

Manuscript Number: FORECO15087R1

Title: The synchronicity of masting and intermediate severity fire effects favors beech recruitment

Article Type: FLA Full Length Article

Keywords: Wildfire; disturbance ecology; seed germination; *Fagus sylvatica* L.; European Alps; temperate forests

Corresponding Author: Dr. Davide Ascoli, Ph.D.

Corresponding Author's Institution: University of Torino

First Author: Davide Ascoli, Ph.D.

Order of Authors: Davide Ascoli, Ph.D.; Giorgio Vacchiano, Ph.D.; Janet Maringer; Giovanni Bovio, Prof.; Marco Conedera, Ph.D.

Abstract: The fire ecology of European beech (*Fagus sylvatica* L.) is poorly understood. We analyzed beech recruitment after a mast year in recently burnt and unburnt stands to answer to the questions: (i) Does post-fire mast seed production and recruitment in beech depend on fire severity, and (ii) which are the processes by which fire and the environment affect beech seed production, germination and seedling emergence and establishment in the first year after masting?

We selected three beech stands in the Southwestern Alps, burnt in either the winter of 2012 or 2013 but before the 2013 beech mast year. In the summer of 2013, at each stand, we established 30 sampling plots stratified by fire severity based on the percent basal area loss of beech (low; intermediate; high). Another 10 plots per stand were assigned to a control (unburnt) group. In the spring of 2014, we counted cupules, seeds, germinated seeds, and emergent seedlings (i.e., rooted in mineral soil) in four squares (0.4 x 0.4 m) at each plot. In the summer of 2014, at each plot, we measured stand characteristics (i.e., a circular area of 12-m in a planar radius) and counted established seedlings in 12 squares (1x1 m).

Control stands had 448 ± 38 cupules m⁻² and 489 ± 44 seeds m⁻² with a germination rate of 11%. In comparison to the control, production of cupules and seeds was significantly lower only under high fire severity (-75% and -63%, respectively). At intermediate and low severity sites, cupule and seed production were similar to unburnt sites, while seed germination and seedling emergence were higher. At intermediate severity sites established seedlings (86000 ± 10574 seedlings ha⁻¹) were significantly more frequent than the control. Generalized linear and additive models demonstrated that intermediate disturbance of litter and canopy cover favored beech regeneration.

Mixed severity fires are an important ecological factor for the natural regeneration of beech. Such insights in beech disturbance ecology can help improve silviculture and post-fire restoration of Alpine forests. The synergy between fire and masting raises new questions concerning the role of fire in temperate beech forests.

Grugliasco, 18th May 2015

Forest Ecology and Management
Editor-in-Chief

ID#: FORECO15087

Authors: Davide Ascoli, Giorgio Vacchiano, Janet Maringer, Giovanni Bovio, Marco Conedera

Title: The synchronicity of masting and intermediate severity fire effects favors beech recruitment

Dear Editor:

We have completed the revision of manuscript FORECO15087. Replies to the general and specific points raised by both reviewers are addressed in our "Reply to reviewers" file. We used a 'quote and response' including line numbers to cross reference the manuscript with the points raised by the reviewers.

We fully revised all manuscript sections to articulate the novelty and impact of our studies. We restructured several parts of the narrative chapters and we additionally provide a linguistic revision of the text by the English Language Editing service available from Elsevier's WebShop.

Sincerely,

Davide Ascoli

Corresponding author:

Davide Ascoli

Address: via Paolo Braccini 2, 10095 Grugliasco (TO), Italy.

E-mail: d.ascoli@unito.it

Tel.: +39 0116705553

Fax: +39 0116705556

1 **The synchronicity of masting and intermediate severity fire effects favors beech recruitment**

2

3 Davide Ascoli^{1*}, Giorgio Vacchiano¹, Janet Maringer^{2,3}, Giovanni Bovio¹, Marco Conedera³

4 ¹ University of Torino, DISAFA, Largo Paolo Braccini 2, Grugliasco (TO), Italy

5 ² Institute for Landscape Planning and Ecology, University of Stuttgart, Germany

6 ³ WSL Swiss Fed. Res. Inst., Res. Group Insubric Ecosystems, Bellinzona, Switzerland

7 *Correspondence author. E-mail: d.ascoli@unito.it; Fax: +390116705556

8

9 **Running headline:** The synchronicity of masting and fire favors beech recruitment

10

11 **Abstract**

12 The fire ecology of European beech (*Fagus sylvatica* L.) is poorly understood. We analyzed beech
13 recruitment after a mast year in recently burnt and unburnt stands to answer to the questions: (i)
14 Does post-fire mast seed production and recruitment in beech depend on fire severity, and (ii) which
15 are the processes by which fire and the environment affect beech seed production, germination and
16 seedling emergence and establishment in the first year after masting?

17 We selected three beech stands in the Southwestern Alps, burnt in either the winter of 2012 or 2013
18 but before the 2013 beech mast year. In the summer of 2013, at each stand, we established 30
19 sampling plots stratified by fire severity based on the percent basal area loss of beech (low;
20 intermediate; high). Another 10 plots per stand were assigned to a control (unburnt) group. In the
21 spring of 2014, we counted cupules, seeds, germinated seeds, and emergent seedlings (i.e., rooted in
22 mineral soil) in four squares (0.4 x 0.4 m) at each plot. In the summer of 2014, at each plot, we
23 measured stand characteristics (i.e., a circular area of 12-m in a planar radius) and counted
24 established seedlings in 12 squares (1x1 m).

25 Control stands had 448 ± 38 cupules m^{-2} and 489 ± 44 seeds m^{-2} with a germination rate of 11%. In
26 comparison to the control, production of cupules and seeds was significantly lower only under high

27 fire severity (-75% and -63%, respectively). At intermediate and low severity sites, cupule and seed
28 production were similar to unburnt sites, while seed germination and seedling emergence were
29 higher. At intermediate severity sites established seedlings (86000 ± 10574 seedlings ha^{-1}) were
30 significantly more frequent than the control. Generalized linear and additive models demonstrated
31 that intermediate disturbance of litter and canopy cover favored beech regeneration.

32 Mixed severity fires are an important ecological factor for the natural regeneration of beech. Such
33 insights in beech disturbance ecology can help improve silviculture and post-fire restoration of
34 Alpine forests. The synergy between fire and masting raises new questions concerning the role of
35 fire in temperate beech forests.

36

37 **Keywords:** Wildfire, disturbance ecology, seed germination, *Fagus sylvatica* L., European Alps,
38 temperate forests

39

40 **1. Introduction**

41 European beech (*Fagus sylvatica* L.) is a shade-tolerant species with seedlings that can establish
42 under a closed canopy (Wagner *et al.*, 2010). However, regeneration in such conditions is scarce,
43 suppressed, and prone to early mortality (Nilsson, 1985; Topoliantz and Ponge, 2000; Collet *et al.*,
44 2008; Wagner *et al.*, 2010). Beech recruitment can take advantage of changes to the physical
45 environment induced by anthropogenic or natural disturbances (Agestam *et al.*, 2003; Wagner *et al.*,
46 2010; Kramer *et al.*, 2014; Nagel *et al.*, 2014). These changes include well-documented
47 disturbances, such as shelterwood cutting and windthrow, the effects of which in European beech
48 forests are mostly understood (Nocentini, 2009; Packham *et al.*, 2012; Šebková *et al.*, 2012; Kramer
49 *et al.*, 2014; Motta *et al.*, 2014; Nagel *et al.*, 2014). These disturbances expose the mineral soil and
50 create prevailing diffuse light conditions. Mineral soil favors seed germination and rooting of
51 emergent seedlings (Harmer, 1995; Agestam *et al.*, 2003; Olesen and Madsen, 2008; Wagner *et al.*,
52 2010; Silva *et al.*, 2012), while diffuse light promotes seedling growth, survival, and establishment
53 by increasing photosynthetic efficiency (Minotta and Pinzauti, 1996; Madsen and Larsen, 1997;
54 Tognetti *et al.*, 1998; Collet *et al.*, 2008; Nagel *et al.*, 2010). When these effects synchronizes with a
55 peak in seed production (mast year), seedling emergence is highly abundant, and the probability of
56 successful establishment increases (Olesen and Madsen, 2008; Simon *et al.*, 2011; Packham *et al.*,
57 2012; Silva *et al.*, 2012).

58 In contrast, the effects of fire disturbance on beech masting, seed germination, seedling emergence
59 and establishment have been poorly researched (Paula *et al.*, 2009). This finding may be observed
60 due to historical and ecological reasons. In the last several centuries, beech was positively selected
61 and intensively managed throughout Europe due to the high economic value of the wood (Geßler *et al.*,
62 2007; Nocentini, 2009; Valsecchi *et al.*, 2010; Wagner *et al.*, 2010; Packham *et al.*, 2012).
63 Prolonged biomass exploitation, fragmentation of the anthropogenic forest landscape, and efficient
64 fire suppression policies altered fire regimes in central and northern Europe (Pyne, 1982;
65 Drobyshev *et al.*, 2014; Valese *et al.*, 2014). For example, in the Alps, fire negatively selects

66 managed beech stands (Pezzatti *et al.*, 2009). Moreover, beech forests have a relatively low
67 flammability and sustain large fires only during exceptionally dry periods, such as the heat wave in
68 the summer of 2003 (Ascoli *et al.*, 2013; Valese *et al.*, 2014). As a result, in the last century the
69 scientific and forest management community had notably few opportunities to observe and
70 understand the ecological role of fire in beech forests, as well as in other temperate forests of central
71 Europe (Paula *et al.*, 2009; Conedera *et al.*, 2010; Adamek *et al.*, 2015). Despite a corresponding
72 lack of exhaustive and systematic research on fire ecology of the species, beech is generally
73 considered to be fire sensitive because it lacks typical fire adaptive traits, such as thick bark, high
74 resprouting ability, and an aerial or soil seed bank (Giesecke *et al.*, 2007; Packham *et al.*, 2012).
75 Indeed, high intensity fire can have stand replacing effects in beech forests (Herranz *et al.*, 1996;
76 Ascoli *et al.*, 2013). Furthermore, beech dominance is restricted by frequent fires, e.g., events with a
77 return interval <50 years (Delarze *et al.*, 1992). This finding is particularly relevant in the Alps
78 when we consider the recent trend toward unusually large fires in beech stands (Ascoli *et al.*, 2013;
79 Valese *et al.*, 2014) and in view of the predicted future increase in intensity and frequency of fire
80 events (Wastl *et al.*, 2013).

81 Conversely, paleoecological long-term studies do not support evidence for a high sensitivity of
82 beech to fire (Tinner *et al.*, 2000; Bradshaw and Lindbladh, 2005; Tinner and Lotter, 2006;
83 Giesecke *et al.*, 2007). Tinner *et al.* (2000) classified beech as fire sensitive because of a negative
84 relationship of its pollen with increasing charcoal influxes but confirmed its ability to avoid local
85 extinction in case of increased fire frequency. Moreover, Bradshaw and Lindbladh (2005) found
86 that the spread of beech in northern Europe during the Holocene was linked to disturbance by fire
87 prior to stand establishment. Recent field observations confirmed the potential of the species to take
88 advantage of single fire events of mixed severity (van Gils *et al.*, 2010; Maringer *et al.*, 2012;
89 Ascoli *et al.*, 2013). However, the scarcity of available studies (Paula *et al.*, 2009) and the
90 heterogeneity of studies in terms of environmental conditions, stand structures, and fire severity,
91 call for a better understanding of post-fire regeneration dynamics in beech. Such understanding can

92 inform post-fire restoration practices in beech forests (Ascoli *et al.*, 2013) and improve the efficacy
93 of silvicultural systems aiming at enhancing beech resilience by emulating natural disturbances
94 (Wagner *et al.*, 2010; Nagel *et al.*, 2014).

95 In this paper, we focus on early regeneration dynamics following masting in recently burnt (1 to 2
96 years) Alpine beech stands by answering two questions:

- 97 (i) Does post-fire mast seed production and seedling recruitment in beech depend on fire severity?
98 (ii) How do fire and the environment affect beech seed production, germination and seedling
99 emergence and establishment in the first year after masting?

100

101 **2. Materials and Methods**

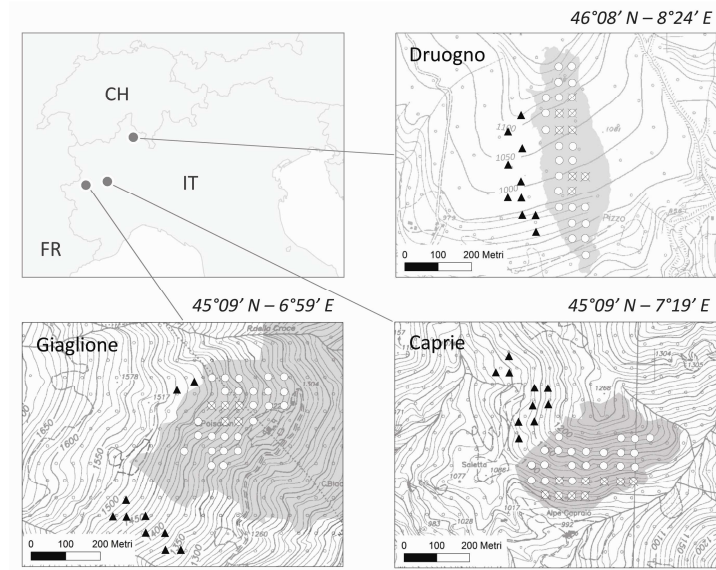
102 *2.1. Study area*

103 We conducted the study in three beech forests in the Southwestern Alps (Figure 1). Winter and
104 early spring surface fires of anthropogenic origin burnt in 2012 in the municipalities of Giaglione
105 (45°09'N, 6°59'E) and Caprie (45°09'N, 7°19'E), and in 2013 in the municipality of Druogno
106 (46°08'N, 8°24'E), Italy. Fires started at low elevation and spread up-slope driven by wind and
107 topography, alternating head and backfire phases and developing a low to moderate fireline
108 intensity (<100 to 2000 kW m⁻¹), typical of anthropogenic fires in Alpine broadleaved forests
109 (Valese *et al.*, 2014). This resulted in mixed fire severities, i.e., a varied degree of tree mortality,
110 litter consumption, and mineral soil exposure (Keeley, 2009).

111 The three forests were former beech coppices converted to high forests during the last 50 years. Pre-
112 fire basal area ranges from 25.9 to 27.9 m² ha⁻¹ (Table 1). Beech is dominant (87% basal area), with
113 sporadic *Betula pendula* Roth, *Laburnum alpinum* J.Presl, *Larix decidua* Mill., *Pinus sylvestris* L.,
114 and *Quercus petraea* (Mattuschka) Liebl. All sites are south facing and lie on crystalline rocks
115 (gneiss), but differ slightly in elevation and annual precipitation (Table 1).

116 A beech masting occurred in the 2013 growing season in all three study sites.

117



118 Figure 1 – Upper left: geographical position of study sites. Panels: fire perimeters (light grey) (data: Italian
 119 Forest Service), and location of sampling plots in burnt (white circles) and unburnt (black triangles) areas.
 120 Crossed circles represent sampling points excluded from the analysis because of unplanned winter salvage
 121 logging.

122
 123 Table 1 – Characteristics of fire events and study sites. P_{30d} : cumulative rainfall in the last 30 days before
 124 fire; T_{max} : maximum air temperature during the fire; Wind: wind gust speed during the fire. BA_{beech} : mean
 125 basal area (\pm SE) of pre-fire beeches; P_{03-13} : mean annual precipitation of the observation period 2003-2013.
 126 Data sources: Arpa Piemonte (weather data), Italian Forest Service (fire date and area).

Site (Municipality)	Fire Date (d/m/a)	P_{30d} / T_{max} / Wind (mm / °C / km h ⁻¹)	Burnt area (ha)	BA_{beech} (m ² ha ⁻¹)	Aspect (°N)	Slope (%)	Elevation (m a.s.l.)	P_{03-13} (mm yr ⁻¹)	Plots
Druogno	26/03/12	82 / 6 / 52	9.5	25.9 ±1.4	150 ±4	59 ±2	1131 ±6	1460	32
Giaglione	31/03/12	17 / 21 / 38	40.5	26.2 ±1.5	125 ±7	67 ±2	1430 ±8	880	35
Caprie	16/01/13	2 / 2 / -	16.7	27.9 ±1.2	162 ±9	70 ±2	1085 ±11	1014	31

127

128 2.2. Sampling design

129 During a preliminary survey, we provisionally divided the burnt stands into high, intermediate and
 130 low fire severity areas to distribute the sampling plots according to fire severity. This was based on
 131 a subjective assessment of tree mortality as a proxy for fire severity (Miller *et al.*, 2009; Ascoli *et*

132 *al.*, 2013; Morgan *et al.*, 2014; Vacchiano *et al.*, 2014). Indeed, tree mortality affects seed
133 production and the forest light regime, it is also one of the primary parameters used to measure fire
134 severity in species with poor resprouting ability (Keeley, 2009; Morgan *et al.*, 2014).

135 To balance the experimental design, we established ten circular plots (planar radius =12 m) per fire
136 severity area (i.e., 30 plots per fire site), according to a 30 x 30 m grid in each site. Additionally, we
137 established ten plots in the adjacent unburnt beech forests (controls), selected in portions of the
138 forest with similar slope, elevation, aspect, stand density, and management history to minimize
139 differences in seed production and seedling predation (Figure 1). Due to unplanned salvage logging,
140 mostly in high severity areas, 22 plots were subsequently excluded from the study (Figure 1). The
141 total number of plots surveyed was 32, 35, and 31 in Druogno, Giaglione and Caprie, respectively
142 (Table 1).

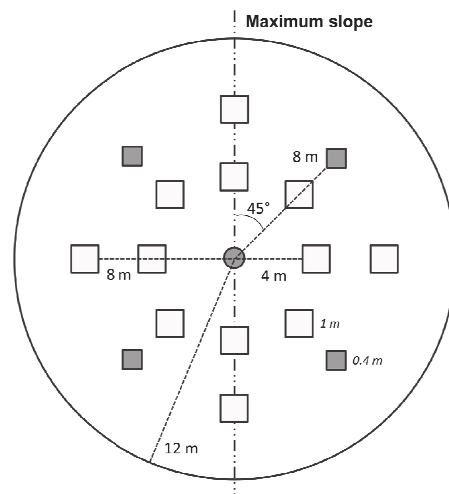
143

144 2.3. *Field survey and lab analysis*

145 In each plot we measured elevation, aspect, slope, and elevation difference from the lowest plot in
146 the site. To capture the different regeneration phases, we established a number of sub-plots (Figure
147 2) and carried out measurements at different times of the growing season, according to the
148 following scheme:

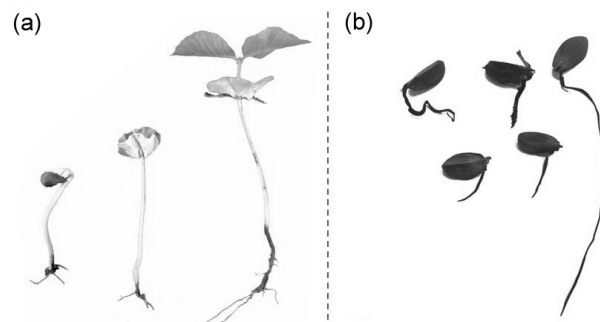
149 a) In spring 2014, after the snow melt, we collected all cupules and seeds from four square sub-plots
150 (40 x 40 cm) located 8 m from the plot center along four orthogonal axes at angles of 45° relative to
151 the slope direction (Figure 2). In each sub-plot we measured slope, percent cover and depth of litter,
152 and counted the number of emergent beech seedlings, i.e., germinated seeds with vital roots at the
153 time of sampling (Figure 3a). Cupules and seeds were subsequently counted in the lab, and seeds
154 were additionally categorized as whole, damaged (i.e., predated or fractured), or germinated with
155 non-vital roots (Figure 3b). Whole seeds were put in germination chambers with an 8-hour light
156 cycle and 20°C temperature on moist paper filters for 50 days (Suszka *et al.*, 2000). The seeds were
157 subsequently classified as germinating or non-germinating.

158 b) In the summer of 2014, we measured the percent cover by litter, bare soil, coarse woody debris,
159 and herb layer vegetation (i.e., grasses, forbs) in each circular plot. We measured the diameter at
160 130 cm height (dbh) of each mature tree (dbh >7 cm) and classified tree crown vitality (Schomaker
161 *et al.*, 2007) as either healthy (>50% live crown) or poor (<50%). We quantified canopy cover by
162 taking a hemispherical photograph 1 m above the soil from the plot center; percent canopy cover
163 was calculated in the lab by the software Gap Light Analyzer (Frazer *et al.*, 1999). In 12 square sub-
164 plots (100 x 100 cm), located at 4 to 8 m from the plot center (Figure 2), we counted one-year old
165 seedlings of beech and other tree species.
166



167 Figure 2 – Sampling units within each 12 m-radius plot. The grey circle shows the center of the plot. Dark
168 grey squares: 0.4 m sub-plots used to count cupules, seeds and emergent seedlings. White squares 1.0 m sub-
169 plots used to count established seedlings. Dashed lines: distances from the plot center.

170



171 Figure 3 – (a) Germinated beech seeds with developed roots and cotyledons; (b) Germinated beech seeds
172 with partial or complete root necrosis.

173

174 2.4. Data analysis

175 In the pre-analysis stage, we refined the fire severity stratification of plots by k-means clustering
176 into three fire severity groups: (high, intermediate, and low. This analysis splits the objects (plots)
177 into a predefined number of clusters (i.e., three fire severity groups), and iteratively assigns cluster
178 membership of each object to maximize the ratio of between-cluster to within-cluster variance of a
179 chosen focus attribute (Quinn and Keough, 2002). Our focus attribute was the relative loss of beech
180 basal area, commonly used to characterize fire severity (Keeley, 2009; Miller *et al.*, 2009; Morgan
181 *et al.*, 2014). Relative loss of basal area was calculated as the ratio between the basal area of beech
182 with poor crown vitality (live crown <50%) and the total beech basal area. K-means clustering
183 resulted in an unbalanced experimental design (high severity =18 plots; intermediate=26 plots;
184 low=24 plots; control=30 plots). The mean percent basal area loss was 89%, 42%, 14%, 5% in high,
185 intermediate, low and in control plots, respectively.

186 To assess the effect of fire on seed production and regeneration, we computed plot-level mean
187 frequencies of cupules, seeds, germinated seeds, emergent seedlings, and established seedlings and
188 compared them across fire severity groups and the Control by ANOVA with LSD post-hoc
189 comparison. Study site was used as a random factor. Response variables were log-transformed
190 when necessary to ensure normality and homoscedasticity between groups.

191 To assess the processes by which fire and other environmental variables affect seed production and
192 regeneration, we modeled plot frequencies of cupules, seeds, germinated seeds, emergent seedlings,
193 and established seedlings as a function of litter abundance, light, competition, and topography.

194 Predictors were chosen according to ecological hypotheses we intended to test (Table 2).

195 Precipitation was not included as a predictor because we did not consider it to be a limiting factor:

196 cumulative precipitation in the study period (2013-09 to 2014-08) was 910, 1350, and 1759 mm,

197 and from seedling emergence to last survey (2014-03 to 2014-08), it was 450, 795, and 805 mm in

198 Giaglione, Caprie and Druogno, respectively (data source: Arpa Piemonte).

199 All response and predictor variables were screened for outliers using Cleveland dotplots (Zuur *et*
200 *al.*, 2010). Predictors were scaled to improve model convergence and ensure comparability of
201 effect sizes (i.e., beta coefficients). We checked for bivariate interactions between model predictors
202 by coplots (Zuur *et al.*, 2010), that is by assessing whether the slope of response-predictor
203 regression was sensitive to the covariates that were thought to interact. We found no evidence for
204 interaction. Following a preliminary test on the dispersion of the response variables (i.e., ratio of
205 residual deviance to degrees of freedom), we rounded all frequencies to the next integer and used
206 Generalized Linear Mixed Models (GLMM) where the response was assumed to follow a negative
207 binomial distribution. The model fitting algorithm automatically estimated the theta parameter.
208 Except for the cupule model, we used as offset in each GLMM the plot-level mean frequency of the
209 preceding regeneration stage (e.g., emergent seedlings as offset for established seedlings) (Table 2).
210 The study site was set as a random variable.

211 We decided not to conduct a model selection method (e.g., stepwise procedure or information
212 theoretic approach) for the following reasons: i) we were interested in testing *a priori* hypotheses
213 (Table 2) and not in applying arbitrary statistical rules for deciding which variables should be
214 included or removed from the model; ii) stepwise algorithms suffer from known statistical issues
215 (e.g., increase type I error due to multiple hypothesis testing) (Quinn and Keough, 2002); iii) we use
216 models in a descriptive rather than in a predictive framework. However, predictors were screened
217 for collinearity (Pearson correlation > 0.6) to avoid p-value inflation. For example, the herb layer
218 cover and canopy cover from Gap Light Analyzer were highly correlated ($R = -0.84$). In this case,
219 we retained canopy cover as the only explanatory variable because it has major cascading effects on
220 post-fire dynamics, including herb abundance, which, in turn, can compete with beech seedlings at
221 burnt sites (Maringer *et al.*, 2012; Ascoli *et al.*, 2013). Similarly, bare soil cover was excluded from
222 all models because it was collinear to litter abundance (-0.78).

223 For response variables whose GLMM Pearson's residuals had significant non-linear trends against
224 model covariates, i.e., smoothing spline with $p < 0.05$ (Zuur *et al.*, 2009), we fitted generalized

225 additive mixed models (GAMM) using auto-initializing penalized thin-plate regression splines
226 (base dimension $k=1$) (Wood, 2006). No models had more than one smoothing term.
227 Under all models, we assessed the significance of the random factor by comparing the full model
228 against a neutral model with the random factor only (F-test). We assessed model performance by
229 scrutinizing observed vs. fitted and deviance residuals plots, and model explicative power by
230 computing percent deviance explained (Nakagawa and Schielzeth, 2013). Finally, we assessed
231 effect sizes by computing standardized regression parameters; confidence intervals and p-values
232 were computed by restricted maximum likelihood (REML) to consider the loss in degrees of
233 freedom resulting from estimating fixed effects (Harville, 1977).
234 Modeling was carried out using the functions *glmer* (for GLMMs) and *gamm4* (for GAMMs) from
235 packages *lme4* and *gamm4* (Bates *et al.*, 2014; Wood, 2014) for R 3.1 (R Core Team 2015).

236

237

238

239

240 Table 2 – Predictors used (X), discarded because of collinearity (X*), and not used (–) in regression models.
 241 For each predictor we provide a description, the related hypothesis we wanted to test, and measurement
 242 units. Hypothesis testing was based on looking for statistical support for the null hypothesis, i.e., no
 243 relationship between the predictor and the response.
 244

Predictor	Variable description	Alternative hypothesis	Response Units	Cupules n m ⁻²	Seeds n m ⁻²	Germinated seeds n m ⁻²	Emergent seedlings n m ⁻²	Established seedlings n m ⁻²
<i>canCov</i>	Canopy cover estimated with the Gap Light Analyzer	As a proxy of beech vitality, it affects positively cupule and seed production. As a proxy of light, it affects positively seed germination, seedling recruitment and establishment.	%	X	X	X	X	X
<i>oth-ba-live</i>	Basal area of live tree species other than beech	As a proxy of competition of other tree species on beech, it affects negatively all variables.	M ² ha ⁻¹	X	X	X	X	X
<i>oth-reg</i>	Seedling density of tree species other than beech	As a proxy of competition of other species on beech after recruitment, it affects negatively seedlings establishment.	N m ⁻²	–	–	–	–	X
<i>litter</i>	Litter abundance at the sub-plot scale (scaling from 0 to 1 of the variable resulting from litter cover multiplied per litter depth)	Litter abundance affects positively accumulation of both cupules and seeds. Has a negative effect on seed germination. As a proxy of soil cover, it affects negatively seedling recruitment.	0-1	X	X	X	X	–
<i>soil</i>	Bare soil cover at the sub-plot scale	It affects positively seedling recruitment.	%	X*	X*	X*	X*	–
<i>cwd</i>	Coarse woody debris cover at the plot scale	It provides suitable sites for seed germination, seedlings recruitment and establishment.	%	–	–	X	X	X
<i>herb layer</i>	Grasses and forbs cover	It affects negatively beech seedlings	%	–	–	–	X*	X*
<i>asp</i>	Side aspect azimuth at the plot scale	As a proxy of southerly exposed sites (i.e., cos(°N) < 0), it affects negatively beech regeneration because of more xeric conditions.	cos(°N)	X	X	X	X	X
<i>d-level</i>	Elevation relative to the lowest plot at each study site	As a proxy of position along the slope, it affects negatively cupule and seed number because of accumulation at lower sites.	m	X	X	–	–	–
<i>elevation</i>	Quote of the plot	It affects negatively all variables because lower temperatures at higher elevation.	m a.s.l.	X	X	X	X	X
<i>slope-Sp</i>	Slope steepness at the sub-plot scale	As a proxy of surface erosion, it affects negatively all variables.	%	X	X	X	X	–
<i>slope-P</i>	Slope steepness at the plot scale	As a proxy of surface erosion, it affects negatively all variables.	%	–	–	–	–	X
<i>offset</i>	Plot means of response variables	Account for the influence of the previous regeneration phase.	n m ⁻²	–	cupules	seeds	germinated seedlings	emergent seedlings

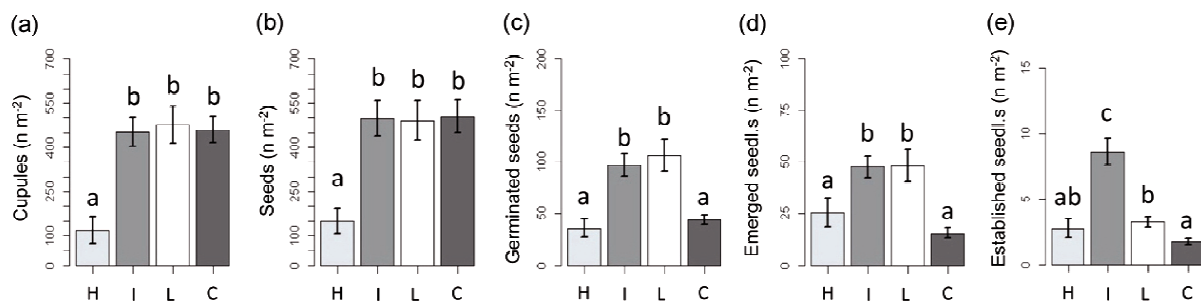
245

246 Results

247 3.1. Post-fire mast seed production and recruitment dependence on fire severity

248 Seed production and recruitment differed significantly between the three fire severity groups (high,
249 intermediate, low) and the unburnt control (Figure 4). High fire severity resulted in a significantly
250 lower production of cupules ($F=14.5$; $p<0.001$) and seeds ($F=10.6$; $p<0.001$) relative to all other
251 groups. Interestingly, cupule and seed production did not differ between the intermediate and low
252 severity groups compared to the control (Figure 4a, b).

253



254 Figure 4 – Means (\pm SE) of the following variables: (a) cupules m^{-2} ; (b) seeds m^{-2} ; (c) germinated seeds m^{-2} ;
255 (d) emergent seedlings m^{-2} ; (e) established seedlings m^{-2} . Different letters show significant differences
256 ($p<0.05$) between fire severity groups (high – H; intermediate – I; low – L; unburnt control – C).

257

258 In contrast, the intermediate and low severity groups had more germinated seeds ($F=36.3$; $p<0.001$)
259 and emergent seedlings ($F=28.8$; $p<0.001$) than the high severity and control groups (Figure 4c, d).
260 Established seedlings were significantly more abundant ($F=23.4$; $p<0.001$) in the intermediate
261 severity group than in the high severity and control groups (Figure 4e).

262 Site as a random factor was significant for cupules ($F=9.2$; $p<0.01$) and seeds ($F=21.4$; $p<0.01$),
263 which were more abundant in Druogno, and for germinated seeds, which were fewer at Caprie
264 ($F=6.1$; $p<0.01$). However, site was no longer significant for emergent and established beech
265 seedlings.

266

267 3.2. Processes by which fire and the environment affect beech seed production, germination and
 268 seedling emergence and establishment in the first year after masting

269 GLMMs and GAMMs had a dispersion close to 1 and a satisfactory explanatory power with
 270 deviance explained in most cases >60% (Table 3). The high deviances are partly due to the use of
 271 offsets. Canopy cover and litter abundance, which linearly decreased from the control to the high
 272 fire severity group (Spearman's R = -0.76 and -0.59, respectively), played a significant role in all
 273 recruitment stages of beech, as evidenced by GLMMs and GAMMs models (Table 3). The shape of
 274 their relationship with response variables was either linear (with positive or negative slope) or
 275 unimodal (significant smoothing term), depending on the response variable.

276

277 Table 3 – Generalized mixed models of beech recruitment in different stages. The model form (GLMM, or
 278 GAMM), beta coefficient value, sign and significance of covariates, random factor significance, and fitness
 279 metrics (proportion of deviance explained and dispersion) are displayed. Names of covariates follow Table 2.

Response	cupules	seeds	germinated seedlings	emergent seedlings	established seedlings
Model form	GAMM	GLMM	GAMM	GLMM	GAMM
Covariates					
<i>canCov</i>	(s)***	- 0.77 **	- 0.10 ***	- 0.69 **	(s)*
<i>oth-ba-live</i>	- 0.58 *	- 0.02	+ 0.01	+ 0.29	- 0.01
<i>oth-reg</i>	–	–	–	–	- 0.01
<i>litter</i>	+ 0.75 **	- 0.48 *	(s)***	- 0.31 *	–
<i>cwd</i>	–	–	+ 0.01	+ 0.37 *	+ 0.09*
<i>asp</i>	- 0.78 **	- 0.31	+ 0.13	+ 0.37 *	+ 0.17
<i>d-level</i>	- 0.21	- 0.02	–	–	–
<i>elevation</i>	+ 0.12	- 0.65 ***	- 0.08 *	- 0.12	+ 0.01
<i>slope-Sp</i>	- 0.64 *	+ 0.24	+ 0.09 *	+ 0.65 **	–
<i>slope-P</i>	–	–	–	–	- 0.01
Random factor					
<i>Study site</i>	()*	()*	()**	()**	()
Fitness metrics					
<i>Proportion of Deviance Explained</i>	0.75	0.96	0.72	0.84	0.70
<i>Dispersion</i>	0.82	1.20	1.01	1.04	0.89

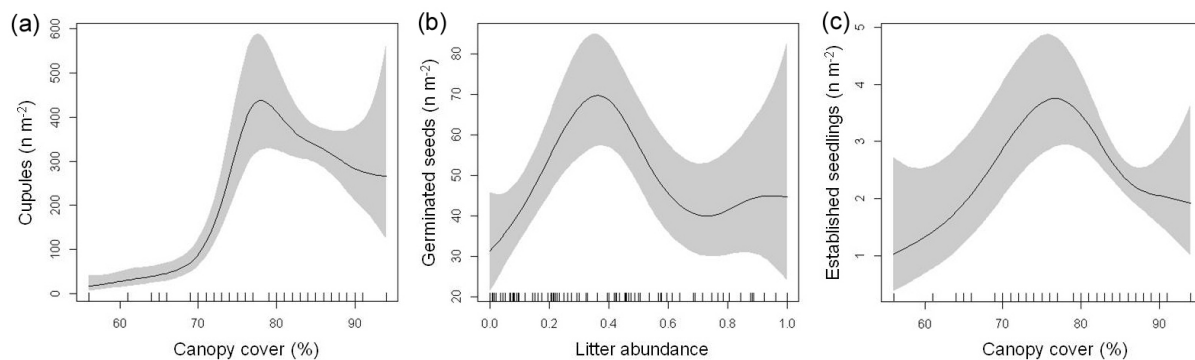
280 Notes: (s) Significant smooth term

281 Significance of predictors: * p ≤0.1); ** p ≤0.01); *** p ≤0.001).

282

283 Not all alternative hypotheses (Table 2) could be supported. Cupules were significantly associated
 284 to a unimodal smoother for canopy cover: fructification increased until canopy cover reached
 285 ~75%, and afterwards gently decreased (Figure 5a). Cupules were also linearly related to aspect
 286 (i.e., were fewer on north-facing sites), litter (were increased with higher litter accumulations), and
 287 slope (were increased on steeper slopes) and by interspecific competition (were fewer with
 288 increasing competition). Position along the slope was not significant (Table 3).

289



290 Figure 5 – Relationship between response variables (± 2 SE) and predictors with significant smoothers in
 291 GAMMs, with other variables in the model held constant. (a) The estimated contribution of canopy cover to
 292 cupules m⁻²; (b) The estimated contribution of litter abundance to germinated seeds m⁻²; (c) the estimated
 293 contribution of canopy cover to established seedlings m⁻². Each tick above the x-axis denotes an observation
 294 with that value.

295

296 When offset by cupule abundance, seed abundance decreased linearly with increasing canopy cover
 297 and elevation (Table 3). Seed germination was nonlinearly related to litter abundance, and higher at
 298 intermediate litter levels (Figure 5b). Also in this case canopy cover had a negative linear effect
 299 (Table 3). Similarly, seedling emergence linearly decreased with increasing canopy cover and litter
 300 abundance, while coarse woody debris, northern aspect, and slope had a significant positive effect
 301 (Table 3). Finally, seedling establishment was positively affected by coarse woody debris and was
 302 nonlinearly related to canopy cover, with intermediate cover levels (70-80%) promoting the highest
 303 seedling survival (Figure 5c).

304 Consistent with the ANOVA results, the study site as a random factor had a stronger effect on
305 cupules, seed production and germination ($p < 0.01$), had a weaker effect on seedling emergence (p
306 $= 0.04$) and was non-significant for seedling establishment. This finding may suggest that site-
307 related factors in our experiment had decreasing importance during the regeneration process in
308 comparison to other predictors, such as litter abundance and canopy cover.

309

310 **4. Discussion**

311 *4.1. Cupule and seed production*

312 Even if they were highly damaged and decaying, adult beech trees in the study sites produced fruits
313 and seeds. Observed mean cupules ($468 \pm 40 \text{ m}^{-2}$) and seed ($500 \pm 44 \text{ m}^{-2}$) abundance in the
314 intermediate and low fire severity were within the range of the unburnt sites. In addition, they were
315 also consistent with reported production in mast years of European beech forests not affected by fire
316 (Nilsson, 1985; Nilsson and Wastljung, 1987; Topoliantz and Ponge, 2000; Overgaard *et al.*, 2007;
317 Olesen and Madsen, 2008; Nopp-Mayr *et al.*, 2012; Silva *et al.*, 2012). Beech trees do not display
318 traits of active fire resistance, such as a thick bark. Consequently, fire often causes bark necrosis
319 and cambial death, followed by rapid wood decay under the attack of saprophytic fungi (Conedera
320 *et al.*, 2010; van Gils *et al.*, 2010; Ascoli *et al.*, 2013). Nonetheless, our results show that beech is
321 able to mast profusely, even under fire-induced damage, confirming reports of abundant masting
322 following edaphic, climatic, or silvicultural stress (Hinrichsen, 1987; Innes, 1994; Topoliantz and
323 Ponge, 2000; Packham *et al.*, 2012; Silva *et al.*, 2012). However, fruiting decreased in the high fire
324 severity group, indicating a threshold above which resources are too depleted to maintain a high
325 reproductive output.

326 In contrast, seed production also decreased when canopy cover was higher than 85%. Studies of
327 beech (Madsen and Larsen, 1997) and other forest cover types (Krannitz and Duralia, 2004; Ayari
328 and Khouja, 2014) found a similar relationship, caused by a reduction of photosynthetically active
329 radiation and air temperature, either at the individual branch or at the whole tree level. This could

330 also explain the significant reduction of cupules that we detected on northern aspects and in the
331 presence of higher competition from other species, as in seeds at higher elevations.

332 We found more cupules on plots with more litter and gentler slopes. We interpret this finding as a
333 result of the mechanical movement of cupules due to the slope and/or running water, which can be
334 mitigated by a deeper litter on a gentle slope. In contrast, seed abundance was negatively affected
335 by litter accumulation, perhaps because it facilitates rodent tunneling and seed predation (Wagner *et*
336 *al.*, 2010; Nopp-Mayr *et al.*, 2012). Additionally, the study site was significantly related to cupule
337 and seed abundance, probably because of the better site quality and consequently higher production
338 at Druogno.

339

340 4.2. Recruitment

341 Despite comparable seed production, beech recruitment was more successful in burnt forests than in
342 unburnt forests. Such a non-proportional relation between seed production and regeneration
343 abundance accords with previous studies of unburnt forests which found that microsite conditions
344 were the main factors controlling seedling amount (Nilsson, 1985; Innes, 1994; Silva *et al.*, 2012).
345 Indeed, similar to other sources of disturbance (Topoliantz and Ponge, 2000; Collet *et al.*, 2008;
346 Simon *et al.*, 2011; Kramer *et al.*, 2014; Nagel *et al.*, 2014), fire alters microsite conditions in a way
347 that promotes germination as well as seedling emergence and establishment, thus resulting in higher
348 recruitment in comparison to the unburnt control. There are several explanations for the stimulatory
349 effect of fire disturbance on germination: higher soil moisture due to alleviated belowground
350 competition, as previously observed following thinning (Madsen and Larsen, 1997; Ammer *et al.*,
351 2002); a stable moisture regime and soil temperatures favorable to beechnut germination due to the
352 mineral soil exposure (Ammer *et al.*, 2002; Agestam *et al.*, 2003); the lower probability of seed loss
353 by parasitic fungi or insects due to the reduction of litter habitats (Madsen, 1995); fire-induced
354 mitigation of phytotoxic effects by plant chemicals and exudates (Wagner *et al.*, 2010).

355 Emergent seedlings were more abundant under moderate litter disturbance. In fact, loose litter
356 protects beech seedlings from dehydration (Ammer *et al.*, 2002) and, at the same time, is
357 sufficiently porous for seedling roots to reach the mineral soil (Harmer, 1995; Wagner *et al.*, 2010).
358 If the litter layer is deep and dense, the root can break or dry out before reaching the soil (Watt,
359 1923; Agestam *et al.*, 2003; Olesen and Madsen, 2008; Simon *et al.*, 2011; Silva *et al.*, 2012), or
360 incur necrosis because of autotoxic effects by extracellular self-DNA, that may limit beech
361 regeneration on conspecific litter (Mazzoleni *et al.*, 2015). Therefore, fire benefits seed germination
362 and seedling emergence in beech by partially consuming litter and exposing the organic or mineral
363 soil horizon.

364 Finally, and similar to after the effect of cutting or windthrow (Minotta and Pinzauti, 1996; Tognetti
365 *et al.*, 1998; Topoliantz and Ponge, 2000; Nagel *et al.*, 2010), intermediate severity fires favor
366 diffuse light conditions that enhance seedling establishment. The mean seedling density in the
367 intermediate fire severity group ($86000 \pm 10574 \text{ ha}^{-1}$) was comparable to that observed after a seed
368 cut carried out in beech stands soon after a mast year (Madsen and Larsen, 1997; Agestam *et al.*,
369 2003; Olesen and Madsen, 2008), or in windthrown areas after a mast year (Simon *et al.*, 2011).
370 Such conditions did not occur in the low fire severity sites or in the unburnt control, where stronger
371 shading due to high tree density probably limits establishment, as observed in numerous studies of
372 unburnt beech forests (Nilsson, 1985; Madsen and Larsen, 1997; Topoliantz and Ponge, 2000;
373 Collet *et al.*, 2008; Olesen and Madsen, 2008; Wagner *et al.*, 2010).

374 Surprisingly, in the case of high severity fires, the density of established seedlings was comparable
375 to that in the unburnt control plots. The reduced amount of seeds produced at high severity sites was
376 partially compensated for by the high rate of seed germination and seedling emergence and
377 establishment. This seemed to overcome the negative influence of herbaceous competition
378 observed in previous studies at increasing fire severity (Maringer *et al.*, 2012; Ascoli *et al.*, 2013),
379 and of soil drying due to direct irradiation through the sparser canopy (Minotta and Pinzauti, 1996;
380 Tognetti *et al.*, 1998; Agestam *et al.*, 2003). The abundance of coarse woody debris at high fire

381 severity sites probably mitigated excessive solar radiation and soil moisture losses (Vacchiano *et*
382 *al.*, 2014), thereby favoring seedling establishment.

383

384 4.3. Synchronicity of masting and fire in beech

385 We observed advantages for beech recruitment when masting synchronizes with short-term fire
386 effects. Successful regeneration due to the synchronicity between masting and fire have been
387 reported for several tree species displaying more obvious fire-adapted traits, such as *Eucalyptus*
388 *delegatensis* R.T. Baker (O'Dowd and Gill, 1984), *Pinus ponderosa* Dougl. ex Laws (Krannitz and
389 Duralia, 2004), *Picea glauca* Moench (Peters *et al.*, 2005), *Abies concolor* (Gord. and Glend.)
390 Lindl. ex Hildebr (van Mantgem *et al.*, 2006), *Picea engelmannii* Parry (Pounden *et al.*, 2014), and
391 other members of *Fagaceae* such as *Nothofagus cunninghamii* (Hook.) Oerst (Burgman *et al.*,
392 2004), *Quercus prinus* L. (Iverson *et al.*, 2008), or *Quercus rubra* L. and *Quercus montana* Willd.
393 (Abrams and Johnson, 2013). Most of these studies stress the ephemeral nature of favorable post-
394 fire microsite conditions for seedling establishment (Pounden *et al.*, 2014) and observe an inverse
395 relationship between the elapsed time since the fire and recruitment success (Peters *et al.*, 2005; van
396 Mantgem *et al.*, 2006). This finding was observed after cutting and soil preparation in beech stands
397 (Madsen, 1995; Agestam *et al.*, 2003; Provendier and Balandier, 2008) because of the negative
398 effects of increasing grass competition and litter accumulation. This also happens after a fire
399 (Maringer *et al.*, 2012; Ascoli *et al.*, 2013), thus stressing the importance of the synchronicity
400 between masting and disturbance effects.

401 Are there any common drivers behind the synchronicity of masting and fire in beech? Masting in
402 beech is driven by external factors such as climate variations. Typically, a mast year (my) is
403 induced by a succession of a year (my -2 years) with low summer temperatures and high
404 precipitation, followed by a year (my -1 year) with high summer temperatures and low precipitation
405 (Piovesan and Adams, 2001; Overgaard *et al.*, 2007; Drobyshev *et al.*, 2014). Interestingly, this
406 temperature-precipitation pattern (wet at my -2 years, dry at my -1 year) increases also the

407 probability of fire occurrence. In fact, higher precipitation (my -2 years) may reduce wildfire
408 probability in the short run but increase wildfire probability in the long run via higher biomass
409 production (Swetnam and Betancourt, 1998; Westerling *et al.*, 2003). If the period of biomass
410 accumulation is followed by a dry and hot season (my -1 year), biomass becomes available for
411 combustion and synchronized large fires can occur over extended areas (Zumbrunnen *et al.*, 2009;
412 Fernandes *et al.*, 2014; Williams *et al.*, 2015).

413 Notably, the full beech mast in year 2004, which was one of the widest mast crops observed
414 throughout central Europe in the last two decades (Belmonte *et al.*, 2008; Mund *et al.*, 2010), was
415 preceded by an exceptional fire season in the summer of 2003, which stands out from the summer
416 fire statistics of central Europe of recent decades (Schmuck *et al.*, 2014). Another hint was found in
417 Sweden, where positive pressure anomalies the summer before a mast year (my -1 year) are
418 positively correlated to both large forest fires (Drobyshev *et al.*, 2015) and beech mast crops in the
419 following year (Drobyshev *et al.*, 2014).

420 In line with the “environmental prediction” hypothesis for mast seeding (Kelly, 1994), some studies
421 suggest a possible evolutionary advantage of using a warm, dry summer as a cue for producing a
422 high seed crop, as severe drought can lead to large-scale mortality of trees, increasing the beneficial
423 effect of diffuse light for seedling establishment (Williamson and Ickes, 2002; Piovesan and
424 Adams, 2005; Souza *et al.*, 2010). In addition to this hypothesis, we suggest that fire disturbance
425 synchronizes with drought and has the potential to magnify this effect to the advantage of beech
426 recruitment. Fire has been suggested to operate as an evolutionary driver of mast seeding in other
427 tree species (Peters *et al.*, 2005; Pouden *et al.*, 2014), including *Picea abies* Karst (Selås *et al.*,
428 2002), a species with masting that is often synchronized with beech (Geburek *et al.*, 2012; Nopp-
429 Mayr *et al.*, 2012).

430

431 **5. Conclusions**

432 The present study provides important insights into the mechanisms responsible for successful
433 recruitment following mixed severity fires in the montane beech forests of Europe (van Gils *et al.*,
434 2010; Maringer *et al.*, 2012; Ascoli *et al.*, 2013). At high fire severity sites, cupule and seed
435 production were significantly lower than at unburnt stands, while seed germination and seedling
436 emergence were unchanged. Consequently, the only effect of fire was to reduce seed production in
437 the most severely burnt sites. At intermediate and low severity sites, cupule and seed production
438 were similar to unburnt sites, while seed germination and seedling emergence were higher.

439 Mixed severity fires generate microsite conditions that promote seed germination and seedling
440 emergence, such as a loose litter, exposed mineral soil and facilitation by deadwood. Moreover, fire
441 promotes diffuse light conditions via canopy opening, which favors beech seedlings already in the
442 first post-fire growing season, particularly at intermediate (i.e., 70-80%) canopy cover.

443 This and previous studies (van Gils *et al.*, 2010; Maringer *et al.*, 2012; Ascoli *et al.*, 2013) improve
444 our knowledge of the fire ecology of *Fagus sylvatica*. These studies demonstrate that beech can
445 persist in a mixed severity fire regime characterized by fire return intervals long enough to allow
446 trees to reach reproductive maturity (i.e., >50 years), such as those identified by long-term
447 paleoecological studies in Central and Northern Europe (Tinner *et al.*, 1999; Bradshaw and
448 Lindbladh, 2005; Tinner and Lotter, 2006; Giesecke *et al.*, 2007).

449 From a practical point of view, these findings are useful to define ecologically based criteria to
450 restore beech forests affected by wildfire. Often, post-fire restoration in beech, and in other Alpine
451 forest stands, fails to recognize the important ecological legacy that decaying trees represent. This
452 results in simplistic prescriptions such as salvage logging, which disrupts the regeneration niche
453 provided by fire and in costly artificial regeneration measures (Ascoli *et al.*, 2013; Vacchiano *et al.*,
454 2014). Our study stresses the importance of decaying trees hit by fire and of their delayed mortality,
455 which promotes regeneration first by producing seeds in mast years, and later by the sheltering
456 action of decaying snags and logs. In this context, the ratio between declining (<50% live crown)
457 and overall basal area of beech may be used to quantify fire severity in the growing seasons after

458 fire, which is a critical aspect for successful post-fire restoration (Morgan *et al.*, 2014). Based on
459 these findings and previous results (Conedera *et al.*, 2010; Ascoli *et al.*, 2013), we suggest the
460 following thresholds of live basal area loss to assess fire severity 1-3 years after fire: low severity
461 <20%; intermediate 20-80%; high >80%. These may also be applied to silvicultural systems aiming
462 to implement disturbance-like treatments that may imitate the effects of mixed severity fires, as
463 recommended in the case of wind disturbance (Nagel *et al.*, 2014).

464 Current knowledge is insufficient to determine whether the regeneration strategy observed for beech
465 is a true adaptation to fire or rather is an “exaptation” (Gould and Vrba, 1982), i.e., a trait selected
466 by other agents (e.g., wind) causing similar effects on stand structure. Severe, infrequent wind
467 disturbances play a primary role in the regeneration of temperate beech forests (Kramer *et al.*, 2014;
468 Nagel *et al.*, 2014). Our study shows that fire also has a positive effect on beech seedling
469 establishment when masting synchronizes with fire effects. These results open up new questions
470 about a possible ‘disturbance-predictive’ form of masting in beech, whereby mast crops are
471 produced in years with exceptionally hot and dry summers, as such climatic conditions portend
472 periods of increased fire occurrence, as proposed for other plant species (Selås *et al.*, 2002; Wright
473 *et al.*, 2014). Additionally, other fire-specific effects may facilitate beech recruitment, e.g., by
474 increasing nutrient mobilization and uptake due to charcoal and by increasing nitrification in the
475 forest soil (Ball *et al.*, 2010), which, in turn, favors masting (Miyazaki *et al.*, 2014) and seedling
476 growth (Wagner *et al.*, 2010) due to a higher amount of available nitrogen. Further analyses are
477 warranted to test these hypotheses.

478

479 **Acknowledgments**

480 This study was partially supported by the Swiss Federal Office for the Environment (FOEN).
481 Field and laboratory work was carried out with the support of Francesco Fraia (WSL Swiss Fed.
482 Res. Inst., Res. Group Insubric Ecosystems), Marc Font (University of Lleida), and Fabio Meloni
483 and Roberta Berretti (DISAFA, University of Torino).

484 We are grateful to two anonymous reviewers for careful revision and useful suggestions.

485

486 **References**

- 487 Abrams, M.D., Johnson, S.E., 2013. The Impacts of Mast Year and Prescribed Fires on Tree
488 Regeneration in Oak Forests at the Mohonk Preserve, Southeastern New York, USA. *Natural Areas*
489 *Journal* 33, 427-434.
- 490 Adamek, M., Bobek, P., Hadincova, V., Wild, J., Kopecky, M., 2015. Forest fires within a
491 temperate landscape: A decadal and millennial perspective from a sandstone region in Central
492 Europe. *Forest Ecology and Management* 336, 81-90.
- 493 Agestam, E., Eko, P.M., Nilsson, U., Welander, N.T., 2003. The effects of shelterwood density and
494 site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. *Forest Ecology and*
495 *Management* 176, 61-73.
- 496 Ammer, C., Mosandl, R., El Kateb, H., 2002. Direct seeding of beech (*Fagus sylvatica* L.) in
497 Norway spruce (*Picea abies* L. Karst.) stands - effects of canopy density and fine root biomass on
498 seed germination. *Forest Ecology and Management* 159, 59-72.
- 499 Ascoli, D., Castagneri, D., Valsecchi, C., Conedera, M., Bovio, G., 2013. Post-fire restoration of
500 beech stands in the Southern Alps by natural regeneration. *Ecological Engineering* 54, 210-217.
- 501 Ayari, A., Khouja, M.L., 2014. Ecophysiological variables influencing Aleppo pine seed and cone
502 production: a review. *Tree Physiology* 34, 426-437.
- 503 Ball, P.N., MacKenzie, M.D., DeLuca, T.H., Holben, W.E., 2010. Wildfire and Charcoal Enhance
504 Nitrification and Ammonium-Oxidizing Bacterial Abundance in Dry Montane Forest Soils. *Journal*
505 *of Environmental Quality* 39, 1243-1253.
- 506 Bates, D., Maechler, M., Bolker, B., Walker S., Christensen, R.H.B., Singmann, H., (...) & Rcpp L.
507 2014. Package 'lme4'. R Foundation for Statistical Computing, Vienna.
- 508 Belmonte, J., Alarcon, M., Avila, A., Scialabba, E., Pino, D., 2008. Long-range transport of beech
509 (*Fagus sylvatica* L.) pollen to Catalonia (north-eastern Spain). *International Journal of*
510 *Biometeorology* 52, 675-687.
- 511 Bradshaw, R.H.W., Lindbladh, M., 2005. Regional spread and stand-scale establishment of *Fagus*
512 *sylvatica* and *Picea abies* in Scandinavia. *Ecology* 86, 1679-1686.

513 Burgman, M., Graham, K., Fox, J.C., Hickey, J. 2004. Chapter 4. Myrtle (*Nothofagus cunninghamii*
514 (Hook.) Oerst.), in: Fox, J.C., Regan, T.J., Bekessy, S.S., (...) & Burgman, M. (Eds.), Linking
515 landscape ecology and management to population viability analysis. Report 2: Population viability
516 analyses for eleven forest dependent species. The University of Melbourne, pp. 94-121.

517 Collet, C., Piboule, A., Leroy, O., Frochet, H., 2008. Advance *Fagus sylvatica* and *Acer*
518 *pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-
519 standards forest. *Forestry* 81, 135-150.

520 Conedera, M., Lucini, L., Valse, E., Ascoli, D., Pezzatti, G., 2010. Fire resistance and vegetative
521 recruitment ability of different deciduous trees species after low-to moderate-intensity surface fires
522 in southern Switzerland. In, *Proceedings of the VI International Conference on Forest Fire*
523 *Research*. Coimbra, Portugal, pp. 15-18.

524 Delarze, R., Caldelari, D., Hainard, P., 1992. Effects of fire on forest dynamics in southern
525 switzerland. *Journal of Vegetation Science* 3, 55-60.

526 Drobyshev, I., Bergeron, Y., Linderholm, H.W., Granström, A., Niklasson, M., 2015. A 700-year
527 record of large fire years in northern Scandinavia shows large variability and increased frequency
528 during the 1800 s. *Journal of Quaternary Science* 30, 211-221.

529 Drobyshev, I., Niklasson, M., Mazerolle, M.J., Bergeron, Y., 2014. Reconstruction of a 253-year
530 long mast record of European beech reveals its association with large scale temperature variability
531 and no long-term trend in mast frequencies. *Agricultural and Forest Meteorology* 192, 9-17.

532 Fernandes, P.M., Loureiro, C., Guiomar, N., Pezzatti, G.B., Manso, F.T., Lopes, L., 2014. The
533 dynamics and drivers of fuel and fire in the Portuguese public forest. *Journal of Environmental*
534 *Management* 146, 373-382.

535 Frazer, G.W., Canham, C., Lertzman, K., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging
536 software to extract canopy structure and gap light transmission indices from true-colour fisheye
537 photographs, users manual and program documentation. Simon Fraser University, Burnaby, British
538 Columbia, and the Institute of Ecosystem Studies, Millbrook, New York 36.

539 Geburek, T., Hiess, K., Litschauer, R., Milasowszky, N., 2012. Temporal pollen pattern in
540 temperate trees: expedience or fate? *Oikos* 121, 1603-1612.

541 Geßler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2007. Potential
542 risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees-Structure and Function*
543 21, 1-11.

544 Giesecke, T., Hickler, T., Kunkel, T., Sykes, M.T., Bradshaw, R.H.W., 2007. Towards an
545 understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of Biogeography* 34, 118-
546 131.

547 Gould, S.J., Vrba, E.S., 1982. Exaptation-a missing term in the science of form. *Paleobiology*, 4-15.

548 Harmer, R., 1995. Natural regeneration of broadleaved trees in Britain .3. germination and
549 establishment. *Forestry* 68, 1-9.

550 Harville, D.A., 1977. Maximum likelihood approaches to variance component estimation and to
551 related problems. *Journal of the American Statistical Association* 72, 320-338.

552 Herranz, J.M., MartinezSanchez, J.J., DeLasHeras, J., Ferrandis, P., 1996. Stages of plant
553 succession in *Fagus sylvatica* L and *Pinus sylvestris* L Forests of Tejera Negra Natural Park
554 (Central Spain), three years after fire. *Israel Journal of Plant Sciences* 44, 347-358.

555 Hinrichsen, D., 1987. The forest decline enigma. *Bioscience* 37, 542-546.

556 Innes, J.L., 1994. The occurrence of flowering and fruiting on individual trees over 3 years and their
557 effects on subsequent crown condition. *Trees-Structure and Function* 8, 139-150.

558 Iverson, L.R., Hutchinson, T.F., Prasad, A.M., Peters, M.P., 2008. Thinning, fire, and oak
559 regeneration across a heterogeneous landscape in the eastern US: 7-year results. *Forest Ecology and*
560 *Management* 255, 3035-3050.

561 Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested
562 usage. *International Journal of Wildland Fire* 18, 116-126.

563 Kelly, D., 1994. The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution* 9, 465-
564 470.

565 Kramer, K., Brang, P., Bachofen, H., Bugmann, H., Wohlgemuth, T., 2014. Site factors are more
566 important than salvage logging for tree regeneration after wind disturbance in Central European
567 forests. *Forest Ecology and Management* 331, 116-128.

- 568 Krannitz, P.G., Duralia, T.E., 2004. Cone and seed production in *Pinus ponderosa*: A review.
569 *Western North American Naturalist* 64, 208-218.
- 570 Madsen, P., 1995. Effects of soil water content, fertilization, light, weed competition and seedbed
571 type on natural regeneration of beech (*Fagus sylvatica*). *Forest Ecology and Management* 72, 251-
572 264.
- 573 Madsen, P., Larsen, J.B., 1997. Natural regeneration of beech (*Fagus sylvatica* L.) with respect to
574 canopy density, soil moisture and soil carbon content. *Forest Ecology and Management* 97, 95-105.
- 575 Maringer, J., Wohlgemuth, T., Neff, C., Pezzatti, G.B., Conedera, M., 2012. Post-fire spread of
576 alien plant species in a mixed broad-leaved forest of the Insubric region. *Flora* 207, 19-29.
- 577 Mazzoleni, S., Bonanomi, G., Incerti, G., Chiusano, M.L., Termolino, P., Mingo, A., Senatore, M.,
578 Giannino, F., Carteni, F., Rietkerk, M., Lanzotti, V., 2015. Inhibitory and toxic effects of
579 extracellular self-DNA in litter: a mechanism for negative plant-soil feedbacks? *New Phytologist*
580 205, 1195-1210.
- 581 Miller, J.D., Knapp, E.E., Key, C.H., Skinner, C.N., Isbell, C.J., Creasy, R.M., Sherlock, J.W.,
582 2009. Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to
583 three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA.
584 *Remote Sensing of Environment* 113, 645-656.
- 585 Minotta, G., Pinzauti, S., 1996. Effects of light and soil fertility on growth, leaf chlorophyll content
586 and nutrient use efficiency of beech (*Fagus sylvatica* L) seedlings. *Forest Ecology and Management*
587 86, 61-71.
- 588 Miyazaki, Y., Maruyama, Y., Chiba, Y., Kobayashi, M.J., Joseph, B., Shimizu, K.K., Mochida, K.,
589 Hiura, T., Kon, H., Satake, A., 2014. Nitrogen as a key regulator of flowering in *Fagus crenata*:
590 understanding the physiological mechanism of masting by gene expression analysis. *Ecology*
591 *Letters* 17, 1299-1309.
- 592 Morgan, P., Keane, R.E., Dillon, G.K., Jain, T.B., Hudak, A.T., Karau, E.C., Sikkink, P.G., Holden,
593 Z.A., Strand, E.K., 2014. Challenges of assessing fire and burn severity using field measures,
594 remote sensing and modelling. *International Journal of Wildland Fire* 23, 1045-1060.
- 595 Motta, R., Garbarino, M., Berretti, R., Bjelanovic, I., Borgogno Mondino, E., Čurović, M., Keren,
596 S., Meloni, F., Nosenzo, A., 2014. Structure, spatio-temporal dynamics and disturbance regime of

597 the mixed beech–silver fir–Norway spruce old-growth forest of Biogradska Gora (Montenegro).
598 Plant Biosystems, 1-10.

599 Mund, M., Kutsch, W.L., Wirth, C., Kahl, T., Knohl, A., Skomarkova, M.V., Schulze, E.D., 2010.
600 The influence of climate and fructification on the inter-annual variability of stem growth and net
601 primary productivity in an old-growth, mixed beech forest. *Tree Physiology* 30, 689-704.

602 Nagel, T.A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-
603 growth forest landscape of southeastern Europe. *Ecological Applications* 24, 663-679.

604 Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in
605 an old-growth Fagus-Abies forest of Bosnia-Herzegovina. *Plant Ecology* 208, 307-318.

606 Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R² from
607 generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4, 133-142.

608 Nilsson, S.G., 1985. Ecological and evolutionary interactions between reproduction of beech fagus-
609 sylvatica and seed eating animals. *Oikos* 44, 157-164.

610 Nilsson, S.G., Wastljung, U., 1987. Seed predation and cross-pollination in mast-seeding beech
611 (fagus-sylvatica) patches. *Ecology* 68, 260-265.

612 Nocentini, S., 2009. Structure and management of beech (*Fagus sylvatica* L.) forests in Italy.
613 *Iforest-Biogeosciences and Forestry* 2, 105-113.

614 Nopp-Mayr, U., Kempter, I., Muralt, G., Gratzner, G., 2012. Seed survival on experimental dishes in
615 a central European old-growth mixed-species forest - effects of predator guilds, tree masting and
616 small mammal population dynamics. *Oikos* 121, 337-346.

617 O'Dowd, D.J., Gill, A.M., 1984. Predator satiation and site alteration following fire: mass
618 reproduction of alpine ash (*Eucalyptus delegatensis*) in southeastern Australia. *Ecology*, 1052-1066.

619 Olesen, C.R., Madsen, P., 2008. The impact of roe deer (*Capreolus capreolus*), seedbed, light and
620 seed fall on natural beech (*Fagus sylvatica*) regeneration. *Forest Ecology and Management* 255,
621 3962-3972.

622 Overgaard, R., Gemmel, P., Karlsson, M., 2007. Effects of weather conditions on mast year
623 frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry* 80, 553-563.

624 Packham, J.R., Thomas, P.A., Atkinson, M.D., Degen, T., 2012. Biological Flora of the British
625 Isles: *Fagus sylvatica*. *Journal of Ecology* 100, 1557-1608.

626 Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoğlu, Ç., Lloret, F., Buhk, C., Ojeda, F., Luna, B.,
627 Moreno, J., Rodrigo, A., 2009. Fire-related traits for plant species of the Mediterranean Basin:
628 *Ecological Archives* E090-094. *Ecology* 90, 1420-1420.

629 Peters, V.S., MacDonald, S.E., Dale, M.R.T., 2005. The interaction between masting and fire is key
630 to white spruce regeneration. *Ecology* 86, 1744-1750.

631 Pezzatti, G.B., Bajocco, S., Torriani, D., Conedera, M., 2009. Selective burning of forest vegetation
632 in Canton Ticino (southern Switzerland). *Plant Biosystems* 143, 609-620.

633 Piovesan, G., Adams, J.M., 2001. Masting behaviour in beech: linking reproduction and climatic
634 variation. *Canadian Journal of Botany-Revue Canadienne De Botanique* 79, 1039-1047.

635 Piovesan, G., Adams, J.M., 2005. The evolutionary ecology of masting: does the environmental
636 prediction hypothesis also have a role in mesic temperate forests? *Ecological Research* 20, 739-743.

637 Pouden, E., Greene, D.F., Michaletz, S.T., 2014. Non-serotinous woody plants behave as aerial
638 seed bank species when a late-summer wildfire coincides with a mast year. *Ecology and Evolution*
639 4, 3830-3840.

640 Provendier, D., Balandier, P., 2008. Compared effects of competition by grasses (Graminoids) and
641 broom (*Cytisus scoparius*) on growth and functional traits of beech saplings (*Fagus sylvatica*).
642 *Annals of forest science* 65, 1.

643 Pyne, S.J., 1982. A cultural history of wildland and rural fire. In. Princeton University Press,
644 Princeton, MS, USA.

645 Quinn, G.P., Keough, M.J., 2002. *Experimental design and data analysis for biologists*. Cambridge
646 University Press.

647 R Core Development Team 2013. R: A language and environment for statistical computing.
648 Version 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria).

649 Wood, S., Scheipl, F., & Wood, M.S. 2014. Package 'gam4'.

650 Schmuck, G., San-Miguel-Ayanz, J., Camia, A., Durrant, T.H., Boca, R., Libertá, G., Petroligkis,
651 T., Di Leo, M., Rodriguez-Aseretto, D., Boccacci, F., 2014. Forest Fires in Europe, Middle East and
652 North Africa 2013. In. European Commission - Joint Research Centre, Luxemburg.

653 Schomaker, M.E., Zarnoch, S.J., Bechtold, W.A., Latelle, D.J., Burkman, W.G., Cox, S.M., 2007.
654 Crown-condition classification: a guide to data collection and analysis. In. USDA, Southern
655 Research Station, pp. 1-92.

656 Selås, V., Piovesan, G., Adams, J.M., Bernabei, M., 2002. Climatic factors controlling reproduction
657 and growth of Norway spruce in southern Norway. *Canadian Journal of Forest Research* 32, 217-
658 225.

659 Silva, D.E., Mazzella, P.R., Legay, M., Corcket, E., Dupouey, J.L., 2012. Does natural regeneration
660 determine the limit of European beech distribution under climatic stress? *Forest Ecology and*
661 *Management* 266, 263-272.

662 Simon, A., Gratzer, G., Sieghardt, M., 2011. The influence of windthrow microsites on tree
663 regeneration and establishment in an old growth mountain forest. *Forest Ecology and Management*
664 262, 1289-1297.

665 Souza, A.F., de Matos, D.U., Forgiarini, C., Martinez, J., 2010. Seed crop size variation in the
666 dominant South American conifer *Araucaria angustifolia*. *Acta Oecologica-International Journal of*
667 *Ecology* 36, 126-134.

668 Suszka, B., Muller, C., Bonnet-Masimbert, M., 2000. *Semi di latifoglie forestali: dalla raccolta alla*
669 *semina*. Calderini-Edagricole Editore.

670 Swetnam, T.W., Betancourt, J.L., 1998. Mesoscale disturbance and ecological response to decadal
671 climatic variability in the American Southwest. *Journal of Climate* 11, 3128-3147.

672 Tinner, W., Conedera, M., Gobet, E., Hubschmid, P., Wehrli, M., Ammann, B., 2000. A
673 palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. *Holocene* 10, 565-
674 574.

675 Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B., Conedera, M., 1999. Long-term forest fire
676 ecology and dynamics in southern Switzerland. *Journal of Ecology* 87, 273-289.

677 Tinner, W., Lotter, A.F., 2006. Holocene expansions of *Fagus silvatica* and *Abies alba* in Central
678 Europe: where are we after eight decades of debate? *Quaternary Science Reviews* 25, 526-549.

679 Tognetti, R., Minotta, G., Pinzauti, S., Michelozzi, M., Borghetti, M., 1998. Acclimation to
680 changing light conditions of long-term shade-grown beech (*Fagus sylvatica* L.) seedlings of
681 different geographic origins. *Trees-Structure and Function* 12, 326-333.

682 Topoliantz, S., Ponge, J.F., 2000. Influence of site conditions on the survival of *Fagus sylvatica*
683 seedlings in an old-growth beech forest. *Journal of Vegetation Science* 11, 369-374.

684 Vacchiano, G., Stanchi, S., Marinari, G., Ascoli, D., Zanini, E., Motta, R., 2014. Fire severity,
685 residuals and soil legacies affect regeneration of Scots pine in the Southern Alps. *Science of the*
686 *Total Environment* 472, 778-788.

687 Valese, E., Conedera, M., Held, A., Ascoli, D., 2014. Fire, humans and landscape in the European
688 Alpine region during the Holocene. *Anthropocene* 6, 63-74.

689 Valsecchi, V., Carraro, G., Conedera, M., Tinner, W., 2010. Late-Holocene vegetation and land-use
690 dynamics in the Southern Alps (Switzerland) as a basis for nature protection and forest
691 management. *Holocene* 20, 483-495.

692 van Gils, H., Odoi, J.O., Andrisano, T., 2010. From monospecific to mixed forest after fire? An
693 early forecast for the montane belt of Majella, Italy. *Forest Ecology and Management* 259, 433-439.

694 van Mantgem, P.J., Stephenson, N.L., Keeley, J.E., 2006. Forest reproduction along a climatic
695 gradient in the Sierra Nevada, California. *Forest Ecology and Management* 225, 391-399.

696 Wagner, S., Collet, C., Madsen, P., Nakashizuka, T., Nyland, R.D., Sagheb-Talebi, K., 2010. Beech
697 regeneration research: From ecological to silvicultural aspects. *Forest Ecology and Management*
698 259, 2172-2182.

699 Wastl, C., Schunk, C., Lupke, M., Cocca, G., Conedera, M., Valese, E., Menzel, A., 2013. Large-
700 scale weather types, forest fire danger, and wildfire occurrence in the Alps. *Agricultural and Forest*
701 *Meteorology* 168, 15-25.

702 Watt, A.S., 1923. On the ecology of British beechwoods with special reference to their
703 regeneration. *Journal of Ecology* 11, 1-48.

704 Westerling, A.L., Gershunov, A., Brown, T.J., Cayan, D.R., Dettinger, M.D., 2003. Climate and
705 wildfire in the western United States. *Bulletin of the American Meteorological Society* 84, 595-604.

706 Williams, A.P., Seager, R., Macalady, A.K., Berkelhammer, M., Crimmins, M.A., Swetnam, T.W.,
707 Trugman, A.T., Buening, N., Noone, D., McDowell, N.G., Hryniw, N., Mora, C.I., Rahn, T., 2015.
708 Correlations between components of the water balance and burned area reveal new insights for
709 predicting forest fire area in the southwest United States. *International Journal of Wildland Fire* 24,
710 14-26.

711 Williamson, G.B., Ickes, K., 2002. Mast fruiting and ENSO cycles - does the cue betray a cause?
712 *Oikos* 97, 459-461.

713 Wood, S., 2006. *Generalized additive models: an introduction with R*. CRC press.

714 Wood, S., Scheipl, F., & Wood, M.S. 2014. Package 'gam4'.

715 Wright, B.R., Zuur, A.F., Chan, G.C.K., 2014. Proximate causes and possible adaptive functions of
716 mast seeding and barren flower shows in spinifex grasses (*Triodia* spp.) in arid regions of Australia.
717 *Rangeland Journal* 36, 297-308.

718 Zumbrunnen, T., Bugmann, H., Conedera, M., Buergi, M., 2009. Linking Forest Fire Regimes and
719 Climate-A Historical Analysis in a Dry Inner Alpine Valley. *Ecosystems* 12, 73-86.

720 Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed effects models and
721 extensions in ecology with R*. Springer Science & Business Media.

722 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common
723 statistical problems. *Methods in Ecology and Evolution* 1, 3-14.

724 Šebková, B., Šamonil, P., Valtera, M., Adam, D., Janík, D., 2012. Interaction between tree species
725 populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. *Forest
726 Ecology and Management* 280, 9-19.

727

728 **Web references**

729 Arpa Piemonte: <http://www.arpa.piemonte.it/banca-dati-meteorologica>. Last access: 17-May-2015.

Reply to Reviewer#1

<p>I have only one major objection to the introduction part. The authors should improve the motivation of the study. It is clear that this phenomenon is poorly studied, but the fire disturbance ecology itself and its relevance to Holocene vegetation development in Europe offer far big potential for better Intro. It would be really pity to devalue such a good paper, by only average if not below-average Introduction.</p>	<p>The introduction section was fully revised according to suggestions.</p>
<p>L56 - L60 Fire also belongs to natural or anthropogenic disturbance - please improve the reasoning in this paragraph</p>	<p>This paragraph was modified (see lines 44 to 59). We improved the reasoning on one of the key messages of our study, i.e., while there is a considerable amount of studies on the effects of disturbances such as wind and shelterwood cutting, very few knowledge about fire effects is currently available for beech forests.</p>
<p>L 152 ... better herb layer vegetation</p>	<p>Done: see line 159</p>
<p>Fig 2 All plots were on big slopes. How did you measure the distances? ... as planar projection or along surface?</p>	<p>To what concerns sub-plot to assess cupules, seeds, seedling emergence (0.4 m quadrats) and seedlings establishment (1 m quadrats), distances were measured along the slope surface without correcting for the slope. As regards the circular plot (12 m radius) used to measure stem density and basal area, the planar distance of 12 m was corrected by the slope. This should be now clearer at line 135.</p>
<p>L168. How did you distinguish the late recruitment stages - e.g. emergent and established seedlings?</p>	<p>We assessed emergent seedlings in spring 2014, while established seedlings were assessed in summer 2014 (i.e., 5 months later). This is explained now from line 149 to line 165.</p>
<p>L182. It would be better to present the predictors earlier than only on L 189</p>	<p>The section 2.4 Data analysis was changed. From line 191 to line 235 we describe the modeling analysis related to paper objective two: assess the processes by which fire and other environmental variables affect seed production and regeneration. Models predictors are now presented at the beginning of this part, from line 194 to line 198.</p>
<p>L. 194 the arguments for not using of selection methods like forward&backward seems to be sound, but did you considered also to the multimodel inference approach (e.g. Burnham et al (2011) and Symonds et Moussalli (2011) Behav Ecol Sociobiol 65), which solve most of your objections?</p>	<p>We read the papers suggested by Reviewer#1. It is true that an IT approach would address the model and parameter selection more effectively than stepwise algorithms. However, as we stated at lines 211, we are not operating in a model selection / model comparison mode. Our study is experimental in nature, and not purely observational, even if the treatment was "applied" by fire and not by the experimenter. Moreover, we started with some clear null hypotheses, not trivial in their formulation, and involving a limited set of potential parameters that were screened for collinearity to avoid p-value inflation. After reading the suggested literature, and other recent papers on the frequentist vs. IT-based approach (e.g.,</p>

	Johnson & Omland 2004, Mundry 2011, Murtaugh 2014, and the recent forum on the 2014 issue of ecology), we chose to continue using p-values in both the ANOVA and GLMM/GAMM analysis.
L. 229 High severity of fire caused high mortality of adult trees, which results in lower production ... it sounds quite trivial, does not?	Often research comes to obvious results. Still this result is an experimental evidence which confirms common believes.
Fig. 4 Improve description of what letters above graphs (a), (b) etc. mean.	We improved the description of the meaning of letters in the graph as regards both letters in brackets related to different studied variable, and letters related to the post-hoc test results.

Reply to Reviewer#2

I feel that the paper could be improved by increasing focus on this broader aim/relevance in the discussion and conclusions (i.e. "Beech is considered to be poorly adapted to fire but this study shows..."). At the moment the overall message/contribution/impact of the paper is not clearly articulated.	We fully revised the introduction, discussion and conclusion sections to articulate the novelty and impact of our studies. As suggested by the Reviewer#2 we focused on the key point that beech seems to display strategies to cope with fires of mixed severity despite lacking of obvious fire adaptive traits.
The text lacks clarity and flow, and requires a stronger narrative to help the reader follow the key ideas and message. Additionally the grammar and sentence structure still requires proof-reading – I have made some suggestions and corrections but this is not exhaustive.	We restructured several parts of the narrative chapters and we additionally provide a linguistic revision of the text by the Elsevier language editing service. We believe that we now meet the expectation of the reviewer in this sense.
The discussion of the possible link between fire events and masting events needs careful work. It appears to me that the authors are suggesting that fire events may act as either a cue for mast events, or as a possible evolutionary driver of masting. This discussion requires very careful revision. There is little evidence to support this hypothesis in the literature (and indeed, a key reference used in this manuscript (Piovesan and Adams, 2005) is controversial. The new data presented by the paper also does not appear to support the hypothesis - In Figure 3 cupule and seed numbers (a measure of masting intensity) are the same in control (unburnt) plots as in Intermediate and Low intensity burnt plots. I would expect a much more detailed and cautious discussion of this idea.	We provide here after and in the text a more detailed discussion of our hypothesis about the link between fire and masting in beech. The first point to clarify is: we are not suggesting that fire acts as a cue of flowering, and thus of mast seeding (e.g. as it is in Australian Xanthorrhoeaceae). Indeed, our data do not support this hypothesis. This misunderstanding was due to the lack of clarity in our assertions, particularly at lines 299-303 and 411-414 (previous version), which are now modified (see lines 320- 323 and 464-472). Rather, in line with the "Environmental prediction hypothesis" for mast seeding (Kelly, 1994), we expand concepts of those studies which look at drought not only as cue for floral induction, but also as a disturbance agent which produces a favorable environment for seedling recruitment, thus exerting a selective pressure on mast seeding selection (Williamson and Ickes, 2002; Souza <i>et al.</i> , 2010; Fletcher, 2015). Piovesan and Adams (2005) suggested the same concept for beech. We expand these concepts from drought to fire: whereby mast crops are produced in years with exceptionally hot and dry summers, such climatic conditions portend periods of increased fire likelihood*. Our idea is that

fire disturbance synchronizes with drought and has the potential to enhance its effect at the advantage of beech seedling recruitment. We support the hypothesis formulated for other species (Selas *et al.*, 2002; Peters *et al.*, 2005; Pouden *et al.*, 2014) that drought and fire, together with others selective pressures (i.e., pollen coupling, seed predators) may have contributed to select masting behavior in beech.

*Evidences to support this statement are:

1) In beech, a synchronized masting results from the influence of a rainy, cold growing season two years before the concerned mast year (my-2), followed by a dry and warm growing season in the year preceding the mast (my-1). Concurrently, higher precipitation (m-2) may reduce wildfire probability in the short run, but increases wildfire probability in the long run via higher biomass production. If the period of biomass accumulation is followed by a dry and hot season (m-1), biomass becomes available for combustion and synchronized large fires can occur over extended areas. This relationship was found by several studies, both in North America (Swetnam and Betancourt, 1998; Westerling *et al.*, 2003; Williams *et al.*, 2015) and Europe (Zumbrunnen *et al.*, 2009; Fernandes *et al.*, 2014).

2) Drought indices in year my-1 were found to correlate positively with a masting the year after, e.g., Palmer Drought Severity Index (PDSI) in Piovesan and Adams (2001), Drought Index (DI) in Drobyshv et al. (2014). The same indices are often used as fire danger indexes to forecast fire (Westerling *et al.*, 2003).

3) Drobyshv *et al.* (2014) found that the year immediately preceding a mast year (my-1) was characterized by a regional high pressure anomaly centered in southern Scandinavia. Similarly, large forest fires years in Sweden are associated with the same positive pressure anomalies (Drobyshv *et al.*, 2015). In the same studies from Southern Sweden, the 1820-1860 period had high frequency of mast years (< 4 years between each mast) (Drobyshv et al. 2014), which overlaps with the period 1820-1850 that had more frequent large fires (Drobyshv et al. 2015).

4) Positive phases of the Summer North Atlantic Oscillation Index (SNAO) (Folland *et al.*, 2009) seem to overlap with periods of increased mast year frequency, and vice versa (i.e., 1750-1775, 1820-1850, 1900-1925, 1975-2006 in Drobyshv et al.

2014). At the same time, positive SNAO is responsible for summer regional drought and heat waves (from southern UK and southern Sweden to Central Europe and Alps) (Della-Marta *et al.*, 2007), which in turn are responsible of increased fire activity in this region, e.g. heat wave and fire in Central EU in 2003 (UNEP 2004, (Schmuck *et al.*, 2014) and large full mast year throughout central Europe in 2004.

References

- Della-Marta, P.M., Luterbacher, J., von Weissenfluh, H., Xoplaki, E., Brunet, M., Wanner, H., 2007. Summer heat waves over western Europe 1880-2003, their relationship to large-scale forcings and predictability. *Climate Dynamics* 29, 251-275.
- Drobyshev, I., Bergeron, Y., Linderholm, H.W., Granström, A., Niklasson, M., 2015. A 700-year record of large fire years in northern Scandinavia shows large variability and increased frequency during the 1800 s. *Journal of Quaternary Science* 30, 211-221.
- Fernandes, P.M., Loureiro, C., Guiomar, N., Pezzatti, G.B., Manso, F.T., Lopes, L., 2014. The dynamics and drivers of fuel and fire in the Portuguese public forest. *Journal of Environmental Management* 146, 373-382.
- Fletcher, M.-S., 2015. Mast seeding and the El Niño-Southern Oscillation: a long-term relationship? *Plant Ecology* 216, 527-533.
- Folland, C.K., Knight, J., Linderholm, H.W., Fereday, D., Ineson, S., Hurrell, J.W., 2009. The summer North Atlantic Oscillation: past, present, and future. *Journal of Climate* 22, 1082-1103.
- Kelly, D., 1994. The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution* 9, 465-470.
- Peters, V.S., MacDonald, S.E., Dale, M.R.T., 2005. The interaction between masting and fire is key to white spruce regeneration. *Ecology* 86, 1744-1750.
- Pounden, E., Greene, D.F., Michaletz, S.T., 2014. Non-serotinous woody plants behave as aerial seed bank species when a late-summer wildfire coincides with a mast year. *Ecology and Evolution* 4, 3830-3840.
- Schmuck, G., San-Miguel-Ayanz, J., Camia, A., Durrant, T.H., Boca, R., Libertá, G., Petroliagkis, T., Di Leo, M., Rodriguez-Aseretto, D., Boccacci, F., 2014. *Forest Fires in Europe, Middle East and North Africa 2013*.
- Selas, V., Piovesan, G., Adams, J.M., Bernabei, M., 2002. Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 32, 217-225.
- Souza, A.F., de Matos, D.U., Forgiarini, C., Martinez, J., 2010. Seed crop size variation in the dominant South American conifer *Araucaria angustifolia*. *Acta Oecologica-International Journal of Ecology* 36, 126-134.
- Swetnam, T.W., Betancourt, J.L., 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of*

	<p>Climate 11, 3128-3147.</p> <p>Westerling, A.L., Gershunov, A., Brown, T.J., Cayan, D.R., Dettinger, M.D., 2003. Climate and wildfire in the western United States. Bulletin of the American Meteorological Society 84, 595-604.</p> <p>Williams, A.P., Seager, R., Macalady, A.K., Berkelhammer, M., Crimmins, M.A., Swetnam, T.W., Trugman, A.T., Buening, N., Noone, D., McDowell, N.G., Hryniw, N., Mora, C.I., Rahn, T., 2015. Correlations between components of the water balance and burned area reveal new insights for predicting forest fire area in the southwest United States. International Journal of Wildland Fire 24, 14-26.</p> <p>Williamson, G.B., Ickes, K., 2002. Mast fruiting and ENSO cycles - does the cue betray a cause? Oikos 97, 459-461.</p> <p>Zumbrunnen, T., Bugmann, H., Conedera, M., Burgi, M., 2009. Linking Forest Fire Regimes and Climate-A Historical Analysis in a Dry Inner Alpine Valley. Ecosystems 12, 73-86.</p>
<p>Abstract</p> <p>18 We selected three beech stands in the Southwestern Alps</p>	<p>Done: see line 17</p>
<p>Introduction</p> <p>Overall the introduction is very short and repeats some key ideas. The paper could be much improved by fully developing and discussing the key motivations of the research/knowledge gaps/potential contribution and impact. The results presented later are very interesting, but the Introduction does not currently convey this potential.</p>	<p>The introduction section was fully revised according to reviewer's suggestions.</p>
<p>55 Relevance of the Drobyshev reference unclear. This paper reconstructed masting events using climate and tree ring data.</p>	<p>We agree with the reviewer and removed the Drobyshev reference.</p>
<p>56-59 Repetition of ideas from the previous paragraph (lines 45-47)</p>	<p>This and previous paragraphs were changed to avoid repetition of concepts. In previous paragraphs, we address shelterwood cutting and wind disturbances effects on beech recruitment, and how changes to the physical environment after disturbance can advantage beech recruitment. Only in this paragraph we improve the reasoning on one of the key points of our study, i.e., while there is a considerable amount of studies on the effects of disturbances such as wind and cutting, very few knowledge about fire effects is currently available for beech forests.</p>
<p>60-62 I feel that this is the key central message of the paper, and the area where the greatest contribution can be made</p>	<p>We expanded the two paragraphs following this key central message to clearly frame and articulate the contribution and impact of our research.</p>
<p>68 Replace "studies results" (clumsy) with "conclusions"?</p>	<p>This paragraph was removed in the revised version of the introduction. See lines 89 to 92.</p>
<p>75-78 If this a key idea/motivation for the research then it should be introduced and developed earlier</p>	<p>We expanded our reasoning about paleoecological studies and how our research can clarify results of these studies: i) the persistence of beech despite</p>

	increases in fire frequency during the Holocene; ii) the spread of beech in northern Europe during the Holocene was linked to disturbance by fire prior to stand establishment.
82 seed germination, and seedling emergence and establishment in the first post-mast year?	Done. See line 99.
83 Does the fire severity	The sentence was removed.
Material and methods Overall the methodology needs clarifying – it is too difficult to follow the procedure employed. A clearer focus and justification for the sampling procedure and statistical approach is required.	We fully revised the methods section and we hope now the clarity is improved.
110 The source for the climate data needs a reference or more details on the source (e.g. website?)	We added the link to weather data in the Web references list. Open the link with Internet Explorer as there are problems of compatibility between Chrome and Java.
112 Winterly Winter	Done: see line 103
113 started from at the	Done: see line 106
120 30 circular plots?	Done: see line 135
151 Are these the same plots (it would appear not)? How many were there? This is where I start to struggle to follow the methodology. Section 2.2 explains the sampling design, but here we appear to be introduced to more sample plots that are not mentioned before. It is not clear what these 250 m ² plots are for.	We agree with the reviewer that section 2.3 was not clear. We established 40 plots per study site (30 plots in the burnt and 10 in unburnt sites). At each plot we collected data in units of different size and area arranged according to Figure 2. Sub-plots of 0.16 m ² and 1 m ² were used to assess seedling emergence and establishment, respectively. Circular plots with a planar radius of 12 m (there was a refuse in reporting the plot size 250 m ²) were used to assess stand characteristics. We reedited section 2.3 making it clearer now, we hope.
156 the software GAP Light Analyzer	Done: see line 163
158 Figure 2. The caption is very unclear. How about: Figure 2. Scheme showing the sampling within each 12 m radius plot used for assessing stand characteristics and recruitment. The grey circle shows the centre of the plot. The dark grey squares represent the 0.4m microplots used to assess seeds and seedling emergence. The white squares represent the 1.0m microplots used to assess established seedlings. Dashed lines represent distances from the plot centre.	We changed the figure caption partly following Reviewer#2 suggestions.
160 “Plot to assess the stand area” – not clear what stand area is?	Fig. 2 caption is now changed according to Reviewer#2 suggestions.
167 These variable names need to be included in S 2.3 so we know exactly what they are and how they were measured.	Variable names were removed from the text as we realized they were not needed. They now appear only in Table 2 and in Table 3.
175 Repeating line 127-128	The sentence was removed.
187 I don’t know what this means? Plot means of what?	We used as offset the plot-averaged frequencies of the preceding regeneration stage. We clarified this at line 208-210.
191 Table 2	Done: see line 210

193 (see pages 139-140 in Quinn and Keough 2002)	Done: see line 215
221 Why are <i>soil</i> and <i>non-woody</i> listed if they are never used in the models?	Non-woody vegetation and bare soil cover were excluded from all models because they were collinear with canopy cover ($r = -0.62$) and litter abundance (-0.78), respectively (see line 217-222). However, we included them in Table 2 because they were initially included as potential predictors of beech regeneration and related hypotheses were formulated. However, they are now evidenced in Table 2 by using the sign X* in order to explicit that they were excluded from the analysis because of collinearity.
Results Overall the results section needs of clarification. The results themselves seem strong and are interesting, but the key ideas are not communicated clearly.	We revised the results section and added sub sections to communicate clearly key results.
224 Start with a more general overview of what the study had done? This first section could be written more clearly, focusing on the key results	We changed the first paragraph of the results section. The results of the K-mean analysis were moved to the method section as they belong to the pre-analysis phase of data. We added sub sections, and we now start the first sub section focusing on key results.
227 Try to write this in a more general way – something like: ANOVA and LSD revealed significant differences in measures of recruitment success between the four groups (High, Intermediate, Low and Control), indicating that...	We rewrote the sentence in a more general way: “Seed production and recruitment differed significantly among the three fire severity groups (high, intermediate, low) and the unburnt control (Figure 4)”. See lines 248-249.
229 I would have considered the more novel/interesting result is that cupule and seed production was <i>not lower</i> in I and L plots compared to C – this is the main emphasis late so it should be here too.	We emphasized this key result here according to the reviewer’s suggestion (see lines 251 to 252).
240 Figure 4 is fascinating – really interesting results	Thanks
255 Table 3 needs reformatting – perhaps include solid horizontal lines to separate the three sections (Covariates, Random factor and Metrics)?	Table 3 was formatted according to the reviewer’s suggestions.
258 It is difficult to assess the relative importance of each term (other than using the significance code)	We added to Table 3 the beta coefficient of predictors
258 It is not fully clear to me why GLMM and GAMM were both used (or were both presented). As they show pretty much the same thing, and the GAMM models explain more deviance then why not just use them for <i>cupule</i> , <i>fs-Ger</i> and <i>fd-Est</i> . At the moment I think the two models tend to distract from the key message of the paper	We removed the GLMM column when GAMM was used instead of GLMM.
266 Replace (Left), (Centre) and (Right) with (a), (b) and (c)	Done
270 at the base of the graph on the x-axis	Done
272 “Accounting for the rate between seeds and	We clarified the sentence as follows: “When offset by

<p>cupules” Not clear what this “rate” means/ I assume it has something to do with the use of offsets?</p>	<p>cupule abundance, seed abundance decreased linearly with increasing canopy cover and elevation”. See lines 296.</p>
<p>301-303 I do not feel that there is enough evidence to support this assertion. 2013 was a mast year anyway, and no evidence is presented to support the assertion that the tree allocated resources primarily to reproduction when confronted with this stress. Indeed, the case cue will have been cued the previous year (before the fire). It may be that following the fire the surviving trees do switch their resource allocation to seed production at the expense of growth etc. but data is not presented to support this. It would be extremely interesting if this data did exist though.</p>	<p>We agree with the Reviewer#2 that we have no data to support this statement. We changed our assertion remarking only that our findings are in line with previous observations that stressed beech trees (because of drought and deceases) can still produce mast crops. See lines 320-323.</p>
<p>338 or incur in necrosis again because</p>	<p>Done: see line 360</p>
<p>347 in the unburnt control plots, where stronger shading</p>	<p>Done: see line 371</p>
<p>351 Surprisingly, in the case</p>	<p>Done: see line 374</p>
<p>352 the unburnt control plots</p>	<p>Done: see line 375</p>
<p>362 Need to be much clearer what is meant by a “positive interaction” between beech masting and fire effects. “Interaction” implies that both entities influence each other – this is not the case here (masting does not influence fire).</p>	<p>We agree that “interaction” implies that both entities influence each other, and this is not the case. We used the term interaction partly influenced by the paper of Peters et al. (2005): “The interaction between Masting and Fire Is Key to White Spruce Regeneration” (we cited). We changed the term “interaction” with “synchronicity” throughout the text, including the title. This term is used in several papers to describe the effects of masting on animal population dynamics, i.e., the synchronicity between mast events and population fluctuations. We believe this term can help in explaining one of the key points of our discussion, i.e. that the synchronicity of beech masting and fire effects produce positive outcome in terms of regeneration and requires further research.</p>
<p>The paper provides strong evidence that fire influences the recruitment of beech, which based on my understanding of the manucrypt I would summarise as being the result of three processes: 1) In high intensity fires, cupule and seed production is significantly reduced compared to unburnt stands. However in high intensity fires the seeds that are produced are equally likely to germinate, emerge and establish as in unburnt stands. <i>Consequently, the only effect of fire on masting is to reduce seed production in the most severely burnt plots.</i> 2) Cupule and seed production is not affected by fire in intermediate and low intensity fires compared to control plots. However, compared to</p>	<p>Yes, these are our main results. We used this clear and straightforward summary suggested by the Reviewer#2 to highlight main study results in the conclusion section (see lines 434 to 442).</p>

<p>control plots, the germination success of seeds is higher, as is the emergence of seeds. 3) The establishment of seedlings is higher in Intermediate plots than any of the other treatments.</p>	
<p>369 Which What</p>	<p>This sentence was removed.</p>
<p>Conclusions 385-387 This the key idea and potential strength of the paper – greater focus is required on how the results of this paper can (and do) address this question.</p>	<p>We added a paragraph to the conclusion section where we focus on how the study results can improve our understanding of the ecology of beech in relation to fire and consequently post-fire restoration practices and silviculture in beech forests (see lines 443 to line 463)</p>
<p>389 Figure 4 implies that cupule and seed production equally high in I, L and C plots, so this statement cannot be true – seed production does not peak at I.</p>	<p>We agree with Reviewer#2, cupule production does not peak at intermediate severity but at intermediate canopy cover (Figure 4a), probably because of increased light (see discussion at line 326-331). This assertion was removed.</p>
<p>411-414 This study does not find an interaction between masting and fire, or an effect of fire in promoting seed production.</p>	<p>We changed this assertion in accordance with the replies to previous comments of Reviewer#2. Our study find a successful seedling establishment when fire effects coincide with a mast year. This result stimulate the question: which is the meaning of such a positive synchronism. Based on previous studies (see the reply to the third comment of Reviewer#2), we hypothesize a ‘disturbance-predictive’ form of masting in beech, whereby mast crops are produced in years with exceptionally hot and dry summers, as such climatic conditions portend periods of increased fire likelihood, which in turn expand the effect of drought in producing a favorable environment for seedling recruitment.</p>

Highlights

- We studied beech recruitment after a masting in burnt and unburnt stands of the Alps
- We quantified fire severity by basal area loss, litter cover and canopy opening
- Seed production declined only where fire severity was high
- Intermediate severity favored beech recruitment by litter shortage, gaps and deadwood
- We advance the hypothesis of a ‘disturbance-predictive’ form of masting in beech

[Click here to download KML File \(for GoogleMaps\): doc.kml](#)