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Low naturalness of Swiss broadleaf forests increases their susceptibility to disturbances

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ABSTRACT

The tree species composition of Swiss forests is influenced by both environmental conditions and centuries of forest management, resulting in varying degrees of naturalness. Here, we estimate the naturalness of Swiss forests by comparing the tree species composition (i.e., dominance and presence/absence of tree species) recorded by the national forest inventory with the idealised species composition of the potential natural forests. We aimed to (1) evaluate the naturalness of different forest types, (2) identify the main drivers of low naturalness and (3) investigate the influence of naturalness on the susceptibility to disturbances. Based on our analysis, 45 % of Swiss forests had a tree species composition classified as 'not natural' while 42 % were classified as 'natural' or 'close to natural'. The vast majority (65 %) of the forests classified as 'not natural' were potential European beech (*Fagus sylvatica* L.) and other broadleaf forests which are currently dominated by conifers. In addition, at higher elevations, forests often showed a higher proportion of European larch (*Larix decidua* Mill.) than expected, based on the potential natural forest. Overall, forests classified as 'natural' had a significantly lower risk of being affected by stand-level disturbance events. Potential natural European beech and other broadleaf forests were significantly less affected by disturbances, namely insect outbreaks and wind throw, when comparing 'natural' to 'not natural' (i.e., afforested with conifers). The observed dieback and associated loss of ecosystem function of conifer afforestations (mainly Norway spruce; *Picea abies* (L.) H. Karst.) in the Swiss plateau is likely a combination of climatic stress and higher pathogen/parasite pressure. These Norway spruce afforestations already experience a significantly elevated temperature of about 2.5 °C compared to their climatic optimum (i.e., primary natural distribution within Switzerland), representing a large-scale, long-term transplantation experiment. We discuss the question of whether similar diebacks and problems of maladaptation are to be expected for many other species, including European beech, due to accelerated climate warming during the 21st century and the slow transformation of long-lived systems such as forests. Consequently, an adaptation of current management practices might be needed to allow a faster transition of forests minimizing the risk of large-scale diebacks.

1. Introduction

Species distribution and dynamic vegetation models predict dramatic shifts in tree habitat ranges and community compositions due to changes of climate and land-use (e.g., Lenoir et al., 2020; Scherrer et al., 2020). Recent drought spells broadly confirm respecting model results (e.g., Allen et al., 2015; Frei et al., 2022; Schuldt et al., 2020) and jeopardize the provision of essential ecosystem services of forests in the long run (e.g., Jandl et al., 2019; Lindner et al., 2014). As a result, forest management practices are adapted to create more resilient 'climate-smart' forests (e.g., Bowditch et al., 2020; Mathys et al., 2021; Santopuoli et al., 2021) ensuring continued ecosystem services (e.g., Nabuurs et al., 2017; Temperli et al., 2020; Verkerk et al., 2020). In Switzerland, forests have been actively managed for centuries with shifting primary ecosystem services (e.g., wood production, protective function, recreation, biodiversity), resulting in different degrees of naturalness (i.e., various degrees of anthropogenic influence on tree species composition and stand structure). In recent decades, most Swiss forests have been managed by a 'close-to-nature' silviculture system (Bürgi, 2015; Spathelf, 1997) favouring natural regeneration in small gaps by direct regrowth (Abegg et al., 2020). This 'close-to-nature' silviculture should increase naturalness and create forests that would adapt to changing environmental conditions and thereby securing continuous ecosystem services (Brang et al., 2014; Spathelf et al., 2015). In line with this idea, the Swiss forestry law (WaG, SR 921.0) states that tree recruitment or planting should be based on site-adapted species (i.e., species of the potential natural forest community). Consequently, information about the potential natural forest community is necessary, a condition that is

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currently covered by a nationwide classification of Swiss forest sites called NaiS-System (Nachhaltigkeit und Erfolgskontrolle im Schutzwald; Frehner et al., 2009; Frey et al., 2021). The NaiS site type (NST; i.e., idealised potential natural vegetation with characteristic tree species composition) of a given location is determined by experts based on abiotic conditions (e.g., elevation, geographic region, soil water availability and pH), site/topographic factors (e.g., big boulders, streams, avalanche tracks) and by the composition of the understory vegetation. The naturalness of a site can be determined by comparing the potential tree composition of an NST and the observed 'real' tree species composition. In this study, naturalness is solely evaluated based on the composition of canopy-forming trees. The composition of the canopy-forming trees is influenced by both the site conditions and management decisions directly driving the naturalness of a site (sometimes also called hemeroby; see Winter, 2012 for a discussion on the conceptual differences of naturalness and hemeroby). Low naturalness is therefore dependent on the amount of canopy tree species that are non-site-specific or even non-native (e.g., Bürgi and Schuler, 2003).

Naturalness of forests is regularly assessed both in monitoring programs and research projects using highly variable methods and criteria (e.g., Brändli et al., 2020; Côté et al., 2019; McRoberts et al., 2012). So far, most of those studies are targeted at conservation (e.g., identifying old-growth forests for protection; Chiarucci and Piovesan, 2020; Moravčík et al., 2010), biodiversity assessments (e.g., ecological value; Winter, 2012) or evaluations of the sustainability of forest management (Winter, 2012). Here, we introduce the idea of naturalness as an indicator of stability, resilience, and resistance of a forest stand by linking naturalness with site-specificity. The concept of site-specificity assumes that only those trees are best adapted to climate and soil conditions and resistant to disturbances that grow naturally at a site (Brang et al., 2014; Frischbier et al., 2019). Nevertheless, it is unclear if forests with lowered naturalness are indeed more susceptible to drought stress or destructive disturbance events than natural forest stands (Eilmann and Rigling, 2012; Lévesque et al., 2014). An analysis on the forest's susceptibility to disturbances in relation to the degree of naturalness requires spatial data on the current species composition, the idealised natural forest composition as well as on disturbance frequencies.

Here, we use data of the Swiss National Forest Inventory in combination with information on the idealised natural forest composition (1) to estimate the naturalness of different types of forests, (2) to evaluate the main drivers reducing naturalness (i.e., which species occur most often 'out of place') and (3) to quantify the relation between the degree of naturalness and the susceptibility to disturbances and subsequent risk of ecosystem failure.

2. Methods

2.1. National forest Inventory data (NFI)

We used data of the fourth Swiss National Forest Inventory (NFI4; 2009–2017), recorded on a 1.4 × 1.4 km systematic permanent sampling grid covering the whole forested area of Switzerland (13,169 km2; Brändli et al., 2020; Cioldi et al., 2020). A terrestrial NFI plot assessment consists of several elements (Lanz et al., 2019) of which we only refer to the 50 × 50 m interpretation area with the circular plot in its centre. In this interpretation area the proportion of all canopy-forming tree species of the reference stand (i.e., the stand including the plot centre, in case the interpretation area is intersected by multiple stands; Fischer and Traub, 2019), the disturbance impact and agent during the last 20 years (i.e., since the second NFI) and the assigned NaiS site type (NST_{exp}; ARGE Frehner et al., 2020; Frey et al., 2021) were determined. Only trees reaching at least 2/3 of the maximum stand height were considered canopy-forming. The disturbance impact was estimated in the field and the disturbance agent was evaluated based on interviews with the local foresters. We only considered larger (i.e., 'stand-level') disturbances affecting at least 20 % of the interpretation area. The NST_{exp} was defined by experts that visited 40 % of the NFI sample plots and concluded community identities by analogy (using factor maps and local knowledge) for the remaining 60 % of the plots, according to the Swiss protective forest classification (NaiS; ARGE Frehner et al., 2020). In cases where several NST_{exp} were mapped within the 50 × 50 m interpretation area, the NST_{exp} of the reference stand (i.e., covering the plot centre) was selected. In total, data on the tree species composition of the canopy, disturbances and NST_{exp} were available for 4959 NFI sample plots (excluding shrublands, Fig. 1).

2.2. Idealised natural forest compositions (NST)

Based on floristic composition, site quality and structural characteristics, NST depicts the idealised tree species composition (including recruitment) in natural forests at the optimum developmental stage, i.e. in balance with the dominant environmental conditions (for example, climate, topography, soil; Frey et al., 2021). There are more than 250 NST defined for Switzerland, each with its own requirements on tree species composition. For each NST all tree species occurring in Switzerland (N = 75, both native and non-native) are classified into four categories (a) 'dominant tree species of the natural forest', (b) 'important supplementary species of the natural forest', (c) 'acceptable element of the natural forest' and (d) 'species not part of the natural forest' (Table S1).

In addition to the expert-based point information on the NST_{exp} of the NFI sample plots, we also used a map of the predicted NST_{exp} for the entire forested area of Switzerland (25 m resolution). The map is based on the aforementioned point information about NST_{exp} of the NFI sample plots and used machine learning algorithms in combination with a large range of climatic, soil, topographic, distance and geographic position variables to predict the NST_{exp} across space and time (for details on model construction and performance see Scherrer et al., 2021a).

All the calculations were done on the level of individual NSTs (N = 224). However, for summary figures and analysis the large number of NSTs was simplified into 24 categories based on the dominant tree species and further aggregated to seven main forest types (i.e., Arolla Pine and European Larch forests, Norway spruce forests, Silver fir-Norway spruce forests, Silver fir-European beech forests, European Beech forests, Mountain and Scots pine forests, Additional deciduous forests; Table S2).

2.3. Observed forest type (NST_{obs})

In addition to the NST_{exp} determined by the experts we also calculated the NST best matching the species composition recorded in the NFI (NST_{obs}). This allowed us to see what forest type should be present based on site condition (NST_{exp}, i.e., the potential natural forest) and is present due to site history and management (NST_{obs}). For each site, the matching score (NST_{score}) of all possible NST was calculated based on

$$NST_{score} = \frac{dom_{obs} + 0.5sup_{obs} + 0.1acc_{obs} - not_{obs}}{dom_{exp} + 0.5sup_{exp} + 0.1acc_{exp}}$$

where dom_{obs} are the number of 'dominant tree species of the natural forest' observed, sup_{obs} the number of 'important supplementary species of the natural forest' observed, acc_{obs} the number of 'acceptable element of the natural forest' observed, and not_{obs} the number of 'species not part of the natural forest' observed. This sum was standardized by the maximum possible score, i.e., the number of species expected to be present in an idealised natural forest (dom_{exp}, sup_{exp}, acc_{exp}). The NST with the highest NST_{score} was considered the best match with the observed species composition (NST_{obs}) of a given site. In case two NST_{obs} had the same matching score, the one with the lower maximum possible score was selected.

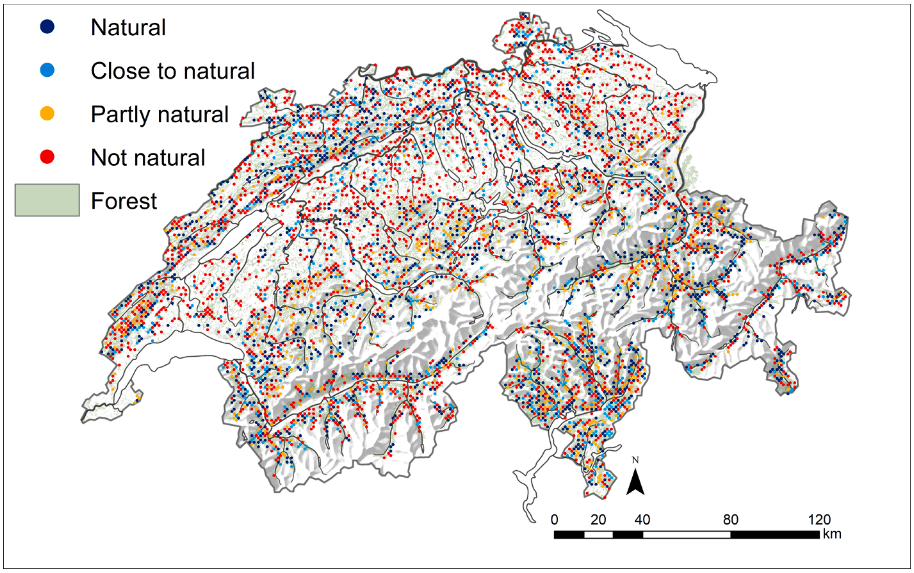

Fig. 1. Spatial distribution of the 4959 NFI sample plots across Switzerland and their estimated naturalness.

2.4. Time series data on bark beetle damage

In addition to the disturbance data of the NFI sample plots we also used nationwide time-series data on bark beetle damage collected by foresters. Switzerland was at the time of data analysis divided into 92 administrative forest units (Forstkreise) ranging in size from 475 to 65,800 ha (median = 8800 ha). For each of the administrative forest units data on bark beetle damage (volume of damaged wood in m^3) is available from 1984 to 2019. These data were used in combination with the map of the predicted NST_{exp} to analyse (1) which factors (e.g., size of administrative forest unit, proportion of coniferous forests) best explain the amount of bark beetle damage and (2) whether changing patterns across the last 40 years were detectable.

2.5. Assessment of naturalness

The naturalness of a forest site was assessed by comparing the reported tree species composition of the canopy layer based on NFI data with the idealised natural tree species composition based on the NST_{exp} of the site. We decided to base our assessment of naturalness on the composition of canopy-forming trees for several reasons: (1) large seed trees are dominating the structure of forest stands influencing many important aspects such as light availability and micro-climate, (2) the canopy-forming trees are the key element to many important ecosystem services of forests (e.g., timber production, carbon storage and protective function) and (3) both detailed data on current tree species composition as well as idealised natural forest composition were available for all NFI sites while data on other taxa were missing. Ignoring other important aspects of naturalness (e.g., additional taxa, soil conditions) might be problematic for some ecosystem services (e.g., biodiversity, water filtration). However, here we focus on the susceptibility to disturbances and ecosystem services mainly associated with trees (e.g., timber production, carbon storage or protective function).

We distinguished four categories of naturalness: (1) 'natural forest', (2) 'close to natural forest', (3) 'partly natural forest' and (4) 'not natural forest' based on the criteria of Table 1.

2.6. Naturalness and susceptibility to disturbances

Based on the plot data of the NFI the influence of naturalness on disturbance frequency was analysed by chi-square tests. We tested for an overall influence of naturalness on disturbance frequency as well as combinations of specific forest types and disturbance agents.

Table 1
Overview of the criteria used to evaluate the naturalness of a forest stand.

	Natural forest	Close to natural forest	Partly natural forest	Not natural forest
Dominant tree species: all tree species represented in canopy	X	X		
Dominant tree species: ≥ 1 tree species has highest canopy cover	X	X	X	
Important supplementary species: ≥ 1 tree species present	X			
Important supplementary species: canopy cover > cover *acceptable species*	X			
Unsuitable (not site-specific) tree species: canopy cover = 0 %	X			
Unsuitable (not site-specific) tree species: canopy cover < 5 %	X	X	X	

In addition to our assessments based on the regular sampling grid of the NFI, the correspondence of non-natural conifer stands (i.e., non-site-specific conifers) on bark beetle damage was analysed at the level of administrative forest units (N = 92). For each administrative forest unit, the area of conifer and broadleaf-dominated NST_{exp} was extracted as well as the proportion of coniferous trees within these NST_{exp}. The information on the proportion of coniferous trees was provided by remote sensing (Waser et al., 2021). Waser et al. (2021) used countrywide winter and summer Sentinel-1 backscatter data, cloud-free summer Sentinel-2 images and a Digital Terrain Model (DTM) to model and subsequently map dominant leaf type (broadleaved and coniferous trees) employing two machine learning approaches (Random Forest and deep learning). The NST_{exp} were based on the before mentioned model (Scherrer et al., 2021a). In a first step, we used a linear model to explore which factor (i.e., forest area, area of coniferous forest, area of coniferous forest in NST_{exp} dominated by conifers, area of coniferous forest in NST_{exp} dominated by broadleaves and year) had the strongest influence on bark beetle damage across all years and forest units. In a second step, we analysed the influence of these factors separately for each year in the period 1984 – 2019 to detect potential temporal changes.

3. Results

3.1. How natural are Swiss forests?

Based on our evaluation criteria 45 % of all NFI sample plots were considered 'not natural' forests, while 30 %, 13 % and 12 % were considered 'natural', 'close to natural' and 'partly natural', respectively (Fig. 2). NFI sample plots with a NST_{exp} dominated by broadleaf were much more often 'not natural' (56 %) than plots with a NST_{exp} dominated by conifers (26 %; Fig. 2, Fig. S1). The vast majority of 'not natural' plots were assigned to beech forest communities (N = 1081, 48 %, Fig. S2).

For forests classified as 'natural' or 'close to natural' the NST_{obs} (i.e., based on NFI tree cover) was mostly identical to the NST_{exp} (Fig. 3a,b). The only slight differences were observed on continuous gradients from European beech to silver fir-European beech and from silver fir-European beech to silver fir-Norway spruce forests (Fig. 3a,b). In contrast for 'partly natural' and 'not natural' sites the difference between NST_{exp} and NST_{obs} was massive (Fig. 3c,d). For the sites classified as 'partly natural', the main difference between NST_{exp} and NST_{obs} was due to the amount of Norway spruce. Many silver fir-European beech forests were classified as silver fir-Norway spruce forests and silver fir-Norway spruce forests as pure Norway spruce forests (Fig. 3c,d). In addition, several of the 'additional deciduous forest types' (i.e., broadleaf forests not dominated by beech) were classified differently based on the dominant species (Fig. S3). Most forests classified as 'not natural' had an NST_{exp} of European beech forests but were observed to contain a high proportion of conifers, namely Norway spruce and partly silver fir (Fig. 3d). Consequently, these forests had observed forest types of either silver fir or Norway spruce-dominated forest types.

The highest proportion of 'not natural' forests were found on the Swiss Plateau, a lower elevation region that is naturally dominated by broadleaf forests but has traditionally been afforested with conifers (mainly Norway spruce) for timber production (Fig. S4). This effect of Norway spruce afforestation can also be seen along the elevation gradient (Fig. S5). The highest proportion of 'natural' or 'close to natural' forest can be found between 1400 and 1700 m a.s.l. where the two commercially most important conifers (i.e., Norway spruce and silver fir) naturally dominate stands (Fig. S5). At lower elevations, the higher proportion of 'not natural' forests is driven by conifer afforestation while at the higher elevations the European Larch is often overrepresented at sites with NST_{exp} of Arolla pine or Norway spruce dominated forests (Fig. S3).

3.2. Naturalness and susceptibility to disturbance

Of the studied 4959 NFI sample plots 13.3 % (658) had a recorded

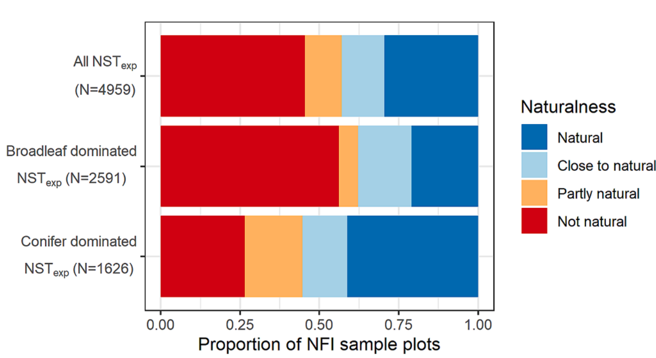

Fig. 2. Proportion of NFI sample plots classified according to the NST_{exp} and degree of naturalness assessed based on observed tree species composition. For a detailed analysis per forests type (including mixed forests) see Fig. S2.

disturbance event within the last 20 years. The main disturbance agents were wind (54 %), insects (mostly bark beetle; 17 %) and snow (17 %) while fire and drought only play marginal roles (Table 2). NFI sample plots classified as 'natural' were significantly less often disturbed ($p < 0.001$) and plots classified as 'partly natural' significantly more often ($p < 0.05$; Table 2). Across all forest types there was no significant effect of naturalness on specific disturbance agents. However, forest types naturally dominated by broadleaf species (i.e., European beech forests, additional deciduous forests, and silver fir-European beech forests) were significantly less often disturbed when classified as natural (Table S3). European beech forests were particularly affected by insect attacks and other disturbances when classified as 'not natural' (Table S3). Spruce dominated forests were less affected by wind throw when classified as 'not natural' (Table S3).

The wood volume (m^3) damaged by bark beetle attack per administrative forest unit was mostly influenced by the area of non-natural conifer forests (i.e., forest stands dominated by conifers on NST_{exp} of broadleaves) with a highly significant interaction of area of non-natural conifer forests and year (Table S4). However, the model across all years had generally very limited explanatory power ($R^2 = 0.16$). The analysis of individual years revealed that the strong interaction of the area of non-natural conifer stands and year is explained by the increasing variable importance and explanatory power of this variable since 2000 (Fig. 4b,c). While the total volume of damaged wood was highly influenced by major disturbance events, the main variables explaining the damage within individual administrative forests units significantly shifted over time (Fig. 4). Since around 2005, the amount of non-natural conifer stands is the most important variable and, in several years, able to explain more than 50 % of the observed variability among administrative forest units (R^2 greater than 0.5, Fig. 4c).

4. Discussion

Several Central European countries assess some form of naturalness as part of their national forest inventories (McRoberts et al., 2012). Based on the systematic, nation-wide sample of the Swiss NFI the tree species composition of 43 % of the forests in Switzerland are 'natural' or 'close-to-natural'. This is slightly higher than the proportion reported in the NFIs of Germany (36 %; BMEL, 2022) and Austria (25 %; Prem, 2015) using comparable approaches based on tree species composition (Prem, 2015; Riedel et al., 2017). So far, these assessments of naturalness are not put in relation to the susceptibility to disturbance or resilience of forest stands. In Switzerland almost half the forest must be considered 'not natural' regarding the canopy tree composition. The deviation from the expected natural composition (NST_{exp}) was largest at low elevations where large proportions of conifers cover potential broadleaf sites. This increased proportion of conifers in NST_{exp} naturally dominated by broadleaves had a direct impact on the vulnerability to disturbances making those forests the most susceptible to larger disturbance events (Dobbertin et al., 2002; Temperli et al., 2020; Wohlgemuth et al., 2022), namely wind throw and insect attacks.

4.1. Main factors influencing naturalness

More than 80 % of the forest stands classified as 'not natural' had an NST_{exp} dominated by broadleaves. This was mainly due to a large proportion of conifers within these stands leading to more than 60 % being classified as conifer forests based on the observed tree species composition (NST_{obs}). The high proportion of conifers, mainly Norway spruce and silver fir, is a result of past and current management (Bürgi and Schuler, 2003). These forest stands are mainly located in the Swiss plateau where the terrain is flat and accessibility is high allowing for highly productive forests (Brändli et al., 2020) and lower harvesting costs (Bont et al., 2022). As a result of the demand of the Swiss wood industry conifer afforestations in the Swiss plateau were a common practice during the 19th and 20th century (Bürgi and Schuler, 2003).

Fig. 3. Comparison of the NST_{exp} and NST_{obs} for the NFI sample plots with different naturalness. The left side indicates NST_{exp} and the right side NST_{obs}. Lines changing their forest types indicate mismatches between NST_{exp} and NST_{obs}.

Table 2
Number of NFI sample plots affected by different disturbance agents grouped according to their naturalness. Combinations of disturbance agents and naturalness that are significantly more often (+) or less often (-) observed than expected by chance are highlighted in bold (Chi-square tests). +++/— $p < 0.001$, +/- $p < 0.05$.

	Natural	Close to natural	Partly natural	Not natural
Undisturbed	**1309^{+++}**	580	**478^{-}**	1934
Disturbed	**152$^{—}$**	91	**99^{+}**	316
Wind	87	54	44	172
Insects	24	14	20	54
Snow	28	17	23	46
Drought	0	2	2	7
Fire	2	0	2	1
Other	11	4	8	36

Most of the Norway spruce afforestation stems from the mid-19th century using various proveniences and autochthone stands dominated by conifers are very rare in the Swiss plateau (Ellenberg and Klötzli, 1972; Portier et al., 2021). As the Swiss forestry law favours (natural) regeneration with site-adapted tree species (i.e., species of the NST_{exp}) and forest management in Switzerland adopts a 'close-to-nature' silvicultural system (Spathelf et al., 2015) the historic Norway spruce afforestation are slowly transitioned into broadleaf forests (Spiecker, 2004). However, due to the longevity of trees and the slow regeneration process, this will take decades if not centuries and Norway spruce remains the main timber species in Switzerland up to today (Bundesamt für Statistik, 2018).

At high elevations the main factor influencing naturalness was the European larch which dominated more stands than naturally expected (i.e., based on NST_{exp}). This overrepresentation is partly a land use legacy of farmers favouring European Larch over Norway spruce to create more open forest and sunlit forest floors that enable more productive grazing (Meyer, 1951). The European larch is also profiting from a high disturbance frequency (i.e., avalanches, clearings and fires) and lower susceptibility to snow-related damages and diseases (Meyer, 1955).

4.2. Naturalness and disturbances susceptibility

Stands classified as 'natural' had a significantly lower susceptibility to disturbances than all other categories of naturalness. However, the degree of naturalness did not necessarily influence the susceptibility to disturbance as 'not natural' stands were, overall, not the most vulnerable ones. The lack of an overall effect for 'not natural' forest stands on the susceptibility to disturbances might, at least partly, be explained by both positive (e.g., wind disturbance in NST_{exp} of Norway spruce forests) and negative effects (e.g., insect outbreaks in NST_{exp} of Beech forests) of low naturalness in different forest types cancelling each other out (Table S3). Forest stands with an NST_{exp} dominated by broadleaves were most affected by disturbances (especially wind throw and insect attacks) when not classified as 'natural'. This is a direct result of the unnaturally high proportion of conifers in these stands as the two most frequent disturbance agents wind throw and insect attacks mainly affected Norway spruce (Scherrer et al., 2022; Usbeck, 2015). Scherrer et al. (2022) showed that the effect of wind throw and bark beetle attacks is especially strong in Norway spruce stands planted outside of the 'natural' distribution of Norway spruce (e.g., here at lower elevations in NST_{exp} of beech forests). Similarly, we found that the amount of non-natural conifer stands is a main contributing factor to the amount of bark beetle damage observed within an administrative forest unit. More importantly, the effect of non-natural conifers stands on bark beetle damage

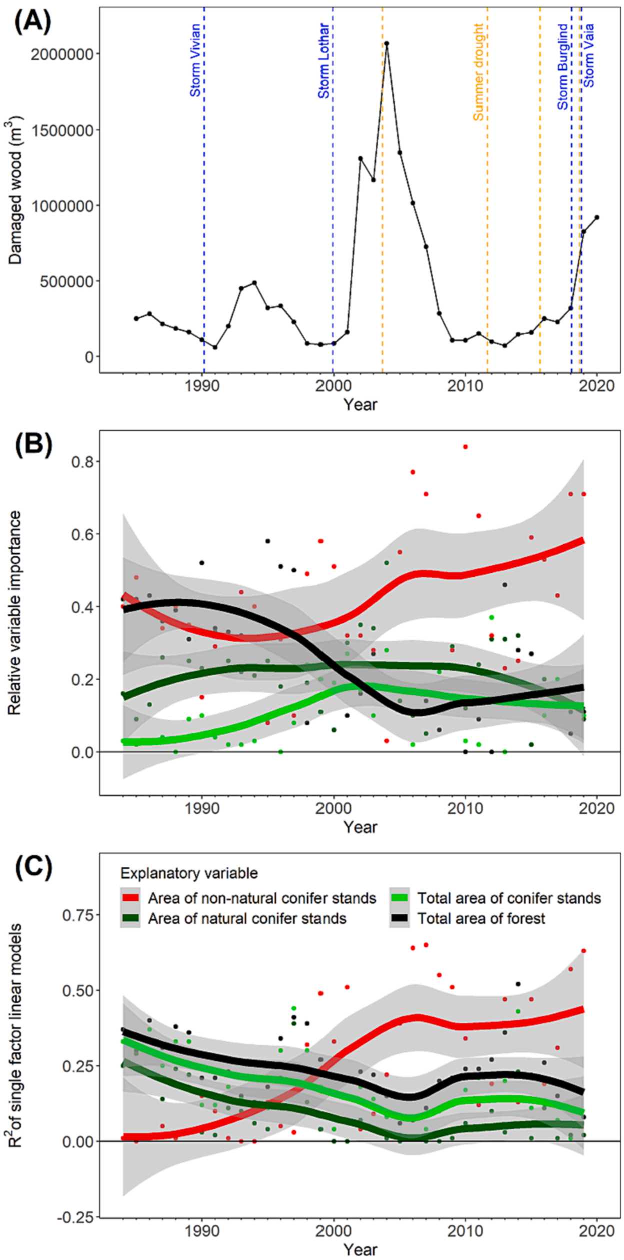

Fig. 4. Bark beetle damage on different types of conifer stands. (A) Wood volume (m^3) damaged by bark beetle attack across all forested areas in Switzerland as reported by local foresters from 1984 to 2019. Blue and orange dotted lines indicate the timing of large storms and summer drought events, respectively (B) the relative importance of different predictor variables for each year, and (C) the explanatory power of a single variable (R^2) for damaged wood volume per administrative forest unit from 1984 to 2019. The trendlines were fitted with a loess function and the shaded areas indicate 95% CI.

was strongly increasing in recent years leading to an elevated risk of large-scale ecosystem failure in forests still dominated by Norway spruce afforestations.

At higher elevations stands with an NST_{exp} dominated by Norway spruce had a lower susceptibility to disturbances (i.e., wind throw) when classified as 'not natural'. This is the result of Norway spruce being substituted by European larch due to a mixture of natural (e.g., avalanches, snow) and anthropogenic influences (e.g., forest pastures). The deciduous nature of the European larch makes the species much less susceptible to winter storms compared to Norway spruce.

4.3. Stability of forests under climate change

From a scientific perspective, the lowland afforestation of non-autochthone conifers during the 19th and 20th century represents a large-scale, long-term transplantation experiment. Norway spruce-dominated forests in the Swiss plateau are especially susceptible to disturbance events (Scherrer et al., 2022; Wohlgemuth et al., 2022) resulting in high mortality rates. In 'good' years, the Norway spruce afforestations in the Swiss plateau are highly productive but quickly show signs of 'maladaptation' under drought stress or storms (Schuldt et al., 2020; Usbeck, 2015). Bark beetles (*Ips typographus*) are highly successful in infecting these 'pre-stressed' Norway spruce afforestations profiting from the warm lowland conditions allowing multiple insect generations per year (Stadelmann et al., 2014). The observed dieback and associated loss of ecosystem function of Norway spruce afforestations in the Swiss plateau is therefore likely a combination of climatic stress and higher pathogen/parasite pressure amplified by interactions of wind throw and drought spells. Many of these low-elevation Norway spruce stands might also consist of rather old and evenly aged trees with limited regeneration further increasing their susceptibility to bark beetle attacks (Wermelinger, 2004). These Norway spruce afforestations already experienced a significantly elevated temperature of about 2.5 °C compared to their natural climatic optimum (i.e., based on the primary natural distribution within Switzerland, Students *t*-test, $p < 0.001$; Fig. S6). This raises the question of whether similar diebacks and problems due to maladaptation are to be expected for many other species, including European beech, due to accelerated climate warming during the 21st century, as predicted by vegetation models (Zimmermann et al., 2014; Zimmermann et al., 2016).

In 2018, a prolonged drought period led to widespread defoliation and dieback events in beech forests across Europe (Frei et al., 2022; Nussbaumer et al., 2020; Obladen et al., 2021; Schuldt et al., 2020; Walthert et al., 2021). Although, the ability of European beech trees and stands to quickly recover and adapt to future droughts is debated (Leuschner, 2020; Rohner et al., 2021), the large-scale dieback of 2018 was seen as a warning signal by many foresters and decision makers. As a result, a number of different plantation experiments were initialised to find the most promising tree species for forests under future climate conditions (Frei et al., 2018). In addition to potential changes in tree species compositions, also shifts in management practice might be essential to better adapt forests to changing climatic conditions (Spathelf et al., 2015). Recent studies indicate, that the currently used close-to-nature silviculture characterized by small gap sizes mostly enhances direct ingrowth (i.e., ingrowth of the dominant seed trees) especially in dense beech forests (Scherrer et al., 2021b). This management regime creates very stable forests in terms of species composition but might enhance maladaptation issues when climate conditions are rapidly changing as the lack of larger scale disturbances potentially pretends new species from establishing (Scherrer et al., 2022; Scherrer et al., 2020). As a result, stands might be fine at many places due to the high resilience and longevity of dominant trees but the chances of large-scale diebacks as results of stress-induced disturbances might increase, leading to a shift in ecosystem services (mainly a loss of wood supply). The example of lowland Norway spruce afforestation and the recent beech dieback during the 2018 summer drought highlight the danger of large-scale mortality events due to changing environmental conditions and raise the question if a more proactive transition of forests is necessary to transform forests in the light of climate warming. Warmer summers with prolonged drought periods are likely to increase but uncertainty in climate predictions remains large and forest management should aim towards a more diverse (spreading the risk) and drought-adapted tree species composition.

CRediT authorship contribution statement

Daniel Scherrer: Methodology, Formal analysis, Writing – original draft, Visualization. **Andri Baltensweiler:** Resources, Writing – review & editing. **Matthias Bürgi:** Resources, Writing – review & editing. **Christoph Fischer:** Data curation, Writing – review & editing. **Golo Stadelmann:** Resources, Writing – review & editing. **Thomas Wohlgemuth:** Conceptualization, Writing – original draft, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The raw data of the Swiss NFI can be provided free of charge within the scope of a contractual agreement.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120827.

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