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Resilience of European beech forests (*Fagus sylvatica* L.) after fire in a global change context

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Plain language summary

Trees are the dominant species in forests, which provide many ecological, economical and socio-cultural services. Because of their longevity and settledness, forest managers have to know their reaction to future climate change. In our study, we focused on beech (*Fagus sylvatica* L.), one of the most important tree species in Europe, and its species-specific reaction to forest fires.

For Review Only

1 **Resilience of European beech forests (*Fagus sylvatica* L.) after fire in a global**
2 **change context**

3

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17

18 **Abstract**

19 As global climate change is predicted to affect disturbance regimes, uncertainties exist in
20 the reaction of ecosystems historically less disturbed by fire. Marginally studied are
21 regeneration processes in beech (*Fagus sylvatica* L.) forests, one of the most ecological
22 and economically important tree species in Europe. Our primary object was to describe
23 successional pathways in burnt beech forests and detect factors influencing beech
24 regeneration. We applied a chronosequence method to study retrospective successional
25 pathways in burnt beech forests, located in the Southern European Alps. We found
26 abundant beech regeneration, often in co-occurrence with pioneer woody species, in fire
27 sites of mixed burn severity. Both mutually benefited from each other until 20 years
28 postfire when the abundance of the pioneers started to decline. Fires of mixed burn
29 severity resulted in similar effects like after shelter-wood cuts, favouring beech
30 regeneration in early and advanced stages under denser and lighter canopies, respectively.
31 In contrast, high burn severity caused dense layers of early post-fire colonizers (e.g.
32 ferns, shrubs, grass), which might delay beech regeneration for several decades. We
33 conclude that except fires of extraordinary high burn severity, single fire events favour
34 beech regeneration. Episodic forest fires seem therefore not to represent a major threat to
35 the resilience of beech populations under current climatic changes.

36

37 Keywords: wildfires, beech fire ecology, burn severity, tree communities

38

39 **1 Introduction**

40 Climate change will alter future weather patterns (IPCC 2014) and might act
41 synergistically with changes in the land-use. As one result, fire regimes are expected to
42 react dynamically to alterations of the climate-weather-fuel system in terms of fire
43 intensity, seasonality, frequency, and burnt area (Overpeck *et al.* 1990; Flannigan *et al.*
44 2000).

45 First signs of mentioned climatic changes are already recognizable in different fire-prone
46 ecosystems. For instance, more and larger stand-replacing fires have disturbed forests in
47 the western U.S. during the last 20 years (Westerling *et al.* 2006; Dennison *et al.* 2014).

48 In western Mediterranean ecosystems, current fires are more drought-driven and less fuel
49 limited compared to the fires before the 1970ies (Pausas and Fernández-Muñoz 2012).
50 Recent studies focus on changes in fire regimes in highly humanized fire-prone regions
51 (Brotons *et al.* 2013; Luo *et al.* 2013).

52 However, climate and land-use change are global phenomena and fires might
53 increasingly impact also forest ecosystems and species that are historically less prone to
54 fire. This was for instance the case of beech forests in the Southern Alps that experienced
55 exceptionally numerous and large fires during the hot and dry summer 2003 (Ascoli *et al.*
56 2013). Similarly to a majority of tree species growing in the Alps and Central Europe,
57 beech lacks obvious fire resistance or fire-adaptation traits such as a thick bark, a strong
58 resprouting ability, serotiny, or smoke germination cue. Thus mature beech trees are
59 considered highly susceptible to fire (Peters 1997; Packham *et al.* 2012). Nevertheless,
60 paleo-records of beech in the Alps demonstrate its persistence to fire on the long term,
61 even during periods of significant increase in fire frequency (Tinner *et al.* 1999; Tinner *et*

62 *al.* 2000). Furthermore, recent short-term studies on the postfire beech ecology indicate a
63 good potential of beech stands to naturally regenerate after fire events (van Gils *et al.*
64 2010; Maringer *et al.* 2012). Observed processes of postfire beech regeneration may
65 differ as a function of burn severity and postfire management. For instance, low to
66 moderate burn severities increase the survivability of seed providing beech trees and
67 result in favourable short-term germination conditions that initiate rapid beech
68 regeneration processes (Ascoli *et al.* 2015). On the other end, severe fires cause early
69 deaths of beech trees, which might inhibit beech regeneration (Ascoli *et al.* 2013).
70 Unfortunately, to date, little is known about mid-term regeneration processes of beech
71 forests disturbed by fire. Knowledge on the environmental factors triggering postfire
72 beech regeneration processes is of paramount importance for forest managers in view of
73 the expected general increase in fire frequency and intensity (Moriondo *et al.* 2006;
74 Krawchuk *et al.* 2009; IPCC 2014).

75 In order to fill this knowledge gap, we investigated factors affecting tree regeneration in
76 fire disturbed beech stands of the Southern foothill of the European Alps along a climatic
77 gradient in terms of both precipitation and temperature. We used a sample of 36 beech
78 stands burnt between 1970 and 2012 to address the following questions:

- 79 (i) Does beech successfully regenerate in burnt forest stands, i.e. how resilient is
80 beech after fire?
- 81 (ii) Do postfire regenerating pioneer tree species limit beech regeneration?
- 82 (iii) Which are the positive and negative ecological drivers of postfire beech
83 regeneration?

84 2 Material and methods

85 2.1 Study area

86 This study was conducted in the Southern Alps where a general precipitation gradient
87 exists from the drier west (Susa in Piedmont, Italy: 07°3'0"E, 45°08'0"N, Ø temperature
88 12.3°C yr⁻¹, Σ precipitation 778 mm a⁻¹; Arpa Piedmont 2015) to the wetter north-east
89 (Locarno Monti in Ticino, Switzerland: 08°47'43"E, 46°10'12"N, Ø temperature 12.4°C
90 a⁻¹, Σ precipitation 1897 mm yr⁻¹; MeteoSwiss 2015; figure 1). In winter and early spring,
91 northern foehn winds cause episodically relative humidity below 20% accompanied by
92 significant temperature rises (Spinedi and Isotta 2005). These factors favour surface fires,
93 mostly caused by human negligence and usually starting from the lower chestnut belt at
94 300–900 m a.s.l., and spreading into the adjacent beech belt at 900–1400 m a.s.l. (Valese
95 *et al.* 2014). Prolonged droughts in the summertime are rare because dry spells do not last
96 longer than thirty consecutive days (Isotta *et al.* 2014). Therefore, summer fires are
97 scarce in average years, though may occur with particular intensity in case of
98 extraordinary prolonged drought, as was the case in summer 2003 (Valese *et al.* 2014).
99 Average summer (JJA) temperatures are around 20°C accompanied by precipitation sums
100 of 495 mm in the Ticino and 158 mm in Piedmont, respectively (Arpa Piedmont 2015;
101 MeteoSwiss 2015).

102 2.2 Selection of fire sites

103 Along the described precipitation gradient, we selected fire sites that potentially occurred
104 in beech stands as registered since 1970 in the forest fire database of Switzerland
105 (Pezzatti *et al.* 2010) and the Forestry State Corp Database of Italy (Corpo Forestale dello
106 Stato/ Ministero delle Politiche Agricole, Alimentari e Forestali), and overlaid them with

107 regional vegetation maps (Camerano *et al.* 2004; Ceschi 2006) using ArcGIS (version
108 10.0; ©ESRI). In summer 2011, we examined 94 of the selected fire sites across the
109 following criteria: (i) burnt area of beech forest larger than 0.25 ha, (ii) no signs of
110 additional fires during the last 50 years, (iii) no signs of wood pasture or salvage logging,
111 (iv) no postfire artificial regeneration (plantations), (v) pre-fire stands dominated by
112 beech with >95% of the stems, and (vi) crystalline bedrock (Gneiss, Orthogneiss; König
113 1967). From the examined 94 fire sites, 36 satisfied the selection criteria and were
114 considered for the final sampling design. The topographical location of the fire sites
115 regarding ranges in elevation (700–1500 m a.s.l.) and geography (south-west to north-
116 east) resulted in a mean temperature and precipitation gradient from 4–9.4°C and 979–
117 1488 mm, respectively (see appendix A). Thus, the 36 fire sites belonged to the drier and
118 wetter bio-climatic regions of Piedmont and Insubria (Oberdorfer 1964; figure 1).

119 [place figure 1]

120 2.3 *Sample and field assessment*

121 Corresponding to the burn size, we placed one to three transects spaced 50 m apart in
122 elevation along the contour lines (figure 2). Along the transects, circle plots of 200 m²
123 were defined in distances of 30 m, starting in the burnt beech forests in 10 m distance to
124 the burn edge. In each transect a minimum of one control plot was located beyond the
125 edge in the unburnt beech forest, except for six fire sites where it was not possible (see
126 appendix A). According to the final number of plots, the burn size (**AREA**; table 1)
127 within each beech stand was categorized as small (< 4 sample plots), medium (4–9
128 sample plots) or large (> 9 sample plots).

129 Starting from the plot centre, the tree regeneration was assessed in concentric circles of
130 variable sizes (12.5 m², 50 m², 100 m², 200 m²) corresponding to the presence of at least
131 10 post-fire beech individuals or to a maximum circle size of 200 m² (figure 2).
132 Regeneration densities were separately pooled and upscaled to stems ha⁻¹ for the target
133 species beech, and for pioneer woody species with a high annual production of wind-
134 dispersed seeds. Remaining woody species combining traits of barochorous or
135 zoochorous seed dispersal, and a highly variable annual seed production were
136 summarized as “other” (table 2).

137 [place figure 2]

138 2.4 Data collection

139 *Field survey*

140 Between July 2012 and September 2013, a total of 234 plots were assessed in the burnt
141 beech forests and 39 in the unburnt (control plots). Each 200 m²-plot was characterized
142 by slope (**SLOPE**), aspect (**ASP**), elevation (**ELE**), and micro-topography (concave,
143 plane, convex; **TOPO**). Additionally, distances (m) were recorded between the plot
144 centre and burnt edge (**EDGE**) and the closest uphill seed providing beech mother tree
145 (**MOTHER**), respectively. Early postfire colonizers (**EARLY**) such as common broom
146 (*Cytisus scoparius* (L.) LINK), common bracken (*Pteridium aquilinum* (L.) KUHN), and
147 purple moor grass (*Molinia arundinacea* SCHRANK) were assessed in terms of their
148 percental coverage per plot.

149 Coarse woody debris (**CWD**) was only considered if not disintegrated under pressure,
150 and was then assessed following the method of Brown (1974). For this purpose, dead
151 wood was assessed in four different diameter classes (1: 2.5–5 cm, 2: >5–7.5 cm, 3:

152 >7.5–15 cm, 4: >15–30 cm) along the radii of the four cardinal directions, and resulting
153 CWD volumes per plot were finally scaled up to standard values ($\text{m}^3 \text{ha}^{-1}$). Mineral soil
154 samples (N 259) were taken randomly in plots on the fire site and served to measure pH-
155 values (**pH**; 0.01 M CaCl_2 solution).

156 Vegetation structure of pre-fire trees was determined by identifying each tree to the
157 species level, recording the diameter at breast height (1.30 m), the tree height, and the
158 percentage of the crown volume killed. Latter parameter was visually estimated by the
159 volumetric proportion of crown killed compared to the space occupied by the pre-fire
160 crown volume (Hood *et al.* 2007). All diameters at breast heights of pre-fire beeches were
161 pooled plot-wise and scaled up to basal area ($\text{m}^2 \text{ha}^{-1}$).

162 Woody regeneration was also identified to the species level (Ammann 2005; Lauber *et al.*
163 2007), and categorized as seedlings (height ≤ 20 cm) and saplings (height > 20 cm).
164 Seedlings were counted on species level separately for living and dead individuals.
165 Saplings height and dbh ($> 1\text{cm}$) were measured individually for dead and living
166 individuals.

167

168 *Assessment of burn severity*

169 Regarding the assessment of burn severity (Turner *et al.* 1997) at plot level, we faced the
170 difficulty to estimate retrospectively severities in different aged fire events. From the
171 various approaches existing (reviewed in Johnson and Miyanishi 2007; Keeley 2009), we
172 selected crown volume (Lampainen *et al.* 2004) and basal area of killed trees (Larson and
173 Franklin 2005) as components to build a severity range that is weighted by postfire years.
174 Accordingly, we defined low burn severity independently from the burn age, if canopy

175 loss and killed basal area of trees per plot were below 5% and 20%, respectively.
176 Contrastingly, high burn severity was indicated by extensive canopy loss and basal area
177 killed, both above 50% in the first postfire decade or if both parameters increased steadily
178 to more than 90% in the following years. We assigned moderate burn severity if both
179 canopy opening and basal area of killed trees ranged between 20% and a maximum of
180 90% during the whole time since the fire event.

181

182 *Climate variables*

183 Precipitation and air temperature were obtained for each fire site from the WorldClim
184 Database (Hijmans *et al.* 2005). Average long-term sums of precipitation (**PREC**) and
185 means of temperature (**TEMP**) refer to the period from 1950–2010. For local climatic
186 conditions, we calculated a detrended correspondence analysis (DCA; Oksanen *et al.*
187 2015) based on tree species composition in the burnt beech forest. The first DCA-axis
188 represents a shift from drier to wetter conditions (**TURN**).

189 *2.5 Data analysis*

190 Resource needs and availability during the regeneration process change with progressive
191 tree development. Thus for the described statistic, the fire sites were categorized together
192 with their corresponding control plots, into different postfire age classes (Horn 1974)
193 based on the date of fire, with “≤ 9 years”, “10–15 years”, “16–21 years”, “22–32 years”,
194 and “>32 years”.

195 To evaluate the influence of explanatory variables (listed in table 1) on postfire beech
196 regeneration, we performed individual models for beech seedlings (**sFAG**) and saplings
197 (**SFAG**). To detect the influence of fire on regeneration processes, we considered for the

198 seedlings and saplings models only fire sites older than one and six years, respectively.
199 Additionally to the density models, we performed a stem height model with averaged
200 beech saplings heights (**hFAG**) at plot-level as response variable. Models were run for
201 both the full data set (N 214), the Insubric (N 148) and Piedmont (N 66) regions to
202 prevent a levelling of regional specific environmental parameters.

203 For model selection, we examined each data set for intra-class correlation (Bliese 2000).
204 This resulted in general linear models (*GLM*) for the tree height models, and generalized
205 mixed effect models (*GLMM*) with burn location as random factor for regeneration
206 models (Pinheiro *et al.* 2015). Data exploration for models performing followed the
207 guidelines of Zuur *et al.* (2010). Therefore, collinearity among covariates was detected by
208 calculating the Pearson correlation factor as well as by the variance of inflation (VIF).
209 Predictors were chosen according to both the ecological relevance and the precision of
210 assessment (measurement vs. estimation). To meet the assumption of collinearity, we
211 excluded the variables **MOTHER** ($r^2 = 0.72$ with **EDGE**), **REG** ($r^2 = 0.8$ with **PREC**),
212 and burn severity (**SEV**) from all beech regeneration models (table 1). The latter was
213 highly correlated with the basal area of survived pre-fire trees (**BASAL**) and with the
214 cover of early postfire colonizers (**EARLY**). For the regional specific models, we
215 excluded **TEMP** ($r^2 = -0.7$ with **AGE**), and **mCLIM** ($r^2 = 0.77$ with **pH**, $r^2 = -0.56$ with
216 **EARLY**) for Piedmont, and **TEMP** ($r^2 = -0.8$ with **PREC**) for Insubric models.

217 For model performance, regeneration densities as response variables were transformed
218 with the Box-Cox transformation (Fox and Weisberg 2015), an often used and more
219 general approach in ecological modelling (e.g. Krebs 1999). Continuous explanatory
220 variables were standardized to allow model comparison between regions (Wimmer and

221 Dominick 2010). Both, regeneration and growth analyses were conducted by starting
222 with variables of significant effects, and integrating additional variables and interactions.
223 For model comparisons, we calculated the maximum likelihood (ML) and provided
224 ANOVA tests. The best model was finally run with restricted maximum likelihood
225 (REML) to compute standard errors and p-values of predictors (Harville 1977).
226 All calculations were carried out using the statistical software R Version 3.0.2 (R
227 Development Core Team 2014).

228 [place table 1]

229

230 3 Results

231 3.1 Forest structure

232 Of the examined burnt beech forest plots, 14.5% were assigned to low, 44% to moderate
233 and 40% to high-severity burns. In the burnt beech stands mean basal area of pre-fire
234 trees survived the fires was $19.36 \text{ m}^2 \text{ ha}^{-1}$, ranging from 2.56 m^2 to $56.1 \text{ m}^2 \text{ ha}^{-1}$.
235 Contrastingly, the basal area in the unburnt beech forests was in average double as high
236 ($39.4 \text{ m}^2 \text{ ha}^{-1}$). With regard to the different classes of postfire age, basal area of living
237 pre-fire trees in low severity fire sites ranged between 33.5 and $56.1 \text{ m}^2 \text{ ha}^{-1}$, and was
238 therefore up to more than ten times higher than basal area in high burn severity sites
239 (figure 3).

240 [place figure 3]

241 3.2 Postfire tree regeneration

242 A total of 32 woody species were found to be regenerating in the burnt beech forests, of
243 which 11 were also present in the unburnt forests (table 2). Out of these species, 32%
244 showed pronounced pioneer tree traits with stem densities ranging from below 1 stems
245 ha^{-1} up to $2343 \text{ stems ha}^{-1}$ in the burnt beech forests, while they were totally absent in the
246 unburnt beech forests (table 2).

247 The target species beech dominated in terms of densities and frequency in the burnt as
248 well as in the unburnt forests. It regenerated in all fire sites and in 91.2% of the
249 investigated burnt plots (table 2). Here, both seedlings and saplings grew with average
250 densities of $7,059$ and $7,233 \text{ stems ha}^{-1}$, respectively, which was double as high than in
251 the unburnt beech forests. Beech regeneration was missing in only 8.8% of the burnt
252 plots. Half of these plots burnt just the previous vegetation period and beech regeneration

253 densities were there in general low (50–350 stems ha⁻¹). The remaining plots without
254 beech regeneration burnt more than 10 years ago with an extraordinary high severity and
255 display now a dense coverage of early postfire colonizers such as common bracken,
256 common broom and purple moor grass.

257 Next to beech, only pioneer birch (*Betula pendula* ROTH) grew also abundant in 60% of
258 the investigated plots with an average sapling density of 2,343 stems ha⁻¹, which
259 corresponds to one third of the beech density. In seedlings, high densities were recorded
260 for Scotch laburnum (*Laburnum alpinum* J.PRESL, Ø 4,193 stems ha⁻¹) and ash (*Fraxinus*
261 *excelsior* L., Ø 2,699 stems ha⁻¹). In three fire sites with mostly high burn severity, a rare
262 number of invasive alien plant species with pioneer character were found such as empress
263 tree (*Paulownia tomentosa* (THUNB.) STEUD.), tree of heaven (*Ailanthus altissima* (MILL.)
264 SWINGLE), and black locust (*Robinia pseudoacacia* L).

265 [place table 2]

266 *Temporal dynamic of tree regeneration*

267 With view on the different postfire ages, beech seedlings densities were half as abundant
268 (10,092 ± 2795 stems ha⁻¹) than pioneer trees during the first 9 years postfire (figure 4).
269 The latter peaked (21,373 ± 9399 stems ha⁻¹) within this period but rapidly declined to
270 small numbers in older fire sites. In contrast, the numbers of beech seedlings were quite
271 similar in younger fire sites (up to 20 years) and dropped down to an average density of
272 2135 ± 599 stems ha⁻¹ later in succession (> 32 years postfire). Saplings of beech and
273 pioneer trees reached nearly similar densities (5812 ± 1978 and 7515 ± 1667 stems ha⁻¹)
274 ten to fifteen years postfire. In correspondence to pioneer seedlings of the first decade
275 postfire, saplings densities peaked ten to fifteen years postfire and steadily decreased later

276 in succession. Beech saplings were consequently most abundant in older fire sites, i.e.
277 22–32 years postfire and >32 years postfire, with values of $14,256 \pm 4424$ and $9372 \pm$
278 2070 stems ha^{-1} , respectively. In comparison to the burnt beech stands, beech
279 regeneration was less abundant in the unburnt beech forests with percentages from 10%
280 to 28% (figure 4). Regeneration densities of other trees played a subordinated role in both
281 the burnt and unburnt beech forests.

282 [place figure 4]

283 *Regeneration height*

284 The height of pioneer and beech regeneration rapidly increased after forest fires (figure
285 5). Pioneer trees were two to six times taller than beech saplings, but both were nearly
286 similar in height in the period from 32 years postfire. In the unburnt beech forests,
287 regenerating beech trees reached heights between 1.3 ± 0.32 m and 2.18 ± 0.65 m, and
288 were therefore only half the size of those in the burnt beech forests in the late
289 successional stages.

290 The *dbh* of pioneer species increased faster in comparison to beech trees. Pioneers
291 reached an average *dbh* of 3.3 cm in 16–20 years old burnt beech forests, which
292 correspond to a growth rate of 1 cm per postfire age class. In fire sites of the same age,
293 *dbh* of beech regeneration amounted to only 30–50% of the pioneer *dbh*.

294 [place figure 5]

295 *3.3 Drivers of postfire beech regeneration*

296 With view on the different regeneration stages (seedlings vs. saplings), seedlings
297 generally grew denser under a closer canopy of living pre-fire beeches, but were mainly
298 restricted by denser cover of early postfire colonizers (common bracken, common broom,

299 purple moor grass) (table 3). Next to those general factors, the full model indicated
300 significant regional differences due to the positive correlation with the amount of
301 precipitation (PREC). In particular in the Insubric region, seedlings densities were
302 negatively correlated with aspect (higher on north to east facing sites), postfire age (AGE;
303 higher in younger burnt beech forests), and with the distance to the burn edge (EDGE;
304 higher closer to intact forests). The best model explained 64% of the variation (deviance
305 D^2) in beech seedlings densities. In the Piedmont, seedling regeneration of beech was
306 positively correlated (quadratic term) to soil pH (higher densities with increasing pH) and
307 elevation (ELE). The linear term of the latter was negatively correlated with beech
308 seedlings densities (high densities on intermediate elevation). The overall model for the
309 Piedmont explained 55% of the variation in seedlings density.

310 The cover of early post-fire colonizer and basal area of living pre-fire beeches also
311 showed a significant influence on beech saplings densities. In contrast to the seedlings
312 models, however, the basal areas of living pre-fire beeches were negatively correlated
313 with the saplings density (higher under smaller canopy cover). In accordance with the
314 seedling models, sapling densities were negatively correlated with early postfire
315 colonizer. Additionally, the overall beech sapling densities showed a significant positive
316 correlation with the volume of coarse woody debris. In the Insubric region, beech sapling
317 densities were positively correlated with postfire age and negatively with elevation, with
318 a total of 32% explained variation in stem density. For the Piedmont region, sapling
319 density was negatively correlated with aspect. Together with the mentioned general
320 variables BASAL, EARLY and CWD, the best model for this region explained 63% of
321 the variation in saplings stem density.

322 [place table 3]

323

324 Height growth of beech saplings was generally improved by the height of non-beech
325 regeneration, as revealed by a high positive correlation (table 4). In Insubria, beech height
326 was also significantly and positively correlated with postfire age (taller in older burnt
327 beech forests), and negatively correlated with basal area of living pre-fire beeches (taller
328 under lighter canopy). The best Insubric model explained 72% of variance in beech
329 sapling heights. In the Piedmont, beech sapling heights were positively correlated with
330 elevation (ELE) and the distance to the burns edge (EDGE; taller with increasing
331 distance). In contrast, soil pH and the quadratic term of early post-fire colonizers
332 (EARLY) showed slightly negative correlations. The overall sapling growth model for
333 Piedmont had an explanatory power of 70%.

334 [place table 4]

335 **4 Discussion**

336 *4.1 Presence of beech regeneration*

337 Our results suggest that beech starts to regenerate soon after fire disturbance, which
338 confirms the conclusions of short-term studies in burnt beech forests (Van Gils *et al.*
339 2010; Maringer *et al.* 2012; Ascoli *et al.* 2013; Ascoli *et al.* 2015). The high variability in
340 beech regeneration densities found during different successional stages is comparable to
341 results from shelterwood and wind-throw research. For example, the number of natural
342 beech regeneration ranged from 10,000–70,000 stems ha⁻¹ in a managed forest six years
343 after canopy opening (Mountford *et al.* 2006; Barna 2011), while regeneration densities
344 were even double as high four years after a mast (Bílek *et al.* 2009).

345 As beech regeneration was abundant during all successional stages, we infer that they
346 represent in most cases a solid basis for new forests (Olesen and Madsen 2008). Plots
347 with no beech regeneration were found in one-year-old fire sites that lacked a seed mast
348 year and where regeneration processes have not yet started (Johnson and Miyanishi
349 2007). Lacking beech regeneration in older burnt beech forests related to high burn
350 severity, where dense layers of early postfire colonizers had accumulated (common
351 bracken, common broom and purple moor grass).

352 4.2 *Interaction between pioneer and beech regeneration*

353 Pioneer woody species did not hinder beech from regenerating after forest fire. Both,
354 beech and pioneers co-occurred in considerable abundance for 20 years. During this early
355 growth stage, we found no evidence of competitive exclusion by pioneer woody species.
356 On the contrary, after 20 years beech becomes dominant by eventually outcompeting
357 other woody species. While shade tolerant beech saplings are able to grow tall under the
358 canopy of fast growing pioneer trees and thus benefit from a nurse crop effect in terms of
359 both shade and protection from browsers, continuous beech growth during a next phase
360 results in an crown expansion and successful competition for light (Leder 1993; Walker
361 1999).

362 The observation of rapid beech regeneration in most plots perfectly fits the direct re-
363 growth theory postulated by Romme *et al.* (2011). Beech forests disturbed by a single
364 surface fire seem to recover to the pre-disturbance species composition within a short
365 period of only 40 years. Similar successional paths of beech have been also reported in
366 post-wind-throw studies in Central Europe (Kompa 2004; Kompa and Schmid 2005;
367 Kramer *et al.* 2014).

368 4.3 *Ecological drivers for beech regeneration*

369 *Limiting factors for beech regeneration*

370 Among the factors limiting beech regeneration, we consider the abundance of early
371 postfire colonizers such as common bracken, common broom, and purple moor grass as
372 the most important. Beech regeneration was dense up to an intermediate abundance of
373 early colonizers cover, but was reduced or even almost absent in case of their increasing
374 cover. Similar effects of competitive shrubs and ferns in burnt beech forests were
375 presented in studies from Spain (Herranz *et al.* 1996) and Piedmont (Ascoli *et al.* 2013).
376 Indeed, bracken was detected to delay beech regeneration for several years in France
377 (Koop and Hilgen 1987), and in Switzerland after wind-throw (Brang *et al.* 2015).
378 Gramineous species such as purple moor grass can also exclude beech regeneration by
379 establishing early in spring, building dense root systems and rapidly extracting nutrients
380 and water from the soil (Harmer 1995; Coll *et al.* 2003; Provendier and Balandier 2008).

381

382 *Positive drivers for beech regeneration*

383 In general, beech regeneration was improved under open canopy and in proximity to seed
384 sources as indicated by the basal area of survived pre-fire trees. In particular, while a
385 denser canopy favours beech regeneration in early stages, sapling growth improves under
386 light (e.g. Barna 2011). Our results are consistent with those from shelterwood cuttings,
387 where a dense shelter provides seeds for recruitments and protects seedlings from
388 competition (Petritan *et al.* 2007). Under light shelter and towards the gap centre, sapling
389 density and height growth improved, respectively (Mountford *et al.* 2006; Barna 2011).

390

391 *Climatic factors*

392 In the investigated fire sites, beech regeneration is not limited by climatic factors such as
393 precipitation and temperature. Annual precipitation sums in the study region range
394 between 778 and 1897 mm, which are above the precipitation range of beech forests in
395 Central Europe (520 mm yr⁻¹ to 1030 mm yr⁻¹; Leuschner *et al.* 2006). However, the two
396 regions in the Southern Alps are characterized by sufficient rainfall in summer (Isotta *et*
397 *al.* 2014), and soils on crystalline bedrock (Gneiss, Orthogneiss; König 1967). Thus, the
398 synergetic effect of both rarely allows a water storage capacity below beech's limit (<
399 65–70 l m⁻²; Gärtner *et al.* 2008). Nevertheless, our results indicate denser beech
400 regeneration on northeast rather than on southwest facing slopes, suggesting an effect of
401 local site conditions (humidity in particular) on beech growth and eventually on beech
402 distribution (see Ceschi 2006 for the Insubric region).

403

404 *Regeneration window*

405 Beech seedlings establish soon after a forest fire of mixed severity (van Gils *et al.* 2010;
406 Maringer *et al.* 2012; Ascoli *et al.* 2013). Based on the long surveyed period of this study
407 we can document an increase of beech seedlings densities up to 20 years postfire, and a
408 decline from thereon. At the same time, beech sapling densities continuously increase.
409 Ongoing growth of beech saplings is guaranteed if sufficient light is available.
410 Accordingly, the regeneration window for beech is limited by light. In particular,
411 Szwagrzyk *et al.* (2001) concluded that canopy openings are essential also for shade
412 tolerant beech saplings regarding sapling banks. In their study, the sampling banks were

413 up to 10 years old in a managed Polish beech forest. And Petritan *et al.* (2007) found an
414 open regeneration window of 20 years after shelterwood cut.
415 However, not only the light window for sapling growth seems to be crucial for successful
416 beech regeneration, but also availability of seeds soon after disturbance. Previous short-
417 term studies assessed the positive effect of disturbances synchronized with masting
418 (Madsen and Larsen 1997; Olesen and Madsen 2008; Drobyshev *et al.* 2010), and
419 detected burn severity as a key factor in this process (Ascoli *et al.* 2015). The present
420 study detected dense cover of early post-fire colonizers as limiting beech seed
421 germination or seedling growth and, in contrast, a gradual canopy opening as favouring
422 the growth of beech saplings. Both factors are controlled by burn severity, which
423 influences the speed of the opening and thus the time frame of the regeneration window.
424 This raises the question on environmental factors triggering the pulse of seed germination
425 and subsequent seedlings establishment, in particular the interaction of burn severity,
426 canopy opening, environmental factors and seed mass production, as already examined
427 for other mast-seeding trees (Peters *et al.* 2005; Iverson *et al.* 2008; Abrams and Johnson
428 2013).

429 **5 Conclusion**

430 With the present study we contribute to the knowledge in beech fire ecology by showing
431 successional processes over a period of 43 years postfire. We demonstrated the success of
432 beech over pioneer woody regeneration after single forest fires of mixed burn severity.
433 Our results therefore may explain the findings of the paleo-botanical studies of the
434 Insubric region of persisting beech in times of increased fire frequency (Tinner and
435 Conedera 1995; Tinner *et al.* 2000). Apart from fires with extraordinary high-severity

436 burn, single fire disturbances are revealed to be favourable to beech stand regeneration in
437 the Southern Alps. Either by direct regrowth or by overgrowing pioneer wood, beech
438 regeneration processes seem acting independently from gradients in temperature and
439 precipitation in the study region. Thus episodic forest fires might not represent a major
440 threat to the resilience of beech populations under current climatic changes. In contrary,
441 beech may benefit from fire disturbance, as it was already postulated in post-glacial
442 beech migration processes (Lindbladh *et al.*, 2007; Bradley *et al.*, 2013).

443

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451

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641

642

Appendix A: Investigated fire sites sorted by the climatic regions (Piedmont, Insubria) and the date of fire.
Further listed: class of the burnt area (small<4 plots, medium 4-9 plots, large >9 plots), years postfire (age),
Ø annual temperature (T), Σ annual precipitation (P) (both data WorldClim), and number of plots
investigated in the burnt (N_b) and unburnt beech forests (N_c).

Regions	Municipality	burn size	date of fire	age	E	N	T [°C]	P [mm]	N _b / N _c
Piedmont									
	Sparone	large	28.12.80	34	382545	5030710	6	1109	16/1
	Rosazza	medium	19.01.90	24	418645	5058661	5.8	1195	5/0
	Corio	large	15.02.90	24	385562	5021543	7.5	989	10/2
	Arola	large	04.06.97	16.5	449208	5074546	7.9	1172	13/0
	Varallo	large	11.08.03	10.5	442360	5078456	7.2	1186	11/1
	Condove	large	01.03.08	7	364870	5000781	7.4	979	11/1
	Giaglione*	medium	03.03.12	2	341650	5001664	6.4	1067	8/1
Insubric									
	Indemini	small	07.08.70	42.5	488196	5105864	6.4	1349	3/1
	Minusio	small	04.11.71	41	484123	5116368	4.7	1415	2/1
	Gordevio*	small	09.03.73	40	482190	5116678	6.5	1355	1/0
	Moghegno	small	27.11.73	39	492538	5101434	8.3	1310	3/1
	Gordola	small	28.03.76	37	490491	5116753	6.0	1365	2/1
	Arbedo	large	20.03.76	37	506667	5116933	7.1	1290	13/1
	Astano	small	01.01.81	32	485796	5096454	8.2	1304	2/1
	Indemini	large	01.01.81	32	484488	5104578	5.5	1376	12/1
	Intragna	small	04.01.87	27	477570	5112256	7.6	1318	3/0
	Aurigeno	small	01.08.89	23.5	478824	5118037	8.2	1308	2/1
	Mugena	medium	23.03.90	23	492683	5105828	7.1	1330	6/1
	Novaggio	small	10.03.90	23	486829	5098133	5.4	1371	2/1
	Avegno	small	05.05.90	23	482007	5116521	6.5	1355	2/0
	Pollegio	medium	09.04.95	18	492574	5139100	5.3	1391	5/2
	Tenero	small	21.04.96	17	487212	5116007	8.5	1315	3/0
	Ronco s.A.	medium	15.03.97	16	477225	5110649	6.6	1349	6/1
	Magadino	large	15.04.97	16	491560	5107650	6.9	1335	26/3
	Sonvico	medium	03.04.97	16	501239	5101934	8.8	1300	5/2
	Arbedo	small	14.11.98	14	506770	5115571	8.5	1302	3/2
	Indemini*	small	19.12.98	14	488487	5106098	6.6	1347	1/1
	Gordevio	large	24.04.02	11	482190	5116678	6.5	1355	13/4
	Maggia	small	12.03.02	11	477394	5124084	5.7	1388	3/1
	Bodio	medium	18.03.03	10	495105	5136703	4	1436	5/1
	Dissimo	medium	06.04.03	11	466503	5111215	5	1402	5/1
	Someo	small	06.08.03	9.5	475281	5126733	5.6	1395	3/1
	Villadossola	large	16.03.05	9	440231	5098748	5.6	1305	11/1
	Cugnasco	medium	03.04.06	7	494084	5114855	9.4	1317	4/1
	Ronco s.A.	small	23.04.07	6	477225	5110649	6.6	1349	2/1

Druogno*	large	26.03.12	2	453207	5110682	4.8	1394	12/1
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* Fire sites excluded from mixed effect models

For Review Only

Table 1: Explanatory variables for (mixed effect) models of beech sapling height (hFAG) and regeneration densities (sFAG, SFAG). Predictors used (x) or not used (---) in all models, or excluded from a specific model (•ⁱ: Insubric, •^p: Piedmont) because of collinearity.

Explanatory variables	Abbreviation	Unit	Models		
			hFAG	sFAG	SFAG
<i>topography</i>					
slope	SLOPE	%	x	x	x
aspect	ASP	°	x	x	x
elevation	ELE	m a.s.l.	x	x	x
micro-topography	TOPO	factor	---	x	x
<i>climate and geography</i>					
temperature	TEMP	°C	• ⁱ	• ^{ip}	• ^{ip}
precipitation	PREC	mm	x	x	x
<i>light and nutrients</i>					
soil pH	pH		---	x	x
basal area pre-fire beeches	BASAL	m ² ha ⁻¹	x	x	x
coarse woody debris	CWD	m ³ ha ⁻¹	• ^p	x	x
shift in woody species	mCLIM		---	• ⁱ	• ⁱ
<i>biotic factors</i>					
non-beech density	dREG	N ha ⁻¹	---	x	x
Ø non-beech height	hREG	cm	x	---	---
early postfire colonizer	EARLY	%	x	x	x
<i>input beech seeds</i>					
distance forest edge	EDGE	m	x	x	x
distance mother tree	MOTHER	m	---	• ^{ip}	• ^{ip}
<i>fire related variables</i>					
years postfire	AGE	yr	• ⁱ	•	•
area burnt beech forest	AREA	factor	• ⁱ	• ⁱ	• ⁱ
burn severity	SEV	factor	• ^{ip}	• ^{ip}	• ^{ip}

Table 2: Regeneration densities of woody species in the burnt and unburnt beech forests. Frequency of species presence [%] in the plots [N 234] and the presence of mother-trees (M) indicated by ● are noted for the burnt forests.

Species	Burnt beech forest				Plots [%]	M	Unburnt beech forest	
	N [ha ⁻¹] saplings		N [ha ⁻¹] seedlings				N [ha ⁻¹] regeneration	SE
	Ø	SE	Ø	SE				
Target species								
<i>Fagus sylvatica</i> L.	7059	992	7233	982	91	●	3042	959
Pioneers with wind-dispersal								
<i>Betula pendula</i> Roth	2343	353	390	70	60	●	0	0
<i>Populus tremula</i> L.	184	145	150	140	1	●	0	0
<i>Laburnum alpinum</i> J.Presl	146	62	4193	1936	9		0	0
<i>Salix caprea</i> L.	143	42	83	24	22		0	0
<i>Coryllus avellana</i> L.	63	25	9	4	7		0	0
<i>Alnus glutinosa</i> (L.) Gaertn.	3	3	0	0	<1	●	0	0
<i>Ailanthus altissima</i> (Mill.) Swingle	2	2	0	0	<1		0	0
<i>Populus nigra</i> L.	0	0	1	1	1		0	0
<i>Paulownia tomentosa</i> (Thunb.)	1	1	0	0	<1		0	0
<i>Populus alba</i> L.	0	0	<1	<1	<1		0	0
<i>Robinia pseudoaccacia</i> L.	<1	<1	0	0	<1		0	0
Other trees with barochorous /zoochorous seed dispersal								
<i>Sorbus aucuparia</i> L.	301	166	195	67	25	●	219	209
<i>Sorbus aria</i> Crantz	222	99	79	18	25	●	8	7
<i>Fraxinus excelsior</i> L.	196	89	2699	795	27	●	351	159
<i>Acer opulifolium</i> Chaix.	55	47	120	120	1		0	0
<i>Castanea sativa</i> Mill.	55	12	61	15	24	●	32	19
<i>Acer pseudoplatanus</i> L.	39	19	1012	596	17	●	59	47
<i>Prunus avium</i> L.	14	7	60	19	14	●	8	5
<i>Frangula alnus</i> Mill.	12	9	8	8	<1		0	0
<i>Quercus petraea</i> (Mattuschka)	11	4	35	11	11	●	3	3
<i>Larix decidua</i> Mill.	11	4	27	12	7	●	0	0
<i>Picea abies</i> (L.)	11	5	7	5	3	●	1	1
<i>Pinus sylvestris</i> L.	3	3	1	1	1	●	0	0
<i>Ilex aquifolium</i> L.	2	1	4	3	2		4	3
<i>Pinus strobus</i> L.	2	2	0	0	1		0	0
<i>Juglans regia</i> L.	2	1	0	0	<1		0	0
<i>Acer campestre</i> L.	1	1	3	1	1		0	0
<i>Tilia cordata</i> Mill.	1	1	0	0	<1		0	0
<i>Quercus pubescens</i> Willd.	0	0	7	5	1	●	0	0
<i>Taxus baccata</i> L.	0	0	1	1	1	●	3	3
<i>Acer platanoides</i> L.	0	0	<1	<1	<1		0	0

Table 3: Estimates (β) and standard error (SE(β)) of best mixed-effect models for beech seedling and sapling regeneration, using all data pooled together (Full), and separately for the regions Piedmont and Insubria. Intercept (I) and residuals (Res) of the Standard Deviation are given for the random effect. Variable names are related to those reported in table 1.

D ² Variables	seedlings						saplings					
	full 54%		Piedmont 55%		Ticino 64%		full 47%		Piedmont 63%		Ticino 32%	
	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
<i>fixed effects</i>												
Intercept	12.7***	1.1	11.2***	1.7	18.9***	1.7	18.4***	1.4	19.8***	2.6	13.9***	.9
BASAL	2.1***	.5	2.8***	.9	3.3**	.9	-2.3***	.6	-2.5*	1.1	-1.3*	.5
BASAL ²					-1.4*	.6						
EARLY ²	-2.0***	.4	-1.2•	.6	-2.9***	.8	-2.1**	.5	-2.9***	.7	-1.0•	.5
AGE	-3.1***	.7			-6.5**	1.5	3.5*	1.1			3.2**	.7
ASP					-2.3**	.8	-1.1*	.7	-3.1***	1.1		
EDGE					-1.3**	.8	0.8*	.6				
ELE			-0.8***	1.1							-1.9*	.7
ELE ²			0.3***	.8								
CWD							2.3***	.7	7.8**	2.1	1.1*	.7
CWD ²									-1.6**	.6		
MICRO ₂							2.3*	1.3			0.7•	1.1
MICRO ₃							4.3*	1.5			3.4•	1.4
SLOPE ²							-0.7*	.4				
PH ²			6.1**	1.1								
PREC	2.1	.9										
PREC ²	1.6*	.7										
AGE: EARLY ²					1.9**	.7						

random effect

	I	Res	I	Res	I	Res	I	Res	I	Res	I	Res
burn	2.7	5.6	5.4	6.4	5.8	6.9	4.6	7.1	5.6	6.6	1.5	5.1

Signif. codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' 1

For Review Only

Table 4: Results of the generalized linear model of beech sapling height using all data pooled together (Full), or separately for the regions Piedmont and Insubria. Variable names are related to those reported in table 1.

Variables	Full		Piedmont		Insubria	
Ø height [m]	2.27		0.94		1.80	
D ²	78%		70%		72%	
	β	SE	β	SE	β	SE
Intercept	4.5***	.05	4.3***	.1	4.4***	.05
hREG	0.7***	.1	0.6***	.1	0.4**	.1
AGE	0.7***	.1			1***	.1
ELE	0.4***	.1	0.4***	.1		
EDGE			0.3*	.1		
pH			-0.3***	.1		
EARLY ²			-0.2*	.1		
BASAL					-1.2*	.1
TEMP	0.1**	.1				
PREC	-0.01	.1				
TEMP: PREC	-0.2***	.1				
AGE: hREG	-0.3***	.1				

Signif. codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' 1

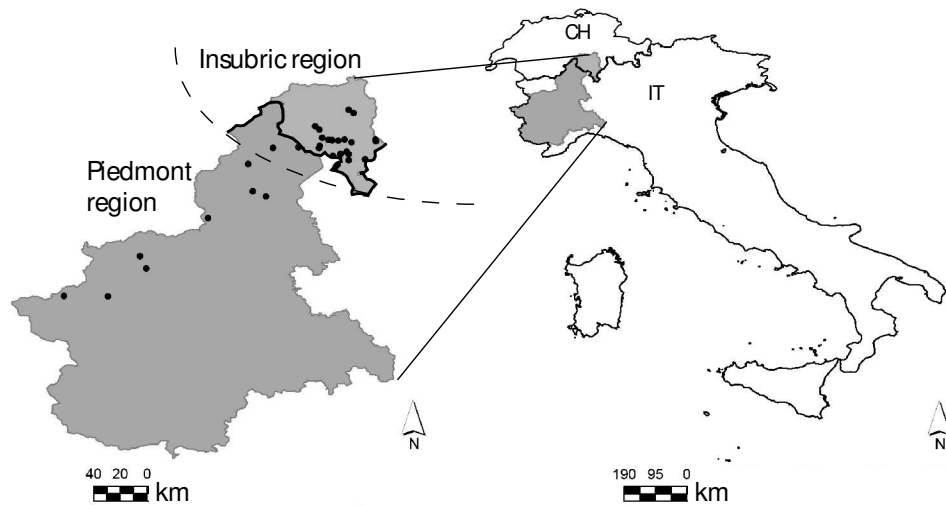


Figure 1: In grey the study region extending on the southern foothill of the Alps from the canton Ticino (Switzerland) to the Piedmont (Italy). Fire sites (black dots) in beech forests subdivided into the drier Piedmont (precipitation $< 1290 \text{ mm a}^{-1}$) and in the wetter Insubric region (precipitation $\geq 1290 \text{ mm a}^{-1}$).

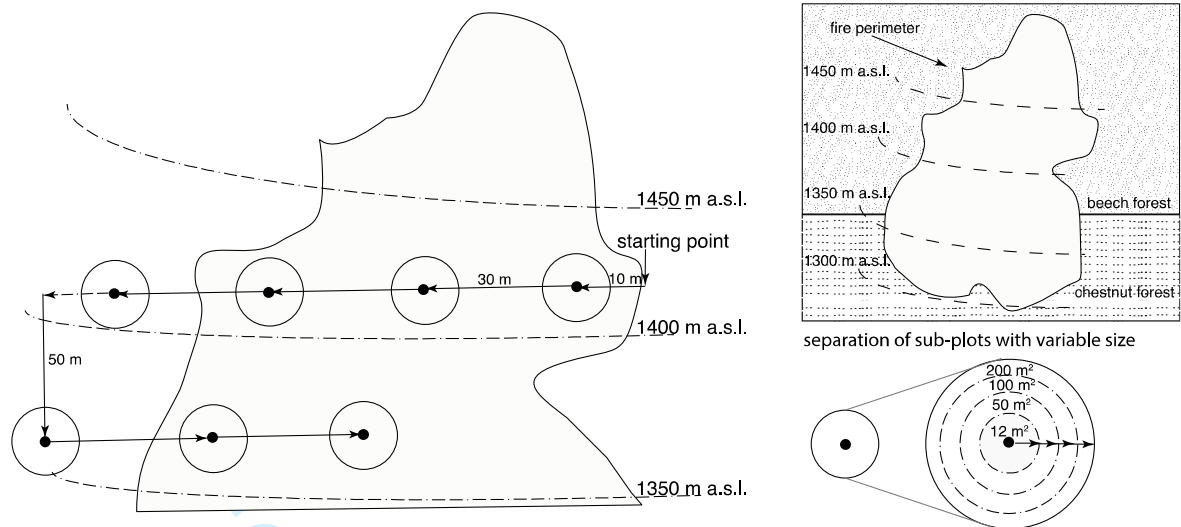


Figure 2: Sampling design in a burnt beech forest that resulted typically from fires starting in the chestnut belt and expanding upslope into the adjacent unburnt beech belt (figure top right). Circular plots of 200 m² were placed in 30 m distance along horizontal transects from the burnt into the unburnt beech forest (figure left), and tree regeneration was assessed in subplots of variable sizes (figure bottom right).

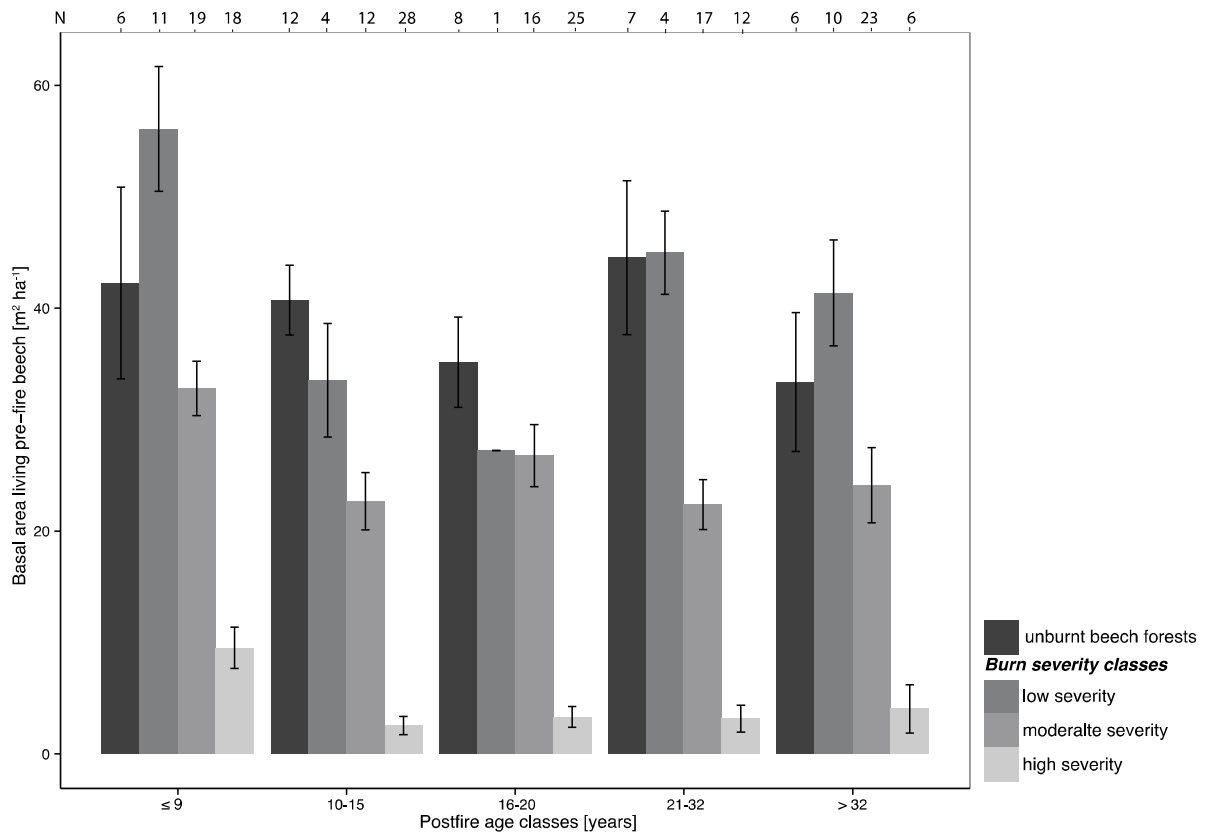


Figure 3: Basal area of living pre-fire beeches in low, moderate and high severity fire sites and the corresponding unburnt beech forests, grouped by postfire age classes.

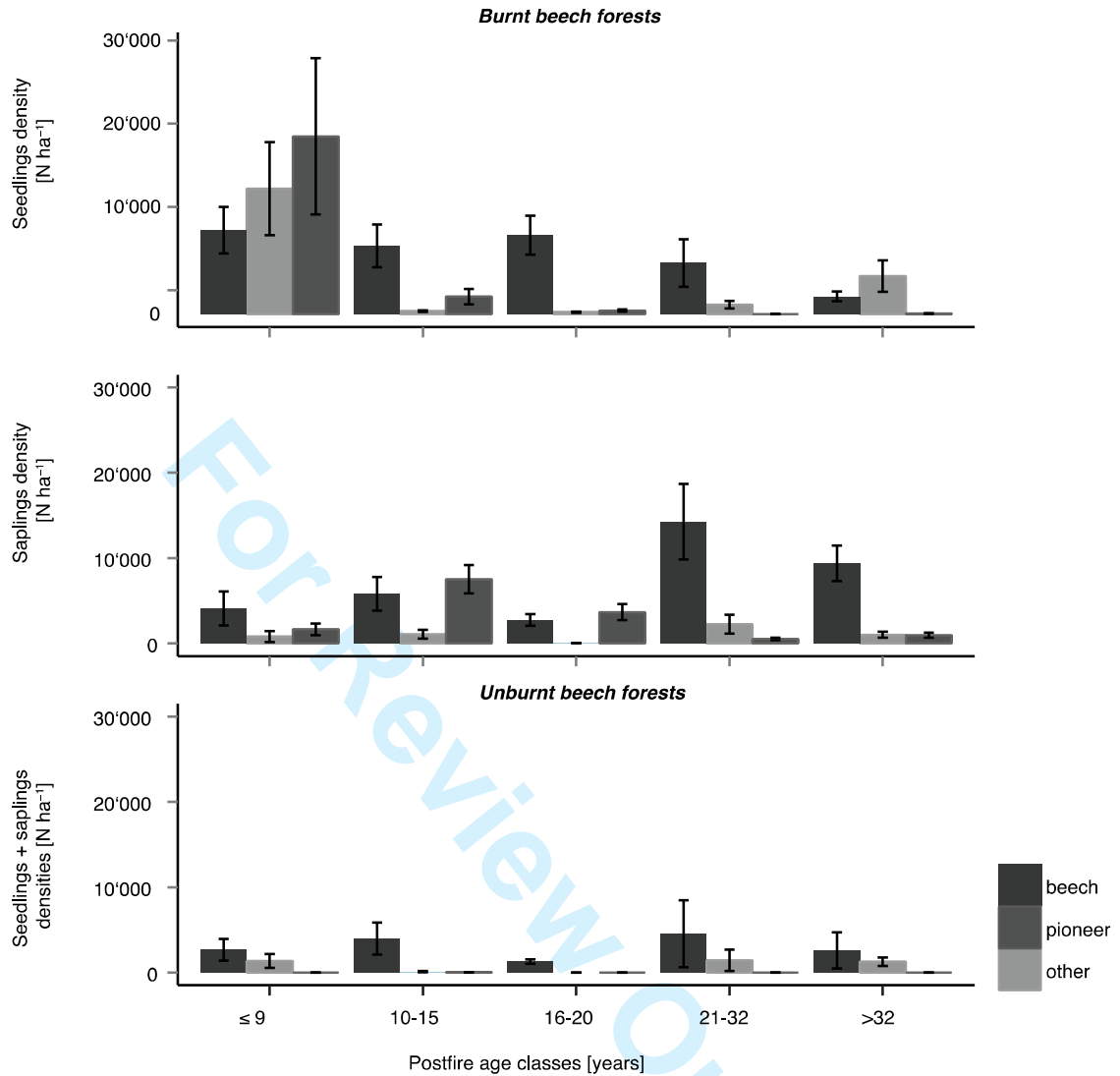


Figure 4: Regeneration densities of seedlings ($\leq 20\text{cm}$) and saplings ($>20\text{cm}$) in burnt and unburnt beech forests, grouped by beech, pioneers and other tree species, and postfire age classes.

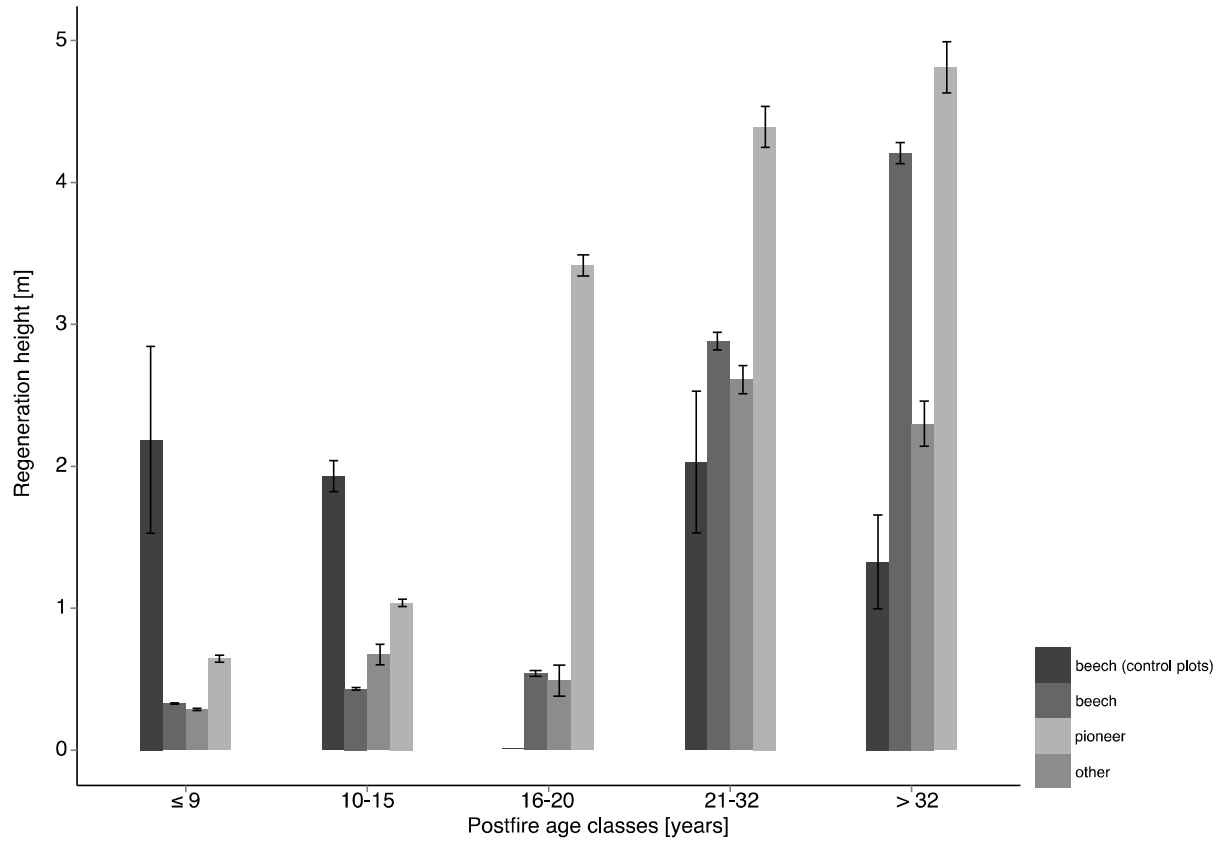


Figure 5: Saplings heights of beech, and saplings belonging to the pioneer and “other” tree species category in the burnt and unburnt beech forests, grouped by postfire age classes.