

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

Davide Ascoli<sup>1\*</sup>, Giorgio Vacchiano<sup>1</sup>, Janet Maringer<sup>2,3</sup>, Giovanni Bovio<sup>1</sup>, Marco Conedera<sup>3</sup>

<sup>1</sup> University of Torino, DISAFA, Largo Paolo Braccini 2, Grugliasco (TO), Italy

<sup>2</sup> Institute for Landscape Planning and Ecology, University of Stuttgart, Germany

<sup>3</sup> WSL Swiss Fed. Res. Inst., Res. Group Insubric Ecosystems, Bellinzona, Switzerland

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

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

## **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  $448 \pm 38$  cupules  $m^{-2}$  and  $489 \pm 44$  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

This document is the accepted manuscript version of the following article:  
Ascoli, D., Vacchiano, G., Maringer, J., Bovio, G., & Conedera, M. (2015). The synchronicity of masting and intermediate severity fire effects favors beech recruitment. *Forest Ecology and Management*, 353, 126-135.  
<https://doi.org/10.1016/j.foreco.2015.05.031>

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

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 ( $86000 \pm 10574$  seedlings  $\text{ha}^{-1}$ ) 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.

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

## 1. Introduction

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

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

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

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

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

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

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

## 2. Materials and Methods

### 2.1. Study area

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

The three forests were former beech coppices converted to high forests during the last 50 years. Pre-fire basal area ranges from 25.9 to 27.9 m<sup>2</sup> ha<sup>-1</sup> (Table 1). Beech is dominant (87% basal area), with sporadic *Betula pendula* Roth, *Laburnum alpinum* J.Presl, *Larix decidua* Mill., *Pinus sylvestris* L., and *Quercus petraea* (Mattuschka) Liebl. All sites are south facing and lie on crystalline rocks (gneiss), but differ slightly in elevation and annual precipitation (Table 1).

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

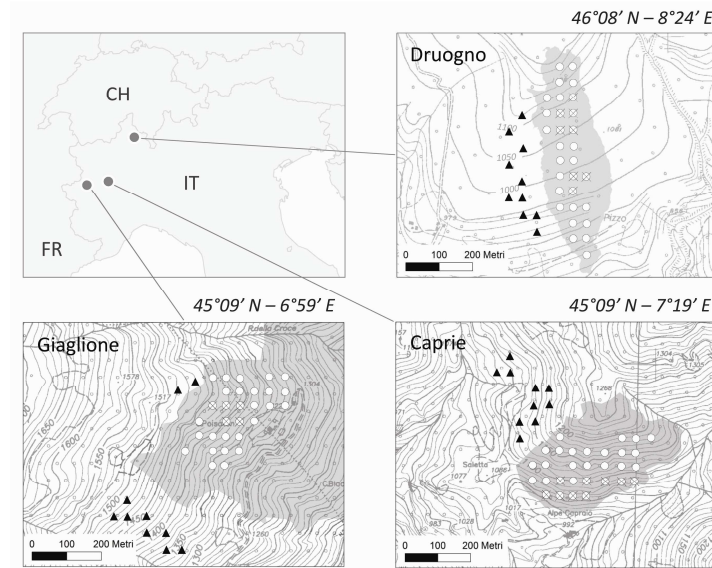


Figure 1 – Upper left: geographical position of study sites. Panels: fire perimeters (light grey) (data: Italian Forest Service), and location of sampling plots in burnt (white circles) and unburnt (black triangles) areas. Crossed circles represent sampling points excluded from the analysis because of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

Table 1 – Characteristics of fire events and study sites.  $P_{30d}$ : cumulative rainfall in the last 30 days before fire;  $T_{max}$ : maximum air temperature during the fire; Wind: wind gust speed during the fire.  $BA_{beech}$ : mean basal area ( $\pm SE$ ) of pre-fire beeches;  $P_{03-13}$ : mean annual precipitation of the observation period 2003-2013. 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 <sup>-1</sup> )	Burnt area (ha)	$BA_{beech}$ (m <sup>2</sup> ha <sup>-1</sup> )	Aspect (°N)	Slope (%)	Elevation (m a.s.l.)	$P_{03-13}$ (mm yr <sup>-1</sup> )	Plots
Druogno	26/03/12	82 / 6 / 52	9.5	25.9 $\pm$ 1.4	150 $\pm$ 4	59 $\pm$ 2	1131 $\pm$ 6	1460	32
Giaglione	31/03/12	17 / 21 / 38	40.5	26.2 $\pm$ 1.5	125 $\pm$ 7	67 $\pm$ 2	1430 $\pm$ 8	880	35
Caprie	16/01/13	2 / 2 / -	16.7	27.9 $\pm$ 1.2	162 $\pm$ 9	70 $\pm$ 2	1085 $\pm$ 11	1014	31

## 2.2. Sampling design

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

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

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

### 2.3. Field survey and lab analysis

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

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

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

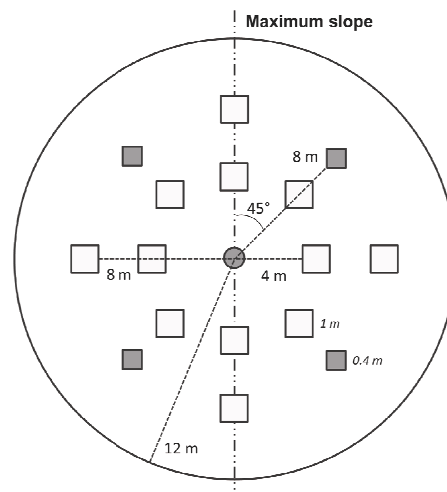


Figure 2 – Sampling units within each 12 m-radius plot. The grey circle shows the center of the plot. Dark grey squares: 0.4 m sub-plots used to count cupules, seeds and emergent seedlings. White squares 1.0 m sub-plots used to count established seedlings. Dashed lines: distances from the plot center.

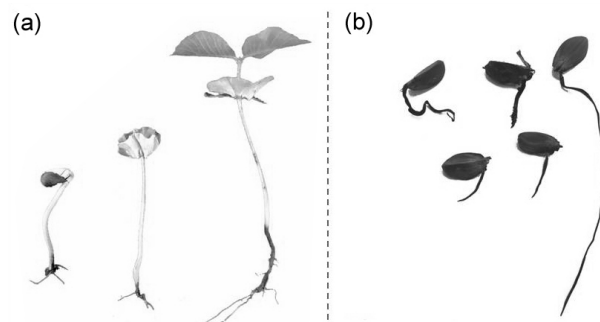


Figure 3 – (a) Germinated beech seeds with developed roots and cotyledons; (b) Germinated beech seeds with partial or complete root necrosis.

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).

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

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

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

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

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 <sup>-2</sup>	Seeds n m <sup>-2</sup>	Germinated seeds n m <sup>-2</sup>	Emergent seedlings n m <sup>-2</sup>	Established seedlings n m <sup>-2</sup>
<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 <sup>2</sup> ha <sup>-1</sup>	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 <sup>-2</sup>	–	–	–	–	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 <sup>-2</sup>	–	cupules	seeds	germinated seedlings	emergent seedlings

## Results

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

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

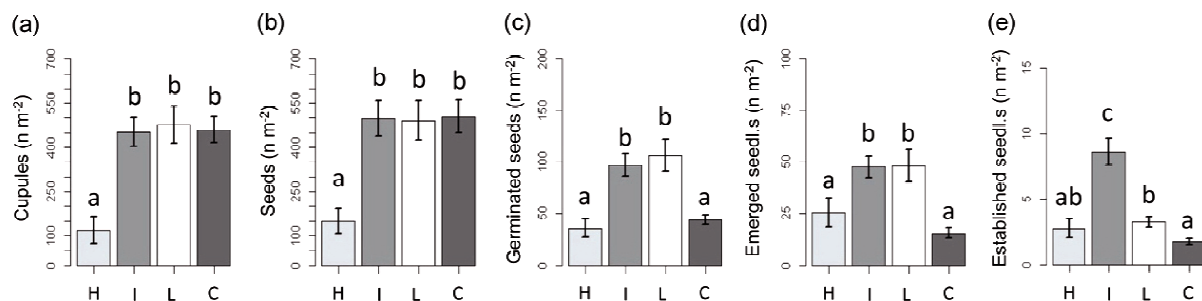


Figure 4 – Means (±SE) of the following variables: (a) cupules m<sup>-2</sup>; (b) seeds m<sup>-2</sup>; (c) germinated seeds m<sup>-2</sup>; (d) emergent seedlings m<sup>-2</sup>; (e) established seedlings m<sup>-2</sup>. Different letters show significant differences ( $p<0.05$ ) between fire severity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

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

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

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

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

Table 3 – Generalized mixed models of beech recruitment in different stages. The model form (GLMM, or GAMM), beta coefficient value, sign and significance of covariates, random factor significance, and fitness 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

Notes: (s) Significant smooth term

Significance of predictors: \*  $p \leq 0.1$ ; \*\*  $p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ .

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

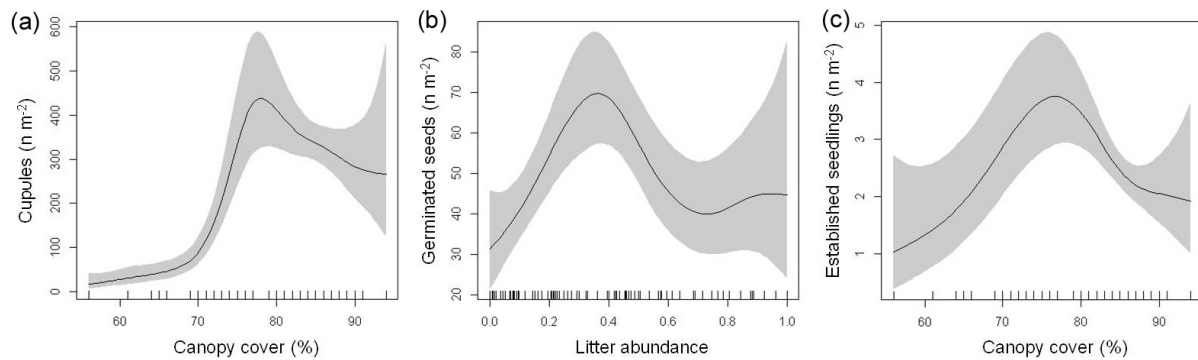


Figure 5 – Relationship between response variables ( $\pm 2SE$ ) and predictors with significant smoothers in GAMMs, with other variables in the model held constant. (a) The estimated contribution of canopy cover to cupules m<sup>-2</sup>; (b) The estimated contribution of litter abundance to germinated seeds m<sup>-2</sup>; (c) the estimated contribution of canopy cover to established seedlings m<sup>-2</sup>. Each tick above the x-axis denotes an observation with that value.

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

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

## 4. Discussion

### 4.1. Cupule and seed production

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

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

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

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

#### 4.2. Recruitment

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

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

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

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

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

#### 4.3. Synchronicity of masting and fire in beech

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

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

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

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

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

## 5. Conclusions

The present study provides important insights into the mechanisms responsible for successful recruitment following mixed severity fires in the montane beech forests of Europe (van Gils *et al.*, 2010; Maringer *et al.*, 2012; Ascoli *et al.*, 2013). At high fire severity sites, cupule and seed production were significantly lower than at unburnt stands, while seed germination and seedling emergence were unchanged. Consequently, the only effect of fire was to reduce seed production in the most severely burnt sites. At intermediate and low severity sites, cupule and seed production were similar to unburnt sites, while seed germination and seedling emergence were higher. Mixed severity fires generate microsite conditions that promote seed germination and seedling emergence, such as a loose litter, exposed mineral soil and facilitation by deadwood. Moreover, fire promotes diffuse light conditions via canopy opening, which favors beech seedlings already in the first post-fire growing season, particularly at intermediate (i.e., 70-80%) canopy cover. This and previous studies (van Gils *et al.*, 2010; Maringer *et al.*, 2012; Ascoli *et al.*, 2013) improve our knowledge of the fire ecology of *Fagus sylvatica*. These studies demonstrate that beech can persist in a mixed severity fire regime characterized by fire return intervals long enough to allow trees to reach reproductive maturity (i.e., >50 years), such as those identified by long-term paleoecological studies in Central and Northern Europe (Tinner *et al.*, 1999; Bradshaw and Lindbladh, 2005; Tinner and Lotter, 2006; Giesecke *et al.*, 2007). From a practical point of view, these findings are useful to define ecologically based criteria to restore beech forests affected by wildfire. Often, post-fire restoration in beech, and in other Alpine forest stands, fails to recognize the important ecological legacy that decaying trees represent. This results in simplistic prescriptions such as salvage logging, which disrupts the regeneration niche provided by fire and in costly artificial regeneration measures (Ascoli *et al.*, 2013; Vacchiano *et al.*, 2014). Our study stresses the importance of decaying trees hit by fire and of their delayed mortality, which promotes regeneration first by producing seeds in mast years, and later by the sheltering action of decaying snags and logs. In this context, the ratio between declining (<50% live crown) and overall basal area of beech may be used to quantify fire severity in the growing seasons after

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

Current knowledge is insufficient to determine whether the regeneration strategy observed for beech is a true adaptation to fire or rather is an “exaptation” (Gould and Vrba, 1982), i.e., a trait selected by other agents (e.g., wind) causing similar effects on stand structure. Severe, infrequent wind disturbances play a primary role in the regeneration of temperate beech forests (Kramer *et al.*, 2014; Nagel *et al.*, 2014). Our study shows that fire also has a positive effect on beech seedling establishment when masting synchronizes with fire effects. These results open up new questions about a possible ‘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 occurrence, as proposed for other plant species (Selås *et al.*, 2002; Wright *et al.*, 2014). Additionally, other fire-specific effects may facilitate beech recruitment, e.g., by increasing nutrient mobilization and uptake due to charcoal and by increasing nitrification in the forest soil (Ball *et al.*, 2010), which, in turn, favors masting (Miyazaki *et al.*, 2014) and seedling growth (Wagner *et al.*, 2010) due to a higher amount of available nitrogen. Further analyses are warranted to test these hypotheses.

## Acknowledgments

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

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

485

## References

- Abrams, M.D., Johnson, S.E., 2013. The Impacts of Mast Year and Prescribed Fires on Tree Regeneration in Oak Forests at the Mohonk Preserve, Southeastern New York, USA. *Natural Areas Journal* 33, 427-434.
- Adamek, M., Bobek, P., Hadincova, V., Wild, J., Kopecky, M., 2015. Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. *Forest Ecology and Management* 336, 81-90.
- Agestam, E., Eko, P.M., Nilsson, U., Welander, N.T., 2003. The effects of shelterwood density and site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. *Forest Ecology and Management* 176, 61-73.
- Ammer, C., Mosandl, R., El Kateb, H., 2002. Direct seeding of beech (*Fagus sylvatica* L.) in Norway spruce (*Picea abies* L. Karst.) stands - effects of canopy density and fine root biomass on seed germination. *Forest Ecology and Management* 159, 59-72.
- Ascoli, D., Castagneri, D., Valsecchi, C., Conedera, M., Bovio, G., 2013. Post-fire restoration of beech stands in the Southern Alps by natural regeneration. *Ecological Engineering* 54, 210-217.
- Ayari, A., Khouja, M.L., 2014. Ecophysiological variables influencing Aleppo pine seed and cone production: a review. *Tree Physiology* 34, 426-437.
- Ball, P.N., MacKenzie, M.D., DeLuca, T.H., Holben, W.E., 2010. Wildfire and Charcoal Enhance Nitrification and Ammonium-Oxidizing Bacterial Abundance in Dry Montane Forest Soils. *Journal of Environmental Quality* 39, 1243-1253.
- Bates, D., Maechler, M., Bolker, B., Walker S., Christensen, R.H.B., Singmann, H., (...) & Rcpp L. 2014. Package 'lme4'. R Foundation for Statistical Computing, Vienna.
- Belmonte, J., Alarcon, M., Avila, A., Scialabba, E., Pino, D., 2008. Long-range transport of beech (*Fagus sylvatica* L.) pollen to Catalonia (north-eastern Spain). *International Journal of Biometeorology* 52, 675-687.
- Bradshaw, R.H.W., Lindbladh, M., 2005. Regional spread and stand-scale establishment of *Fagus 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., Frochot, 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 R<sup>2</sup> 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 silvatica 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 ‘*gamm4*’.

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.

- 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.
- Williamson, G.B., Ickes, K., 2002. Mast fruiting and ENSO cycles - does the cue betray a cause? *Oikos* 97, 459-461.
- Wood, S., 2006. *Generalized additive models: an introduction with R*. CRC press.
- Wood, S., Scheipl, F., & Wood, M.S. 2014. Package 'gamm4'.
- Wright, B.R., Zuur, A.F., Chan, G.C.K., 2014. Proximate causes and possible adaptive functions of mast seeding and barren flower shows in spinifex grasses (*Triodia* spp.) in arid regions of Australia. *Rangeland Journal* 36, 297-308.
- Zumbrunnen, T., Bugmann, H., Conedera, M., Buerger, M., 2009. Linking Forest Fire Regimes and Climate-A Historical Analysis in a Dry Inner Alpine Valley. *Ecosystems* 12, 73-86.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1, 3-14.
- Šebková, B., Šamonil, P., Valtera, M., Adam, D., Janík, D., 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. *Forest Ecology and Management* 280, 9-19.
- Web references**
- Arpa Piemonte: <http://www.arpa.piemonte.it/banca-dati-meteorologica>. Last access: 17-May-2015.

## 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