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Canopy Disturbances Catalyse Tree Species Shifts in Swiss Forests

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Canopy disturbances catalyse vegetation shifts in Swiss forests

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Manuscripts

Canopy disturbances catalyse vegetation shifts in Swiss forests

Short title: Canopy disturbances catalyse vegetation shifts

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Authors contribution

TW initiated the idea and DS developed the methods; DS and CF analysed the data; DS, TW and MC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

The data used in this manuscript will be stored in the EnviDat repository upon acceptance. The raw data from the Swiss NFI can be provided free of charge within the scope of a contractual agreement (http://www.lfi.ch/dienstleist/daten-en.php).

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Abstract

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

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

Manuscript highlights

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

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Introduction

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

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2018). On the other hand, reports supporting rapid vegetation shifts due to climate warming often refer to opportunistic case studies and neglect the vast majority of other forests, where possible substantial changes may remain unobserved (Jump and others 2007; Brandl and others 2020).

Both simulation studies (e.g., Liang and others 2018; Scherrer and others 2020) as well as forest surveys (e.g., Peñuelas and Boada 2003; Rigling and others 2013; Brice and others 2019; Brice and others 2020) suggest that disturbances and extreme events (natural or anthropogenic) are a key component in facilitating forest transitions under climate change by creating favourable conditions for opportunistic species better adapted to the novel (and presumed future) climatic conditions. Whether such events leading to tree and stand mortality alter forest trajectories or simply result in ingrowth (i.e., infilling by the already dominant species; e.g., Kramer and others 2014) might be highly dependent on complex interactions of environmental conditions, disturbance agents and their severity (Seidl and others 2017; Jentsch and von Heßberg 2019; Nikolova and others 2019). Furthermore, forest stands differ in their susceptibility/vulnerability to specific disturbance agents (e.g., wind, fire, pest or avalanches) as a function of their age and development stage, which leads to a multitude of potential post-disturbance forest trajectories, additionally modulated by the local or regional dominant disturbance regimes, environmental conditions (e.g., high vs low elevation) and understory dynamics (Bolte and others 2014).

To find evidence for representative disturbance-induced forest changes, we used the unique nationwide data from the Swiss National Forest Inventory (NFI; Fischer and Traub 2019) covering several bioclimatic regions (i.e., Jura, the Plateau, the Northern Alps, the Western and Eastern Central-Alps and the Southern Alps) and spanning an elevation gradient from 240 to 2400 m a.s.l. All main Swiss forest types are represented in this systematic inventory allowing us a statistically representative overview of disturbance events and species-specific post-disturbance dynamics, e.g., changes in basal area and recruitment density over an average period of 25-years. We focused on four prevalent natural disturbance agents (i.e., wind, insect outbreaks, forest fires, and prolonged drought events) likely to increase in frequency with future environmental change (Seidl and others 2017) in order to investigate:

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(1) how do natural disturbance agents differ in frequency among different biogeographic regions, climatic conditions, and forest types, (2) which species were most affected by different disturbance agents and (3) are there any differences between pre- and post-disturbance tree species composition (adult trees and recruitment) that may suggest potential vegetation shifts?

Material and methods

Study region and climate data

The study area is Switzerland, encompassing a territory of 41,285 km² of which 31.9% (13,169 km²) is forested (Cioldi and others 2020). Forests range from about 200 to 2400 m a.s.l. with the lower elevations dominated by broadleaves and the higher elevations by conifers (Figure S1). Corresponding with regions and with steep elevation gradients around the Alpine arc, the climate strongly varies. In the north of the Alps, the climate is mainly influenced by the Atlantic Ocean, from where mild, humid winds blow. In Zurich-Affoltern at 443 m a.s.l., winters are mild (0.3 °C in January) and summers warm (18.8 °C in July), with annual precipitation of 1054 mm. In the south of the Alps, the climate is influenced by the Mediterranean system with temperatures 2–3 °C warmer than in the North, and annual precipitation usually exceeds 1600 mm (Locarno-Monti; 366 m a.s.l.). Central Alpine valleys are dry with nationwide lowest annual precipitation (603 mm, Sion; MeteoSwiss 2020). In accordance with this climate heterogeneity, Switzerland is categorized into six biogeographic regions (Gonseth and others 2001; Figure 1). To take into account the existing climatic spatial heterogeneity, we used the annual mean temperature (°C) and the annual precipitation sum (mm) derived from gridded climatic data calculated at a 100 x 100 m resolution for the reference period of 1981–2010 as spatial layers (meteoswiss.ch; Zubler and others 2014).

Forest inventory data

We used data of the Swiss National Forest Inventory (NFI), recorded on a 1.4 km x 1.4 km systematic permanent sample grid covering the whole country, during the second NFI (NFI2; 1993–1995) and the fourth NFI (NFI4; 2009–2017), respectively. Previous to analyses, we removed all plots classified as

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shrub land or not visited in both NFI2 and NFI4, eventually retaining the 5521 accessible forest plots. Passing from NFI2 to NFI4 the protocol of terrestrial data collection slightly changed as well as the survey period did, which switched from a three-year assessment window to a nine-year-window (continuous inventory since NFI4; Brändli and Hägeli 2019; Lanz and others 2019). The vast majority of Swiss forests were since centuries and still are managed following a 'close-to-nature' silvicultural approach (Spathelf and others 2015). The commandment of privileging natural tree recruitment or planting of native site-adapted species when natural regeneration is difficult is even embodied in the national forest law. As a result, large monoculture plantations are very rare as are non-native tree species (Table S1), which are only present on 2.4% of NFI-plots and contribute less than 0.6% to the basal area of Swiss forests (Brändli and others 2020).

A terrestrial NFI-plot consists of several plot elements. Standing and lying trees are measured using two concentric circular plots (500 m^2 and 200 m^2). On the large plot all trees with a diameter at breast height (DBH) ≥36 cm are measured, while on the small plot also trees and shrubs with a DBH ≥12 cm and <36 cm are measured (Lanz and others 2019). Tree recruitment is defined as individuals ≥ 10 cm height and <12 cm DBH and was assessed using concentric circles with different sizes. In NFI2 two satellite plots with two concentric circles differing in radius were used (r = 1–2.12 m; Stierlin 1994) and in NFI4 one satellite plot with four concentric circles was used (r = 0.9–4 m; Düggelin and Keller 2017). We used the total available dataset, as preliminary analyses showed changes in sampling design between NFI2 and NFI4 to have no significant impact on recruitment density per hectare. Different size of the satellite plots might impact analysis of species diversity, which, however, is not in focus of the present study. On the interpretation area of 50 x 50 m (0.25 ha) around the plot centre disturbances and the potential natural forest community were determined. After estimating the extension of existing damages in the field, the disturbance agent was evaluated by interviews with the local foresters (Stierlin 1994; Düggelin and Keller 2017). The potential natural forest communities (PNC) were defined by experts that visited 25% of the NFI sample plots and concluded community identities by analogy (using factor maps and local knowledge) for the remaining 75% of the plots, according to

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the Swiss protection forest classification (NaiS; ARGE Frehner and others 2020). These PNC depict the expected idealised natural tree species composition (including recruitment) when the forest stands are totally in balance with the dominant environmental conditions (e.g., climate, topography, soil) as expressed by the present understory species (Frey and others 2020). In this study we use 17 simplified PNC defined according to the main tree species (e.g. sub-montane beech forests or sub-alpine spruce forests). A forest stand is then defined as natural when the occurring dominant tree species based on NFI data (i.e., based on basal area) is identical to the PNC (e.g., *Picea abies* has highest basal area per ha on NFI-plots belonging to the sub-alpine spruce forest PNC). However, due to present and/or past management decisions, differences may exist between the actual dominating species and the PNC species. To prevent confusion between dominant taxa and the PNC of a NFI-plot we will use in this paper the scientific taxon name for the dominant species (e.g., *Picea abies*, *Fagus sylvatica*) and the English names for the PNC (e.g., spruce forest and beech forest).

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

Data pre-processing

Of the 56 tree species that were recorded in the NFI-plots, only few are very abundant and contributed to the vast bulk of biomass while the majority of species are rare or added little biomass. We therefore reclassified all species into twelve taxa: *Abies alba* (silver fir), *Picea abies* (spruce), *Pinus cembra* (Swiss stone pine), *Larix* spp.(larch), *Pinus* spp. (pine), other conifers, *Castanea sativa* (sweet chestnut), *Fagus sylvatica* (European beech), *Acer* spp. (Maple), *Fraxinus* spp. (ash), *Quercus* spp. (oak), other broadleaves (for details see Table S1). The dominant taxa for each plot was defined based on the BA represented. For each species, we calculated the climatic envelop on the base of the gridded values of the annual mean temperatures and precipitation. Further, we divided the tree recruitment into

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individuals with DBH < 4 cm (saplings) and individuals with DBH 4 - 11.9 cm (pole stage) as these size groups represent very different age cohorts and amount of (self-)thinning.

Defining disturbed plots

To distinguish between naturally disturbed NFI sample plots (hereafter called 'naturally disturbed') and all others ('not naturally disturbed') we used the following criteria: 'naturally disturbed' if a) the NFI field team reported a damage affecting at least 10% of the interpretation area, and b) the local forester reported a specific disturbance agent for the plot (e.g., wind, fire). Plots with a contradiction between the foresters' report and the NFI field team observations were removed from further analysis, leaving us with 5092 plots. Most of these mismatches were the result of minor disturbances already invisible at the time of the next NFI visit. In this study, we were interested in obvious, i.e. canopy disturbances with the potential to catalyse vegetation shifts and consequently these small-scale and very low-severity disturbances were not analysed. In the cases where more than a single disturbance event and/or disturbance agent affected a NFI-sample plot, we determined the main disturbance agent by comparison of the area damage caused by each disturbance agent. For the later classification of plots into different disturbance agents, the main damage type (as determined by maximum area damaged) was used.

'Not naturally disturbed' plots were further subdivided based on the information of the NFI into 'undisturbed' that is without any recorded natural disturbance and human intervention in the past 25 years, 'treated' that are plots where planned silvicultural treatments occurred, and 'salvage logging', which resulted from mortality/damage events related to smaller natural disturbances (i.e., less than 10% of the interpretation area affected). This classification allowed us to test if a larger-scale natural disturbance leads to a different vegetation trajectory compared to a human induced disturbance (i.e., 'treated' and 'salvage logging') or no intervention and no disturbance at all (i.e., 'undisturbed').

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Data analysis

To test if certain site conditions (i.e., biogeographic region, dominant taxa or PNC) were linked to a specific natural disturbance agent we used Chi-squared analysis. Additionally, we conducted a niche analysis to test if the disturbances occurred more often at the edge of the climatic envelope of taxa. This analysis was based on the hypothesis that populations at the ecological limits are more stressed by environmental conditions or biotic interactions and therefore might be more susceptible to certain disturbance agents. To define the location of each NFI-plot within the climatic envelope (temperature vs precipitation) of each target species we used the niche innerness index from the ecospat R-package (Di Cola and others 2017).

The effect of disturbance agents on the different considered taxa and on the broader groups broadleaves vs. conifers was analysed by comparing the absolute and relative BA changes (Wilcoxon-test). To test if and where disturbances may catalyse future vegetation shifts (i.e., change in forest composition) we compared the species-specific recruitment density (for saplings and pole-stage trees) on 'naturally disturbed' and 'not naturally disturbed' sites. Additionally, we used mixed-effects models to check for combined effects of site and species-specific factors on BA changes of the adult tree species and on the tree recruitment density. All statistical analysis were conducted in R 3.6.1 (R Core Team 2020).

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Results

Distribution of natural disturbance events

Of the 5092 NFI plots, 2024 (40%) were classified as 'undisturbed', 1600 (31%) as 'treated' and 778 (15%) as 'salvage logging'. Subsequently, 690 (14%) were classified as 'naturally disturbed' of which 411 (59%) were disturbed by wind, 110 (16%) by insects (predominantly bark beetle), 101 (15%) by snow/avalanches, 8 (1.2%) by fire, 11 (1.6%) by drought and 49 (7.2%) by other agents including mass movements such as landslides (39), flooding (4) and rock fall (3), phytopathogens (2) and cattle (1). Out of the 690 'naturally disturbed' plots, 163 (24%) were affected by several disturbance events

during the observation period (Table S2). The majority of these multiple disturbance events were combinations of wind and insects (72%) in which usually a wind disturbance favoured an insect outbreak few years later. Another notable source of multiple disturbances were snow and drought, which both reoccurred in at same plots over the years.

Natural disturbance events were significantly more frequent in the 'Plateau' and the 'Northern Alps' and less frequent than expected by chance in the 'Jura' and 'Southern Alps' (Figure 2). This finding is, however, confounded with the extensive storm damage area produced by storm Lothar (winter 1999) that mainly affected the 'Plateau' and 'Northern Alps' and resulted to be by far the most impactful natural disturbance event during the observation period (8% of all NFI-plots). The 'Northern Alps' were significantly more affected by bark beetles, while forest fires occurred significantly more often in the 'Southern Alps' (Figure 2). Storm Lothar also led to a strong synchronisation of wind and insect disturbed plots as over 85% of the wind affected sites were recorded in 1999 and 85% of the insect affected sites during the 5 years following the storm (2000-2005, Figure S2). As a side effect of this 'synchronisation' of wind and insect damage, our analysis becomes much more consistent as the time interval between disturbance event and NFI observation showed low variability and therefore regrowth and tree recruitment stages are comparable.

Sample plots dominated by *P. abies* were by far the most affected by natural disturbances (63% of all disturbed plots), which especially holds for wind and insects (>80%; Figure 2) primarily in the 'Plateau' and 'Northern Alps'. Plots dominated by *C. sativa* more often suffered from drought (Figure 2). In contrast, plots dominated by *F. sylvatica* or *Larix* spp. were significantly less often affected by any disturbances. Additionally, stands dominated by *Pinus* spp. (mostly *Pinus sylvestris*) were over-proportionally affected by drought in the dry valleys of the 'Western Central-Alps' but not nationwide. This susceptibility of *Pinus* spp. to drought was further highlighted by the analysis based on niche innerness showing that drought disturbance more often occurred at the edge of *Pinus* spps' environmental distribution (dry and hot end; Table S3; Figure 3). All other disturbance agents affected the taxa randomly across their environmental space (Figure 3).

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Plots with a PNC of silver fir-Norway spruce forests were significantly more often affected by disturbances than any other community, and in particular by wind, insects and snow (Figure 2). Wind also over-proportionally affected PNCs of beech and silver fir-beech forests, while drought over-proportionally disturbed plots with a PNC of hornbeam and oak forests (Figure 2). More than 75% of the wind disturbed plots with a PNC of beech forest were dominated by another tree species (mainly *P. abies* and, to a lesser degree, *A. alba*). In fact, *P. abies* dominated stands were significantly more often affected by wind disturbance when found on sites with PNCs dominated by broadleaves (e.g., potential natural beech forests; $X^2 = 8.7242$, df = 1, p-value = 0.00314).

Disturbance effects on species composition

Between 1995 and 2017, the total BA of Swiss forests as well as the BA per ha increased from 34.8 M m^2 and 31.0 m^2ha^{-1} to 37.5 M m^2 and 32.7 m^2ha^{-1}, respectively. However, the subset of NFI-plots used in our study showed a more pronounced BA increase of +2.4 m^2ha^{-1}. This difference is explained by the fact that the NFI-plots omitted in our analysis showed a decrease in BA (-7.4 m^2ha^{-1}) and represent disturbed/damaged plots often followed by 'salvage logging', which were removed from the dataset due to missing information on disturbance agents. The observed BA change mostly represented an increase of broadleaf trees (+1.5 m^2ha^{-1}, +15%), while coniferous trees remained almost constant (+0.9 m^2ha^{-1}, +5%; Table S4) increasing the BA contribution of broadleaves by 2%. If merely 'not naturally disturbed' plots were considered, BA of both conifers and broadleaf species increased proportionally (+15.3% for conifers and +17.0% for broadleaves), but conifers were much more affected by natural disturbances than broadleaves (-39.4% for conifers and -4.9% for broadleaves; Table S4). The two dominant natural disturbance agents (wind and insect outbreaks) mainly affected dense conifer stands dominated by *P. abies* (63% of disturbed plots), particularly in the 'Plateau' and 'Northern Alps' (Figure 2), leading to a drastic reduction in BA of *P. abies* (-45%; Table S5, Figure 4). *Pinus* spp. was the only taxa that decreased in BA on 'naturally disturbed' and on 'not naturally disturbed' plots and was especially affected by wind and drought disturbances (Table S5, Figure 4). The only broadleaf species

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showing a tentative disturbance effect on BA was *C. sativa* suffering from drought in the 'Southern Alps' (Table S6, Figure 4).

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

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

Post-disturbance vegetation trajectories

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

Due to the relatively small sampling area and the associated extrapolation to the hectare, data on tree recruitment was highly stochastic and variable. As a result, only very few significant disturbance-induced and species-specific changes in vegetation trajectories could be detected. On PNCs of broadleaves that were mostly stocked with conifers, wind disturbance led to a shift of the vegetation trajectory towards more broadleaves recruitment over the last 20 years (Figure 5). No such shift in tree recruitment was observed on wind-disturbed and insect-attacked sites naturally dominated by spruce (Figure 5). In sites affected by drought, recruitment by *Pinus* ssp. decreased in favour of *Quercus* spp.,

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especially in the 'Western Central-Alps' while in the 'Southern Alps' the recruitment of *C. sativa* decreased on drought-prone sites (Table S9-12; Figure 4). *Castanea sativa* was also the only species showing consistent decrease in tree recruitment (saplings and pole-stage trees) both on 'naturally disturbed' and 'not naturally disturbed' plots with the notable exception of post-fire tree recruitment (Table S11-12; Figure 4). 'Undisturbed plots' showed no consistent change in tree recruitment, while both 'treated' and 'salvage logging' plots seem to favour the recruitment of broadleaves over conifers (Figure 6).

Discussion

Canopy disturbances as catalysts of forest vegetation shifts

Over the last 25 years the Swiss forests showed a shift from conifer towards a higher proportion of broadleaf species especially at lower elevations. This life form shift was driven by extensive natural or anthropogenic (i.e., silvicultural treatments) canopy disturbances (> 0.1 ha), or a combination of the two (salvage logging), as forest trajectories did not change in 'undisturbed' plots. Additionally, in the warmest and driest regions of Switzerland, comparisons indicate that extreme droughts led to diverging forest trajectories affecting mostly chestnut groves and oak-pine forests.

Fatal attraction: P. abies outside of their natural range

While the overall contribution to BA of most species only slightly changed (±0.7%) between 1995 and 2017, a considerable if not dramatic change was observed in *P. abie*s (-2.9%) and stands dominated by *P. abies* were confirmed to be especially susceptible to certain natural disturbances (62% of all natural disturbance events), which resulted in a shift towards more broadleaf species. This is not surprising when considering the general susceptibility of *P. abies* to both windthrow (e.g., Hanewinkel and others 2011) and the European spruce bark beetle (Ips typographus; e.g., Wermelinger 2004; Faccoli and Bernardinelli 2014), including the interaction of beetle attacks in spruce forests weakened by wind disturbance or prolonged drought (Stadelmann and others 2013; De Groot and others 2018; Dobor and others 2020).

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In our study large-scale wind damage in spruce stands occurred predominantly during the Lothar storm (1999), which mostly affected forests at low elevations within the range of the natural beech and silver fir-beech communities. No major storm occurred during the observation period in montane and subalpine Norway spruce forests. In mountain spruce forests affected by Vivian (storm at higher elevation, predominantly in the Central Alpine valleys; 1990) the post-disturbance regeneration trajectories were dominated by *P. abies* (Schönenberger 2002). In contrast, in the Lothar-affected lowlands and foothills of the Pre-Alps, where *P. abies* is mostly out of the natural range as it was frequently planted in the past and promoted in the frame of adopted German silvicultural systems (Bürgi and Schuler 2003), the post-disturbance trajectories indicate a decrease in *P. abies*. This pattern was additionally reinforced by the abundant bark beetle outbreaks that occurred on plots previously affected by wind disturbance during the heatwave in summer 2003 (Forster and Meier 2010; Stadelmann and others 2014).

Our data on tree recruitment suggest that on low elevation sites, where forests are naturally dominated by broadleaves, disturbances significantly altered forest trajectories away from *P. abies* (and conifers in general) towards more broadleaf species. The shift in vegetation trajectories towards more broadleaves recruitment was stronger after wind than insect disturbance. Bark beetle usually mainly attack trees older than 50 years, leaving younger trees healthy (Wermelinger 2004) and therefore limiting the potential for a dramatic shift in vegetation trajectories. Nevertheless, salvage logging to control bark beetle infestations and intensified harvests of *P. abies* to avoid financial loss due expected further lowering of wood prices supported this trend (Kläy 2015). As the most influential disturbance events happened around 15–20 years ago the shift in vegetation trajectories was mostly visible in the well-established pole-stage that are nowadays dominated by broadleaves. This indicates that, at low elevations, broadleaf species are competitively superior to *P. abies,* as had been demonstrated in post-windthrow patches (Kramer and others 2014). The increased reliance on natural regeneration in the second half of the 20th century (Burgi 1999) has also contributed to their recent re-expansion. Additionally, at lower elevations foresters started to transition forests away from *P. abies*

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by species regulation in the juvenile phase (up to thickets) and through targeted thinning. Since most future climate change scenarios predict an increased frequency of extreme weather events such as large storm systems, prolonged droughts and heatwaves, linked disturbances (e.g., Seidl and others 2017) need to be considered. Insect attacks likely increase, as wind-disturbed and climatically stressed trees become more susceptible (Brandl and others 2020), and warmer temperatures stimulate bark beetle population dynamics resulting in more generations and higher densities during one season (Stadelmann and others 2013; Jakoby and others 2016). At higher elevations, disturbances did not seem to negatively affect the recruitment of conifers both after wind and insect disturbances, which indicates that in these cooler forest habitats a direct regrowth of the stand-forming coniferous species. This is in line with findings of Kramer and others (2014) on regeneration in gaps produced by windthrow across Switzerland.

Impressive though rare: fire and drought

In contrast to damage by wind and insect outbreaks, other disturbance agents or extreme events such as fire and drought were rarely observed during the study period and affected only a small proportion of the Swiss forest area (< 0.2% of plots) mostly located in the warmest ('Southern Alps') and driest biogeographic Swiss regions ('Western Central-Alps'). In the dry valleys of the 'Western Central-Alps' drought has negatively affected *P. sylvestris* that has for long dominated slopes at low elevation due to traditional land-use practices (pasture and litter collection; Gimmi and others 2010) towards the dry limits of forest growth (Etzold and others 2019). Land-use change in the past decades in combination with repeated extreme drought events increased tree mortality (e.g., Rigling and others 2013) and benefit the more drought-resistant and shade-tolerant downy oak (*Q. pubescens*). In fact, combined drought-shade effects to drought-tolerant *P. sylvestris* (Niinemets and Valladares 2006), hampers successful recruitment (Bachofen and others 2019). Similar transitions from pines to oaks are reported for dry regions in Italy (Vacchiano and Motta 2015) and Spain (e.g., Zavala and others 2000; Galiano and others 2010; Carnicer and others 2014; Morán-López and others 2014).

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In the 'Southern Alps' drought mostly affected forests dominated by the *C. sativa*. The chestnut groves in southern Switzerland are the result of a long-term land use practice aimed at producing both fruits for the self-sustainment and wood (Krebs and others 2012), which encouraged the chestnut cultivation at the limits of the tree and in some cases even at the edge of its fundamental niche (Muster and others 2007). Similar to the pine-dominated forests in the Valais, the suspension of any management input made the chestnut groves particularly susceptible to the colonization by other more site-specific tree species, exposing the light-demanding *C. sativa* trees to competition, climatic stress, and specific diseases (Conedera and others 2001). On the most dry and exposed sites, this resulted also in an enhanced summer drought susceptibility as revealed by the 2003 summer drought and heat wave (Conedera and others 2009). All this induces a shift towards the PNC, i.e. corresponding to beech on rich sites at higher elevation and to broadleaf mixed forests dominated by lime (*Tilia* spp.) as well as maple trees (*Acer* spp.) in the lowlands (Conedera and others 2000; Muster and others 2007). Fire displays, on contrary, the opposite effect by enhancing the recruitment of the disturbance-adapted *C. sativa* that profits from its extreme resprouting capacity and outcompetes other fire-sensitive broadleaves (Delarze and others 1992), including invasive evergreen species (Grund and others 2005).

So far, both drought and fire affected the forest dynamics trajectory only in NFI plots in the warmest and driest parts of the country that are dominated by certain species as a result of century long management effects (i.e., *C. sativa* and *P. sylvestris*) that partially grow at their ecological limits. The question arises how disturbances may affect the most widespread forest types such as spruce and beech forests in the future. Conspicuous drought damage in both beech and spruce forests during the recent summer drought periods (2018, 2019; Schuldt and others 2020) suggest that drought may assume a central role in shaping future forest trajectories in Swiss Forests. Evidences of forest fires impacting usually fire-avoiding forest types such as beech stands are also increasing in recent decades (Maringer and others 2016).

Limits of the study

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In this study, we used the data collected on revisited plots of the Swiss forest inventory. Beside the great advantage of the long time span of the observations (up to 25 years) and the permanent character of the plots, the used data presents also some limits. The shift of the survey from a periodic three-years lasting survey (NFI2) to a continuous, nine-years lasting field activity (NFI4) implies that the period of observation may vary by up to eight years among plots. In addition, the survey protocol of the recruitment slightly changed between the two inventories and the retrospective approach in reconstructing and assessing the disturbances that occurred on each plot may represent a source of imprecision.

Systematic samples such as the NFI produce representative results in terms of quantitative rankings. However, important small-scale phenomenon such as the local spread of neophytes (Maringer and others 2012; Conedera and others 2018), the dynamic of rare species or the study of detailed post-disturbance ecological processes require targeted and species-specific approaches (e.g., Allen and others 2010; Moser and others 2010; Rigling and others 2013; Maringer and others 2020; Schuldt and others 2020).

Conclusions

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

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the chestnut groves in the Southern Alps). Overall, our data suggest that the forest trajectory after a disturbance favours recruitment of species of the natural forest community. In particular, in disturbed *P. abies* stands at the low-lands, broadleaf species regenerate most successfully, while in *P. abies* stands at higher elevations, direct regrowth of this and other coniferous species prevails. Undisturbed forest stands, on contrary, persisted in their species composition, and the constrained tree recruitment under canopy was mostly comprised of the species dominating the stand. Tree regeneration under dense canopies is always sparse and only a few species are able to build up an abundant 'seedling bank' in a closed and shady stand (Grubb 1977; Savage and others 1996). Most species rather regenerate in pulses realized in canopy gaps (Zackrisson and others 1995; Jentsch and White 2019). In a small gap, however, the chance that seeds from new species arrive during the window of opportunity for seedling establishment is a stochastic event and most gaps will be filled with seedlings from the already present dominant species (Moser and others 2010). Therefore, in undisturbed forests the 'biotic component' of the dominating tree species rather than the abiotic conditions are driving species selection. Larger-scale disturbances, on the other hand, seem to level the playing field allowing more species to establish and favour those (among which many opportunistic ones) that are adapted to the current environmental conditions and can increase resistance against future disturbances (e.g., repeated insect outbreaks; Sommerfeld and others 2020). Larger-scale disturbances might therefore act as essential catalysts to enable/accelerate the transition of forest ecosystems in adaptation to changing environmental conditions (Brice and others 2019; Brice and others 2020).

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Figure Legends

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

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.

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

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

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

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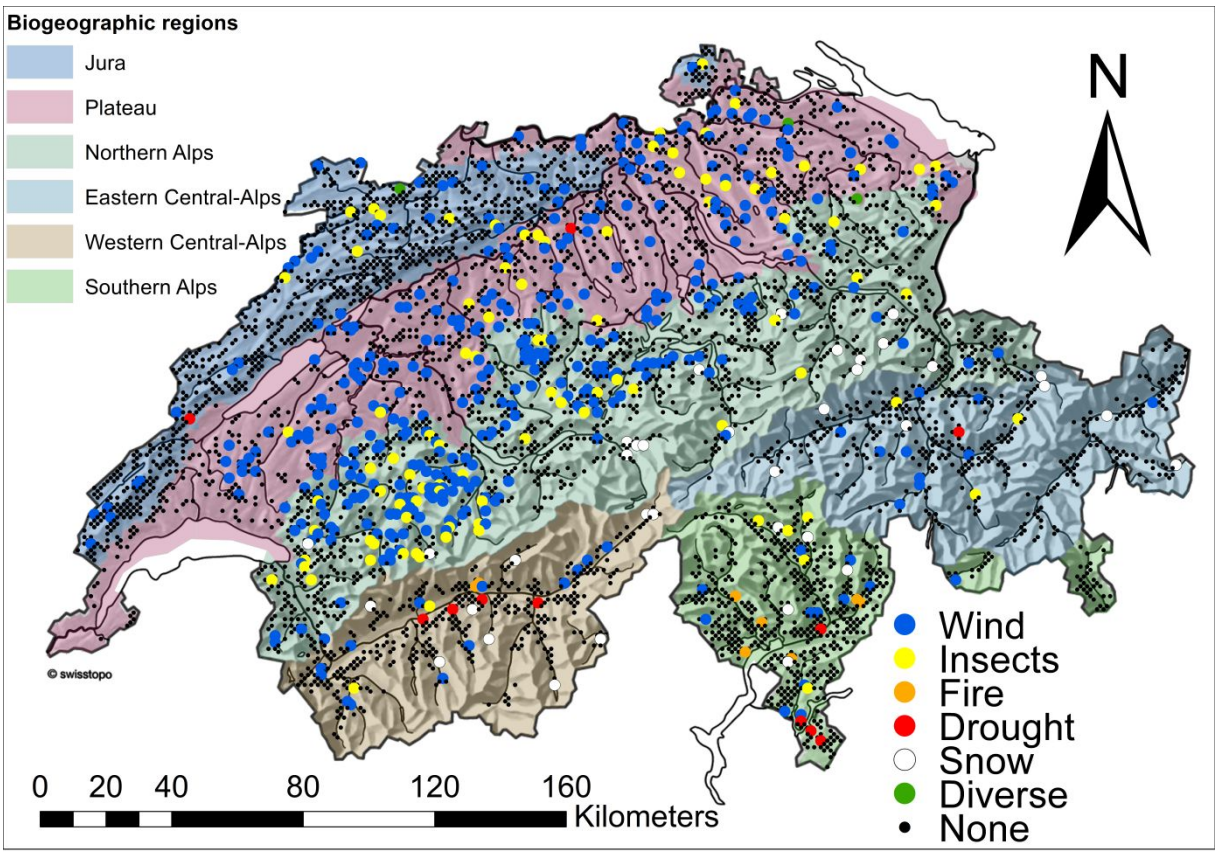
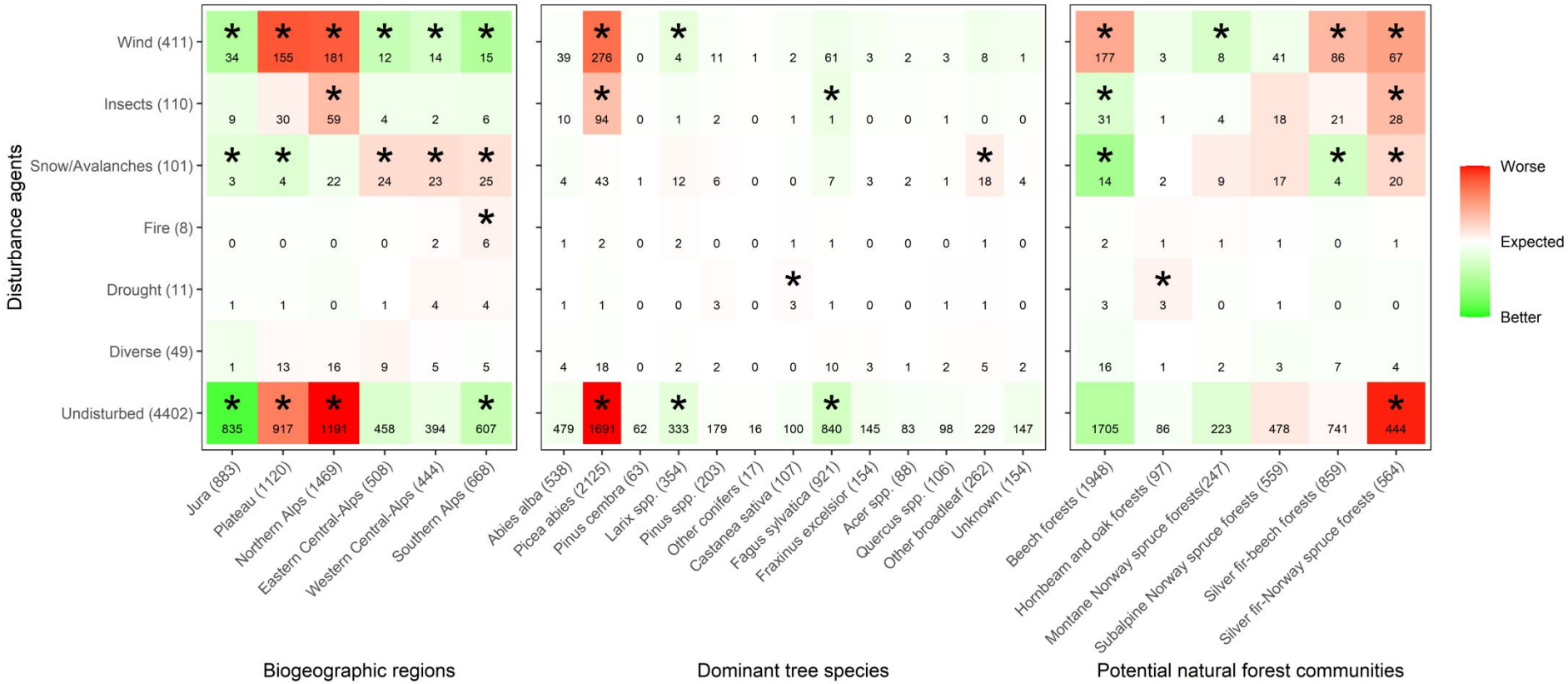


Figure 1: Biogeographic regions of Switzerland (Gonseth and others 2001) and geographic positions of NFI-sample plots used in this study. Different point colours indicate the type of natural disturbance recorded in the period 1993–2017 and the shade colours different biogeographic regions. None = 'Not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



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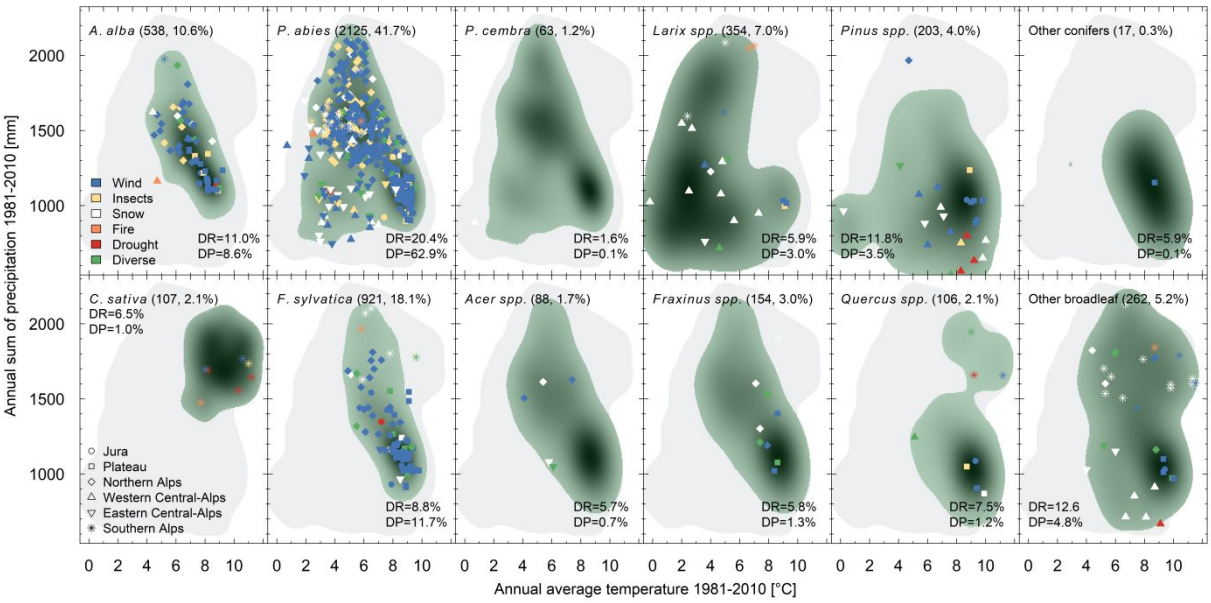

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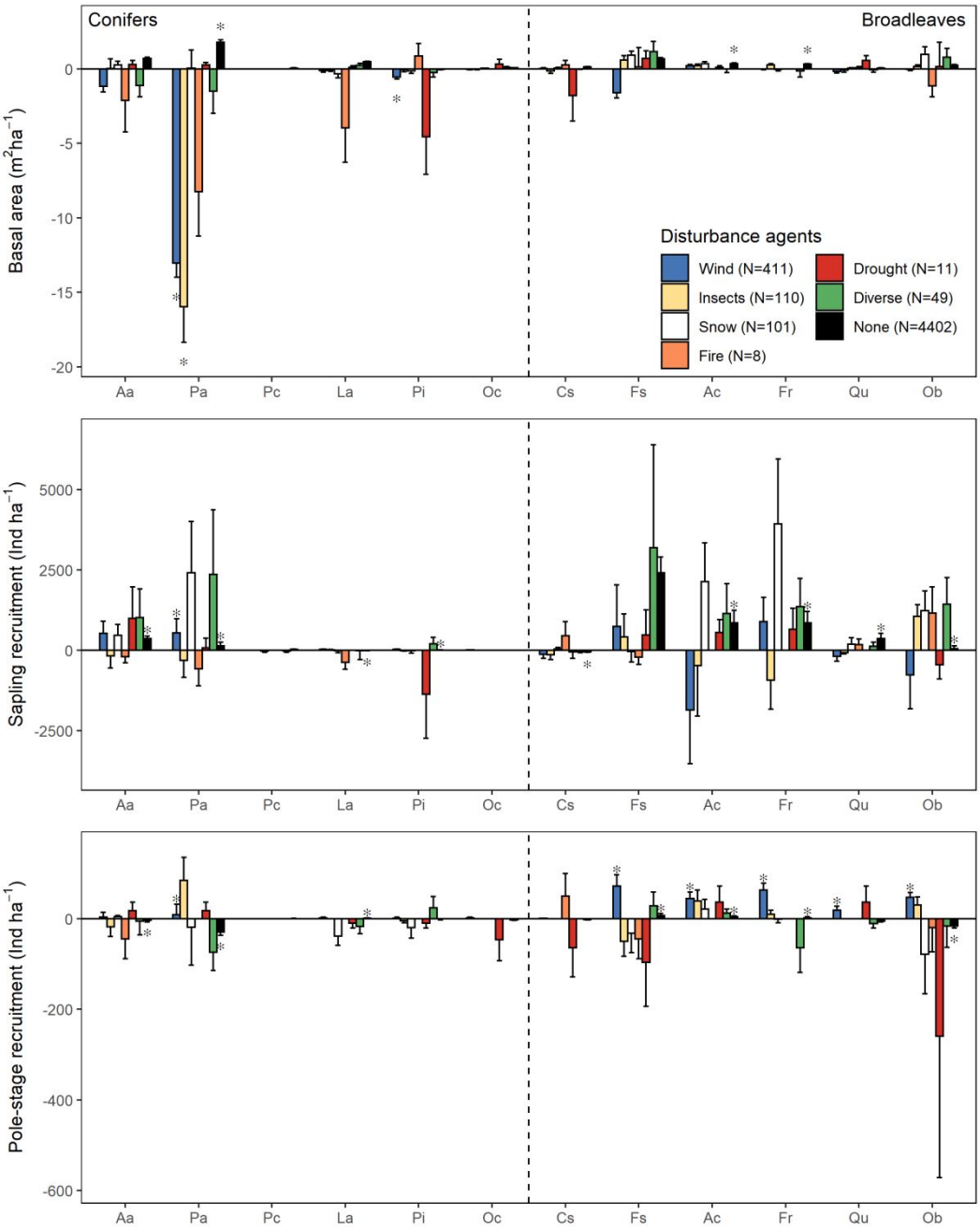

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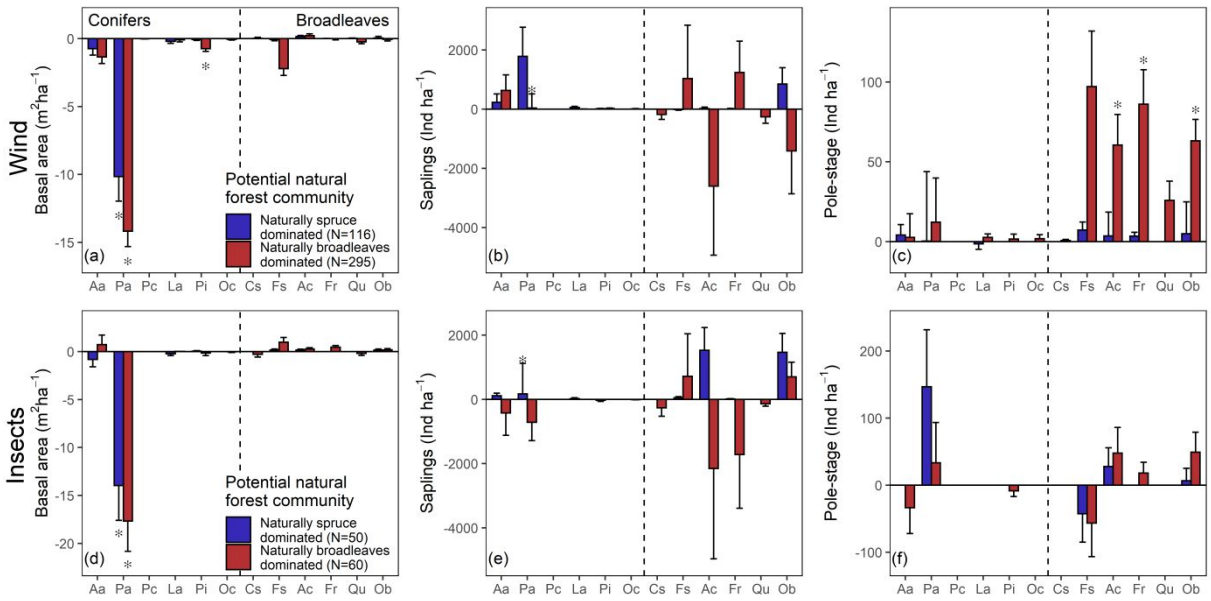

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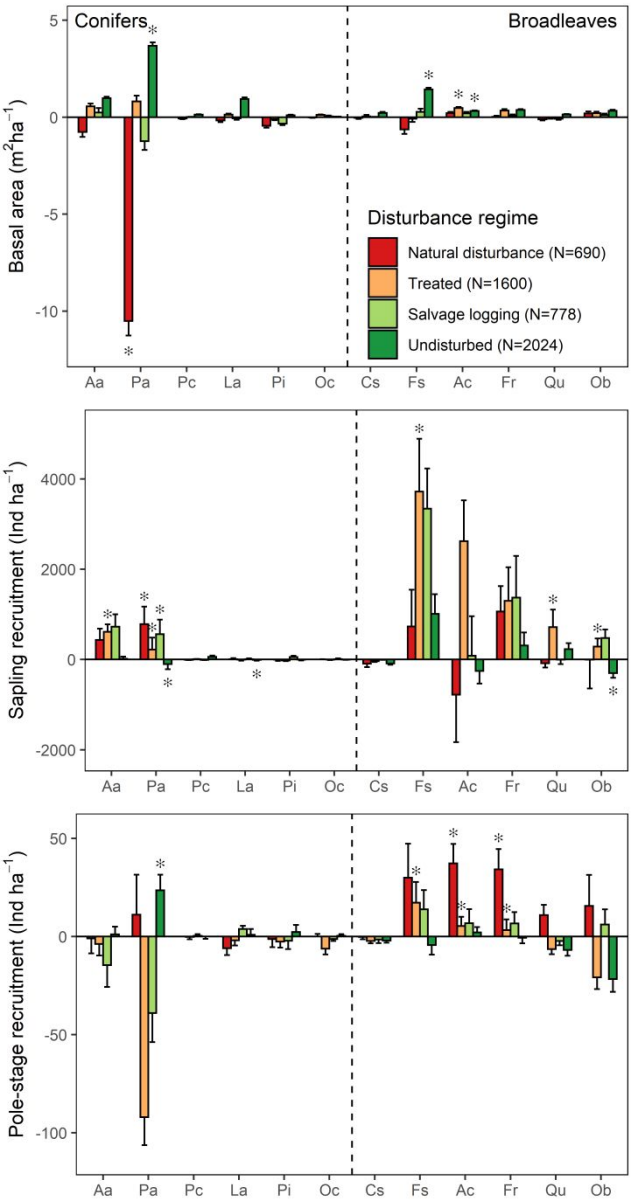

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