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

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Abstract

Predicting the timing and amount of tree mortality after a forest fire is of paramount importance for post-fire management decisions, such as salvage logging or reforestation. Such knowledge is particularly needed in mountainous regions where forest stands often serve as protection against natural hazards (e.g., snow avalanches, rockfalls, landslides). In this paper, we focus on the drivers and timing of mortality in fire-injured beech trees (*Fagus sylvatica* L.) in mountain regions. We studied beech forests in the southwestern European Alps, which burned between 1970 and 2012. The results show that beech trees, which lack fire-resistance traits, experience increased mortality within the first two decades post-fire with a timing and amount strongly related to the burn severity. Beech mortality is fast and ubiquitous in high severity sites, whereas small- (DBH <12 cm) and intermediate- diameter (DBH 12-36 cm) trees face a higher risk to die in moderate-severity sites. Large-diameter trees mostly survive, representing a crucial ecological legacy for beech regeneration. Mortality remains low and at a level similar to unburnt beech forests for low burn severity sites.

Beech trees diameter, the presence of fungal infestation and elevation are the most significant drivers of mortality. The risk of beech to die increases toward higher elevation and is higher for small- than for large-diameter trees. In case of secondary fungi infestation beech faces generally a higher risk to die. Interestingly, fungi that initiate post-fire tree mortality differ from fungi occurring after mechanical injury. From a management point of view, the insights about the controls of post-fire mortality provided by this study should help in planning post-fire silvicultural measures in montane beech forests.

Keywords: beech fire ecology; fungal infestation; southwestern Alps

1 Introduction

Climate change and 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-sensitive forest ecosystems (Bachelet et al., 2007; Fischer et al., 2010; Schumacher and Bugmann, 2006). In many fire-sensitive 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), raising questions about how to predict the rate of fire-injured tree mortality within the framework of planning post-fire silvicultural measures such as salvage logging and reforestation (Brown et al., 2003; Ledgard and Davis, 2004; Kobziar et al., 2006; Keyser et al., 2008; Moreira et al., 2012). Models that predict post-fire mortality, as a result of various driving factors, have been developed mainly for tree species in 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 species that dominate in less fire-sensitive regions. From a forest management perspective, a major problem arises from the lack of data and experience regarding the vulnerability and resilience of such forest stands under increasing fire disturbance.

European beech (*Fagus sylvatica* L.), for example, represents a tree species with high economic and ecological value in Europe, and forests of beech are usually considered less fire-sensitive (Pezzatti et al., 2013). However, during the exceptional drought of 2003 (e.g. Beniston, 2004), beech stands in the southwestern Alps experienced numerous and atypical large forest fires. These fires may indicate a shift in fire regime driven by climate change (Valese et al., 2014).

To date, species survival strategies after fire are poorly understood, and post-fire silvicultural measures are usually limited to salvage logging followed by reforestation in very rare cases. Generally, beech is considered to be highly susceptible to fire due to its lack of fire-resistance (e.g. thick bark) and fire-adaptation (e.g. resprouting capability) traits (Peters, 1997; Packham et al., 2012). In fact, studies report that beech resprouts after fire, but the resulting shoots tend to dieback and hardly constitute a valuable new generation (van Gils et al. 2008; Conedera et al., 2010; Espelta et al. 2012; Maringer et al., 2012).

Furthermore, beech regeneration (from seeds) relies on seed dispersal by gravity and animals, and establishment is often close to the nearest seed-bearing tree (Wagner et al., 2010; van Couwenberghe et al., 2010). Consequently, natural beech regeneration becomes more limited within increasing burned area and greater distance from a seed source. Recent studies, however, suggest that beech stands exhibit surprisingly high resilience after single fire events (Ascoli et al., 2013; Maringer et al., subm.). The fire-surviving strategy, in this case, 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 mature surviving trees are critical for new cohort recruitment and 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 severe fire (Conedera et al., 2007; Ascoli et al., 2013). There is, however, a lack of knowledge regarding factors driving such delayed mortality, and especially the predictability of its timing. Such information would help forest managers in planning complex post-fire measures related to: (i) whether or not intervene with silvicultural measures, (ii) timing of the needed interventions, and (iii) the number of trees to salvage (Ascoli et al., 2013). Following the guiding principle that post-fire management decisions should be based on site- and species-specific ecological processes, we focus in this paper on the major drivers that influence post-fire beech mortality. In particular we ask:

(1) What are the mid-term 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 biotic and abiotic 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 elevational 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 coppice management to high-stand forests (Nocentini, 2009).

The area of investigation is characterized by a climate gradient that ranges from the drier Piedmont region with an annual precipitation of 778 mm and 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 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 conditions when the relative humidity drops below 20% and is accompanied by significant temperature increases (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 spread into high-elevation beech forests. In general, however, beech forests burn very infrequently and have an average fire return interval of about 500 to 1,000 years (Pezzatti et al., 2010).

Total winter (December, January, February) precipitation ranges from 158 mm (Piedmont) to 495 mm (Ticino) in our study area (Arpa Piedmont; MeteoSwiss, 2015). Generally dry winters contrast with humid summers (June, July, August) where dry spells normally do not last longer than 30 consecutive days (Isotta et al., 2014). Summer fires rarely occur in climatically average years, but may ignite by lightning or humans and spread with particular intensity during times of extraordinary and prolonged drought, such as the summer 2003 (Ascoli et al., 2013; Valese et al., 2014).

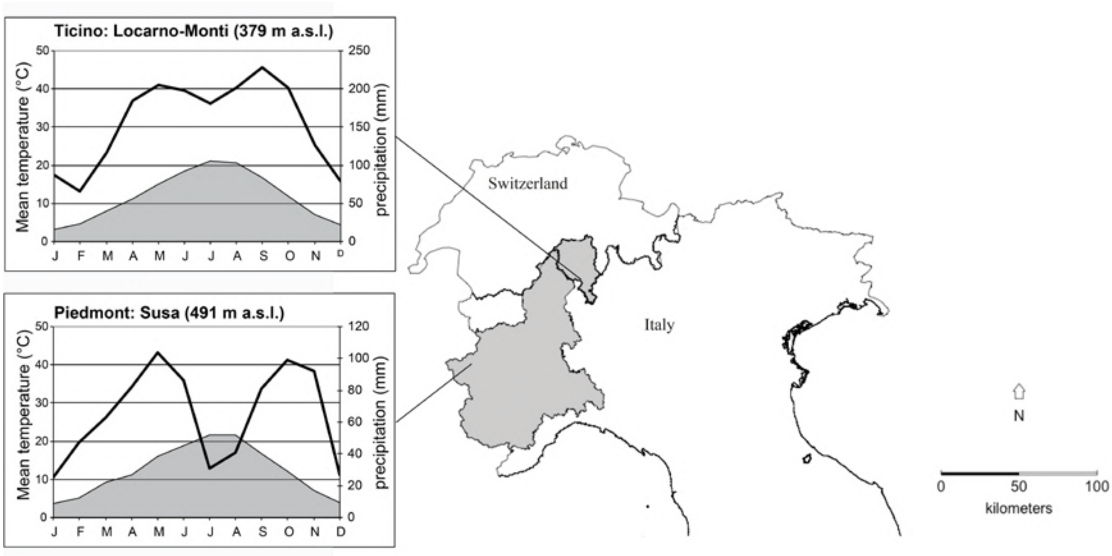

Figure 1: The study region on the southwestern slopes of the Alps located in Canton Ticino (Switzerland) and Piedmont Region (Italy) marked in grey with representative climate diagrams.

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 (Corpo Forestale dello Stato - Ministero delle Politiche Agricole, Alimentari e Forestali) for the purpose of identifying sites that burned after 1970. In order to reduce bedrock and hence soil-related variation, we limited our selection to beech forests on crystalline bedrock. To this end, we overlaid the fire perimeter data with detailed regional forest maps and geological maps (Ceschi, 2006; Camerano et al., 2004) in a geographical information system (GIS) (version 10.0; © ESRI). This procedure identified 94 potentially suitable stands for the investigation. All were inspected in summer 2011 to select sites that met the following criteria: (i) pre-fire stands dominated by beech (i.e., stem densities of beech >95%), (ii) area burned within the beech forest >0.25 ha, (iii) no additional fires in the stand during the last 50 years, as reported in the forest fire database, and no sign of recent fires during the preliminary field assessment (e.g., no trees with fire scars in the forest adjacent to the selected fire site), (iv) no evidence that the site supported a pre-fire wooded pasture, as indicated by large solitaire beech trees with large crowns and low limbs, and (v) no evidence of post-fire management, such as salvage logging or artificial regeneration. Of the 94 identified fire sites, 36 satisfied all of the selection criteria (Appendix A).

2.3 Data collection

Sampling design

Depending on the area burned and accessibility of the beech stands, 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). The number of transects was limited to three per fire site in order to avoid overrepresentation of a single fire event. Along the transects, circular plots of 200 m^2 were placed 30 m apart, starting at a distance of 10 m from the unburned forest. Wherever possible, a minimum of one and a maximum of four control plots per site were placed within the adjacent, unburned beech forest (see Figure 2). Fieldwork was conducted between July 2012 and September 2013, and a total of 233 and 39 plots were assessed in burned and unburned beech forests, respectively (Appendix A).

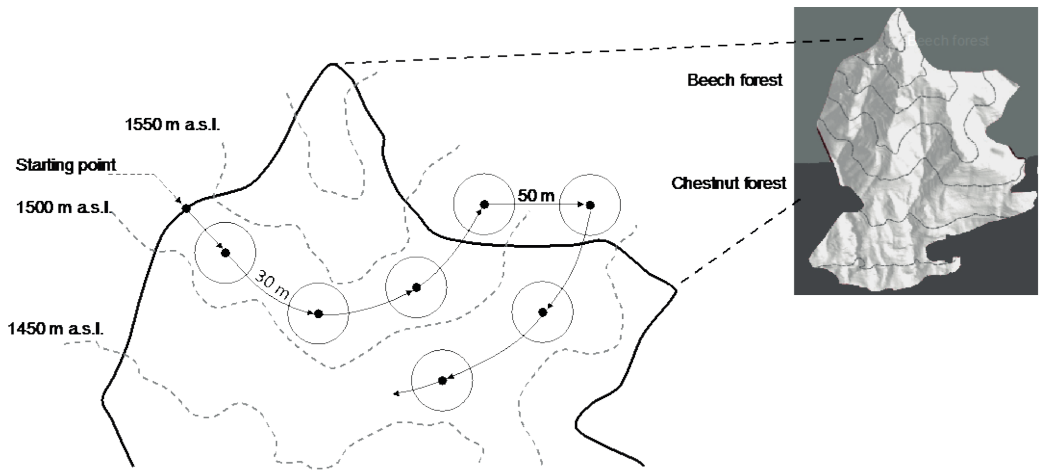

Figure 2: Sampling design in the upper part of the burned beech forest (right figure). Circular plots of 200 m^2 were placed 30 m apart along horizontal transects from the burned into the unburned beech forest (left figure).

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). During field survey, every mature (pre-fire) tree was classified as alive or dead. Dead individuals were further distinguished as dead standing trees (snags and dead standing tree with crown portions but without visible green foliage) and dead fallen trees (logs; Figure 3). We attempted to identify each tree (alive, dead) with diameter at breast height (DBH) ≥8 cm at the species level, but this was sometimes not possible because of the progressed wood decay stage. DBH was measured to the nearest centimeter for all standing trees, and the average diameter was recorded for logs. For standing beech individuals, data collection further included growth habit (monocormic or polycormic); tree height; percentage of crown volume killed; decay stage of the wood; fungal activity; and height of the fire scar, or in the absence of a fire-scar, the proportion of damaged bark. Tree growth habit 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 with the volume occupied by the pre-fire crown (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 on the entire stem of each beech using a one-to-four abundance class (none, few, partial, mass). 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).

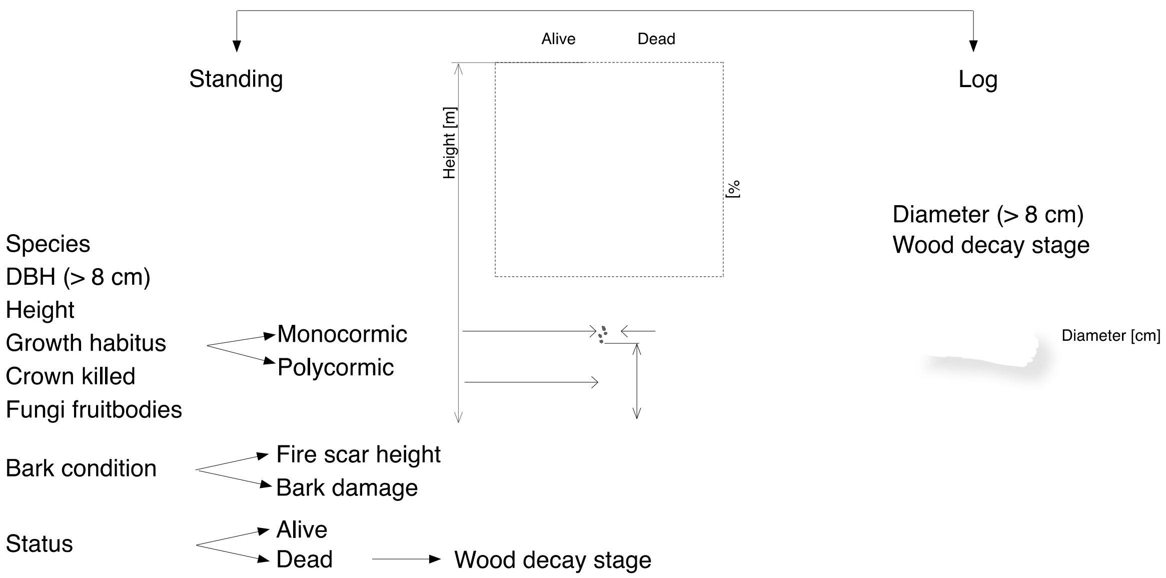

Figure 3: Scheme of the measured variables for living and dead standing trees and for logs.

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 were 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

Various approaches have been used to determine burn severity (reviewed in Johnson and Miyanishi 2007; Keeley 2009; Morgan et al., 2014). Because we faced the difficulty of estimating fire severity during different fire events occurring over four decades, we used the loss of tree-crown volume (Lampainen et al., 2004) and basal area (Larson and Franklin 2005) with respect to the ratio of post-fire/pre-fire living trees as the most suitable proxy. For burns older than 10 years, pre-fire conditions were assessed exclusively from the control plots. In recently burned areas (≤ 10 years) pre-fire stand characteristics were determined by the number of visible dead trees and logs in the burned plot. Plots were considered to be in the low-severity burn category if they showed less than 5% crown volume loss and less than 20% basal area loss. High- severity conditions were inferred from extensive crown loss (> 50%) and basal area killed (> 60%). Plots with intermediate losses in terms of crown and basal area belonged to the moderate-severity burn class (examples of low-, moderate- and high-severity sites are given in Appendix C).

2.4 Data aggregation for descriptive statistics

Dominant forest structure was characterized as the proportion of post-fire polycormic trees to total trees: (i) high-stand forests (< 33% polycormic trees), (ii) transitional stands between former unevenly-aged coppices and high-stand forests (33-66% polycormic trees), and (iii) unevenly-aged coppices (> 66% polycormic trees).

In order to describe temporal patterns of post-fire mortality, fire sites (including the control plots) were aggregated according to the time since the fire event. For this purpose, the study period was divided in 5 post-fire periods ('≤ 9 years', '10–15 years', '16–21 years', '22–32 years', and '32–43 years post-fire') following existing literature on the subject (Delarze et al. 1992; Cohn et al., 2015). Finally, standing mature beech trees were grouped into four DBH-classes (small-diameter: 8-12 cm, intermediate-diameter: 12-24 cm, 24-36 cm, and large-diameter: ≥ 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 and dead standing trees.

2.5 Beech mortality models

We assessed the risk of beech mortality using mixed-logit models - a model type belonging to the generalized linear mixed-effects model family (GLMM). Models were individual tree-based, using the vitality status (alive or dead) of the standing beech as the response variable, and site-, plot- and individual-trees characteristics as explanatory variables. Potential risk factors (explanatory variables) included total annual precipitation (**PREC**), annual mean temperature (**TEMP**) and fire season (**SW**) at the site level; micro-topography (**TOPO**), slope (**SLO**), elevation (**ELE**), and aspect (**ASP**) at the plot level; and tree size (**DBH, HEIGHT**), growth habit (**POLY**), and fungi fructification (**FUNGI**) at tree level (Table 1). All continuous risk factors were z-score transformed $[x' = \frac{x-\bar{x}}{sd(x)}]$ to calculate and compare the mixed-logit models. The models relate 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 (X), and y_i the random effect. The offset function corrects the number of mortality events for different YPF values (Boeck et al., 2014) what claims for the use of the complementary log-log as link function.

As a general rule, tree characteristics, such as stem diameter and height, were recalculated based on 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. Fungi infestation normally starts within the second year after the fire (Conedera et al., 2007; Conedera et al., 2010), and it 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 the influence of factors affecting beech mortality might be altered as a function of burn severity, we performed models separately for low, moderate, and high 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 unburned forests (*control-model*). Data exploration followed the guidelines of Zuur et al. (2010), which suggest the use of Pearson's correlation coefficient and the variance inflation factor (VIF) to detect collinearity among variables. 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 (Table 1). All continuous predictors were visualized and afterwards implemented in the models as linear and/or quadratic terms.

2.6 Model performance and selection

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

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

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). GLMM model selection refers to the lowest information-theoretical approach based on the correct Akaike information criterion (AIC; Venables and Ripley, 1999). Explanatory variables were retained if significantly different from zero ($p \leq 0.05$). Coefficients of determination (R^2) were calculated after the method of Nakagawa and Schielzeth (2013).

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 burned (B) [1] and unburned (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 habit	POLY	0/1	•	•
fungi cover	FUNGI	0/1	•	•
fire related characteristics				
fire season	SW	0/1	•	•

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

3 Results

3.1 Forest structure

Most (61%) of the burned forest stands were classified as high-stand forests, a minority (16%) as coppices, and the remainder were intermediate in structure. In total, 3,504 mature trees (DBH > 8 cm) were recorded, of which beech comprised 88 and 93% of the trees in burned and unburned forests, respectively. Other tree species rarely (< 4%) grew within the pure beech stands (Appendix B).

3.2 Post-fire beech mortality

Half of the beech trees assessed in burned plots (N = 2,845) died whereas only 10% of the trees in unburned forests were dead. Fungi infestation in burned areas occurred in

23% of living beech trees, and 72% of dead individuals. We found at least 10 different fungal species on the stems of fire-injured beech (see Table 3). The average basal area of standing dead beech trees in burned 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} depending the years since fire (Figure 4). Among fire severity classes, absolute basal area values varied greatly, and mortality showed different temporal patterns. Tree mortality in low-severity sites was quite similar to that in unburned forests, while tree mortality increased with burn severity and peaked 10 to 15 years after a fire. The highest overall loss of basal area (up to 85% of the initial value) occurred in high-severity sites, followed by moderate-severity sites (up to 63%).

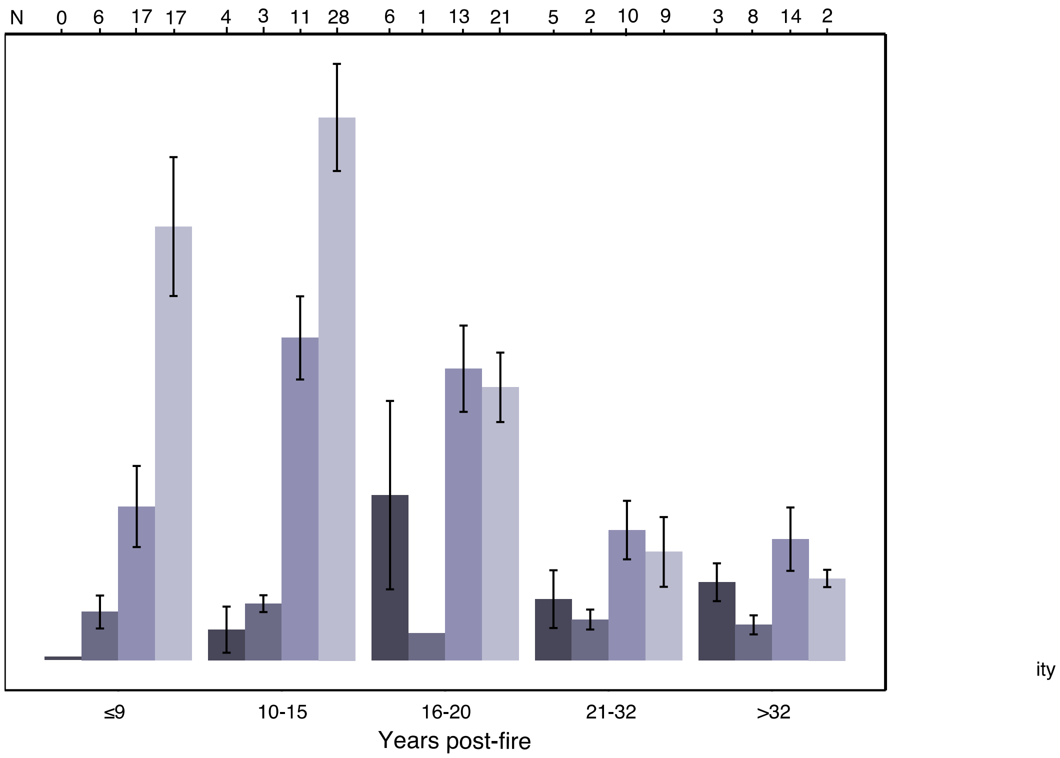

Figure 4: Mean (±SE) basal area of standing dead pre-fire beech in low-, moderate-, and high-severity sites, and the corresponding unburned plots as a function of years post-fire.

Using unburned forests as a 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 diameter. In low-severity sites, tree mortality was usually limited to small-diameter (DBH < 12 cm) beech, whereas in moderate-severity burns, intermediate-sized (DBH 12-36 cm) trees were also affected. Beech mortality was high and affected all tree sizes in high-severity plots, where mortality started immediately after the fire and continued up to two decades post-fire with the ratio of mortality odds always greater than 2.8 (Figure 5 A). In contrast, in moderate-severity plots, the odds of mortality for small-diameter beech was two to six times higher than for intermediate-sized individuals and four to 11 times higher than for large-diameter trees (DBH > 36 cm). These differences in the mortality rate were clear within the first 15 years post-fire, when mortality was highest (Figure 5 B). Similar patterns were observed in low-severity sites, where the odds of death for small-diameter trees were generally higher than for large-diameter trees (Figure 5 C). In these sites, the probability of a large-diameter individual dying was near zero, whereas that of intermediate-diameter tree ranged between 0.03 and 0.56.

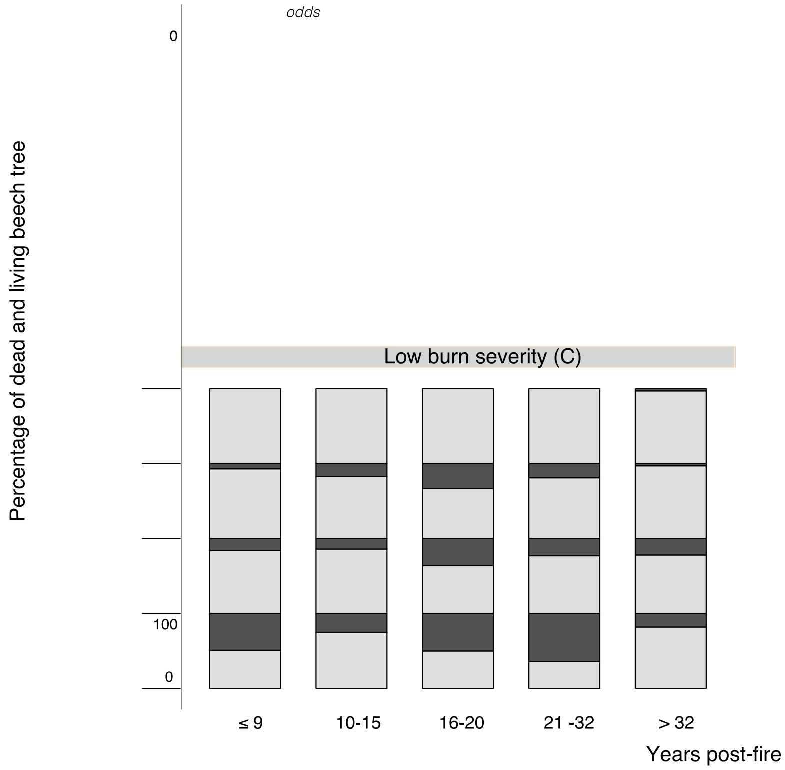

Figure 5: Percentage of survived (light grey) and dead (dark grey) beech for small (DBH < 12 cm), intermediate-sized (DBH = 12 – 24 cm), large (DBH = 24 – 36 cm), and very large (DBH > 36 cm) individuals, separated for different burn severities and years post-fire. The odds ratio of mortality is also shown to the right of each column.

3.3 Drivers of beech mortality

The best models of beech mortality clearly described the mortality rate for fire-injured beech, with FUNGI (fungi fruitbodies), DBH, and ELE (elevation) as common factors (Table 2). FUNGI had a positive and significant ($p < 0.001$) effect on beech mortality in all three burn-severity models, indicating an increasing risk of mortality after visible fungal activity, as measured by the formation of fungal fruiting bodies. The odds ratio of beech mortality after fungi fructification was 7.2 in the moderate-model, which was twice that of the low-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 toward trees with large diameters. The odds of large-diameter beech trees surviving a low-severity fire was three times higher than for a moderate-severity event; no detectable correlation existed between mortality and DBH in the high-model. The correlation between beech mortality and the quadratic term of DBH was positive. Also, the linear predictor in the control-model (unburned forests) was positive, indicating increased mortality for small- and large-diameter beech trees. Polycormic growth habit (POLY) reduced the mortality risk factor in moderate- and high-models, but not in the low-model.

In addition to tree characteristics, several site factors correlated with beech mortality. The linear and quadratic terms of elevation (ELE) were significantly and positively correlated with beech mortality in all three fire-severity models. The quadratic term of TEMP negatively correlated with beech mortality in the moderate- and high-models, respectively. Furthermore, positive correlations with beech mortality were found for PREC in the low- and moderate-model and ASP was important in the high-model. In summary, the explanatory power of the low-model containing all four variables (DBH, FUNGI, ELE, PREC) was 38%. Beech mortality was explained by six variables (FUNGI, DBH, POLY, ELE, TEMP, PREC) with an explanatory power of 23% in the moderate-model, and by five variables (FUNGI, POLY, ELE, TEMP, ASP) 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, followed by elevation (negatively correlated) and aspect (positively). All three variables explain 47% of the variation in beech mortality.

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

Models	Burned forests			Unburned 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	0.14**	1.9***	94***	0.02***
FUNGI	3.37***[1.7-6.5]	7.2***[5.4-9.6]	6.8***[3.5-12.9]	ns
DBH	0.25***[0.2-0.4]	0.8**[0.6-0.9]	ns	0.07***[0.02-0.18]
DBH^2	ns	ns	ns	2.02***[1.56-2.82]
POLY	ns	0.6***[0.4-0.8]	0.5*[0.3-0.9]	ns
ELE	3.6**[1.5-7.6]	ns	0.5*	0.35*[0.1-0.86]
ELE^2	3.85**[1.5-9.3]	0.9*[0.7-1.2]	ns	ns
$TEMP^2$	ns	0.8*[0.7-0.9]	0.6**[0.4-0.8]	ns
PREC	ns	1.8***[1.3-2.5]	ns	ns
$PREC^2$	1.6*[1.1-2.5]	ns		ns
ASP	ns	ns	1.7*[1-2.9]	3.14*[1.3-12.4]
random term	Var (x)[SD]	Var (x)[SD]	Var (x)[SD]	Var (x)[SD]
Plot	1.2[1.1]	0.3[0.5]	1.2[1]	2.8[1.7]
$R^2_{\text{fixed effects}}$	38%	23%	17%	47%
$R^2_{\text{fixed + random effects}}$	56%	27%	35%	69%

Signif. codes: '***' 0.001 '**' 0.01 '*' 0.05 '•' 0.1 'ns' 1. odds-ratio <1 negative relationship, odds-ratio >1 positive relationship, abbreviations see Table 1

4 Discussion

4.1 Post-fire stand dynamics

The selected stands showed typical beech forest structural characteristics for the southwestern Alps, with overlapping transition stages from coppices to high forest stands (Nocentini, 2009; Ascoli et al., 2013). In these stands, fires of mixed severity caused changes in forest structure by triggering mortality in half of the pre-fire beech. In general, fire-induced beech mortality increased with time in the first two post-fire decades. Similar lags in mortality after fire have also been observed in other broadleaved species (Harrod et al., 2000; Shafiei et al., 2010; Catry et al., 2010; Adel et al., 2013; Bravo et al., 2014).

As already reported for other tree species (e.g., Keyser et al., 2008; van Mantgem et al., 2013), the extent and pace of beech mortality in our study highly depended on tree size. We observed that risk of mortality was highest in small-diameter trees (DBH < 12 cm) and decreased to larger diameter individuals (DBH > 36 cm). With increasing time since fire (> 20 years post-fire), the mortality rate decreased toward a nearly natural level (control plots). Similar patterns in mortality rates have been reported for Oriental beech (*Fagus orientalis* LIPSKY) forests 37 years after a fire (Shafiei et al., 2010; Adel et al., 2013).

4.2 Triggers of post-fire beech mortality

Among the drivers of post-fire beech mortality, the presence of visible fungal activity in terms of fruit body formation was most important. The accelerating effect of secondary fungal activity in the dieback process of fire-injured trees 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. *Fagus* bark cracks after exposure to heat and subsequent boring by insects and other arthropods; both disrupt the phloematic tissues and put the cambium and sapwood at high risk of secondary fungi infestation.

To protect vital tissues, injured trees have to quickly compartmentalize wounded parts of the trunk by creating ‘defense walls’ that retard or block air and microorganisms (Shigo and Marx, 1977; Liese and Dujesiefken, 1996). Beech, in contrast to other broadleaved species, is relatively slow to undertake compartmentalization. Its bark opens soon after heat exposure (Conedera et al., 2010) and compartmentalization processes may not occur until three years after injury (Dujesiefke et al., 2005). In the intervening period, beech is highly susceptible to secondary fungal infestation.

The damage of woody tissue by fire and the likelihood of post-fire colonization by active and fructifying fungi appear to be crucial in inducing mortality. In this respect, our results confirm the findings of Conedera et al. (2010), which indicate that forests exposed to moderate-severity burns are the most vulnerable to secondary fungal infestation (i.e., the odds ratio is higher than under low- or high-severity burn conditions).

The sampling design adopted in this study does not permit a conclusive statement on the role of particular fungi species in the process of post-fire beech mortality or the ecological factors that drive fungi colonization. Nonetheless, our results indicate that the sheer presence of any fungal fruitbodies may be more important than their type or amount (Hecht et al., 2015). In accordance with Hecht et al. (2015), our study suggests that the season of injury (winter vs. summer) has no influence on beech mortality. Thus, the opportunity for fungal infestation exists over several seasons and years.

Interestingly, in this study, the fungal species colonizing fire scars appear to be different than those infesting mechanically injured trees (Table 3; see Standovár and Kenderes (2003) and Hecht et al. (2015) for a review on fungi on mechanical-injured beech trees and Conedera et al. (2007) for fire-related fungi). The existence of specific, fire-related fungi infesting beech trees is thus confirmed. Questions remain, however, concerning the specific ecological conditions needed at the time of fungal colonization and the impact of different species on the mortality process.

Next to fungi infestation, 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 small-diameter trees than for large-diameter ones has often been noted for other tree species (McHugh and Kolb, 2003; Kobziar et al., 2006; Shafiei et al., 2010; Brando et al., 2012). Gutsell and Johnson (1996) note that small-diameter trees have mostly their whole circumference burned, hence most parts of the cambium killed, and they are unable to create fire scars as a defense mechanism. The enhanced fire resistance of large trees is generally attributed to their thicker bark (increasing with age), which isolates the cambium from lethal heat radiation (Gutsell and Johnson, 1996; Lawes et al., 2013; Hély et al., 2003). However, to date little is known about the relationship between European beech bark thickness and tree size. For Oriental beech, a close relative, 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 thick bark on the bole of the trees, a trait that is evident also in large European beech trees in the Alps. This thickening may help protect living tissue from the heating caused by surface fires of relatively low intensity (Figure 6). Large European beech trees have more structured, creviced, and rough bark than small-diameter beech (Russo et al., 2010; Dymytrova et al., 2014), and these characteristics increase thermal insulation and thus resistance to fire injury (Fahnestock and Hare, 1964; Nicolai, 1986; Bauer et al., 2010; Odhiambo et al., 2014). In addition, large trees have large crowns, no low limbs, and limited litter yield around their boles (Yaussy et al., 2004), which increases their survivability after surface fires.

Figure 6: Old beech trees with structured, creviced, and rough bark at the stem base that protects living tissues from the heating due to patchy surface fires (right figure; Piedmont, Italy; D. Ascoli)

In high-severity sites, beech mortality was widespread, except in polycormic trees. In part, this observation may be related to the leeward effect of fire spread on trunk damage (Gutsell and Johnson, 1996). In multiple stem individuals, shoots exposed to the fire front are often preserved from bark-killing heat radiation, whereas those on the leeward side of the flame front are subjected to longer exposure to heat radiation. Individuals with multiple shoots may profit from shifts in resource allocation from roots of the killed shoots (Tanentzap et al., 2012), which may enhance the recovery potential of the tree. In this way, polycormic individuals have an advantage to survive fire that single-stemmed individuals do not.

Elevation is the third important factor in triggering beech mortality in burned and unburned forests. The study area has optimal levels of precipitation for beech growth (Ellenberg and Leuschner, 2010), and elevation and related temperatures are the major physical constraints on growth. Beech is naturally limited along an elevation gradient by low temperature in May (Seynave et al. 2008) and by short growing seasons in general. Therefore, it is not surprising that elevation, as a representation of growing season temperature, emerges as a significant variable in this study.

Table 3: Main ecological characteristics of fungi infection in injured beech trees (fungi infection in mechanically-injured beech trees are based on the literature review of Standovár et al., 2003; Hecht et al., 2015)

Species	Short biological description
Fungi on fire-injured trees	
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]
Fomes fomentarius (L. ex Fr.) Gill.	White rot of beech wood and other broadleaf species; occurs on living, standing trees and leads to progressive wood decay. The infested tree normally breaks at its weakest point.[h]
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 trees or on living trees. 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 trees, which are exposed to light. Sabrobiont on dead standing or lying trees, which still have pieces of bark. [d]
Fungi on mechanically-injured trees	
Cylinddrobasidium evolvens	Wood-decaying fungi
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]
Hypoxylon fragiforme	Wood-decaying fungi growing on dead trees.
Hypoxylon cohaerens	Wood-decaying fungi.
Inonotus radiatus (Sw. ex Fr.) Karst.	The main host is alder (*Alnus* sp.) but also occurs on dying beech trees.[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]
Inonotus cuticularis (Bull.) P. Karst.	Causes brown rot, mainly on beech trees in barely disturbed forests.[d]
Laetiporus sulphureus (Bull.) Bond. Ex Sinq.	Wood-decaying fungi. [e]
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 beech trees.[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] Zarzyński, (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); [i]Shortle et al. (1996); [j] Conedera et al. (2007)

4.3 **Limits of the study**

Logistic regressions usually predict tree mortality by relating tree death to: (i) fire intensity (Keyser et al., 2008), (ii) bark thickness (Brando et al., 2012), (iii) tree characteristics including DBH, total tree height, crown position, and (iv) immediate damages on root, stem and foliage (cf. Wyant et al., 1986). The degree of damage a tree can withstand varies among species-, site- and fire-specific characteristics (Catry et al., 2010). Latter both include solar radiation, precipitation, drought, temperature, severe frost events, and wind speed in the post-fire environment as site-specific parameters as well as fire-weather, fuel condition and topography as fire-characteristics (see review in Lines et al., 2010).

The rapid rate of post-fire beech mortality and wood decay did not allow us to include all of these variables in our model, given the difficult to assess them in all plots of our chronosequence. For example, important factors like the amount of bark damage and crown volume killed could not be considered. These missing variables may account for the decreasing explanatory power of the mortality models with increasing rapidity of post-fire stand dynamics. In fact, while 38% of the variance in tree mortality was explained in the low-model, the explanatory power decreased to 23% in the moderate-model and dropped to 17% in the high-model. In contrast, the control-model reached an explanatory power of 47%. In addition, because we were not able to precisely date the year in which an individual died, we were unable to analyze the influence of harsh weather conditions during the post-fire period.

5 **Conclusions**

In this study, we used a retrospective approach to examine post-fire dynamics and fire-related beech mortality in 36 sites in the southwestern Alps. Despite some methodological limits in our chronosequence approach, we provide important new insights on the fire ecology and post-fire mortality of European beech.

The major drivers of tree mortality in this study were related to a combination of factors: (i) the proportion of woody tissue damaged as a consequence of tree diameter in relation to burn severity, (ii) the likelihood that trees were colonized by active (fructifying) fungi, and (iii) the elevation of the site, as it relates to temperature. The observed mortality process in fire-disturbed beech stands began with a dynamic phase (< 20 years post-fire), when beech trees progressively degenerated and died, and a more stable phase (> 20 years post-fire) when few surviving trees died as a result of the fire.

Most large-diameter trees survived for several years after mixed-severity fires, and even if damaged they provided seeds for a new regeneration. In addition, suitable post-fire environmental conditions (e.g., mineral soil bed, intermediate light conditions) provided a seedbed for favorable seed germination and successful seedling establishment (Ascoli et al., 2015; Maringer et. al, subm.). Our research did not focus specifically on the role of specific fungal species in the dieback process of fire-injured beech trees, and further research is needed to understand the timing and ecology of post-fire fructifying fungi infestation.

Our study demonstrates that beech can persist in a mixed-severity fire regime, which contradicts the common perception that the species has no ability to cope with fire. Our findings may help to develop ecologically based silvicultural treatments that mimic natural post-disturbance stand dynamics (Nagel et al., 2014). Simplistic prescriptions, such as salvage logging standing dead trees, should be avoided (Ascoli et al. 2013) in favor of site-specific measures to restore the particular forest. In particular, standing living beech trees should be left on the burn site in order to provide seeds and shelter for beech regeneration (for details see Ascoli et al. 2013, 2015; Maringer et. al, subm.). Logs play also an important function in providing local shade, enhancing soil moisture, and releasing nutrients for beech regeneration.

In places where stand disruption and log accumulation should be controlled because of safety (e.g. in steep terrain) or silvicultural (accelerating the regeneration process) reasons, forests managers should assess the burn severity class (ratio of dead to overall basal tree area) and related stand mortality dynamics within the third year after a fire. Criteria to evaluate the mortality process are the diameter of surviving beech trees in relation to the burn severity, site elevation, and evidence of fungi fruitbodies on open bark. In the case of low- to moderate-severity fires, managers can take advantage of positive fire effects, such as litter removal and charcoal input, and apply a business-as-usual approach to forest regeneration (i.e., employing shelterwood system with seed cuts in mast years). Where beech stands serve a direct protective function, log accumulations following tree collapse after moderate- and high-severity fires might increase the danger of natural hazards (especially in case of downhill shifting log piles). Foresters may prevent these problems with preventive directional tree felling along the contour lines of the slopes. In case of large patches of high-severity fires, foresters may think about accelerating regeneration by planting beech seedlings within few years after fire (1-3 years).

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 burned (N_b) and unburned 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 burned and unburned forests sorted by the target species (beech), and trees showing dispersal strategies that rely on wind, gravity, and animals. 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.

Species	Burned forests			Unburned forests		
	∑ 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

Appendix C

Figure C.1: Low-severity burn site 10 years post-fire (D.Ascoli)

Figure C.2: Moderate-severity burn site six years post-fire (D.Ascoli)

Figure C.3: High-severity burn site four years post-fire (D.Ascoli)

Acknowledgements

This study was partially supported by the Swiss Federal Office for the Environment (FOEN). Fieldwork assistance was carried out with the support of Franco Fibbioli, Simone Giavi, Marianne Steffen, Lisa Berghäuser, Jordi Murgadas from the Swiss Federal Institute for Forest, Snow and Landscape Research, and Sven Hofmann from the University of Karlsruhe (Germany). Thanks go to Curtis Gautschi who took care of revising the English version. Finally, we acknowledge the helpful comments of two anonymous reviewers and Prof. Cathy Whitlock on earlier visions of the manuscript.

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