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1 **Drivers of persistent post-fire recruitment in European beech forests**

2

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26

27 **Abstract**

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

46

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

49

## 50 **1 Introduction**

51 Climate change is reorganizing disturbance regimes of forest ecosystems (Seidl et al.,  
52 2014), sometimes interacting synergistically with changes in land use and forest  
53 management (Overpeck et al., 1990; Flannigan et al., 2000). Alterations in the  
54 climate-weather-fuel system will influence fire regimes, not only in fire-prone  
55 systems but also in forest ecosystems that have not historically experienced fires  
56 (Schumacher et al., 2006). In order to understand the resistance and resilience of  
57 forests to novel disturbance regimes such as fires in forest communities in which tree  
58 species lack obvious fire adaptations, a broader understanding in species-specific fire  
59 ecology is needed (Maringer et al., 2016a, Maringer et al., 2016b).

60 A key factor determining forest resilience to fire is the regeneration strategy, which is  
61 dependent on propagule availability and the suitability of the environment for  
62 germination and establishing, as well as for sprouting (Grubb, 1977; Gutsell and  
63 Johnson, 2007). The interaction of propagule availability and suitable environmental  
64 factors determines the recruitment window. Given dispersal constraints, plant species  
65 that establish *in situ* after fire disturbance can take advantage of increased resource  
66 availability such as light, nutrients, and reduced competition (Bond and van Wilgen,  
67 1996; Davis et al., 2000). In fire-prone regions, where stand-replacing fires are  
68 common, vegetation displays fire-adaptive traits for a rapid *in situ* establishment, e.g.,  
69 sprouting from the root collar and seed release from either soil or aerial seed banks  
70 (Keeley, 2012). Such fire-adapted species compete with generalists, i.e., species  
71 producing high annual number of seeds in order to colonize open gaps created by  
72 stand-replacing fires.

73 However, in forests dominated by species that lack specific fire-adaptive or generalist  
74 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  
77 provide 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  
80 intra- and inter-annual patterns (Allen et al., 2017), a pattern that occurs from the  
81 tropics to the boreal zone (Koenig and Knops, 2000). The coincidence of a mast year  
82 closely following a fire is a key factor in successful post-fire recruitment, especially if  
83 a burn is stand-replacing (Peters et al., 2005; Wright and Zuur, 2014). The duration of  
84 a recruitment window might be broadened in less fire-prone ecosystems, where seed  
85 trees 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  
88 protect vital tissue from lethal heat during the fire and its sprouting capacity declines  
89 with tree age (Wagner et al., 2010). Depending on the proportion of injured tissue and  
90 the likelihood of subsequent fungi infestation, tree mortality may be delayed by up to  
91 20 years post-fire (Maringer et al., 2016a). This ensures *in situ* production of the  
92 aerial seed bank after the fire event (Maringer et al., 2016b), and previous research  
93 showed that beech regeneration after fire is strongly promoted by a subsequent mast  
94 event (Ascoli et al., 2015). However, beech masts irregularly, with a mast event on  
95 average every 3 – 8 years, although mast events may fail to occur for over a decade  
96 (Packham et al., 2012; Nussbaumer et al., 2016; Ascoli et al., 2017a). As a  
97 consequence, a short temporal recruitment window and the absence of mast events  
98 may delay post-fire beech regeneration, or even result to a failure of regeneration. In  
99 contrast, a longer recruitment window would suggest a higher potential long-term

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

109

## 110 2 Material and methods

### 111 2.1 Study region

112 Forest fires occur occasionally in Mediterranean beech forests (Herranz et al., 1996;  
113 van Gils et al., 2010), in the European Alps, and in the Jura Mountains (Maringer et  
114 al., 2016b; Stubenböck, 2016). In our study we selected 38 beech forest sites that  
115 burnt once since 1970 across the European Alps in the Swiss Cantons Glarus,  
116 Solothurn, and Ticino as well as in the contiguous Italian region of Piedmont (see Fig.  
117 1; Supplementary material A Table 1).

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

129 The climate in the study region is strongly influenced by the Alps. Climate in the  
130 North of the Alps has an Atlantic character, with a mean annual temperature of 9.7 °C  
131 (climate station Attiwil 47.26N / 7.79 E; Glarus 47.03N / 9.07 E, see Fig. 1) and  
132 annual precipitation sum of 934 mm a<sup>-1</sup> at Attiwil and 1421 mm a<sup>-1</sup> at Glarus in the  
133 Northern Pre-Alps. Towards the South, mean annual temperatures increase by 1.0–3.5  
134 °C (Meteo Swiss, 2019; Agenzia Regionale per la protezione Amientale, 2019).

135 Annual precipitation along the Southern foothills of the Alps amounts to  
136 approximately 1800 mm in Ticino and decreases in the southeastern part of the Alps  
137 (970 mm a<sup>-1</sup> in Valdieri) (Agenzia Regionale per la protezione Ambientale, 2019;  
138 Meteo Swiss, 2019).

139 Within the wide climatic amplitude of beech communities (Willner et al., 2017),  
140 beech dominates the forests from 150 m to 1500 m a.s.l. in the cooler Northern Alps  
141 (Englisch, 2006) and occupies the intermediate elevation belt between 900 and 1500  
142 m a.s.l. in the warmer Southern Alps (Ceschi, 2006). Beech forests in the Northern  
143 Alps grow mainly on calcareous bedrock, while they are found on crystalline  
144 basement in the Southern Alps, except in the southernmost parts of Canton Ticino and  
145 in parts of the Piedmont. Thus, the resulting soils are calcic cambisol on limestone  
146 and crypto-humus-podzol with thick humus layers on silicate rock material (Blaser et  
147 al., 2005).

## 148 **2.2 Data collection and preparation**

### 149 *2.2.1 Study design and assessed variables*

150 Fires burnt after 1969 were selected from the forest fire data base of Switzerland  
151 (Pezzatti et al., 2010) and the State Forestry Crops of Italy (Corpo Forestale dello  
152 Stato/ Ministero delle Politiche Agricole, Alimentari e Forestali, 2005). In total, 104  
153 potential burnt stands were identified and inspected in the summer 2011 and 2017 to  
154 select sites that satisfied all of the following four criteria: (i) burnt area larger than 0.5  
155 ha in beech-dominated forests (beech stem density > 90% of total), (ii) with only one  
156 single fire record during the last 100 years, (iii) no evidence of pre-fire wood pasture  
157 (indicated by large solitaire beech trees with low limbs), and (iv) no evidence of post-  
158 fire management and silvicultural measures in both the burnt and adjacent unburnt  
159 stands.



160 Based on these criteria, we selected 37 sites (Supplementary material A). At each site,  
161 we used 200 m<sup>2</sup> plots to assess recruitment in burnt areas and, where possible,  
162 adjacent unburnt areas in the same forest. Sampling took place during summer  
163 2012/13 and 2017/18, following the protocol described in Maringer et al. (2016a). In  
164 total, we assessed data in 137 plots in burnt areas (1–14 per stand, mean = 3.7) and 25  
165 in the adjacent unburnt forests (0–2 per stand, mean = 0.7), using the latter as  
166 references. For each circular plot, we assessed factors that might influence beech  
167 recruitment. We measured topographical parameters (aspect, slope, elevation, micro-  
168 topography [plane, convex, concave]; see Table 1 for abbreviation and explanation),  
169 competing ground vegetation (veg.comp; percentage of *Pteridium aquilinum*, *Cytisus*  
170 *scoparius*, *Molinia arundinacea*) that potentially hinder successful germination and  
171 establishment of beech seeds (Bílek et al., 2009), percentage of bare soil (bare soil)  
172 and percentage of soil covered by litter (litter) as a potential barrier for seedlings’  
173 roots reaching the mineral soil layer before the litter dries out in spring and summer  
174 (Harmer, 1995). The volume of coarse woody debris (CWD) was estimated following  
175 the method of Brown (1974) and van Wagner (1982) in order to consider its potential  
176 role influencing soil moisture and the shading effect on seedlings (Harmon et al.,  
177 2004; Bílek et al., 2009).

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

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

### 188 2.2.2 *Processing of tree ring cores*

189 A total of 20 beech recruits were sampled within each 200 m<sup>2</sup> plot, paying attention to  
190 include the variety of the regeneration structure (e.g. including the smallest and the  
191 tallest, which are assumed to roughly represent the youngest and the oldest,  
192 respectively). In cases where fewer than 20 beech individuals were present in the plot,  
193 all were sampled.

194 The year of germination for the youngest recruitments (age  $\leq$  4 years) was determined  
195 in the field counting their annual growth units as defined by terminal bud scars  
196 (Heuret et al., 2003). Older individuals were cut or cored (5 mm coring devices) close  
197 to the root collar. Cores were glued on supports in order to avoid deformation during  
198 the drying process, and both tree discs and cores were dried for 48 hours. Samples  
199 were abraded with sandpaper (100 grit), and finally prepared with chalk, liquid color,  
200 and razor blades to enhance the contrast of the anatomical features. Annual tree rings  
201 were then counted under a binocular following reference pictures of Schweingruber  
202 (1987).

### 203 2.2.3 *Assignment of climate variables*

204 Sufficient soil moisture in spring and early summer promotes beech seed germination  
205 and early recruitment (Harmer, 1995; Pukacka and Ratajczak, 2014). Therefore, we  
206 calculated the annual cumulative Standardized Precipitation-Evapotranspiration Index  
207 (SPEI) for the period February to August as a proxy for water availability (Vicente-  
208 Serrano et al., 2012). When calculating the SPEI we considered the water balance as

209 the difference between precipitation and potential evapotranspiration (PET). PET was  
210 calculated using the Thornthwaite equation in the R-package SPEI (Beguería and  
211 Vicente-Serrano, 2017).

#### 212 *2.2.4 Assigning beech mast intensities*

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

#### 223 *2.2.5 Reconstructing time-dependent environmental variables*

224 We took advantage of a space-for-time approach, in which the time between the fire  
225 event and the field assessment differed between sites. On this basis we were able to  
226 reconstruct the temporal trends of environmental conditions in the post-fire period for  
227 each plot, which was classified as low-, moderate or high severity burns based on the  
228 proportion of the basal area lost in the post-fire period (for definition and  
229 methodological details see Maringer et al. (2016b); examples of low-, moderate- and  
230 high severity burns are given in Supplementary material B), assuming that plots in  
231 the nearby unburnt forests represent the equivalent development of the forest in the  
232 absence of fire. After plotting the variable assessed in each plot against the years post-  
233 fire separately for each burn severity class (i.e., low, medium, high severity), we

234 estimated the overall temporal trend using loess-smoothing curves. We assessed the  
235 annual values for each time-dependent variable from the year of fire to the field  
236 observation separately for each plot by following the shape of the overall loess-  
237 smoother (see Supplementary material C fig. 1– fig. 3).

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

## 241 **2.3 Data analysis**

### 242 *2.3.1 Data pre-processing*

243 To describe temporal trends in the age structures of the post-fire recruits in the burnt  
244 and unburnt forests we aggregated the years post-fire into five epoch classes: ‘≤ 9  
245 years’, ‘10-15 years’, ‘16-21 years’, ‘21-32 years’, ‘> 32 years’ (see Maringer et al.,  
246 2016b). Variation in age distribution within fire severity classes (low-, moderate- and  
247 high severity) and the unburnt forests was analyzed using a Kolmogorov-Smirnov test  
248 ( $p < 0.05$ ).

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

256 2.3.2 *Model construction*

257 Since our analysis is based on the number of beech recruits established each year, we  
258 counted more zeros (69%) than expected for the Poisson distribution leading to  
259 overdispersion (Zuur et al., 2009). Therefore, we used a zero-inflated (ZI) count  
260 model, which combines a count response variable (Poisson or Negative binomial  
261 distributed) and a distribution with point mass of one at zero. The count part is known  
262 as the conditional model and is similar to a generalized linear model. The zero part  
263 describes the probability of observing an extra zero (i.e., structural zero) that is not  
264 generated by the conditional model (Lambert, 1992).

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

270 The ZI model was implemented in the R package glmmTMB (Magnusson et al.,  
271 2019) that allows the inclusion of random-effects. As a first step we developed several  
272 null models (without explanatory variables) to test for the best random structure and  
273 distribution for the count process. Models were compared based on the Akaike's  
274 Information Criterion (AIC) (Burnham and Anderson, 2004).

275 For variable selection, we first focused on the conditional model part and calculated  
276 models using only one predictor and the best random structure (single-models). In a  
277 second step, models were calculated that combined significant variables out of the  
278 single-model step, verifying the AIC improvement and likelihood-ratio chi-squared  
279 test. During the process of variable selection, low variation was found between the  
280 estimated values of a full mast (category 3) and extraordinary high seed production

281 (category 4). Therefore, we merged both to one category in order to reduce the  
282 degrees of freedom. After finding the best conditional model, all non-significant  
283 variables from the single-model step were added back to confirm that they are not  
284 statistically significant. In a last step interaction terms were added and kept in the  
285 models in case of significance. The same procedure was then applied to the zero-  
286 inflation component of the model.

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

## 292 **3 Results**

### 293 **3.1 Frequency of mast years**

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

### 298 **3.2 Germination frequency and age structure**

299 In total, we assessed the year of germination for 2322 beech seedlings – 83.3%  
300 belonging to the burnt forests, 16.7% to the unburnt forests. Most of the recruits  
301 established within the first 15 years post-fire in moderate (63.5% of all recruits) and  
302 high (85%) severity burns, while germination occurred irregularly in low severity  
303 burns and the unburnt forests throughout the observation period (Fig. 3). Most recruits  
304 (73.4%) in the unburnt forests established after intermediate or full mast years one

305 year prior to seed germination. In rare cases, as for the peak 40 years post-fire in the  
306 unburnt forests, a high number of germination took place two years after a full mast  
307 event. In contrast, in the burnt forests ca. 50% of the sampled recruits germinated in  
308 the year following an intermediate or full mast year (55%, 58% and 50% in low,  
309 moderate and high burn severity sites, respectively).

310 In the unburnt forests, the mean age of recruits was 2.2 years and did not vary with  
311 time since the adjacent forests burnt (Fig. 4). The age structure did not significantly  
312 differ in the unburnt forest, except the period 21 – 32 years. This contrasts to the burnt  
313 forests, where the age of recruits steadily increased with time since fire. Within the  
314 first 9 years post-fire, the age difference between the burnt and unburnt forests was  
315 approximately 1 year and differed significantly at the 0.05%-level (Fig. 4). The age  
316 differences steadily increased, and were always significantly different between the  
317 burnt and unburnt forests throughout the entire observation period. The recruits in the  
318 burnt forests were on average 2.8 – 6.3 years, 3.2 – 6 years, and 6.2 – 11.7 years older  
319 than in the unburnt forests, 10 – 15 years, 16 – 20 years and 21 – 32 years post-fire,  
320 respectively. The highest age differences were observed 32 year after fire, recruits in  
321 the burnt forest were more than 10 years older than equivalent recruits in unburnt  
322 forests. At the same time, as the mean age increased the age variance in the burnt  
323 forests increased steadily showing recruit's ages ranging from 1 year to 42 years after  
324 32 years post-fire.

### 325 **3.3 Factors influencing beech recruitments**

326 The most parsimonious model consisted of a negative binomial zero-inflated  
327 generalized linear mixed-effect model (NBZI-GLMM) relating the number of the  
328 recruits to years interval (ObservInterv), Standardized Precipitation-  
329 Evapotranspiration Index (SPEI), mast intensity (mast), tree cover above 1.3 m

330 (layer.III), cover of ground vegetation (veg.comp), as well as interactions of mast  
331 intensity with layer.III, and mast intensity with veg.comp (Table 2). Fire site was  
332 considered as a random structure in the conditional part, but not in the zero-inflation  
333 part. In the latter, the probability to observe an extra zero was only related to the  
334 increasing tree cover (layer.III, i.e., higher absence of recruits in darker stands).

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

#### 349 **3.4 Longevity of the fire-induced recruitment window for beech**

350 The model results reveal that the recruitment window is mainly influenced by mast  
351 intensity interacting with the overall tree cover (layer.III) and competing ground  
352 vegetation (veg.comp). Therefore, we plotted the presence and absence of  
353 recruitments against mast intensity in relation to tree cover (Fig. 5 A) and interfering  
354 ground vegetation (Fig. 5 B). Figure 5A shows that with 95% confidence beech



355 establish over all mast intensities when canopy cover range between 38% and 70%.  
356 Contrastingly, beech fails to establish with 95% confidence under tree cover ranging  
357 from 55% to 73% regardless of the mast intensity.

358 In figure 5B the cover of ground vegetation replaces tree cover on the y-axis. It is  
359 notable that 50% (inter quantile range) of beech recruits establish after a full mast  
360 year even in the presence of interfering ground vegetation with up to 50% (Fig. 5 B).  
361 The success diminishes with decreasing mast intensity to 37%, 36% and 19% in case  
362 of intermediate-, minor-, and no-mast year, respectively.

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

## 368 **4 Discussion**

### 369 **4.1 Main drivers of post-fire beech recruitment**

370 The delayed post-fire mortality of beech after mixed severity fires (Maringer et al.,  
371 2016a) ensures *in situ* seed production and allows beech to take advantage of the  
372 favorable recruitment conditions in the post-fire environment. Surprisingly, the model  
373 did not retain basal area of surviving beeches, indicating that a limited number of  
374 trees can provide sufficient seeds in mast years to guarantee regeneration and leaving  
375 enough light for establishment at the same time. Seed production by surviving trees  
376 may be promoted by changes in the post-fire environment. For example, as a general  
377 rule fire increases nutrient availability in the soil (DeBano, 1990), and this combined  
378 with related increases in carbohydrate production may stimulate flower initiation

379 (Allen et al., 2017) and seed maturation (e.g., Hoch et al., 2013). For beech  
380 specifically, individuals remaining vital after a burn of low to medium severity  
381 (Maringer et al., 2016a) may be able to extend the lateral crown after gap creation,  
382 increasing photosynthesis and subsequently seed production (Emborg et al., 2000).  
383 Minor-, intermediate- and particularly full mast years are highly significantly and  
384 positively related to the post-fire recruitment success (Table 2). The dominant and  
385 significant effect of regional masting events is in line with the general trend in beech  
386 masting controlled by large-scale weather patterns (Ascoli et al., 2017b). Therefore,  
387 according to our results there is no clear evidence of specific, fire-induced stress  
388 masting in burnt beech stands. Rather, fire stimulates an increased seed production in  
389 fire-injured beech stands during large-scale masting events (Ascoli et al., 2015). This  
390 extends the short-term post-fire effects observed by Ascoli et al. (2015) over multiple  
391 decades.

392 Successful beech recruitment after low seed production was observed in our study site  
393 (Table 2), consistent with the results reported by Övergaard (2009). However, the  
394 likelihood of successful recruitment clearly increased with mast intensity. This could  
395 be related to the higher number of seeds produced during a full mast year, which  
396 increases the probability that some seeds survive predation (Olesen and Madsen,  
397 2008; Övergaard, 2009; Schulze et al., 2010; Zwolak et al., 2016), and resulting  
398 recruits have a higher survival probability (Madsen and Hahn, 2008). During years of  
399 high seed production (full mast) the seed quantity is so high that despite of interfering  
400 ground vegetation (veg.comp; Koop and Hilgen, 1987; den Ouden, 2000) and shading  
401 tree cover (layer.III) some beech recruitments are able to establish (Table 2). In  
402 contrast, in cases of lower seed availability (intermediate mast), the shading trees  
403 (layer.III) and competing vegetation (veg.comp) tend to have an inhibitory effects on

404 seed establishment as already reported for shelterwood cutting (Övergaard, 2009;  
405 Silva et al., 2012).

406 Finally, the overall tree cover (layer.III) is the only variable retained in the zero-  
407 inflation model, meaning that the probability of observing a zero (i.e., no recruitment)  
408 increases under denser shelter (Ammer et al., 2002; Wagner et al., 2010). Such  
409 shading effect can result either from complete canopy closure of the fire-surviving  
410 trees or from earlier established beech regeneration that have grown to dense saplings-  
411 to pole stages. As a result, low light availability and strong intra-specific competition  
412 combine to inhibit the establishment of cohorts of beech regeneration.

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

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

## 427 **4.2 Prolonged post-fire recruitment window**

428 The positive effects of natural and anthropogenic-induced disturbances on suitable  
429 environmental conditions for beech seed germination and establishment are broadly  
430 documented in the literature (e.g., Agestam et al., 2003; Nagel and Svoboda, 2008;  
431 Wagner et al., 2010; Maringer et al., 2016b; Orman et al., 2018). Similarly to other  
432 non-serotinous species, such as *Picea glauca* and *P. engelmannii* (Michaletz et al.,  
433 2012; Pouden et al., 2014), we found that for beech the disturbance-induced  
434 recruitment window is better utilized in coincidence with mast years (Olesen and  
435 Madsen, 2008; Ascoli et al., 2015). The present study extends existing knowledge by  
436 demonstrating that beech recruitment in burnt forests mainly originated from several  
437 regeneration pulses and created an uneven-aged structure within the first 40 years  
438 post-fire. This is dependent on the delayed mortality of fire-injured beeches, induced  
439 by the heterogeneous fire behavior in mountain beech forests (Maringer et al., 2016a,  
440 and see examples in Supplementary material B). This ensures a persistent seed input  
441 over several years to decades (Övergaard, 2009). In combination with intermediate  
442 light conditions (canopy covers of 38% to 70%, see Fig. 5) staggered beech  
443 regeneration is promoted (Harmer, 1995; Wagner et al., 2010).

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

## 449 **4.3 Practical consequences and implications for beech forests in the future**

450 Our study indicates that masting-related seed inputs along with the availability of light  
451 are of paramount importance for post-fire beech regeneration. Depending on the

452 silvicultural objectives, forest managers should (i) leave fire-injured surviving trees as  
453 possible on the burn site to act as seed sources, (ii) pay attention to upcoming mast  
454 years, which are triggered by large-scale weather patterns (Ascoli et al., 2017b), and  
455 (iii) assure enough light conditions in the post-masting season.

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

460 1) Beech regeneration depends on very local seed sources (Wagner et al., 2010;  
461 Maringer et al., 2016b) which are not guaranteed after stand-replacing fires. If  
462 fire regimes in beech forests shift to higher-severity or more frequent fires,  
463 immediate tree mortality particularly in immature stands may result in shifts in  
464 forest composition as a result of failed beech regeneration.

465 2) The rapid die-back of beech trees after severe fires (Maringer et al., 2016a)  
466 rapidly opens the tree canopy, providing enough light to promote competing  
467 ground vegetation, which can delay beech regeneration for several decades  
468 (Koop and Hilgen, 1987).

469 3) Based on our results, post-fire recruitment success is reduced in years with dry  
470 springs and summers, which might reduce the regeneration capacity post-fire  
471 under climate change. However, our results show that this effect is relatively  
472 weak, and the long regeneration window (up to three decades post-fire)  
473 provides multiple opportunities for sufficiently moist years to coincide with  
474 masting to facilitate regeneration before the recruitment window closes.

475 4) The range in mast year frequency (3 – 8 years; Ascoli et al., 2017a) appears to  
476 be sufficient to ensure successful regeneration post-fire. However, future

477 changes in the frequency of full mast years are still uncertain (Monks et al.,  
478 2016) and would have a strong influence on recruitment (mast is the most  
479 important term in the model). A reduction in mast frequency in these forests  
480 could reduce resilience to novel fire disturbance.

#### 481 **4.4 Limits of the study**

482 The delayed mortality of fire-injured beeches accompanied with rarely occurring mast  
483 years (3 – 8 years; Ascoli et al., 2017a) makes it difficult to study the longevity of  
484 post-fire recruitment windows and the influencing factors. Therefore, we chose the  
485 space-for-time approach that allowed us to extend the observation period over more  
486 than four decades. We were able to study the germination success and recruitment  
487 patterns of 2,322 post-fire beech recruits ranging from 1 to 42 years in age.

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

493 Well known short-term effects of fire such as the exposure of the mineral soil layer  
494 and the increased mineralization and nutrient release due to higher soil temperatures  
495 in the stand openings (Röhrig et al., 1978; Harmer 1995; Maringer et al., 2016b) are  
496 not explicitly measured in our study. Further effects such as the lowering of the  
497 pathogenic inoculum of fungi attacking beech seeds and seedlings, and toxic agents  
498 such as the extracellular self-DNA that usually accumulates in the litters and upper  
499 soil layers of mature beech stands (Szewczyk and Szwagrzyk, 2010; Barna, 2011;  
500 Mazzoleni et al., 2015) were also unmeasured. This is due on the long-term

501 perspective (four decades of our space for time approach on one hand and to the lack  
502 of specific parameters of proxies to characterize these effects in our protocol).  
503 Finally, determining the year of germination of suppressed, slow growing or browsed  
504 beech saplings by counting the annual rings was difficult due to irregular, very narrow  
505 rings, and the possibility of missing tree rings. The very short chronologies preclude  
506 cross-dating. Hence, dating precision of such specimens may result in  $\pm 1$  year error,  
507 which may reduce the explanatory power ( $R^2 = 0.31$ ) of the model.

## 508 **5 Conclusion**

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

518 Our results indicate that beech forests in central Europe are currently resilient to novel  
519 fire disturbance, as a consequence of the prolonged post-fire recruitment window.  
520 However, post-fire beech resilience may decline under future climate if dry or drought  
521 periods increase, fires become more severe, competitive pressure by ground  
522 vegetation and/ or invading pioneer tree species increases, or the frequency of mast  
523 years decreases. Higher frequency of large-scale stand replacing fires in particular

524 may significantly reduce beech seed input via barochory or zoochory, and a  
525 subsequent shift towards other forest species, including invading exotic pioneer trees.



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779

780

781 **Figure captions**

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

786 [double column – back and white]

787

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

792 [1.5 column – black and white]

793

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

798 [1.5 column – black and white]

799

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

803 [1.5 column – black and white in the printed version, colored in the online  
804 publication]

805

806

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

814 [2 column – black and white]

815

**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 <sup>2</sup> ha <sup>-1</sup>
Coarse woody debris	CWD	m <sup>3</sup> ha <sup>-1</sup>
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

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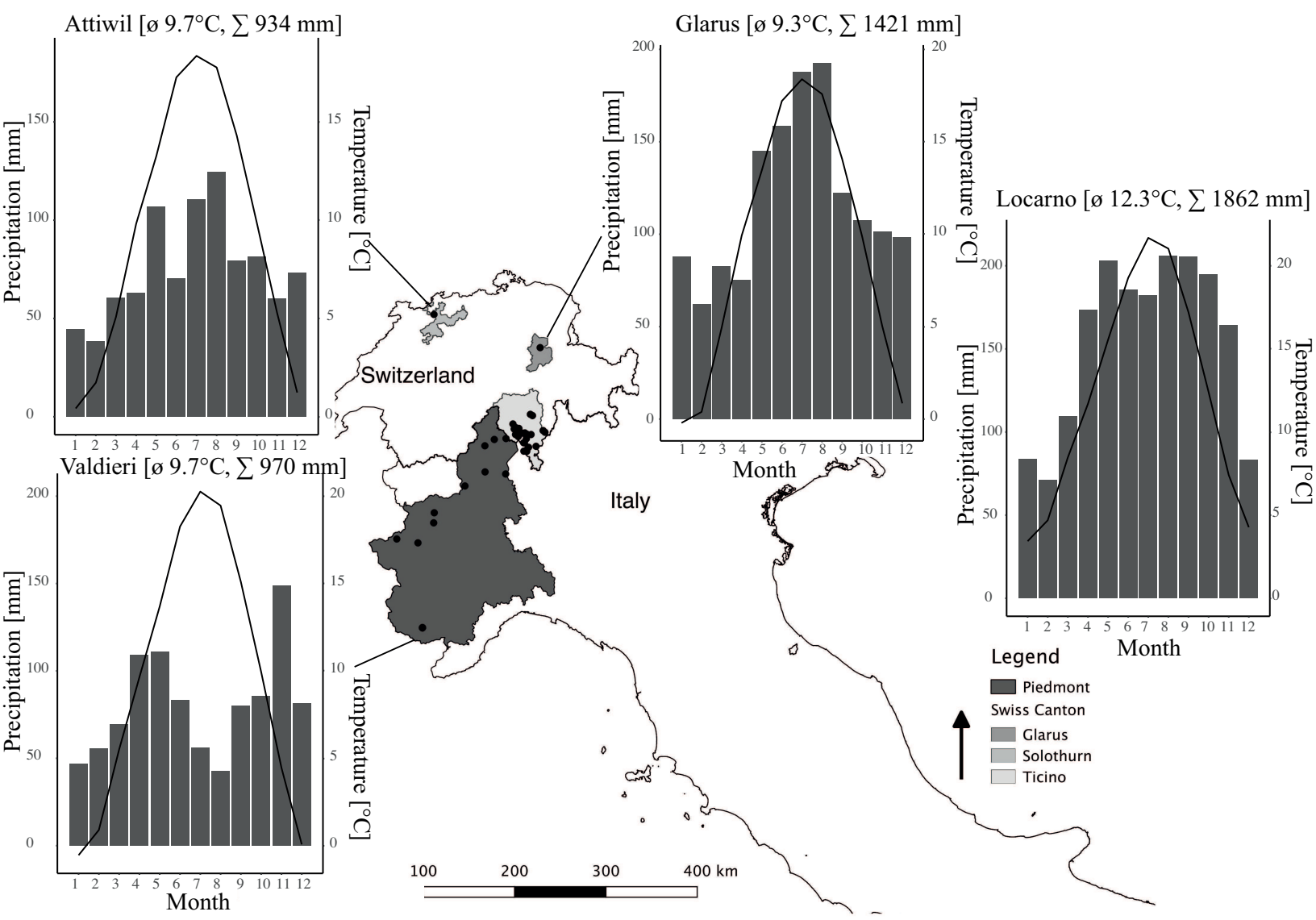


**Table 2: Estimates and standard error of the best negative binomial zero-inflated mixed effect model with the conditional and zero-inflated part.**

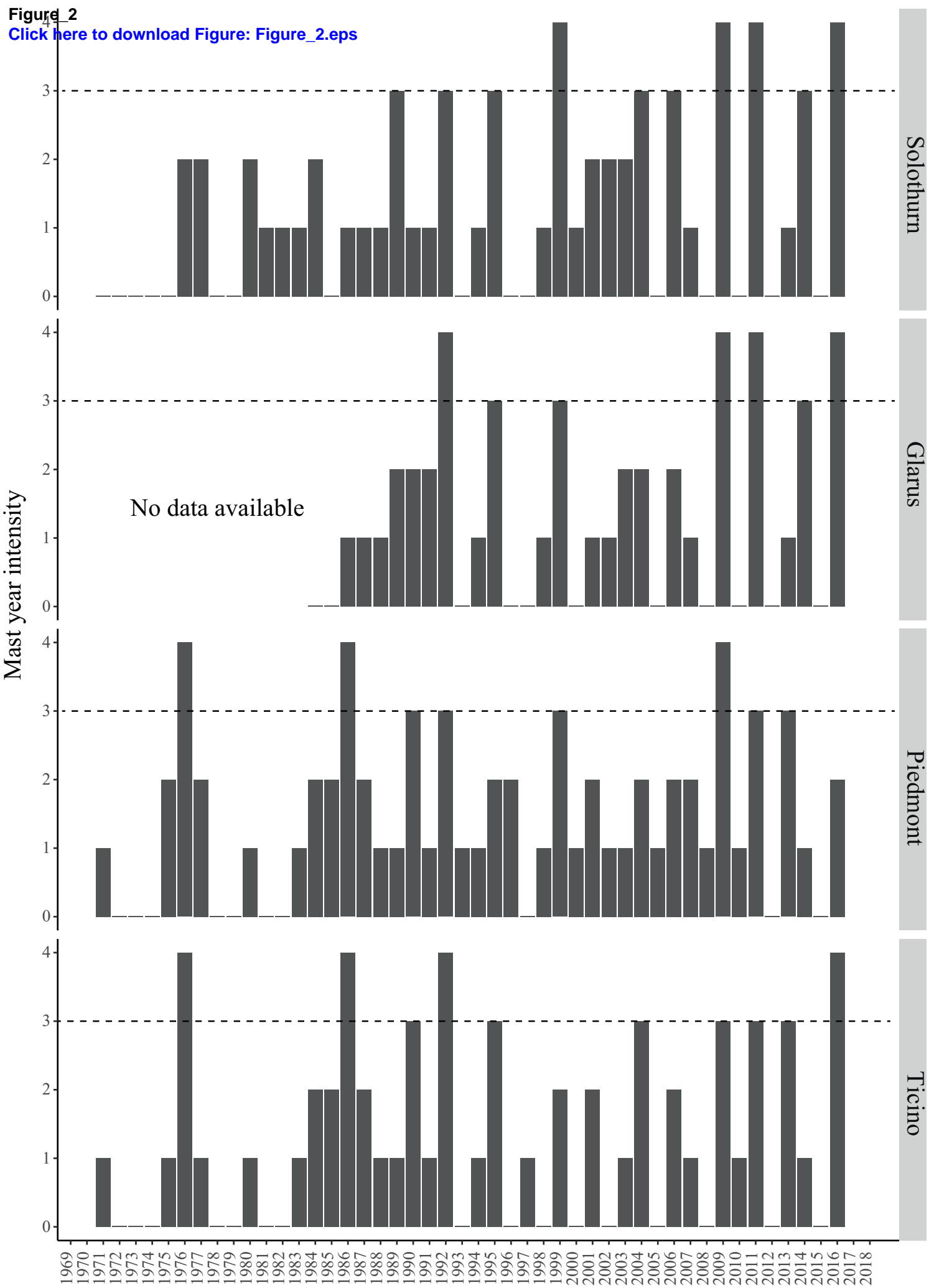
Variable	Estimate [Std.Error]	z-value[sign.level]
<b>Conditional model</b>		
Intercept	-3.3 [ $\pm 0.12$ ]	-25.7 [***]
ObsvInterv	-0.5 [ $\pm 0.05$ ]	-9.9 [***]
SPEI	0.09 [ $\pm 0.03$ ]	2.5 [*]
Layer.III	-0.17 [ $\pm 0.09$ ]	-1.7 [•]
Sporadic mast	0.3 [ $\pm 0.1$ ]	2.9 [**]
Half mast	0.46 [ $\pm 0.11$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

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

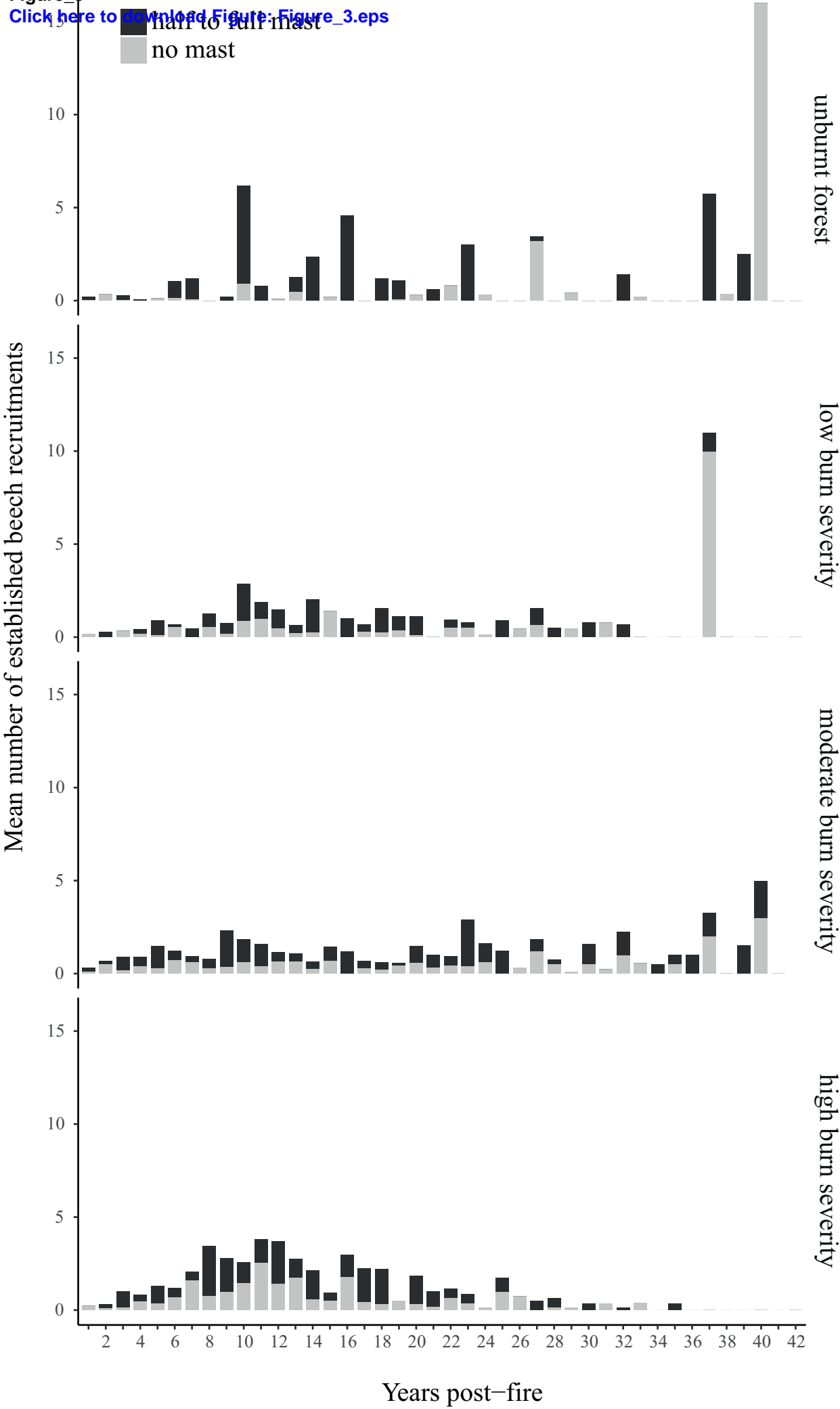
**Figure\_1**  
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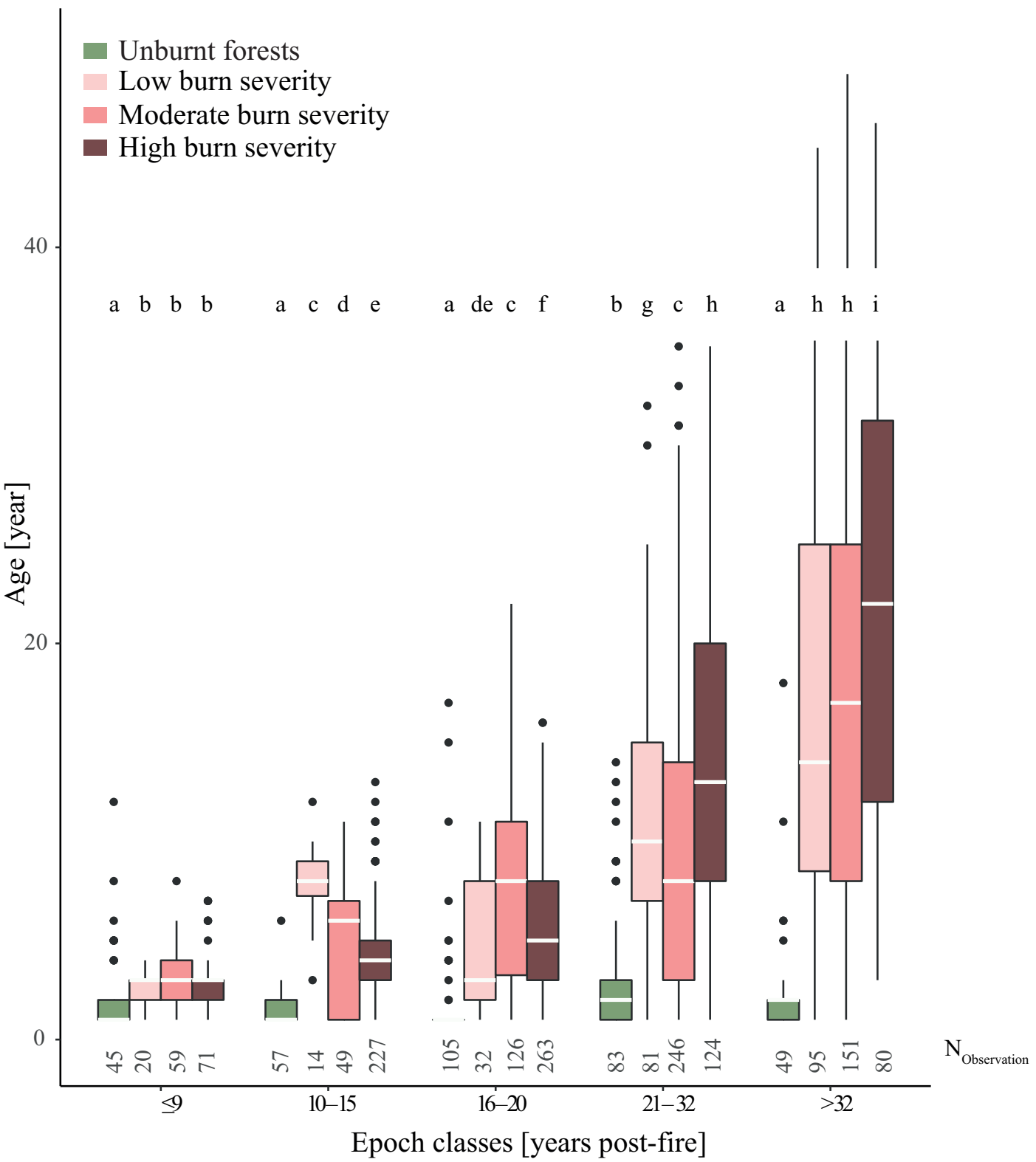
**Figure 2**  
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**Figure 3**  
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Figure\_4  
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**Figure\_5**  
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