

Drivers of persistent post-fire recruitment in European beech forests

Janet Maringer^{A*}, Thomas Wohlgemuth^B, Andrew Hacket-Pain^C, Davide Ascoli^D,
Roberta Berretti^D, Marco Conedera^A

^A Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Insubric
Ecosystems, A Ramél 18, CH-6593 Cadenazzo, Switzerland; janet.maringer@wsl.ch;
marco.conedera@wsl.ch

^B Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Disturbance
Ecology, Züricherstrasse 111, CH-8903 Birmensdorf, Switzerland;
thomas.wohlgemuth@wsl.ch

^C Department of Geography and Planning, School of Environmental Science,
University of Liverpool, Liverpool, L69 7ZT, UK;
andrew.hacket-pain@liverpool.ac.uk

^D Department of Agriculture, Forest and Food Sciences, Largo Paolo Braccini 2,
10095 Grugliasco, Italy; d.ascoli@unito.it; roberta.berretti@unito.it

*Corresponding author, phone +41 91 821 52 30, janet.maringer@wsl.ch

This document is the accepted manuscript version of the following article:
Maringer, J., Wohlgemuth, T., Hacket-Pain, A., Ascoli, D., Berretti, R., & Conedera, M.
(2020). Drivers of persistent post-fire recruitment in European beech forests. *Science of
the Total Environment*, 699, 134006 (12 pp.).<https://doi.org/10.1016/j.scitotenv.2019.134006>

This manuscript version is made available under the CC-BY-NC-ND 4.0 license
<http://creativecommons.org/licenses/by-nc-nd/4.0/>

Abstract

Climate change is expected to alter disturbance regimes including fires in European beech (*Fagus sylvatica* L.) forests. Regarding the resilience of beech forests to fire it is questionable whether seeds of this non-serotinous obligate masting seeder find advantageous conditions in a post-fire environment. The probability of recruitment success has been shown to increase when fire coincides with a mast year. However, the fire-induced recruitment window is poorly defined, and it is unclear how other interacting factors influence its duration. We used a space-for-time approach to model the relationships between post-fire beech recruitment, timing of seed mast events, and interacting environmental conditions using a zero-inflated model. Our results show that recruitment peaks 5–12 years after a fire, and continues throughout three decades post-fire. Beech recruitment in the post-fire period is driven by mast intensity interacting with (i) canopy opening as a consequence of progressive post-fire tree mortality and (ii) coverages of competing ground vegetation. Spring-summer moisture showed a weak positive effect on beech recruitment. We conclude that fires increase light availability, which in coincidence with a mast event results in pulses of beech recruitment. The delayed post-fire mortality of beech creates a recruitment window lasting for up to three decades, resulting in a higher-than-expected resilience of beech to individual fire disturbances.

Keywords: *Fagus sylvatica*, mast years, European Alps, burn severity, disturbance regime, forest regeneration

1 Introduction

Climate change is reorganizing disturbance regimes of forest ecosystems (Seidl et al., 2014), sometimes interacting synergistically with changes in land use and forest management (Overpeck et al., 1990; Flannigan et al., 2000). Alterations in the climate-weather-fuel system will influence fire regimes, not only in fire-prone systems but also in forest ecosystems that have not historically experienced fires (Schumacher et al., 2006). In order to understand the resistance and resilience of forests to novel disturbance regimes such as fires in forest communities in which tree species lack obvious fire adaptations, a broader understanding in species-specific fire ecology is needed (Maringer et al., 2016a, Maringer et al., 2016b).

A key factor determining forest resilience to fire is the regeneration strategy, which is dependent on propagule availability and the suitability of the environment for germination and establishing, as well as for sprouting (Grubb, 1977; Gutsell and Johnson, 2007). The interaction of propagule availability and suitable environmental factors determines the recruitment window. Given dispersal constraints, plant species that establish *in situ* after fire disturbance can take advantage of increased resource availability such as light, nutrients, and reduced competition (Bond and van Wilgen, 1996; Davis et al., 2000). In fire-prone regions, where stand-replacing fires are common, vegetation displays fire-adaptive traits for a rapid *in situ* establishment, e.g., sprouting from the root collar and seed release from either soil or aerial seed banks (Keeley, 2012). Such fire-adapted species compete with generalists, i.e., species producing high annual number of seeds in order to colonize open gaps created by stand-replacing fires.

However, in forests dominated by species that lack specific fire-adaptive or generalist traits the resilience of those forests is questionable, especially if fire occurs as novel

75 disturbance. Populations of such species can only persist after fire if either surviving
76 individuals from the burn area, or individuals from surrounding unburnt forests provide
77 enough seeds to establish a new generation (Greene and Johnson, 2000).

78 The situation is further complicated in masting tree species. Masting is characterized
79 by the production of synchronized and highly variable seed crops with distinctive intra-
80 and inter-annual patterns (Allen et al., 2017), a pattern that occurs from the tropics to
81 the boreal zone (Koenig and Knops, 2000). The coincidence of a mast year closely
82 following a fire is a key factor in successful post-fire recruitment, especially if a burn
83 is stand-replacing (Peters et al., 2005; Wright and Zuur, 2014). The duration of a
84 recruitment window might be broadened in less fire-prone ecosystems, where seed trees
85 survive surface fires of low to medium severity.

86 Such low to medium severity fires have been observed in European beech (*Fagus*
87 *sylvatica* L.) forests. Beech lacks typical fire-adaptive traits; its thin bark cannot protect
88 vital tissue from lethal heat during the fire and its sprouting capacity declines with tree
89 age (Wagner et al., 2010). Depending on the proportion of injured tissue and the
90 likelihood of subsequent fungi infestation, tree mortality may be delayed by up to 20
91 years post-fire (Maringer et al., 2016a). This ensures *in situ* production of the aerial
92 seed bank after the fire event (Maringer et al., 2016b), and previous research showed
93 that beech regeneration after fire is strongly promoted by a subsequent mast event
94 (Ascoli et al., 2015). However, beech masts irregularly, with a mast event on average
95 every 3 – 8 years, although mast events may fail to occur for over a decade (Packham
96 et al., 2012; Nussbaumer et al., 2016; Ascoli et al., 2017a). As a consequence, a short
97 temporal recruitment window and the absence of mast events may delay post-fire beech
98 regeneration, or even result to a failure of regeneration. In contrast, a longer recruitment
99 window would suggest a higher potential long-term resilience of these forests to an

100 increasing frequency of fire. Therefore, we hypothesize that beech may benefit from
101 the combined effect of delayed mortality and post-fire changes in environmental
102 conditions (e.g., light conditions, ground vegetation, bare soil), which create a long-
103 lasting recruitment window. With the help of a retrospective space-for-time approach
104 we assessed post-fire stand and environmental conditions over four decades in order to
105 identify the main drivers for beech recruitment. In this context, we define recruitment
106 window as the period by which seeds germinate, individuals establish and are still
107 contributing to the existing population at time of the field survey.

108

2 Material and methods

2.1 Study region

Forest fires occur occasionally in Mediterranean beech forests (Herranz et al., 1996; van Gils et al., 2010), in the European Alps, and in the Jura Mountains (Maringer et al., 2016b; Stubenböck, 2016). In our study we selected 38 beech forest sites that burnt once since 1970 across the European Alps in the Swiss Cantons Glarus, Solothurn, and Ticino as well as in the contiguous Italian region of Piedmont (see Fig. 1; Supplementary material A Table 1).

From a pyrologic perspective, both Piedmont and Ticino belong to the Southern Alpine fire regime that is characterized by high fire frequencies in dry spring months (March–April), with fires that in rare cases extend over more than 1000 ha. In contrast, the Cantons Glarus and Solothurn belong to the Northern Alps where fire frequencies are low and burn areas rarely exceed 1 ha (Conedera et al., 2018). The majority of these fires are anthropogenic-induced (Conedera, 2009). Usually those fires start from the wildland-urban interface and extend into adjacent forests as rapidly spreading surface fires (Conedera et al., 2015) consuming the loose debris (litter, dead branches) and the understory vegetation (tree seedlings, herbs). Thereby the fire front and the related fire impact on vegetation are spatially heterogenous, creating a mosaic of different burnt and unburnt patches (see Supplementary material B Fig. 1).

The climate in the study region is strongly influenced by the Alps. Climate in the North of the Alps has an Atlantic character, with a mean annual temperature of 9.7 °C (climate station Attiwil 47.26N / 7.79 E; Glarus 47.03N / 9.07 E, see Fig. 1) and annual precipitation sum of 934 mm a⁻¹ at Attiwil and 1421 mm a⁻¹ at Glarus in the Northern Pre-Alps. Towards the South, mean annual temperatures increase by 1.0–3.5 °C (Meteo Swiss, 2019; Agenzia Regionale per la protezione Amientale, 2019). Annual

precipitation along the Southern foothills of the Alps amounts to approximately 1800 mm in Ticino and decreases in the southeastern part of the Alps (970 mm a⁻¹ in Valdieri) (Agenzia Regionale per la protezione Ambientale, 2019; Meteo Swiss, 2019). Within the wide climatic amplitude of beech communities (Willner et al., 2017), beech dominates the forests from 150 m to 1500 m a.s.l. in the cooler Northern Alps (Englisch, 2006) and occupies the intermediate elevation belt between 900 and 1500 m a.s.l. in the warmer Southern Alps (Ceschi, 2006). Beech forests in the Northern Alps grow mainly on calcareous bedrock, while they are found on crystalline basement in the Southern Alps, except in the southernmost parts of Canton Ticino and in parts of the Piedmont. Thus, the resulting soils are calcic cambisol on limestone and crypto-humus-podzol with thick humus layers on silicate rock material (Blaser et al., 2005).

2.2 Data collection and preparation

2.2.1 Study design and assessed variables

Fires burnt after 1969 were selected from the forest fire data base of Switzerland (Pezzatti et al., 2010) and the State Forestry Crops of Italy (Corpo Forestale dello Stato/Ministero delle Politiche Agrocole, Alimentari e Forestali, 2005). In total, 104 potential burnt stands were identified and inspected in the summer 2011 and 2017 to select sites that satisfied all of the following four criteria: (i) burnt area larger than 0.5 ha in beech-dominated forests (beech stem density > 90% of total), (ii) with only one single fire record during the last 100 years, (iii) no evidence of pre-fire wood pasture (indicated by large solitaire beech trees with low limbs), and (iv) no evidence of post-fire management and silvicultural measures in both the burnt and adjacent unburnt stands. Based on these criteria, we selected 37 sites (Supplementary material A). At each site, we used 200 m² plots to assess recruitment in burnt areas and, where possible, adjacent unburnt areas in the same forest. Sampling took place during summer 2012/13 and

2017/18, following the protocol described in Maringer et al. (2016a). In total, we assessed data in 137 plots in burnt areas (1–14 per stand, mean = 3.7) and 25 in the adjacent unburnt forests (0–2 per stand, mean = 0.7), using the latter as references. For each circular plot, we assessed factors that might influence beech recruitment. We measured topographical parameters (aspect, slope, elevation, micro-topography [plane, convex, concave]; see Table 1 for abbreviation and explanation), competing ground vegetation (veg.comp; percentage of *Pteridium aquilinum*, *Cytisus scoparius*, *Molinia arundinacea*) that potentially hinder successful germination and establishment of beech seeds (Bílek et al., 2009), percentage of bare soil (bare soil) and percentage of soil covered by litter (litter) as a potential barrier for seedlings' roots reaching the mineral soil layer before the litter dries out in spring and summer (Harmer, 1995). The volume of coarse woody debris (CWD) was estimated following the method of Brown (1974) and van Wagner (1982) in order to consider its potential role influencing soil moisture and the shading effect on seedlings (Harmon et al., 2004; Bílek et al., 2009).

Further, belowground competition for water and nutrients (Bílek et al., 2009) was estimated by calculating the basal area (BA) of trees surviving the fire, which were identified by visible fire scars and DBH larger than the means. The aggregated height of already-established post-fire beech (aggHeightBeech) and pioneer tree (aggHeightPioneer) regeneration (with a height <1.3 m) was calculated as a measure of the competing stand for the newly incoming seedlings (Fei et al., 2006).

Since light is one of the main factors influencing establishment of beech recruitments (Ammer et al., 2002), we estimated canopy cover (in %) as a surrogate for light transmission for the lower (1.3–5 m, layer.I) and upper (> 5 m, layer.II) stand layers, separately, as well as for the sum of both (i.e., layer.I + layer.II = layer.III).

2.2.2 *Processing of tree ring cores*

A total of 20 beech recruits were sampled within each 200 m² plot, paying attention to include the variety of the regeneration structure (e.g. including the smallest and the tallest, which are assumed to roughly represent the youngest and the oldest, respectively). In cases where fewer than 20 beech individuals were present in the plot, all were sampled.

The year of germination for the youngest recruitments ($\text{age} \leq 4$ years) was determined in the field counting their annual growth units as defined by terminal bud scars (Heuret et al., 2003). Older individuals were cut or cored (5 mm coring devices) close to the root collar. Cores were glued on supports in order to avoid deformation during the drying process, and both tree discs and cores were dried for 48 hours. Samples were abraded with sandpaper (100 grit), and finally prepared with chalk, liquid color, and razor blades to enhance the contrast of the anatomical features. Annual tree rings were then counted under a binocular following reference pictures of Schweingruber (1987).

2.2.3 *Assignment of climate variables*

Sufficient soil moisture in spring and early summer promotes beech seed germination and early recruitment (Harmer, 1995; Pukacka and Ratajczak, 2014). Therefore, we calculated the annual cumulative Standardized Precipitation-Evapotranspiration Index (SPEI) for the period February to August as a proxy for water availability (Vicente-Serrano et al., 2012). When calculating the SPEI we considered the water balance as the difference between precipitation and potential evapotranspiration (PET). PET was calculated using the Thornthwaite equation in the R-package SPEI (Beguería and Vicente-Serrano, 2017).

2.2.4 *Assigning beech mast intensities*

In order to determine the influence of annual seed production (masting) on the

abundance of beech recruitments, we extracted mast intensities for each studied region (Glarus, Solothurn, Ticino, Piedmont) separately from the MASTREE database (Ascoli et al., 2017a). In MASTREE the mast intensity is recorded on an ordinal scale ranging from no seed production (class 1) to very high production (class 5). When MASTREE contained multiple entries from different sources for one region in one year, we calculated the mean mast intensities. Further, we shifted the numbers to a scale from 0 (no mast) to 4, and defined minor (1), intermediate (2) and full (3–4) mast years. Since most beech seeds germinate only in the spring after seed fall, the mast intensity variable referred to the previous year.

2.2.5 *Reconstructing time-dependent environmental variables*

We took advantage of a space-for-time approach, in which the time between the fire event and the field assessment differed between sites. On this basis we were able to reconstruct the temporal trends of environmental conditions in the post-fire period for each plot, which was classified as low-, moderate or high severity burns based on the proportion of the basal area lost in the post-fire period (for definition and methodological details see Maringer et al. (2016b); examples of low-, moderate- and high severity burns are given in supplementary material B), assuming that plots in the nearby unburnt forests represent the equivalent development of the forest in the absence of fire. After plotting the variable assessed in each plot against the years post-fire separately for each burn severity class (i.e., low, medium, high severity), we estimated the overall temporal trend using loess-smoothing curves. We assessed the annual values for each time-dependent variable from the year of fire to the field observation separately for each plot by following the shape of the overall loess-smoother (see Supplementary material C fig. 1– fig. 3).

Considering that early and mid-term mortality of regeneration is high (Collet and Le Moguedec, 2007), we used ‘observation interval’ (ObsvInterv) – the number of years from the fire until the field assessment, as a proxy for recruitment mortality.

2.3 Data analysis

2.3.1 Data pre-processing

To describe temporal trends in the age structures of the post-fire recruits in the burnt and unburnt forests we aggregated the years post-fire into five epoch classes: ‘ ≤ 9 years’, ‘10-15 years’, ‘16-21 years’, ‘21-32 years’, ‘ > 32 years’ (see Maringer et al., 2016b). Variation in age distribution within fire severity classes (low-, moderate- and high severity) and the unburnt forests was analyzed using a Kolmogorov-Smirnov test ($p < 0.05$).

Prior to the model construction, data exploration followed the guidelines of (Zuur et al., 2010), using the Pearson’s correlation coefficient (cut level $r^2 > 0.49$) and the variance inflation factor (VIF) to test collinearity among variables. Bare soil was highly inversely correlated with litter ($VIF > 3$) and was therefore excluded from further analysis. For the purpose of model comparison, all continuous variables were z-score transformed. Statistical analyses were performed in R Version 3.3.3 (R Development Core Team, 2019).

2.3.2 Model construction

Since our analysis is based on the number of beech recruits established each year, we counted more zeros (69%) than expected for the Poisson distribution leading to overdispersion (Zuur et al., 2009). Therefore, we used a zero-inflated (ZI) count model, which combines a count response variable (Poisson or Negative binomial distributed) and a distribution with point mass of one at zero. The count part is known as the

conditional model and is similar to a generalized linear model. The zero part describes the probability of observing an extra zero (i.e., structural zero) that is not generated by the conditional model (Lambert, 1992).

Due to the pseudo-replicated observations at each plot and fire site that causes dependency to the dataset, we additionally tested fire site and plots as separated and nested random structures. Finally, we included the total number of beech recruits sampled per plot as an offset to allow the use of a Poisson or Negative binomial response (Bolker, 2019).

The ZI model was implemented in the R package glmmTMB (Magnusson et al., 2019) that allows the inclusion of random-effects. As a first step we developed several null models (without explanatory variables) to test for the best random structure and distribution for the count process. Models were compared based on the Akaiques Information Criterion (AIC) (Burnham and Anderson, 2004).

For variable selection, we first focused on the conditional model part and calculated models using only one predictor and the best random structure (single-models). In a second step, models were calculated that combined significant variables out of the single-model step, verifying the AIC improvement and likelihood-ratio chi-squared test. During the process of variable selection, low variation was found between the estimated values of a full mast (category 3) and extraordinary high seed production (category 4). Therefore, we merged both to one category in order to reduce the degrees of freedom. After finding the best conditional model, all non-significant variables from the single-model step were added back to confirm that they are not statistically significant. In a last step interaction terms were added and kept in the models in case of significance. The same procedure was then applied to the zero-inflation component of the model.

We assessed the model's goodness-of fit by plotting (i) a quantile-quantile plot of the residuals, (ii) the residuals versus the predicted variable, and (iii) the residuals against each explanatory variable. Normality in the distribution of the residuals was tested with a Kolmogorow- Smirnow -test ($p < 0.05$) as provided by the R-package DHARMA (Hartig, 2019). The R^2 was estimated using the package sjstats (Lüdtke, 2019).

3 Results

3.1 Frequency of mast years

Mast years occurred in all the study regions in 1992, 2009 and 2011 (Fig. 2). Additionally, mast years were observed in 1976, 1986, 1990 and 2013 in the Southern Alps. Regionally limited mast years were detected in 1995 (Ticino, Glarus, Solothurn), 1999 (Solothurn, Glarus, Piedmont), and 2004 (Solothurn, Ticino).

3.2 Germination frequency and age structure

In total, we assessed the year of germination for 2322 beech seedlings – 83.3% belonging to the burnt forests, 16.7% to the unburnt forests. Most of the recruits established within the first 15 years post-fire in moderate (63.5% of all recruits) and high (85%) severity burns, while germination occurred irregularly in low severity burns and the unburnt forests throughout the observation period (Fig. 3). Most recruits (73.4%) in the unburnt forests established after intermediate or full mast years one year prior to seed germination. In rare cases, as for the peak 40 years post-fire in the unburnt forests, a high number of germination took place two years after a full mast event. In contrast, in the burnt forests ca. 50% of the sampled recruits germinated in the year following an intermediate or full mast year (55%, 58% and 50% in low, moderate and high burn severity sites, respectively).

In the unburnt forests, the mean age of recruits was 2.2 years and did not vary with time since the adjacent forests burnt (Fig. 4). The age structure did not significantly differ in the unburnt forest, except the period 21 – 32 years. This contrasts to the burnt forests, where the age of recruits steadily increased with time since fire. Within the first 9 years post-fire, the age difference between the burnt and unburnt forests was approximately 1 year and differed significantly at the 0.05%-level (Fig. 4). The age differences steadily increased, and were always significantly different between the burnt and unburnt forests throughout the entire observation period. The recruits in the burnt forests were on average 2.8 – 6.3 years, 3.2 – 6 years, and 6.2 – 11.7 years older than in the unburnt forests, 10 – 15 years, 16 – 20 years and 21 – 32 years post-fire, respectively. The highest age differences were observed 32 year after fire, recruits in the burnt forest were more than 10 years older than equivalent recruits in unburnt forests. At the same time, as the mean age increased the age variance in the burnt forests increased steadily showing recruit's ages ranging from 1 year to 42 years after 32 years post-fire.

3.3 Factors influencing beech recruitments

The most parsimonious model consisted of a negative binomial zero-inflated generalized linear mixed-effect model (NBZI-GLMM) relating the number of the recruits to years interval (ObservInterv), Standardized Precipitation-Evapotranspiration Index (SPEI), mast intensity (mast), tree cover above 1.3 m (layer.III), cover of ground vegetation (veg.comp), as well as interactions of mast intensity with layer.III, and mast intensity with veg.comp (Table 2). Fire site was considered as a random structure in the conditional part, but not in the zero-inflation part. In the latter, the probability to observe an extra zero was only related to the increasing tree cover (layer.III, i.e., higher absence of recruits in darker stands).

As the estimated z-values indicate, the influence of full mast on recruitment frequency was nearly double with respect to minor and intermediate mast, making it the most important explanatory variable (Table 2). In contrast, veg.comp was negatively related to recruitment abundance (i.e. fewer recruits under denser cover of ground vegetation). Further, SPEI was significantly positively related to beech recruitment (i.e. recruitment was lower in drier years), while the years of observation significantly negatively affected the abundance of beech recruits (i.e., increasing mortality with years post-fire). Moreover, the effect of intermediate mast years on beech recruitment was negative in stands with lower light availability (mast intensity interacting with layer.III). A positive interaction was detected in the conditional model between mast intensity and veg.comp. Here, the number of recruitments increased in a full mast year under denser vegetation cover. All fixed variables included in the conditional part of the model explained 31% of the variance in beech seed germination and establishment.

3.4 Longevity of the fire-induced recruitment window for beech

The model results reveal that the recruitment window is mainly influenced by mast intensity interacting with the overall tree cover (layer.III) and competing ground vegetation (veg.comp). Therefore, we plotted the presence and absence of recruitments against mast intensity in relation to tree cover (Fig. 5 A) and interfering ground vegetation (Fig. 5 B). Figure 5A shows that with 95% confidence beech establish over all mast intensities when canopy cover range between 38% and 70%. Contrastingly, beech fails to establish with 95% confidence under tree cover ranging from 55% to 73% regardless of the mast intensity.

In figure 5B the cover of ground vegetation replaces tree cover on the y-axis. It is notable that 50% (inter quantile range) of beech recruits establish after a full mast year even in the presence of interfering ground vegetation with up to 50% (Fig. 5 B). The

success diminishes with decreasing mast intensity to 37%, 36% and 19% in case of intermediate-, minor-, and no-mast year, respectively.

By accounting for years elapsed post-fire (Fig. 5 C), the model revealed that beech recruits started to establish in the growing season following a fire and peaked 5 to 12 years post-fire. Noticeable is the longevity of the establishment window, with regular recruitment associated with mast years throughout the first 32 years post-fire, after which recruitment became rare.

4 Discussion

4.1 Main drivers of post-fire beech recruitment

The delayed post-fire mortality of beech after mixed severity fires (Maringer et al., 2016a) ensures *in situ* seed production and allows beech to take advantage of the favorable recruitment conditions in the post-fire environment. Surprisingly, the model did not retain basal area of surviving beeches, indicating that a limited number of trees can provide sufficient seeds in mast years to guarantee regeneration and leaving enough light for establishment at the same time. Seed production by surviving trees may be promoted by changes in the post-fire environment. For example, as a general rule fire increases nutrient availability in the soil (DeBano, 1990), and this combined with related increases in carbohydrate production may stimulate flower initiation (Allen et al., 2017) and seed maturation (e.g., Hoch et al., 2013). For beech specifically, individuals remaining vital after a burn of low to medium severity (Maringer et al., 2016a) may be able to extend the lateral crown after gap creation, increasing photosynthesis and subsequently seed production (Emborg et al., 2000).

Minor-, intermediate- and particularly full mast years are highly significantly and positively related to the post-fire recruitment success (Table 2). The dominant and

significant effect of regional masting events is in line with the general trend in beech masting controlled by large-scale weather patterns (Ascoli et al., 2017b). Therefore, according to our results there is no clear evidence of specific, fire-induced stress masting in burnt beech stands. Rather, fire stimulates an increased seed production in fire-injured beech stands during large-scale masting events (Ascoli et al., 2015). This extends the short-term post-fire effects observed by Ascoli et al. (2015) over multiple decades.

Successful beech recruitment after low seed production was observed in our study site (Table 2), consistent with the results reported by Övergaard (2009). However, the likelihood of successful recruitment clearly increased with mast intensity. This could be related to the higher number of seeds produced during a full mast year, which increases the probability that some seeds survive predation (Olesen and Madsen, 2008; Övergaard, 2009; Schulze et al., 2010; Zwolak et al., 2016), and resulting recruits have a higher survival probability (Madsen and Hahn, 2008). During years of high seed production (full mast) the seed quantity is so high that despite of interfering ground vegetation (veg.comp; Koop and Hilgen, 1987; den Ouden, 2000) and shading tree cover (layer.III) some beech recruitments are able to establish (Table 2). In contrast, in cases of lower seed availability (intermediate mast), the shading trees (layer.III) and competing vegetation (veg.comp) tend to have an inhibitory effects on seed establishment as already reported for shelterwood cutting (Övergaard, 2009; Silva et al., 2012).

Finally, the overall tree cover (layer.III) is the only variable retained in the zero-inflation model, meaning that the probability of observing a zero (i.e., no recruitment) increases under denser shelter (Ammer et al., 2002; Wagner et al., 2010). Such shading effect can result either from complete canopy closure of the fire-surviving trees or from

earlier established beech regeneration that have grown to dense saplings- to pole stages. As a result, low light availability and strong intra-specific competition concur in preventing new boosts of beech regeneration to establish.

The model indicates a slight positive influence of spring and summer moisture (SPEI see Table 2) on the overall beech recruitment, which can be related to the required soil moisture for beech seed germination and establishment (Harmer, 1995; Madsen and Larsen, 1997; Bílek et al., 2009; Övergaard, 2009). The effects of dry conditions might be more relevant on limestone, where the water storage capacity is generally lower than on silicate basement. However, our model did not detect any differences in the establishing frequency between limestone and silicate bedrock.

Regeneration mortality, indicated by the proxy ‘observation interval’, is high since mortality risk remains high until an individual reaches the canopy layer (Holzwarth et al., 2013). After seed germination, seedlings may suffer from browsing pressure (Olesen and Madsen, 2008) and harsh environmental conditions (Harmer, 1995; Diettmair et al., 2003). When they reach heights where browsing pressure is low, the self-thinning phase begins until they manage to become dominant in the crown layer (Collet and Le Moguedec, 2007).

4.2 Prolonged post-fire recruitment window

The positive effects of natural and anthropogenic-induced disturbances on suitable environmental conditions for beech seed germination and establishment are broadly documented in the literature (e.g., Agestam et al., 2003; Nagel and Svoboda, 2008; Wagner et al., 2010; Maringer et al., 2016b; Orman et al., 2018). Similarly to other non-serotinous species, such as *Picea glauca* and *P. engelmannii* (Michaletz et al., 2012; Pouden et al., 2014), we found that for beech the disturbance-induced recruitment window is better utilized in coincidence with mast years (Olesen and Madsen, 2008;

Ascoli et al., 2015). The present study extends existing knowledge by demonstrating that beech recruitment in burnt forests mainly originated from several regeneration pulses and created an uneven-aged structure within the first 40 years post-fire. This is dependent on the delayed mortality of fire-injured beeches, induced by the heterogeneous fire behavior in mountain beech forests (Maringer et al., 2016a, and see examples in Supplementary material B). This ensures a persistent seed input over several years to decades (Övergaard, 2009). In combination with intermediate light conditions (canopy covers of 38% to 70%, see Fig. 5) staggered beech regeneration is promoted (Harmer, 1995; Wagner et al., 2010).

In contrast to the unburnt forests, where the life span of beech hardly exceeded 2.2 years, in burnt forests the life expectancy and age differentiation of recruits increased with time since fire (see Fig. 4), confirming the longevity of the recruitment window. In this respect, fire created a recruitment-friendly environment similar to traditional silvicultural treatments (Övergaard et al., 2009).

4.3 Practical consequences and implications for beech forests in the future

Our study indicates that masting-related seed inputs along with the availability of light are of paramount importance for post-fire beech regeneration. Depending on the silvicultural objectives, forest managers should (i) leave fire-injured surviving trees as seed source as long as possible on the burn site, (ii) pay attention to upcoming mast years, which are triggered by large climate weather conditions (Ascoli et al., 2017b), and (iii) assure enough light conditions in the post-masting season.

Further, our study indicates that beech forests affected by fire appear to be rather resilient under present climatic conditions and fire regimes. However, there are some important caveats that determine the resilience of beech forests affected by fire under future climate:

- 1) Beech regeneration depends on very local seed sources (Wagner et al., 2010; Maringer et al., 2016b) which are not guaranteed after stand-replacing fires. If fire regimes in beech forests shift to higher-severity or more frequent fires, immediate tree mortality particularly in immature stands may result in shifts in forest composition as a result of failed beech regeneration.
- 2) The rapid die-back of beech trees after severe fires (Maringer et al., 2016a) rapidly opens the tree canopy, providing enough light to promote competing ground vegetation, which can delay beech regeneration for several decades (Koop and Hilgen, 1987).
- 3) Based on our results, post-fire recruitment success is reduced in years with dry springs and summers, which might reduce the regeneration capacity post-fire under climate change. However, our results show that this effect is relatively weak, and the long regeneration window (up to three decades post-fire) provides multiple opportunities for sufficiently moist years to coincide with masting to facilitate regeneration before the recruitment window closes.
- 4) The range in mast year frequency (3 – 8 years; Ascoli et al., 2017a) appears to be sufficient to ensure successful regeneration post-fire. However, future changes in the frequency of full mast years are still uncertain (Monks et al., 2016) and would have a strong influence on recruitment (mast is the most important term in the model). A reduction in mast frequency in these forests could reduce resilience to novel fire disturbance.

4.4 Limits of the study

The delayed mortality of fire-injured beeches accompanied with rarely occurring mast years (3 – 8 years; Ascoli et al., 2017a) makes it difficult to study the longevity of post-fire recruitment windows and the influencing factors. Therefore, we chose the space-

477 for-time approach that allowed us to extend the observation period over more than four
478 decades. We were able to study the germination success and recruitment patterns of
479 2,322 post-fire beech recruits ranging from 1 to 42 years in age.

480 Due to the retrospective approach, the time-dependent environmental variables have
481 been reconstructed based on the overall temporal trend in the related severity class.
482 Although previous studies demonstrated that such reconstructions are quite robust and
483 reliable (Maringer et al., 2016b), there is still a discrepancy with respect to the data
484 accuracy in comparison to repeated field campaigns.

485 Well known short-term effects of fire such as the exposure of the mineral soil layer and
486 the increased mineralization and nutrient release due to higher soil temperatures in the
487 stand openings (Röhrig et al., 1978; Harmer 1995; Maringer et al., 2016b) are not
488 explicitly measured in our study. Further effects such as the lowering of the pathogenic
489 inoculum of fungi attacking beech seeds and seedlings, and toxic agents such as the
490 extracellular self-DNA that usually accumulates in the litters and upper soil layers of
491 mature beech stands (Szewczyk and Szwagrzyk, 2010; Barna, 2011; Mazzoleni et al.,
492 2015) were also unmeasured. This is due on the long-term perspective (four decades of
493 our space for time approach on one hand and to the lack of specific parameters of
494 proxies to characterize these effects in our protocol).

495 Finally, determining the year of germination of suppressed, slow growing or browsed
496 beech saplings by counting the annual rings was difficult due to irregular, very narrow
497 rings, and the possibility of missing tree rings. The very short chronologies preclude
498 cross-dating. Hence, dating precision of such specimens may result in ± 1 year error,
499 which may reduce the explanatory power ($R^2 = 0.31$) of the model.

5 Conclusion

In this study we used a retrospective space-for-time approach to identify important drivers and duration time of the post-fire recruitment window in beech stands. Our results clearly show that after surface fires of mixed severities, beech recruitment results from multiple regeneration pulses. These pulses are associated with full mast years of beech under suitable light conditions at the forest floor, but are independent of time since fire (at least over three decades). In this context, we conclude that European beech belongs to the class of non-serotinous masting seeders that ensure an *in situ* aerial seed bank after fire, by periodically producing sufficient seed crops in mast years post-fire until damaged trees eventually die.

Our results indicate that beech forests in central Europe are currently resilient to novel fire disturbance, as a consequence of the prolonged post-fire recruitment window. However, post-fire beech resilience may decline under future climate if dry or drought periods increase, fires become more severe, competitive pressure by ground vegetation and/ or invading pioneer tree species increases, or the frequency of mast years decreases. Higher frequency of large-scale stand replacing fires in particular may significantly reduce beech seed input via barochory or zoochory, and a subsequent shift towards other forest species, including invading exotic pioneer trees.

518 **Acknowledgements**

519 This study was partially supported by the Swiss Federal Office for the Environment
520 (FOEN grand number 00.0137.PZ / L424-1645). Fieldwork and laboratory assistance
521 were carried out with the support of Sven Hofman, Franco Fibbioli, Luca Jelmini
522 from the Swiss Federal Institute for Forest, Snow and Landscape Research, James
523 Winder from St Catherine's College, Oxford (UK) and Matteo Garbarino from the
524 University of Torino. Further, we would like to thanks the anonymous reviewers for
525 their helpful thought-provoking impulses, suggestions and comments.

6 Reference list

- Agenzia Regionale per la protezione Amientale, 2019. Climate data Piedmont (Italy). Arpa Piemonte. <http://www.arpa.piemonte.it/reporting/core-set-of-indicators/climate-change/temperature/> (accessed 3/17/2019).
- Agestam, E., Ekö, P.-M., Nilsson, U., Welanders, N. T., 2003. The effects of shelterwood density and site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. *Forest Ecology and Management*. 176, 61–73. DOI: 10.1016/S0378-1127(02)00277-3.
- Allen, R. B., Millard, P., Richardson, S. J., 2017. A resource centric view of climate and mast seeding in trees, in: Cánovas, F.M., Matyssek, R., Lüttge, U. (Eds.), *Progress in Botany*. Springer, Switzerland, pp. 233–268.
- Ammer, C., Mosandl, R., Kateb, H. El., 2002. Direct seeding of beech (*Fagus sylvatica* L.) in Norway spruce (*Picea abies* [L.] Karst.) stands—effects of canopy density and fine root biomass on seed germination. *Forest Ecology and Management*. 159, 59–72. DOI: 10.1016/S0378-1127(01)00710-1.
- Ascoli, D., Vacchiano, G., Maringer, J., Bovio, G., Conedera, M., 2015. The synchronicity of masting and intermediate severity fire effects favors beech recruitment. *Forest Ecology and Management*. 353, 126–135. DOI: 10.1016/j.foreco.2015.05.031.
- Ascoli, D., Maringer, J., Hacket-Pain, A., Conedera, M., Drobyshev, I., Motta, R. et al., 2017a. Two centuries of masting data for European beech and Norway spruce across the European continent. *Ecology*. 98, 1473. DOI: 10.1002/ecy.1785.
- Ascoli, D., Vacciano, G., Turco, M., Conedera, M., Drobyshev, I., Maringer, J., Motta, R., Hacket-Pain, A., 2017b. Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nature Communications*. 8, 2205. DOI: 10.1038/s41467-017-02348-9.

551 Barna, M. 2011. Natural regeneration of *Fagus sylvatica* L.: A review. In
 552 Austrian J For Sci. 72, 71–91.

553 Beguería, S., Vicente-Serrano, Sergio M., 2019. SPEI. Version 1.7: CRAN
 554 Development Team.

555 Bílek, L., Remeš, J., Zahradník, D., 2009. Natural regeneration of senescent
 556 even-aged beech (*Fagus sylvatica* L.) stands under the conditions of Central Bohemia.
 557 Journal of Forest Science. 55, 144–145. DOI: 10.17221/823-JFS.

558 Blaser, P., Zimmermann, S., Luster, J., Walthert, L., Lüscher, P. (Eds.) (2005):
 559 Waldböden der Schweiz: Regionen Alpen und Alpensüdseite. Bern: Haupt-Verlag.

560 Bolker, B., 2019. Getting started with the glmmTMB package. Edited by
 561 CRAN R Development Team. Available online at [https://cran.r-](https://cran.r-project.org/web/packages/glmmTMB/vignettes/glmmTMB.pdf)
 562 [project.org/web/packages/glmmTMB/vignettes/glmmTMB.pdf](https://cran.r-project.org/web/packages/glmmTMB/vignettes/glmmTMB.pdf), checked on
 563 3/17/2019.

564 Bond, W. J., van Wilgen, B. W., 1996. Fire and plants. Springer, Netherlands.

565 Brown, J., 1974. Handbook of inventorying downed woody material. Edited
 566 by USDA forest Service - Rocky Mountain Research Station. Missoula.

567 Burnham, K. P., Anderson, D. R., 2004. Multimodel inference. Sociol Method
 568 Res, 33, 261–304. DOI: 10.1177/0049124104268644.

569 Ceschi, I., 2006. Il bosco nel Canton Ticino. Locarno: Armando Dadó Editore.

570 Collet, C., Le Moguedec, G., 2007. Individual seedling mortality as a function
 571 of size, growth and competition in naturally regenerated beech seedlings. Forestry. 80,
 572 359–370. DOI: 10.1093/forestry/cpm016.

573 Conedera, M., 2009. Implementing fire history and fire ecology in fire risk
 574 assessment: the study case of Canton Ticino (southern Switzerland). Doctoral

575 dissertation. Department of Civil Engineering, Geo and Environmental Science,
576 University of Karlsruhe.

577 Conedera, M., Tonini, M., Oleggini, L., Orozco, C.V., Leuenberger, M.,
578 Pezzatti, G., 2015. Geospatial approach for defining the Wildland-Urban Interface in
579 the Alpine environment. *Computers, Environment and Urban Systems*. 52, 10-20.

580 Conedera, M., Krebs, P., Valse, E., Cocca, G., Schunk, C., Menzel, A. et al.,
581 2018. Characterizing Alpine pyrogeography from fire statistics. *Appl Geogr*. 98, 87–
582 99. DOI: 10.1016/j.apgeog.2018.07.011.

583 Corpo Forestale dello Stato/ Ministero delle Politiche Agricole, Alimentari e
584 Forestali, 2005. Ufficio Territoriale per al Biodiversità di Verona Centro Nazionale
585 Biodiversità Forestale di Peri. Techn. rep. Corpo Forestale dello Stato - Ispettorato
586 generale.

587 Davis, M. A., Grime, J. P., Thompson, K., 2000. Fluctuating resources in plant
588 communities: a general theory of invasibility. *J Ecol*. 88, 528–534. DOI:
589 10.1046/j.1365-2745.2000.00473.x.

590 DeBano, L. F. (Ed.), 1990. The effect of fire on soil properties. With
591 assistance of Alan E. Harvey, Leon F. Neuenschwander. *Proceedings-management*
592 *and productivity of western-montane forest soils*. Forest Service, Intermountain
593 Research Station (Odgen), 1990 April 10-12. United States Department of Agriculture
594 - U.S. Forest Service.

595 Diettmann, C., Zech, W., Elling, W., 2003. Growth variation in common beech
596 (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe
597 - a dendrochronological study. *Forest Ecol Manag*. 173, 63-78.

598 Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000. The structural
 599 dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark.
 600 Forest Ecol Manag. 126, 173–189. DOI: 10.1016/S0378-1127(99)00094-8.
 601 Englisch, M., 2006. European beech (*Fagus sylvatica*) - Portrait of a tree
 602 species. BFW- Praxisinformation. 12, 3–4.
 603 Fei, S., Gould, P. J., Steiner, K.C., Finley, J.C., 2006. Aggregate height—A
 604 composite measure of stand density for tree seedling populations. Forest Ecol Manag.
 605 223, 336–341. DOI: 10.1016/j.foreco.2005.11.014.
 606 Flannigan, M.D., Stocks, B.J., Wotton, B.M., 2000. Climate change and forest
 607 fires. Sci Total Environ. 262, 221–229. DOI: 10.1016/S0048-9697(00)00524-6.
 608 Greene, D.F., Johnson, E.A., 2000. Tree recruitment from burn edges. Can J
 609 Forest Res. 30, 1264–1274.
 610 Grubb, P.J., 1977. The maintenance of species-richness in plant communities:
 611 the importance of the regeneration niche. Biol Rev. 52, 107–145. DOI:
 612 10.1111/j.1469-185X.1977.tb01347.x.
 613 Gutsell, S.L., Johnson, E.A., 2007. Wildfire and tree population processes, in:
 614 (Eds.), Plant Disturbance Ecology. Elsevier Inc., pp. 441–485.
 615 Harmer, R.R., 1995. Natural regeneration of broadleaved trees in Britain III.
 616 Germination and establishment. Forestry. 68, 1–9.
 617 Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin,
 618 J.D. et al., 2004. Ecology of coarse woody debris in temperate ecosystems. In Hal
 619 Caswell (Ed.): Advances in ecological research. Classic papers, vol. 34. Amsterdam,
 620 London: Elsevier Academic Press (Advances in Ecological Research, v. 34), pp. 59–
 621 234.

622 Hartig, F., 2019. DHARMA. Residual diagnostic for hierachical (multi-
 623 level/mixed) regression models: CRAN Development Team. Version 0.2.4.
 624 <https://cran.r-project.org/web/packages/DHARMA/DHARMA.pdf> (accessed
 625 15/01/2019).

626 Herranz, J.M., Martinez-Sanchez, J.J., Las Heras, J. de; Ferrandis, P., 1996.
 627 Stages of plant succession in *Fagus sylvatica* L. and *Pinus sylvestris* L. forests of
 628 Tejera Negra National Park (Central Spain), three years after fire. Israel Journal of
 629 Plant Sciences. 44, 347–358. DOI: 10.1080/07929978.1996.10676656.

630 Heuret, P., Guédon, Y., Guérard, N., Barthélémy, D., 2003. Analysing
 631 branching pattern in plantations of young red oak trees (*Quercus rubra* L., Fagaceae).
 632 Ann Bot-London. 91, 479–492. DOI: 10.1093/aob/mcg046.

633 Hoch, G., Siegwolf, R.T.W., Keel, S.G., Körner, C., Han, Q., 2013. Fruit
 634 production in three masting tree species does not rely on stored carbon reserves.
 635 Oecologia. 171, 653–662. DOI: 10.1007/s00442-012-2579-2.

636 Holzwarth, F., Kahl, A., Bauhus, J., Wirth, C., 2013. Many ways to die –
 637 partitioning tree mortality dynamics in a near-natural mixed deciduous forest. J Ecol
 638 101, 220-230.

639 Keeley, J.E., 2012. Fire in Mediterranean climate ecosystems – a comparative
 640 overview. Israel Journal of Ecology & Evolution. 58, 123-135.

641 Koenig, W.D., Knops, J.M., 2000. Patterns of annual seed production by
 642 northern hemisphere trees: a global perspective. American Naturalist. 155, 59-69.

643 Koop, H., Hilgen, P., 1987. Forest dynamics and regeneration mosaic shifts in
 644 unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). Forest Ecol
 645 Manag. 20, 135–150. DOI: 10.1016/0378-1127(87)90155-1.

646 Lambert, D., 1992. Zero-Inflated Poisson Regression, with an Application to
 647 Defects in Manufacturing. *Technometrics*. 34. DOI: 10.2307/1269547.

648 Lüdecke, D., 2019. Collection of Convenient Functions for Common
 649 Statistical Computations. Version 0.17.4: CRAN Development Team. [https://cran.r-](https://cran.r-project.org/web/packages/sjstats/sjstats.pdf)
 650 [project.org/web/packages/sjstats/sjstats.pdf](https://cran.r-project.org/web/packages/sjstats/sjstats.pdf). (assessed 18/01/2019)

651 Madsen, P., Hahn, K., 2008. Natural regeneration in a beech-dominated forest
 652 managed by close-to-nature principles — a gap cutting based experiment. *Can J*
 653 *Forest Res.* 38, 1716–1729. DOI: 10.1139/X08-026.

654 Madsen, P., Larsen, J.B., 1997. Natural regeneration of beech (*Fagus sylvatica*
 655 L.) with respect to canopy density, soil moisture and soil carbon content. *Forest*
 656 *Ecology and Management* 97 (2), pp. 95–105. DOI: 10.1016/S0378-1127(97)00091-
 657 1.

658 Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M.
 659 et al., 2019. *glmmTMB*. Version 0.2.3: CRAN Development Team.

660 Maringer, J., Ascoli, D., Küffer, N., Schmidtlein, S., Conedera, M., 2016a.
 661 What drives European beech (*Fagus sylvatica* L.) mortality after forest fires of
 662 varying severity? *Forest Ecol Manag.* 368, 81–93. DOI:
 663 10.1016/j.foreco.2016.03.008.

664 Maringer, J., Conedera, M., Ascoli, D., Schmatz, D.R., Wohlgemuth, T.,
 665 2016b. Resilience of European beech forests (*Fagus sylvatica* L.) after fire in a global
 666 change context. *Int. J. Wildland Fire.* 25, 699. DOI: 10.1071/WF15127.

667 Mazzoleni, S., Bonanomi, G.; Incerti, G., Chiusano, M. L., Termolino, P.,
 668 Mingo, A. et al., 2015. Inhibitory and toxic effects of extracellular self-DNA in litter:
 669 a mechanism for negative plant-soil feedbacks? *The New Phytologist.* 205, 1195–
 670 1210. DOI: 10.1111/nph.13121.

671 Meteo Swiss, 2019. Climate data Switzerland. Edited by Meteo Swiss.
672 <https://www.meteoswiss.admin.ch/home.html?tab=overview> (accessed 3/17/2019).
673 Michaletz, S.T., Johnson, E.A., Mell, W.E., Greene, D.F., 2012. Timing of fire
674 relative to seed development controls availability of non-serotinous aerial seed banks.
675 Biogeosciences Discuss. 9, 16705–16751. DOI: 10.5194/bgd-9-16705-2012.
676 Monks, A., Monks, J.M., Tanentzap, A.J., 2016. Resource limitation
677 underlying multiple masting models makes mast seeding sensitive to future climate
678 change. New Phytologist, 210, 419-430.
679 Nagel, T.A., Svoboda, M., 2008. Gap disturbance regime in an old-growth
680 Fagus – Abies forest in the Dinaric Mountains, Bosnia-Herzegovina. Can J Forest
681 Res. 38, 2728–2737. DOI: 10.1139/X08-110.
682 Nussbaumer, A., Waldner, P., Etzold, S., Gessler, A., Benham, S., Thomsen,
683 I.M., Jørgensen, B.B., Timmermann, V., Verstraeten, A., Sioen, G., Rautio, P.,
684 Ukonmaanaho, L., Skudnik, M., Apuhtin, V., Braun, S., Wauer, A., 2016. Patterns of
685 mast fruiting of common beech, sessile and common oak, Norway spruce and Scots
686 pine in Central and Northern Europe. Forest Ecol Manag. 363, 237-251.
687 Olesen, C.R., Madsen, P., 2008. The impact of roe deer (*Capreolus*
688 *capreolus*), seedbed, light and seed fall on natural beech (*Fagus sylvatica*)
689 regeneration. Forest Ecol Manag. 255, 3962–3972. DOI:
690 10.1016/j.foreco.2008.03.050.
691 Orman, O., Dobrowolska, D., Szwagrzyk, J., 2018. Gap regeneration patterns
692 in Carpathian old-growth mixed beech forests – Interactive effects of spruce bark
693 beetle canopy disturbance and deer herbivory. Forest Ecol Manag. 430, 451–459.
694 DOI: 10.1016/j.foreco.2018.08.031.

695 Övergaard, R., 2009. A method for natural regeneration of beech (*Fagus*
 696 *sylvatica* L.) practices in Southern Sweden. Umeå: Swedish University of Agricultural
 697 Sciences Faculty of Forest Sciences (Studia forestalia Suecica, 218).
 698 <http://pub.epsilon.slu.se/3992/1/SFS218.pdf> (accessed 30/09/2018).
 699 Overpeck, J.T., Rind, D., Goldberg, R., 1990. Climate-induced changes in
 700 forest disturbance and vegetation. *Nature*. 343, 51–53. DOI: 10.1038/343051a0.
 701 Packham, J.R., Thomas, P.A., Atkinson, M.D., Degen, T., 2012. Biological
 702 flora of the British Island: *Fagus sylvatica*. *J Ecol.* 100, 1557-1608.
 703 Peters, V.S., Macdonals, E.S., Dale, M.R.T., 2005. The interaction between
 704 masting and fire is key to White spruce regeneration. *Ecology*. 86, 1744–1750.
 705 Pezzatti, G., Reinhard, M., Conedera, M., 2010. Swissfire: Die neue
 706 Schweizerische Waldbranddatenbank. *Schweizerische Zeitschrift für Forstwesen*.
 707 161, 465-469.
 708 Pounden, E., Greene, D.F., Michaletz, S.T., 2014. Non-serotinous woody
 709 plants behave as aerial seed bank species when a late-summer wildfire coincides with
 710 a mast year. *Ecol Evol.* 4, 3830–3840. DOI: 10.1002/ece3.1247.
 711 Pukacka, S., Ratajczak, E., 2014. Factors influencing the storability of *Fagus*
 712 *sylvatica* L. seeds after release from dormancy. *Plant Growth Regul.* 72, 17–27. DOI:
 713 10.1007/s10725-013-9832-5.
 714 R Development Core Team, 2019. R: A language and environment for
 715 statistical computing. Version 3.5.3: R Development Core Team.
 716 Röhrig, E., Bartels, H., Gussone, H.-A., Ulrich, B. 1978. Untersuchungen zur
 717 natürlichen Verjüngung der Buche (*Fagus sylvatica*). Universität Göttingen,
 718 Göttingen. Institut für Waldbau, für Forestbotanik und für Bodenkunde und
 719 Waldernährung.

720 Schulze, E.D., Hessenmöller, D., Seele, C., Wäldchen, J., von Lüpke, N.,
 721 2010. Die Buche. Eine Kultur- und Wirtschaftsgeschichte. Biologie in unserer Zeit.
 722 40, 171–183. DOI: 10.1002/biuz.201010421.

723 Schumacher, S., Reineking, B., Sibold, J., Bugmann, H., 2006. Modeling the
 724 impact of climate and vegetation on fire regimes in mountain landscapes. Landscape
 725 Ecol. 21, 539–554. DOI: 10.1007/s10980-005-2165.

726 Schweingruber, F.H., 1987. Microscopic wood anatomy: Structural
 727 variability of stems and twigs in recent and fossil woods from Central Europe. Zug:
 728 Züricher AG.

729 Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerk, P.J., 2014. Increasing
 730 forest disturbances in Europe and their impact on carbon storage. Nat Clim Change. 4,
 731 806–810.

732 Silva, D.E., Rezende Mazzella, P., Legay, M., Corcket, E., Dupouey, J. L.,
 733 2012. Does natural regeneration determine the limit of European beech distribution
 734 under climatic stress? Forest Ecol Manag. 266, 263–272. DOI:
 735 10.1016/j.foreco.2011.11.031.

736 Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed
 737 effects models and extensions in ecology with R. Springer, New York.

738 Stubenböck, F., 2016. Effekt von Waldbrand auf die Mortalität und
 739 Regenerationsfähigkeit von Schutzwald im inneralpinen Raum am Fallballspiel
 740 Absamer Vorberg. Master-Thesis. Universität für Bodenkultur Wien, Wien. Institut
 741 für Wald- und Bodenwissenschaften - Institut für Waldbau.

742 Szewczyk, J., Szwagrzyk, J., 2010. Spatial and temporal variability of natural
 743 regeneration in a temperate old-growth forest. Ann For Sci. 67, 202. DOI:
 744 10.1051/forest/2009095.

745 van Gils, H., Odoi, J.O., Andrisano, T., 2010. From monospecific to mixed
 746 forest after fire? *Forest Ecol Manag.* 259, 433–439. DOI:
 747 10.1016/j.foreco.2009.10.040.

748 Vicente-Serrano, S.M., Beguería, S., Lorenzo-Lacruz, J., Camarero, J.J.,
 749 López-Moreno, J.I., Azorin-Molina, C., et al., 2012. Performance of drought indices
 750 for ecological, agricultural, and hydrological applications. *Earth Interact.* 16, 1–27.
 751 DOI: 10.1175/2012EI000434.1.

752 van Wagner, C.E., 1982. Practical aspect of the line intersect method.
 753 Petawawa National Forestry Institute. Canadian Forestry Service. Chalk River,
 754 Ontario, Canada.

755 Wagner, S., Collet, C., Madsen, P., Nakashizuka, T., Nyland, R.D., Sagheb-
 756 Talebi, K., 2010. Beech regeneration research: From ecological to silvicultural
 757 aspects. *Forest Ecol Manag.* 259, 2172–2182. DOI: 10.1016/j.foreco.2010.02.029.

758 Willner, W., Jiménez-Alfaro, B., Agrillo, E., Biurrun, I., Campos, J.A., Čarni,
 759 A., et al., 2017. Classification of European beech forests: a Gordian Knot? *Appl Veg*
 760 *Sci.* 20, 494–512. DOI: 10.1111/avsc.12299.

761 Wright, B.R., Zuur, A.F., 2014. Seedbank dynamics after masting in mulga
 762 (*Acacia aptaneura*): Implications for post-fire regeneration. *J Arid Environ.* 107, 10–
 763 17. DOI: 10.1016/j.jaridenv.2014.03.008.

764 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to
 765 avoid common statistical problems. *Methods Ecol Evol.* 1, 3–14. DOI:
 766 10.1111/j.2041-210X.2009.00001.x.

767 Zwolak, R., Bogdziewicz, M., Wróbel, A., Crone, E.E., 2016. Advantages of
 768 masting in European beech: timing of granivore satiation and benefits of seed caching

769 support the predator dispersal hypothesis. *Oecologia*. 180, 749–758. DOI:
770 10.1007/s00442-015-3511-3.

771

772

Figure captions

Fig 1: Study sites (black dots) across the European Alps in the Swiss Canton Glarus, Solothurn and Ticino as well as the Italian region of Piedmont. Temperature and precipitation diagrams characterize the climate conditions of the study region (Agenzia Regionale per la protezione Amientale 2019; Meteo Swiss 2019).

[double column – back and white]

Fig 2: Intensity of mast years for the Swiss Cantons Glarus, Solothurn, Ticino and the Italian region of Piedmont. Rescaled mast intensities based on the MASTREE data base (Ascoli et al. 2017) indicate no mast events (0), minor (1), intermediate (2) and full mast years (3-4).

[1.5 column – black and white]

Fig 3: Mean numbers of established beech recruitments in the years post-fire in low-, moderate-, and high burn severity sites as well as in the unburnt forests. Dark bars indicate the occurrence of an intermediate or full mast year, while the light grey bars show no to minor mast in the previous year of germination.

[1.5 column – black and white]

Fig 4: Temporal trends in recruitments ages in low-, moderate-, and high severity burns and in the unburnt forests as reference. Samples sharing a common letter are not significantly different at the 0.05%-level.

[1.5 column – black and white in the printed version, colored in the online publication]

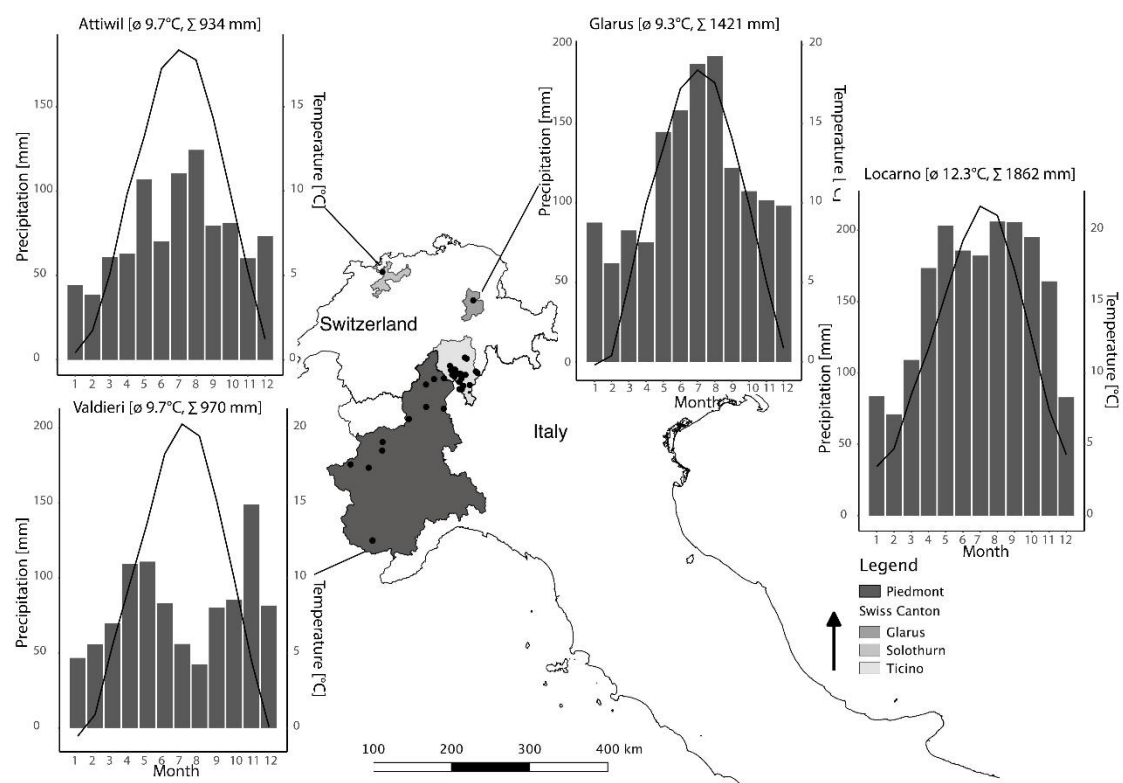
798

799 Fig 5: Recruitment window for beech is visualized by plotting the main influence
800 factors (percentage of both tree cover [A] and competing ground vegetation [B]) against
801 mast intensity, separately for the presence and absence of beech recruitments. Light and
802 bold dashed lines indicate the 95%-Confidence intervals and inter quantile ranges over
803 all mast years, respectively. Mean annual germination frequency [C] is shown for the
804 years post-fire in combination with loess smoothing curves for tree cover and
805 competing ground vegetation.

806 [2 column – black and white]

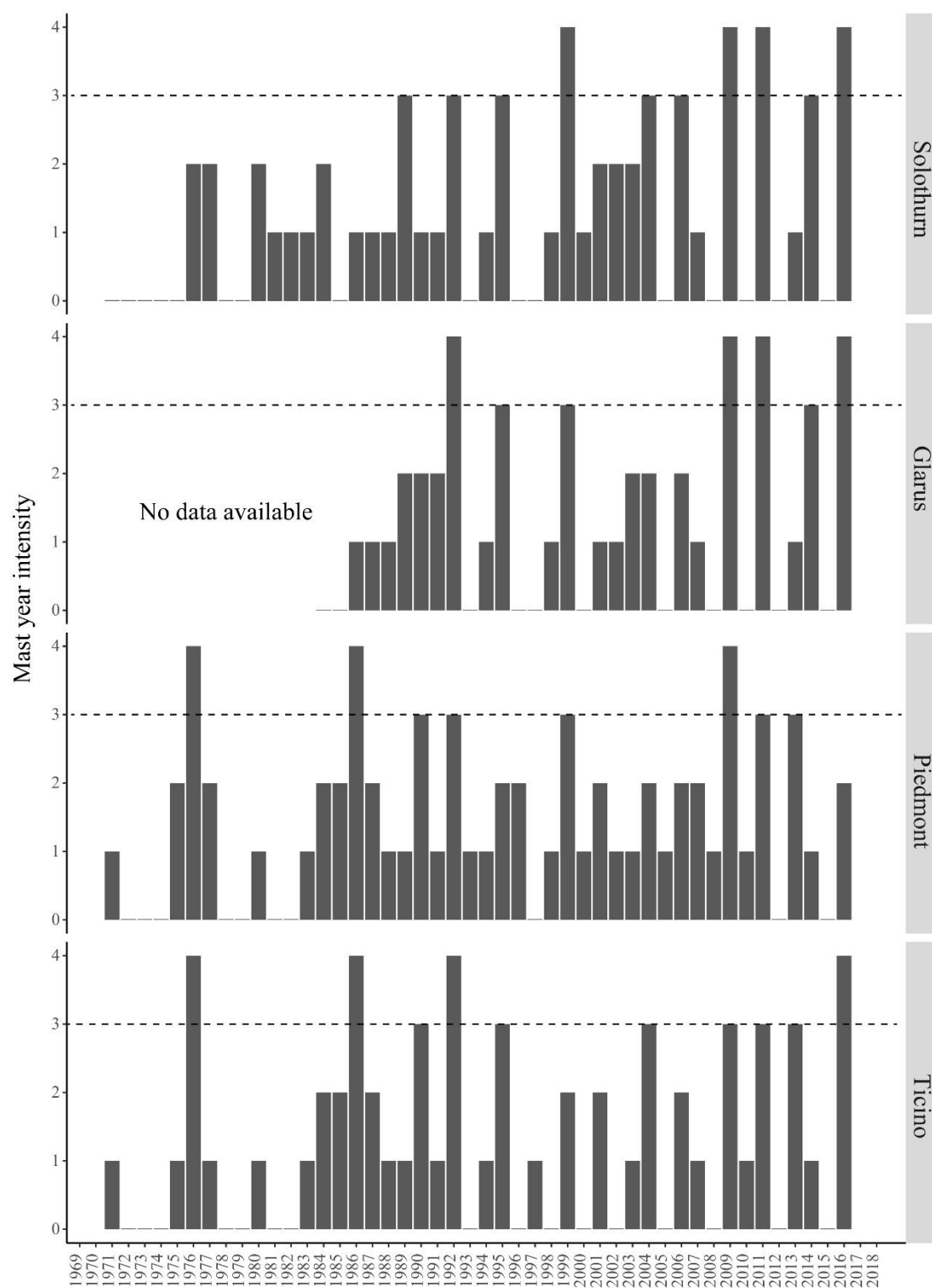
807

808 Fig. 1



809

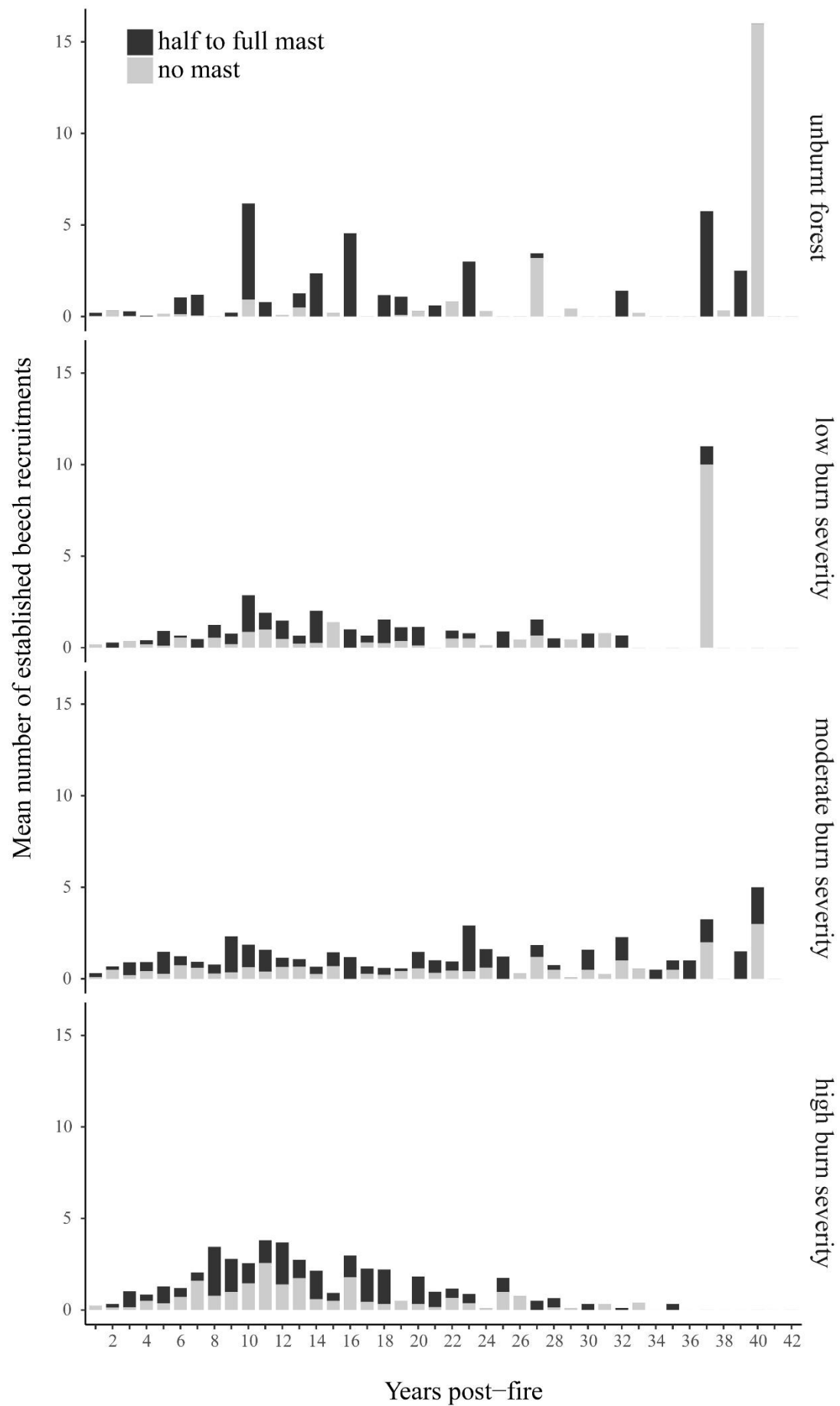
810



812

813

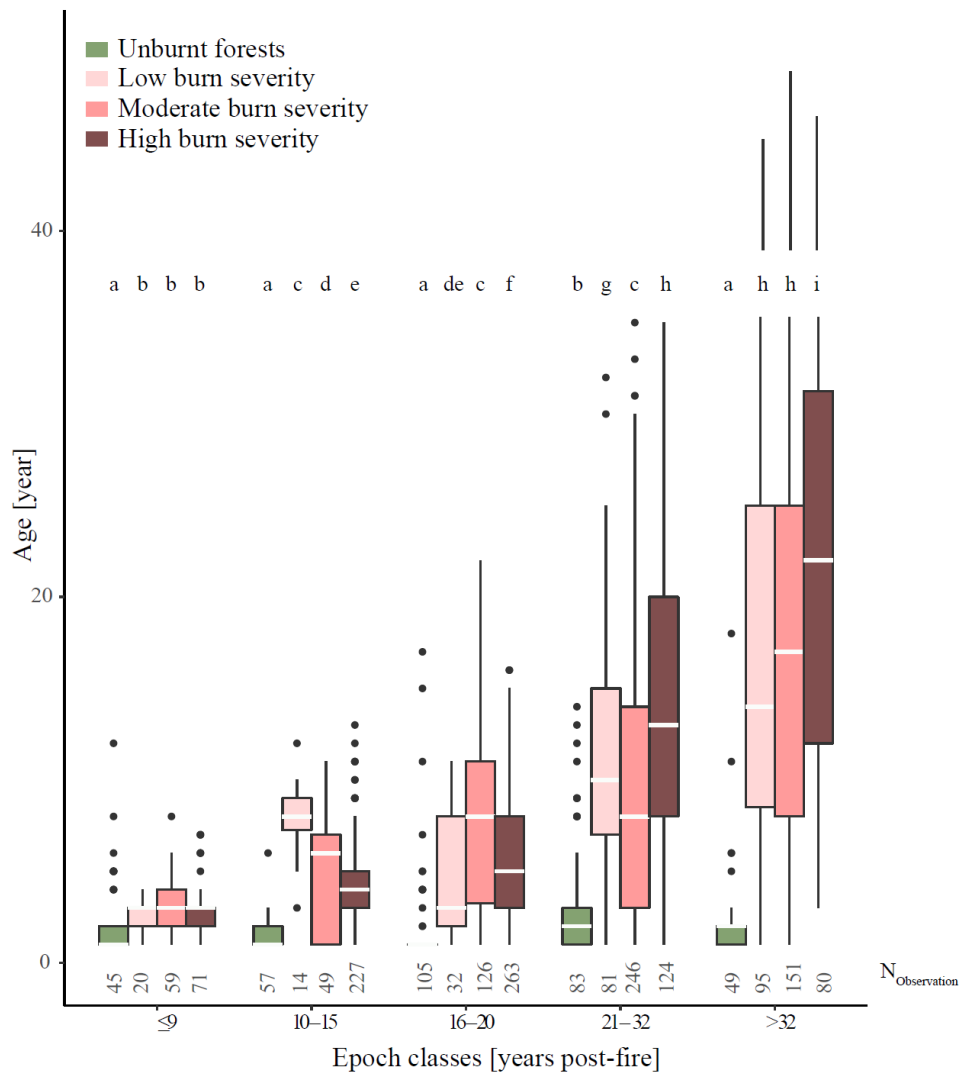
814 Fig. 3



815

816

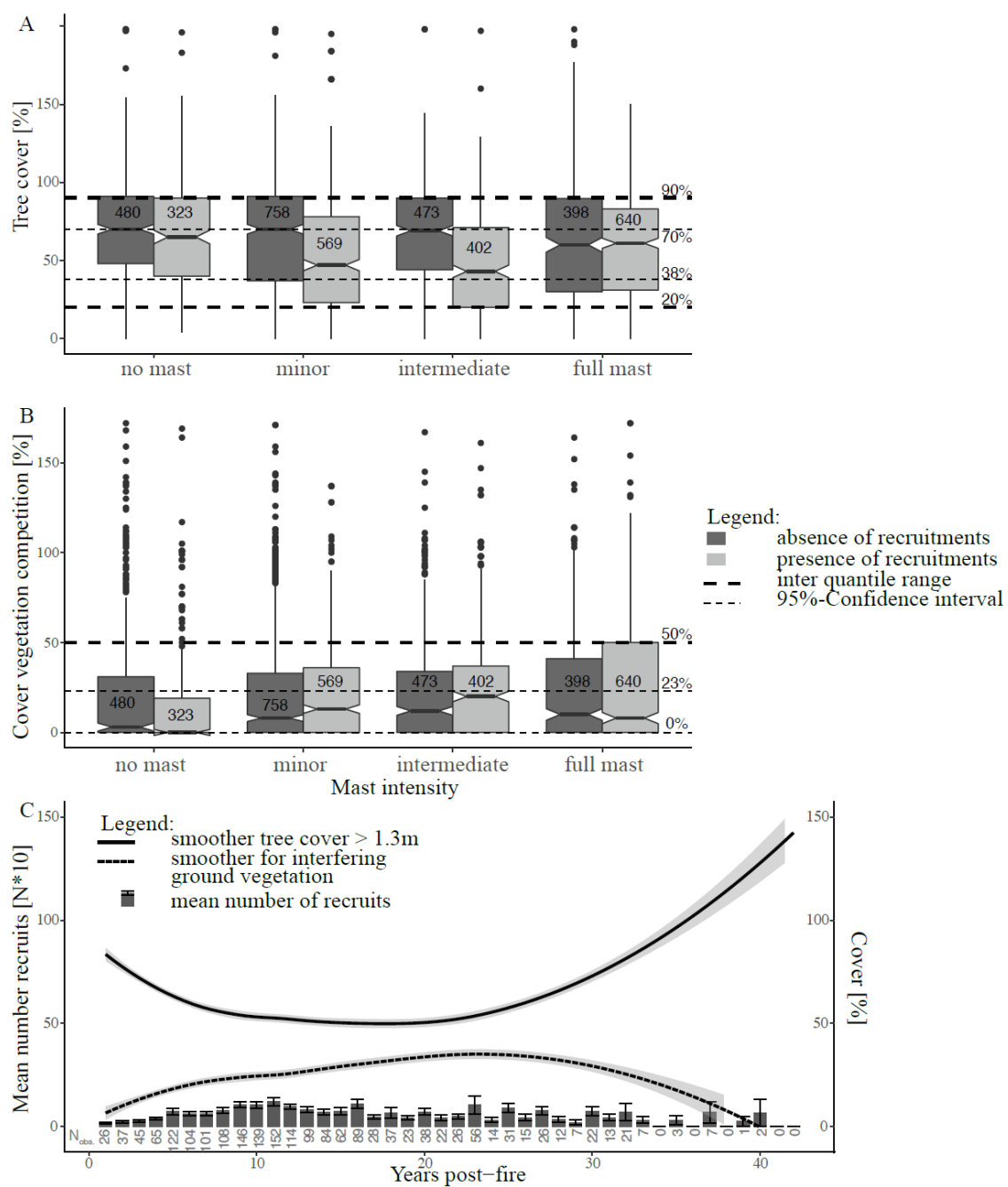
817 Fig.4



818

819

820 Fig. 5



821

822

Table 1: Time-dependent and time-independent variables tested in the Zero-inflated generalized linear mixed-effect model.

Variable	Abbreviation	Unit
<i>Response variable</i>		
Annual number of recruitments		
<i>Time-independent</i>		
Slope	Slope	%
Aspect	Aspect	°
Elevation	Elevation	m a.s.l.
Micro-topography	MicroTopo	Plane, convex, concave
Rock material	Rock	Silicate, limestone
<i>Time-dependent</i>		
Litter	Litter	%
Bare soil	Bare soil	%
Basal area	BA	m ² ha ⁻¹
Coarse woody debris	CWD	m ³ ha ⁻¹
Mast intensity	Mast	0 – no mast 1 – light 2 – intermediate 3-4 – full
Cumulated standardized precipitation evapotranspiration index (SPEI) (February to August)	SPEI	
Tree cover > 5 m	layerII	%
Tree cover 1.3 – 5m	layerI	%
Tree cover >1.3	layerIII	%
Aggregated height of beech	aggHeight_beech	m
Aggregated height of pioneer species	aggHeight_pioneer	M
Interfering ground vegetation	Veg.comp	%
Observation interval	ObsvInterv	years

Table 2: Estimates and standard error of the best negative binomial zero-inflated mixed effect model with the conditional and zero-inflated part.

Variable	Estimate [Std.Error]	z-value[sign.level]
Conditional model		
Intercept	-3.3 [± 0.12]	-25.7 [***]
ObsvInterv	-0.5 [± 0.05]	-9.9 [***]
SPEI	0.09 [± 0.03]	2.5 [*]
Layer.III	-0.17 [± 0.09]	-1.7 [•]
Sporadic mast	0.3 [± 0.1]	2.9 [**]
Half mast	0.46 [± 0.11]	3.9 [***]
Full mast	0.73 [± 0.1]	7.02 [***]
Veg.comp	-0.26 [0.09]	-2.8 [**]
Layer.III : light mast	-0.12 [± 0.1]	-1.7 [n.s.]
Layer.III : intermediate mast	-0.3 [± 0.12]	-2.4 [*]
Layer.III : full mast	0.2 [± 0.11]	1.9 [•]
Sporadic mast :	0.18 [± 0.1]	1.7 [•]
veg.comp		
Half mast : veg.comp	0.23 [± 0.1]	1.9 [•]
Full mast : veg.comp	0.36 [± 0.1]	3.4 [***]
Zero-inflated model		
Intercept	-1.6 [± 0.5]	-3.17 [***]
Layer.III	0.4 [± 0.17]	2.7 [**]
Random effect		
Fire site	Variance 0.07	

Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '•' 0.1, 'n.s.' 1; : interaction term