significance
Disturbance	1	12.231	<b>&lt;0.001***</b>
Type	3	24.987	<b>&lt;0.001***</b>
Residual	107		

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325

326 In the RDA based on species composition data (Fig.5a) RDA axes explained 33.2% of the total  
327 variation, and the first and second ordination axes were significant (Table 5). Habitat type and  
328 disturbance resulted both significant in the constrained ordination (Table 6). Variation Partitioning  
329 showed that also in this case only habitat type significantly explains variation in functional diversity  
330 (Fig. 5b).





338 Fig.5. a) RDA of species composition; b) compositional Variation Partitioning.

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342 Table 5. RDA statistics. Only first axis is significant. RDA axes explain 35.7% of the total variation.

343

	% Exp Variance	% Cum Exp Variance	% Exp <b>Varianc e/Total</b>	% Cum <b>Exp Varianc e/Total</b>	Significa nce
Rda1	0.832	0.832	0.276	0.276	<b>0.001***</b>
Rda2	0.113	0.945	0.037	0.315	<b>0.001***</b>
Rda3	0.033	0.979	0.011	0.325	0.146 <sup>NS</sup>
Rda4	0.020	1.000	0.006	0.332	0.339 <sup>NS</sup>
Total		R <sup>2</sup> =0.33			0.001***
		2			

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345

346 Table 6. RDA statistics. Summary of explanatory variable significance.

347

Variable	df	F	Significance
Disturbance	1	8.769	<b>&lt;0.001***</b>
Type	3	14.805	<b>&lt;0.001***</b>
Residual	107		

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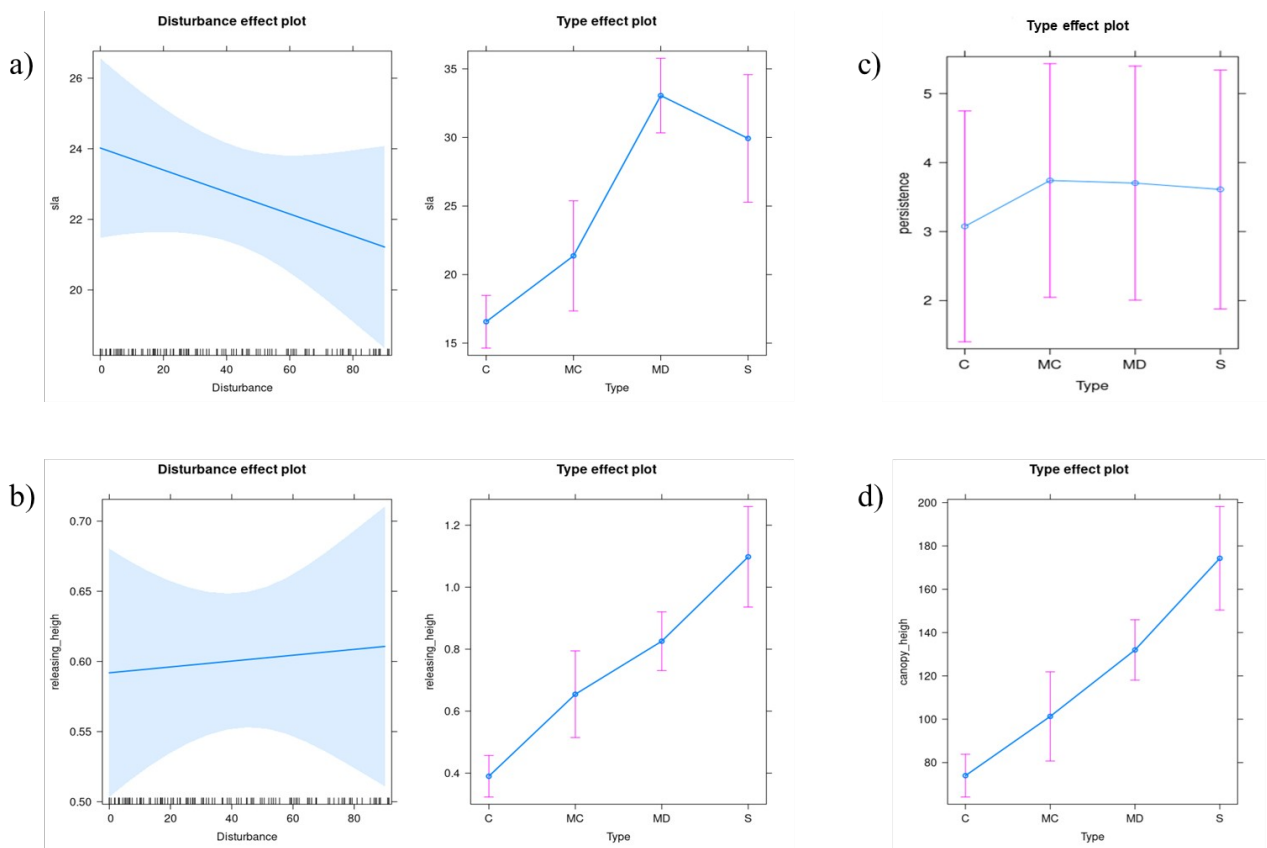
350 GLMs for SLA revealed a negative relationship with disturbance and a positive relationship  
351 with the increase in the habitat fertility, from coniferous to swamp forest stands, while for releasing  
352 height they showed a positive relationship with disturbance and a strong positive relationship with the  
353 increase in habitat fertility (Fig.6, Supplementary Material). For persistence of clonal connections and  
354 canopy height only the relationship with habitat type was significant, with an initial increase from



355 coniferous habitats to mixed-coniferous ones followed by a levelling in the case of persistence, and a  
 356 strong and almost linear increase of values with increasing habitat fertility for canopy height. All the  
 357 other quantitative traits did not exhibit significant response either to disturbance or habitat type (results  
 358 not shown).

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363 Fig. 6. Variation trend along the disturbance gradient and among habitat type for a) SLA and b) releasing height  
 364 and along habitat type only for c) persistence of clonal connections and d) canopy height.

365

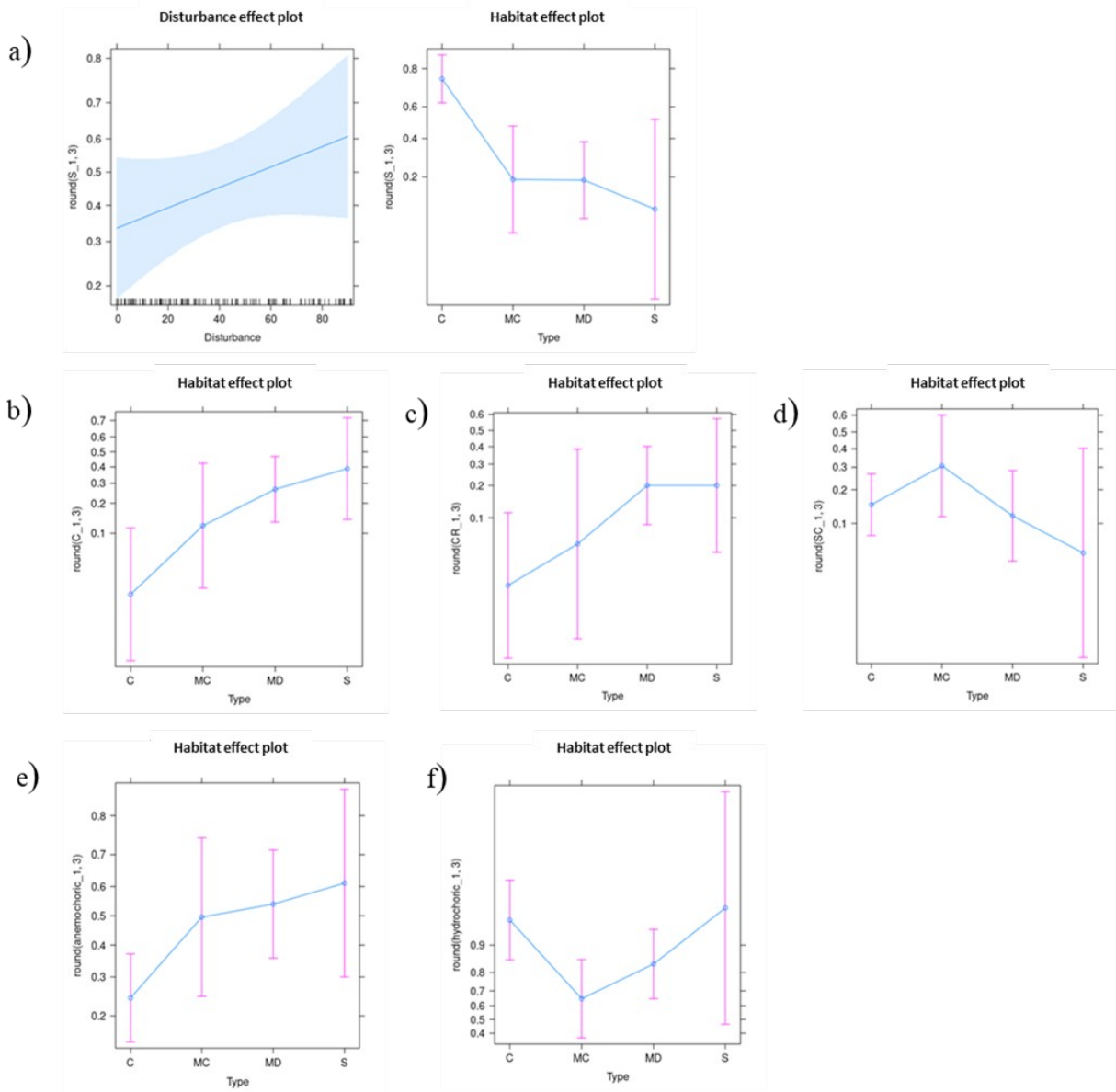
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376 species with increasing habitat fertility and an initial decrease of the share of hydrochorically dispersed  
 377 species from coniferous to mixed coniferous habitat, followed by a sharp increase with further  
 378 increasing of habitat fertility (Fig.7).

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384 Fig.7. Variation trend along disturbance gradient and habitat type for stress-tolerant (a) and along habitat type  
385 only for competitive (b), CR (c); CSR (d); anemochoric (e) and hydrochoric (f).

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## 391 Discussion

392

### 393 Response of functional diversity metrics to wind disturbance

394

395        Each of the tested functional diversity metrics revealed a different response to disturbance  
396 depending on the habitat type, which made it not possible to define a general pattern.

397        In coniferous stands wind disturbance determined a significant decrease of functional  
398 divergence while leaving functional richness almost unaltered. This means windstorm caused an  
399 expansion of the share of those species lying towards the centre of the functional spectrum which were  
400 already present in the community and the disappearance of those lying at its ends. We can hypothesize  
401 the function groups which expanded their share consisted of forest generalists, e.g. *Rubus idaeus* L.,  
402 and their expansion was determined by the decline of the share of more specialized species, i.e. shade  
403 tolerant and light-demanding ones. Such decline can be accounted for by the fact that, after disturbance,  
404 the forest stand was no longer dense enough for shade-tolerant species, yet, due to the abundant forest  
405 regeneration, it was not open enough for light-demanding species either. The higher competitiveness of  
406 generalists in comparison with specialized species is well documented (Denelle et al., 2020). In their  
407 study on long-term human disturbance in tropical forests, Sanaphre-Villanueva et al. (2017) showed

408 that disturbance indeed favoured generalist species, but this did not result in functional homogenization  
409 of the ecosystem, while, in our case, the expansion of generalists in coniferous forest habitats appears  
410 to cause a functional homogenization of the community. Chelli et al. (2021), in their work on coppice  
411 forests, highlighted that higher amounts of dead wood are related to a shift of functional diversity  
412 patterns from convergence to divergence for traits such as reproductive height, seed mass, specific leaf  
413 area and leaf area. In our case, although coniferous stands were those characterized by the highest  
414 amount of dead wood among all tested habitats following the windstorm, no positive effect of  
415 abundance of dead wood on functional divergence was observed.

416 For mixed-coniferous habitats, the strong increase in functional richness and the simultaneous  
417 lack of changes in functional divergence suggest that disturbance here allowed for the entry of species  
418 lying again at the centrum of the functional spectrum, but unlike in coniferous habitats, these  
419 generalists did not expand their share at the cost of more specialized species. In these case our results  
420 are in line with those of Sanaphre-Villanueva et al. (2017), but they are again in contrast with those of  
421 Chelli et al (2021), since here too the high amount of dead wood generated by the windstorm did not  
422 show any enhancing effect on functional divergence.

423 In mixed-deciduous habitats, the decrease of functional richness was paired with a decrease of  
424 functional divergence, which suggests the species sharing a similar multifunctional setting which  
425 disappeared from the community lied at one of the extremes of the functional spectrum and consisted  
426 of the shade-tolerant species, the ones which are most negatively affected by the changed  
427 environmental conditions. Also in this case, we can hypothesize the niche left empty by the  
428 disappearance of the shade-tolerant species was filled by the expansion of generalists, which led again  
429 to a homogenization of the community.

430 In swamp habitats wind disturbance left functional richness and divergence unaffected. This  
431 may be accounted for by the lower sensitivity of this forest habitat to wind disturbance, as well as to the

432 higher resilience of swamp species to changing light conditions. Such species depended rather on water  
433 than on light availability, so that changes in canopy openness did not exert a significant impact on the  
434 community.

435 Overall, these results did not match our expectations, especially in the case of coniferous and  
436 mixed-deciduous habitats. The observed patterns can be accounted for by the fact that after 13 years  
437 from the windstorm event the effect of wind disturbance was screened and possibly counterbalanced by  
438 the rapid forest regeneration.

439  
440 Species richness response to wind disturbance and correlation with functional richness

441 While changes in functional diversity patterns differed depending on habitat type, species  
442 richness following wind disturbance increased in all habitats but the coniferous one, with the highest  
443 increase observed in mixed-coniferous and swamp forests. The positive effect of wind disturbance on  
444 species diversity confirms the results of Cooper-Ellis et al. (1999), Ulanova (2000) and Palmer et al.  
445 (2000.), as well as what reported by Thom & Siedl (2015), who showed that natural disturbances  
446 positively affect various diversity indices and increase species richness on average by 35.6%.

447 The strong correlation between species richness and functional richness found in our study  
448 confirms our expectations, as well as the results of previous studies (Biswas & Mallik, 2011).  
449 However, such correlation was stronger for poor habitats, i.e. coniferous and mixed-coniferous forest  
450 stands, than for fertile habitats, i.e. mixed-deciduous and swamp forests. In fact, in coniferous stands  
451 we did not observe any increase in either species richness or functional richness, whereas in the mixed-  
452 coniferous stands the increase in species richness was mirrored by an increase in Functional Richness.  
453 This strong correlation suggests that in poor habitats the addition of any new species to the set of  
454 already existing ones is likely to create a new group of species with similar multifunctional setting.  
455 Where the correlation was less strong, like in mixed-deciduous and swamp stands, the increase in

456 species richness was not paired with an increase in functional richness, which, on the contrary,  
457 decreased. This apparent inconsistency can be accounted for assuming that in fertile habitats the  
458 species which entered the community shared the same functional setting of species already present in  
459 the community. Besides, in mixed-deciduous habitats, this determined an expansion of such groups at  
460 the cost of those lying at the edge of the functional spectrum, i.e. shade-tolerant species, which would  
461 explain the decrease of both functional richness and functional divergence observed in mixed-  
462 deciduous habitats.

463

464 Relative importance of disturbance and habitat type on functional diversity

465 By performing RDA and Variation partitioning analyses we tried to assess the relative  
466 contribution of disturbance severity, habitat type and spatial distance to variations in functional  
467 diversity and compositional diversity, but our results did not show a univocal response, highlighting  
468 that both habitat and disturbance can equally likely represent the main driver of changes in diversity,  
469 being strongly collinear. In fact, windstorm effects were strongly related to the habitat type, with stand  
470 characterized by a higher proportion of deciduous trees increasingly resistant to disturbance  
471 (Szwagrzyk et al., 2017). Similar results, with differences in disturbance severity largely explained by  
472 habitat type, were found also in previous studies (Peterson & Rebertus 1997, Ilisson et al. 2005;  
473 Anyomi et al., 2017). Because of that, the impact of the disturbance severity on forest floor diversity  
474 was indiscernible from that of habitat constraints. So the question of the relative contribution of habitat  
475 and disturbance in forest ecosystems cannot be answered unless comparing habitats with a similar  
476 sensitivity to a specific disturbance agent.

477

478 Variation trends of life trait values following wind disturbance



479 GLMs allowed us to test the variation of each individual functional traits separately along the  
480 disturbance gradient and the fertility gradient represented by the various habitat types. From the  
481 analyses emerged that the majority of traits remained unaffected by variations in disturbance severity,  
482 while many of them varied depending on habitat type. Only SLA and seed releasing height  
483 significantly responded to the disturbance severity gradient, besides varying among habitats.

484 SLA exhibited a strong decrease along with increasing disturbance, according to our  
485 expectation, and increased with increasing habitat fertility, though its values were lower for swamp  
486 than for mixed-deciduous forests. This can be explained considering that swamp stands are  
487 characterized by a high patchiness in the distribution of microsites available for trees to grow, so that  
488 such forest type is usually more open than mixed-deciduous stands, which are denser and shadier. The  
489 lower light intensity on the forest floor of mixed-deciduous habitats accounts for the highest values of  
490 SLA observed in plants occurring this habitat type. Canopy height shows just a very slight increase  
491 with increasing disturbance, but a strong and linear increase with increasing habitat fertility.  
492 Persistence of clonal connections and releasing height only showed a significant variation in relation to  
493 the habitat type and displayed an almost identical pattern, with values increasing from coniferous to  
494 mixed-coniferous and then decreasing with further increase of habitat fertility. Such pattern may be  
495 rather the result of the dominance by a particular species (like *Vaccinium myrtillus* L.) in mixed-  
496 coniferous stands, than of specific environmental constraints.

497 The SLA decrease with increasing disturbance severity confirmed our expectations, as well as  
498 what already highlighted by Prado Júnior et al. (2015) in seasonal Brazilian forests. At the same time  
499 the lack of response of clonal traits, in particular persistence of clonal connections and lateral spread,  
500 contrasted with our expectations of a decrease of these traits with increasing disturbance. In fact,  
501 regeneration from aboveground vegetative sources (e.g., lateral extension, runners) is typical of plant  
502 communities where the disturbance agent affects mainly tree canopy (Roberts, 2004) and changes

503 along the disturbance gradient as a consequence of the increased light availability and uniformity of  
504 distribution would be reasonable to observe. The lack of response of clonal traits could be explained by  
505 the retaining by blowdowns of a certain degree of environmental patchiness, even after light has  
506 become much more uniformly distributed due to stand disruption, or by its restoration, due to the rapid  
507 forest regeneration.

508 Unlike SLA, seed releasing height exhibited significant increase with increasing disturbance  
509 severity, which can be accounted for by the enhanced vegetation development due to the increase in  
510 light availability following stand disruption. The fact, that seed releasing height was positively  
511 associated with increasing disturbance severity, while plant height was not, could be accounted for by  
512 the architecture of grasses (like *Deschampsia flexuosa* (L.) Trin. and *Calamagrostis arundinacea* (L.)  
513 Roth), which are abundant in more disturbed habitats. The foliage in most grasses is set much lower  
514 above the ground than the inflorescence and the structures containing seeds.

515 The lack of a significant response of bud bank size, lateral spread, seed mass and share of  
516 annual species to the disturbance severity gradient, as well as the strong negative response of SLA,  
517 contrasts with the results of Herben et al. (2017), who showed a strong decrease in bud bank size values  
518 with increasing disturbance severity, a strong increase of lateral spread, a moderate decrease of seed  
519 mass, a strong increase of the share of annual species and a moderate increase of SLA. At the same  
520 time, our results confirm the strong positive relationship with habitat fertility of both SLA and Canopy  
521 Height already observed in their study. However, Herben et al. (2017) studied several different habitat  
522 types, so that their results did not specifically refer to forest communities. Besides, they examined  
523 several types of both anthropogenic and natural disturbance and did not practically assess the actual  
524 degree of disturbance from direct observation, but based on personal knowledge and experience of  
525 typical disturbance severity in certain habitats.

526           While the share of annuals and biennial/perennials did not exhibit significant variations either  
527 along the disturbance gradient or among different habitats, plant strategies as well as dispersal modes  
528 significantly varied together with the habitat type. We observed an obvious trend of increasing the  
529 share of C species from the coniferous forest type to the swamp forest type, which was predictable,  
530 since in poor habitats there are very few strong competitors, while in more productive habitats their  
531 share increases. The only significant relationship with both disturbance severity and habitat type was  
532 observed for the stress-tolerant species, whose share was highest in coniferous forests and lowest in  
533 swamp forests and increased together with increasing disturbance both overall and within the  
534 coniferous habitat type. The S species abundantly occurring in the coniferous forest type (*Calluna*  
535 *vulgaris*, *Vaccinium vitis-idaea*, *Deschampsia flexuosa*) are also light-demanding species, so they are  
536 more common in places where the forest canopy cover had been strongly reduced by disturbance.  
537 Similar, although weaker tendency was found in mixed coniferous habitat type. In more productive  
538 habitats (mixed deciduous and swamp habitat types) the S plants are rare and they are not the light-  
539 demanding ones, so the relationship between disturbance severity and the presence of S plants is  
540 negative, but weak and insignificant. In case of ruderals (R plants) there was no significant relationship  
541 both with disturbance severity and habitat type. We need to take into account, that ruderals are very  
542 likely to appear and thrive immediately after wind disturbance, but they disappear soon after. In this  
543 study, conducted 13-14 years after disturbance they are long gone, replaced by typical forest plants.  
544 The share of anemochoric species almost linearly increased with increasing soil fertility, namely from  
545 coniferous to swamp habitat types, while the share of hydrochoric species decreased from coniferous  
546 habitats to mixed coniferous and then increased to reach the highest value in swamp habitat types. The  
547 high share of hydrochoric species in coniferous forest type is probably an artifact, as there is hardly any  
548 water available for seed transport in dry habitats. Yet some species occurring in coniferous habitat types  
549 are characterized by both anemochory and hydrochory (see TRY database), so in dry habitats they rely

550 mostly on wind dispersal, while in wet habitats, especially close to water streams, they can be dispersed  
551 mainly by water.

552         Looking at the results of this study overall, we need to consider that many changes in species  
553 composition of the herbaceous layer occur in the first 2-3 years after disturbance, when the light-  
554 demanding species are able to colonize the openings created by canopy tree mortality (Szwagrzyk et al.  
555 2016; Daniels & Larson, 2019). However, these changes can be only temporary, not affecting the  
556 composition and structure of forest community in a long run. The patterns of functional diversity and  
557 trait variation highlighted by this study refer to an advanced stage of forest regeneration, when a low  
558 canopy layer, made up by tall saplings and young trees, begins to be formed. In fact, according to  
559 literature, forest communities start returning to their original state within 6-15 years form the  
560 disturbance event (Cooper-Ellis et al., 1999; Palmer et al., 2010; Szwagrzyk et al., 2018; Daniels &  
561 Larson (2019).

562

## 563 Conclusions

564         Our results show that wind disturbance effects on functional diversity are not univocal and that  
565 they strongly depend on habitat type. However, changes in functional diversity did not show a trend  
566 consistent with the habitat gradient and the strictly related disturbance severity gradient, as might have  
567 been expected. In fact, while wind disturbance caused a functional homogenization of the community  
568 in habitats that significantly differ in their environmental features like coniferous and mixed-deciduous  
569 ones, it did not in mixed-coniferous nor in swamp ones. The reason behind these inconsistencies is an  
570 issue which deserves further investigation. Management practices simulating wind disturbance in order  
571 to stimulate undergrowth diversity should thus take into account the individual forest habitat features,  
572 i.e. their resistance and resilience to wind disturbance events. Based on the results of our study, it

573 appears that wind disturbance exerts a generally positive effects on mixed-coniferous habitats, since it  
574 increases there both species and functional richness. In such habitat type, simulation of wind  
575 disturbance as a management practice can be expected to be appropriate, while it should be considered  
576 with caution in coniferous and mixed-deciduous habitats.

577         Contrary to functional diversity, species richness showed rather consistent patterns across the  
578 tested habitat types, since it increased in all of them but the coniferous one, which confirms the positive  
579 effects of windstorms on biodiversity, even on the long run. The relative impact of habitat type and  
580 disturbance severity on patterns of functional diversity remains unclear because of the strong  
581 correlation among disturbance severity and habitat types. Most examined traits did not show any  
582 relationship with the disturbance gradient, except SLA, seed releasing height and share of stress-  
583 tolerant species. We suggest that repeated monitoring at different time intervals form the disturbance  
584 events is needed to reliably assess the changes in diversity and species composition in disturbed forest  
585 communities.

586

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588

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