Resprouting in European beech confers resilience to high frequency fire

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European beech (*Fagus sylvatica* L.) can regenerate successfully from seeds after mixed-severity fires with mid-to-long fire return intervals (> 60 years). However, if fire return interval is lower than the age of sexual maturity, post-fire seeding will be limited, leaving vegetative resprouting as the only viable option for recovery. This means that the forecasted increase in fire frequency driven by climate change may erode beech forest resilience to fire. Here we surveyed tree regeneration in a European beech forest affected by two consecutive fires, in 2003 and 2017, and applied experimental clipping of tree saplings to address the following questions: (1) What is the fire resistance and post-fire recovery via resprouting of tree saplings? (2) Which factors drive post-fire resprouting of beech saplings? (3) Does post-fire clipping of tree saplings increase the probability of survival and resprouting vigor? We monitored 2,195 beech saplings and 953 saplings of other tree species during three consecutive years, from 2018 to 2020. Almost all beech saplings were top-killed by fire, and two-thirds of them died completely. However, three years after the second fire, 30% of beech saplings survived by resprouting from the base. Post-fire resprouting was less likely in small-diameter saplings and in those more injured by fire. Overall, the second fire did not cause a major decline of beech regeneration and consequently did not alter the dominant species composition of post-fire recovery. Given the low specific resistance to fire, post-fire resprouting of saplings is therefore a key component of beech resilience to short-interval fires. The effects of clipping on post-fire survival and resprouting vigor were very limited, suggesting the unsuitability of actively clearing burned beech regeneration as a post-fire management prescription. In conclusion, basal resprouting from beech saplings after fire-induced top-kill led to a higher-than-expected resilience of beech to short-interval fires (i.e., *circa* 15 years).

Introduction

Climate and land use changes are affecting fire frequency, extent, seasonality and possibly severity across global forest biomes (Seidl et al., 2017; Halofsky et al., 2020; Mantero et al., 2020; Pausas and Keeley, 2021). Such changes in fire regimes can lead to strong impacts on forest ecosystems (Reyer et al., 2015) by favoring certain species or causing abrupt transitions towards different plant communities (Johnstone et al., 2016). Resilience can be defined in different ways (Nikinmaa et al., 2020), including the capacity of a system to reorganize and return to a prior state after a disturbance (Connell and Ghedini, 2015). Recurrent high-severity fires can dramatically reduce forest resilience through the loss of biological legacies that drive post-fire recovery (Kleinman et al., 2019; Turner et al., 2019). Therefore, we need to evaluate the resilience of forests to altered fire regimes in order to support forest processes and functions through effective management actions in a global change context.

Historically, the European Alps were not considered as a fire-prone region (Valese et al., 2014; Conedera et al., 2018; Müller et al., 2020). Nonetheless, fire disturbance increased in the last decades due to land abandonment favoring fuel accumulation and landscape connectivity (Bebi et al., 2017; Ascoli et al., 2021), as well as increasing temperatures, and severity and frequency of droughts and heatwaves (Gobiet et al., 2014; Dupire et al., 2017; Moris et al., 2020; Morresi et al., 2022), which may eventually result in a fire-regime shift. The first signs of altered fire regimes in European beech (*Fagus sylvatica* L.) forests are reported on southern slopes of the Alps (Maringer et al., 2016a).

European beech is highly susceptible to fire due to its thin bark (Bär and Mayr, 2020) and poor post-fire resprouting capacity of mature trees (Conedera et al., 2010; Maringer et al., 2012;

Ascoli et al., 2013). Mature beech forests are, however, resilient to mixed-severity fires with mid- to long-fire return intervals (>60 years). Under such regimes, post-fire tree mortality is delayed, abundant seeding occurs during mast years, and fire creates suitable conditions for seed germination and seedling establishment (Ascoli et al., 2015; Maringer et al., 2020). Post-fire beech regeneration is particularly abundant when mast years shortly follow fire disturbance (Vacchiano et al., 2021), although the suitable window for both seed germination and seedling establishment lasts for at least 20 years after the fire (Maringer et al., 2020; 2021). Nonetheless, an increase in fire frequency may erode beech forest resilience by modifying the structure, composition and survival of successive post-fire regeneration (Delarze et al., 1992). When the fire return interval is lower than the time needed for most individuals to reach sexual maturity (i.e., about 40-60 years in European beech; Wagner et al., 2010), post-fire seeding is limited and beech regeneration must rely on resprouting from buds at the root collar (Conedera et al., 2010; Figure 1). Timely post-fire cutting is recommended for other broadleaf species to prevent basal stem desiccation and stimulate proventitious and adventitious buds and shoots growth (Providoli et al., 2002; Moreira et al., 2009b). However, there is no experimental evidence on the survival and resprouting capacity of young beech exposed to fire disturbance.

In October 2017, a series of large wildfires spread over the western Italian Alps during a severe and prolonged drought, including the Val Susa Fire (4,018 ha; Morresi et al., 2022). Part of the Val Susa Fire burned an area previously affected by another wildfire during the heatwave of summer 2003 (Ascoli et al., 2013). This brought us the opportunity to examine post-2017 survival and resprouting of tree seedlings and saplings that had established after the 2003 fire. In addition, we established a clipping experiment on burned tree regeneration to investigate the suitability of clearing for enhancing post-fire resprouting of young trees. In this study, we explore the resilience of post-fire European beech regeneration to short-interval fires (i.e., *circa*

15 years). We specifically addressed the following questions: (1) What is the fire resistance and post-fire recovery via resprouting (resilience) of tree saplings in a European beech forest? (2) Which factors drive post-fire resprouting of European beech saplings? (3) Does post-fire clipping of tree saplings increase the probability of survival and resprouting vigor?

[Figure 1]

Materials and methods

Study area

The study site covers an area of approximately four ha and is located in the Susa Valley, Piedmont region, in the western Italian Alps (45º9'33"N, 7º9'45"E; Figure 2). The altitude ranges from 1043 to 1135 m a.s.l., the slope from 17º to 43º, and the aspect from north-east to south-east. The area is characterized by a sub-oceanic climate, with an average annual temperature of 8.7 ºC and an average annual precipitation of 904 mm in the period 1970-2000 (Fick and Hijmans, 2017). The wooded vegetation is dominated by an oligotrophic beech forest accompanied by other tree species, including European larch (*Larix decidua*), silver birch (*Betula pendula*), Italian maple (*Acer opulifolium*) and sycamore maple (*Acer pseudoplatanus*).

The fire regime of mountain beech forests in the Alps is characterized by small (<50 ha) winter (November-April) surface fires with long fire return intervals (>60 years; Valese et al., 2014; Maringer et al., 2016b; Conedera et al., 2018). The study site, conversely, was affected by two wildfires in a period of 14 years, both driven by extreme climate events. The first fire event started in August 2003 in the wildland-urban interface at 547 m a.s.l. and spread up to 1800 m a.s.l., burning a total of 484 ha (Ascoli et al., 2013). This wildfire occurred during an extreme heatwave in summer 2003 in Central Europe (Schär et al., 2004) that caused an exceptional fire activity throughout the Alps, including numerous large fires (Valese et al., 2014; Dupire et al., 2017). The second fire event, commonly referred as the "Val Susa Fire", occurred in October 2017 and burned a total of 4,018 ha. This fire was exceptionally large and 66% of the burned area was covered by forest (Ascoli et al., 2021). The great extent of fires in autumn 2017 in the western Italian Alps was related to the severe and prolonged drought that affected the region that year (Morresi et al., 2022). Both the heatwave in 2003 and the drought in 2017 have been classified as climate extremes linked to climate change (Schär et al., 2004; Bo et al., 2020). In both fire events, fire behavior in the study area was characterized by low-to-moderate intensity (<500 kW m^{-1}) surface fires.

The forest had not been affected by fire since at least 1960. Before the fire in 2003, the forest was a stored coppice (about 55 years old) with a beech density of 1250 stems ha^{-1}, a mean diameter of 25 cm and a basal area of 61 m^2 ha^{-1} (Ascoli et al., 2013). Within the study site, severity of the fire in 2003 was moderate (dead basal area between 20% and 80%; Ascoli et al., 2015). After the fire in 2003, beech natural regeneration from seeds was abundant (> 20,000 saplings ha^{-1}) favored by a beech mast event in 2006, accompanied by abundant regeneration of light-demanding pioneer species such as *Salix caprea*, *Laburnum anagyroides*, *Betula pendula*, *Populus tremula* and *Acer opulifolium* (Ascoli et al., 2013). In 2017, when the second fire occurred, many saplings were > 10 years old and some adult beech trees had already died due to direct fire damage or fungal activity in a prolonged post-fire dieback process (Maringer et al., 2016b).

Sampling design

We visited the study site in winter 2018 to find areas satisfying the following criteria: (1) clear signs of the passage of both fires (2003 and 2017); (2) European beech as the dominant tree species before 2003; (3) moderate-to-high post-fire tree mortality due to the 2003 fire; (4) no post-fire management; (5) occurrence of post-fire natural regeneration following the 2003 fire. This initial inspection was based on fire legacies, such as surviving trees, snags and downed woody debris following the 2003 fire, and exposed mineral soil, ash and charred tree regeneration following the 2017 fire. We then randomly selected 30 points within the areas that fulfilled the previous requirements. At each point, we established a pair of adjacent 4x4-m plots (30 pairs, 60 plots). In one of the paired plots (i.e., treatment plot) all seedlings and saplings were clipped (i.e., the stems were cut at the base; see Appendix 2 for photos) in winter 2018 (i.e., the first dormant season after fire) to remove the aboveground biomass, while in the other plot we did not apply any treatment (i.e., control plot; Figure 2). Additionally, we established three plots within an area that burned in 2003 but not in 2017. We clipped all the seedlings and saplings within these three additional plots to obtain a second treatment group that represents the effect of cutting juveniles that were not burned by recurrent fire.

[Figure 2]

Data collection

The data used in this study were collected at four different times. In winter 2018 (T0), each plot was characterized by its slope (with a clinometer), aspect (with a compass), elevation (from a digital elevation model) and two proxies of burn severity: percent of ground cover by litter (average of visual estimations in four 1-m^2 quadrants), and depth of the litter layer (average of measurements with a ruler at 56 points along diagonals of the four 1-m^2 quadrants). For each tree seedling and sapling that established before the 2017 fire, we recorded the following information: species, burn severity (high or low) based on the presence of charred and damaged bark, root collar diameter (with a caliper), and height above ground (with a meter) at which the stem was clipped for those in treatment plots. Most, if not all, of the seedlings and saplings established naturally from seeds after the fire in 2003. Unless otherwise stated, hereafter both size classes (seedlings and saplings) will be referred to as "saplings". Each sapling was then tagged to be monitored through time. In total, we sampled 2,195 beech saplings (982 in control and 1,213 in treatment plots) and 953 saplings of other tree species (408 in control and 545 in treatment plots).

In summer 2018 (T1; the first growing season after fire), we counted the number of post-fire basal resprouts in each sapling. Each resprout was assigned to a height class (<20, 20-40, 40-60, and >60 cm) and resprouting type (proventitious, adventitious, and belowground). At plant level, we determined the stem status (i.e., the condition of the aboveground biomass affected by the most recent fire) of each sapling in control plots, based on the presence of live foliage, into two classes: apparently dead (i.e., topkill), and alive. We also took a hemispherical photograph one m above the ground at the plot center; the percent of canopy openness was quantified with "Hemiphot.R" (ter Steege, 2018).

In summer 2019 (T2), the stem status of each sapling was again assessed following the same approach described above for T1 sampling. The height of the tallest post-fire resprout in each sapling was also measured with a meter. In summer 2020 (T3), the stem status of each sapling and height of tallest post-fire resprout were assessed for a third time. Exclusively for beech saplings, we also counted the number of live post-fire resprouts.

Data preparation

We labeled each pre-fire sapling according to two criteria: (1) stem status (i.e., alive or top-killed), and (2) presence of basal resprouting after the most recent fire. We followed the conceptual model of Moreira et al. (2009a) to define four types of post-fire responses according to a gradient of fire severity as follows: mode 1 (no top-kill and no resprouting), mode 2 (no top-kill and resprouting), mode 3 (top-kill and resprouting) and mode 4 (top-kill and no resprouting). Resprouts found dead at the moment of field survey were not taken into consideration to evaluate the response mode.

Saplings with response modes 1, 2 and 3 survived the most recent fire, but only saplings with response modes 2 and 3 resprouted successfully. All saplings in control plots were labeled into these four post-fire response modes over three years: summer 2018 (T1), summer 2019 (T2) and summer 2020 (T3). On the contrary, saplings within plots that received the clipping treatment were labeled into two classes: (1) those that resprouted (i.e., at least one resprout was still alive when measurements were taken), and (2) those that did not resprout, or with no surviving resprout at the time of measurements. As a result of delayed resprouting (i.e., resprouting starting in the second or third growing season after the fire), some saplings apparently dead (mode 4) at T1 were alive at T2 and T3. Analogously, some live saplings (modes 1, 2 and 3) at T1 were found dead (mode 4) at T2 and T3 due to whole-plant delayed mortality, and consequently some saplings died later on despite the initial resprouting success or aboveground survival.

We used three variables to measure resprouting capacity in each sapling: the height of the tallest resprout (max height), the total number of live resprouts (n resprouts), and a proxy of resprouting vigor (vigor index) calculated as the product of maximum height and number of resprouts (Moreira et al., 2012). Empirical studies support the use of indices derived from the combination of the total number of resprouts and measurements taken only from the main resprout (i.e., maximum height in this study) as reliable proxies of post-disturbance resprouting vigor (e.g., Cruz et al., 2003a; Moreira et al., 2012; Jaureguiberry et al., 2020). Given that each resprout measured at T1 was assigned to a height class, we used the following values to estimate maximum height at T1: 10 cm for height class 1, 30 cm for height class 2, 50 cm for height class 3, and 70 cm for height class 4. At T2 and T3, maximum heights were measured with an accuracy of 1 cm. Although all the species of the saplings were recorded, for the purpose of this study we pooled all species except *Fagus sylvatica*, separating saplings into two species classes (i.e., European beech and other species).

Data analyses

All the statistical analyses were carried out using the R software environment (version 4.1.0; R Core Team, 2021). To answer the first research question, we calculated the percentage of saplings in each of the four post-fire resprouting modes at T1, T2 and T3, separately for European beech and the other species. In addition, we calculated summary statistics for resprouting vigor, tree density, and species composition. Only saplings within the control plots were used in this part of the analyses. We followed a resistance-resilience framework to quantify fire resistance and post-fire recovery separately (Connell and Ghedini, 2015; Hodgson et al., 2015; Nimmo et al., 2015). Saplings with response mode 1 and 2 were resistant given that the main stem did not die from fire, while saplings with response mode 3 experienced top-kill but recovered via resprouting. Therefore, here we quantified post-fire sapling survival through two different mechanisms, aboveground survival from fire (resistance), and fire-induced resprouting following top-kill (resilience).

We tested the influence of post-fire clipping by calculating differences in post-fire survival (i.e., proportion of saplings that survived the fire by resisting top-kill or recovering through resprouting) and resprouting vigor (i.e., maximum height, number of resprouts, vigor index) between saplings in control vs. treatment plots. Effect sizes were estimated separately for European beech and other species in two different years (T1 and T3). First, we applied bias-corrected and accelerated (bca) bootstrap (5000 resamples with replacement) to build: (1) 95% confidence intervals (CI) of mean survival, mean maximum height, mean number of resprouts, and mean vigor index for both groups (control and treatment) using the function "ci_mean" from the R package "confintr" (Mayer, 2020); and (2) 95% CI of the mean difference between groups for all the four variables using the function "mean_diff" from the R package "dabestr" (Ho et al., 2019). Second, we calculated Cohen's d (Ellis, 2012) and its 95% CI to obtain a standardized measure of effect size for resprouting vigor using the function "cohens_d" from the R package "effectsize" (Ben-Shachar et al. 2020). We followed Sawilowsky (2009) to interpret d (i.e., d<0.2 very small effect; d=0.2-0.5 small; d=0.5-0.8 moderate; d=0.8-1.2 large; d>1.2 very large). Similarly, Cohen's h (Cohen, 1988) was used as a standardized measure of the difference of survival rates between control and treatment groups.

We applied Generalized Linear Mixed Models (GLMM) to assess the influence of several predictor variables (Table 1) on post-fire beech resprouting. Thus, only data from beech saplings were used in this part of the analyses. We applied mixed models due to the hierarchical structure (saplings sharing the same values at plot level, such as topography and density) and temporal dependency (repeated measures at sapling level, such as T1 and T3) of the data. Intra-class correlation coefficient (ICC) values > 0.19 and > 0.39 at plot and plant level, respectively, illustrate the non-independence of our dataset (Nakagawa et al., 2017). Plot and sapling were therefore used as random intercepts in all models. Two response variables were modelled: post-fire resprouting (yes or no) and resprouting vigor index (described above). For each response variable we built a model with all saplings, and one using data exclusively from saplings in the clipping treatment (i.e., four models). Before modeling, data exploration was carried out following the protocol described in Zuur et al. (2010). We did not detect high collinearity between predictors, although we found some evidence of two-way interactions.

Continuous predictors were standardized to ensure comparability of effect sizes (i.e., beta coefficients). We used a binomial distribution (with a logit link function) and a gamma distribution (with a log link function) to model the probability of resprouting and resprouting vigor, respectively. We assessed two-way interactions between predictors by calculating p-values of the interaction terms, comparing models with and without interactions using Chi-square tests, Akaike Information Criterion (AIC) and Bayesian Information Criteria (BIC), and plotting predicted vs. observed values. When Pearson's residuals had significant ($p < 0.05$) non-linear trends against predictors (Zuur et al., 2009), we fitted a Generalized Additive Mixed Model (GAMM) with analogous design. Model assumptions were assessed graphically using Pearson residuals (Zuur et al., 2009). No predictor selection was performed because the models were not intended for prediction. Model performance was evaluated with the variance explained by fixed (marginal R^2) and both random and fixed factors (conditional R^2; Nakagawa and Schielzeth, 2013; Nakagawa et al., 2017). Finally, effects sizes were estimated using standardized beta coefficients, odds-ratios and their 95% CI, and plots of marginal effects (Lüdecke, 2021). Modeling was carried out using the function "glmer" from the R package "lme4" for GLMM (Bates et al., 2015) and the function "gamm4" from the package "gamm4" for GAMM (Wood and Scheipl, 2020).

[Table 1]

Results

Post-fire response modes and resilience

Death of beech saplings (mode 4) was the most common response to fire in the immediate (T1) and subsequent years (T2 and T3), while top-kill and resprouting (mode 3) was the second most common response (Table 2). We observed a decrease in beech apparent mortality (mode 4) from 69.5% at T1 to 65.5% at T3, as well as a decrease in aboveground survival (modes 1 and 2) from 8.1% at T1 to 3.8% at T3, and an increase in post-fire resprouting after top-kill (mode 3) from 22.4% at T1 to 30.7% at T3 (Table 2). These trends exist because some saplings were classified into different response modes over time. For instance, 46.8% of beech saplings with response mode 3 (top-kill and resprouting) at T3 were classified as apparently dead (mode 4) at T1 (Table S1), showing that delayed resprouting was common in beech. Non-beech saplings consisted mostly of *Salix caprea* (34%), *Betula pendula* (28%), *Laburnum anagyroides* (20%) and *Acer opulifolium* (15%). For these species, mortality increased over time from 30.1% at T1 to 44.3% at T3, and the proportion of plants resprouting after top-kill decreased from 43.9% at T1 to 32.1% at T3 due to delayed fire-induced mortality (Table 2).

[Table 2]

The response of beech to fire was characterized by a low resistance (the aboveground part survived in 3.8% of saplings at T3), and a relatively moderate resilience (30.7% of beech saplings recovered through resprouting; Table 3). Other tree species showed a higher degree of survival than beech (55.6% vs. 34.5%) due to a higher fire resistance (23.6% vs. 3.8%), and a slightly higher resilience (32.1% vs. 30.7%) three years after the fire (Table 3). In addition, the initial resprouting vigor of beech was inferior in terms of both number of resprouts and height (Table 2). Consequently, fire decreased the proportion of beech within the species composition of the post-fire regeneration, from 70.6% before the second fire, to 59.9% of all surviving saplings in 2020. Nonetheless, three years after the second fire the density of beech was still around 7,000 saplings ha^{-1}, with almost 20,000 beech resprouts ha^{-1} (Table 3).

[Table 3]

Fire and clipping effects on resprouting

Beech survival (i.e., the percentage of resistant and resilient saplings) was higher under the clipping treatment than in the control group (Table 4), although the mean difference (treatment minus control) was higher at T1 (16.2% [12.0%; 20.5%]) than at T3 (7.8% [3.5%; 12.1%]). The mean difference in immediate survival in other tree species was very small (2.4% [-3.4%; 8.0%]), and by T3 the mean survival under treatment was lower than in the control group (42.6% [38.3%; 46.8%] vs. 55.6% [50.7%; 60.5%]), indicating a negative effect of the treatment on the subsequent survival (Table 4). Since we pooled all the species except beech, we did not separate effect sizes by individual species, and thus it is likely that the treatment affected survival of every species unequally.

Given that 29.4% of the initial beech resprouts in treatment plots were adventitious (i.e., developed from previously non-meristematic tissues), we suspected that proventitious resprouts (originated from meristem tissue) may have had a higher survival over time (Table S2). However, we found no evidence of this, and 72.0% [60.0%; 80.0%] of beech saplings with only adventitious resprouts as well as 73.4% [68.1%; 77.6%] of beech saplings with only proventitious resprouts at T1 were still alive at T3 in the treatment group. On the other hand, beech saplings that were clipped but not burned experienced a very high initial survival (94.3% [90.2%; 96.3%]) compared with beech saplings in the control group (30.5% [27.6%; 33.3%]; Table S3).

[Table 4]

Beech saplings from treatments plots had a higher initial mean number of resprouts than saplings from control plots (4.9 [4.5; 5.4] vs. 2.6 [2.3; 2.8]), although at T3 the difference (3.3 [3.0; 3.6] vs. 3.0 [2.8; 3.2]) was weak (Table 5). Regarding the maximum height and vigor index of beech saplings, in general we observed small positive effects of the clipping treatment in both years T1 and T3 (Table 5). The data also shows a positive effect of the treatment on number of resprouts (mean difference 4.0 [3.1; 5.1]) and vigor index (1.8 [1.3; 2.4]) of other species at T1, but not on maximum resprouting height (Table S4).

[Table 5]

Drivers of post-fire beech resprouting

Mixed models showed that several drivers were associated with post-fire beech resprouting. Probability of resprouting decreased with slope (Table 6). Burn severity, clipping and diameter showed stronger size effects than slope (Figures 3A, 3B, 3C). The odds of resprouting were more than three times higher in saplings that experienced low burn severity than those with high severity (Table 6). Likewise, clipping increased the odds of resprouting by approximately three times. The effect of clipping was mediated by time since fire. In control plots, the probability of finding live resprouts increased with time, while in saplings that received the clipping treatment, time reduced this probability (Figure 3C). The shape of the relationship between diameter and resprouting was apparently unimodal, although with high levels of uncertainty for the largest diameters. Probability of resprouting increased until diameter reached approximately 4-5 cm, but decreased with larger diameters (Figure 3B). Similarly, clipping, time since fire and diameter were positively associated with vigor of post-fire beech resprouting (Figures 3D, 3E, 3F). Additionally, we found a weak negative relationship between pre-fire density and resprouting vigor (Table 6). On the other hand, there was no evidence for a relationship between clipping height and post-fire resprouting (Table 6). The variance explained by fixed and random factors was > 65 % in all the models.

[Figure 3]

[Table 6]

Discussion

Resilience of European beech juveniles to fire

European beech saplings showed a low resistance to fire. More than 95% of beech saplings were top-killed, and complete mortality (i.e., no resprouting after top-kill) reached 65.5% three years after the fire (Tables 2, 3). In particular, the bark of beech saplings was often damaged and cracked after exposure to fire heat (Maringer et al., 2016b; Appendix 2). We also observed a delayed mortality of beech stems (i.e., death occurred two or three years after the fire), although it only affected around 10% of beech saplings (Table S1). The high percentage of top-kill evidences the low degree of fire resistance of European beech saplings. European beech is highly susceptible to fire due to the thin and poorly insulating bark that protects the cambium from lethal temperatures during a fire (Bär and Mayr, 2020). While bark thickness growths with tree diameter (e.g., Bauer et al., 2021) so that larger beech trees are more likely to survive fire (Maringer et al., 2016b; 2021), small-diameter beech trees tend to have the whole circumference scorched and larger parts of the cambium killed, reducing their capacity to create fire scars to survive (Maringer et al., 2016b). Thus, the small dimension of beech saplings (i.e., mostly root collar diameters < 10 cm) and the low fire protection of beech traits explain the high rate of top-kill observed for this species after a fire of low-to-moderate fire intensity.

Resilience of beech juveniles to fire came from post-fire resprouting. Three years after the fire, approximately 30% of beech saplings were able to resprout from the base. Studies from the European Alps report a scarce post-fire resprouting capacity of mature beech trees (Conedera et al., 2010; Ascoli et al., 2013; Maringer et al., 2016). However, our results suggest that post-fire beech resprouting is more common in juveniles (Bond and Midgley, 2001). Interestingly, we found that almost half of the saplings in control plots that survived after top-kill did not resprout in the first growing season following the fire, but in the second one. This delayed resprouting suggests that initial resprouting is not necessarily a good indicator of the post-fire resprouting capacity of beech saplings (Moreira et al., 2012).

The moderate post-fire resprouting success of beech saplings (i.e., approximately 30%) may be due to common causes of resprouting failure, such as high burn severity, low bud protection, and limited stored resources to fund regrowth (Clarke et al., 2013). Beech saplings in the high burn severity class had a lower probability of resprouting (Figure 3A). Some saplings may have suffered fire-induced cambium necrosis of the stem base or xylem cavitation, leading to plant mortality (Midgley et al., 2011; Nolan et al., 2021). Another possible cause of post-fire resprouting failure in beech is the low degree of protection of dormant basal buds. In fire-prone ecosystems, species with unprotected or low bud protection have a higher risk of dying after a fire (Charles-Dominique et al., 2015). European beech epicormic buds are located on the bark surface (Colin et al., 2012; Meier et al., 2012). If basal buds have the same relative position to bark surface, they are unprotected against fire and easily killed (Charles-Dominique et al., 2015; Burrows and Chisnall, 2016), unless they are located below or near the soil surface and as a result partially insulated (Pausas et al., 2018). Here, we cannot attribute mortality to damage to either cambial tissues or basal buds, but fire was clearly more lethal than basal clipping for beech (Pausas et al., 2016). In fact, the survival probability of non-burned beech saplings under clipping was three times higher than burned beech saplings within control plots (Table S3).

We found strong evidence that sapling size had a positive effect on post-fire resprouting vigor. Nonetheless, the relationship between diameter and probability of post-fire resprouting was not linear (Figure 3B). While there was a positive association between probability of resprouting and diameter up to 4 cm, this probability decreased in individuals with larger diameters. Two opposite factors may explain the shape of the relationship between post-fire resprouting and sapling size. On one side, larger trees have a higher level of fire resistance (Moreira et al. 2009a; Nolan et al., 2020), and a larger amount of non-structural carbohydrates in belowground organs

(Moreira et al., 2012; Piper and Paula, 2020; Nolan et al., 2021). Therefore, larger beech plants probably benefit from a higher insulating capacity, a larger bud bank and larger reserves in the root system, all of which may increase post-fire survival and resprouting vigor. On the other side, European beech is a relatively poor resprouter (Conedera et al., 2010; Vacchiano et al., 2017), and resprouting of adult beech trees decreases with increasing diameter and age (Vacchiano et al., 2017). A decrease in resprouting ability with increasing size is common in other tree species, although the mechanisms responsible for this decline are unclear (Vesk, 2006; Vacchiano et al., 2017; Fairman et al., 2019; Jaureguiberry et al., 2020). Although age may have a negative effect on beech resprouting that might already manifest at early stages, this hypothesis needs to be supported by stronger evidence given the limited age and size of the beech plants studied here. In addition, sample size and model accuracy for beech saplings with root collar diameter >5 cm were limited in this study.

Effects of post-fire management

In the first growing season after the fire, clipped beech saplings were more likely to survive and resprout, and produced more resprouts than saplings in the control group. However, three years after the fire, the differences in survival and vigor between the control and treatment groups dropped (Tables 4, 5). In the third growing season after the fire, survival of clipped beech saplings was only 3.5 to 12.1% higher than non-clipped saplings. On the other hand, clipping did not improve the initial post-fire survival of other tree species pooled together, and even reduced their survival three years after the fire.

The change in effect size of clipping on beech survival resulted from two separate trends (Figure 3C). On one side, increasing survival over time in the control group was due to delayed resprouting, especially in the second growing season after the fire. On the other side, similar to the control group, clipped saplings also experienced delayed mortality, but only 10% of live clipped saplings resprouted after the first growing season. Delayed resprouting was not enough to compensate for late mortality, and therefore cumulative survival of the clipped group decreased over the 3-year period.

Variables related to the clipping experiment such as clipping height and canopy openness did not affect post-fire beech resprouting (Table 6). First, it is likely that fire killed most of the stems before clipping, so that clipping height did not influence the demand and mobilization of resources from the remaining aboveground biomass (Fischer et al., 2022). Second, while light availability may limit the growth of resprouts in some species frequently exposed to wildfires (Cruz et al., 2003b; Casals and Rios, 2018; Monfort-Bague et al., 2020), we found no evidence that canopy openness was related to resprouting probability and vigor. Nevertheless, small dead and live stems might shelter beech resprouts during the first years, similar to the shelter provided by woody debris and fast-growing pioneer tree species (Ascoli et al., 2013; Maringer et al., 2016a).

Clipping occurred in April 2018, at the end of the dormant season. Thus, we cannot assess here the influence of treatment timing. While coppicing before the beginning of the growing season is often considered optimal to maximize resprouting vigor (Ducrey and Turrel, 1992; Spinelli et al., 2017), the effects of cutting season were rarely found significant by previous research (Hmielowski et al., 2014; Fischer et al., 2022). Another aspect that we could not explore here is the potential interaction between timing of fire and treatment (Regier et al., 2010). For instance, applying a clipping experiment a few weeks after a winter fire may not have the same effect as an early-spring clipping after a summer fire, especially in the first growing season.

The fire of 2017 occurred in late October during a severe drought, when non-structural carbohydrates may have been at low levels due to drought stress and the end of the growing season (Espelta et al., 2012; Piper and Paula, 2020). A different experimental design will be needed to explore whether pre-fire drought limits post-fire resprouting.

Post-fire cutting of dead and damaged trees is a commonly suggested silvicultural practice to promote tree recovery through resprouting (Catry et al., 2012; Espelta et al., 2012). The post-fire clipping experiment intended to stimulate basal resprouting by eliminating the burned aboveground biomass (Catry et al., 2012) and increasing light availability (Casals and Rios, 2018). In addition, the clipping treatment tried to trigger the development of adventitious buds, in case fire reduced or eliminated completely the proventitious buds at the root collar. Clipping increased post-fire resprouting in the first post-fire growing season, and adventitious resprouts represented almost 30% of all initial resprouts in clipped beech saplings (Table S2). However, based on our results, we cannot recommend post-fire clipping of saplings in beech forests. First, the positive effects in terms of post-fire survival and vigor in beech saplings were too small after three years. If the trend continues, the effect may not persist in the following years. Second, in our study area, the levels of post-fire resprouting in the control group were satisfactory, and additional treatments were not necessary to prompt recovery of post-fire regeneration. Finally, manual or mechanical cutting of saplings is an expensive treatment in high mountain areas. Small ecological improvements may not justify the costs of this type of treatment.

Forest dynamics after high frequency fire

The second fire in 2017 changed the structure and composition of the natural regeneration that established after the first fire in 2003, although these changes did not appear to reverse the post-fire trajectory of recovery towards a beech forest. The second fire killed around 60% of saplings, reducing the total density of natural regeneration from almost 30,000 to 12,000 saplings ha^{-1}. This fire also lowered the relative density of beech saplings from 70% in 2017 (pre-fire) to 60% in 2020 (three years after the fire). Almost all beech saplings were top-killed, while pioneer species were more resistant to top-kill. The higher degree of fire resistance in pioneer species may be due to a thicker bark in juvenile stages (e.g., birch; Vacchiano et al., 2014; Bär and Mayr, 2020), and the fact these tree species had larger diameters since they established quickly after the first fire and grew faster than beech (Ascoli et al., 2013; Maringer et al., 2016a). On the other hand, beech and pioneer species had a similar degree of post-fire resprouting three years after the second fire (i.e., approximately 30% of saplings kept live resprouts). Pioneer species had a resprouting probability twice as high as beech in the first growing season, but also experienced a higher delayed mortality than beech in the following two years (Table 3). These post-fire dynamics (e.g., delayed resprouting and delayed mortality) over a short period highlight the importance of continuous monitoring.

Studies from the European Alps demonstrated that beech forests are rather resilient to single fires of mixed severity under recent climatic conditions as a result of successful regeneration of beech from seeding (Maringer et al., 2016a; 2020). Nevertheless, Maringer et al. (2020) suggested that more frequent fires, particularly in immature beech stands, could result in shifts in species composition because of failed beech regeneration. This hypothesis assumes that the post-fire resprouting capacity of beech juveniles is low and post-fire beech regeneration depends on a prolonged post-fire recruitment window provided by mast seeding *in situ* from mature beech trees. Conversely, our data prove that beech saplings are able to resprout from the root collar after being top-killed by fire of low-to-moderate intensity. The first three years of monitoring show that despite the low fire resistance (i.e., high levels of top-kill), sufficient beech saplings were able to survive and resprout after the fire (accompanied by pioneer species) to restock beech in the following decades. In fact, shade-tolerant beech seedlings and saplings benefit from the nurse effect of neighboring fast-growing pioneer species in post-fire environments (Ascoli et al., 2013; Maringer et al., 2016a). Accordingly, our results indicate that two consecutive fires of low-to-moderate intensity, separated by 14 years, will not cause a major decline of beech. In other words, we found no evidence that altered fire frequency may drive European beech past a tipping point into a different forest type, or even cause a transition to shrubland or grassland (Reyer et al., 2015). To this regard, post-fire resprouting of saplings seems a key component of beech resilience to high frequency fire (Figure 1).

This study could serve as an early example of the resilience of European beech forests to altered fire frequency driven by climate change. There are, however, some caveats regarding the resilience of beech forests that can be derived from our study:

1. The second fire reduced the density of saplings, lowered the relative proportion of beech in the regeneration, and most of the surviving saplings had to restart growth from basal resprouts. Therefore, structure and composition of the regeneration following the first fire may be vital to ensure resilience to the successive fire. If beech regeneration after the first fire is scarce (e.g., in large stand-replacing fires), a second fire in a short period may increase the likelihood of a shift into a different forest type (Maringer et al., 2020).

2. Time between fire events is an important factor given that size of beech saplings is a strong driver of post-fire resprouting. However, it is unclear how fire interval can affect resilience because of the potential non-linear association between beech size and resprouting capacity. Mid fire intervals (e.g., 30-40 years) may result in a higher resprouting failure, than the one

described here, driven by older beech juveniles. The post-fire resprouting capacity of young beech trees across a wide range of diameters should be further assessed.

3. Fire severity is an important driver of post-fire resprouting. The levels of post-fire resprouting reported here are indicative of low-to-moderate fire intensity. High-intensity fire may limit much more severely the resprouting capacity of young beech individuals.

Limits of the study

The main limitation of the analyses is that our observations are restricted to one study area. We are not aware of other beech forests that experienced such a short fire interval in the region (Maringer et al., 2016a). Consequently, our findings should be interpreted as preliminary until new studies confirm and extend our results to additional study areas.

We did not test the effects of weather on post-fire resprouting. The influence of dry conditions on post-fire beech recruitment from seeds may be relatively weak (Maringer et al., 2016a; 2020). However, we do not know whether severe post-fire drought events could trigger high mortality in resprouting beech saplings (Espelta et al., 2012).

We focused on post-fire resprouting. The rapid growth and high density of resprouts may limit the opportunity for new seedling recruitment. However, pulses of regeneration from seeds, favored or not by the second fire, may occur in the next years (Maringer et al., 2020).

Finally, our study covered a short period of three years. Thus, our results represent an early indicator of the resilience of beech forests to short-interval fires. Further monitoring is needed to expand the knowledge from short- to mid-term post-fire dynamics (e.g., 5 to 20 years). A space-for-time approach could be applied (Maringer et al., 2020), although frequent fires in the same location are currently rare in European beech forests.

Implications for forest resilience and management under global change

Higher fire frequency, driven by climate change, increases the “immaturity risk” by which seed supply may be insufficient to recover a specific forest type if young trees did not reach reproductive maturity (Keeley et al., 1999; Johnstone et al., 2016; Turner et al., 2019). Short-interval fires can reduce the density of post-fire tree seedlings and modify the species composition (Bowman et al., 2014; Turner et al., 2019; Whitman et al, 2019), as well as decrease the likelihood of basal and epicormic resprouting (Fairman et al., 2019). In this regard, our study shows a similar trend, with a reduction in the total density of post-fire saplings, although without a substantial change in species composition. Nonetheless, we do not interpret these results as an indicator of reduced European beech resilience to future fire regimes, but as a higher-than-expected resilience to short-interval fires of this non-serotinous obligate masting seeder due to post-fire survival of saplings through basal resprouting.

The unexpected capacity of European beech saplings to resprout after fire-induced top-kill is most likely not evolutionary linked to fire (Pausas and Keeley, 2014). In fact, resprouting is a general trait of temperate angiosperms through the sapling stage of development (Del Tredici, 2001). Vesk (2006) found that seedlings of tree species have a high probability of resprouting under different disturbance types, including fire, while the probability of resprouting after top-kill fires is lower in mature trees. Our study suggests that resprouting in beech saplings confers resilience to short-interval fires because resprouting of juveniles favors the recovery of the regeneration established initially by post-fire seeding. This has important implications for the resilience to future fire regimes. Since the higher resprouting capacity of juvenile trees is often overlooked in non-fire-prone ecosystems, other forests dominated by cool temperate deciduous species may also have this additional mechanism of resilience against altered fire regimes. There are important uncertainties though, such as the increasing risk of resprouting failure and whole-tree mortality under repeated short-interval fires (Karavani et al., 2018; Fairman et al., 2019; Nolan et al., 2021). Here we only studied two short-interval fires (ca. 15 years), but under three or four recurrent short-interval fires, the capacity of the same young beech individuals to resprout again may be seriously limited.

From a management point of view, our findings on the capacity of beech saplings to produce post-fire vital resprouting shoots reinforce previous conclusions by Maringer et al. (2020) on the high resilience of beech forest to fire disturbances as a result of post-fire seeding from surviving trees. When such mechanisms are in place, additional silvicultutal practices (e.g., clearing) would not significantly improve the recovery of beech forest stands affected by short-interval fires, causing a negative cost-benefit balance.

Conclusions

Our findings reveal the potential of post-fire resprouting of beech saplings in response to short fire interval. Firstly, despite the low beech resistance to fire (i.e., almost all beech saplings were top-killed by fire and around two thirds died completely), approximately 30% of beech saplings survived by resprouting from the base after being top-killed. Interestingly, delayed beech resprouting in the second growing season was common. Secondly, post-fire resprouting was inferior in small-diameter beech saplings and in those more injured by fire. Finally, the positive effect of the clipping experiment on post-fire survival and resprouting resulted to be small. Based on our results, we do not recommend clearing burned regeneration as a prescription for post-fire beech management.

The goal of this study was to explore the resilience of European beech to short-interval fires. Two successive wildfires affected the study area in a period of 14 years. The first one during an extreme heat wave and the second one after a severe drought. Successful beech regeneration from seeding ensured recovery from the first fire (Ascoli et al., 2013), while sufficient post-fire resprouting of beech saplings after the second fire is maintaining the successional trajectory of recovery (this study). In short, two different traits, seeding from mature trees and resprouting from young individuals, enhance resilience of European beech forests to frequent fires. We conclude that European beech can persist after two consecutive low-to-moderate-intensity fires with short interval. Future studies must confirm our initial findings, and the resilience of beech forests to further alterations of the fire regime, such as larger and more severe fires, remains to be tested. Areas affected by large stand-replacing fires, which limit post-fire beech recruitment from seeds (Maringer et al., 2020), followed by short-interval, moderate-to-high severity fires may experience more persistent shifts in species composition.

Data availability

The data and code underlying this article will be shared on request to the corresponding author.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest

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Table 1 Variables used in the regression models.

Variable	Description	Unit	Sampling	Hypothesis
RESPONSE				
Resprouting	Presence of live resprouts	yes-no	Sapling T1 & T3	
Vigor	Resprouting vigor	index	Sapling T1 & T3	
PREDICTOR				
Treatment type				
Treatment	Type of treatment	control-clipping	Plot T0	Cutting stems stimulates resprouting (+)
Clipping height	Height above ground of clipping	cm	Sapling T0	Cutting stems stimulates resprouting (-)
Topography				
Slope	Steepness	º	Plot T0	Proxy of soil fertility (-)
Aspect	Cosine of degrees from north	cos(ºN)	Plot T0	Proxy of soil moisture (-)
Elevation	Altitude above sea level	m a.s.l.	Plot T0	Proxy of temperature (-)
Burn severity				
Litter cover	Proportion of ground covered by litter	0-1	Plot T0	Proxy of burn severity (+)
Litter depth	Depth of litter layer	cm	Plot T0	Proxy of burn severity (+)
Burn severity - plot	Proportion of saplings with low severity	0-1	Plot T0	Proxy of burn severity (+)
Burn severity - plant	Bark damage	high-low	Sapling T0	Proxy of burn severity (-)
Density				
Canopy openness	Proportion of unobscured sky	0-1	Plot T1	Proxy of light availability (+)
Pre-fire density	Total number of saplings of all species	n	Plot T0	Proxy of competition (-)
Plant size				
Diameter	Root collar diameter	cm	Sapling T0	Proxy of fire resistance (+)
Time				
Time	Years since fire	year		For resprouting (-); for vigor (+)

(+) positive effect; (-) negative effect.

Table 2 Post-fire responses and resprouting vigor in control plots.

Post-fire response	Density (saplings/ha)	Proportion saplings (%)	Mean max height (m)	Mean n resprouts per sapling	Mean vigor index
Beech T1					
Mode 1	1312	6.4	–	–	–
Mode 2	354	1.7	0.17	3.7	0.58
Mode 3	4583	22.4	0.17	2.5	0.47
Mode 4	14208	69.5	–	–	–
Beech T2					
Mode 1	750	3.7	–	–	–
Mode 2	292	1.4	0.37		
Mode 3	6875	33.6	0.29		
Mode 4	12542	61.3	–	–	–
Beech T3					
Mode 1	583	2.8	–	–	–
Mode 2	208	1.0	0.76	2.9	2.06
Mode 3	6271	30.7	0.46	3.0	1.48
Mode 4	13396	65.5	–	–	–
Other spp T1					
Mode 1	562	6.6	–	–	–
Mode 2	1646	19.4	0.45	4.9	2.26
Mode 3	3729	43.9	0.52	4.9	2.63
Mode 4	2562	30.1	–	–	–
Other spp T2					
Mode 1	937	11.0	–	–	–
Mode 2	1146	13.5	1.25		
Mode 3	3167	37.3	1.48		
Mode 4	3250	38.2	–	–	–
Other spp T3					
Mode 1	1187	14.0	–	–	–
Mode 2	812	9.6	1.73		
Mode 3	2729	32.1	1.83		
Mode 4	3771	44.3	–	–	–

Table 3 Resistance and resilience to fire in control plots.

Variable	Beech	Other spp	Total
Pre-fire			
N saplings	982	408	1,390
Density (saplings/ha)	20,458	8,500	28,958
Proportion saplings (%)	70.6	29.4	100
T1			
N surviving saplings	300	285	585
Density (saplings/ha)	6,250	5,938	12,188
Proportion saplings (%)	51.3	48.7	100
N resprouts	608	1,267	1,875
Density (resprouts/ha)	12,667	26,396	39,063
Proportion resprouts (%)	32.4	67.6	100
Resistance (%)	8.1	26.0	13.4
Resilience (%)	22.4	43.9	28.7
Survival (%)	30.5	69.9	42.1
T3			
N surviving saplings	339	227	566
Density (saplings/ha)	7,063	4,729	11,792
Proportion saplings (%)	59.9	40.1	100
N resprouts	926		
Density (resprouts/ha)	19,292		
Resistance (%)	3.8	23.6	9.6
Resilience (%)	30.7	32.1	31.1
Survival (%)	34.5	55.6	40.7

Table 4 Effect sizes of the clipping treatment on post-fire survival.

Variable	Control	Treatment	Mean difference	Cohen's h
Beech				
N saplings	982	969		
T1 survival (%)	30.5 [27.6; 33.3]	46.7 [43.6; 49.8]	16.2 [12.0; 20.5]	0.33 [0.25; 0.42]
T3 survival (%)	34.5 [31.5; 37.5]	42.3 [39.1; 45.2]	7.8 [3.5; 12.1]	0.16 [0.07; 0.25]
Other spp				
N saplings	408	545		
T1 survival (%)	69.9 [65.4; 74.1]	72.3 [68.6; 76.0]	2.4 [-3.4; 8.0]	0.05 [-0.07; 0.18]
T3 survival (%)	55.6 [50.7; 60.5]	42.6 [38.3; 46.8]	-13.1 [-19.6; -6.7]	-0.26 [-0.39; -0.14]

Note: 95% CI are given in brackets.

Table 5 Effect sizes of the clipping treatment on post-fire European beech resprouting vigor.

Variable	Control		Treatment		Mean difference		Cohen's d	
T1								
N saplings	237		453					
Max height (m)	0.17	[0.16; 0.19]	0.14	[0.13; 0.15]	-0.03	[-0.05; -0.01]	-0.27	[-0.42; -0.11]
N resprouts	2.6	[2.3; 2.8]	4.9	[4.5; 5.4]	2.4	[1.9; 2.9]	0.59	[0.43; 0.75]
Vigor index	0.5	[0.4; 0.6]	0.8	[0.7; 0.9]	0.3	[0.2; 0.5]	0.27	[0.11; 0.43]
T3								
N saplings	311		410					
Max height (m)	0.47	[0.45; 0.50]	0.52	[0.50; 0.55]	0.05	[0.01; 0.09]	0.22	[0.07; 0.36]
N resprouts	3.0	[2.8; 3.2]	3.3	[3.0; 3.6]	0.3	[0.0; 0.6]	0.12	[-0.03; 0.27]
Vigor index	1.5	[1.4; 1.7]	1.8	[1.6; 2.0]	0.3	[0.1; 0.6]	0.18	[0.03; 0.33]

Note: 95% CI are given in brackets. The values reported for maximum height, number of resprouts and vigor index correspond to mean values.

Table 6 Mixed models of post-fire European beech resprouting.

Model	Resprouting GAMM		Resprouting T GLMM		Vigor GLMM		Vigor T GLMM	
Variable	Beta	OR [95% CI]	Beta	OR [95% CI]	Beta	OR [95% CI]	Beta	OR [95% CI]
Treatment clipping	**1.22*** **	**3.38 [1.63; 7.03]**	–	–	**0.26** **	**1.29 [1.07; 1.56]**	–	–
Clipping height	–	–	-0.14	0.87 [0.74; 1.03]	–	–	-0.04	0.96 [0.87; 1.06]
Slope	**-0.62*** **	**0.54 [0.37; 0.78]**	**-0.86* **	**0.42 [0.18; 0.99]**	0.05	1.05 [0.96; 1.16]	-0.02	0.98 [0.86; 1.13]
Aspect	0.04	1.05 [0.68; 1.60]	0.28	1.32 [0.44; 4.00]	-0.02	0.98 [0.88; 1.09]	0.06	1.06 [0.87; 1.29]
Elevation	-0.36	0.70 [0.46; 1.06]	0.08	1.09 [0.42; 2.79]	-0.01	0.99 [0.90; 1.10]	0.07	1.07 [0.91; 1.26]
Litter cover	0.07	1.07 [0.76; 1.51]	0.12	1.13 [0.51; 2.50]	0.04	1.04 [0.95; 1.14]	0.06	1.06 [0.91; 1.22]
Litter depth	0.11	1.11 [0.73; 1.70]	-0.12	0.89 [0.28; 2.83]	0.05	1.05 [0.95; 1.17]	0.03	1.03 [0.86; 1.23]
Burn severity - plot	-0.18	0.83 [0.59; 1.18]	0.59	1.80 [0.86; 3.74]	-0.06	0.95 [0.86; 1.04]	0.04	1.05 [0.91; 1.20]
Burn severity - plant low	**1.11*** **	**3.05 [1.98; 4.70]**	**3.02*** **	**20.5 [5.67; 74.3]**	0.14	1.15 [1.00; 1.33]	0.03	1.03 [0.83; 1.28]
Canopy openness	-0.16	0.85 [0.56; 1.29]	-0.32	0.72 [0.30; 1.76]	0.03	1.03 [0.92; 1.15]	0.00	1.00 [0.86; 1.16]
Pre-fire density	-0.29	0.75 [0.47; 1.19]	-0.29	0.75 [0.22; 2.53]	**-0.14* **	**0.87 [0.77; 0.98]**	-0.13	0.88 [0.73; 1.06]
Diameter	**(s)*** **		**1.39*** **	**4.03 [2.36; 6.86]**	**0.36*** **	**1.44 [1.35; 1.54]**	**0.52*** **	**1.68 [1.50; 1.87]**
Time	**0.37*** **	**1.45 [1.26; 1.67]**	**-0.26** **	**0.77 [0.64; 0.93]**	**0.57*** **	**1.77 [1.70; 1.84]**	**0.48*** **	**1.61 [1.53; 1.70]**
Time x clipping	**-0.56*** **	**0.57 [0.46; 0.70]**	–	–	–	–	–	–
R^2								
Marginal	0.19		0.28		0.39		0.41	
Conditional	0.69		0.86		0.70		0.67	

T: clipping treatment.

OR: odds ratio (exponentiated beta coefficients).

(s): smooth term.

Statistically significant predictors are in bold. Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Dashes are given for variables not included in the models.

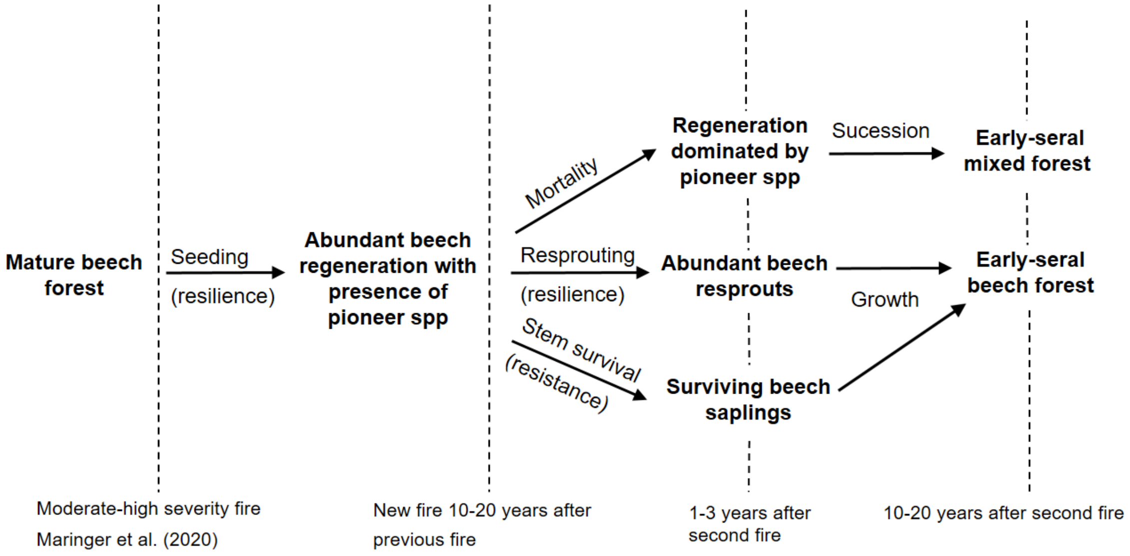

Figure 1 Theoretical trajectories of European beech forests following high frequency fire.

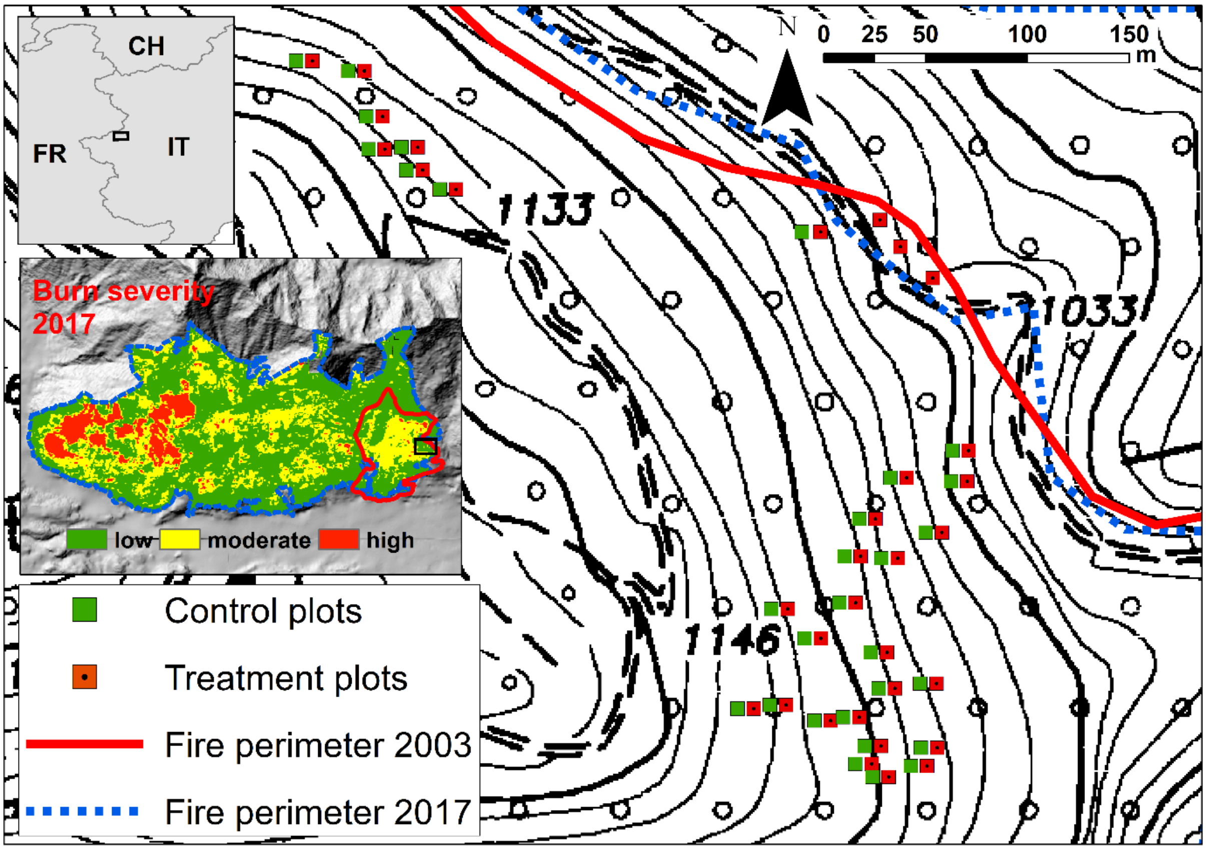

Figure 2 Position of the field plots in the study area.

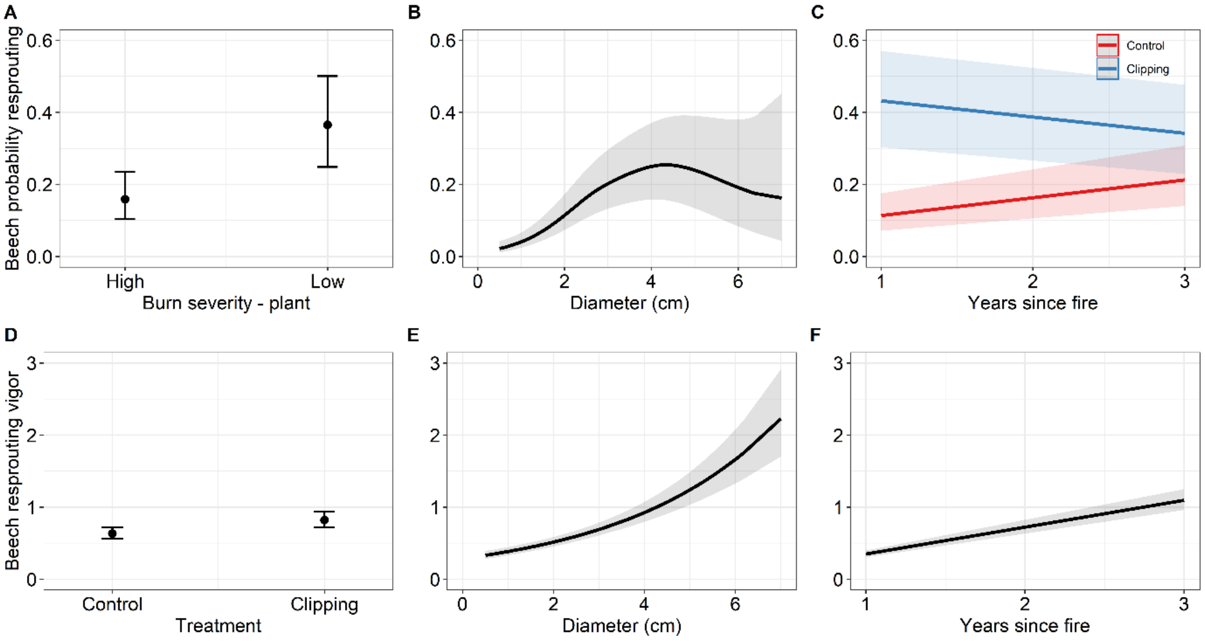

Figure 3 Relationships between response variables and predictors. These marginal effect plots represent model predictions (y-axis) along a single predictor (x-axis) holding constant the rest of predictors (i.e., continuous variables are set to their mean, while factors are set to their reference level). Error bars and shade areas symbolize 95% CI of the predictions.