What drives European beech (Fagus sylvatica L.) mortality after forest fires of varying severity?

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Abstract: Predicting the timing and the amount of tree mortality after a forest fire is of paramount importance for forest management decisions related to post-fire measures. Such knowledge is particularly needed in mountainous regions where forest stands often serve as protection against natural hazards. In this paper, we focus on drivers and temporal trends in mortality processes of fire-injured beeches (Fagus sylvatica L.). We studied beech forests in the Southern European Alps, which burnt between 1970 and 2012. The results show that beech trees—which obviously lack fire-resistance traits—experience increased mortality within the first two decades post-fire after fires of moderate and high burn severity. Beech mortality was ubiquitous in high severity sites, whereas taller beeches had a higher survivability after fires of moderate severity, representing a crucial ecological legacy for natural beech regeneration. In contrast, mortality remains low and at a level similar to unburnt beech forests for low burn severity sites.
Among mortality drivers, fungal infestation and the presence of fungal sporulation in particular was found to be most significant. Interestingly, fungi initiating post-fire tree mortality appeared to differ from fungi occurring after mechanical injury. From a practical point of view, insight gained regarding post-fire mortality is of great help in planning post-fire silvicultural measures.

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***Cover Letter**

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Stuttgart, 17th October 2015

Dear Editor,

We wish to submit an original research article entitled "What drives lead to European beech (*Fagus sylvatica* L.) mortality after forest fires of varying severities?" for consideration by the journal Forest Ecology and Management.

We confirm that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere. The article has been read and approved by all authors.

In this paper, we report on the timing and drivers of beech mortality after forest fires of varying severity. This is of importance with regards to forest management decisions related to post-fire measures. Such knowledge is particularly needed in mountainous regions where forest stands often serve as protection against natural hazards.

We believe this topic is appropriate for publication by Forest Ecology and Management because it links fire-ecological processes with forest management decisions, and makes further contributions to a broader understanding of beech fire ecology. A parallel study focusing on post-fire regeneration processes after a mast year has recently been published in the journal of Forest Ecology and Management (doi:10.1016/j.foreco.2015.05.031).

We have no conflicts of interest to disclose. If you find that the manuscript is appropriate for your journal, we suggest the following reviewers:

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I thank you and the reviewers in advance for your efforts in evaluating and reviewing this manuscript. I look forward to your review.

Sincerely,

Janet Maringer

What drives European beech (*Fagus sylvatica* L.) to death after forest fires of varying severities?

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Abstract

Predicting the timing and the amount of tree mortality after a forest fire is of paramount importance for forest management decisions related to post-fire measures. Such knowledge is particularly needed in mountainous regions where forest stands often serve as protection against natural hazards. In this paper, we focus on drivers and temporal trends in mortality processes of fire-injured beeches (*Fagus sylvatica* L.). We studied beech forests in the Southern European Alps, which burnt between 1970 and 2012. The results show that beech trees—which obviously lack fire-resistance traits—experience increased mortality within the first two decades post-fire after fires of moderate and high burn severity. Beech mortality was ubiquitous in high severity sites, whereas taller beeches had a higher survivability after fires of moderate severity, representing a crucial ecological legacy for natural beech regeneration. In contrast, mortality remains low and at a level similar to unburnt beech forests for low burn severity sites.

Among mortality drivers, fungal infestation and the presence of fungal sporulation in particular was found to be most significant. Interestingly, fungi initiating post-fire tree mortality appeared to differ from fungi occurring after mechanical injury. From a practical point of view, insight gained regarding post-fire mortality is of great help in planning post-fire silvicultural measures.

Keywords: beech fire ecology; fungal infestation; wood decay; Southern European Alps

1 Introduction

Climate change and the related predictions of a warmer and drier climate (IPCC, 2014) lead to increasing concerns about the future impact of wildfires on forest resistance and resilience in both fire-prone and less fire-prone forest ecosystems (Bachelet et al., 2007; Fischer et al., 2010; Schumacher and Bugmann, 2006). In fire-prone regions, the size and intensity of wildfires have already increased in recent decades (e.g., Westerling et al., 2006; Sullivan et al., 2011; Sarris et al., 2014). This has raised questions on how to predict fire-injured tree-mortality rates in the framework of planning post-fire restoration measures (Brown et al., 2003; Ledgard and Davis, 2004; Kobziar et al., 2006; Keyser et al., 2008; Moreira et al., 2012). Models explaining driving factors and predicting post-fire tree mortality have been developed mainly for fire-prone ecosystems (e.g., McHugh and Kolb, 2003; Ledgard and Davis, 2004; Rigolot, 2004; Kobziar et al., 2006; Sieg et al., 2006; Hood et al., 2007; Fernandes et al., 2008; Stevens-Rumann et al., 2012). Comparatively little attention has been paid to tree species that dominate in less fire-prone regions. From a forest management perspective, one of the major problems arises from the lack of data and experience regarding the vulnerability and resilience of such forest stands under increasing fire disturbances.

European beech (*Fagus sylvatica* L.), for example, represents a tree species with high economic and ecological value in Europe whose forest stands are usually considered less prone to fire (Pezzatti et al., 2013). However, during the exceptional drought in 2003 (e.g. Beniston, 2004), beech stands in the Southern Alps experienced numerous and atypically large forest fires, indicating a potential shift in fire regime together with climate change (Valese et al., 2014). To date, the species' post-fire survival strategies are poorly understood. Mature beeches are generally considered highly susceptible to fire because of a lack of fire resistance or fire-adaptation traits, such as thick bark or persistent resprouting capability (Peters, 1997; Packham et al., 2012). Furthermore, beech relies on gravity and rodent seed dispersal, which makes its regeneration limited by the distance to the nearest seed-bearing tree or by the distance to the forest edge (Wagner et al., 2010; van Couwenberghe et al., 2010). Consequently, the greater the burnt area and the further away an off-site seed source is, the more limited natural beech regeneration may be. Recent studies suggest, however, that beech stands exhibit surprisingly high resilience after single fire events (Ascoli et al., 2013; Maringer et al., subm.). This fire surviving strategy is mainly based on rapid *in situ* seed production when mast years coincide with suitable germination conditions in the post-fire environment (e.g., improved light conditions and reduced litter cover on the soil, Ascoli et al., 2015). Thus, post-fire density and spatial distribution of surviving seed trees are of paramount importance for new cohort recruitments and represent the basis for the rapid recovery of beech forests.

It is well known that the timing of post-fire beech mortality depends on fire intensity. Beech mortality may occur immediately after very severe fires or be delayed by several years after low to moderate fire severity (Conedera et al., 2007; Ascoli et al., 2013). There is, however, a lack of knowledge regarding factors that drive such delayed post-fire beech mortality, and with respect to the predictability of its timing. Such information would support forest managers in making decisions related to post-fire measures, such as salvage logging, and fuel treatment (Ascoli et al., 2013).

In the present study, we focus on the key questions of detecting the major drivers influencing delayed post-fire beech mortality. In particular we ask:

(1) Are there any temporal trends in fire-caused beech mortality?

(2) Which tree-specific traits (e.g., tree size) enhance the survivability of fire-injured beech trees?

(3) What are the main factors associated with beech mortality after fire disturbance?

2 Materials and methods

2.1 Study area

The present study was conducted in the neighboring regions of Piedmont (Italy) and Ticino (Switzerland) located in the Southwestern European Alps (Figure 1). Both regions are characterized by a marked elevation gradient along which forest vegetation types are distributed. Beech dominated forests occupy the intermediate elevation belt ranging from 600-1,000 m a.s.l. to 1,300-1,700 m a.s.l. depending on the locality and aspect (Camerano et al, 2004; Ceschi, 2006). These forests are mostly in the process of transformation from former unevenly-aged coppice management to high-stand forests (Nocentini, 2009).

The area of investigation is characterized by a gradient of precipitation that ranges from the drier Piedmont region with an annual precipitation of 778 mm and a mean annual temperature of 12.3°C (Susa meteorological station: 07°3’0”E, 45°08’0”N; Arpa, Piedmont) to the wetter Canton Ticino, with an annual precipitation of 1,897 mm and a similar mean annual temperature of 12.4°C (Locarno-Monti meteorological station: 08°47’43”E, 46°10’12”N; observation period 1981-2010; MeteoSwiss, 2015). In winter and early spring, northern foehn winds cause episodic relative humidity of below 20% accompanied by significant temperature rises (Isotta et al., 2014). These conditions favor winter surface fires, which are mostly induced by humans. Such fires usually start at the wildland-urban interface (Conedera et al., 2015) and episodically spread into more highly elevated beech forests (800-1,500 m a.s.l.). Total winter

(DJF) precipitation ranges from 158 mm (Piedmont) to 495 mm (Ticino) (Arpa Piedmont; MeteoSwiss, 2015). The generally dry winters contrast with the humid summers (JJA) where dry spells normally do not last longer than thirty consecutive days (Isotta et al., 2014). Therefore, summer fires rarely occur in climatically average years, but may ignite (by both lightning and humans) and spread with particular intensity during extraordinary and prolonged drought, such as in the summer 2003 (Ascoli et al., 2013; Valese et al., 2014).

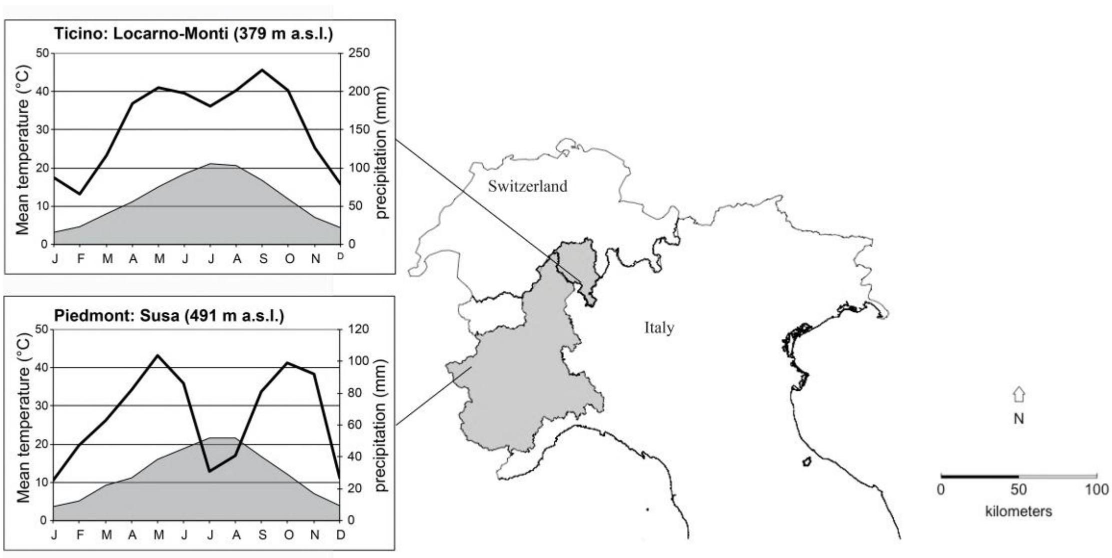

Figure 1: The study region on the southern slope of the Alps located in Canton Ticino (Switzerland) and Piedmont Region (Italy) marked in grey with representative climate diagrams.

2.2 Selection of fire sites

We examined the Swiss forest fire database (Pezzatti et al., 2010) and those of the Italian State Forestry Corps (Ufficio Territoriale per la Biodiversità di Verona Centro Nazionale Biodiversità Forestale di Peri) for the purpose of identifying fire sites that burnt after 1970. In order to keep the sample uniform, we limited our selection to beech forests on crystalline bedrock. To this end, we overlaid the obtained fire perimeters with detailed regional forest and geological maps (Ceschi, 2006;

Camerano et al., 2004) in a geographical information system (GIS) (version 10.0; © ESRI). In total, we obtained 94 potential beech stands affected by individual fires that we inspected in summer 2011 to select fire sites that matched all of the following criteria: (i) pre-fire stands dominated by beech with >95% of their stems, (ii) burnt area within the beech forest of >0.25 ha, (iii) no signs of additional fires during the last 50 years, (iv) no evidences of pre-fire wood pasture, and (v) no post-fire artificial regeneration (plantations). From the examined 94 fire sites, 36 satisfied all of the selection criteria and were retained for the field survey in the years 2012 and 2013 (Appendix A).

2.3 Data collection

Sampling design

We placed between one and three transects in each fire site, spaced 50 m apart in elevation and following the contour lines (see Figure 2). Along the transects, circle plots of 200 m^2 were placed 30 m apart, starting at a distance of 10 m from the unburnt forest. Wherever possible, a minimum of one and a maximum of 4 control plots per fire site were placed within the adjacent, unburnt beech forest (see Figure 2). Fieldwork was conducted between July 2012 and September 2013, and a total of 234 and 39 plots were assessed in burnt and unburnt beech forests, respectively (Appendix A).

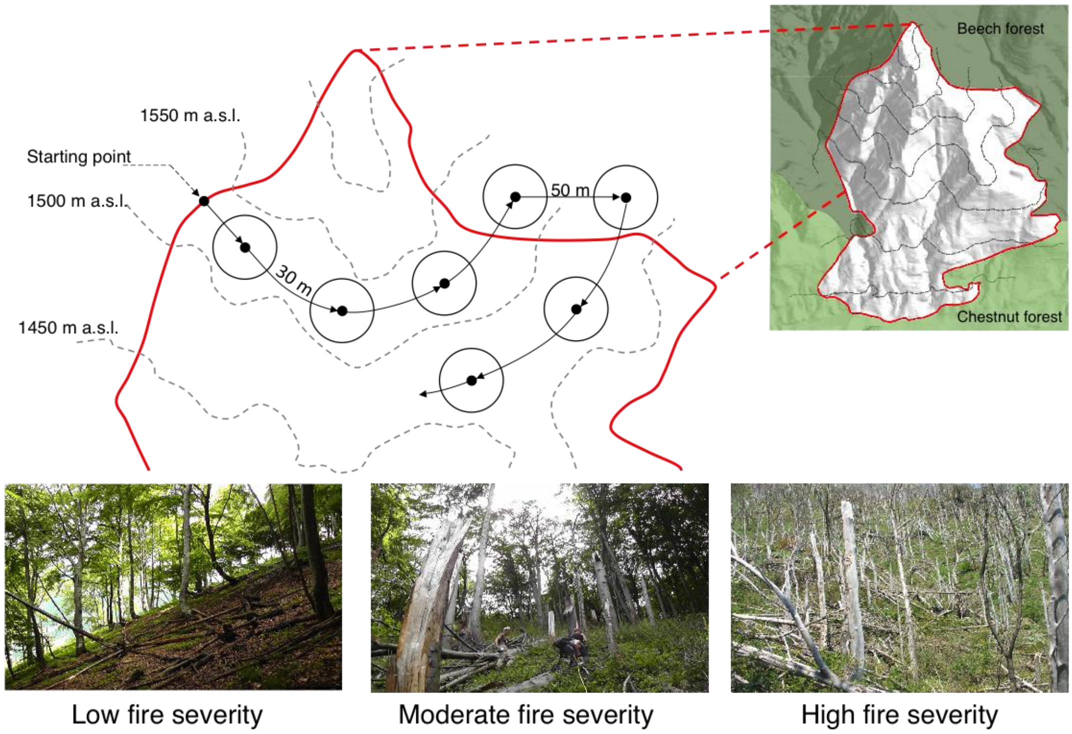

Figure 2: Sampling design in the upper part of the burnt beech forest. Circular plots of 200 m^2 were placed 30 m apart along horizontal transects from the burnt into the unburnt beech forest (figure left). Each plot is further characterized in terms of burn severity as a function of the portion of dead beeches (photographs).

Field measurements: plot characteristics and stand structure

Each 200-m^2 plot was characterized by its slope, aspect, elevation, and micro-topography (concave, plane, convex). Every pre-fire tree was classified as alive or dead. Dead individuals were further distinguished as dead standing trees (dead standing tree with crown portions but without visible green foliage and snags) and dead fallen trees (logs). We attempted to identify each tree (alive, dead) with diameter at breast height (DBH) ≥8 cm at the species level, which was sometimes not possible because of the progressed wood decay stage. DBH was measured to the nearest cm for all standing trees, and the average diameter was recorded for logs. For standing beech individuals, data collection further included growing habitus (monocormic, polycormic), tree height, percentage of crown volume killed, decay stage of the wood, height of the fire scar, proportion of damaged bark, and fungal activity. Tree growing habitus was defined as polycormic if two or more resprouts grew out of the same stool. The percentage of crown volume killed was visually estimated by the volumetric proportion of crown killed compared to the space occupied by the pre-fire crown volume (Hood et al., 2007). In order to assess the contribution of fungi infestation to the mortality process (Conedera et al., 2007; Conedera et al., 2010), fungal fructification (fruit bodies) was assessed quantitatively by assigning one of four abundance classes (none, few, partial, mass) to each beech tree. A subset of the fungal specimens was collected, put in paper bags, and transported to the laboratory for species determination according to Krieglsteiner (2000), Gerhard (2005) and Klug and Lewald-Brudi (2012). For all dead standing trees and logs, the decay stage of the wood was classified according to following classes: (1) cambium still fresh, (2) knife penetrates low, cambium disappeared, (3) knife penetrates into the fiber direction, but not transversely, or (4) knife penetrates in both directions.

Assessment of climatic variables

Precipitation and temperature can influence tree mortality (Lines et al., 2010) and both variables may occur as secondary stressors in fire-injured trees. Therefore, precipitation and air temperature data was obtained for each fire site from the WorldClim Database (Hijmans et al., 2005). Yearly precipitation and temperature averages refer to the period 1950–2010.

Assessment of burn severity

In accordance with a parallel study by Maringer et al. (subm.), we assessed burn severity by calculating the basal area of post-fire/pre-fire living trees. For old (>10 years post-fire) fire sites, pre-fire conditions were assessed exclusively from the control plots, while in recently burnt areas (≤ 10 years), pre-fire stand characteristics were determined by the number of visible dead trees in burnt plots. We defined low burn severity in plots with less than 5% crown volume loss and less than 20% basal area loss. In contrast, high burn severity was indicated by extensive crown loss (> 50%) and basal area killed (> 60%). All plots with intermediate losses in terms of crown and basal area were assigned to the moderate severity class.

2.4 Data aggregation

To describe temporal trends in fire-caused beech mortality, sites were categorized according to the number of years passed since the fire event, i.e., "≤ 9 years", "10–15 years", "16–21 years", "22–32 years", and "32-43 years", always including the corresponding control plot in the unburnt beech forest. Plots were additionally classified according to their proportion of poly- to monocormic trees: (i) stands evolved into high forests (< 33% polycormic trees), (ii) stands in the transition phase between former unevenly-aged coppices and high forests (33-66% polycorm trees), and (iii) unevenly-aged coppices (> 66% polycorm trees). Finally, standing pre-fire beeches were grouped into four DBH-classes (8-12 cm, 12-24 cm, 24-36 cm, and ≥ 36 cm; Frehner et al., 2005). For all DBH-classes, stem density (N ha^{-1}) and basal area (m^2 ha^{-1}) were calculated separately for living trees and dead standing trees, respectively.

2.5 Beech mortality model construction

We assessed the risk of beech mortality using mixed-logit models (GLMM). Since models were individual tree-based using the vitality status (alive or dead) of the standing beeches as a response variable, within-plot data violated the rule of independency. Thus, plots were included as a random effect for intercepts, in addition to potential risk factors (explanatory variables) characterizing site-, plot- and individual-trees. These included total annual precipitation (**PREC**) and annual mean temperature (**TEMP**) at site level, micro-topography (**TOPO**), slope (**SLO**), elevation (**ELE**), and aspect (**ASP**) at plot level, as well as tree size (**DBH, HEIGHT**), growth habitus (**POLY**), and fungi fructification (**FUNGI**) at tree level. Continuous risk factors were standardized to calculate the mixed-logit models, which related the probability π_{ijk} of mortality for an individual beech tree *j* in a particular plot *i* over the number of years post-fire (YPF) *k* to the mentioned risk factors ($X_1, \ldots, X_n$) as follows:

$$\log(\pi_{ijk}/1 - \pi_{ijk}) = ß_o + \text{offset}(\log(\text{YPF}_{ik})) + ß_1 X_{(\text{treeIndex})ij} + \ldots + ß_n X_{(\text{siteIndex})i} + y_i$$

where $ß_o$ represents the overall intercept, $ß_1$ to $ß_n$ the regression parameters for the corresponding variables, and y_i the random effect. The offset function corrects the number of mortality events for different YPF values (Boeck et al., 2014). Continuous predictors (X) were visualized and afterwards implemented in the models as linear and/or quadratic terms.

As a general rule, values referring to tree characteristics such as stem diameter and height were recalculated based on the year of fire. Average annual growth rates (Z'Graggen, 1992; Eidg. Anstalt für das forstliche Versuchswesen (EAFV), 1983) were subtracted from **DBH** and **HEIGHT** for all years post-fire (Table 1). Fungi infestation normally starts within the second year post-fire (Conedera et al., 2007; Conedera et al., 2010) and was therefore regarded as an initial parameter. In contrast, proportions of bark damage and the length of the fire scar were excluded from the modeling approach, because immediate fire effects were impossible to reconstruct for older fire events due to the rapid progression of wood decay.

Assuming that factors affecting beech mortality might alter their influence as a function of burn severity, we performed models separately for low, moderate, and high burn severities (hereafter referred to as low-model, moderate-model, high-model). To validate the influence of fire on beech mortality, a separate model was conducted for the unburnt forests (*control*). Data exploration followed the guidelines of Zuur et al. (2010), which suggest detecting collinearity among variables by using Pearson's correlation coefficient and the variance inflation factor (VIF). After excluding **HEIGHT** ($r^2 > 0.8$ with **DBH**) from all models and **TEMP** ($r^2 > -0.7$ with **PREC**) from the low-severity model, all VIFs were below 3, indicating the absence of any critical collinearity.

2.6 Model performance and selection

By choosing a GLMM, the data assumed a two-level hierarchical structure with pre-fire trees at level 1 nested within plots at level 2. Hence, variables were categorized at level 1 and 2, and model selection started by considering only standardized level 1 variables.

After finding significant explanatory variables at level 1, level 2 variables were then included in models and both were tested for interactions. During this process, low variations were found for the estimated values for **FUNGI** with four expressions (none, low, few, high). Consequently, this variable was converted into a dummy variable (0/1).

GLMM model selection referred to the lowest information-theoretic approach based on the correct Akaike information criterion (AIC; Venables and Ripley, 1999), and explanatory variables were retained if significantly different from zero ($p \leq 0.05$). Model diagnostics checked for the best-fitting models based on deviance residuals that were plotted against the fitted values and all variables included and not included in the model to detect unusual patterns in residuals (Zuur et al., 2010).

All analyses were performed using R statistics software (R Development Core Team, 2014). Logistic regression models were fitted and validated using the lme4 (Pinheiro et al., 2015) and VGAM (Yee et al., 2015) packages. Graphical outputs were mainly produced using the packages lattice (Deepayan, 2008) and ggplot2 (Wickham and Chang, 2015), and maps were created using map and GIS tools (Brownrigg, 2015; Brunsdon and Chen, 2015).

Table 1: Risk factors included (•) and excluded (--) in the calculated mixed-logit models (GLMM) for burnt (B)[1] and unburnt (UB) plots.

			Models	
Variables	Abbreviation	Unit	B	UB
response variable				
beech living status	STATUS	0=alive, 1=dead	•	•
topography				
slope	SLOPE	%	•	•
aspect	ASP	°	•	•
elevation	ELE	m a.s.l.	•	•
micro-topography	TOPO	factor	•	•
climate				
temperature	TEMP	°C	•[2]	•
precipitation	PREC	mm	•	•
tree characteristics				
diameter at breast height	DBH	cm	•	•
height	HEIGHT	m	--	--
growth habitus	POLY	0/1	•	•
fungi cover	FUNGI	0/1	•	•

[1] calculated separately for low, moderate, and high burn severity
[2] not used in the low-model

3 Results

3.1 Forest structure

Most (61%) of the burnt forest stands were classified as high stand forests, a minority (16%) as unevenly-aged coppices, with the remainder within the transition phase. In total, 3,504 mature trees were recorded, of which beech consisted of 88% and 93% in the burnt and unburnt forests, respectively. Other tree species rarely (< 4%) grew within the pure beech stands (Appendix B).

3.2 Post-fire beech mortality

From the overall number of beech trees assessed in burnt plots (N = 2,845), half died due to fire impact, whereas in unburnt forests, only 10% of the recorded trees were classified as dead. Fungi infestation occurred in 23% of survived beeches, and 72% of dead trees. We found at least 10 different fungal species on the stems of fire-injured beeches (see Table 3). As reported in Figure 3, the average basal area of standing dead beeches in burnt forests was 14.1 ± 0.95 m^2 ha^{-1}, ranging from 1.9 m^2 ha^{-1} to 37.6 m^2 ha^{-1} over the years post-fire. Tree mortality in low burn severity sites is quite similar to that in unburnt forests, while tree mortality increases with burn severity and peaks 10 to 15 years post-fire. The highest overall basal area losses (up to 85% of the initial value) occurred in high severity sites, followed by moderate severity sites (up to 63%).

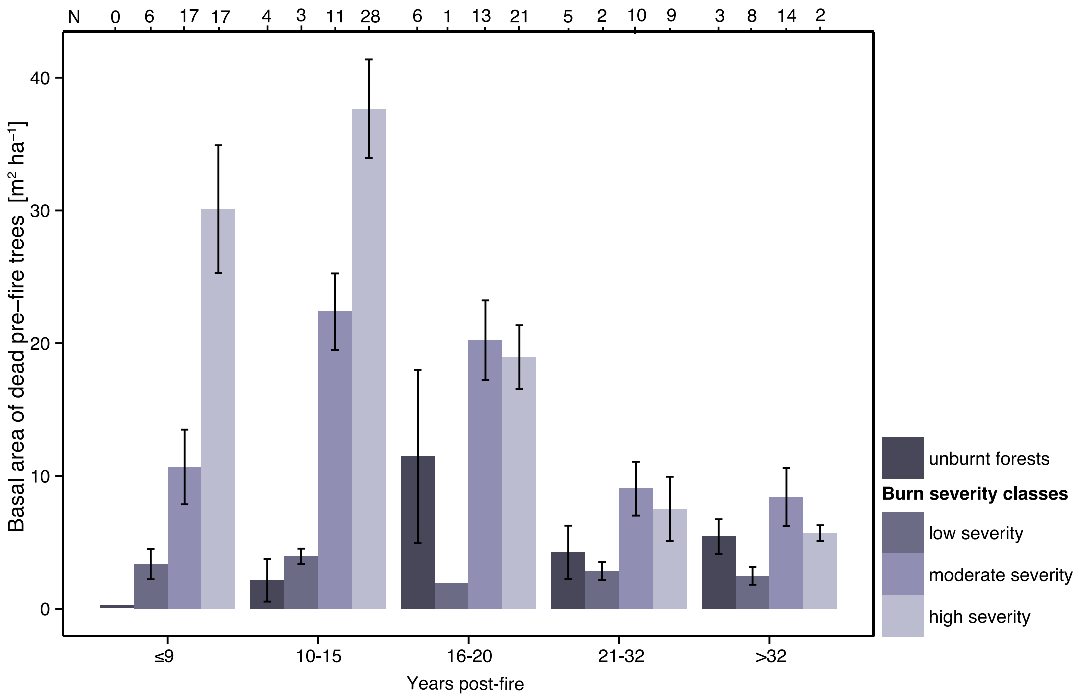

Figure 3: Mean (±SE) basal area of standing dead pre-fire beeches in low-, moderate-, and high severity sites, and the corresponding unburnt plots as a function of years post-fire.

Taking unburnt forests as the reference, the odds of beech mortality (i.e., the ratio of the probability of dying vs. surviving) was 42, 5, and 2.3 times greater in high-, moderate-, and low severity sites, respectively. Within the burn severity classes, the extent and timing of beech mortality varied as a function of tree size. In low-severity sites, tree mortality was usually limited to small beeches, whereas in the case of moderate severity, intermediate-sized beeches were also affected. Finally, beech mortality was high and affected all tree sizes in high severity plots. There, mortality started immediately after fire disturbance and continued up to two decades post-fire with mortality odds ratios always greater than 2.8 (Figure 4 A). In contrast, in moderate severity plots, the odds of mortality for small (DBH < 12 cm) beeches were two to six times higher than for intermediate-sized, and four to eleven times higher than for large and tall beeches (DBH > 36 cm). These differences in the mortality rate are clear within the first 15 years post-fire, when mortality is higher than in subsequent years (Figure 4 B). Similar patterns were observed in low severity sites, where the odds of death for small beeches were generally higher than for tall and large beeches (Figure 4 C). In these fire sites, the probability of large-beech mortality was near zero, while intermediate-sized beech mortality ranged between 0.03 and 0.56 throughout the whole observation period.

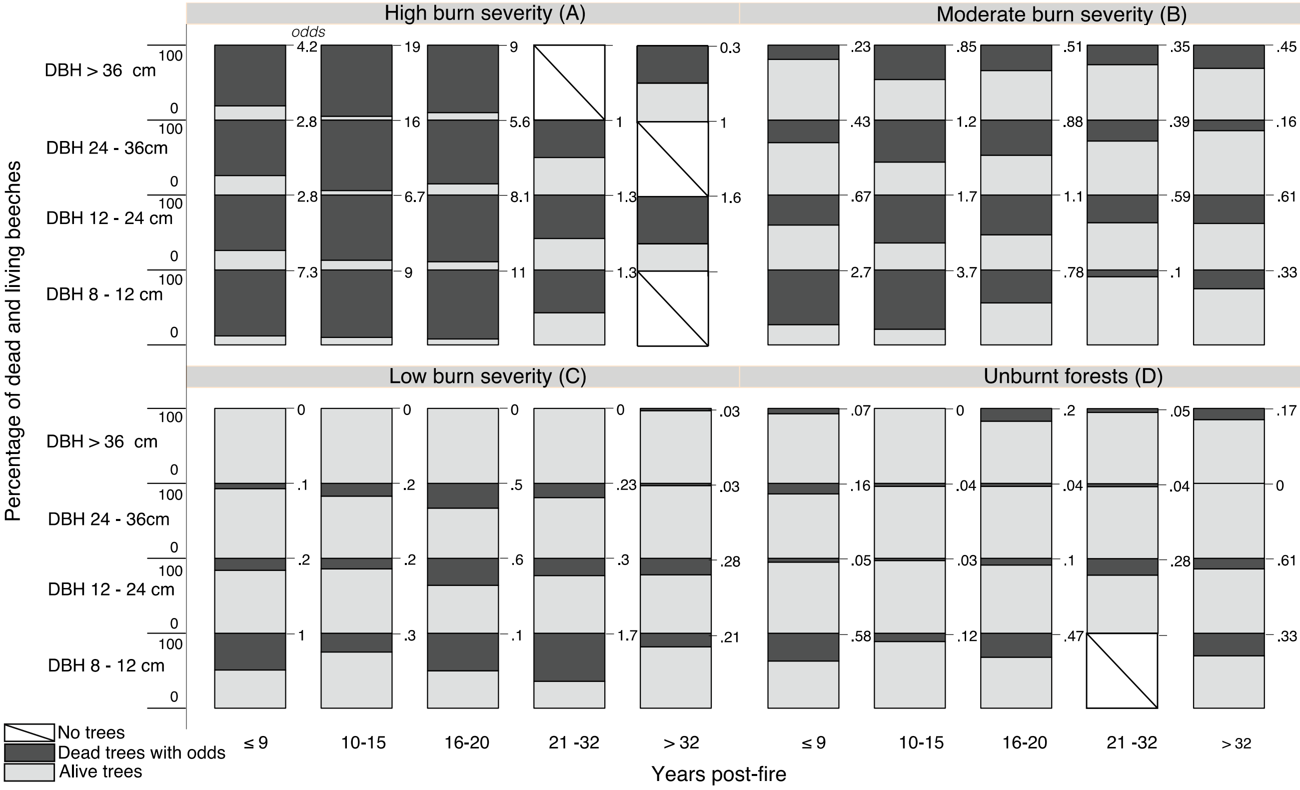

Figure 4: Percentage of survived (light grey) and dead (dark grey) beeches for small (DBH < 12 cm), intermediate-sized (DBH = 12 – 24 cm), large (DBH = 24 – 36 cm), and very large (DBH > 36 cm) individuals, separated for different burn severities and years post-fire. The odds ratios of mortality are also shown to the right of each column.

3.3 Deadwood characteristics

In the first decade post-fire, the majority of standing dead trees (70%) and logs (54%) showed slight to intermediate decomposition (Figure 5). Over the years post-fire, the proportion of intermediate and advanced wood decay stages steadily increased, finally ranging between 64% (10-15 years post-fire) and 87% (> 32 years post-fire) for standing dead trees, and exceeding 90% for logs 16 years post-fire. As a result, in the first two decades post-fire, the number of standing dead trees was ten times higher than logs. After the second decade post-fire, both the number of standing dead trees and logs decreased by approximately 80%. Figure 5 clearly illustrates that dead standing trees appear to dominate in the first 20 years post-fire.

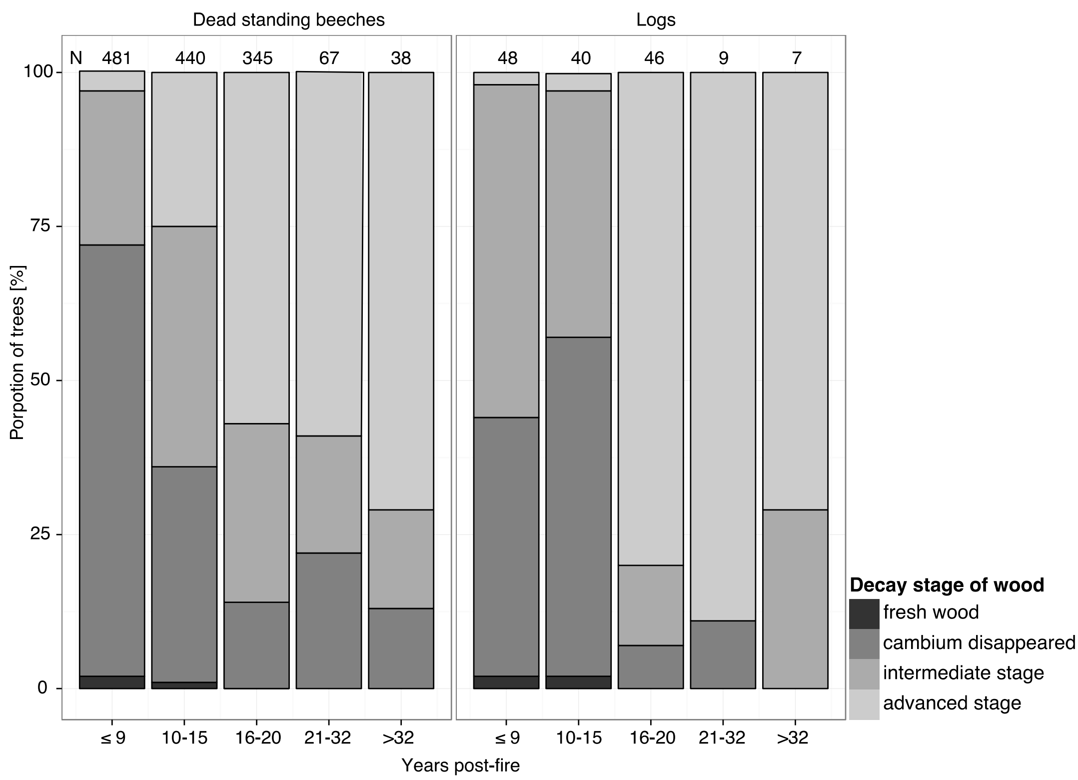

Figure 5: Decay stages of wood for standing dead trees and logs as a function of years post-fire.

3.4 Drivers of beech mortality

The best beech mortality models clearly describe the mortality rate for fire-injured beeches, with FUNGI (fungi fruitbodies), DBH, and ELE (elevation) as common factors (Table 2). FUNGI had a positive and highly significant ($p < 0.001$) effect on beech mortality in all three burn severity models, indicating an increased risk of mortality after visible fungal activity in terms of fruit body formation. The odds ratio of beech mortality after fungi fructification was 14.8 in the moderate-severity model, which was four times that of the low-model and double that of the high-severity model.

In addition to fungi fructification, DBH was significantly and negatively correlated with beech mortality in the low- and moderate-models, indicating a consistently decreasing risk of mortality with increasing DBH. The odds of tall beech survival after a low severity fire was four-times higher than for moderate burn severity, whereas no detectable correlation existed between mortality and DBH in the high-model. The correlation between beech mortality and the quadratic term of DBH was found to be positive in addition to the linear predictor in the control-model (unburnt forests), indicating increased mortality for tall and thin beeches. Polycormic growth habitus (POLY) reduced the mortality risk factor in moderate- and high-models, but not in the low-model.

Site factors only marginally correlated with beech mortality, except for ELE. The linear and quadratic terms of ELE were weakly but significantly and positively correlated with beech mortality in all three fire-severity models. The explanatory power of the low-model containing all three variables (DBH, FUNGI, ELE) was 38%. The quadratic term of TEMP weakly and negatively correlated with beech mortality in the moderate- and high-models, respectively. Furthermore, positive correlations with beech mortality were found for PREC in the moderate-model and ASP in the high-model. In summary, beech mortality was explained by six (FUNGI, DBH, POLY, ELE, TEMP, PREC) variables with an explanatory power of 32% in the moderate-model, and by five (FUNGI, POLY, ELE, TEMP, ASP) variables with an explanatory power of 17% in the high-model.

From the above-mentioned variables, the linear and quadratic terms of DBH had the most explanatory power in the control-model. With DBH as the only highly significant variable, the model had an explanatory power of 66%, whereas the weakly (0.1%-level) correlated variables ELE and ASP only marginally improved the model.

Table 2: Results of the mixed-logit models for the burnt and unburnt forests separated for low (low-model), moderate (moderate-model) and high (high model) burn severities.

Models	Burnt forests			Unburnt forests
	Low-model Odds ratio [conf. interval]	*Moderate-model* Odds ratio [conf. interval]	*High-model* Odds ratio [conf. interval]	*Control* Odds ratio [conf. interval]
fixed term				
Intercept	34^{-1}***[86^{-1}-15^{-1}]	53^{-1}***[93^{-1}- 40^{-1}]	1.5^{-1}[3.3^{-1}-1.8]	51^{-1}***[176^{-1}-22^{-1}]
FUNGI	4.6***[2.2-9.9]	14.8***[9.8-21.5]	7.4***[3.8-14.3]	ns
DBH	5^{-1}***[8.3^{-1}-3.1^{-1}]	1.7^{-1}***[1.8^{-1}-1.3^{-1}]	ns	4.7^{-1}***[8.2^{-1}-2.8^{-1}]
DBH^2	ns	ns	ns	1.7***[1.4-2.1]
POLY	ns	2.0^{-1}***[2.9^{-1}-1.3^{-1}]	2.2^{-1}*[4.5-1.3]	ns
ELE	2.8*[1.1-6.7]	ns	2.1^{-1}*[4.1^{-1}-1.2]	1.9^{-1}•[4^{-1}-1]
ELE^2	2.3*[1.1-4.7]	1.3**[1.1-1.5]	ns	ns
$TEMP^2$	ns	1.2^{-1}*[1.5^{-1}-1]	1.8^{-1}**[2.7^{-1}-1.2^{-1}]	ns
PREC	ns	1.6***[1.2-2.2]	ns	ns
$PREC^2$	ns	ns	ns	ns
ASP	ns	ns	1.7*[1-2.9]	1.8•[1.1^{-1}-4.3]
random term	Var (x)[SD]	Var (x)[SD]	Var (x)[SD]	Var (x)[SD]
Plot	1.7[1.3]	0.5[0.6]	1.1[1]	2.6[1.6]
$D^2_{\text{fixed effects}}$	38%	32%	17%	66%
$D^2_{\text{fixed + random effects}}$	55%	38%	35%	80%

Signif. codes: '***' 0.001 '**' 0.01 '*' 0.05 '•' 0.1 'ns' 1. Abbreviations see Table 1

4 Discussion

4.1 Post-fire stand dynamics

The selected stands showed typical beech forest structural characteristics for the Southern Alps, with interlocking transition stages from unevenly-aged coppices to high forest stands (Nocentini, 2009; Ascoli et al., 2013). In these stands, fires of mixed severity induced significant forest structure changes by causing mortality in half of the pre-fire beeches. In general, most fire-caused beech mortality occurs within the first two decades post-fire. Such short-term mortality has also been observed in studies of other fire-injured broadleaf stands (Harrod et al., 2000; Ledgard et al., 2004; Shafiei et al., 2010; Catry et al., 2010; Bravo et al., 2014). Moreover, our findings are in accordance with a companion study (Maringer et al., subm.) that observed a post-fire regeneration window spanning the first two decades post-fire, when the regeneration takes advantages of progressive canopy openings and particularly suitable germination beds.

As already reported in numerous studies for other tree species (e.g., Keyser et al., 2008; van Mantgem et al., 2013) the extent and pace of beech mortality highly depend on tree size. We observed a decreasing risk of mortality for beeches from thinner (DBH < 12 cm) to tall and large (DBH > 36 cm) individuals. With increasing time since fire (> 20 years post-fire), the mortality rate for beeches decreases toward a nearly natural level (control plots). Similar observations are reported for Oriental beech (*Fagus orientalis* LIPSKY) forests 37 years after a fire (Shafiei et al., 2010; Adel et al., 2013).

Standing dead beeches, snags in particular, accounted for the majority of the resulting dead wood, which is typical for burnt forests (Lampainen et al., 2004; Brown et al., 2013). The number of dead standing trees and especially the amount of logs—which usually have contact with the soil surface—rapidly decrease with time since fire, due to the fast decomposition rate of beech wood relative to standardized time intervals (Kahl, 2008; Lombardi et al., 2008).

4.2 Triggers of post-fire beech mortality

Among the detected drivers of post-fire beech mortality, the presence of visible fungal activity in terms of fruit body formation revealed to be the most relevant. The accelerating effect of secondary fungal activity in the dieback process of fire-injured beeches is well known, not only for European beech (Conedera et al., 2007; Conedera et al., 2010; van Gils et al., 2010) but also for American beech (*Fagus grandifolia* Ehrh.) (Tubbs and Houston, 1990). Thin bark is one characteristic of the genus *Fagus* that renders beech species particularly susceptible to fire scar formation (Tubbs and Houston, 1990; Peters, 1997; Hicks, 1998; Packham et al., 2012) and thus potentially to secondary fungal infestation. Fungi infestation causes rapid decay in the exposed wood tissues in fire scars, reducing trunk mechanical stability and, in turn, the time and likelihood of successful scar overgrowth and healing.

This is likely the reason why beech diameter as a risk factor was found to play only a secondary role in the modeling of post-fire beech mortality patterns, although tree size is linearly and negatively correlated to beech mortality in low- and moderate-models. The fact that tree mortality caused by fire is higher for thinner trees than for larger ones has often been stated in the literature for different tree species (McHugh and Kolb, 2003; Kobziar et al., 2006; Shafiei et al., 2010; Brando et al., 2012). Most studies relate the higher mortality rate of thinner trees to bark thickness and tree height, which usually increase with tree age (Gutsell and Johnson, 1996; Lawes et al., 2013). However, to date little is known about the relationship between European beech bark thickness and tree size. For Oriental beech, a close relative to the target species, Bonyad et al. (2012) discovered a strong positive correlation between DBH and bark thickness. Shekholeslami et al. (2011) investigated Oriental beech bark thickness along the trunk and found thicker bark on the bole of the trees, a trait that is evident also for larger beeches in the Alps (Figure 6). Studies on large European beeches have found more structured, creviced, and rough bark (Russo et al., 2010; Dymytrova et al., 2014), characteristics which have been found to increase thermal insulation and thus resistance to fire injury (Fahnestock and Hare, 1964; Nicolai, 1986; Bauer et al., 2010; Odhiambo et al., 2014). Also considering that larger beeches have large crowns, low limbs, and limited litter yield around their boles (Yaussy et al., 2004), it is understandable that survivability increases for large individuals after surface fires of low to moderate intensity.

Figure 6: Old beech with structured, creviced, and rough bark (left figure) and a cross section with a thick and relatively rough bark (right figure; Piedmont, Italy; D. Ascoli)

In summary, the combination of the portion of woody tissue exposed through fire scars and the likelihood of being colonized by active and fructifying fungi appear to be crucial in inducing the mortality process in fire-injured beeches. In this respect, the results of our modeling approach confirm the findings of Conedera et al. (2010), indicating that the moderate-burn severity class is the most sensitive to secondary fungal infestation (odds ratios four and two times higher with respect to low and high severity, respectively).

Our sampling design does not permit a conclusive analysis of the role played by fungi species and their particular timing of infestation. Once colonized, the visible abundance of fungal fructifications does not appear to be an indicator of enhanced risk of mortality, as revealed by our modeling approach. Similarly, neither the season of the fire event (vegetation rest or growing season) nor the fungal species concerned play an apparent role, given that the lethal issue of fungal activity is not dependent on the fire date (data not shown) or the fungal species.

Interestingly, in this study, the assessed fungal species colonizing fire scars appear to differ from those infesting mechanically injured beeches (Table 3; see Standovár and Kenderes (2003) for a review and Conedera et al. (2007) for fire related fungi). The existence of specific, fire-related fungi infesting beeches is thus confirmed. The question remains, however, regarding the specific ecological conditions needed at colonization time, and the different impact of each fungal species in the mortality process of beech trees. Even though we did not directly measure the abundance of fungal sporulation in the present study, we postulate that the sheer presence of fungal fruit bodies may be more important than the amount of fungal fruit bodies. This relationship is yet to be tested in further field work.

Table 3: Main ecological characteristics of fungi infection in injured beeches (fungi infection in mechanically-injured beeches are based on the literature review of Standovár et al., 2003)

Species	Short biological description
Fungi on fire-injured beeches	
Armillaria spec. (Fries) Staude	----
Cerrena cf. unicolor (Bull.) Murrill	Spaced forest stands on humid soils.[d]
Daldinia concentrica (Bolton) Cest. & de Not.	Specifically adapted to wildfire and can be invisible for many decades.[j]
Inonotus nodulosus (Fr.) P. Karst	Usually occurs on humid soil during late successional forest stages.[d]
Irpex lacteus (Fr.)	Usually abundant in fire scars where it causes white rot finally causing the stem to break.[j]
Oudemansiella mucida (Schrad.) Höhn.	Sabrobiont, occurs in the early wood-decay stage on dead standing beeches or on living beeches. Especially in regions with high humidity. [d]
Schizophyllum commune (Fr.)	Often occur after "sun burn" on broadleaf trees.[j]
Stereum hirsutum (Willd.) Pers.	Pioneer species fruits often after fires in deciduous forests.[j]
Trametes hirsuta (Wulfen) Pilát	Occurs on injured beeches, which are exposed to light. Sabrobiont on dead standing or lying trees, which still have pieces of bark. [d]
Fomes fomentarius (L. ex Fr.) Gill.	White rot of beech wood and other broadleaf species; occurs on living, standing beeches and leads to progressive wood decay. The infested tree normally breaks at its weakest point.[h]
Fungi on mechanically-injured beeches	
Daedalea quercina (L.) Fr.	Causing brown rot often leading to huge wood loss inside the stem.[a]
Fomitopsis pinicola (Sw. ex Fr.) Gill.	Unable to invade living sapwood, but wounded trees are easily colonized.[b]
Ganoderma applanatum (Pers.) Pat.	Causes white heart rot and is dispersed by a specialized mycophagous fly.[c]
Inonotus radiatus (Sw. ex Fr.) Karst.	The main host is alder (*Alnus* sp.) but also occurs on dying beeches.[d]
Laetiporus sulphureus (Bull.) Bond. Ex Sinq.	Intensive wood decay in the tree's trunk causing static problems mainly in the root crown. [e]
Inonotus cuticularis (Bull.) P. Karst.	Causes brown rot, mainly on beeches in barely disturbed forests.[d]
Inonotus obliquus (Pers.) Pilát	Cause white heart rot. The fungus penetrates the tree through poorly-healed wounds.[f] Decay may continue for 10–80+ years inside a living host tree.[d]
Meripilus giganteus (Pers.) P.Karst	Causes intensive white rot, mainly on beech and oak wood.[d]
Nectria galligena Bres.	Causes cancer disease. Entry of the pathogen is facilitated by the beech scale insect (*Cryptococcus fagisuga*). [d]
Nectria ditissima Tul.	Similar to *N. galligena*.[d]
Oxyporus populinus (Fr.) Donk.	Causes white heart rot, especially in the basal part of the stem. [d]
Pholiota squarrosa Huds. ex Fr.	Infests weakened beeches.[g]
Polyporus squamosus Huds. ex Fr.	Cause white rot, often along the wounds where spores colonized the stem.[d]
Pleurotus ostreatus (Jacq. ex Fr.) Kummer	Often found on dying or dead standing deciduous broadleaf trees. [d]

[a]Zarzyn´ski (2007); [b]Schwarze and Baum (2000); [c] Webster and Weber (2007); [d] Krieglsteiner (2000); [e] Reinartz and Schlag (2002); [f] Lee et al. (2008); [g] Shigo (1970); [h] Kahl (2008); [j] Conedera et al. (2007)

4.3 **Limits of the study**

The retrospective approach of this study combined with the resulting rapidity of post-fire beech mortality may have caused a bias in the possibility and precision of assessing pre-fire stand characteristics and tree decaying-related variables, especially for fire sites older than 20 years post-fire. This may account for the decreasing explanatory power of models with increasing rapidity of post-fire stand dynamics, even though we discarded problematic variables such as the proportion of bark damage by fire and fire scar height. In fact, while 38% of the variance in tree mortality was explained in the low-model, explanatory power decreased to 32% in the moderate-model and dropped to 17% in the high-model. In contrast, the control-model reached an explanatory power of 66%.

Furthermore, fungi were not systematically assessed at the species level on each tree, which hampered our ability to provide a detailed analysis of the timing and impact of single species in the decay process, and the role of species occurrence under specific post-fire environmental conditions.

5 **Conclusions**

In this study, we used a retrospective approach for reconstructing the post-fire dynamics and main drivers of fire-related beech mortality in 36 differently-aged fire sites in the Southern Alps. Despite the discussed methodological limits of the approach, we were able to answer the main questions of the study, providing important new insights regarding beech fire ecology and post-fire beech mortality in particular.

Fire-induced beech mortality was found to be very high within the first two decades post-fire. Thus, the process can be explained in terms of a dynamic phase (< 20 years post fire), when beeches mostly die, and a more stable phase (> 20 years post-fire) when nearly no so-far-surviving beeches die as a consequence of fire impact. Consequently, gap formation is gradual, providing a 20-year window for beech regeneration under increasing light conditions. This finding is useful for the development of ecologically-based silvicultural post-fire treatments.

Major mortality drivers were found to be the combination of the proportion of woody tissue exposed as a consequence of fire scars and the likelihood of being colonized by active (fructifying) fungi. In the case of low to moderate burn severity, tree size may contribute to a reduction in the proportion of stems exposed to fungal infestation. Unfortunately, our research did not focus specifically on the role of single fungal species in the dieback process of fire-injured beeches. Further research is therefore needed on the temporal occurrence and ecology of specific post-fire fructifying fungi in beech forests.

This study demonstrates that beech can persist in a mixed-severity fire regime. Tall and large beeches survive for at least several years after low to moderate severe fires. These conditions mostly contribute to seed production and dispersal in mast years (e.g., Nilsson and Wastljung, 1987) and thus immediately provide seeds in the environment. At this stage, the seedbed is favorable to beech seed germination and seedling establishment (Ascoli et al., 2015).

From a practical point of view, it should be possible for forest managers to assess the burn severity class (ratio of dead to living trees) and related stand mortality dynamics within the third year post-fire. Target parameters for the evaluation of the mortality process are the diameters of survived trees in relation to the burn severity and evidence of open bark, which serves as entry points for fungal infection. Furthermore, our results show that very tall and large beeches mostly survive even after high severe fires at least for several years. These remnant beeches are important as seed source for emerging regeneration. Therefore, they have to preserve when planning post-fire management measures.

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Appendix A

Table A.1: Investigated fire sites sorted by region (Piedmont, Ticino) and the date of fire. Items listed: years post-fire (age), UTM coordinates (WGS84), Ø annual temperature (T), ∑ annual precipitation (P) (T and P: WorldClim data base; Hijmans et al., 2005), and the number of plots investigated in the burnt (N_b) and unburnt beech forests (N_c).

Regions Municipality	Date of fire	Age	E	N	T [°C]	P [mm]	N_b/ N_c
Piedmont							
Sparone	28.12.80	34	382545	5030710	6	1109	16/1
Rosazza	19.01.90	24	418645	5058661	5.8	1195	5/0
Corio	15.02.90	24	385562	5021543	7.5	989	10/2
Arola	04.06.97	16.5	449208	5074546	7.9	1172	13/0
Dissimo	06.04.03	11	466503	5111215	5	1402	5/1
Varallo	11.08.03	10.5	442360	5078456	7.2	1186	11/1
Villadossola	16.03.05	9	440231	5098748	5.6	1305	11/1
Condove	01.03.08	7	364870	5000781	7.4	979	11/1
Giaglione	03.03.12	2	341650	5001664	6.4	1067	8/1
Druogno	26.03.12	2	453207	5110682	4.8	1394	12/1
Ticino							
Indemini	07.08.70	42.5	488196	5105864	6.4	1349	3/1
Minusio	04.11.71	41	484123	5116368	4.7	1415	2/1
Gordevio	09.03.73	40	482190	5116678	6.5	1355	1/0
Moghegno	27.11.73	39	492538	5101434	8.3	1310	3/1
Gordola	28.03.76	37	490491	5116753	6.0	1365	2/1
Arbedo	20.03.76	37	506667	5116933	7.1	1290	13/1
Astano	01.01.81	32	485796	5096454	8.2	1304	2/1
Indemini	01.01.81	32	484488	5104578	5.5	1376	12/1
Intragna	04.01.87	27	477570	5112256	7.6	1318	3/0
Aurigeno	01.08.89	23.5	478824	5118037	8.2	1308	2/1
Mugena	23.03.90	23	492683	5105828	7.1	1330	6/1
Novaggio	10.03.90	23	486829	5098133	5.4	1371	2/1
Avegno	05.05.90	23	482007	5116521	6.5	1355	2/0
Pollegio	09.04.95	18	492574	5139100	5.3	1391	5/2
Tenero	21.04.96	17	487212	5116007	8.5	1315	3/0
Ronco s.A.	15.03.97	16	477225	5110649	6.6	1349	6/1
Magadino	15.04.97	16	491560	5107650	6.9	1335	26/3
Sonvico	03.04.97	16	501239	5101934	8.8	1300	5/2
Arbedo	14.11.98	14	506770	5115571	8.5	1302	3/2
Indemini	19.12.98	14	488487	5106098	6.6	1347	1/1
Gordevio	24.04.02	11	482190	5116678	6.5	1355	13/4
Maggia	12.03.02	11	477394	5124084	5.7	1388	3/1
Bodio	18.03.03	10	495105	5136703	4	1436	5/1
Someo	06.08.03	9.5	475281	5126733	5.6	1395	3/1
Cugnasco	03.04.06	7	494084	5114855	9.4	1317	4/1
Ronco s.A.	23.04.07	6	477225	5110649	6.6	1349	2/1

Appendix B

Table B.1: Distribution of mature tree species in the burnt and unburnt forests sorted by the target species (beech), and trees showing wind-, gravity-, and animal seed dispersal strategies. The amount of dead trees related to the total number of trees of a particular species (∑ N) is expressed in the proportion of mortality (mort. [%]). Species proportion [%] indicates the proportion of particular species out of the total number of trees.

	Burnt forests			Unburnt forests		
Species	∑ N	Mort. [%]	Species proportion [%]	∑ N	Mort. [%]	Species proportion [%]
Target species						
Fagus sylvatica L.	2845	53	88	887	13	93
Pioneers with wind-dispersal seeds						
Betula pendula ROTH	129	44	4	20	30	2
Larix decidua MILL.	66	62	2	14	36	1
Sorbus aria (L.) CRANTZ	16	69	1	5	0	<1
Alnus glutinosa (L.) GAERTN.	4	75	<1	0	100	0
Corylus avellana L.	1	0	<1	0	100	0
Populus tremula L.	1	0	<1	0	100	0
Sorbus aucuparia L.	1	0	<1	0	0	0
Laburnum alpinum FABR.	0	0	0	14	64	1
Trees with gravity- /animal-dispersal seeds						
Castanea sativa MILL.	57	70	2	11	9	1
Quercus petraea (MATTUSCHKA)	30	40	1	2	0	<1
Fraxinus excelsior L.	6	33	<1	0	100	0
Picea abies (L.) H.KARST.	6	0	>1	0	100	0
Pinus sylvestris L.	3	0	<1	0	100	0
Prunus avium L.	2	0	<1	4	75	<1
Taxus baccata L.	2	0	<1	0	100	0
Acer pseudoplatanus L.	1	0	<1	1	0	<1
Quercus pubescens WILLD.	1	100	<1	0	0	0

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