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## Canopy Disturbances Catalyse Tree Species Shifts in Swiss Forests

**This is a pre print version of the following article:**

*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/1792161> since 2021-06-26T05:22:17Z

*Published version:*

DOI:10.1007/s10021-021-00649-1

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(Article begins on next page)

## Canopy disturbances catalyse vegetation shifts in Swiss forests

Journal:	<i>Ecosystems</i>
Manuscript ID	Draft
Types:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Scherrer, Daniel; Swiss Federal Institute for Forest Snow and Landscape Research, Forest Dynamics / Forest Resources and Management Ascoli, Davide; Università degli Studi di Torino, Department of Agriculture Forestry and Food Sciences Conedera, Marco; Swiss Federal Institute for Forest Snow and Landscape Research, Insubric ecosystems Fischer, Christoph; Swiss Federal Institute for Forest Snow and Landscape Research, Forest Resources and Management Maringer, Janet; Swiss Federal Institute for Forest Snow and Landscape Research, Insubric ecosystems Moser, Barbara; Swiss Federal Institute for Forest Snow and Landscape Research, Forest Dynamics Simeonova Nikolova, Petia; Swiss Federal Institute for Forest Snow and Landscape Research, Forest Resources and Management Rigling, Andreas; Swiss Federal Institute for Forest Snow and Landscape Research, Forest Dynamics; ETH Zurich Department of Environmental Systems Science, Institute of Terrestrial Ecosystems Wohlgemuth, Thomas; Swiss Federal Institute for Forest Snow and Landscape Research, Forests Dynamics
Key Words:	Castanea sativa, drought, insect outbreaks, national forest inventory, Picea abies, Pinus sylvestris, vegetation shift, wind throw

# 1 **Canopy disturbances catalyse vegetation shifts in Swiss forests**

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5 2 Short title: Canopy disturbances catalyse vegetation shifts

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8 3 Daniel Scherrer<sup>1</sup>, Davide Ascoli<sup>2</sup>, Marco Conedera<sup>3</sup>, Christoph Fischer<sup>1</sup>, Janet Maringer<sup>3</sup>, Barbara  
9 Moser<sup>1</sup>, Petia Simeonova Nikolova<sup>1</sup>, Andreas Rigling<sup>1,4</sup>, Thomas Wohlgemuth<sup>1</sup>

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11  
12  
13 5 <sup>1</sup> Swiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903 Birmensdorf,  
14 Switzerland

15  
16  
17  
18 7 <sup>2</sup> Department of Agriculture, Forest and Food Sciences, University of Torino, Largo Paolo Braccini 4,  
19 Grugliasco (TO), Italy

20  
21  
22  
23 9 <sup>3</sup> Swiss Federal Institute for Forest, Snow and Landscape Research WSL, c/o campus di ricerca, CH-6593  
24 Cadenazzo, Switzerland

25  
26  
27  
28 11 <sup>4</sup> Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zurich,  
29 Universitätstrasse 16, CH-8092 Zurich, Switzerland

30  
31  
32  
33  
34 14 Corresponding author:

35  
36  
37 15 Daniel Scherrer

38  
39  
40 16 Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

41  
42  
43 17 Telefon: +41 44 739 29 37

44  
45  
46 18 [daniel.scherrer@wsl.ch](mailto:daniel.scherrer@wsl.ch)

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## 50 51 52 20 **Authors contribution**

53  
54  
55 21 TW initiated the idea and DS developed the methods; DS and CF analysed the data; DS, TW and MC  
56 led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval  
57 for publication.  
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2 24 **Data availability**  
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4  
5 25 The data used in this manuscript will be stored in the EnviDat repository upon acceptance. The raw  
6  
7 26 data from the Swiss NFI can be provided free of charge within the scope of a contractual agreement  
8  
9 27 (<http://www.lfi.ch/dienstleist/daten-en.php>).  
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For Peer Review

## 28 **Abstract**

29 Widely observed inertia of forest communities contrasts with climate change projections that suggest  
30 dramatic alterations of forest composition for the coming decades. Disturbances might be a key  
31 process to catalyse forest adaptation to environmental change by creating the opportunities for 'new'  
32 species to establish. To test this assumption, we compared two assessments (1993-1995, 2008-2017)  
33 from the Swiss National Forest Inventory to evaluate which forests were opened by natural canopy  
34 disturbance (i.e., wind, insect outbreaks, fire and drought) and if these disturbances altered forest  
35 trajectories both in terms of species-specific basal area and tree recruitment densities. Disturbances  
36 affected 14% of the Swiss forests, with wind and insect outbreaks being the most frequent (75 %) and  
37 fire and drought being rare (< 1.5%). Disturbances led to a shift from conifer to broadleaf tree species  
38 at low elevation, in particular in dense *P. abies* stands, but no change was observed at higher  
39 elevations. The composition of undisturbed sites persisted during the same time period. Our results  
40 demonstrate that undisturbed forests widely resist climatic change as an effect of direct ingrowth by  
41 stand-forming species. Disturbance events seem necessary to create opportunities for climatically  
42 'better suited and site-adapted' species to (re-)establish and therefore potentially catalyse forest  
43 adaptation to environmental changes. We detected a reduction of species that were cultivated outside  
44 their primary natural range (*P. abies*) or depended on traditional management practices (*P. sylvestris*,  
45 *C. sativa*), which may represent an early signal on how the projected increase in disturbance frequency  
46 and severity might alter forests.

47 **Keywords:** *Castanea sativa*, drought, insect outbreaks, national forest inventory, *Picea abies*, *Pinus*  
48 *sylvestris*, vegetation shift, wind throw

## 49 **Manuscript highlights**

- 50 • Disturbances create regeneration windows for better site-adapted species
- 51 • Post-disturbance forest dynamics reverse earlier socio-economic-driven management
- 52 • Low elevation forests shift away from spruce towards more broadleaf species

## 53 Introduction

54 Climate change is expected to affect species distributions (Pereira and others 2010; Lindner and others  
55 2014; Dyderski and others 2018). Resulting changes in forest structures and species compositions may  
56 potentially alter ecosystem processes and related services, claiming for an adaptation of management  
57 practices (Millar and others 2007; Civantos and others 2012; Brang and others 2014). Many models  
58 predict dramatic changes in forests over the coming decades (e.g., elevational or latitudinal shifts of  
59 species; Gehrig-Fasel and others 2007; Dyderski and others 2018; Jandl and others 2019), altered  
60 frequencies of disturbances (Seidl and others 2017) and post-disturbance changes in vegetation (e.g.,  
61 as a consequence of drought-induced mortality; Allen and others 2015; McDowell and others 2020).  
62 On the other hand, representative surveys have observed only marginal changes under ongoing  
63 climate warming during the last decades (e.g., Lenoir and others 2008; Lenoir and others 2010b;  
64 Bertrand and others 2011; Küchler and others 2015; Scherrer and others 2017; Etzold and others  
65 2019). In European forests, shifts in distribution ranges of tree species have been mostly assessed at  
66 their present latitudinal or altitudinal limits (e.g., Grundmann and others 2011; Bolte and others 2014;  
67 Hernández and others 2014), with larger effects in species restricted to mountain habitats or with  
68 faster population turnover (Lenoir and others 2008; Dyderski and others 2018). This discrepancy  
69 between model simulations and recent field observations of late-successional species could be  
70 explained by four main factors all related to the longevity of dominant tree species: 1) slow  
71 regeneration processes due to long persistence of the optimal phase of dominant trees, high plasticity  
72 and rare mast fructification (e.g., Bertrand and others 2011; Ascoli and others 2017; Copenhaver-Parry  
73 and others 2020), 2) limited dispersal (e.g., Svenning and Skov 2007; Lenoir and others 2010a), 3)  
74 limited establishment due to competition, fluctuating resource availability, and forest management  
75 (e.g., Bertrand and others 2016; Nikolova and others 2019; Shi and others 2020), and 4) lack of gap-  
76 creating disturbances generating opportunities for the recruitment of (new) species (Grubb 1977). All  
77 these factors hinder rapid climate driven changes in forest composition and thereby may contribute  
78 to an increasing amount of extinction and colonisation debt (Talluto and others 2017; Liang and others

1  
2 79 2018). On the other hand, reports supporting rapid vegetation shifts due to climate warming often  
3  
4 80 refer to opportunistic case studies and neglect the vast majority of other forests, where possible  
5  
6 81 substantial changes may remain unobserved (Jump and others 2007; Brandl and others 2020).  
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9 82 Both simulation studies (e.g., Liang and others 2018; Scherrer and others 2020) as well as forest surveys  
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11 83 (e.g., Peñuelas and Boada 2003; Rigling and others 2013; Brice and others 2019; Brice and others 2020)  
12  
13 84 suggest that disturbances and extreme events (natural or anthropogenic) are a key component in  
14  
15 85 facilitating forest transitions under climate change by creating favourable conditions for opportunistic  
16  
17 86 species better adapted to the novel (and presumed future) climatic conditions. Whether such events  
18  
19 87 leading to tree and stand mortality alter forest trajectories or simply result in ingrowth (i.e., infilling by  
20  
21 88 the already dominant species; e.g., Kramer and others 2014) might be highly dependent on complex  
22  
23 89 interactions of environmental conditions, disturbance agents and their severity (Seidl and others 2017;  
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25 90 Jentsch and von Heßberg 2019; Nikolova and others 2019). Furthermore, forest stands differ in their  
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27 91 susceptibility/vulnerability to specific disturbance agents (e.g., wind, fire, pest or avalanches) as a  
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29 92 function of their age and development stage, which leads to a multitude of potential post-disturbance  
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31 93 forest trajectories, additionally modulated by the local or regional dominant disturbance regimes,  
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33 94 environmental conditions (e.g., high vs low elevation) and understory dynamics (Bolte and others  
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35 95 2014).  
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41 96 To find evidence for representative disturbance-induced forest changes, we used the unique  
42  
43 97 nationwide data from the Swiss National Forest Inventory (NFI; Fischer and Traub 2019) covering  
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45 98 several bioclimatic regions (i.e., Jura, the Plateau, the Northern Alps, the Western and Eastern Central-  
46  
47 99 Alps and the Southern Alps) and spanning an elevation gradient from 240 to 2400 m a.s.l. All main  
48  
49 100 Swiss forest types are represented in this systematic inventory allowing us a statistically representative  
50  
51 101 overview of disturbance events and species-specific post-disturbance dynamics, e.g., changes in basal  
52  
53 102 area and recruitment density over an average period of 25-years. We focused on four prevalent natural  
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55 103 disturbance agents (i.e., wind, insect outbreaks, forest fires, and prolonged drought events) likely to  
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57 104 increase in frequency with future environmental change (Seidl and others 2017) in order to investigate:  
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1  
2 105 (1) how do natural disturbance agents differ in frequency among different biogeographic regions,  
3  
4 106 climatic conditions, and forest types, (2) which species were most affected by different disturbance  
5  
6 107 agents and (3) are there any differences between pre- and post-disturbance tree species composition  
7  
8 108 (adult trees and recruitment) that may suggest potential vegetation shifts?  
9

## 109 **Material and methods**

### 110 *Study region and climate data*

111 The study area is Switzerland, encompassing a territory of 41,285 km<sup>2</sup> of which 31.9% (13,169 km<sup>2</sup>) is  
112 forested (Cioldi and others 2020). Forests range from about 200 to 2400 m a.s.l. with the lower  
113 elevations dominated by broadleaves and the higher elevations by conifers (Figure S1). Corresponding  
114 with regions and with steep elevation gradients around the Alpine arc, the climate strongly varies. In  
115 the north of the Alps, the climate is mainly influenced by the Atlantic Ocean, from where mild, humid  
116 winds blow. In Zurich-Affoltern at 443 m a.s.l., winters are mild (0.3 °C in January) and summers warm  
117 (18.8 °C in July), with annual precipitation of 1054 mm. In the south of the Alps, the climate is  
118 influenced by the Mediterranean system with temperatures 2–3 °C warmer than in the North, and  
119 annual precipitation usually exceeds 1600 mm (Locarno-Monti; 366 m a.s.l.). Central Alpine valleys are  
120 dry with nationwide lowest annual precipitation (603 mm, Sion; MeteoSwiss 2020). In accordance with  
121 this climate heterogeneity, Switzerland is categorized into six biogeographic regions (Gonseth and  
122 others 2001; Figure 1). To take into account the existing climatic spatial heterogeneity, we used the  
123 annual mean temperature (°C) and the annual precipitation sum (mm) derived from gridded climatic  
124 data calculated at a 100 x 100 m resolution for the reference period of 1981–2010 as spatial layers  
125 (meteoswiss.ch; Zubler and others 2014).

### 126 *Forest inventory data*

127 We used data of the Swiss National Forest Inventory (NFI), recorded on a 1.4 km x 1.4 km systematic  
128 permanent sample grid covering the whole country, during the second NFI (NFI2; 1993–1995) and the  
129 fourth NFI (NFI4; 2009–2017), respectively. Previous to analyses, we removed all plots classified as  
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1  
2 130 shrub land or not visited in both NFI2 and NFI4, eventually retaining the 5521 accessible forest plots.  
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4 131 Passing from NFI2 to NFI4 the protocol of terrestrial data collection slightly changed as well as the  
5  
6 132 survey period did, which switched from a three-year assessment window to a nine-year-window  
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8 133 (continuous inventory since NFI4; Brändli and Hägeli 2019; Lanz and others 2019). The vast majority of  
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10 134 Swiss forests were since centuries and still are managed following a 'close-to-nature' silvicultural  
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12 135 approach (Spathelf and others 2015). The commandment of privileging natural tree recruitment or  
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14 136 planting of native site-adapted species when natural regeneration is difficult is even embodied in the  
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16 137 national forest law. As a result, large monoculture plantations are very rare as are non-native tree  
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18 138 species (Table S1), which are only present on 2.4% of NFI-plots and contribute less than 0.6% to the  
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20 139 basal area of Swiss forests (Brändli and others 2020).

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25 140 A terrestrial NFI-plot consists of several plot elements. Standing and lying trees are measured using  
26  
27 141 two concentric circular plots (500 m<sup>2</sup> and 200 m<sup>2</sup>). On the large plot all trees with a diameter at breast  
28  
29 142 height (DBH)  $\geq 36$  cm are measured, while on the small plot also trees and shrubs with a DBH  $\geq 12$  cm  
30  
31 143 and  $< 36$  cm are measured (Lanz and others 2019). Tree recruitment is defined as individuals  $\geq 10$  cm  
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33 144 height and  $< 12$  cm DBH and was assessed using concentric circles with different sizes. In NFI2 two  
34  
35 145 satellite plots with two concentric circles differing in radius were used ( $r = 1-2.12$  m; Stierlin 1994) and  
36  
37 146 in NFI4 one satellite plot with four concentric circles was used ( $r = 0.9-4$  m; Düggelein and Keller 2017).  
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40 147 We used the total available dataset, as preliminary analyses showed changes in sampling design  
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42 148 between NFI2 and NFI4 to have no significant impact on recruitment density per hectare. Different size  
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44 149 of the satellite plots might impact analysis of species diversity, which, however, is not in focus of the  
45  
46 150 present study. On the interpretation area of 50 x 50 m (0.25 ha) around the plot centre disturbances  
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48 151 and the potential natural forest community were determined. After estimating the extension of  
49  
50 152 existing damages in the field, the disturbance agent was evaluated by interviews with the local  
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52 153 foresters (Stierlin 1994; Düggelein and Keller 2017). The potential natural forest communities (PNC)  
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54 154 were defined by experts that visited 25% of the NFI sample plots and concluded community identities  
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56 155 by analogy (using factor maps and local knowledge) for the remaining 75% of the plots, according to  
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1  
2 156 the Swiss protection forest classification (NaiS; ARGE Frehner and others 2020). These PNC depict the  
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4 157 expected idealised natural tree species composition (including recruitment) when the forest stands  
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6 158 are totally in balance with the dominant environmental conditions (e.g., climate, topography, soil) as  
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8 159 expressed by the present understory species (Frey and others 2020). In this study we use 17 simplified  
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10 160 PNC defined according to the main tree species (e.g. sub-montane beech forests or sub-alpine spruce  
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12 161 forests). A forest stand is then defined as natural when the occurring dominant tree species based on  
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14 162 NFI data (i.e., based on basal area) is identical to the PNC (e.g., *Picea abies* has highest basal area per  
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16 163 ha on NFI-plots belonging to the sub-alpine spruce forest PNC). However, due to present and/or past  
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18 164 management decisions, differences may exist between the actual dominating species and the PNC  
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20 165 species. To prevent confusion between dominant taxa and the PNC of a NFI-plot we will use in this  
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22 166 paper the scientific taxon name for the dominant species (e.g., *Picea abies*, *Fagus sylvatica*) and the  
23  
24 167 English names for the PNC (e.g., spruce forest and beech forest).

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26 168 From roughly 300 different NFI attributes recorded on each plot, we only extracted the species-specific  
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28 169 basal area of trees with DBH  $\geq 12$ cm (BA,  $\text{m}^2\text{ha}^{-1}$ ), the species-specific density of tree recruitment ( $\text{m}^2\text{ha}^{-1}$ ),  
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30 170 the damaged area per ha due to disturbance events (%), the disturbance agent, the date of the last  
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32 171 timber harvest and the potential natural forest community.

### 33 34 35 36 37 38 39 172 *Data pre-processing*

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42 173 Of the 56 tree species that were recorded in the NFI-plots, only few are very abundant and contributed  
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44 174 to the vast bulk of biomass while the majority of species are rare or added little biomass. We therefore  
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46 175 reclassified all species into twelve taxa: *Abies alba* (silver fir), *Picea abies* (spruce), *Pinus cembra* (Swiss  
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48 176 stone pine), *Larix* spp. (larch), *Pinus* spp. (pine), other conifers, *Castanea sativa* (sweet chestnut), *Fagus*  
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50 177 *sylvatica* (European beech), *Acer* spp. (Maple), *Fraxinus* spp. (ash), *Quercus* spp. (oak), other  
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52 178 broadleaves (for details see Table S1). The dominant taxa for each plot was defined based on the BA  
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54 179 represented. For each species, we calculated the climatic envelop on the base of the gridded values of  
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56 180 the annual mean temperatures and precipitation. Further, we divided the tree recruitment into  
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2 181 individuals with DBH < 4 cm (saplings) and individuals with DBH 4 - 11.9 cm (pole stage) as these size  
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4 182 groups represent very different age cohorts and amount of (self-)thinning.  
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7 183 *Defining disturbed plots*  
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10 184 To distinguish between naturally disturbed NFI sample plots (hereafter called 'naturally disturbed') and  
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12 185 all others ('not naturally disturbed') we used the following criteria: 'naturally disturbed' if a) the NFI  
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14 186 field team reported a damage affecting at least 10% of the interpretation area, and b) the local forester  
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16 187 reported a specific disturbance agent for the plot (e.g., wind, fire). Plots with a contradiction between  
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18 188 the foresters' report and the NFI field team observations were removed from further analysis, leaving  
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20 189 us with 5092 plots. Most of these mismatches were the result of minor disturbances already invisible  
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22 190 at the time of the next NFI visit. In this study, we were interested in obvious, i.e. canopy disturbances  
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24 191 with the potential to catalyse vegetation shifts and consequently these small-scale and very low-  
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26 192 severity disturbances were not analysed. In the cases where more than a single disturbance event  
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28 193 and/or disturbance agent affected a NFI-sample plot, we determined the main disturbance agent by  
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30 194 comparison of the area damage caused by each disturbance agent. For the later classification of plots  
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32 195 into different disturbance agents, the main damage type (as determined by maximum area damaged)  
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34 196 was used.  
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40 197 'Not naturally disturbed' plots were further subdivided based on the information of the NFI into  
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42 198 'undisturbed' that is without any recorded natural disturbance and human intervention in the past 25  
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44 199 years, 'treated' that are plots where planned silvicultural treatments occurred, and 'salvage logging',  
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46 200 which resulted from mortality/damage events related to smaller natural disturbances (i.e., less than  
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48 201 10% of the interpretation area affected). This classification allowed us to test if a larger-scale natural  
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50 202 disturbance leads to a different vegetation trajectory compared to a human induced disturbance (i.e.,  
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52 203 'treated' and 'salvage logging') or no intervention and no disturbance at all (i.e., 'undisturbed').  
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2 205 *Data analysis*  
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5 206 To test if certain site conditions (i.e., biogeographic region, dominant taxa or PNC) were linked to a  
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7 207 specific natural disturbance agent we used Chi-squared analysis. Additionally, we conducted a niche  
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9 208 analysis to test if the disturbances occurred more often at the edge of the climatic envelope of taxa.  
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11 209 This analysis was based on the hypothesis that populations at the ecological limits are more stressed  
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13 210 by environmental conditions or biotic interactions and therefore might be more susceptible to certain  
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15 211 disturbance agents. To define the location of each NFI-plot within the climatic envelope (temperature  
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17 212 vs precipitation) of each target species we used the niche innerness index from the ecospat R-package  
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19 213 (Di Cola and others 2017).  
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23 214 The effect of disturbance agents on the different considered taxa and on the broader groups  
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25 215 broadleaves vs. conifers was analysed by comparing the absolute and relative BA changes (Wilcoxon-  
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27 216 test). To test if and where disturbances may catalyse future vegetation shifts (i.e., change in forest  
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29 217 composition) we compared the species-specific recruitment density (for saplings and pole-stage trees)  
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31 218 on 'naturally disturbed' and 'not naturally disturbed' sites. Additionally, we used mixed-effects models  
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33 219 to check for combined effects of site and species-specific factors on BA changes of the adult tree  
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35 220 species and on the tree recruitment density. All statistical analysis were conducted in R 3.6.1 (R Core  
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37 221 Team 2020).  
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42 222 **Results**  
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45 223 *Distribution of natural disturbance events*  
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48 224 Of the 5092 NFI plots, 2024 (40%) were classified as 'undisturbed', 1600 (31%) as 'treated' and 778  
49  
50 225 (15%) as 'salvage logging'. Subsequently, 690 (14%) were classified as 'naturally disturbed' of which  
51  
52 226 411 (59% ) were disturbed by wind, 110 (16% ) by insects (predominantly bark beetle), 101 (15% ) by  
53  
54 227 snow/avalanches, 8 (1.2% ) by fire, 11 (1.6% ) by drought and 49 (7.2%) by other agents including mass  
55  
56 228 movements such as landslides (39), flooding (4) and rock fall (3), phytopathogens (2) and cattle (1).  
57  
58 229 Out of the 690 'naturally disturbed' plots, 163 (24%) were affected by several disturbance events  
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1  
2 230 during the observation period (Table S2). The majority of these multiple disturbance events were  
3  
4 231 combinations of wind and insects (72%) in which usually a wind disturbance favoured an insect  
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6 232 outbreak few years later. Another notable source of multiple disturbances were snow and drought,  
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8 233 which both reoccurred in at same plots over the years.

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11 234 Natural disturbance events were significantly more frequent in the 'Plateau' and the 'Northern Alps'  
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13 235 and less frequent than expected by chance in the 'Jura' and 'Southern Alps' (Figure 2). This finding is,  
14  
15 236 however, confounded with the extensive storm damage area produced by storm Lothar (winter 1999)  
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17 237 that mainly affected the 'Plateau' and 'Northern Alps' and resulted to be by far the most impactful  
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19 238 natural disturbance event during the observation period (8% of all NFI-plots). The 'Northern Alps' were  
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21 239 significantly more affected by bark beetles, while forest fires occurred significantly more often in the  
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23 240 'Southern Alps' (Figure 2). Storm Lothar also led to a strong synchronisation of wind and insect  
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25 241 disturbed plots as over 85% of the wind affected sites were recorded in 1999 and 85% of the insect  
26  
27 242 affected sites during the 5 years following the storm (2000-2005, Figure S2). As a side effect of this  
28  
29 243 'synchronisation' of wind and insect damage, our analysis becomes much more consistent as the time  
30  
31 244 interval between disturbance event and NFI observation showed low variability and therefore  
32  
33 245 regrowth and tree recruitment stages are comparable.

34  
35 246 Sample plots dominated by *P. abies* were by far the most affected by natural disturbances (63% of all  
36  
37 247 disturbed plots), which especially holds for wind and insects (>80%; Figure 2) primarily in the 'Plateau'  
38  
39 248 and 'Northern Alps'. Plots dominated by *C. sativa* more often suffered from drought (Figure 2). In  
40  
41 249 contrast, plots dominated by *F. sylvatica* or *Larix* spp. were significantly less often affected by any  
42  
43 250 disturbances. Additionally, stands dominated by *Pinus* spp. (mostly *Pinus sylvestris*) were over-  
44  
45 251 proportionally affected by drought in the dry valleys of the 'Western Central-Alps' but not nationwide.  
46  
47 252 This susceptibility of *Pinus* spp. to drought was further highlighted by the analysis based on niche  
48  
49 253 innerness showing that drought disturbance more often occurred at the edge of *Pinus* spp's'  
50  
51 254 environmental distribution (dry and hot end; Table S3; Figure 3). All other disturbance agents affected  
52  
53 255 the taxa randomly across their environmental space (Figure 3).  
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2 256 Plots with a PNC of silver fir-Norway spruce forests were significantly more often affected by  
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4 257 disturbances than any other community, and in particular by wind, insects and snow (Figure 2). Wind  
5  
6 258 also over-proportionally affected PNCs of beech and silver fir-beech forests, while drought over-  
7  
8 259 proportionally disturbed plots with a PNC of hornbeam and oak forests (Figure 2). More than 75% of  
9  
10 260 the wind disturbed plots with a PNC of beech forest were dominated by another tree species (mainly  
11  
12 261 *P. abies* and, to a lesser degree, *A. alba*). In fact, *P. abies* dominated stands were significantly more  
13  
14 262 often affected by wind disturbance when found on sites with PNCs dominated by broadleaves (e.g.,  
15  
16 263 potential natural beech forests;  $\chi^2 = 8.7242$ ,  $df = 1$ ,  $p\text{-value} = 0.00314$ ).

#### 20 264 *Disturbance effects on species composition*

23 265 Between 1995 and 2017, the total BA of Swiss forests as well as the BA per ha increased from 34.8 M  
24  
25 266  $\text{m}^2$  and  $31.0 \text{ m}^2\text{ha}^{-1}$  to 37.5 M  $\text{m}^2$  and  $32.7 \text{ m}^2\text{ha}^{-1}$ , respectively. However, the subset of NFI-plots used  
26  
27 267 in our study showed a more pronounced BA increase of  $+2.4 \text{ m}^2\text{ha}^{-1}$ . This difference is explained by the  
28  
29 268 fact that the NFI-plots omitted in our analysis showed a decrease in BA ( $-7.4 \text{ m}^2\text{ha}^{-1}$ ) and represent  
30  
31 269 disturbed/damaged plots often followed by 'salvage logging', which were removed from the dataset  
32  
33 270 due to missing information on disturbance agents. The observed BA change mostly represented an  
34  
35 271 increase of broadleaf trees ( $+1.5 \text{ m}^2\text{ha}^{-1}$ ,  $+15\%$ ), while coniferous trees remained almost constant ( $+0.9$   
36  
37 272  $\text{m}^2\text{ha}^{-1}$ ,  $+5\%$ ; Table S4) increasing the BA contribution of broadleaves by 2%. If merely 'not naturally  
38  
39 273 disturbed' plots were considered, BA of both conifers and broadleaf species increased proportionally  
40  
41 274 ( $+15.3\%$  for conifers and  $+17.0\%$  for broadleaves), but conifers were much more affected by natural  
42  
43 275 disturbances than broadleaves ( $-39.4\%$  for conifers and  $-4.9\%$  for broadleaves; Table S4). The two  
44  
45 276 dominant natural disturbance agents (wind and insect outbreaks) mainly affected dense conifer stands  
46  
47 277 dominated by *P. abies* (63% of disturbed plots), particularly in the 'Plateau' and 'Northern Alps' (Figure  
48  
49 278 2), leading to a drastic reduction in BA of *P. abies* ( $-45\%$ ; Table S5, Figure 4). *Pinus* spp. was the only  
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51 279 taxa that decreased in BA on 'naturally disturbed' and on 'not naturally disturbed' plots and was  
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53 280 especially affected by wind and drought disturbances (Table S5, Figure 4). The only broadleaf species  
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1  
2 281 showing a tentative disturbance effect on BA was *C. sativa* suffering from drought in the 'Southern  
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4 282 Alps' (Table S6, Figure 4).

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6  
7 283 A detailed analysis of sites affected by wind or insect disturbances revealed that both, plots naturally  
8  
9 284 dominated by *P. abies* (i.e., PNC of spruce forests) as well as plots naturally dominated by broadleaves  
10  
11 285 showed a dramatic decrease of *P. abies* BA. However, the effect on *P. abies* was significantly stronger  
12  
13 286 on sites naturally dominated by broadleaves ( $-56 \pm 4\%$  for wind,  $-37 \pm 9\%$  for insect) than on sites with  
14  
15 287 PNC of spruce forest ( $-21 \pm 7\%$  for wind,  $-24 \pm 14\%$  for insects; Wilcoxon rank sum test with continuity  
16  
17 288 correction  $W = 19375$ ,  $p < 0.001$  for wind,  $W = 1719$ ,  $p = 0.04$  for insects; Figure 5).

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21 289 In contrast to the 'naturally disturbed' plots, the 'undisturbed' plots (i.e., no human intervention or  
22  
23 290 natural disturbance) showed a significant increase in BA of late-successional species *P. abies* and *F.*  
24  
25 291 *sylvatica* (Figure 6). Both 'salvage logging' and 'treated' showed little effects on BA with only *Acer spp.*  
26  
27 292 significantly increasing on 'treated' plots (Figure 6).

### 28 293 *Post-disturbance vegetation trajectories*

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33 294 Sapling density was higher in NFI4 than in NFI2 (+30%, Table S7) while the density of pole-stage trees  
34  
35 295 was lower (-6%, Table S8). Surprisingly, the number of plots without any saplings increased from 20%  
36  
37 296 to 34% while the number of plots without pole-stage individuals decreased from 57% to 47% (Table  
38  
39 297 S7-8). On 'naturally disturbed' plots mean sapling-density was reduced and pole-stage-density  
40  
41 298 increased compared to 'not naturally disturbed' plots (Table S7-8).

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45 299 Due to the relatively small sampling area and the associated extrapolation to the hectare, data on tree  
46  
47 300 recruitment was highly stochastic and variable. As a result, only very few significant disturbance-  
48  
49 301 induced and species-specific changes in vegetation trajectories could be detected. On PNCs of  
50  
51 302 broadleaves that were mostly stocked with conifers, wind disturbance led to a shift of the vegetation  
52  
53 303 trajectory towards more broadleaves recruitment over the last 20 years (Figure 5). No such shift in tree  
54  
55 304 recruitment was observed on wind-disturbed and insect-attacked sites naturally dominated by spruce  
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57 305 (Figure 5). In sites affected by drought, recruitment by *Pinus ssp.* decreased in favour of *Quercus spp.*,  
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1  
2 306 especially in the ‘Western Central-Alps’ while in the ‘Southern Alps’ the recruitment of *C. sativa*  
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4 307 decreased on drought-prone sites (Table S9-12; Figure 4). *Castanea sativa* was also the only species  
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6 308 showing consistent decrease in tree recruitment (saplings and pole-stage trees) both on ‘naturally  
7  
8 309 disturbed’ and ‘not naturally disturbed’ plots with the notable exception of post-fire tree recruitment  
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10 310 (Table S11-12; Figure 4). ‘Undisturbed plots’ showed no consistent change in tree recruitment, while  
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12 311 both ‘treated’ and ‘salvage logging’ plots seem to favour the recruitment of broadleaves over conifers  
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14 312 (Figure 6).  
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## 18 313 **Discussion**

### 21 314 *Canopy disturbances as catalysts of forest vegetation shifts*

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24 315 Over the last 25 years the Swiss forests showed a shift from conifer towards a higher proportion of  
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26 316 broadleaf species especially at lower elevations. This life form shift was driven by extensive natural or  
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28 317 anthropogenic (i.e., silvicultural treatments) canopy disturbances (> 0.1 ha), or a combination of the  
29  
30 318 two (salvage logging), as forest trajectories did not change in ‘undisturbed’ plots. Additionally, in the  
31  
32 319 warmest and driest regions of Switzerland, comparisons indicate that extreme droughts led to  
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34 320 diverging forest trajectories affecting mostly chestnut groves and oak-pine forests.  
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### 38 321 *Fatal attraction: P. abies outside of their natural range*

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41 322 While the overall contribution to BA of most species only slightly changed ( $\pm 0.7\%$ ) between 1995 and  
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43 323 2017, a considerable if not dramatic change was observed in *P. abies* (-2.9%) and stands dominated by  
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45 324 *P. abies* were confirmed to be especially susceptible to certain natural disturbances (62% of all natural  
46  
47 325 disturbance events), which resulted in a shift towards more broadleaf species. This is not surprising  
48  
49 326 when considering the general susceptibility of *P. abies* to both windthrow (e.g., Hanewinkel and others  
50  
51 327 2011) and the European spruce bark beetle (*Ips typographus*; e.g., Wermelinger 2004; Faccoli and  
52  
53 328 Bernardinelli 2014), including the interaction of beetle attacks in spruce forests weakened by wind  
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55 329 disturbance or prolonged drought (Stadelmann and others 2013; De Groot and others 2018; Dobor  
56  
57 330 and others 2020).  
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2 331 In our study large-scale wind damage in spruce stands occurred predominantly during the Lothar storm  
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4 332 (1999), which mostly affected forests at low elevations within the range of the natural beech and silver  
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6 333 fir-beech communities. No major storm occurred during the observation period in montane and  
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8 334 subalpine Norway spruce forests. In mountain spruce forests affected by Vivian (storm at higher  
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10 335 elevation, predominantly in the Central Alpine valleys; 1990) the post-disturbance regeneration  
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12 336 trajectories were dominated by *P. abies* (Schönenberger 2002). In contrast, in the Lothar-affected  
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14 337 lowlands and foothills of the Pre-Alps, where *P. abies* is mostly out of the natural range as it was  
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16 338 frequently planted in the past and promoted in the frame of adopted German silvicultural systems  
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18 339 (Bürgi and Schuler 2003), the post-disturbance trajectories indicate a decrease in *P. abies*. This pattern  
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20 340 was additionally reinforced by the abundant bark beetle outbreaks that occurred on plots previously  
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22 341 affected by wind disturbance during the heatwave in summer 2003 (Forster and Meier 2010;  
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24 342 Stadelmann and others 2014).

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29 343 Our data on tree recruitment suggest that on low elevation sites, where forests are naturally  
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31 344 dominated by broadleaves, disturbances significantly altered forest trajectories away from *P. abies*  
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33 345 (and conifers in general) towards more broadleaf species. The shift in vegetation trajectories towards  
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35 346 more broadleaves recruitment was stronger after wind than insect disturbance. Bark beetle usually  
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37 347 mainly attack trees older than 50 years, leaving younger trees healthy (Wermelinger 2004) and  
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39 348 therefore limiting the potential for a dramatic shift in vegetation trajectories. Nevertheless, salvage  
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41 349 logging to control bark beetle infestations and intensified harvests of *P. abies* to avoid financial loss  
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43 350 due expected further lowering of wood prices supported this trend (Kläy 2015). As the most influential  
44  
45 351 disturbance events happened around 15–20 years ago the shift in vegetation trajectories was mostly  
46  
47 352 visible in the well-established pole-stage that are nowadays dominated by broadleaves. This indicates  
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49 353 that, at low elevations, broadleaf species are competitively superior to *P. abies*, as had been  
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51 354 demonstrated in post-windthrow patches (Kramer and others 2014). The increased reliance on natural  
52  
53 355 regeneration in the second half of the 20<sup>th</sup> century (Bürgi 1999) has also contributed to their recent re-  
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55 356 expansion. Additionally, at lower elevations foresters started to transition forests away from *P. abies*  
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1  
2 357 by species regulation in the juvenile phase (up to thickets) and through targeted thinning. Since most  
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4 358 future climate change scenarios predict an increased frequency of extreme weather events such as  
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6 359 large storm systems, prolonged droughts and heatwaves, linked disturbances (e.g., Seidl and others  
7  
8 360 2017) need to be considered. Insect attacks likely increase, as wind-disturbed and climatically stressed  
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10 361 trees become more susceptible (Brandl and others 2020), and warmer temperatures stimulate bark  
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12 362 beetle population dynamics resulting in more generations and higher densities during one season  
13  
14 363 (Stadelmann and others 2013; Jakoby and others 2016). At higher elevations, disturbances did not  
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16 364 seem to negatively affect the recruitment of conifers both after wind and insect disturbances, which  
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18 365 indicates that in these cooler forest habitats a direct regrowth of the stand-forming coniferous species.  
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20 366 This is in line with findings of Kramer and others (2014) on regeneration in gaps produced by  
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22 367 windthrow across Switzerland.  
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27 368 *Impressive though rare: fire and drought*  
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30 369 In contrast to damage by wind and insect outbreaks, other disturbance agents or extreme events such  
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32 370 as fire and drought were rarely observed during the study period and affected only a small proportion  
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34 371 of the Swiss forest area (< 0.2% of plots) mostly located in the warmest ('Southern Alps') and driest  
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36 372 biogeographic Swiss regions ('Western Central-Alps'). In the dry valleys of the 'Western Central-Alps'  
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38 373 drought has negatively affected *P. sylvestris* that has for long dominated slopes at low elevation due  
39  
40 374 to traditional land-use practices (pasture and litter collection; Gimmi and others 2010) towards the dry  
41  
42 375 limits of forest growth (Etzold and others 2019). Land-use change in the past decades in combination  
43  
44 376 with repeated extreme drought events increased tree mortality (e.g., Rigling and others 2013) and  
45  
46 377 benefit the more drought-resistant and shade-tolerant downy oak (*Q. pubescens*). In fact, combined  
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48 378 drought-shade effects to drought-tolerant *P. sylvestris* (Niinemets and Valladares 2006), hampers  
49  
50 379 successful recruitment (Bachofen and others 2019). Similar transitions from pines to oaks are reported  
51  
52 380 for dry regions in Italy (Vacchiano and Motta 2015) and Spain (e.g., Zavala and others 2000; Galiano  
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54 381 and others 2010; Carnicer and others 2014; Morán-López and others 2014).  
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2 382 In the 'Southern Alps' drought mostly affected forests dominated by the *C. sativa*. The chestnut groves  
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4 383 in southern Switzerland are the result of a long-term land use practice aimed at producing both fruits  
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6 384 for the self-sustainment and wood (Krebs and others 2012), which encouraged the chestnut cultivation  
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8 385 at the limits of the tree and in some cases even at the edge of its fundamental niche (Muster and others  
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10 386 2007). Similar to the pine-dominated forests in the Valais, the suspension of any management input  
11  
12 387 made the chestnut groves particularly susceptible to the colonization by other more site-specific tree  
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14 388 species, exposing the light-demanding *C. sativa* trees to competition, climatic stress, and specific  
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16 389 diseases (Conedera and others 2001). On the most dry and exposed sites, this resulted also in an  
17  
18 390 enhanced summer drought susceptibility as revealed by the 2003 summer drought and heat wave  
19  
20 391 (Conedera and others 2009). All this induces a shift towards the PNC, i.e. corresponding to beech on  
21  
22 392 rich sites at higher elevation and to broadleaf mixed forests dominated by lime (*Tilia* spp.) as well as  
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24 393 maple trees (*Acer* spp.) in the lowlands (Conedera and others 2000; Muster and others 2007). Fire  
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26 394 displays, on contrary, the opposite effect by enhancing the recruitment of the disturbance-adapted *C.*  
27  
28 395 *sativa* that profits from its extreme resprouting capacity and outcompetes other fire-sensitive  
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30 396 broadleaves (Delarze and others 1992), including invasive evergreen species (Grund and others 2005).  
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32  
33 397 So far, both drought and fire affected the forest dynamics trajectory only in NFI plots in the warmest  
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35 398 and driest parts of the country that are dominated by certain species as a result of century long  
36  
37 399 management effects (i.e., *C. sativa* and *P. sylvestris*) that partially grow at their ecological limits. The  
38  
39 400 question arises how disturbances may affect the most widespread forest types such as spruce and  
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41 401 beech forests in the future. Conspicuous drought damage in both beech and spruce forests during the  
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43 402 recent summer drought periods (2018, 2019; Schuldt and others 2020) suggest that drought may  
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45 403 assume a central role in shaping future forest trajectories in Swiss Forests. Evidences of forest fires  
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47 404 impacting usually fire-avoiding forest types such as beech stands are also increasing in recent decades  
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50 405 (Maringer and others 2016).  
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57 406 *Limits of the study*  
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2 407 In this study, we used the data collected on revisited plots of the Swiss forest inventory. Beside the  
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4 408 great advantage of the long time span of the observations (up to 25 years) and the permanent  
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6 409 character of the plots, the used data presents also some limits. The shift of the survey from a periodic  
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8 410 three-years lasting survey (NFI2) to a continuous, nine-years lasting field activity (NFI4) implies that  
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10 411 the period of observation may vary by up to eight years among plots. In addition, the survey protocol  
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12 412 of the recruitment slightly changed between the two inventories and the retrospective approach in  
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14 413 reconstructing and assessing the disturbances that occurred on each plot may represent a source of  
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16 414 imprecision.

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20 415 Systematic samples such as the NFI produce representative results in terms of quantitative rankings.  
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22 416 However, important small-scale phenomenon such as the local spread of neophytes (Maringer and  
23  
24 417 others 2012; Conedera and others 2018), the dynamic of rare species or the study of detailed post-  
25  
26 418 disturbance ecological processes require targeted and species-specific approaches (e.g., Allen and  
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28 419 others 2010; Moser and others 2010; Rigling and others 2013; Maringer and others 2020; Schuldt and  
29  
30 420 others 2020).

## 31 32 33 34 421 **Conclusions**

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37 422 Most future climate scenarios predict warmer and drier conditions across Switzerland and Europe in  
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39 423 general (Zubler and others 2014) and an increasing risk of prolonged droughts (Spinoni and others  
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41 424 2018), forest fires (Pezzatti and others 2016) and large storms (Collins and others 2019). However,  
42  
43 425 while models often predict dramatic changes in forests with ongoing climate change (e.g., Lindner and  
44  
45 426 others 2014; Dyderski and others 2018), representative studies observe no or only slow transitions  
46  
47 427 (e.g., Gehrig-Fasel and others 2007; Lenoir and others 2010b; Küchler and others 2015). Despite the  
48  
49 428 limits of the present approach, we detected natural disturbance as a major trigger of vegetation shifts  
50  
51 429 in Swiss forests in the current global change context. At present, post-disturbance vegetation shifts  
52  
53 430 occur where the dominant species has been cultivated out of its natural range due to economic reasons  
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55 431 (i.e., *P. abies* in the lowland of the Plateau). Additionally, forests seem increasingly at risk in hitherto  
56  
57 432 traditional ranges of management (i.e., widespread pure pine stands at low elevations in the Valais or

1  
2 433 the chestnut groves in the Southern Alps). Overall, our data suggest that the forest trajectory after a  
3  
4 434 disturbance favours recruitment of species of the natural forest community. In particular, in disturbed  
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6 435 *P. abies* stands at the low-lands, broadleaf species regenerate most successfully, while in *P. abies*  
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8 436 stands at higher elevations, direct regrowth of this and other coniferous species prevails. Undisturbed  
9  
10 437 forest stands, on contrary, persisted in their species composition, and the constrained tree recruitment  
11  
12 438 under canopy was mostly comprised of the species dominating the stand. Tree regeneration under  
13  
14 439 dense canopies is always sparse and only a few species are able to build up an abundant 'seedling  
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16 440 bank' in a closed and shady stand (Grubb 1977; Savage and others 1996). Most species rather  
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18 441 regenerate in pulses realized in canopy gaps (Zackrisson and others 1995; Jentsch and White 2019). In  
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20 442 a small gap, however, the chance that seeds from new species arrive during the window of opportunity  
21  
22 443 for seedling establishment is a stochastic event and most gaps will be filled with seedlings from the  
23  
24 444 already present dominant species (Moser and others 2010). Therefore, in undisturbed forests the  
25  
26 445 'biotic component' of the dominating tree species rather than the abiotic conditions are driving species  
27  
28 446 selection. Larger-scale disturbances, on the other hand, seem to level the playing field allowing more  
29  
30 447 species to establish and favour those (among which many opportunistic ones) that are adapted to the  
31  
32 448 current environmental conditions and can increase resistance against future disturbances (e.g.,  
33  
34 449 repeated insect outbreaks; Sommerfeld and others 2020). Larger-scale disturbances might therefore  
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36 450 act as essential catalysts to enable/accelerate the transition of forest ecosystems in adaptation to  
37  
38 451 changing environmental conditions (Brice and others 2019; Brice and others 2020).  
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For Peer Review

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2 701 **Figure Legends**  
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5 702 **Figure 1:** Biogeographic regions of Switzerland (Gonseth and others 2001) and geographic positions of  
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7 703 NFI-sample plots used in this study. Different point colours indicate the type of natural disturbance  
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9 704 recorded in the period 1993–2017 and the shade colours different biogeographic regions. None = ‘Not  
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11 705 naturally disturbed’.

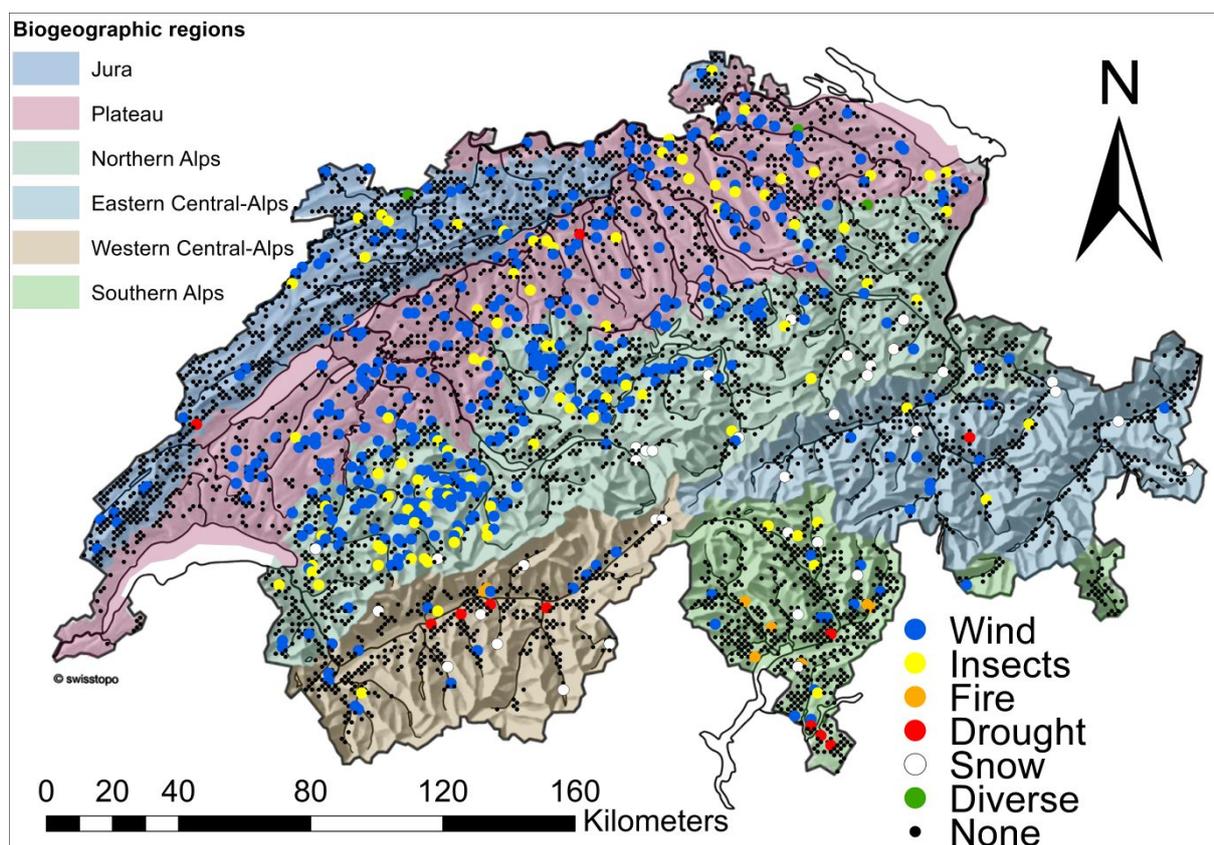
12  
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14 706 **Figure 2:** Matrix of different disturbances agents and biogeographic regions (left), dominant tree  
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16 707 species (middle) and potential natural forest community (right). The colours indicate interactions that  
17  
18 708 were worse (red) or better (green) than statistically expected. The asterisks indicated significant  
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20 709 differences between expectations and observations based on chi-squared tests. The numbers indicate  
21  
22 710 the number of observations.

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26 711 **Figure 3:** Climatic preferences of different taxa based on occurrence records (green area) within the  
27  
28 712 climate of all NFI sample plots (grey area). Plots are marked by colours for different disturbance agents  
29  
30 713 and by symbols for biogeographic regions. Both the grey and green area are MCP spanning 95% of all  
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32 714 occurrences. The number in brackets indicate the absolute number and proportion as dominant taxa  
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34 715 across the 5092 NFI plots. DR = Disturbance ratio reflecting the proportion of plots of this taxa affected  
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36 716 by disturbance events. DP = Disturbance proportion reflects the proportion of disturbance events  
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38 717 associated with a certain taxa.

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42 718 **Figure 4:** Change in basal area ( $\text{m}^2\text{ha}^{-1}$ ; top), sapling recruitment (stems  $\text{ha}^{-1}$  with height  $>10$  cm and  
43  
44 719 DBH  $< 4$  cm; middle) and pole-stage recruitment (stems  $\text{ha}^{-1}$  with DBH 4–11.9 cm; bottom) between  
45  
46 720 NFI2 and NFI4 records on sample plots affected by different disturbances agents (with number of plots;  
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48 721 None = ‘Not naturally disturbed’). Coloured bars indicate the mean, black bars the standard errors.  
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50 722 Asterisks mark significant changes (pairwise-Wilcoxon with Holm correction,  $p < 0.05$ ). Aa = *Abies alba*,  
51  
52 723 Pa = *Picea abies*, Pc = *Pinus cembra*, La = *Larix* spp., Pi = *Pinus* spp., Oc = other conifers, Cs = *Castanea*  
53  
54 724 *sativa*, Fs = *Fagus sylvatica*, Ac = *Acer* spp., Fr = *Fraxinus* spp., Qu = *Quercus* spp., Ob = other broadleaves.  
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2 725 **Figure 5:** Change in basal area ( $\text{m}^2\text{ha}^{-1}$ ; a,d), sapling recruitment (stems  $\text{ha}^{-1}$  with height >10 cm and  
3  
4 726 DBH < 4 cm; b,e) and pole-stage recruitment (stems  $\text{ha}^{-1}$  with DBH 4-11.9 cm; c,f) between NFI2 and  
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6 727 NFI4 records on sample plots affected by wind (a,b,c) and insect disturbance (d,e,f) grouped into plots  
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8 728 naturally dominated by spruce (blue, montane/sub-alpine Norway spruce forests and Silver fir-Norway  
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10 729 spruce forests) and naturally dominated by broadleaves (red). Aa = *Abies alba*, Pa = *Picea abies*, Pc =  
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12 730 *Pinus cembra*, La = *Larix* spp., Pi = *Pinus* spp., Oc = other conifers, Cs = *Castanea sativa*, Fs= *Fagus*  
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14 731 *sylvatica*, Ac = *Acer* spp., Fr= *Fraxinus* spp., Qu = *Quercus* spp., Ob = other broadleaves.

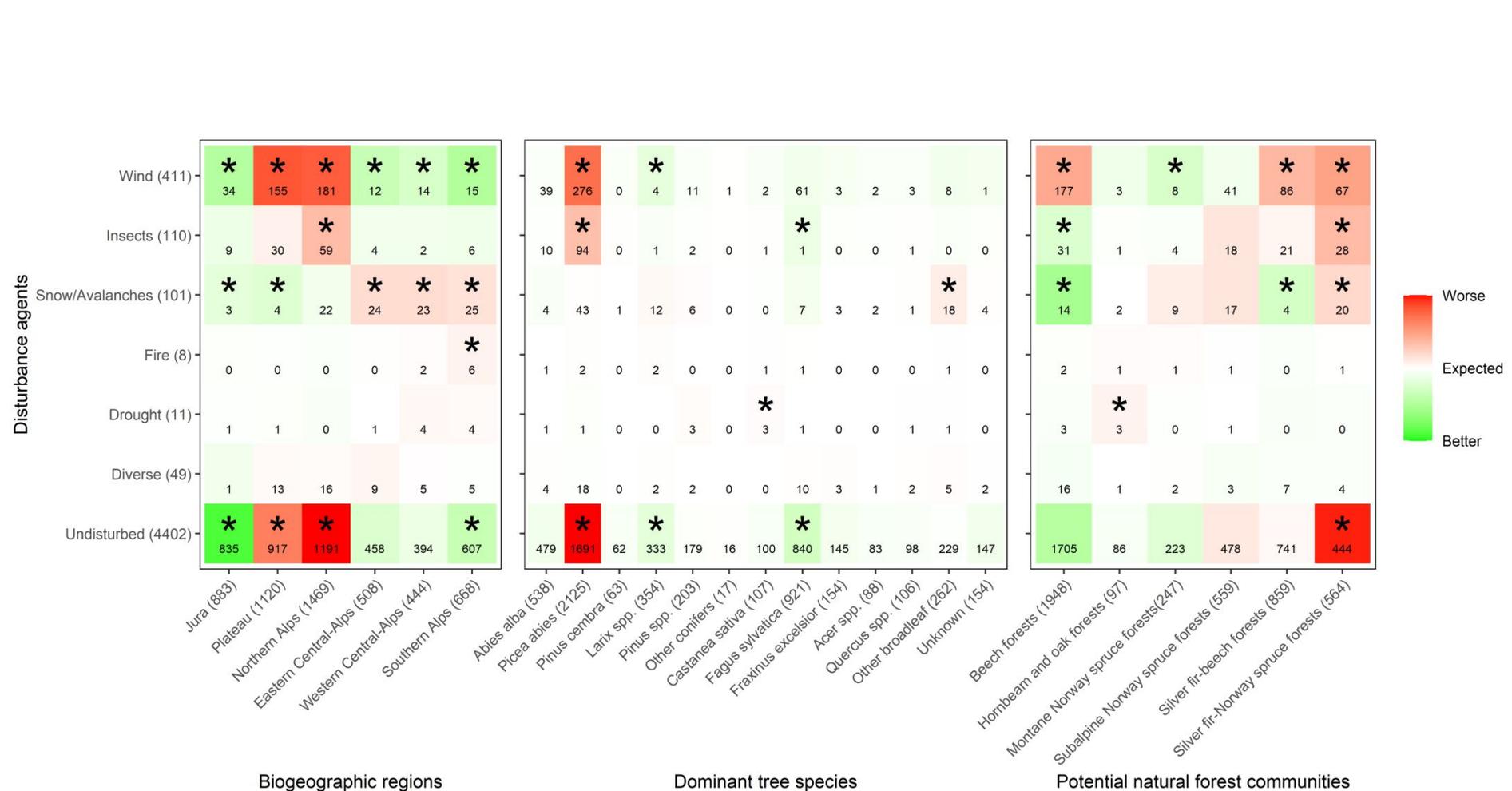
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18 732 **Figure 6:** Change in basal area ( $\text{m}^2\text{ha}^{-1}$ ; top), sapling recruitment (stems  $\text{ha}^{-1}$  with height >10 cm and  
19  
20 733 DBH < 4 cm; middle) and pole-stage recruitment (stems  $\text{ha}^{-1}$  with DBH 4-11.9 cm; bottom) between  
21  
22 734 NFI2 and NFI4 records on 'naturally disturbed', 'salvage logging', 'treated' and 'undisturbed' sample  
23  
24 735 plots. Coloured bars indicate the mean, black bars the standard errors. Asterisks mark significant  
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26 736 changes (pairwise-Wilcoxon with Holm correction,  $p < 0.05$ ). Aa = *Abies alba*, Pa = *Picea abies*, Pc =  
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28 737 *Pinus cembra*, La = *Larix* spp., Pi = *Pinus* spp., Oc = other conifers, Cs = *Castanea sativa*, Fs= *Fagus*  
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30 738 *sylvatica*, Ac = *Acer* spp., Fr= *Fraxinus* spp., Qu = *Quercus* spp., Ob = other broadleaves.



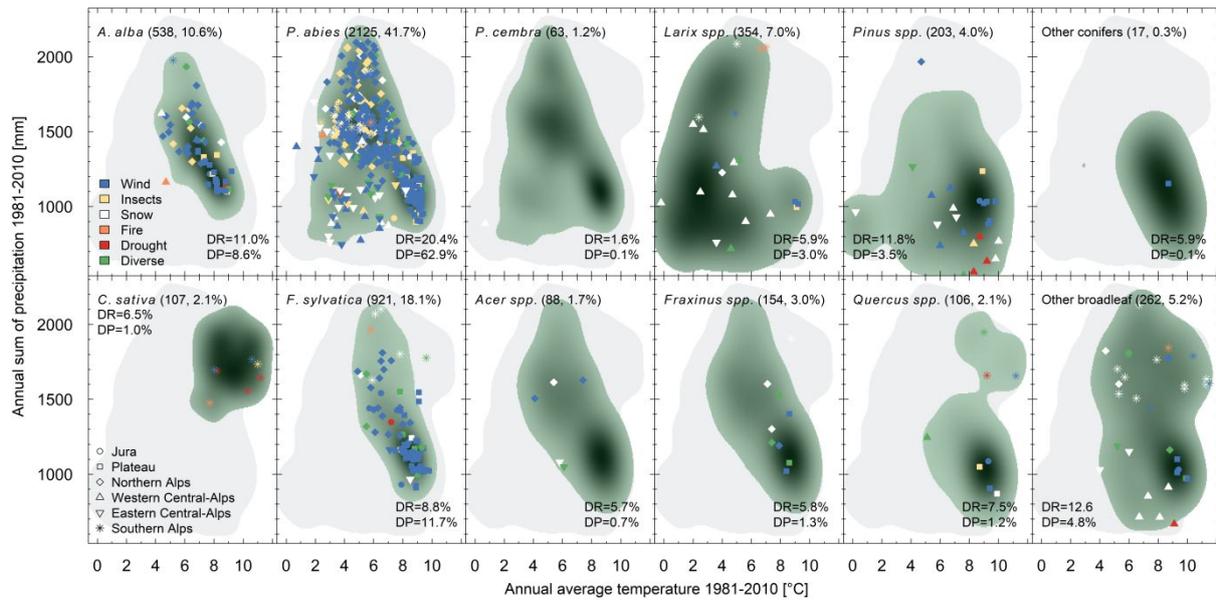
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740 **Figure 1:** Biogeographic regions of Switzerland (Gonseth and others 2001) and geographic positions of  
 741 NFI-sample plots used in this study. Different point colours indicate the type of natural disturbance  
 742 recorded in the period 1993–2017 and the shade colours different biogeographic regions. None = 'Not  
 743 naturally disturbed'.

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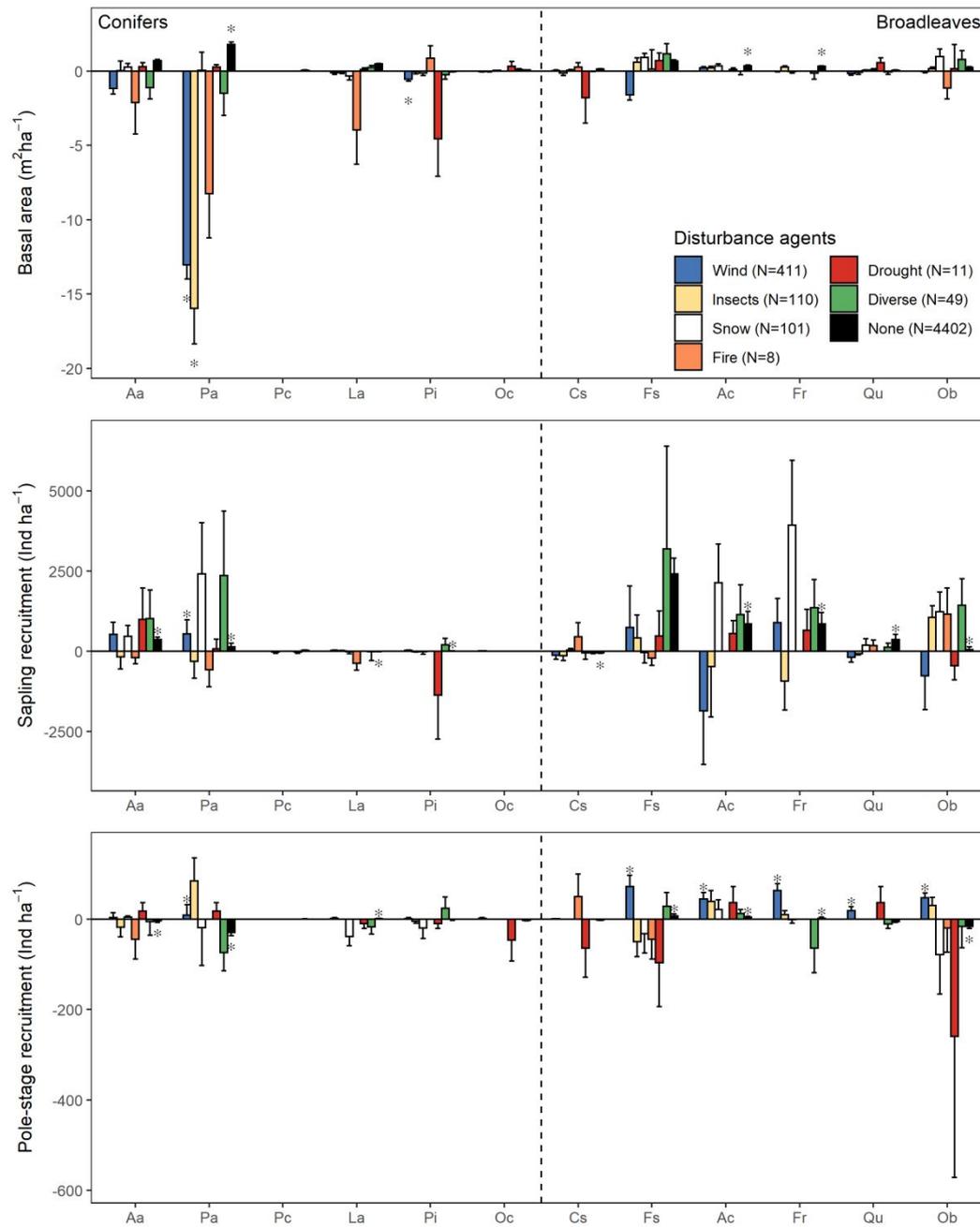
**Figure 2:** Matrix of different disturbances agents and biogeographic regions (left), dominant tree species (middle) and potential natural forest community (right). The colours indicate interactions that were worse (red) or better (green) than statistically expected. The asterisks indicated significant differences between expectations and observations based on chi-squared tests. The numbers indicate the number of observations.



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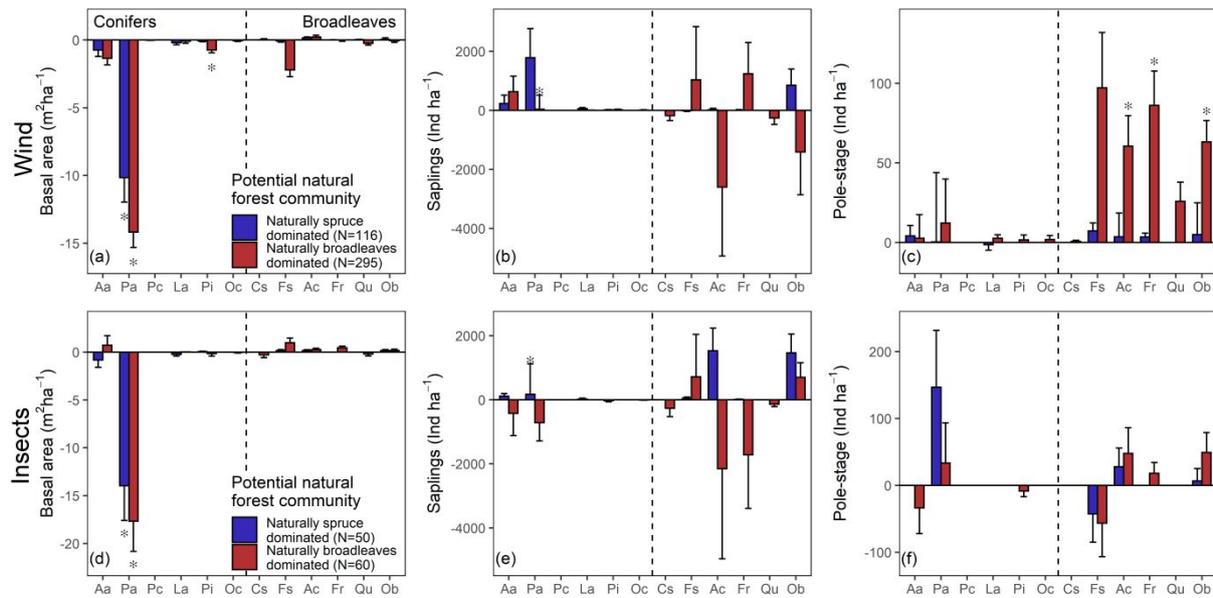
751 **Figure 3:** Climatic preferences of different taxa based on occurrence records (green area) within the  
 752 climate of all NFI sample plots (grey area). Plots are marked by colours for different disturbance agents  
 753 and by symbols for biogeographic regions. Both the grey and green area are MCP spanning 95% of all  
 754 occurrences. The number in brackets indicate the absolute number and proportion as dominant taxa  
 755 across the 5092 NFI plots. DR = Disturbance ratio reflecting the proportion of plots of this taxa affected  
 756 by disturbance events. DP = Disturbance proportion reflects the proportion of disturbance events  
 757 associated with a certain taxa.

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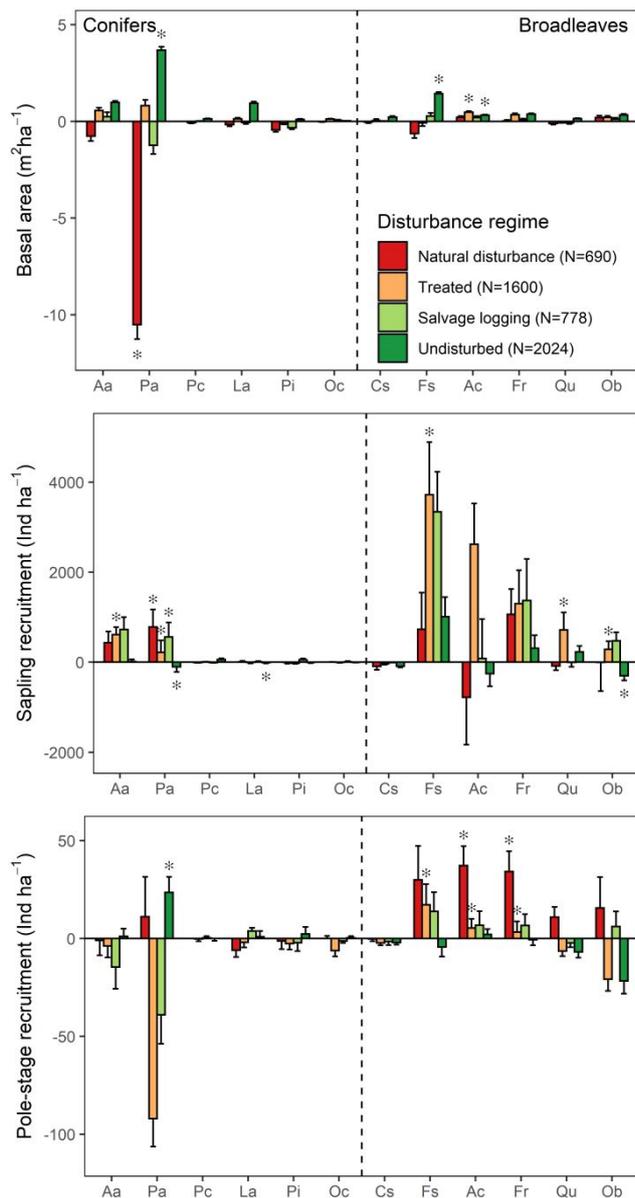
760 **Figure 4:** Change in basal area ( $\text{m}^2 \text{ha}^{-1}$ ; top), sapling recruitment (stems  $\text{ha}^{-1}$  with height  $>10$  cm and  
 761 DBH  $< 4$  cm; middle) and pole-stage recruitment (stems  $\text{ha}^{-1}$  with DBH 4-11.9 cm; bottom) between  
 762 NFI2 and NFI4 records on sample plots affected by different disturbances agents (with number of plots;  
 763 None = 'Not naturally disturbed'). Coloured bars indicate the mean, black bars the standard errors.  
 764 Asterisks mark significant changes (pairwise-Wilcoxon with Holm correction,  $p < 0.05$ ). Aa = *Abies alba*,  
 765 Pa = *Picea abies*, Pc = *Pinus cembra*, La = *Larix* spp., Pi = *Pinus* spp., Oc = other conifers, Cs = *Castanea*  
 766 *sativa*, Fs = *Fagus sylvatica*, Ac = *Acer* spp., Fr = *Fraxinus* spp., Qu = *Quercus* spp., Ob = other broadleaves.



767

768 **Figure 5:** Change in basal area ( $m^2 ha^{-1}$ ; a,d), sapling recruitment (stems  $ha^{-1}$  with height >10 cm and  
 769 DBH < 4 cm; b,e) and pole-stage recruitment (stems  $ha^{-1}$  with DBH 4-11.9 cm; c,f) between NFI2 and  
 770 NFI4 records on sample plots affected by wind (a,b,c) and insect disturbance (d,e,f) grouped into plots  
 771 naturally dominated by spruce (blue, montane/sub-alpine Norway spruce forests and Silver fir-Norway  
 772 spruce forests) and naturally dominated by broadleaves (red). Aa = *Abies alba*, Pa = *Picea abies*, Pc =  
 773 *Pinus cembra*, La = *Larix* spp., Pi = *Pinus* spp., Oc = other conifers, Cs = *Castanea sativa*, Fs = *Fagus*  
 774 *sylvatica*, Ac = *Acer* spp., Fr = *Fraxinus* spp., Qu = *Quercus* spp., Ob = other broadleaves.

775



776

777 **Figure 6:** Change in basal area (m<sup>2</sup>ha<sup>-1</sup>; top), sapling recruitment (stems ha<sup>-1</sup> with height >10 cm and  
 778 DBH < 4 cm; middle) and pole-stage recruitment (stems ha<sup>-1</sup> with DBH 4-11.9 cm; bottom) between  
 779 NFI2 and NFI4 records on 'naturally disturbed', 'salvage logging', 'treated' and 'undisturbed' sample  
 780 plots. Coloured bars indicate the mean, black bars the standard errors. Asterisks mark significant  
 781 changes (pairwise-Wilcoxon with Holm correction, p < 0.05). Aa = *Abies alba*, Pa = *Picea abies*, Pc =  
 782 *Pinus cembra*, La = *Larix* spp., Pi = *Pinus* spp., Oc = other conifers, Cs = *Castanea sativa*, Fs = *Fagus*  
 783 *sylvatica*, Ac = *Acer* spp., Fr = *Fraxinus* spp., Qu = *Quercus* spp., Ob = other broadleaves.