

Resistance and resilience of European beech
forests (*Fagus sylvatica* L.) after forest fire

Von der Fakultät für Architektur und Stadtplanung der Universität
Stuttgart zur Erlangung der Würde eines Doktors der
Ingenieurwissenschaften (Dr.-Ing.) genehmigte Abhandlung

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Tag der mündlichen Prüfung 20. Oktober 2016

Institut für Landschaftsplanung und Ökologie der Universität
Stuttgart
2016

for my grandfather
and Marco *Thanks

Erklärung des Verfassers

Hiermit erkläre ich, dass ich, abgesehen von den ausdrücklich bezeichneten Hilfsmitteln und den Ratschlägen von jeweils namentlich genannten Personen, die Dissertation selbstständig verfasst habe.

Stuttgart, den 03. Mai 2016
Janet Maringer

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Abbreviations

BP	Before Present
e.g.	Exempli gratia (for example)
GIS	Geographical Information System
°C	Temperature (Degree Celsius)
T ₀₇	Temperature in June
ha	Hectare (1 hectare = 10,000 m ²)
pH	Potential of Hydrogen
sd	Standard deviation
se	Standard error
yr	Year
kyr	Tousand years
N	Sample number
l m ²	Liter per square meter
kW m ⁻¹	Kilowatts per meter
m ³ ha ⁻¹	Cubic meters per hectare
mm yr ⁻¹	Millimeter per year
days yr ⁻¹	Days per year
stems ha ⁻¹	Stems per hectare

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Summary

BACKGROUND

Global climate change and the pattern of tree species are broadly discussed in science due to the tree's high ecological and economical values. The present study focuses on beech (*Fagus sylvatica* L.), one of the most important deciduous tree species in Europe, and its species-specific reaction to single forest fire.

In the light of global change-type drought effects, the danger of wildfires is predicted to increase also in historically less fire-prone regions. The large fires affecting beech forests of the southwestern European Alps during the heatwave in 2003 are one example. This raises questions on the best post-fire measures to ensure continued provision of ecosystem services, particularly in areas where beech forests serve a direct protection against natural hazards (e.g. rock-fall). Silvicultural measures aim to be based on ecological processes, but to date little is known about the resistance and resilience of beech forests after forest fire.

RESEARCH QUESTIONS

In order to describe the resistance and resilience processes in beech forests after fire, the present study addresses the following questions:

- What are the rates and quantities in the mortality of fire-injured beech trees and their related drivers?

- What are the temporal trends in post-fire regeneration densities?
- Which factors trigger post-fire beech regeneration processes?
- Are there mid-term lacks in the protective capacity against rockfall in mixed-severity beech stands?

STUDY REGION

The study was conducted in the southwestern Alps in the neighboring regions of the Canton Ticino (Switzerland) and the province of Piedmont (Italy). Here, winters are generally dry and sunny. The fire danger increases during Northern Foehn conditions, when the humidity drops below 20%. Forest fires usually start at the wildland-urban interface and burn as surface fires the loose debris in the deciduous forests. In order to study the mid-term processes after fire in beech forests, 36 stands burned between 1970 and 2012 (chronosequence approach) were chosen exclusively on crystalline bedrock.

METHOD

Parameters reflecting conditions of fire-injured trees were recorded on 200 m²-plots (N=234). Starting from the center of the plots, subplots of variable sizes (from 12-200 m²) were placed to record woody regeneration. Additionally, 2500 dendrochronological investigations on woody regeneration were taken. Finally, site- and tree-specific (DBH \geq 8 cm) parameters were implemented in the rockfall model *Rockfor.net* (Berger & Dorren, 2007) to assess the temporal evolution of the protective capacity against rockfall of burned beech forests. Different scenarios were calculated assessing the forests' protective capacities against rocks with volumes of 0.05, 0.2 and 1 m³, with mean slope gradients of 27°, 30°, and 35° and with forested slope lengths of 75 and 150 m.

MAIN RESULTS

Post-fire beech mortality

The results show, that beech mortality, if any, occurred delayed within the first 20 years post-fire. Small-diameter (DBH <12 cm) beech trees mostly suffered in low-severity burns, while intermediate- (DBH 12-36 cm) and large-diameter (DBH > 36 cm) beeches remain alive. With increasing burn severity, the risk of mortality raised for medium-diameter beeches. Beech mortality was ubiquitous throughout all diameter classes in high-severity burns. Thereby, the survivability of an individual beech tree is a function of the proportion of injured bark tissue and the likelihood of wood decaying fungi to infest exposed tissue. In higher elevated burns, beech tends to suffer more from fire than lower elevated.

Post-fire tree regeneration

At the same time as fire-injured beeches collapse, new tree regeneration emerge in all burns. Beech regeneration dominated in the investigated burns and often co-occur with other woody species (mainly *Betula pendula* Roth). Both mutually benefit from each other until 20 years post-fire. Afterwards, beech increased in dominance by out-competing the more light-demanding regeneration of other tree species. Most important factors influencing beech regeneration densities are the canopy density of remnant beeches, the density of ground vegetation and the elevation of the fire site. The gradual canopy opening promote beech regeneration in different development stages. Seedling (height < 20 cm) benefit from dense shelters of remnant beeches, whereas saplings (height \geq 20 cm) grow under more sparse canopies. Apart therefrom, dense layers of early post-fire colonizers, like common bracken (*Pteridium aquilinum*), common broom (*Cytisus scoparius*), purple moor grass (*Molinia caerulea*) hinder successful beech regeneration.

Forest protection capacity

The time elapsing between the decreasing protective capacity of fire-injured mature beeches and the slow increasing protective capacity

of emerging new tree regeneration cause lacks in the forest protective capacity of burned beech forests. Since the mortality rate in low-severity burns is limited to small-diameter trees, the protective capacity against rockfall is similar to the unburned forests. On the contrary, the protective capacity is rather low (<50%) between 10 and 30 years post-fire in moderate- and high-severity burns.

Practical consequences for forest management

Since dead wood played an important role in beech regeneration and in the protective capacity against rockfall, it should be generally left on the burns. In case the forest stand serve as direct protection forest, silvicultural or technical measures might be necessary. Beside the installation of rockfall nets or dams, small-scale felling of dying trees and the placement of stems in oblique direction to the slope can mitigate the reduction of protection provided by the forest. In burns of high severity, where mortality of seed providing trees is fast and early post-fire colonizers develop dense layers, direct seeding accompanied by weed control may be necessary.

CONCLUSION

In conclusion, beech mortality is delayed over a period of 20 years post-fire after mixed-severe fires– representing a crucial ecological legacy for natural beech regeneration. This creates a regeneration window of nearly 20 years, in which beech regeneration benefits from favorable site conditions, like exposed mineral soil, less competition, and intermediate light conditions. Hence, beech forests profit from single forests fires by initiating processes of rejuvenation. Exceptions are made for beech forests serving a direct protection against rockfalls. In case protection forests are disturbed by moderate or high severe fires, post-fire measures might be necessary depending on the coast-benefit ratio.

Zusammenfassung

PROBLEMSTELLUNG

In der Dissertation wird der Frage nachgegangen, wie resistent Buchenwälder (*Fagus sylvatica* L.) gegenüber Waldbrand sind und wie schnell sich gebrannte Buchenwälder nach einmaligen Feuern regenerieren können. Im Rahmen der klimatischen Veränderungen wird die zukünftige Standorteignung der Buche in ihrem angestammten Verbreitungsgebiet wissenschaftlich hinterfragt. Bei der Betrachtung stehen häufig direkt wirkende abiotische und biotische Faktoren, wie Temperatur- und Niederschlagsänderungen, im Vordergrund. Weniger Beachtung findet dagegen die Frage, inwiefern veränderte Störungsregime die Buchenpräsenz beeinflussen könnten.

Feuer ist neben Windwurf die häufigste Störungsart in Europa und Klimaszenarien prognostizieren bis zum Ende des 21. Jahrhunderts ein erhöhtes Waldbrandrisiko auch in Regionen, die heute nur selten von Feuer betroffen sind. Damit kann nicht ausgeschlossen werden, dass zukünftig vermehrt auch Buchenbestände durch Feuer gestört werden, wie es auf der Alpensüdseite im Hitzesommer 2003 bereits der Fall war. Vor dem Hintergrund, dass waldbauliche Maßnahmen nachhaltig sein sollen, stellt sich die Frage wie die Buche nach einem Waldbrand reagiert. Für die forstliche Praxis ist dabei die zeitliche Entwicklung der Buchenwälder von großem Interesse, besonders in Gebieten in denen Buchenwälder als Schutz gegen Steinschlag dienen.

FORSCHUNGSFRAGEN

Vor diesem Hintergrund werden in der vorliegenden Arbeit folgende Hauptfragen diskutiert:

- Wie schnell und durch welche Standortfaktoren beeinflusst sterben feuergeschädigte Buchen ab?
- Welche zeitliche Entwicklung nimmt die Gehölzregeneration und von welchen Faktoren wird im Speziellen die Buchenregeneration beeinflusst?
- Welche Risiken sind in Buchenschutzwäldern mit Waldbrand verbunden, mit speziellem Blick auf die Gefahrenabwehr gegenüber Steinschlag?

METHODEN

Um die mittelfristige Entwicklung (40 Jahre) gebrannter Buchenwälder studieren zu können wurde eine Chronosequenz aus 36 Buchenwäldern gebildet, welche zwischen 1970 und 2012 brannten. Die Untersuchungsflächen wurden auf der Alpensüdseite gewählt, wo es umfangreiche Daten zu Waldbränden in Buchenwäldern auf Silikatgestein im schweizerischen Tessin und italienischen Piemont gibt.

Daten zu Bestandsdynamiken und Regenerationsprozessen wurden auf 234 Plots mit einer Größe von 50–200 m² erhoben. Auf diesen Flächen wurden zusätzlich rund 2500 dendrochronologische Jahrringproben an der nach Waldbrand aufkommenden Buchenverjüngung vorgenommen.

Zur Eruierung der allgemeinen Schutzfunktion gebrannter Buchenwälder wurden Daten zum Baumbestand (beides mit Brusthöhendurchmesser [BHD] ≥ 8 cm) und Standortparameter in das Steinschlagsimulationsmodell Rockfor.net (Dörren und Berger, 2007) implementiert, und Szenarien mit unterschiedlichen Steingrößen (0.05, 0.2 und 1 m³), Hangneigungen (27°, 30°, 35°) und bewaldeten Hanglängen (75 und 150 m) gerechnet.

HAUPTERGEBNISSE

Folgen von Feuer auf den Buchenaltbestand

In den ersten 20 Jahren nach einem Waldbrand starben rund die Hälfte aller vom Feuer geschädigten Buchen. Generell zeigte sich, dass die Mortalitätsrate mit zunehmender Brandschwere¹ zunimmt und mit zunehmenden Brusthöhendurchmesser der Buchen abnimmt. Auf Flächen mit geringer Brandschwere starben rund die Hälfte aller dünnen Buchen ($BHD \leq 12$ cm), wohingegen mitteldicke (BHD 12-36 cm) und dicke Buchen ($BHD \geq 36$ cm) zu 80% überlebten. Dagegen steigt die Mortalitätsrate für dünne und mitteldicke Buchen nach einem mittelschweren Brand, und trifft die meisten Buchen unabhängig ihres Durchmessers. Als Konsequenz brechen Buchenwälder nach einem schweren Brand rasch zusammen. Ungeachtet der Schwere eines Waldbrandes erhöht sich das Risiko für Buchen nach einem Waldbrand zu sterben, wenn sich die Borke öffnet und das darunter liegende Gewebe mit aktiven (d.h. fruchtkörperbildenden) holzzersetzenden Pilzen infiziert wird.

Verjüngung nach Feuer

In den untersuchten Flächen zeigte sich, dass sich Jungbuchen zusammen mit anderen Gehölzarten (vornehmlich *Betula pendula*) rasch nach einem Brand aus Samen regenerieren. Die Bestandesdichten letztgenannter nahmen stetig nach einem Brand ab, wobei die Buche immer mehr an Dominanz gewann. Die Modelergebnisse zeigen, dass die Buchenregeneration stark von der Nähe zu vorhandenen Samenbäumen abhängt, sowie vom Aufkommen störungsangepasster Arten. Von dem sich langsamen öffnenden Kronendach des Buchenaltbestandes profitieren zunächst die Buchenkeimlinge (Höhe < 20 cm). Der das Feuer überlebende Altbestand stellt die erforderlichen Samen zur Verfügung und bietet Schutz gegenüber rauen Witterungsverhältnissen. Mit zunehmender Zeit profitierten Buchensämlinge (Höhe ≥ 20 cm) vom Zusammenbrechen des Buchenaltbestands und

¹Brandschwere zeigt sich in der Wirkung von Feuer auf ein bestimmtes Ökosystem

damit von besseren Lichtverhältnissen.

Im Falle ausgedehnter und rasch zusammenbrechender Waldbestände (z.B. im Fall von sehr schweren Bränden) wurden häufig dichte Bestände von störungsangepassten Arten vorgefunden, wie bspw. *Pteridium aquilinum* (L.) KUHN, *Molinia arundinacea* SCHANK und *Cytisus scoparius* (L.) LINK. Aus den Ergebnissen der statistischen Modelle ging hervor, dass störungsangepasste Arten stark hemmend auf die Buchenregeneration wirken. In einigen Fällen (3%) blieb die Buchenregeneration vollständig aus.

Konsequenz für die Schutzfunktion der Wälder gegen Steinschlag
Ergebnisse des Steinschlagmodells ergaben, dass sich aus dem Zeitverzug zwischen Zusammenbruch des Buchenaltbestandes und der aufkommenden Regeneration nach Feuer, vorübergehende Einbußen in der Schutzfunktion dieser Wälder gegenüber Steinschlagergebnissen ergeben. Auf Flächen mit geringer Brandschwere starben meist nur dünne Buchen, weshalb die Schutzfunktion von mittelgroßen bis sehr großen Buchen übernommen wird. Basierend auf den Berechnungen im Steinschlagmodell resultiert eine zeitlich ähnliche Entwicklung der Schutzkapazität für alle gerechneten Szenarien in leicht gebrannten Beständen, wie für ungebrannte Wälder. Nach einem mittleren und schweren Brand starben vermehrt mittelgroße bis große Buchen ab. Die Aufnahmen zeigten jedoch, dass zur gleichen Zeit das Dickenwachstum des Jungwuchses noch nicht für eine umfassende Schutzfunktion ausreichte, weshalb die berechnete Schutzfunktion in diesen Beständen vermindert war. Die Stärke einer solchen verminderten Schutzwirkung hängt von der Steingröße und von der Länge und Neigung des bewaldeten Hanges ab. Laut Berechnungen war sie im Extremfall zwischen 10 und 30 Jahren nach einem Waldbrand bis auf unter 50% des Normalzustandes gesunken.

Empfehlungen für forstliche Maßnahmen

Generell sind forstliche Eingriffe nach einem Waldbrand nicht nötig, außer der betroffene Bestand dient direkt als Schutzwald. Neben der Installation von Steinschlagschutznetzen oder -wällen, könnten

nach einer Kosten-Nutzen-Abschätzung, forstliche Eingriffe von Nöten sein. Speziell das Fällen von absterbenden Buchen und das hangparallele Aufstapeln der Stämme könnte die Schutzwirkung zumindest temporär erhöhen. Zur Förderung einer schnellen Baumregeneration, könnte die Reduktion störungsangepasste Krautvegetation in Kombination mit künstlicher Ansamung hilfreich sein.

FAZIT

Zusammenfassend lässt sich sagen, dass der Buchenaltbestand verzögert über einen Zeitraum von 20 Jahren zusammenbricht. Infolge ist der Sameneintrag für eine erfolgreiche Buchenregeneration gesichert. Innerhalb dieses Zeitfensters profitiert die Buchenregeneration von den Standortbedingungen nach einem Brand (Mineralboden, weniger Konkurrenz, mittlere Lichtverhältnisse). Deshalb sind einmalige Brände durchaus nützlich um Regenerationsprozesse zu initiieren und so einer Bestandsüberalterung entgegen zuwirken. Ein spezieller Blick sollte jedoch auf Schutzwälder gelegt werden, in denen nach mittleren und schweren Bränden gegebenenfalls schutzfördernde Maßnahmen ergriffen werden müssen.

Chapter 1

Introduction

Global climate change and the distribution of tree species are broadly discussed in science because of tree's high ecological and economical values (Zimmermann et al., 2009). The present study focuses on beech (*Fagus sylvatica* L.), one of the most important deciduous tree species in Europe, and its specific post-fire reaction to forest fires in a global change context.

The anthropogenic climate change, caused by the emission and accumulation of greenhouse gases in the atmosphere, lead to a general warming of the global climate system. As a consequence, global temperature rise by reduced day-to-day variability. Warmer temperatures increase the moisture storage capacity of the atmosphere, which lead to a higher variability in the range of heavy precipitation (Pachauri et al., 2014). Those processes are predicted to influence on the one hand the distribution of species (Zimmermann et al., 2009), and on the other hand disturbance regimes in terms of frequency, magnitude and seasonality (Flannigan et al., 2000; White & Jentsch, 2001; Moriondo et al., 2006; Schumacher & Bugmann, 2006)

Trees are particularly sensitive to both changing climatic conditions and disturbance regimes, because of their longevity and sedentariness. Under consideration of their ecosystem services (ecolog-

ical, economical and socio-cultural), it is of general concern how they might respond to direct and indirect climatic changes. Generally it is assumed, that climate drives the distribution and abundances of trees (e.g. Guisan & Zimmermann, 2000; Boucher-Lalonde et al., 2012). Therefore, climate variables are often used to define species-specific ecological niches in order to predict the related biogeographical distribution (Guisan & Zimmermann, 2000). Niche modeling, in turn, can be used to understand how environmental changes may affect species' occurrences (Pearson & Dawson, 2003; Heikkinen et al., 2006).

However, the shift of the tree species distribution area is seldom related to climatic mean values. They are much more the response to alterations in frequencies and intensities of climatic extremes (Pulliam 2000; Bigler et al., 2006; Fuhrer et al., 2006; Zimmermann et al., 2009), such as disturbance events (Peterson, 2000; Nagel et al., 2006; Krawchuk et al., 2009; Hennon et al., 2012). Hence, the extinction or expansion of the species distribution area results from selective pressure on intra-specific genetic diversity and / or from changes of the inter-specific competition (Kramer et al., 2010; Lindner et al., 2010; Mette et al., 2013). As a consequence niche modeling in turn should consider, next to habitat related factors, also realistic disturbance scenarios (Overpeck et al., 1990). For this purpose information is needed about the species-specific reaction to a particular disturbance agent.

First signs of altering disturbance regimes are already recognizable. For instance, winter storms increased in magnitude and frequency in the last 50 years in Europe (Usbeck et al., 2010; Seidl et al., 2011). And more and larger stand-replacing fires have disturbed forests in western United States over the last 20 years than during the previous 20 years (Westerling et al., 2006; Dennison et al., 2014). In western Mediterranean ecosystems, fires today are more drought-driven and less fuel-limited than fires before 1970 (Pausas & Fernández-Muñoz, 2012). In the light of climate change, disturbances are increasingly likely to impact also forest ecosystems and species that have historically been less affected by a particular dis-

turbance agent. For example, beech (*Fagus sylvatica* L.) forests in the southwestern Alps experienced exceptionally numerous and large fires during the hot and dry summer of 2003 (Ascoli et al., 2013). Such extreme summer heat waves are expected to increase in frequency during the 21st century in Central Europe (Schär et al., 2004).

As climate change moved into the focus of attention, the stand-specific suitability of beech has been questioned due to the species high economical and ecological value in Central Europe (Rennenberg et al., 2004; Bolte et al., 2009; Lindner et al., 2008). From the ecological perspective, the tree species plays an important role in natural conservation of biological diversity (Assmann et al., 2007; Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit, 2007). It is able to improve and conserve soil functions because of its broad shallow root system (Polomski & Kuhn, 2001) and its relatively fast decomposing litter in humid regions (Czajkowski et al., 2005; Wühlisch, 2008). Regarding its stable wood structure, beech forests are often planted in mountainous regions to protect close-by infrastructure from rockfalls and soil erosion (Schmidt, 2005; Perzl, 2009).

From the economic point of view, beech is the most important deciduous tree species in Central Europe (Germany 15% and Switzerland 18% on the total forest cover) with rising trend in the last 15 years (Brändli, 1999; Deutscher Forstwirtschaftsrat, 2008; Polley et al., 2014). The favoring of beech can be related to changes in the forest policy since the 1980s toward the close-to-nature concept (e.g. Schütz, 1999). Based on this concept many off-site conifer-stands were converted into near-naturally beech forests, with the aim to improve biodiversity and stand stability (e.g. Spiecker et al., 2004; Nagel & Svoboda, 2008; Pretzsch et al., 2013).

Due to the species high economical and ecological value, knowledge is required on the species ecophysiological plasticity to different abiotic and biotic factors. Depending on the locality within its distribution area, some studies advocate its cultivation (Ammer et al., 2005; Mette et al., 2013), while others point to its sensitivity to wa-

ter stress and recommend the plantation of more drought-tolerant plant species (Rennenberg et al., 2004; Fuhrer et al., 2006; Kutnar & Kobler, 2011; Vitale et al., 2012). Most of the studies focus on single direct climate factors and test the plasticity of beech in terms of increasing temperature accompanied by water stress (Huntley et al., 1989; Czajkowski et al., 2005; Leuschner et al., 2006; Franke & Köstner, 2007; Gärtner et al., 2008; Fischer & Neuwirth, 2012; Hartl-Meier et al., 2014; Kreyling et al., 2014), variability in atmospheric CO₂-levels (Henn & Schopf, 2001), and in the species vulnerability to late spring frosts (Kreyling et al., 2011) or a shorter chilling period (Sykes et al., 1996; Schmidt & Wichmann, 2000).

A small part of research draws also attention to beech's reaction to disturbances— mostly concentrating on windthrow (Koop & Hilgen, 1987; Kompa, 2004; Kompa & Schmid, 2005; Collet et al., 2008; van Couwenberghe et al., 2010; Heinrichs et al., 2012; Kramer et al., 2014). Almost unlighted is the reaction of beech to forest fire. Few studies investigated the fire ecology of beech. They focused either on short- (1-3 years; van Gils et al., 2010; Maringer et al., 2012; Ascoli et al., 2013) or long-term (decades to centuries; Tinner et al., 1999; Tinner et al., 2000) responses. To date, little is known about mid-term (40 years) regeneration processes in beech forests disturbed by single fires. Knowledge may increase in importance for forest managers, in particular in the light of global-change-type drought effects (Breshears et al., 2005) raising fire danger also in areas with low fire occurrence at present.

In particular, knowledge in both the survivability of fire-injured beech trees and post-fire regeneration processes can assist managers in making post-fire decisions related to tree removal, reforestation, salvage logging, and wildlife habitats. This might be of special importance in mountain areas, where beech forests often serve as protection against rockfall (Perzl, 2009). Management decisions, in turn, need to be based on the fire ecological behavior of beech in order to avoid unnecessarily and costly technical measures. Additionally, knowledge about the fire ecological behavior of beech is necessary to clarify the species-specific plasticity or adaptability to

the ongoing climate change debate by implementing the reaction to disturbances in niche models.

The present study attempts to develop a more comprehensive understanding of the mid-term resistance and resilience processes in beech forests affected by single surface fires and their protective capacity against rockfall — embedding the topic in the context of climate change. In order to understand “what is going to happen” it is necessary also to understand “what has happened” (Peters, 1997).

Therefore, Chapter 2 starting on page 39 gives a detailed overview of the state of the art of beech’s reaction to climate change in the context of both post-glacial recolonization processes and future climate change. At the end of Chapter 2 the attention is drawn to fire ecology of beech (Section 2.4). Chapter 3 presents the research questions. Thereafter, the post-fire resistance and resilience processes of beech forests are examined based on field observations. A detailed overview of the geographical, geological and climatic conditions in the study area is given in Chapter 4 on page 55ff. The resulting regional specific fire regime is described in Section 4.3. Criteria for selecting the burns in beech forests and the applied sampling design are described in Section 5.1 and 5.2. Statistical techniques and the rockfall model are described in detail in the "Data analysis"- section starting on page 61ff. Chapter 6 starting on page 91 provides results in the resistance and resilience process of burned beech forests and the resulting protective capacities against rockfall. All issues are deeply discussed with literature background in chapter 7 on page 129ff. Finally, Chapter 8 contains concluding remarks, direction for further research and forest management recommendation.

Chapter 2

Background

2.1 Post-glacial recolonization processes

Forest stands are dynamical systems and their present appearance is a result of history, climate, silvicultural practices, and successional processes. From the historical point of view, beech recolonization processes started late in the post-glacial environment. There is evidence that the species survived the last glaciation in scattered refugia across southern Europe, while two main slightly genetic different groups were identified (Magri et al., 2006). Some groups survived in the Carpathian, the southeastern Alps and the Balkan region and contributed to Central European beech populations. Others survived in small-scattered populations in the Mediterranean region that apparently expanded only slowly and in a limited spatial range (Figure 2.1 on page 42).

Taking into account that at the time when beech started to migrate Europe was already covered by dense forests, climate might be not the only driver for beech's post-glacial recolonization process. When looking at the main expansion waves, which started at 8.2-5 thousand years before present [kyr= thousand years; BP= be-

fore present] in southern Europe (Tinner & Lotter, 2006; Valsecchi et al., 2008) and 4-3 kyr BP in Central Europe (Langdon et al., 2003; Barber & Langdon, 2007; Walentowski et al., 2010), climate was characterized as cool and moist (Tinner & Lotter, 2006; Valsecchi et al., 2008). Summer temperatures declined periodically several degrees under the long-term mean, although mean temperatures remained generally higher than today (Walentowski et al., 2010).

Looking at migration patterns on the local scale, favorable environmental conditions concurred with low natural and / or human disturbances, initiating successional processes by opening dense forests (Küster, 1997; Clark et al., 1989; Keller et al., 2002). In the Mediterranean region, e.g., warmer temperatures accompanied by low severe anthropogenic disturbances caused an upward shift of beech populations toward higher elevations, while migration stopped under cooler climate and the absence of disturbances (Muñoz Sobrino et al., 2009). Similar results were observed in the post-glacial recolonization processes in Bulgaria (Tonkov et al., 2008) and Scandinavia (Henry & Swan, 1974; Björkman & Bradshaw, 1996; Bradshaw & Lindbladh, 2005).

To conclude, migration processes of beech in the post-glacial environment were favored in cool and moisture summers, but low severe disturbances have been important for beech's initial spread. Therefore, climate factors determined beech's distribution on a continental scale and low to moderate disturbances regimes favored beech distribution on a regional scale.

2.2 Present distribution area and bioclimatic envelope

Currently, beech seems mostly to be at equilibrium with climate (Huntley et al., 1989; Hanewinkel et al., 2012) and its distribution area ranges from the lowland (-colline) plains in southern Scandinavia, northern Germany and Poland to south England, northwestern France and the Benelux (Figure 2.1). In Central and Western

Europe the tree species grows from the colline to the sub-montane elevation zone and further south, toward warmer and drier climate, in the montane-altimontane elevation zones (1,100—1,900 m a.s.l.) (Bohn & Neuhäusl, 2000/ 2003).

This broad geographical expansion is characterized by mean annual temperatures and precipitation ranging from 3 to 13 °C and 500 mm yr⁻¹ to 1850 mm yr⁻¹, respectively (Kölling et al., 2007). Beech finds its ecological optimum in areas with mean annual temperature of 6 to 12 °C (Fang & Lechowicz, 2006) and annual precipitation of 1200 mm (Huntley et al., 1989; Table 2.1 on page 43).

High temperatures in May (> 17-20 °C, optimum 12-14 °C, Seynave et al., 2008; Mátyás et al., 2010) and July (> 18-25 °C; Mátyás et al., 2010) accompanied by precipitation below 250 mm limit the occurrence of beech further south (Ellenberg & Leuschner, 2010). Toward northern latitudes and the continental regions, beech distribution is limited by mean temperatures in January below -3 °C (optimum - 1 °C, Huntley et al., 1989), frost events of -30 °C and frost on more than 141 days yr⁻¹ (Michiels et al., 2009). On the other hand, the species requires a chilling period of minimum 145 days yr⁻¹ with temperatures below 7 °C (Murray et al., 1989). Despite its climatic requirement, beech tolerates soil pH-values ranging from 3.5-8.5, but avoids water logged or too shallow soils with water storage capacity (AWC) below 65-70 l m⁻² (Leuschner, 2010; Gärtner et al., 2008).

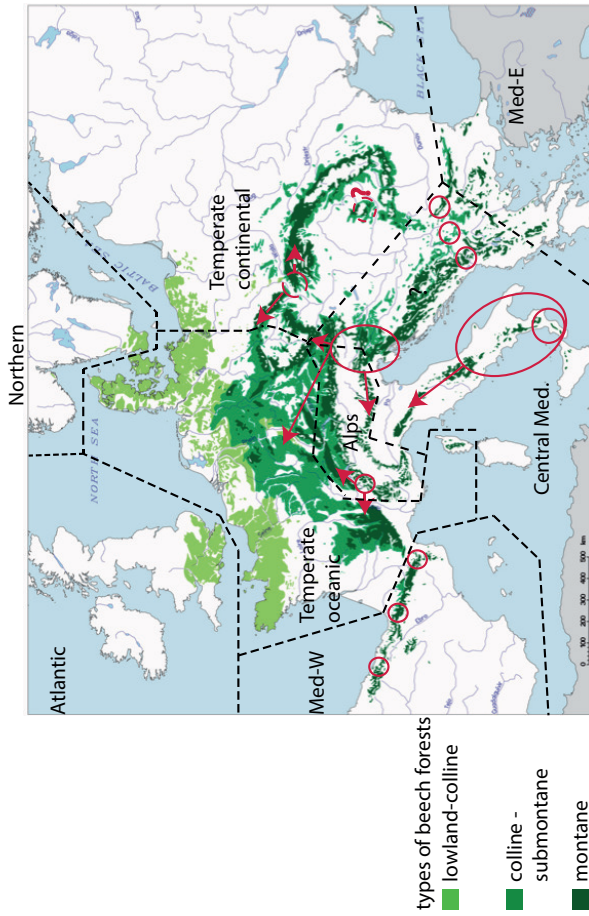


Figure 2.1: Current natural distribution area of beech (*Fagus sylvatica* L.) partially disclosed for the colline-, colline to submontane-, and montane zone (modified after Bohn & Neuhausl 2000/ 2003) divided into the different ecological zones (dashed lines; modified after Schelhaas et al., 2003). The Pleistocene refugia and the main colonization routes are visualized in red circles and red arrows based on Magri et al. (2006).

Table 2.1: Ecological requirements of beech (*Fagus sylvatica*) with optimum, minimum, and maximum ranges for temperature, precipitation and soil pH-values (Huntley et al., 1989; Murray et al., 1989; Fang & Lechowicz, 2006; Kölling et al., 2007; Seynave et al., 2008; Bolte et al., 2010; Ellenberg & Leuschner, 2010; Wagner et al., 2010).

Abiotic parameters	Optimum	Minimum	Maximum
<i>Temperature</i>			
$\text{\O T } [^{\circ}\text{C yr}^{-1}]$	6-12	3	13 (14)
$\text{\O T } [^{\circ}\text{C}]$ in January	-1	-11	3
$\text{\O T } [^{\circ}\text{C}]$ in May	<7	—	—
$\text{\O T } [^{\circ}\text{C}]$ in July	18	—	19
<i>Period [days]</i>			
\sum days $\text{\O T } > 7[^{\circ}\text{C}]$	—	~ 217	—
\sum days $\text{\O T } < 7[^{\circ}\text{C}]$	—	~ 145	—
\sum days $\text{\O T } < 0[^{\circ}\text{C}]$	—	—	~ 141
<i>Precipitation</i>			
\sum P [mm yr ⁻¹]	600-900	450	2000
\sum P [mm] May-Sept.	—	250	—
pH-value	4.5-6	3.5	8.5

2.3 Impact of climate change on beech distribution

2.3.1 Beech forests of the Mediterranean zone

The wide geographical distribution of beech reflects its broad eco-physiological niche in terms of temperature, precipitation and soil conditions. The region where beech populations are expected to decrease, if climate is getting warmer and drier, is the montane zone of the Mediterranean region (Figure 2.1; Huntley et al., 1989; Hanewinkel et al., 2012).

By the end of the 21st century mean annual temperature are expected to increase by 3.5 to 5.5 °C with a peak in summer by

around 5.4°C in the Mediterranean region (Table 2.2 on page 49). Forecast for summer precipitation show a clear declining tendency with prolong droughts and increasing fire danger (Christensen & Christensen, 2007; Loepfe et al., 2012; Pachauri et al., 2014; Kovats et al., 2014; Wu et al., 2015).

Low precipitation during the summer months (see Table 2.2 on page 49) causes distress for beech and may lead to shrinking beech populations. First signs are already observed in southeastern Spain and Central Italy (Jump et al., 2006; Piovesan et al., 2008). Based on this awareness, Peñuelas & Boada (2003) predicted an upward shift of beech populations toward higher elevations. This assumption is supported by low-spatial distribution models (Vitale et al., 2012; Kramer et al., 2010). Contrastingly, in parts of the Mediterranean region with higher precipitation or humidity like the Pyrenees and the more Atlantic influenced Iberian Peninsula, beech populations seems to be stable or even expand (Sierra-Diaz et al., 2012; Garrigüe et al., 2008).

It can be summarized that, the survival rates of beech populations in the Mediterranean region depend on: i) the magnitude and frequency of droughts and forest fires, ii) the genetic adaptability of beech to cope with water stress (particularly in the regeneration stage), iii) the species possibility to reach alternative habitats with favorable conditions, and on iv) the employed forest management systems. Historical studies showed, e.g., that genetic variation of beech survived in scattered refuges during the last glaciation (Magri et al., 2006), but to date little is known about the genetic adaptability to specific environmental factors (Rose et al., 2009; Kreyling et al., 2011; Hofmann et al., 2015). Therefore, the forest policy in the Mediterranean region has a special responsibility in maintaining local beech populations and thus genetic variety.

2.3.2 Beech forests of the temperate oceanic zone

Different affected from the predicted climate change seem beech populations in the temperate oceanic zone (Figure 2.1). Regional cli-

mate forecasts predict increasing mean annual temperatures by +2.0 to 3.5 °C with a peak by +4 °C in summer (Table 2.2 on page 49). Summers are generally getting drier caused by around 15% lower precipitation (except for Scandinavia) with high day-to-day variability (Fuhrer et al., 2006; Christensen & Christensen, 2007; Wastl et al., 2012).

Within the temperate zone, regional differences can be seen. For zones influenced by the Atlantic, the sea-water-masses buffer the temperature-rise and -amplitude between summers and winters (Christensen & Christensen, 2007). Here, beech populations have been stable so far. Even shorter periods of less favorable water supply seem to have no distress on beech populations (García-Plazaola et al., 2008). Increasing temperatures seems to favor beech growth, and the species is recently reported to invade forest stands in Ireland (Hickler et al., 2012). Restricting factors for beech migration further west-expansion might be a shorter chilling period due to warmer winter temperatures (Sykes & Prentice, 1996; Schmidt & Wichmann, 2000).

Beech might be replaced by more drought tolerant species in drier parts of the temperate oceanic zone (low humidity and precipitation 600 mm yr⁻¹), and on sites with soil water storage capacity below 65-70 l m⁻² (Kohler et al., 2006; Bressemer, 2008; Gärtner et al., 2008).

Beech populations in the temperate zone are also exposed to increasing storms and fungal infestations (Räisänen et al., 2004; Leckebusch et al., 2006; Beniston et al., 2007; Jung, 2009; Pinto et al., 2010; Klaus et al., 2011). Beech is mostly susceptible to *Phytophthora*-species (Jung, 2009)– fungi species which cause root-collar rot and aerial bark canker on beeches of all ages. Where present, *Phytophthora*-species inhibit beech regeneration by contaminating the soil (Nechwatal et al., 2011). This is mostly true for beech forests growing on base-rich, fresh and periodically water logged sites (Hartmann & Blank, 2002; Michiels et al., 2009). Apart from soil conditions, warmer temperature and heavy precipitation, however, will favor the expansion of *Phytophthora*-species (Bressemer, 2008; Jung,

2009).

Another common biotic factor that often lead to local beech death are woolly beech scale (*Cryptococcus fagisuga* LINDINGER) in combination with *Nectria coccinea*. Warmer and drier summers are predicted to cause a mass reproduction in woolly beech scale and make beech bark susceptible for infestation by *Nectria*-fungi (Bressem, 2008). Latter is favored by mild and wet winters, which are predicted for the temperate zone. Mostly even-age beech stands, which are additionally stressed by drought and nutritional unbalance, are likely to be killed by *Nectria*-fungi (Niesar et al., 2007; Packham et al., 2012). All above-mentioned pathogens seem to profit from climate change and increase the risk of beech infestations, mainly in mono-culture stands (Schelhaas et al., 2003). Beside fungi infestation, montane beech forests may additionally weakened by increased O₃-levels. These seem to reduce the metabolism of beech and makes the species more vulnerable to secondary disturbances, like fungi infestation and windthrow (Dittmar et al., 2003).

Generally, forest fires may play a minor role in beech forests of the temperate oceanic zone, and fire hazards will increase toward the south and the more continental zone (Wu et al., 2015). However, increasing fire danger in Southern Scandinavia (Schmuck et al., 2004) may force beech migration into Norway spruce stands, similar to post-glacial expansion processes (see chapter 2.1 on page 39).

2.3.3 Beech forests of the temperate continental zone

Toward the more continental zone, mean annual temperatures are predicted to increase by around 4.5 °C accompanied by highly variable amounts of precipitation (Christensen & Christensen, 2007). Projections for winter precipitation show an increasing tendency toward wetter conditions, while summers are getting warmer and drier. Regional climatic models predict major drought events every second year by the end of the 21st century (Gálos et al., 2007) raising also the danger of wildfires (Wu et al., 2015).

First effects of prolonged droughts are given by populations from Hungary, where beech growth is limited at lower elevation, while populations in moister environmental at higher elevation remain stable (Mátyás et al., 2010). In contrast, low spatial-resolution models, however, predict an eastward shift of beech populations under moderate climate change (Hanewinkel et al., 2012; Kramer et al., 2010).

With regard to biotic disturbances, infestation by gypsy moth (*Lymantria dispar* Linnaeus) and nun moth (*L. monacha* Linnaeus) causes beech defoliation over large areas with a great economical impact (Hättenschwiler & Schafellner, 2004). Due to temperature increase both moths are expected to extend their ranges toward north and the more continental regions, while they reach their southern limits in the Mediterranean region under hot and dry weather (Lindner et al., 2008). However, increasing atmospherically CO₂- and N-values might cause changes in the leaf chemistry of tree species making some species more palatable for leaf consuming moths (Henn & Schopf, 2001). With regard to beech, many studies have disproved this hypothesis and pointed out that, e.g., common hornbeam (*Carpinus betulus* L.) and oak species (*Quercus* spec.) are more vulnerable to gypsy and nun moth attacks (e.g. Hättenschwiler & Schafellner, 2004; Henn & Schopf, 2001). Therefore, a host species shift toward more palatable tree species might occur with positive feedbacks for beech.

2.3.4 Beech forests of the European Alps

The future distribution of beech in the Alps may vary among regional climate, geological bedrock, and changes in the disturbance regimes. Due to the relief-rich terrain, climate shows a high spatial variability and temperature has increased roughly 1.6 times the northern hemispheric warming rate (CH2011, 2011). General trends expect temperature increase by 2.7 to 5 °C by the end of the 21st century, accompanied by precipitation increase during winter and slightly decrease in summer (Pachauri et al., 2014; Table 2.2). Exceptions are made for the Southern Alps where the main precipitation are

concentrated in autumn and early winter.

On limestone, beech has to cope with increasing water stress, so that some studies predict the decline of local beech populations (Fuhrer et al., 2006; Seynave et al., 2008; Kutnar & Kobler, 2011), while those growing in better site conditions seem to stay stable (Bugmann, 1997; Wunder et al., 2007; Brang et al., 2011).

With view to disturbances, the Northern Alps are currently frequently disturbed by harmful storms. Investigations of Schiesser et al. (1997), however, detected declining trends in the frequency of storm days and the duration of storm events. Possible reasons are the northward shift of extra tropical cycles whereby the Northern Alps would lie more often outside of continental storm fields or on their southern edge.

Winterly surface fires of anthropogenic origin frequently burn in the southern Alps, whereas the majority of summer fires are lightning-induced. The study of Conedera et al. (2006) shows that lightning-induced summer fires may increase in relevance in the light of climate change. Observations from the last 60 years show, an increasing fire danger for the southern Alps but also for the western and northern Alps (Wastl et al., 2012). This tendency is likely to continue, which is why some studies predict an upward shift of beech populations toward higher elevations (Bugmann, 1997; Schumacher et al., 2006).

Table 2.2: Expected climate changes in relation to the long-term means of summer (JJA) and winter (DJF) temperature (T [°C]) and relative changes in the amount of precipitation (P). Further listed are representative climate stations and their locations [Elevation m a.s.l.] (Christensen & Christensen, 2007; Hijmans et al., 2005).

Region Subregion	Climate station	Elevation	Present climate $\overline{\text{OT}}$ [°C]	\sum P [mm]	Predicted climate change			
					T_{DJF}	T_{JJA}	P_{DJF} P_{JJA}	
<i>Mediterranean region</i>								
Central	Campobasso (I)	807	12.0	628	3.7	5.4	-0.01	-0.43
Western	Pamplona (E)	459	12.5	721	3.0	5.4	-0.04	-0.48
<i>Alpine region</i>								
NW-Alps	Zurich (CH)	555	8.5	1086	3.5	5.0	+0.2	-0.26
S-Alps	Locarno (CH)	379	12.5	1806	3.5	5.0	+0.2	-0.26
E-Alps	Afenz(A)	780	6.8	870	3.5	5.0	+0.2	-0.26
<i>Temperate oceanic region</i>								
Sub-Atlantic	Stettin (PL)	1	8.4	527	3.3	4.1	+0.17	-0.21
Atlantic	Plymouth (GB)	27	10.7	980	1.8	3.1	+0.2	-0.33
Scandinavia	Goeteborg(S)	4	7.8	791	4.1	3	+0.2	+0.03
<i>Temperate continental region</i>								
	Sibiu (RO)	444	8.5	623	4.3	4.5	+0.2	-0.15

2.4 Beech fire ecology

Since the area burned and the intensity of wildfires increased in recent decades (e.g., Westerling et al., 2006; Sullivan et al., 2011; Sarris et al., 2014) questions raised on how to predict tree mortality rates (Ledgard & Davis, 2004; Kobziar et al., 2006; Moreira et al., 2012). Models have been developed explaining driving factors and predicting post-fire tree mortality mainly for fire-prone ecosystems (e.g., McHugh & Kolb, 2003; Ledgard & 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). Little attention has been paid to tree species, like beech, that dominate in historical non fire-prone regions. However, due to climate change the fire danger is expected to increase also in non-fire prone regions, like in the Alps (Wastl et al., 2012). The numerous and large forest fires burned in beech forests in the southwestern Alps during the heatwave of 2003 (Ascoli et al., 2013) serve as one example.

Beech is generally considered highly susceptible to fire because of a lack in fire resistance or fire-adaptive traits, such as a thick bark or a persistent resprouting capability (Peters, 1997; Packham et al., 2012). The mechanism of post-fire survival strategies of the species are poorly understood and this generates a lack in predicting fire-injured beech mortality rates. Recent studies show that the timing of post-fire beech mortality depends on fire intensity¹ (Conedera et al., 2007; Ascoli et al., 2013). Beech mortality may occur immediately after very severe fires or be delayed by several years when fires burn less severe.

Beech's fire survival strategy is mainly based on the rapid *in situ* seed production when mast years synchronize 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). Beech relies on gravity and animal seed dispersal (rodents, birds), which makes its regeneration limited by the distance to the nearest

¹Fire intensity is defined as the heat rate released at the flaming front [kW m^{-1}] (Johnson & Miyanishi, 2007)

seed-bearing tree (Wagner et al., 2010; van Couwenberghe et al., 2010). Consequently, the larger a stand-replacing burn and the further away an off-site seed source is, the more limited natural beech regeneration may be. Paleobotanical studies of beech in the Alps, however, demonstrated its persistence to fire on the long-term (Tinner et al., 1999; Tinner et al., 2000). And short-term studies indicated a good potential of naturally beech regeneration (van Gils et al., 2010; Maringer et al., 2012; Ascoli et al., 2013). However, little attention has been paid to the mid-term regeneration dynamic and related environmental factors driving post-fire beech regeneration processes. A broader understanding in the mid-term resistance and resilience dynamic of burned beech forests would answer questions on post-fire measures to re-establish ancestral ecosystem services such as the forest protection function.

The European Alps form a relief-rich area, where healthy and well-structured beech stands are able to dissipate the kinetic energy from falling rocks (Schmidt, 2005; Perzl, 2009). Therefore, mountain beech forests often serve as protection forests. Beech forests in the southwestern Alps, e.g., hold a share of 16% (Ticino, Switzerland) and 26% (Piedmont, Italy) on the regional overall protection forests against rockfall (Istituto per le Piante da Legno e l'Ambiente, 2012; Brändli & Huber, 2015).

The forests protective functions mainly affect mountain regions. Generally disturbances, such as fire, have the potential to abruptly and substantially reduce the protective capacity of forests, which depends on (1) the intensity and scale of the disturbance, (2) the resistance and resilience of the disturbed stand, and (3) on the post-disturbance management (Bebi et al., 2015). In case of an immediately and comprehensive loss of living trees after the disturbance event, remnant dead wood decreases terrain patency and thus at least partly compensates for the loss in the protective capacity. On the other hand, slow succession rates after a disturbance event and relatively fast decaying dead wood may lead to the temporarily reduced protection capacity against natural hazards (Bebi et al., 2015). The literature review for this study revealed no research concentrat-

ing on temporal trends in the protective capacity of burned beech forests. This in turn is needed to gain knowledge on post-fire measures to improve the forest's protective capacity.

Chapter 3

Research objectives

In order to fill the mentioned knowledge gaps, the present thesis focus on the mid-term resistance and resilience processes of burned beech forests and their protective capacity against rockfall. Therefore, the focus of the research questions (RQs) shift from the collapse of fire-injured beech trees (RQ's 1 & 2) to post-fire regeneration pattern (RQ's 3 to 6). The resulting protective capacity of burned beech forest against rockfall is addresses in RQ 7. The study's research questions are as follows:

1. Changes in forest structure and beech mortality:

RQ 1 What are the rates and quantities in the stand structure of fire-induced beech mortality, and the subsequent wood fragmentations?

RQ 2 Which factors lead to fire-injured beech mortality?

2. Resilience of beech forests:

RQ 3 Does beech regenerate in all investigated burned forest stands?

RQ 4 What are the temporal trends in beech regeneration compared to other woody species?

RQ 5 Which are the positive and negative ecological drivers of the post-fire beech regeneration?

RQ 6 Do pioneer tree species— colonizing burned forests— limit beech regeneration?

3. Forest protection function:

RQ 7 Are there mid-term lacks in the protection capacity against rockfall of burned beech forests?

Based on these research questions, the study sites were selected on the southwestern foothill of the European Alps. Here, extensive data sets on wildfires in beech forests exist in the Swiss Canton Ticino (Pezzatti et al., 2010) and the Italian province Piemonte (Corpo Forestale dello Stato/ Ministero delle Politiche Agricole, Alimentari e Forestali, 2005).

Chapter 4

Study area

4.1 Geography, geology and soils

The study area is located on the south to southwestern European Alps in the Swiss canton of Ticino and the Italian province of Piedmont (Figure 4.1 on page 57). Characteristic for both regions is a marked elevation gradient ranging from the Lake Maggiore (197 m a.s.l.) to the Adula Peak (3402 m a.s.l.) in Ticino and to the Punta Nordend (4609 m a.s.l.) in Piedmont, respectively (Figure 5.1 on page 63). Due to the relief-rich terrain, rockfalls are one of the major natural hazards threatening mountain settlements and roads in both regions (Regione Autonoma Valle d'Aosta - Regione Piemonte, 2011; Ambrosi & Thüring, 2005).

The regional geology is characterized by the tectonics of the Alps, and crystalline basement dominates large parts of the southwestern Alps. In Ticino the Insubric basement is separated from the Penninic nappes through the east-west striking Insubric line, and only small parts show inclusions of calcareous bedrock. Limestone is only present in the very south (Piffner, 2015). In the northern part of the Piedmont, gneiss and mica-schists complexes dominates the geologi-

cal basement, rarely interspersed with limestone. In the very south, around the city Torino, rhyolite dominates the crystalline basement (Istituto Superiore per la Protezione e la Ambientale, 2015).

Soil profiles mostly contain geological debris of gneiss and mica-schists complexes and are characterized by a low base saturation. This reduces the biological activity and leads to delayed litter decay. As a consequence, soils contain mostly of thick organic layers (moder) and they are morphological almost undifferentiated together with the subjacent mineral horizons. Blaser (1973) was able to identify the transfer of sesquioxides into deeper soil layers. He classified the soil as crypto-humus-podzol. Soils with lower aluminium content in relation to ferric oxides are classified as ochre-podzol (Blaser et al., 2005).

4.2 Regional climate

The climatic processes in the study region are strongly influenced by the east-western orientated Alps. The mountain range builds a barrier for cold air masses coming from northern Europe and temperatures of comparable elevations are higher in the southern than in the northern Alps. Mean annual temperatures in the study region are around 12.4 °C. Winters are generally mild with mean temperature of 3.5 °C in January and warm summers with average temperature around 21.7 °C (Figure 4.1 on page 57). Susa (Piedmont; 7°3'0'' E, 45°8'0'' N) in the West is much drier with annual precipitation of 778 mm (ARPA, 2015) than Locarno Monti (Ticino; 8°46'10'' E, 46°10'12'' N) in the North with 1,897 mm (observation period: 1981-2010; MeteoSwiss, 2015). Precipitation peak in the transitional seasons from April to May and from (August) September to October. Generally, periods without rain last not longer than thirty consecutive days in summer (Isotta et al., 2014). This contrasts with winter months (December to February), in which precipitation are particularly low (\sum 99 mm for Piedmont, \sum 220 mm for Ticino). On an average of 40 days yr⁻¹ a katabatic warm and dry wind (North

foehn) drops the relative humidity below 20% (Spinedi & Isotta, 2005).

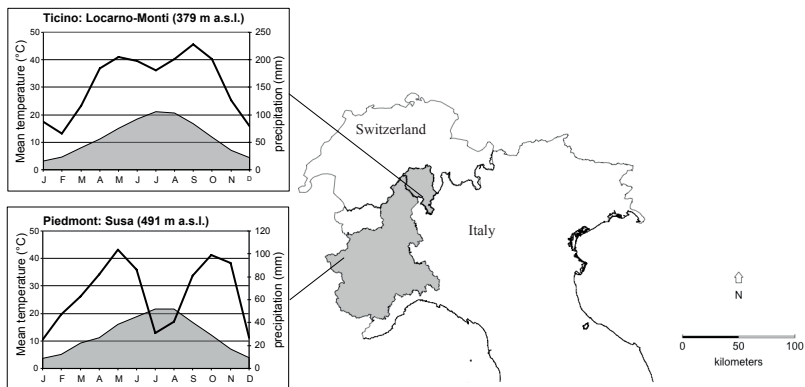


Figure 4.1: Study region with climate diagrams for the wetter canton Ticino (Locarno Monti: 8°46'10'' E, 46°10'12'' N) and the drier Piedmont (Susa: 7°3'0'' E, 45°8'0'' N)

4.3 Forest fires

The fire danger in the southwestern Alps rises during North foehn episodes in winter and spring. In case of ignition, wildfires start from the wildland-urban interface and spread in the adjacent forests (Conedera et al., 2015). They usually take the form of a surface fire, consuming the loose debris (litter, herbs, dead branches) and the understory vegetation (tree seedlings and the surface vegetation).

Thereby the fire front and the related fire impact on vegetation are not spatial uniform; rather it creates a mosaic of differently burned and unburned patches.

Only in rare cases fires becomes more intense resulting in stand-replacing fires (e.g. fire in a mixed-broadleaved forest described in Maringer et al., 2012). Generally, the wintery surface fires start from the lower chestnut belt (300–900 m a.s.l.) and spread into the adjacent beech belt (900–1,700 m a.s.l.), where they often stop (Pezzatti et al., 2009). Beech forests display certain characteristics of fire-resistant forests. They often form high-stand forests with trees showing no low limbs that prevent the vertical spread of flames during a fire. Moreover, a generally low amount of biomass (sparse shrubs and herbs strata) in the understory and the compact litter layer, that maintains the humidity and is poor in oxygen, prevents fires from becoming intense. Finally, the presence of fire-inducing activities is scarce in mountainous beech forests. This leads to lower numbers of forest fires and very low area burned in beech forests of the southwestern Alps than theoretically expected when considering the overall beech forest area (e.g., Pezzatti et al., 2010). Additionally to winter fires, summer fires are rare in average years. They usually burn in the higher elevated conifer belt (>1400 m a.s.l.) mainly caused by lightning.

4.4 Forest cover

The geological and climatic characteristics suggest that both regions (Ticino and Piedmont) are nearly similar from the biogeographical point of view. Ozenda (1988) assigns the Southern foothill of the Alps, in particular Ticino and the northern Piedmont, to the Insubric vegetation complex with the adjacent Piedmont-Alps in the South. Forests cover to 46% and 34% the regions of Ticino and Piedmont, respectively (Inventario nazionale delle foreste e dei serbatoi di Carbonio (INFC 2005), Corpo Forestale dello stato – ispettorato generale; Pezzatti et al., 2009). The main forest types and vegeta-

tion belts correspond to those of the Northern Alps (Ozenda, 1988), except the chestnut (*Castanea sativa* Mill.) forests in the lower elevation belt (300–900 m a.s.l.). Chestnut was introduced by the Etruscan and later intensively cultivated by the Romans (Conedera et al., 2004).

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). Beech forests on acid soil are classified as *Luzulo niveae-Fagetum typicum* with the sub-association *Luzulo niveae-Fagetum dryopteridetosum* in humid sites (Ellenberg & Klötzli, 1972). Generally, beech forests hold a share of 6% in Ticino and 13% in Piedmont of the overall forest cover (Nocentini, 2009; Pezzatti et al., 2009). And many of those forests had been often used as coppices for charcoal production.

Coppices are characterized by differently aged shoots growing out of one stool. The rotation cycle of the shoots is relatively short—approximately 20 years. Coppices provided firewood and charcoal for many centuries. Since the 1950s, however, low costs for alternative energy sources lead to a massive migration process of mountain inhabitants. Most coppices have been left abandonment or actively transformed to high stand forests. Thus, beech forests in the study region have undergone a transformation process from coppices toward high stand forests of different development stages. Currently beech coppices and high stand forests in Piedmont reach proportions of 63% and 26%, respectively. The remaining are still in the transformation process (Nocentini, 2009).

Chapter 5

Materials and methods

5.1 Fire perimeter selection

To gain knowledge on the above named research questions, a retrospective approach extended by statistical models was chosen. Therefore, 36 beech forests burned between 1970 and 2012 were investigated in the summer of 2012 and 2013. This retrospective approach, also known as space-for-time substitution, assumes that different sites with similar age between the disturbance event and the field observation, can be considered as one time sequence (Pickett, 1989). Multiple time sequences in a row build a chronosequence.

Fires burned after 1969 were selected from the forest fire database of Switzerland (Pezzatti et al., 2010) and in the database of the State Forestry Corps of Italy (Corpo Forestale dello Stato/ Ministero delle Politiche Agricole, Alimentari e Forestali, 2005). They were overlaid with local vegetation maps (Camerano et al., 2004; Ceschi, 2006) and geological maps in a geographical information system (ArcGIS; version 10.0; ESRI, 2010) to identify fires in beech stands on crystalline bedrock. In total, 94 candidate burns resulted from the GIS analysis. All of them were inspected in summer 2011 to select sites

that satisfied all of the following criteria:

- area burned in beech forests >0.25 ha,
- no additional fires in the stand during the last 100 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),
- no evidence that the site supported a pre-fire wooded pasture, as indicated by large solitaire beech trees with large crowns and low limbs,
- no evidence of post-fire management, such as salvage logging or artificial regeneration, and
- pre-fire stands dominated by beech (i.e., stem densities of beech $>90\%$).

Since soil types and the subjacent bedrock influence species composition and their coverage, burns were selected exclusively on crystalline bedrock. From the 94 examined burns, 36 satisfied all of the selection criteria, and were considered for the final sampling design (Table 5.1 and Figure 5.1).

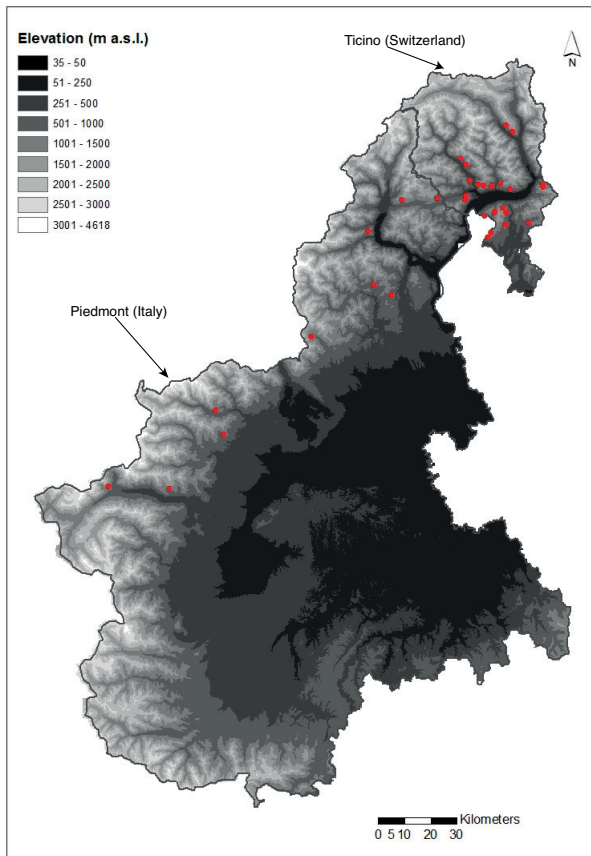


Figure 5.1: Sampled burns showed on an elevation map of Ticino (Switzerland) and Piedmont (Italy) (source: DEM Swisstopo, Bern; Consorzio per il sistema informativo (CSI)– Regione Piemonte)

Table 5.1: Investigated burns sorted by the climatic regions (Piedmont, Insubria) and the date of fire. Further listed: mean elevation [m a.s.l.], class of the burned area (small<4 plots (S), medium 4-9 plots (M), large >9 plots (M)), UTM- coordinates (WGS84), mean annual temperature (T [°C]), sum of annual precipitation (P [mm]) (observation period 1950-2010 from WorldClim Database; Hijmans et al., 2005), and number of plots investigated in the burned (Nb) and unburned beech forests (Nc). Burns marked with * are not considered in the regeneration models.

<i>Regions</i>	Municipality	Elevation	Size	Date of fire	E	N	T	P	Nb/Nc
<i>Piedmont</i>									
	Sparone	1100	L	12/1980	382545	5030710	6	1109	16/1
	Rosazza	1000	M	01/1990	418645	5058661	5.8	1195	5/0
	Corio	1080	L	02/1990	385562	5021543	7.5	898	10/2
	Arola	850	L	06/1997	449208	5074546	7.9	1172	13/0
	Varallo	1300	L	08/2003	442360	5078456	7.2	1186	11/1
	Condove	1100	L	03/2008	364870	5000781	7.4	979	11/1
	Giaglione*	1300	M	03/2012	341650	500164	6.4	1067	8/1
<i>Insubria</i>									
	Indemini	1300	S	08/1970	488196	5105864	6.4	1349	3/1
	Minusto	1000	S	11/1971	484123	5116368	4.7	1415	2/1
	Gordevio*	1450	S	03/1973	482190	5116678	6.5	1355	1/0
	Moghengo	1100	S	11/1973	492538	5101434	8.3	1310	3/1
	Gordola	1060	S	03/1976	490491	5116753	6.0	1365	2/1
	Arbedo	1300	L	03/1976	506667	5116933	7.1	1290	13/1
	Astano	1050	S	01/1981	485796	5096454	8.2	1304	2/1
	Indimini	1300	L	01/1981	484488	5104578	5.5	1376	12/1
	Intragna	1150	S	01/1987	477570	5112256	7.6	1318	3/0
	Aurigeno	900	S	08/1989	478824	5118037	8.2	1308	2/1
	Mugena	900	M	03/1990	492683	5105828	7.1	1330	6/1

<i>Regions</i>									
Municipality	Elevation	Size	Date of fire	E	N	T	P	Nb/Nc	
Novaggio	1300	S	03/1990	486829	5098133	5.4	1371	2/1	
Avegno	1250	S	05/1990	482007	5116521	6.5	1355	2/0	
Pollegio	1250	M	04/1995	492574	5139100	5.3	1391	5/2	
Tenero	950	S	04/1996	487212	5116007	8.5	1315	3/0	
Ronco s.A.	1300	M	03/1997	477225	5110649	6.6	1349	6/1	
Magadino	1200	L	04/1997	491560	5107650	6.9	1335	26/3	
Sonvico	1000	M	04/1997	501239	5101934	8.8	1300	5/2	
Arbedo	1350	S	11/1998	506770	5115571	8.5	1302	3/2	
Indemini*	1300	S	12/1998	488487	5106098	6.6	1347	1/1	
Gordevio	1450	L	04/2002	482190	5116678	6.5	1355	13/4	
Maggia	1380	S	03/2002	477394	5124084	5.7	1388	3/1	
Bodio	1050	M	03/2003	495105	5136703	4	1436	5/1	
Dissimo	1000	M	04/2003	466503	5111215	5	1402	5/1	
Someo	1450	S	08/2003	475281	5126733	5.6	1395	3/1	
Villadossola	1200	L	03/2005	440231	5098748	5.7	1305	11/1	
Cugnasco	700	M	04/2006	494084	5114855	9.4	1317	4/1	
Ronco s.A.	1300	S	04/2007	477225	5110649	6.6	1349	2/1	
Druogno*	1100	L	03/2012	453207	5110682	4.8	1394	12/1	

5.2 Sampling design

Depending on the burn size, one to three transects were defined and spaced 50 m apart in elevation by starting randomly at the forest edge (Figure 5.2 on page 67). Along the transects, circular plots of 200 m² were placed in the burned beech forests, starting with the first plot in 10 m distance to the burn edge, and regularly repeating with 30 m spacing between the centers. This method was performed to sample the edge distance gradient. In each transect a minimum of one control plot and a maximum of four were located beyond the edge in the unburned beech forest, except for six burns where it was not possible because of the steep terrain (Table 5.1). According to the final number of plots, the burn size (**AREA**, see abbreviations in Table 5.2 on page 81) within each beech stand was categorized as small (< 4 sample plots), medium (4–9 sample plots) or large (> 9 sample plots). Tree regeneration was assessed starting from the plot center in concentric circles of variable subplot sizes ([2.5 m²], 50 m², 100 m², 200 m²) to avoid missing beech regenerations. The subplot size was extended stepwise until either a minimum of 10 post-fire beech individuals were found or to a maximum circle size of 200 m² (Figure 5.2).

5.3 Data collection

5.3.1 Field measurements: site characteristics

Against the background that fire behavior varies with topography, each 200 m²-plot was characterized by slope (**SLOPE**), aspect (**ASP**), and micro-topography (concave, plane, convex; **TOPO**). Further, elevation (**ELE**) was measured as a factor representing indirectly both temperature and precipitation gradients. Known to colonize burned areas soon after forest fires (Maringer et al., 2012), common broom (*Cytisus scoparius* (L.) LINK), common bracken (*Pteridium aquilinum* (L.) KUHN), and purple moor grass (*Molinia arundinacea*

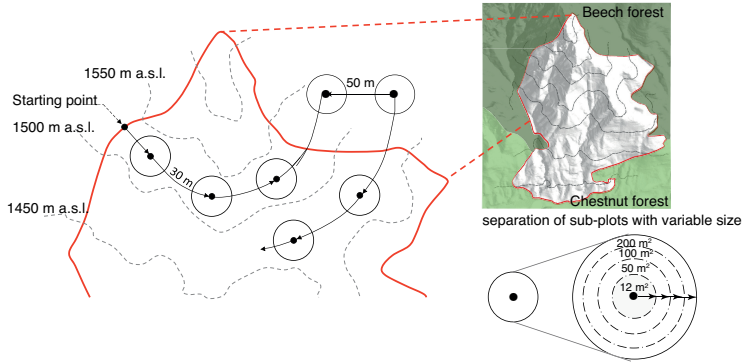


Figure 5.2: Sampling design in a burned beech forest (*Fagus sylvatica* L.) that resulted typically from fires starting in the chestnut (*Castanea sativa* Mill.) belt and expanding upslope into the adjacent beech belt (figure top right). Circular plots of 200 m² were placed in 30 m distance along horizontal transects from the burned into the adjacent beech forest (figure left). Tree regeneration was assessed in subplots of variable sizes as shown on the bottom right.

SCHRANK) were assessed in terms of their overall cover. They are regarded as early post-fire colonizers (**EARLY**), which might inhibit emerging regeneration (Priewasser, 2013) and contribute as surface roughness (Wohlgemuth et al., 2002). Additionally, the distances between the plot center and both the nearest uphill seed providing mother beech tree (**MOTHER**) and the burn edge (**EDGE**) were estimated as indicator for beech seed availability.

5.3.2 Field measurements: stand structure

Assessment of vegetation structures of the pre-fire trees followed the guidelines of the Swiss National Forest Inventory (LFI; Keller, 2005) with specific focus on stand stability parameters (Herold & Ulmer, 2001). Therefore, each tree was classifying as alive or dead (**STATUS**; Figure 5.3 on page Figure 70). Dead individuals were

further distinguished between dead standing trees (snags and dead standing tree with crown portions but without visible green foliage) and fallen dead trees (hereafter referred to as logs). Each standing tree was identified down to the species level (Lauber et al., 2007), and their diameter to breast height (**DBH** at 1.30 m aboveground) was measured to the nearest centimeter and height (**HEIGHT**) to the nearest meter. For logs the average diameter and length was recorded (Figure Figure 5.3 on page Figure 70). Data collection further included for beech the growth habit (monocormic, polycormic), percentage of crown volume killed, decay stage of wood, height of the fire scar, proportion of damaged bark, fungal activity, as well as the number and height of basal shoots (any new growth on the base of a tree). Tree growth habit was defined as polycormic (**POLY**) if two or more stems grew out of one 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 (**FUNGI**) to the mortality process (Conedera et al., 2007; 2010), fungal fructification (fruit bodies) was assessed quantitatively by determining four abundance classes (none, few, partial, mass) on 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); Gerhardt (2005) and Klug & Lewald-Brudi (2012) (fungi species determination was conducted by Nicolas Küffer).

The level of wood decay was estimate in order to estimate the decomposition rate with progressing time. Therefore, each snag and log was assign to one of the following classes by visually assess the morphological characteristics of a tree and by knife penetration of the stem (for more details see Hunter & Schmiegelow, 2011). Trees were assigned to class one if they recently died and still had an intact bark (the cambium is still fresh). Trees in class two are characterized by a broken and patchy bark along the stem. Although the outer layer of the stump has been started to soften so that the

knife penetrates low the dead wood. Bark is completely missing on trees assigned to class three and the outer wood layers disintegrate to some extent so that the knife penetrate into the fibre direction. Finally, trees in class four showed completely disintegrated wood so that the knife penetrates in both the fibre and transversal direction.

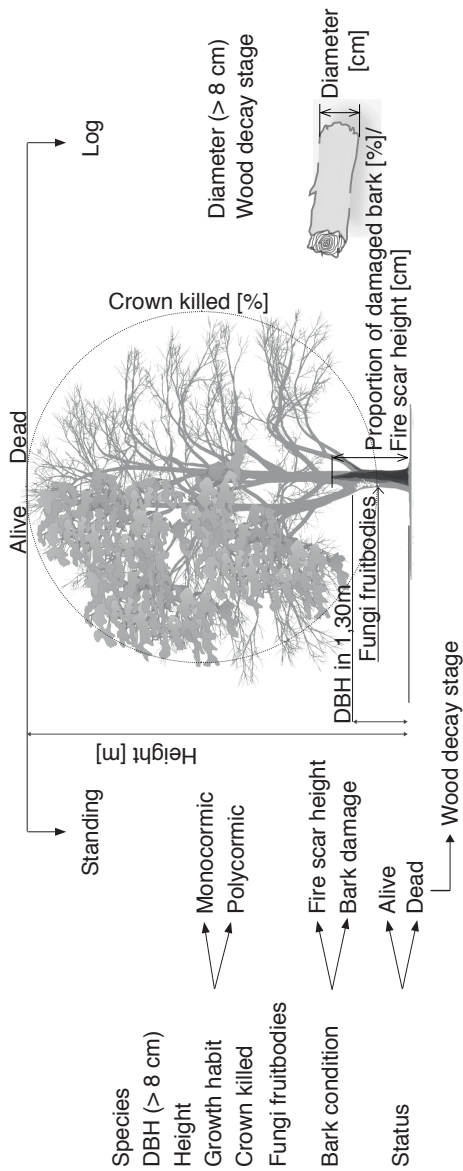


Figure 5.3: Scheme of the measured variables for living and dead standing trees and for logs.

5.3.3 Field measurements: woody regeneration

Woody regeneration was also identified to the species level (Amann, 1967; Lauber et al., 2007), and categorized as seedlings (height \leq 20 cm) and saplings (height $>$ 20 cm). Seedlings were counted on species level separately for living and dead individuals. Saplings were measured individually (height, DBH in case $>$ 1cm) and their vitality was recorded as alive with percentage of physical damage (in 5%-steps) or dead. To detect saplings preferences in growth location, nine different micro-habitats were recorded (level-ground, hump, in a depression, on a log/ stump, beside a stump, under a fallen tree crown, uprooting pit/ mud or on a stone). Densities of seedlings and saplings were upscaled to stems ha^{-1} (stems per hectare), separately for beech, pioneer and "other" woody species. Pioneer trees are characterized by high annual productions of wind-dispersed seeds. Species assign to "others" combine traits of gravity (barochorous) or animal (zoochorous) seed dispersal strategies by showing a highly variable annual seed production.

Dendrochronological samples were randomly taken exclusively for beech on the 200 m^2 -plots. Samples always included the smallest and tallest individual, implying the youngest and oldest, respectively. To avoid the first years after seed germination, the age of beech regenerations younger than four years was determined by counting the growth units (Heuret et al., 2003; Figure 5.4). Older individuals were cut or drill cores of 5 mm diameters were taken close to the root collar (transition zone between stem and root at the ground line of a tree).

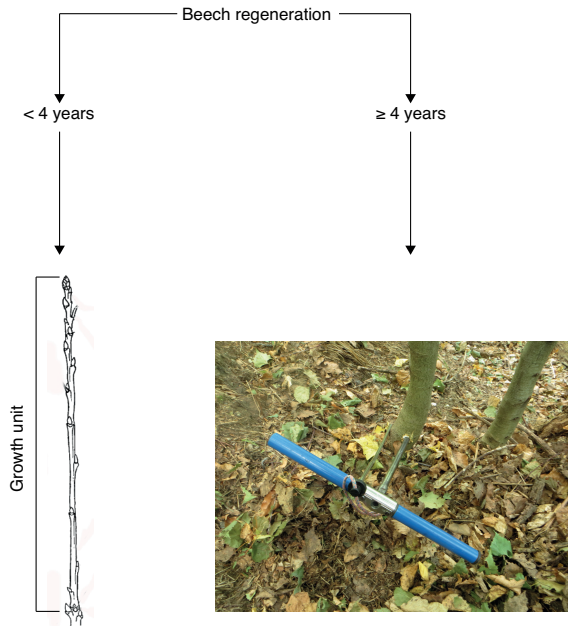


Figure 5.4: Age assessment of beech regeneration. The left part of the figure illustrates the assessment of growth units (modified after Heuret et al., 2003) and the right part the placement of the drill core.

5.3.4 Field measurements: surface fuel and soil

Dead wood may serve as a long-term source for nutrients, increases spatially limited the soil moisture, and provides shade (Harmon et al.,

1986). Therefore, in addition to logs, lying branches and brushwood originating from falling crowns of dead trees with a decay stage below four were assessed after the method of Brown (1974) and Wagner (1982). Pieces in the 200 m²-plots were recorded in different diameter classes (1: 2.5-5 cm, 2: >5-7.5 cm, 3: >7.5-15 cm, 4: >15-30 cm) along the four cardinal directions. The obtained volume was then scaled up to standard hectare values (m³ ha⁻¹) as follow:

$$V = \frac{1.234 \cdot n \cdot d^2 \cdot a \cdot c}{L} \quad (5.1)$$

Where,

V = volume [m³ ha⁻¹]

n = number of intersections for each size class

L = transect length [m]

d = mean diameter of the size class [cm]

a = correction factor which is 1.13 if $d \leq 7.5$ cm, and 1 if $d > 7.5$ cm

c = slope correction factor ($\leq 10\% \rightarrow c = 1$; $11-50\% \rightarrow c = 1.12$; $51-100\% \rightarrow c = 1.41$)

Soil pH may have a strong influence on tree regeneration (Kramer et al., 2014). Therefore, mineral soil samples (N 259) were taken randomly in minimum one and maximum three plots per fire site in two depths: (i) just beneath the litter layer, and (ii) when possible in 30 cm depth.

5.3.5 Assessment of burn severity

Regarding the assessment of burn severity¹ (**SEV**; Turner et al., 1997; Morgan et al., 2014) at plot level, there was the difficulty to estimate retrospectively severities in differently aged fire events. From the various approaches existing (reviewed in Johnson & Miyanishi, 2007; Keeley, 2009; Morgan et al., 2014), losses in crown volume (Lampainen et al., 2004) and in basal area (Larson & Franklin, 2005) were selected with respect to the ratio of post-fire living trees/ overall pre-fire trees as the most suitable proxy and with respect to time since fire (Brown et al., 2013). For old (>10 years) burns, pre-fire conditions were assessed exclusively from the control plots, whereas in recently burned areas (≤ 10 years) pre-fire stand characteristics were assessed combining numbers of visible dead trees in control and burned plots. Plots were defined as low-severity burns when the loss of canopy and basal area was less than 5% and 20%, respectively (Figure 5.5 on page 75). Contrastingly, high burn severity was indicated by extensive canopy loss (> 50%) and basal area killed (> 60%) within the first decade post-fire. All plots displaying an intermediate evolution in canopy and basal area losses were assigned to the moderate severity class.

5.3.6 Climate variables

Precipitation and air temperature were obtained for each investigated burn from the WorldClim Database (Hijmans et al., 2005). Average long-term sums of precipitation (**PREC**) and means of temperature (**TEMP**) refer to the period from 1950–2010 for each fire site. For local site conditions, a detrended correspondence analysis (DCA; Oksanen et al., 2015) was calculated plot-wise based on tree

¹Both fire and burn severity is defined as the magnitude of changes on fuel, vegetation, soil and wildlife habitat induced by fire disturbance. While fire severity describes the short-term effects, burn severity refers to the longer-term effects (see review in Morgan et al., 2014).

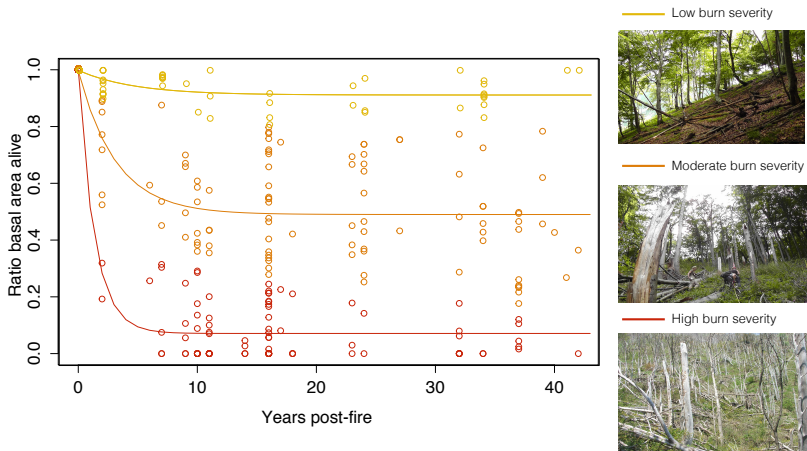


Figure 5.5: Ratio between basal area of beeches survived the fire and either the overall basal area of the same plot (years post-fire ≤ 10) or the overall basal area of the plot in the corresponding unburned forests (years post-fire > 10). Patches burned of low, moderate and high severity are shown in the photographs on the right side of the figure.

species composition in the burned beech forests. The first DCA-axis represents a species diversity turnover (Leps & Smilauer, 2003), which corresponds to a light gradient. Positions along this first axis were used for further analysis (**mCLIM** see Table 5.2 on page 81).

5.3.7 Assessment of the age of beech regeneration

The samples of tree disc and drill cores of beech regeneration were dried 48 hours, than abraded with sandpaper (value 100), prepared with chalk, liquid color, and razor blades for archiving more contrast. Annual tree rings were counted under a binocular after reference pictures of Schweingruber (1987). Dendrochronological samples

were only considered if germination occurred before 2010 to detect germination rates triggered by fire.

5.3.8 Assessment of soil pH-value

The soil samples taken from the burns were dried in the laboratory according to DIN ISO 11464 (Beuth, 2006), milled, and sieved (2 mm sieve). The pH-values were measured using a CaCl_2 -solution (DIN ISO 10390; Deutsche Norm 2005). A total of 259 pH-measurements were conducted.

5.4 Data analysis

5.4.1 Data preparation and aggregation

Classification of the forest stand:

Plots were classified according to their proportion of poly- to monocormic pre-fire beech trees as: (i) stands evolved to high forests (< 33% polycormic trees), (ii) stands in the transition between former unevenly-aged coppices and high forests (33-66% polycorm trees), and (iii) unevenly-aged coppices (> 66% polycorm trees).

In order to describe temporal patterns of post-fire mortality, burns (including the control plots) were aggregated according to the time since the fire event. For this purpose, the study period was divided in five 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).

Classification of mature beeches:

Standing pre-fire beeches were grouped into four DBH-classes (8-12 cm, 12-24 cm, 24-36 cm, and ≥ 36 cm) following the guidelines of the "Sustainability and success monitoring in the protection forests of Switzerland (NaiS)" (Frehner et al., 2005). For all DBH-classes,

stem density (N ha^{-1}) and basal area ($\text{m}^2 \text{ ha}^{-1}$) were calculated separately for living trees and snags (standing dead trees), respectively. Volumes of dead standing beeches were calculated based on the equation used in the Italian National Forest Inventory (Tabacchi et al., 2011):

$$V = b_1 + b_2 \cdot DBH^2 \cdot h \quad (5.2)$$

Where,

$$b_1 = 8.1151 \cdot 10^{-1}$$

$$b_2 = 3.8965 \cdot 10^{-2}$$

h = height [m] DBH = diameter to breast height [cm] (V [dm^3], DBH [cm], h [m])

5.4.2 Regression analysis for beech mortality

Structure of the regression model

The risk of beech mortality was assessed using a mixed-logit model – a model type belonging to the generalized linear mixed-effects model family (GLMM) that clusters observations. Models were individual tree-based ($\text{DBH} \geq 8 \text{ cm}$), 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), fire season (SW) at site level; micro-topography (TOPO), slope (SLO), elevation (ELE), and aspect (ASP) at plot level; and tree size (DBH, HEIGHT), growth habit (POLY), and fungi fructification (FUNGI) at tree level (Table 5.2 on page 81). Values referring to the tree characteristics were recalculated to the year of fire. Therefore, average annual growth rates (Z'Graggen, 1992; Eidg. Anstalt für das forstliche Versuchswesen, 1983) were subtracted from DBH and HEIGHT for all years post-fire. Fungi infestation normally starts within the first three years post-fire (Conedera et al., 2007, 2010)

and was therefore regarded as an initial parameter. Contrary, proportions of bark damage and fire scar height 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 (Kahl, 2008).

All continuous risk factors were z-score² transformed to allow model comparisons (Wimmer & Dominick, 2010). The model relates 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, \dots, X_n) as follows:

$$\text{logit}(\Pi_{ijk}) = \beta_0 + \text{offset}(\log(JsF_{ik})) + \beta_1 \cdot X_{ij,1} + \dots + \beta_n \cdot X_{i,n} + y_i + \epsilon \quad (5.3)$$

Π_{ijk} is one if an individual beech tree is dead or zero if alive. The notation logit stands for the logistic link, which is the natural logarithm of the odds of Π ($\Pi = \frac{p}{1-p}$). The term β_0 represents the overall intercept, β_1, \dots, β_n are regression parameters for the corresponding variables (X_1, \dots, X_n), and y_i is the random effect. The random intercept (y_i) is assumed to be normally distributed with a mean of zero and a variance δ^2 . 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 clog-log as link function.

Assuming that factors driving beech mortality might alter their influence as function of burn severity (Ascoli et al., 2013), models were conducted separately for low (*low-model*: N 545), moderate (*moderate-model*: N 890) and high (*high-model*: N 696) burn severity. To validate the influence of fire on beech mortality, a separated model was conducted for the unburned forests (*control-model*: N 642). Data exploration followed the guidelines of Zuur et al. (2010), which suggest detecting the collinearity among variables based on the Pearson correlation and the variance inflation factor (VIF; further explanation see Zuur et al., 2010). After excluding HEIGHT

² $x' = \frac{x - \text{mean}(x)}{\text{sd}(x)}$

($r^2 > 0.8$ with DBH) from all models and TEMP ($r^2 > -0.7$ with PREC) from the low-model, all VIFs were below 3— indicating the absence of any critical collinearity (Table 5.2 on page 81). All continuous predictors were visualized and afterwards implemented in the models as linear and/or quadratic terms.

Mortality 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. Plots were not nested within burns since models were separately conducted for low-, moderate-, and high-severity plots. 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 & 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 & Schielzeth (2013).

Table 5.2: Explanatory variables used in (mixed effect) models of beech mortality (M), beech sapling height (hFAG), beech seedlings densities (sFAG), and beech saplings densities (SFAG). Predictors used (x) or not used (-) in models, or excluded (●) from a specific model (low: low-model, ●i: Piedmont) because of collinearity.]

Variable	Abbr.	Unit	M	hFAG	sFAG	SFAG
<i>Particularities of trees existed pre-fire</i>						
Growth form	POLY	0/1	x	-	-	-
Diameter to breast height	DBH	cm	x	-	-	-
Height	HEIGHT	m	●	-	-	-
Basal area	BASAL	m ² ha ⁻¹	-	x	x	x
Cover of fungi	FUNGI	none=0, few=1, partial=2, mass=3	x	-	-	-
<i>Particularities of tree regeneration</i>						
non-beech height	hREG	m	-	x	-	-
non-beech densities	dREG	stems ha ⁻¹	-	-	x	x
<i>Particularities of the 200 m²-plots</i>						
Slope	SLOPE	%	x	x	x	x
Aspect	ASP	m a.s.l.	x	x	x	x
Elevation	ELE	concave,	x	x	x	x
Micro-topography	TOPO	plane, con-	x	-	x	x
Brushwood	BW	vex	-	●p	x	x
Early post-fire colonizer	EARLY	m ³ ha ⁻¹	-	x	x	x
Shift in woody species	mCLIM	%	-	-	●i	●i
Distance to forest edge	EDGE	m	-	x	x	x

Variable	Abbr.	Unit	M	hFAG	sFAG	SFAG
Fire season	SW	0/1	x	—	—	—
<i>Particularities of the burns</i>						
Vegetation periods post-fire	AGE	years	—	•i	•	•
Burn size	AREA	small, medium, large	—	•i	•i	•i
Soil pH-value	pH		—	—	x	x
Burn severity	SEV	low, moder- ate, high	—	•ip	•ip	•ip
<i>Distance to seed source</i>						
Distance to mature beech	MOTHER	m				
<i>Climate variables</i>						
Temperature	TEMP	°C	•low	•i	•ip	•ip
Precipitation	PREC	mm	x	x	x	x

5.4.3 Data analysis of beech regeneration from seeds

Germination and survival of beech regeneration strongly depends on the soil water situation, which usually changes after gap creation (Madsen & Hahn, 2008; Bilek et al., 2009; Barna, 2011). In order to detect supposed differences in regeneration densities the data set was separated according to the annual mean precipitation into the drier bio-climatic region of Piedmont (annual precipitation < 1290 mm yr⁻¹) and in the wetter Insubric part (annual precipitation ≥ 1290 mm yr⁻¹; Oberdorfer, 1964; Table 5.1 on page 65). Additionally, individual models were performed for beech seedlings (sFAG) and saplings (SFAG) to evaluate the influence of explanatory variables during different development stages (listed in Table 5.2 on page 81). Only burns older than one and six years were considered for the seedlings and saplings models, respectively, in order to detect only the influence of fire. Additionally, beech stem height model models were performed using averaged beech saplings heights (hFAG) at plot-level as response variable. All models were run for both the full data set (N 208), the Insubric (N 144) and Piedmont (N 64) regions to prevent a levelling of regional specific environmental parameters.

For model selection, each data set was examined for intra-class correlation (Bliese, 2000). This resulted in general linear models (GLM) for tree height analysis (Equation 5.4), and GLMMs with burn location as random factor for regeneration analysis (Pinheiro et al., 2015).

$$Y_i = \beta_0 + \beta_{1i} \cdot X_{1i} + \dots + \beta_{ni} \cdot X_{ni} + \epsilon_i \quad \epsilon_i \sim N(0, \delta^2) \quad (5.4)$$

Y_i = Beech saplings height

$X_{1,\dots,n}$ = Explanatory variables

ϵ_i = Residuals

β_0 = Intercept

$\beta_{1,\dots,n}$ = Regression parameters (slope)

To meet the assumption of collinearity, predictors were chosen based on the VIFs as well as on their ecological relevance. Variables excluded were MOTHER ($r^2 = 0.72$ with EDGE), REG ($r^2 = 0.8$ with PREC), and burn severity (SEV) from all beech regeneration models (Table 5.2 on page 81). The latter was highly correlated with the basal area of survived pre-fire trees (BASAL) and with the cover of early post-fire colonizers (EARLY). For the regional specific models, TEMP ($r^2 = -0.7$ with AGE), and mCLIM ($r^2 = 0.77$ with pH, $r^2 = -0.56$ with EARLY) were excluded for Piedmont, and TEMP ($r^2 = -0.8$ with PREC) for Insubric models.

For GLMM performance, regeneration densities as response variables were transformed with the Box-Cox transformation in order to stabilize the variance (Fox & Weisberg, 2015), an often used and more general approach in ecological modelling (Krebs, 1999). Continuous explanatory variables were standardized to allow model comparison between models (Wimmer & Dominick, 2010). Both, regeneration and growth analyses were conducted by starting with variables of significant effects, and integrating additional variables and interactions (see details in section 5.4.2). For GLMM comparisons, the maximum likelihood (ML) and provided ANOVA tests were calculated. The best GLMM was finally run with restricted maximum likelihood (REML) to compute standard errors and p-values of predictors (Harville, 1977). 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 & Schielzeth (2013).

5.4.4 Model based analysis of the forest protective capacity against rockfall

The underlying principle of the Rockfor.net model

In order to evaluate the protective capacity against rockfall, there are various approaches by evaluating either topographical factors (empirical or statistical models; GIS-based models) or motions of falling rocks over slope surfaces (process-based models; see review in Dorren (2003) for more details). The present study uses the Rockfor.net model developed by Berger & Dorren (2007)– a model particularly sensitive to tree characteristics.

The Rockfor.net model was originally developed to quickly rate the protective capacity of different structured forests and has been often applied in the European Alps (Berger & Dorren, 2007; Wehrli et al., 2006; Kajdiž et al., 2015).

The underlying idea of the model is to compare the theoretical basal area required for absorbing the kinetic energy of downhill moving rocks ($G_{required}$) and the available basal area of a particular forest stand ($G_{available}$). Therefore, the model regards all standing trees distributed in a forest as a virtual tree lines parallel to the contour lines (Figure 5.6). All trees have the same species composition and diameters (weighting of the tree species see Dorren & Berger, 2005), representing the mean values in the original forest stand. The model starts by calculating the total kinetic energy developed by a rock falling down the slope. Then it calculates the energy dissipative capacity of each tree line. The number of trees required to dissipate all kinetic energy are subsequently converted in a required basal area ($G_{required}$) using the mean DBH. In the last step the Rockfor.net model quantifies the protective effect of a forest stand by comparing the required theoretical $G_{required}$ with the available $G_{available}$ (see Berger & Dorren, 2007 for more details).

The contribution of logs was considered also in the Rockfor.net

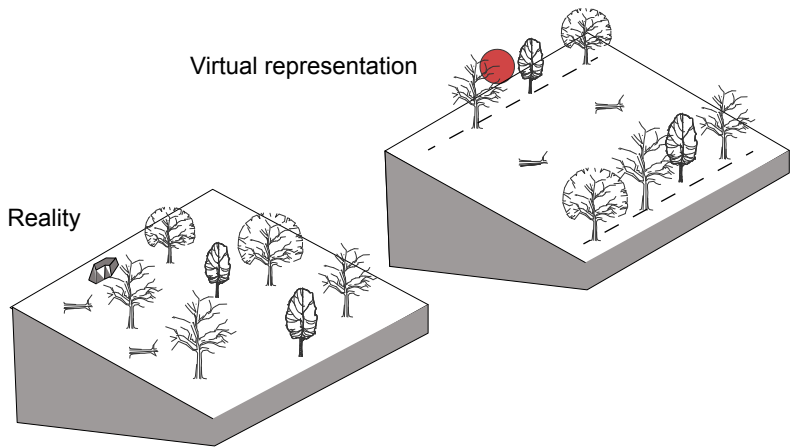


Figure 5.6: Schematic illustration of a burned beech forests on the lefthand side of the figure– showing different tree species, alive, dead or fallen logs. All standing trees and fallen logs distributed in the forest are converted as virtual tree lines parallel to the contour lines in the Rockfor.net model (righthand side of the figure).

model, assuming that their capacity of absorbing kinetic energy is proportional to the ratio between log-diameter and rock size. Olmedo-Manich (2015) demonstrated that deposited tree logs with rock/log diameter ratios between 0.8 and 1.55 favour optimal energy loss. In this study it has been assumed that energy dissipation efficiency is linearly related to the rock/log diameter ratio. The amount of lying logs was estimated in terms of volume (in $\text{m}^3 \text{ha}^{-1}$) in the field. In the Rockfor.net model, this volume was converted into a total log length per hectare and finally into the number of potential logs impacts per hectare (Equation 5.5 was developed by Luuk Dorren). Here it has been assumed that an efficient rock-log contact, meaning with a rock/log diameter ratio of 1 or smaller, is required every 10 m on a slope length of 100 m to stop 100% of the rocks by logs. The following equation was used to calculate the percentage of rocks stopped by logs ($\%R_{stopped}$):

$$R_{stopped} = Eff_{contact} \cdot Vol_{log} \cdot \frac{1}{\pi \cdot (D_t/2)^2} \cdot \frac{1}{100m} \cdot \frac{1}{10} \cdot 100\% \quad (5.5)$$

Where,

$Eff_{contact}$ = rock-log contact efficiency = $\min[1, D_t/ D_b]$

D_t = tree diameter to breast height (in m)

D_b = rock diameter (in m)

Vol_{Log} = volume of lying logs (in $\text{m}^3 \text{ha}^{-1}$)

The contribution of lying branches and brushwood to rockfall energy dissipation is hard to quantify in a model such as the Rockfor.net and was therefore neglected. Temporal changes of their volumes were only graphically visualized. In sum, the Rockfor.net model requires as input parameters both site and forest stand characteristics. Required site characteristics are cliff height (m), length of both the forested and unforested slope on the trajectory of a fallen rock, and mean slope inclination ($^\circ$). Species composition, DBHs and densities of standing trees (including snags) as well as diameter and length of the logs (wood decomposition rate below four) are required

as stand characteristics (see Figure 5.7 on page 88).

Input data preparation and scenario specification

Tree diameters were grouped in four DBH-classes (see section 5.4.1 on page 76) separately for living and dead standing trees and standardized to number of stems per hectare. Large diametered trees are most effectively dissipate the kinetic energy of falling rocks, especially large rocks. On the other hand, small trees significantly increase the probability of rock—tree contacts due to the (generally) large stem densities. Therefore, the required basal area ($G_{required}$) to stop a falling rock within a specific forested slope is weighted for the DBH-classes according to the rock size (Dorren et al., 2015). Moreover, to account for the differences in capacity of different tree types to dissipate the kinetic energy of falling rocks, Rockfor.net converted the proportions of the presence of five different tree "types" in each stand into a mean energy dissipative capacity per study site. The following five tree "types" were taken into account: beech, Norway spruce (*Picea abies* [L.] Karst.), silver fir (*Abies alba* Mill.), other broadleaves, and other conifers (Dorren & Berger, 2005).

Further, standardized rock sizes, mean slope gradients, cliff heights and lengths of forested slopes were used in the process of calculating the protective capacity. Standard rock volumes were defined as 0.05 m³, 0.2 m³, and 1 m³, which corresponds to the rock diameters 0.37 m, 0.58 m and 1 m (Figure 5.7 on page 88) as traditionally used in NaiS (Frehner et al., 2005; Dorren et al., 2015). In order to simulate realistic field conditions, two options of horizontal distances (75 m, 150 m) have been defined in which a rock had to be stopped from the bottom of a cliff to the downslope forest edge. Finally, three different slope gradients were considered representing the 1st (27°) and 3rd quantile (35°), as well as at the mean (30°) of the slope distribution from the surveyed plots (Figure 5.7). Slope inclination was standardized after testing the statistical non-significance between tree stem densities and slopes using a mixed effect model (see Appendix A on page 161).

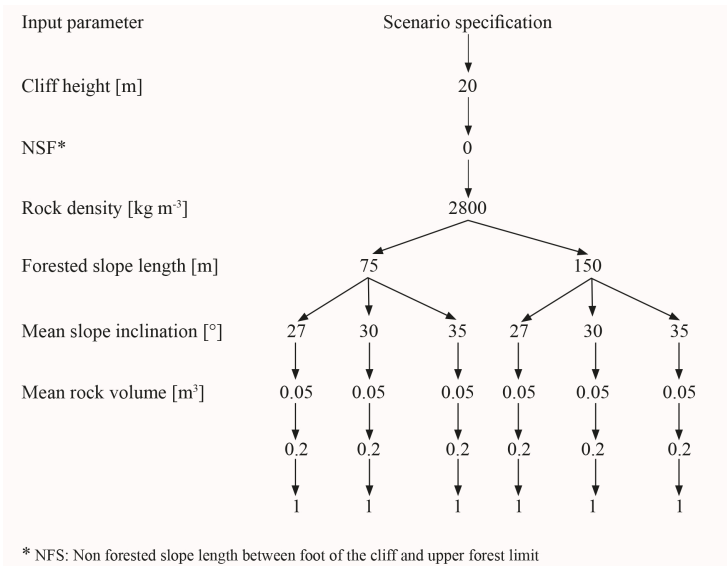


Figure 5.7: Scenario specification for the Rockfor.net model

The estimation of the protective effect as calculated by Rockfor.net represents the probability of a rock to be stopped in the stand, which is expressed in the following categories: $\geq 90\%$ very good protection, 75 - 90% good protection, 50 - 75% adequate protection, 25 - 50% moderate protection, and $< 25\%$ inadequate protection. Whether or not the level of protection provided by a forest stand is sufficient, can only be determined by means of a risk analysis in which the effective risk reduction of the forest is quantified. This is out of the scope of the present study.

Analysis of the simulated results

The protective effectiveness provided by the different scenarios was aggregated for standing trees and for logs at the plot-level, while paying attention to not exceeding the 100% mark. The results were

visualized using standard loess (local regression)-smoothing curves (Chambers & Hastie, 1992) separately for low-, moderate- and high-severity burns with the corresponding unburned forests serving as control. The loess-smoothing curve is a flexible tool making it easy to model complex processes, but it is not feasible to present and to interpret an easy regression function. Therefore, significant temporal trends in those smoothing curves were detected by employing linear regression models with protective effectiveness as response variable and years post-fire as explanatory variable. Since the protective effectiveness is expressed as percentage (probability), the data was transformed³ and years post-fire were included as both the linear and quadratic term. Additionally, Mann-Whitney-Wilcoxon tests were applied for detecting significant differences in distributions of the forest protective effect in different burn severity sites and the corresponding unburned forests separately for each scenario.

5.4.5 Statistical software and packages

All analyses of the simulation results and the statistical models were performed using R, the free software environment for statistical computing (R Development Core Team, 2014). Negative binomial logistic regression models for assessing correlations between stem density and slope inclination were fitted and validated using the `glmADMB` package (Bolker et al., 2013). Logistic regression models for assessing risk factors for beech mortality were fitted and validated using the `lme4` (Pinheiro et al., 2015) and `VGAM` (Yee et al., 2015) package. Regeneration models were conducted using the `nlme` package (Pinheiro et al., 2015). Graphical outputs are mainly based on packages `lattice` (Deepayan, 2008), `ggplot2` (Wickham & Chang, 2015), and maps are visualized with `map`- and GIS tools (Brownrigg, 2015; Brunsdon & Chen, 2015).

³

$$y' = \frac{y}{1 - y} \tag{5.6}$$

Chapter 6

Results

6.1 Site and forests characteristics

Between July 2012 and September 2013, a total of 234 plots were assessed in the burned and 39 in the adjacent unburned beech forests. The elevations of the burns ranged between 700 and 1486 m a.s.l. with mean slope inclinations of $30 \pm 0.34^\circ$. Most (70%) of the burns were exposed to the east ($45\text{--}135^\circ$) and west ($215\text{--}320^\circ$), followed by the south with 21.5%. Rarely (8.2%), burns were located on north-facing slopes. Here, mostly (50%) low severe fires occurred while moderate (40%) and high (45%) severe fires burned predominantly on south-facing slopes. The microrelief of the burns were mostly plane (46%) followed by small depressions (31%), and convex (23%) surfaces. The average coverage of rocks in a burned plot was 2%, ranging from zero to maximum 30%.

Based on the growth habit of beech, the majority (61%) of the burned forests were classified as high stand forests, a minority (16%) as unevenly-aged coppices, with the remainder within the transition phase. From the overall number of plots pre-fire existing beeches dominated in terms of stem densities in the burned (88%) and un-

burned (93%) forests, and were rarely interspersed by other tree species (< 4%; Table 6.1 on page 93). Their overall average tree height (considering $\text{DBH} \geq 8$ cm) was 10.3 ± 0.11 m, and approximately 2 m higher when referring to living trees only.

Table 6.1: Distribution of pre-fire existing tree species in the burned and unburned 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 ($\sum N$) is expressed in the proportion of mortality (Mort. [%]). Species proportion (Spec. [%]) indicates the proportion of particular species out of the total number of trees.

Species	burned forests		Unburned forests	
	$\sum N$	Mort. Spec.	$\sum N$	Mort. Spec.
Target species				
<i>Fagus sylvatica</i> L.	2845	53 88	887	13 93
Pioneers with wind-dispersal seeds				
<i>Betula pendula</i> Roth	129	44 4	20	30 2
<i>Larix decidua</i> Mill.	66	62 2	14	36 1
<i>Sorbus aria</i> (L.) Crantz	16	69 1	5	0 <1
<i>Alnus glutinosa</i> (L.) Gaertn.	4	75 <1	0	100 0
<i>Coryllus avellana</i> L.	1	0 <1	0	100 0
<i>Populus tremula</i> L.	1	0 <1	0	100 0
<i>Sorbus aucuparia</i> L.	1	0 <1	0	0 0
<i>Laburnum alpinum</i> Fabr.	0	0 0	14	64 1
Trees with gravity- / animal-dispersal seeds				
<i>Castanea sativa</i> Mill.	57	70 2	11	9 1
<i>Quercus petraea</i> (Matuschka)	30	40 1	2	0 <1
<i>Fraxinus excelsior</i> L.	6	33 <1	0	100 0
<i>Picea abies</i> (L.) H.Karst	6	0 <1	0	100 0
<i>Pinus sylvestris</i> L.	3	0 <1	0	100 0
<i>Prunus avium</i> L.	2	0 <1	4	75 <1
<i>Taxus baccata</i> L.	2	0 <1	0	100 0
<i>Acer pseudoplatanus</i> L.	1	0 <1	1	0 <1
<i>Quercus pubescens</i> Willd.	1	100 <1	0	0 0

6.1.1 Temporal trends in post-fire beech mortality

Half of the beech trees ($N_{total} = 2,845$) assessed in the burned plots died, whereas only 10% of the trees in the unburned forests were dead (Table 6.1 on page 93). Both—standing and lying dead beeches—reached average volumes of $38 \pm 4 \text{ m}^3 \text{ ha}^{-1}$, whereas logs accounted for only 10%. The number of standing dead trees was ten times higher than logs in the first two decades post-fire. During this period their wood was only slightly decomposed (decay stages < 3 : standing dead= 80%, logs= 54%). With progressing time since fire, the proportion of intermediate (stage 3) and advanced (stage 4) 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). Also the numbers of standing dead trees and logs decreased by approximately 80% from the second decade post-fire on (Figure 6.1).

The average basal area of standing dead beech trees reached values of $14.1 \pm 0.95 \text{ m}^2 \text{ ha}^{-1}$, ranging from $1.9 \text{ m}^2 \text{ ha}^{-1}$ to $37.6 \text{ m}^2 \text{ ha}^{-1}$ depending on the years since fire (Figure 6.2). Among fire severity classes, absolute basal area values varied greatly, and mortality showed different temporal patterns. Mortality of trees in low-severity burns were quite similar to that in the unburned forests, while tree mortality increased with burn severity and peaked 10 to 15 years post-fire. The highest overall loss of basal area (up to 85% of the initial value) occurred in high-severity burns, followed by moderate-severity burns (up to 63%).

The mortality process of fire-injured beech trees was considered more in detail, since foresters need to know which tree sizes mostly suffer from a forest fire. Using the unburned forests as a reference (Figure 6.3 D), the odds of beech mortality was 42, 5, and 2.3 times greater in high-, moderate-, and low-severity burns, respectively. Within the burn severity classes, the extent and timing of beech mortality varied as a function of tree diameter. In low-severity sites (Figure 6.3 C), tree mortality was usually limited

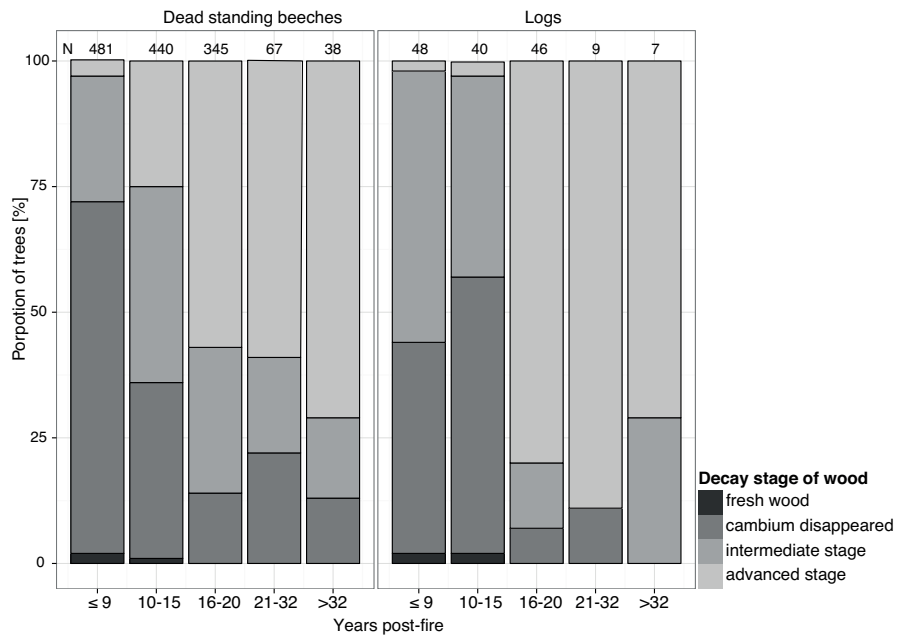


Figure 6.1: Decay stages of wood for standing dead trees and logs as a function of years post-fire.

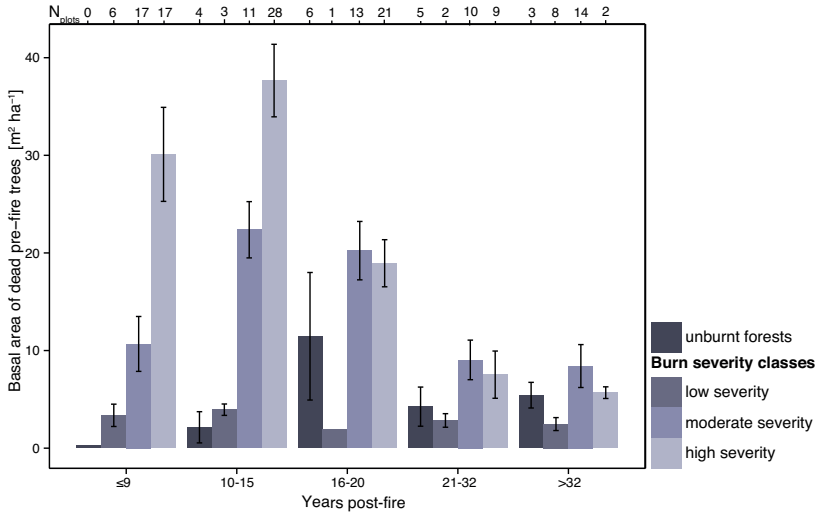


Figure 6.2: Mean (\pm SE) basal area of dead standing fire-injured beeches in low-, moderate-, and high-severity burns, and the corresponding unburned plots as a function of years post-fire.

to small-diameter (DBH <12 cm) beeches, whereas in moderate-severity burns, intermediate-sized (DBH 12-36 cm) trees were also affected (Figure 6.3 B).

Beech mortality was high and affected all tree sizes in high-severity burns, 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 6.3 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. Similar patterns were observed in low-severity burns, where the odds of

death for small-diameter trees were generally higher than for large-diameter trees. In these burns, the probability of a large-diameter individual dying was near zero, whereas that of intermediate-diameter trees ranged between 0.03 and 0.56.

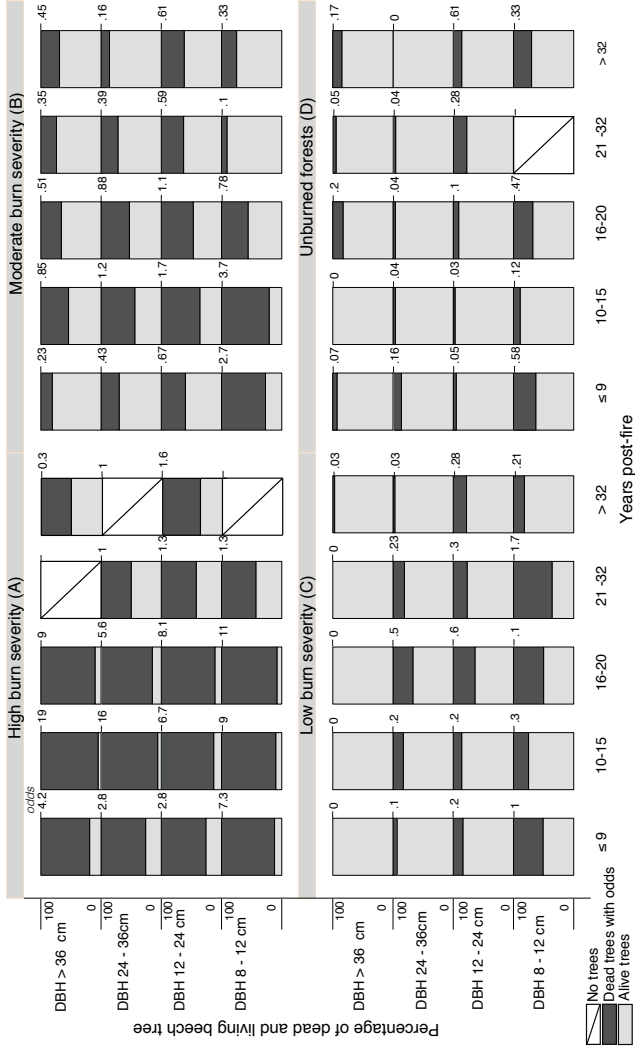


Figure 6.3: Percentage of survived (light grey) and dead (dark grey) beeches for small (DBH < 12 cm), intermediate-sized (DBH = 12 – 24 cm), large (DBH = 24 – 36 cm), and very large (DBH > 36 cm) individuals, separated for different burn severities and years post-fire. The odds of mortality are also shown to the right of each column.

6.1.2 Drivers of beech mortality

The best models of beech mortality clearly described the mortality rate for fire-injured beech, with fungi fruitbodies (FUNGI), diameter to breast height (DBH), and elevation (ELE) as common factors (Table 6.2 on page 101). FUNGI had a positive and significant ($p \leq 0.001$) 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 more than twice that of the low-model (Appendix B).

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 in low-severity burns was three times higher than for a moderate-severity event; no detectable correlation existed between mortality and DBH in the high-model. The linear and quadratic term of DBH was correlated with beech mortality in the control-model, indicating increasing mortality for small- and large-diameter beech trees (Appendix B). Polycormic growth habit (POLY), as an other morphological characteristic, reduced the mortality risk factor in moderate- and high-models, but not in the low-model and control model.

In addition to tree characteristics, several site factors correlated with beech mortality. The linear and quadratic terms of elevation (ELE) were significantly 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 6.2).

Table 6.2: 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	
	<i>Low-model</i>	<i>Moderate-model</i>	<i>High-model</i>	<i>Control</i>
<i>Fixed term</i>				
Intercept	0.14***	1.9***	94***	50.02***
Fungi	3.4***[1.7-6.5]	7.2***[5.4-9.6]	6.8***[3.5-12.9]	ns
Diameter to breast height	0.3***[0.2-0.4]	0.8***[0.6-0.9]	ns	0.07***[0.02-0.18]
Diameter to breast height ²	ns	ns	ns	2***[1.6-2.8]
Polycorm habit	ns	0.6***[0.4-0.8]	0.5[0.3-0.9]	ns
Elevation	3.6**[1.5-7.6]	ns	0.5*[0.4-1.2]	ns
Elevation ²	3.9**[1.5-9.3]	1.2*[0.7-1.2]	ns	ns
Temperature ²	ns	0.8*[0.7-0.9]	0.6**[0.4-0.8]	ns
Precipitation	ns	1.8***[1.3-2.5]	ns	ns
Precipitation ²	1.6*[1.1-2.5]	ns	ns	ns
Aspect	ns	ns	1.7*[1-2.9]	3.1*[1.3-12.4]
<i>Random term</i>	<i>Var(x)/SD/</i>	<i>Var(x)/SD/</i>	<i>Var(x)/SD/</i>	<i>Var(x)/SD/</i>
Plot	1.7[1.3]	0.5[0.6]	1.1[1]	2.6[1.6]
R ² _{fixed effects}	38%	23%	17%	47%

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

odds-ratio <1 negative relationship, odds-ratio >1 positive relationship.

6.2 Post-fire tree regeneration

6.2.1 Germination of beech seeds

At the same time as fire-injured beeches die and collapse to the forest floor, new tree regeneration emerge in the burned sites. Beech seeds germination started soon after the forest fires regardless of the burn severity. Out of the 1717 dendrochronological samples, 42.9% belonged to the moderate-severity burns, followed by 40.4% to the moderate and 13.5% to the low-severity burns. The minority (3.2%) of dendrochronological samples was taken in the unburned forests.

The ratio between seed germination in a particular year to the overall number of germinations differed between the unburned and burned beech forests. After high severe fires 88.5% of the beech seeds germinated within the first 15 years post-fire with a peak by around 10 years post-fire (Figure 6.4). Hereafter, germination rates decreased from 18 to 32 years post-fire. Most (85%) of the beech seeds in moderate-severity burns germinated within the first 20 years post-fire, whereas germination was less and infrequently afterwards. After fires of low burn severity— as visualized by the yellow bars in Figure 6.4 — seed germinated up to 30 years post-fire without a clear temporal tendency. In the unburned forests, beech germination frequency varied within the years and was missing in more than half of the years in the observation period.

6.2.2 Temporal development of tree regeneration

A total of 32 woody species regenerated in the burned forests, of which 11 were also present in the unburned forests (Table 6.3 on page 107). Out of these species, 32% showed pronounced pioneer traits, with densities ranging from below 1 stems ha^{-1} up to 4,380 stems ha^{-1} in the burned beech forests. None were found in the unburned beech forests (Table 6.3 on page 107).

In both the burned and unburned forests beech dominated in terms of densities and frequency. It regenerated in all burns, but

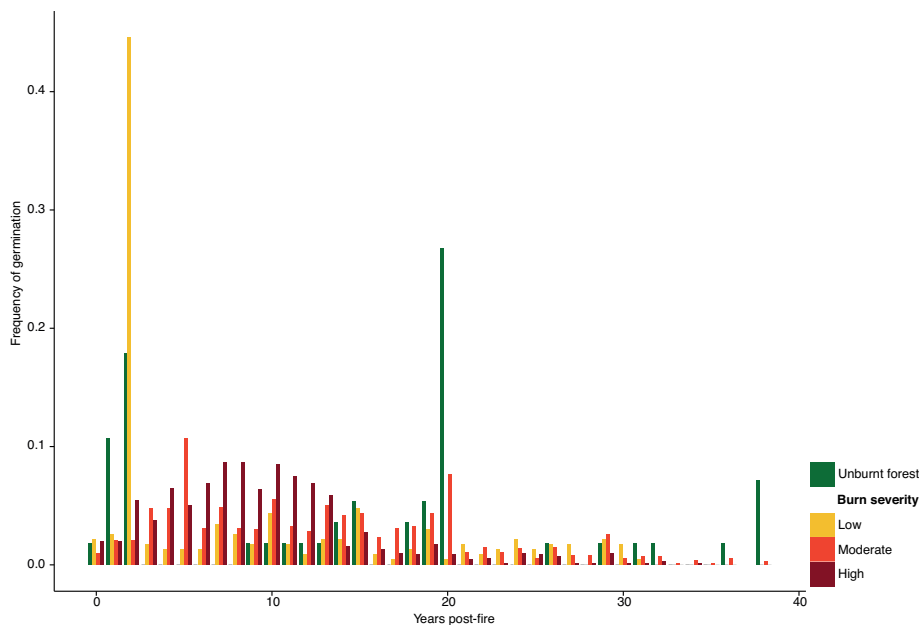


Figure 6.4: Germination rate of beech seeds based on the overall numbers of germination counted in the burned forests grouped by low, moderate, high burn severity. Germination frequency in the corresponding unburned forests is shown in the left part of the figure.

was absent in 9% of the burned plots (Table 6.3 on page 107). Half of the plots without beech regeneration had burned just in the winter prior to the field assessment. Beech regeneration densities in these plots were generally low (50–350 stems ha⁻¹). The remaining plots with no beech regeneration had been burned more than 10 years ago, and plot displayed dense covers of early post-fire colonizers such as common bracken, common broom, and purple moor grass.

However, beech seedlings and sapling reached average densities of 7381 ± 980 stems ha⁻¹ and 9055 ± 1642 stems ha⁻¹, respectively (Table 6.3). Nearly all of the beech regeneration was alive. The average damage rate of beech saplings was 5.6%, which was lower than for other woody species (Table 6.3). Pioneer birch (*Betula pendula* ROTH) was the only tree species also grow abundantly. It was found in 60% of the plots investigated with an average saplings density of $2,331 \pm 365$ stems ha⁻¹. This is to one-third of the density of beech.

For seedlings, high densities were recorded for Scotch laburnum (*Laburnum alpinum* J.PRESL, mean 4380 stems ha⁻¹) and ash (*Fraxinus excelsior* L., mean 3127 stems ha⁻¹). In three burns with mostly high burn severity, a number of invasive alien plants with pioneer character were found, including empress tree (*Paulownia tomentosa* (THUNB.) STEUD.), tree of heaven (*Ailanthus altissima* (MILL.) SWINGLE), and black locust (*Robinia pseudoacacia* L.).

Table 6.3: Regeneration densities of woody species in the burned (B) and unburned (UB) beech forests with percentage of living regeneration and the proportion of damage. Frequency of species presence [%] in the plots [N 234] and the presence of mother-trees (M) indicated by ● are noted for the burned forests. Species names see Appendix G

Species	Site	Seedlings Ø	SE	Alive %	Saplings Ø	SE	Alive %	Damage %	Plots %	M
Target species										
<i>Fagus sylvatica</i>	B	7381	980	100	9055	1642	97	5	91	●
	UB	2852	922	98	281	119	83	13	92	—
Pioneers with wind-dispersal seeds										
<i>Betula pendula</i>	B	378	69	100	2454	365	95	<5	60	●
	UB	0	0	0	0	0	0	0	0	—
<i>Populus tremula</i>	B	149	138	100	183	143	100	<5	1	●
	UB	0	0	0	0	0	0	0	0	—
<i>Laburnum alpinum</i>	B	4380	1930	100	192	77	92	<5	9	—
	UB	0	0	0	0	0	0	0	0	—
<i>Salix caprea</i>	B	82	23	100	144	41	98	10	22	—
	UB	0	0	0	0	0	0	0	0	—
<i>Coryllus avellana</i>	U	9	3	100	65	25	95	6	7	●
	UB	0	0	0	0	0	0	0	0	—
<i>Alnus glutinosa</i>	U	<1	<1	100	4	4	83	0	<1	●
	UB	0	0	0	0	0	0	0	0	—
<i>Ailanthus altissima</i>	U	<1	<1	100	2.3	2.3	100	0	<1	—
	UB	0	0	0	0	0	0	0	0	—
<i>Populus nigra</i>	U	<1	<1	100	<1	<1	100	0	1	—
	UB	0	0	0	0	0	0	0	0	—
<i>Paulownia tomentosa</i>	U	0	0	100	<1	<1	100	0	<1	—
	UB	0	0	0	0	0	0	0	0	—
<i>Populus alba</i>	B	<1	<1	100	0	0	0	0	<1	—
	UB	0	0	0	0	0	0	0	0	—

Species	Site	Seedlings Ø	Seedlings SE	Alive %	Alive Ø	Saplings SE	Alive %	Damage %	Plots %	M
<i>Robinia pseudoacacia</i>	UB	0	0	0	0	0	0	0	0	-
	B	<1	<1	100	0	0	0	0	<1	-
	UB	0	0	0	0	0	0	0	0	-
Other tree species with wind- and animal dispersal seeds										
<i>Sorbus aucuparia</i>	B	194	66	100	314	170	95	5	25	•
	UB	185	165	100	35	33	100	30	8.1	-
	B	80	18	10	234	98	99	4	25	•
<i>Sorbus aria</i>	UB	7	7	100	1	1	100	4	5.4	-
	B	3127	900	100	451	270	100	5	27	•
<i>Fraaxinus excelsior</i>	UB	346	150	100	5	5	100	5	21.6	-
<i>Acer opulifolium</i>	B	119	119	100	55	46	100	0	1	-
<i>Castanea sativa</i>	B	60	15	100	61	15	89	10	24	•
	UB	27	17	100	5	5	100	39	13.5	-
<i>Acer pseudoplatanus</i>	B	1131	603	100	270	234	100	2	17	•
	UB	59	44	100	0	0	0	0	8.1	-
<i>Prunus avium</i>	U	70	21	100	36	22	99	13	14	•
	B	8	5	100	0	0	0	0	8.1	-
<i>Frangulus alnus</i>	B	8	8	100	12	9	100	0	<1	-
	UB	0	0	0	0	0	0	0	0	-
<i>Quercus petraea</i>	B	35	11	100	11	5	100	15	11	•
	UB	3	3	100	0	0	0	2.7	•	-
<i>Larix decidua</i>	B	27	12	100	11	4	100	6	7	•
	UB	0	0	0	0	0	0	0	0	-
<i>Picea abies</i>	B	7	5	100	10	5	100	0	0	-
	UB	<1	<1	100	0	0	0	0	3	•
<i>Pinus sylvestris</i>	B	<1	<1	100	2	2	100	50	0	-
	UB	0	0	0	0	0	0	0	1	•
<i>Ilex aquifolium</i>	U	4	2	100	3	2	100	2	2	-
	UB	2	2	100	1	1	100	0	0	-

Species	Site	Seedlings Ø	Seedlings SE	Alive %	Ø	Saplings SE	Alive %	Damage %	Plots %	M
<i>Pinus strobus</i>	B	<1	<1	100	2	3	100	0	1	-
	UB	0	0	0	0	0	0	0	0	-
<i>Juglans regia</i>	B	0	0	0	2	2	100	0	<1	-
	UB	0	0	0	0	0	0	0	0	-
<i>Acer campestre</i>	B	3	4	100	1	0	100	0	1	-
	UB	0	0	0	0	0	0	0	0	-
<i>Tilia cordata</i>	B	0	0	0	1	0	100	0	<1	-
	UB	0	0	0	0	0	0	0	0	-
<i>Quercus pubescens</i>	B	9	7	100	0	0	0	0	0	•
	UB	0	0	0	0	0	0	0	0	-
<i>Taxus baccata</i>	B	1	0	100	0	0	0	0	1	•
	UB	0	0	0	0	0	0	0	2.7	-
<i>Acer platanoides</i>	B	<1	<1	100	0	0	0	0	1	-
	UB	0	0	0	0	0	0	0	0	0

6.2.3 Changes in tree regeneration in mixed-severity burns

Average beech seedlings densities were $\sim 10,000$ stems ha^{-1} in low and moderate-severity burns, which was more than double that in high-severity burns (Figure 6.5 on page 110). The highest beech seedling densities were mostly recorded in the first post-fire decades, but they declined with time since fire (Figure 6.5). In early post-fire stages, beech seedlings often co-occurred with regeneration of pioneer and other tree species in high and low-severity burns, respectively.

Beech sapling were most dense in moderate-severity burns (Figure 6.5 middle), where they reached densities ranging between 20,000 stems ha^{-1} (10–15 years post-fire) and 13,000 stems ha^{-1} (> 32 years post-fire). These densities were more than double those found in low and high-severity burns (Figure 6.5 middle). In moderate and high-severity burns, beech regeneration often co-occurred within the first post-fire decades with pioneer saplings. After 20 years post-fire, pioneer densities dropped to below 1000 stems ha^{-1} , whereas beech sapling densities ranged between 4000 and 11,000 stems ha^{-1} .

Both saplings of beech and pioneers increased rapidly in height, with pioneers clear taking the lead during the first post-fire decades (Figure 6.6 middle). However, beech saplings also grew fast and were 32 years post-fire nearly as high as the pioneers. Beech saplings were taller in high-severity burns (mean height 6.3 ± 0.23 m) than in moderate (mean height ~ 4 m), and in low-severity burns (mean height ~ 2 m). Considering all burns, pioneers increased faster in DBH than beech saplings (Figure 6.6 bottom). They reached average DBHs of 3.3 ± 0.02 cm at 16–20 years post-fire, which corresponds to a growth rate of 1 cm per post-fire age unit. In burns of the same age, DBH of beech regeneration amounted to only 30–50% of the pioneer DBH.

In the unburned forests, the densities of the beech regeneration were lower than in the burned forests, except for the post-fire age classes older than 20 years. The low number of seedlings in the

unburned forest contributed to the low sapling densities, which were only 10–20% of the densities in the burned sites. The saplings in the unburned forest and in the low-severity burns were around 2 m (Figure 6.6).

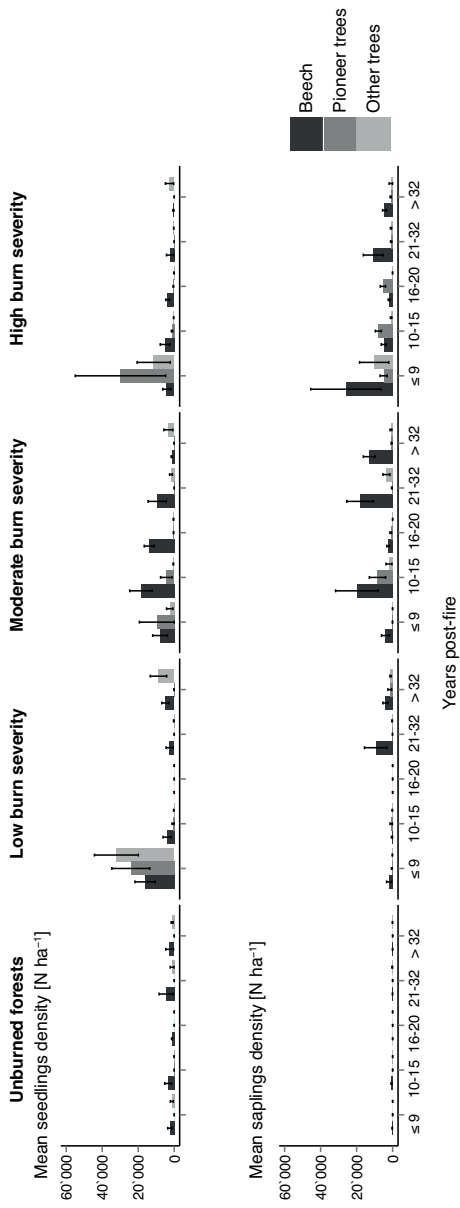


Figure 6.5: Mean (\pm SE) seedlings and saplings densities of beech, pioneer and other tree species grouped by years post-fire and burn severity with the corresponding unburned forests.

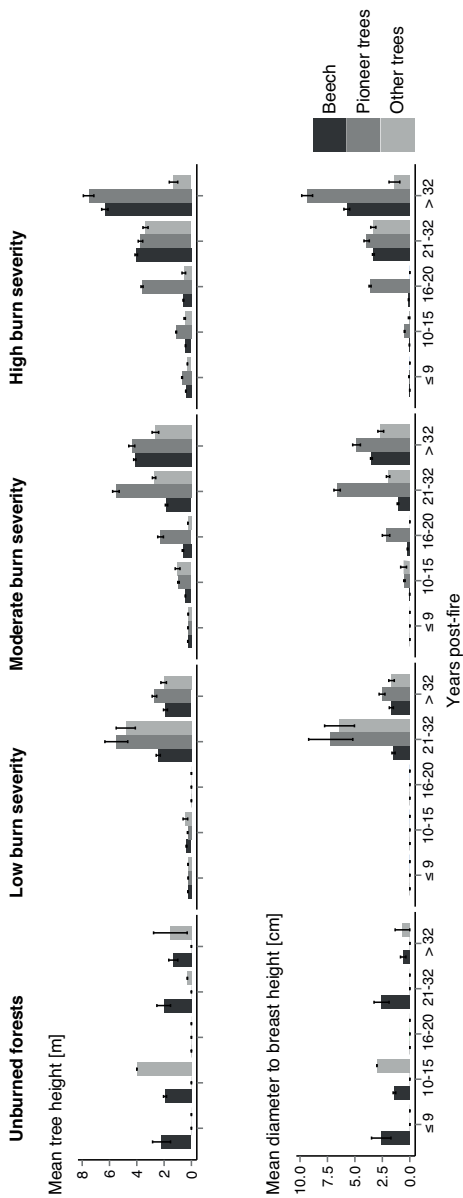


Figure 6.6: Mean (\pm SE) seedlings and saplings heights and diameter to breast height of beech, pioneer and other tree species grouped by years post-fire and burn severity with the corresponding unburned forests.

6.2.4 Drivers of post-fire beech regeneration

Seedlings generally grew denser in the presence of the surviving beeches (BASAL), while their densities were mainly restricted by dense covers of early post-fire colonizers (EARLY; Table 6.4 on page 115). Apart from BASAL and EARLY, beech seedlings' responses to fires differed in some variables in the two regions. In the wetter Insubric region, seedling densities were higher on slopes with North-to East-facing aspect (ASP), on younger burns (AGE), and on sites close to the unburned beech forests (EDGE). The listed variables together explained 64% of the variation (R^2) in the beech seedling density in the Insubric region. The beech seedling densities in the drier Piedmont were correlated to the quadratic factor of soil pH, and to the linear (negatively) and quadratic (positively) factor of elevation (ELE), indicating a peak of beech seedling densities at intermediate elevations. The overall model for Piedmont explained 55% of the variation in seedling density.

The cover of the early post-fire colonizers (EARLY) and the basal area of the surviving beeches (BASAL) not only significantly influenced the seedling models but also the overall beech sapling densities. Sapling densities were unlike the seedlings negatively correlated with basal areas (higher under less dense canopy cover), but like the seedlings also saplings were negatively correlated with the early post-fire colonizers. Moreover, they were positively correlated with the volume of coarse woody debris (higher with more CWD). In the burned sites in the Insubric region, the sapling densities were positively correlated with the post-fire age and elevation. The five variables (BASAL, EARLY, AGE, ELE, CWD) together explained 32% of the variation in sapling density. In the Piedmont region, sapling densities were negatively correlated with aspect (ASP), as well as with BASAL, EARLY, and CWD. The best model explained 63% of the variation in the stem density of saplings (Table 6.4 on page 115).

The growth in height of beech saplings was generally correlated with the height of non-beech saplings (Table 6.5 on page 116). In the

Insubric, beech height was also significantly correlated with post-fire age, with taller trees in older burned beech forests, but negatively correlated with the basal area of the surviving beeches as trees were taller under less dense canopy cover. The best Insubric model explained 72% of the variance (D^2) in beech saplings height. In Piedmont, beech sapling heights were additionally positively correlated with elevation (ELE) and the distance from the burned area's edge (EDGE; taller with increasing distance). In contrast, soil pH and the quadratic term of early post-fire colonizers (EARLY) showed slightly negative correlations. The overall sapling growth model for Piedmont had an explanatory power of 70%.

Table 6.4: Estimates (β) and standard error (SE(β)) of best mixed-effect models for beech seedling and sapling regeneration, using all data pooled together (Full), and separately for the regions Piedmont and Insubric. Intercept (I) and residuals (Res) of the Standard Deviation are given for the random effect.

Variables	Seedlings-models					
	Full 54%	Piedmont 55%	Insubric 64%			
R^2	β	SE	β	SE		
<i>Fixed effects</i>						
Intercept	12.7***	1.1	11.2***	1.7	18.9***	1.7
Basal area	2.1***	.5	2.8***	.9	3.3**	.9
Basal area ²	ns	ns	-1.4*	.6	ns	ns
Colonizer ²	-2.0***	.4	-1.2●	.6	-2.9***	.8
Vegetation periods post-fire	-3.1***	.7	ns	ns	-6.5**	1.5
Aspect	ns	ns	ns	ns	-2.3**	.8
Distance to forest edge	ns	ns	ns	ns	1.3**	.8
Elevation	ns	ns	-0.8***	1.1	ns	ns
Elevation ²	ns	ns	0.3***	.8	ns	ns
Soil pH-value ²	ns	ns	6.1**	1.1	ns	ns
Precipitation	2.1	.9	ns	ns	ns	ns
Precipitation ²	1.6*	.7	ns	ns	ns	ns
<i>Interaction terms</i>						
Years post-fire:	ns	ns	ns	ns	1.9**	.7
Early post-fire colonizer						
<i>Random effects</i>						
Plot	I	Res	I	Res	I	Res
	2.7	5.6	5.4	6.4	5.8	6.9

Variables	Saplings-models					
	Full 47%		Piedmont 63%		Insubric 32%	
	β	SE	β	SE	β	SE
<i>Fixed effects</i>						
Intercept	18.4***	1.4	19.8***	2.6	13.9***	.9
Basal area	-2.3***	.6	-2.5*	1.1	-1.3*	.5
Colonizer ²	-2.1**	.5	-2.9***	.7	-1.0	.5
Vegetation periods post-fire	3.5*	1.1	ns	ns	3.2**	.7
Aspect	-1.1*	.7	-3.1***	1.1	ns	ns
Distance to forest edge	.8*	.6	ns	ns	ns	ns
Elevation	ns	ns	ns	ns	-1.9*	.7
Brushwood	2.3***	.7	7.8**	2.1	1.1*	.7
Brushwood ²	ns	ns	-1.6**	.6	ns	ns
Micro-topography(2)	2.3*	1.3	ns	ns	.7	1.1
Micro-topography(3)	4.3*	1.5	ns	ns	3.4	1.4
Slope ²	-0.7*	.4	ns	ns	ns	ns
<i>Random effects</i>						
Plot	I	Res	I	Res	I	Res
	4.6	7.1	5.6	6.6	1.5	5.1

• Significance level ≤ 0.1 ; * ≤ 0.05 ; ** ≤ 0.01 ; *** ≤ 0.001 ; : interactions
Colonizers= Early post-fire colonizer

Table 6.5: Results of the generalized linear model of beech sapling height using all data pooled together (Full), or separately for the regions Piedmont and Insubric.

Variables	Full	Piedmont	Insubric
\emptyset height [m]	2.27	0.94	1.80
D ²	78%	70%	72%
Intercept	4.5***	4.3***	4.4***
Non-beech height	0.7***	0.6***	0.4**
Vegetation periods post-fire	0.7***	ns	1***
Elevation	0.4***	0.4***	ns
Distance to forest edge	ns	0.3*	ns
Soil pH-value	ns	-0.3***	ns
Early post-fire colonizer ²	ns	-0.2*	ns
Basal area	ns	ns	-1.2*
Temperature	0.1**	ns	ns
Precipitation	-0.01	ns	ns
<i>Interaction terms</i>			
Temperature:	-0.2***	ns	ns
Precipitation:			
Years post-fire:	-0.3***	ns	ns
Non-beech height			

• Significance level ≤ 0.1 ; * ≤ 0.05 ; ** ≤ 0.01 ; *** ≤ 0.001
: interactions

6.2.5 Vegetative regeneration

Beside the fact that beech frequently regenerates from seeds, part of the fire-injured beeches also resprouted. From the survived beeches, 11% resprouted with an average number of 7 shoots per stool. Most (67%) of the shoots were alive. Within the first decade post-fire, the overall number of beech shoots (N 154) was almost three times as high as later in succession (> 16 years post-fire; Figure 6.7). Whereas their heights rapidly increased from below one meter within the first two decades post-fire up to average heights of 2.1 ± 0.21 m after 32 years post-fire (Figure 6.7). Next to beech, also sycamore maple (*Acer pseudoplatanus* L.), birch, ash (*Fraxinus excelsior* L.), sessile oak (*Quercus petraea* (Mattuschka) Liebl.), whitebeam (*Sorbus aria* Crantz.), and sweet chestnut (*Castanea sativa* Mill.) resprouted (Appendix D).

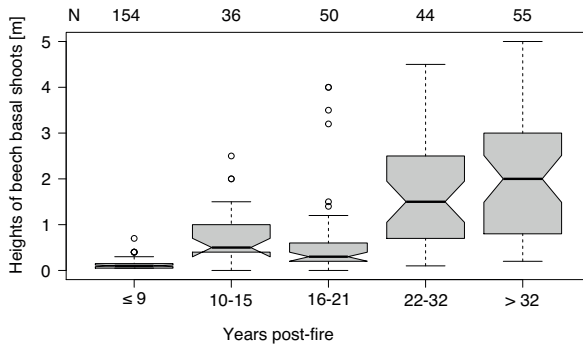


Figure 6.7: Number (N) and heights of living vegetative shoots on pre-fire beeches grouped by years post-fire.

6.3 Forest structure regarding the protective capacity

The previous sections showed, that the probability of fire-injured beeches to die decreases from small- to large-diameter beech trees and increased from low- to high-burn severity. At the same time new tree regeneration emerged— mainly dominated by beech. Considering both processes, the following can be summarized as an interim result:

- The basal area of standing dead beeches in low-severity burns corresponds to the unburned forests. Mostly small-diameter beech trees suffered from fire, while intermediate- and large-diameter beech trees mainly survived. Due to the relative low mortality rate of mature beeches and the resulting small gaps, tree regeneration densities are lower than in moderate- and high-severity burns.
- The amount of dead fire-injured beech trees increased in moderate-severity burns, and peaked within the first 20 years post-fire. Mostly small-diameter and few intermediate-sized beech trees suffered from fire disturbance, while large-diameter beeches mainly survived. New regeneration— dominated by beech— emerged in the gaps. In the early post-fire decades, beech regeneration was mixed with pioneer and other tree species, while latter both declined in densities with progressing time since fire.
- Beech trees in high-severity burns suffered from fire, regardless of the tree diameter. Mortality started immediately after the fire and peaked 10–15 years post-fire. New beech regeneration emerges together with pioneer and other tree species. However, latter both declined in densities with progressing time since fire.

Against this background, it seems that the protective capacity of burned beech forests may decrease temporarily, particularly in

moderate- and high-severity burns. Stand structure in low-severity burns does not change fundamentally, which lead to the hypothesis that the protective capacity correspond to the unburned beech forests, while those in moderate and high severity burns might decrease temporarily. The Rockfor.net model was employed to test this hypothesis. The model uses only trees with diameter to breast height (DBH) ≥ 8 cm. Smaller trees were omitted because of their negligible role in the protective effectiveness (Wehrli et al., 2006). Nevertheless, brushwood and dense layers of early post-fire colonizers may increase temporarily the surface roughness and hence the protective capacity. The contribution of lying branches and brushwood to rockfall energy dissipation is hard to quantify in a model such as the Rockfor.net and was therefore neglected for the purposes of this study. However, temporal changes in fallen branches and brushwood volume were graphically visualized.

6.3.1 Temporal trends in surface unevenness

Early post-fire colonizers grew frequently after fires by reaching average coverages of 28% in moderate-severity burns and 56% in high-severity burns (Figure 6.8). Their coverages steadily increased within the first decade post-fire in moderate-severity burns and peaked by 30%. This corresponds to one half of the cover reached in high-severity burns. Contrastingly, early post-fire colonizers showed no clear temporal tendency and were in average 25% in low-severity burns. In the unburned forests their coverages tended to be close to be zero (Figure 6.8).

Pattern in the volume of fallen dead branches and brushwood were similar in the different burn severity sites with peaks at around 15 years post-fire (Figure 6.9). Afterwards their volumes steadily decreased by reaching similar values recorded for the unburned forests after 30 years post-fire. When considering different burn severities, the volume of fallen branches and brushwood scored highest average values (106 m^3) in high-severity burns; here it was 1.5-times higher than in moderate- (75 m^3) and low-severity (60 m^3) burns, respec-

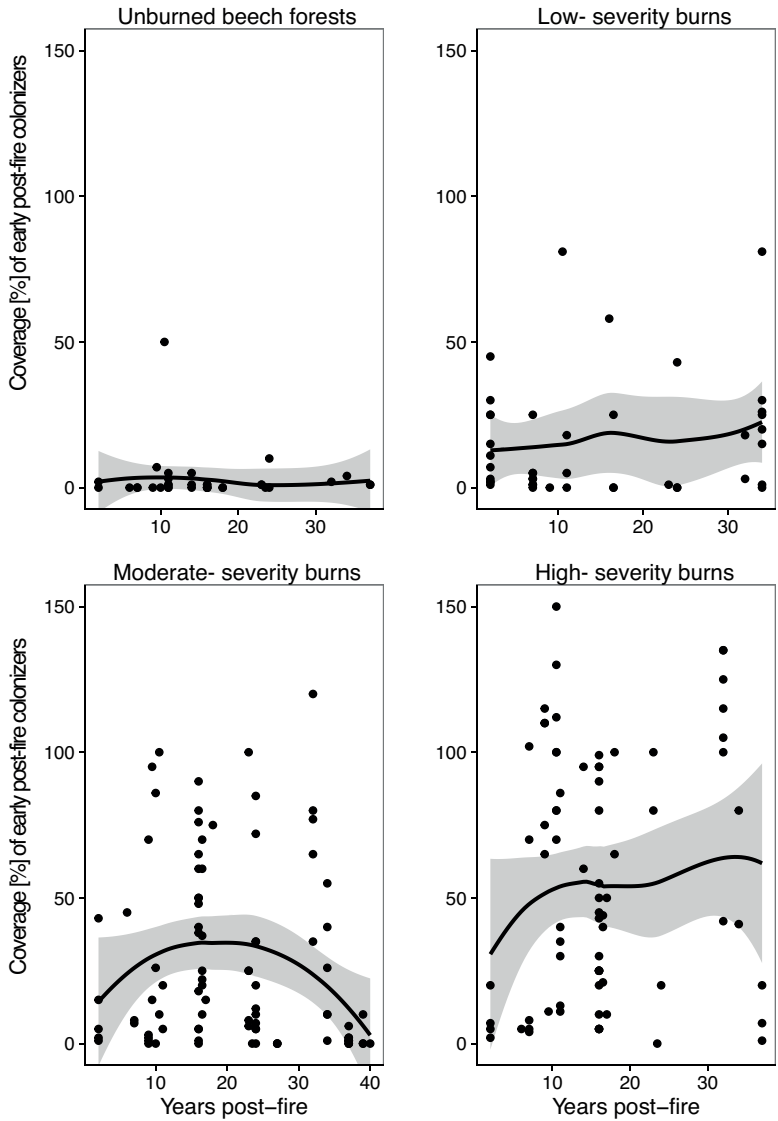


Figure 6.8: Temporal trends for the cover of early post-fire colonizers (sum of *Pteridium aquilinum*, *Cytisus scoparius*, *Molinia arundinacea*) visualized by loess-smoothing curves (black lines) including confidence intervals (grey) for the different burn severity classes and the corresponding unburned forests.

tively. Contrastingly, no clear temporal trend was detected in the unburned forests where volumes of fallen branches and brushwood never exceeded $25 \text{ m}^3 \text{ ha}^{-1}$.

6.3.2 Temporal trends in the forest protection capacity

The Rockfor.net model results highlight the mid-term (first 40 years post-fire) evolution of the protective capacity of burned beech stands as a function of different burn severities, rock sizes, forested slope lengths, and slope inclinations. The average protective capacity aggregated over the years post-fire decreased with increasing rock size, slope inclination, and shortness of the forested slope length (Table 6.6). The protective capacity of low-severity burns did not significantly differ from the unburned forests for most of the scenarios. Whereas, for moderate- and high-severity burns the protective capacity significantly differed from the unburned forests in more than half (67%) of the scenarios (Table 6.6).

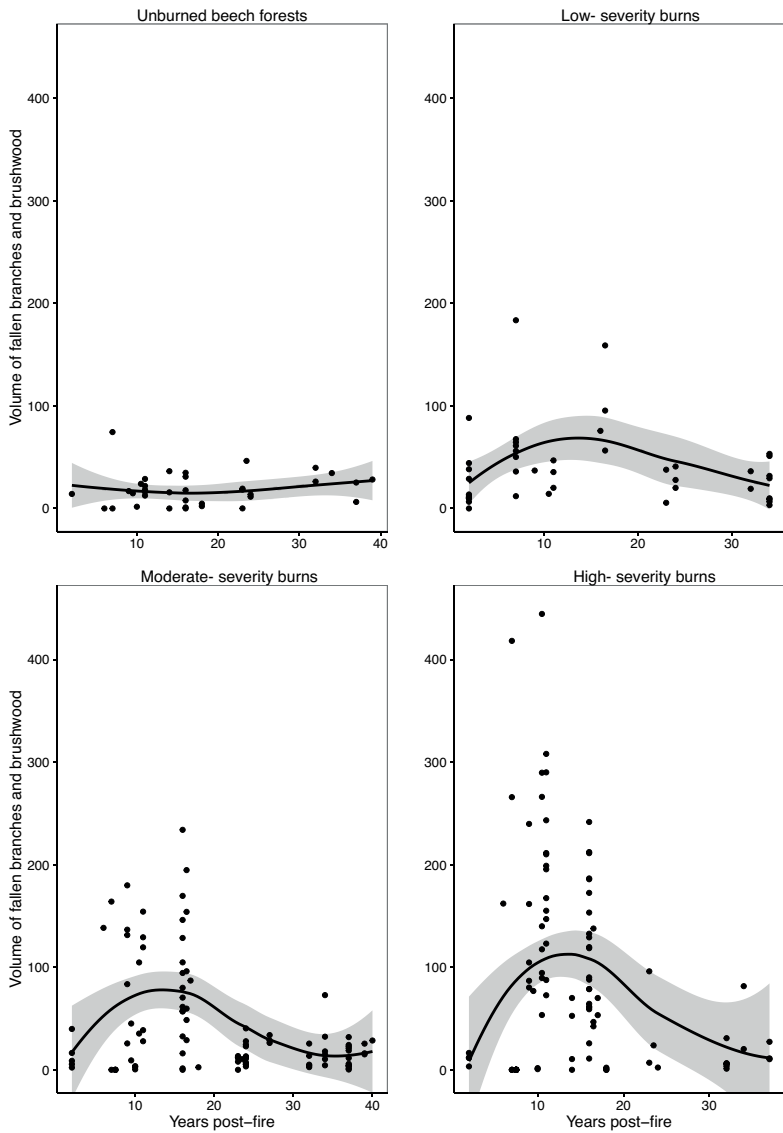


Figure 6.9: Temporal trends in the volumes [$\text{m}^3 \text{ha}^{-1}$] of fallen dead branches and brushwood visualized by loess-smoothing curves (black lines) including confidence intervals (grey) for the different burn severity classes and the corresponding unburned forests.

Table 6.6: Mean protection capacity [%] for the different scenario specifications grouped by low, moderate and high burn severity and the corresponding unburned forests. Similarities (Mann-Whitney-Wilcoxon tests) in the protection capacity between unburned and burned forests of different severities are shown in the superscript.

Forested slope Slope inclination <i>Rock size</i>	<i>Burn severity</i>	75 m			150 m		
		27°	30°	35°	27°	30°	35°
		<i>Mean protective capacity [%]</i>					
0.05 m ³	Unburned	97	95	91	95	95	95
	Low	96 ^(ns)	92 ^(ns)	87 ^(ns)	92 ^(ns)	92 ^(ns)	92 ^(ns)
	Moderate	89 ^(ns)	85 ^(*)	76 ^(**)	88 ^(*)	87 ^(*)	87 ^(*)
0.02 m ³	High	73 ^(*)	68 ^(**)	61 ^(**)	74 ^(*)	73 ^(*)	69 ^(**)
	Unburned	94	84	69	95	94	89
	Low	87 ^(*)	83 ^(ns)	71 ^(ns)	94 ^(ns)	91 ^(ns)	84 ^(ns)
1 m ³	Moderate	77 ^(**)	66 ^(ns)	57 ^(*)	89 ^(ns)	85 ^(*)	71 ^(*)
	High	55 ^(***)	49 ^(**)	40 ^(***)	73 ^(*)	67 ^(**)	(*)
	Unburned	62	48	30	94	75	58
	Low	61 ^(ns)	54 ^(ns)	37 ^(ns)	93 ^(ns)	76 ^(ns)	56 ^(ns)
	Moderate	47 ^(**)	37 ^(ns)	28 ^(ns)	86 ^(ns)	59 ^(*)	39 ^(*)
	High	33 ^(***)	28 ^(**)	23 ^(ns)	65 ^(**)	41 ^(***)	29 ^(**)

• Significance level ≤ 0.1 ; * ≤ 0.05 ; ** ≤ 0.01 ; *** ≤ 0.001

Low and moderate-severity burns yielded a protective capacity more than adequate (above 50%) for small and intermediate-sized rocks regardless of the forested slope length (Figure 6.10 and Figure 6.11). Only in scenarios with rocks of 0.2 m^3 , slope inclination $\geq 30^\circ$ and forested slopes length shorter than 75 m the protective capacity decreased below 50%, mostly between 20 and 30 years post-fire (Figure 6.11 a). In similar scenarios, the protective capacity in high-severity burns ranged between 10% (inadequate) and 45%, and was at a minimum in scenarios combining intermediate-sized rocks with steep and short forested slopes (Figure 6.11 a).

For scenarios with rocks of 1 m^3 and forested slope length of 150 m, the protective capacity of the forests was above 50% (adequate protection) for the unburned and low severe burned forests without any clear temporal trend (Figure 6.12 b). In case of shorter forested slopes, the protective capacity of those forest types ranged only between 25% (satisfying) and 75% (adequate) (Figure 6.12 a). Contrastingly, the protective capacity in moderate and high-severity burns younger than 15 years post-fire rapidly decreased below 50%, reaching its minimum (10% that is inadequate) around 20 years post-fire. As a general rule, the log components contributed only very minimally to the overall protective effect of the analyzed scenarios (see Appendix C; for details on single scenarios and single plots data refer to the Appendix E.)

The linear regression models applied to detect temporal trends in the protective capacity of the burned and unburned forests showed significant correlations between the protective capacity and the linear and quadratic term of the number of post-fire years for most of the moderate and high burn severity scenarios. Such a significant correlation was missing for low-severity burns and the unburned forests (Appendix F).

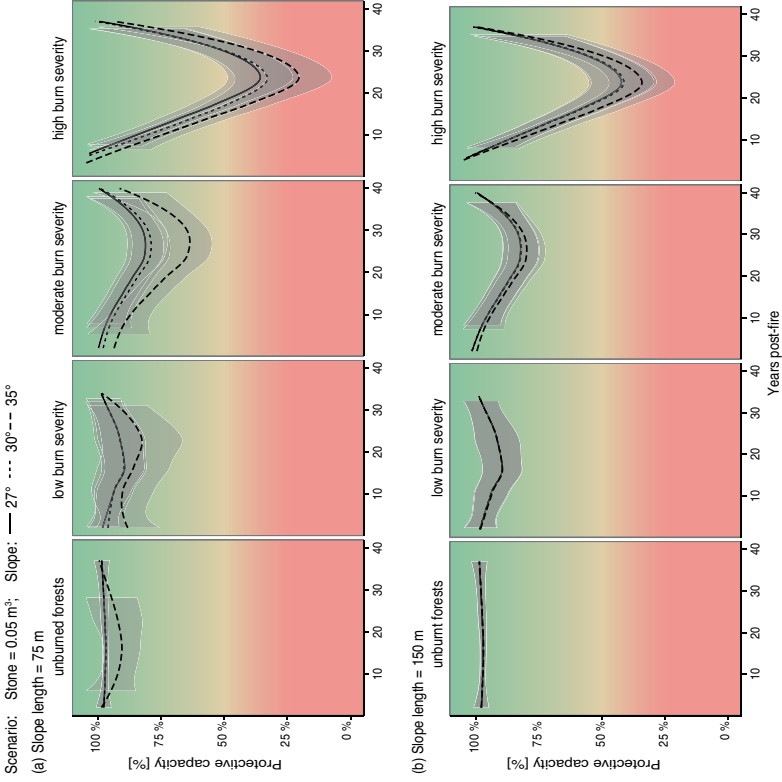


Figure 6.10: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against small rocks [0.05 m³], 75 m (a) and 150 m (b) forested slopes

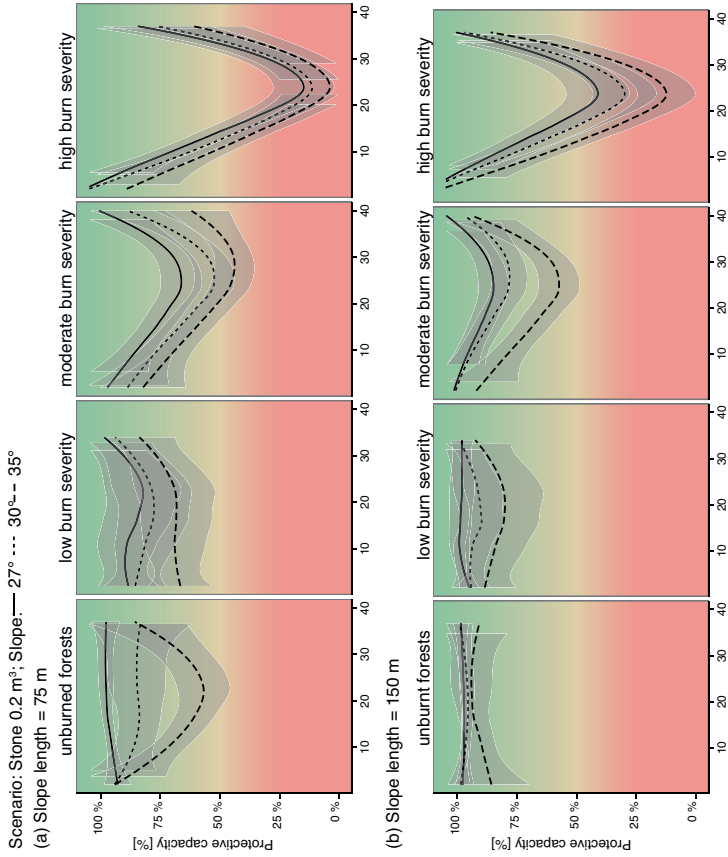


Figure 6.11: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against small rocks [0.2 m³], 75 m (a) and 150 m (b) forested slopes

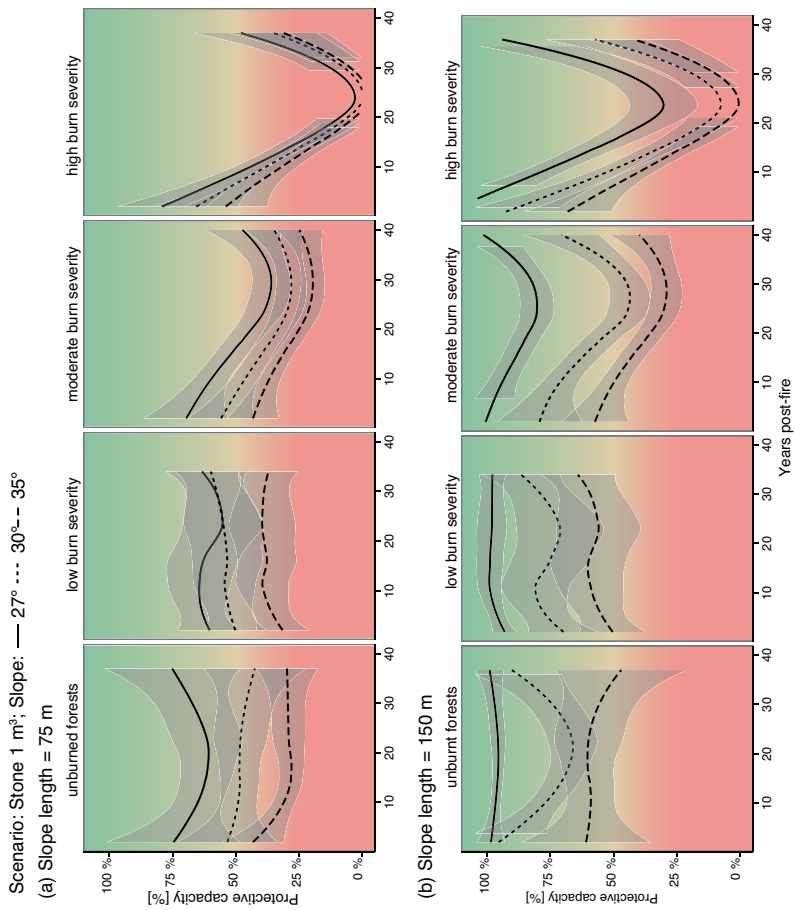


Figure 6.12: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against small rocks [1 m³], 75 m (a) and 150 m (b) forested slopes

Chapter 7

Discussion

7.1 Delayed beech mortality

The examined stands showed typical beech forest structural characteristics for the southwestern Alps, as they are often described in the literature as interlocking transition stages from unevenly-aged coppices to high stand forests (Nocentini, 2009; Ascoli et al., 2013). In these stands, fires of mixed severity caused changes in the forest structure by triggering mortality in half of the pre-fire beeches. Contrarily, dead trees in undisturbed forest account for only 10%, which goes in line with observations of Hunter & Schmiegelow (2011).

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 the study presented highly depended on tree size. The observed 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).

Standing dead beeches—snags in particular—accounted for the majority of the resulting dead wood. Normally standing dead trees dominate up to a decade post-fire (3-15 years post-fire; Brown et al., 2013), due to continuously collapsing dead trees to the forest floor (Shafiei et al., 2010; Lampainen et al., 2004). The low amount of logs in the present study may result from the rapidly decaying beech wood relative to standardized time intervals. The study region is characterized by a warm and humid climate, which in turn promotes the high biological activities (Koop & Hilgen, 1987; Lampainen et al., 2004; Kahl, 2008). Moreover, most burns are located on steep slopes with mean inclination of 65%, which causes downhill moving logs. In less steep areas which are also easy accessible by car, local inhabitants remove the dead wood for private use as it has often been observed in Piedmont (pers. communication D. Ascoli).

7.2 Drivers of post-fire beech mortality

7.2.1 Secondary fungi investation

Among the detected drivers of post-fire beech mortality, the presence of visible fungal activity in terms of fruit body formation (FUNGI) revealed to be very important. 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) but also for American beech (*Fagus grandifolia* Ehrh.) (Tubbs & Houston, 1990).

The thin bark is one characteristic of the genus *Fagus* that renders beech species particularly susceptible to fire-scar formation (Tubbs & Houston, 1990; Peters, 1997; Hicks, 1998; Packham et al., 2012), and thus potentially to secondary fungal infestation. The bark of *Fagus* 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 infes-

tation.

To protect the vital tissues, injured trees have to quickly compartmentalize wounded parts of the trunk by creating "defense walls" to retard or block air and microorganisms (Liese & Dujesiefke, 1996). Beech, in contrast to other broadleaf species, is relatively slow to undertake compartmentalization. Its bark opens soon after heat exposure (Conedera et al., 2010) and compartmentalization processes may last up to three years after injury (Dujesiefke et al., 2005). In the intervening period, beech is highly susceptible to secondary fungal infestation.

Winter temperatures inhibit the compartmentalization, because beech starts to defend when air temperatures are between 5 and 10 °C (Jurasek, 1958). Thus, dispersed fungi spores after a winter fire may increase the risk of beech mortality. However, the present study could not detect any differences in beech mortality between winter and summer fires. This has also been highlighted by Hecht et al. (2015). The authors investigated in the fungal infestation of mechanical-injured beeches and found interestingly other fungi species than those after post-fire (Table 7.1; see Standovár & Kenderes (2003) and Hecht et al. (2015) for mechanical related fungi and Conedera et al. (2007) for fire related fungi). This may indicate the existence of specific, fire-related fungi infesting beeches, which has to be further tested in field experiments.

The combined effect of both 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 regardless of the fire season. In this respect, the results of the present study confirm the findings of Conedera et al. (2010), indicating that moderate- and high-burn severity is the most sensitive to secondary fungal infestation (odds ratios are higher with respect to low-severity burns; Table 6.2 on page 101).

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. The fungal infested wood tissue has not been analyzed

in the present study indicating that the visible abundance of fungi fruitbodies does not appear to be an indicator of enhanced mortality. Therefore, the sheer presence of fungal fruit bodies may be more important than their actual amount (Hecht et al., 2015).

Table 7.1: Main ecological characteristics of fungi on mechanically and fire-injured beeches (fungi infection in mechanically-injured beeches are based on the literature review of Standovár et al., 2003 and Hecht et al., 2015.).
a Zarzyński (2007); *b* Schwarze & Baum (2000); *c* Webster & Weber (2007); *d* Kriegelsteiner (2000); *e* Reinartz & Schlag 2002; *f* Lee et al. (2008); *g* Shigo 1970; *h* Kahl (2008); *i* Shortle et al (1996); *j* Conedera et al. (2007)

Species	Short biological description
FUNGII OF FIRE-INJURED	
BEECHES	
<i>Armillaria</i> spec. (Fries) Staude	Strong facultative pathogen, which infects intact tree tissue directly. Wounding is not necessary. ⁱ
<i>Cerrena</i> cf. <i>unicolor</i> (Bull.) Murrill	Spaced forest stands on humid soils. ^d Specifically adapted to wildfire and can be invisible for many decades. ^j Usually occurs on humid soil during late successional forest stages. ^d
<i>Daldinia concentrica</i> (Bolton) Cest.	Specifically adapted to wildfire and can be invisible for many decades. ^j
<i>Inonotus nodulosus</i> (Fr.) P. Karst	Usually occurs on humid soil during late successional forest stages. ^d
<i>Irpex lacteus</i> (Fr.)	Usually abundant in fire scars where it causes white rot finally causing the stem to break. ^j
<i>Oudemansiella mucida</i> (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
<i>Schizophyllum commune</i> (Fr.)	Often occur after “sun burn” on broadleaf trees. ^j
<i>Stereum hirsutum</i> (Willd.) Pers.	Pioneer species fruits often after fires in deciduous forests. ^j

Species	Short biological description
<i>Trametes hirsuta</i> (Wulfen) Pilát	Occurs on injured beeches, which are exposed to light. Sabrobiont on dead standing or logs, which still have pieces of bark. ^d
<i>Fomes fomentarius</i> (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. ^b
FUNGI ON MECHANICALLY-INJURED BEECHES	
<i>Cylindrobasidium evolvens</i>	Wood decaying fungi
<i>Daedalea quercina</i> (L.) Fr.	Causing brown rot often leading to huge wood loss inside the stem. ^a
<i>Fomitopsis pinicola</i> (Sw. ex Fr.) Gill.	Unable to invade living sapwood, but wounded trees are easily colonized. ^b
<i>Ganoderma appplanatum</i> (Pers.) Pat.	Causes white heart rot and is dispersed by a specialized mycophagous fly. ^c
<i>Hypoxylon fragiforme</i>	Wood decaying fungi. Grows on dead beeches
<i>Hypoxylon cohaerens</i>	Wood decaying fungi.
<i>Inonotus radiatus</i> (Sw. ex Fr.) Karst.	The main host is alder (<i>Alnus</i> sp.) but also occurs on dying beeches. ^d
<i>Inonotus cuticularis</i> (Bull.) P. Karst.	Causes brown rot, mainly on beeches in barely disturbed forests. ^d

Species	Short biological description
<i>Imotus obliquus</i> (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
<i>Laetiporus sulphureus</i> (Bull.) Bond. Ex Sinq.	Intensive wood decay in the tree's trunk causing static problems mainly in the root crown. ^e
<i>Meripilus giganteus</i> (Pers.) P.Karst	Causes intensive white rot, mainly on beech and oak wood. ^d
<i>Nectria galligena</i> Bres.	Causes cancer disease. Entry of the pathogen is facilitated by the beech scale insect (Cryptococcus fagisuga). ^d
<i>Nectria ditissima</i> Tul.	Similar to <i>N. galligena</i> . ^d
<i>Oxyporus populinus</i> (Fr.) Donk.	Causes white heart rot, especially in the basal part of the stem. ^d
<i>Pholiota squarrosa</i> Huds. ex Fr.	Infests weakened beeches. ^g
<i>Polyporus squamosus</i> Huds. ex Fr.	Cause white rot, often along the wounds where spores colonized the stem. ^d
<i>Phialophora</i> ssp.	—
<i>Phoma</i> ssp.	—
<i>Phomopsis</i> spec.	—
<i>Pleurotus ostreatus</i> (Jacq. ex Fr.) Kummer	Often found on dying or dead standing deciduous broadleaf trees. ^d

7.2.2 The influence of tree diameter

Next to fungi infestation, tree size (DBH) is linearly and negatively correlated to beech mortality in low- and moderate-models, whereas no significant correlation was found in the high-(severity)-model. Contrasting to the burn-models, beech mortality was linearly and quadratically correlated with DBH in the control-models. This indicates higher mortality risk for thin as well as for large beeches, which describes the mortality processes initiated in the self-thinning and over-maturity phase, respectively (Holzwarth et al., 2013).

The fact that tree mortality caused by fire is higher for small-diameter trees than for large-diameter ones has often been stated in the literature for different tree species (McHugh & Kolb 2003; Kobziar et al. 2006; Shafiei et al. 2010; Brando et al. 2012). Gutsell & Johnson (1996) highlighted that small-diameter trees have mostly their whole circumference burned, hence most parts of the cambium killed, and they are incapable 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 heating (Gutsell & Johnson, 1996; Hély et al., 2003; 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, 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 may evident also for 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.

Large European beech trees have more structured, creviced, and rough bark (Figure 7.1) 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 & Hare, 1964; Nicolai, 1986; Bauer et al., 2010; Odhiambo et al.,



Figure 7.1: Fire in a beech stand of the southwestern European Alps with leeward burned beech bole [photo by D. Ascoli]

2014). In addition, large beech trees have large crowns, no low limbs, and limited litter yield around their boles (Yaussy et al., 2004), which hinders the fire from vertical spread and thus increases their survivability after surface fires.

7.2.3 Influence of growth habit

In high-severity sites, beech mortality was widespread, except in polycormic trees (POLY). In part, this observation may be related to the leeward effect of fire spread on trunk damage (Gutsell & Johnson, 1996). In multiple stem individuals, shoots exposed to the fire front are often preserved from bark-killing critical heating, whereas those on the leeward side of the flame front are subjected to longer exposure to heat. 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.

7.2.4 Elevation

Elevation (ELE) is the third important factor in triggering beech mortality in burned and unburned forests. Since the study area has optimal levels of precipitation for beech growth (Ellenberg & Leuschner, 2010), elevation indirectly explains temperatures— a major physical constraints on growth. Beech is naturally limited along an elevation gradient by low temperature in May (optimum 11°C–14°C; 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.

7.2.5 Ecological principles in the survivability of beech

To summarise: Forest fires in the southwestern Alps usually take the form of a surface fire, consuming the loose debris and the understory vegetation. Thereby the fire front and the related fire impact on vegetation are not spatial uniform; rather it creates a mosaic of differently burned and unburned patches. As a consequence, a number of tree individuals can survive surface fires— depending on the proportion of injured bark tissue and the likelihood of wood decaying fungi to infest exposed tissues (see Table 6.2 on page 101).

As is generally known, beech has a thin and smooth bark that limits the species to protect their vital tissue from lethal heat radiation. Since small-diameter beeches generally have a thinner and smoother bark than large ones, they face a higher risk to die after forest fires. Exceptions are made for individuals growing on the leeward side of the flame front in a polycormic tree ensemble (see Table 6.2 on page 101). On the leeward side the residence time of the flame is longer than on the windward side, so that heat transfers into the inner layers (Dickinson & Johnson, 2001), cause bark opening and hence secondary fungi infestation. The fungi decay the wood, which finally leads to the collapse of the tree. Thereby, fungi

species infesting fire-injured beeches differ from those described in the literature for mechanical-injured beeches (see Table 7.1 on page 135ff). Finally, the survivability of a beech tree in the post-fire period decreases toward less suitable site conditions, such as, shorter vegetation periods and lower temperature on the upper elevation limit of beech distribution (see Table 6.2 on page 101).

7.3 Beech regeneration

7.3.1 Beech seed germination

Beech seed germination started soon after forest fire, which has been also observed by short-term studies in burned beech forests in the southwestern Alps (Maringer et al., 2012; Ascoli et al., 2013; Ascoli et al., 2015) and Apennine (van Gils et al., 2010). The window for successful seed germination and hence seedlings establishment was slightly shorter in high-severity burns than in moderate-severity burns. This can be related to the relatively fast dieback of seed providing trees and/ or by the fast establishment of competing surface vegetation. The inverse relationship between successful beech recruitment and both favourable post-fire microsite conditions (Delarze et al., 1992) and the time elapsed since fire has also been observed for other tree species (Peters et al. 2005; van Mantgem et al. 2013).

Generally, beech seeds seem to benefit from changing micro-site conditions in the post-fire environment, in particular: (i) the reduced amount of litter and the resulting more exposed mineral soil, (ii) the adequate soil moisture, (iii) the intermediate light conditions, and (iv) the low covers of competing ground vegetation, (Harmer, 1995; Madsen & Hahn, 2008; Barna, 2011). The cumulative effect of the mentioned factors stabilizes both the soil moisture and temperature by favoring beech seed germination and the tap-root formation (Madsen & Hahn, 2008; Ascoli et al., 2013). Beech seeds on bare soil can easily form a tap-root into the mineral layer, and avoiding the break off and dry out as it mostly occurs when rooting through

thick litter layers (Agestam et al., 2003; Olesen & Madsen, 2008; Bilek et al., 2009; Silva et al., 2012). Contrastingly, the unburned beech forests are characterized by low light levels and thick duff layers (Ascoli et al., 2015), which explains the reduced germination of beech seeds and the recruitment of seedlings in the present study.

7.3.2 Resprouting capacity

Beyond the intensive regeneration from seeds, beech marginally resprouts after fire. The resprouting capacity of a tree is generally related to the (i) tree species, (ii) fire characteristics (severity, frequency, season), and (iii) tree characteristics, like size and age (Espelta et al., 2012; DeBano et al., 1998). Beech is known to be a poorly resprouter (Packham et al., 2012), whose resprouting ability declines with tree diameter and probably with age (Wagner et al., 2010). Indeed, 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., 2010; Conedera et al., 2010; Maringer et al., 2012; Espelta et al., 2012).

7.3.3 Interaction between both pioneer and beech regeneration

Both, beech and pioneers regeneration co-occurred in considerable abundance for 20 years post-fire. During this early growth stage, there was no evidence of competitive exclusion by pioneer woody species. On the contrary, from 20 years post-fire onward, beech becomes dominant by outcompeting other woody species. While shade tolerant beech saplings are able to grow tall under the sparse canopy of fast-growing pioneer trees, they may benefit from a nurse crop effect (Ammer et al., 2002) in term of shade and protection from browsers. Continuous beech growth during the next phase results in a crown expansion and successful competition for light (Leder, 1993; Walker, 1999). Moreover, in comparisson to other woody regeneration, beech was only slightly browsed, which may

contribute additionally to beech dominance in the succession process (Björkman, 1996).

The observation of rapid beech regeneration in most plots perfectly fits the direct re-growth theory postulated by Romme et al. (2011). They reported that burned forests are replaced by trees of the same species as existed pre-fire. In the present study, beech forests disturbed by a single surface fire seem to recover to the pre-disturbance species composition within a short period of only 40 years. Similar successional paths of beech have been also reported in post-windthrow studies in Central Europe (Kompa, 2004; Kompa & Schmid, 2005; Kramer et al., 2014).

Only few plots showed no beech regeneration, mostly in one-year-old burns that lacked a seed mast year and where regeneration processes have not yet started (Johnson & Miyanishi, 2007). Lacking beech regeneration in older burned beech forests related to high-burn severity, where dense layers of early post-fire colonizers had accumulated (common bracken, common broom and purple moor grass).

7.4 Ecological drivers for beech regeneration

7.4.1 Competition to early post-fire colonizers

Among the factors limiting beech regeneration, the abundance of early post-fire colonizers was considered as the most important. Beech regeneration was present up to an intermediate coverage of early post-fire colonizers, which can be beneficial for beech regeneration providing shade and browsing protection (Harmer, 1995). However, as cover increased beech regeneration was reduced or even almost absent. This is comparable to post-fire dynamics in the Mediterranean region in which forest regeneration is hindered by dense layers of shrubs– dominating in the first post-fire years (e.g. Trabaud, 1991; Delitti et al., 2005; Marzano et al., 2013). Dense lay-

ers of competitive shrubs and ferns in burned beech forests hindered also successful beech regeneration in studies from Spain (Herranz et al., 1996) and Italy (Ascoli et al., 2013).

Beech seedlings, however, compete for water, nutrients and in particular for light with early post-fire colonizers (Evans et al., 1990). Indeed, bracken was detected to delay beech regeneration for several years in France (Koop & Hilgen, 1987), and in Switzerland after windthrow (Brang et al., 2015). Under a dense layer of bracken beech seed germination is reduced due to released leachates (Priewasser, 2013). Moreover, bracken rapidly develops well-spread horizontal leaves, which in turn reduces the light availability for beech seedlings (Gaudio et al., 2011). Contrary, graminaceous species— such as purple moor grass— has long erected leaves, and competes therefore less than bracken for light. The strategy of purple moor grass is to establish early in spring, build dense root systems, and hence compete with beech seedlings for nutrients and water from the soil (Harmer, 1995; Coll et al., 2003; Provendier & Balandier, 2008; Gaudio et al., 2011).

7.4.2 The role of remnant beech trees

Other possible explanations for a lack of beech regeneration may be rapid canopy opening after fires of high severity with a simultaneous loss of seed-providing trees (Peltier et al., 1997; Bonnet et al., 2005) and immediate exposure to extreme weather conditions (Agestam et al., 2003). A late frost in 1987 in the Insubric region, for example, caused damage in the beech belt (Z'Graggen, 1992). Seedlings growing under dense tree canopies, however, are protected from harmful frost unlike those in deforested areas (Agestam et al., 2003; Mountford et al., 2006). Beech seedling densities seem to be higher closer than further away to seed-bearing trees as indicated by the basal area of the remaining trees (BASAL) and the distance to the forest edge (EDGE). Since beech relies on gravity and animals for seed dispersal, its regeneration is limited by the distance from

the nearest seed-bearing tree and by the distance from the forest edge (Wagner et al., 2010; van Couwenberghe et al., 2010). Consequently, the larger the area burned and the distance from the seed sources, the more natural beech regeneration may be limited.

Contrastingly to beech seedling, saplings growth depend on more light, which is expressed by the negative correlation with basal area of mature beeches (BASAL). As studies of shelterwood cutting have shown, dense shelter provide seeds for recruitment and protects seedlings from competition (Agestam et al., 2003; Petritan et al., 2007; Barna, 2011; Crotteau et al. , 2013), whereas saplings growth improve under light shelter after the second cut and towards the gap center (Mountford et al., 2006).

The positive correlation of beech saplings densities with volumes of dead wood (CWD), reflects also the dependency on light. The downed woody debris, in particular logs, often serve additionally as nurse logs by changing the micro-site conditions and providing shade, nutrients and enhanced soil moisture (Hunter & Schmiegelow, 2011). Therefore, dead wood should be left on the burns to maintain the mid-term nutrient cycle.

7.4.3 Climatic factors

In the present study, beech regeneration was not limited by annual precipitation (PREC). On a local scale this may be due to less root competition from the surviving beeches causing potentially less water stress for beech regeneration (Czajkowski et al., 2005). Regionally, this may be due to the generally rather high annual precipitation (979 to 1436 mm) in the study area, and the high organic content in soils (Blaser et al., 2005). The cumulative effect of both constrains the storage capacity of soil water to levels that would not limit beech growth ($< 65 \text{ l m}^{-2}$; Gärtner et al., 2008; Chakraborty et al., 2013).

Nevertheless, local climate conditions, e.g. aspect (ASP) or elevation (ELE), may influence beech regeneration densities. The in-

investigated beech regeneration grew denser on North-East than on South-West facing slopes, where water stress is likely to be higher (Mountford et al., 2006; Chakraborty et al., 2013). Such local site conditions probably do affect beech growth, and possibly beech distribution as well (see Ceschi (2006) for the Insubric region).

Changes in temperature (TEMP) were indirectly represented due to the elevation gradient (ELE), which had a limiting effect on beech regeneration densities. Generally, climate becomes harsher with increasing elevation, resulting in slower establishment and growth of tree seedlings (Schönenberger et al., 1995). Beech seedlings in particular are sensitive to late frost events (Z'Graggen, 1992), which may explain the decreasing regeneration densities with increasing elevation.

7.4.4 Ecological principles in post-fire beech regeneration

To summarise: Beech forest regeneration is mainly based on the rapid *in situ* seed germination. The shoots on fire-injured beech trees tend to dieback with progressing time since fire and hardly contribute to a valuable new regeneration (see Figure 6.7 on page 117).

Beech seeds germinated frequently (Figure 6.4), particularly when a beech mast year follows a fire (Ascoli et al., 2015). In addition, freshly burned beech forests display very favorable germination conditions for beech seeds, providing exposed mineral soil, limited competition, enhanced soil pH-values and nutrient availability released by the burned biomass (Delarze et al., 1992; Maringer et al., 2012; Ascoli et al., 2015). These favorable conditions and the resulting high seed germination rate contribute to the mid-term dominance of beech regeneration as found in the investigated burns (see Figure 6.5 on page 110).

Regeneration models of the present study show that beech regeneration densities are a function of the basal area of remnant beech trees (BASAL), the distance to the forest edge (EDGE), the vol-

umes of coarse woody debris (CWD), the coverage of early post-fire colonizers (EARLY) and microclimate conditions (ASP; Table 6.4 on page 115). Since beech seeds are limited in their dispersal up to a mean distance of 20 m (seldom 70 m, Wagner et al., 2010), high seedling densities occur close to seed-bearing trees of the forest edge or close to surviving mature beech trees in the burns. Apart from the availability of seeds, remnant trees provide intermediate light conditions and shelter from harsh weather conditions, such as late spring frost (Agestam et al., 2003).

With the progress of the delayed death of fire-injured beech trees, light availability for beech saplings progressively increases enhancing their growth and densities. Additionally, the resulting dead wood on the soil favors beech saplings by providing local shelter from direct light, enhanced soil moisture and by contributing to the long-term nutrient cycle (Hunter & Schmiegelow, 2011). Closely linked to the light conditions on the forest floor is the chance for early post-fire colonizers to establish. Both beech seedlings and saplings can persist intermediate densities of early post-fire colonizers, but in case of rapid canopy opening, early post-fire colonizers build dense layers and may prevent the establishment of beech regeneration (Table 6.4 on page 115).

7.4.5 Climate change may limit beech regeneration

The retrospective approach applied in this study indicates that beech communities affected by fire appear to be rather stable in the present climatic situation as they can regenerate after fires of different severity levels. In the study area, the climate varies little inter-annually in temperature and precipitation, although extreme events may occur such as the summer of 2003 (Schär et al., 2004). By the end of the 21st century, summer precipitation is expected to decrease considerable (-25% in Ticino; CH2011, 2011), leading to longer and more frequent drought episodes, whereas winter precipitation is likely to increase (Rebetez, 1999; Flannigan et al., 2000; CH2011, 2011).

Beech can compensate for annual growth losses over extended periods of drought due to its broad eco-physiological amplitude. Since the environmental conditions in the study region are not expected to change fundamentally, beech will probably persist in its ecological niche (e.g. Ammer et al., 2005; Zimmermann et al., 2009).

The dynamic vegetation model FORCLIM (Bugmann, 1996) also projects beech dominance from current climatic conditions up to 4°C of higher temperature. Beech will only persist in changed climatic conditions, however, if regeneration, in particular germination and early growth, remains successful. Windows of opportunity may shrink due to less frequent optimal germination conditions, while the number of mast years is expected to increase. In conclusion, studies on the tipping points of beech regeneration may improve our understanding of the mechanisms behind the range shifts projected in many current studies (e.g. Hanewinkel et al., 2012; Lindner et al., 2010).

7.5 Modulating effect of burn severity

As mentioned above, the fire behavior in relief-rich areas is heterogeneous and depends further on: (i) fuel availability, (ii) climate, (iii) local weather conditions, and (iv) topography (DeBano et al., 1998). The local fuel load determines the fire intensity and the fire behavior according to its arrangement, amount, moisture content, chemistry and distribution. Local weather conditions, especially wind, and topography influence the oxygen availability for combustion and fuel moisture. Both factors determine the vegetation distribution and can therefore create natural firebreaks. As a consequence, a fire might not affect all trees in the burns in the same way. The resulting local impacts on the forest stands are defined as the fire- (short-term) or burn- (long-term) severity (Morgan et al., 2014).

The situation in moderate-severity burns differs from those in low-severity burns. In the latter, beech seedlings frequently regenerate but the resulting saplings densities are comparatively low (see

Figure 6.5 on page 110). This may result from low light levels on the forest floor due to lateral crown expansion of remnant beech trees. The situation in low-severity burns contrasts to the immediate consumption of beech trees after high severe fires (Figure 6.3 on page 98). Here, fire modulates the site conditions and hence the ecological features driving post-fire tree mortality and regeneration in a way that beech regeneration densities grow next to pioneer- and other-woody regeneration. They mutually benefit from each other, so that the shade-tolerant beech benefits from the nurse-crop effect of the sparse canopy of the fast-growing pioneers (Table 6.5 on page 116, cf. Ammer et al., 2002). The saplings of the pioneers provide shade and protection from browsers and enables beech growth, which finally dominates (> 32 years post-fire) and successfully competes for light (Figure 6.5 on page 110). In extreme cases, however, the fast dying seed-bearing trees causes a rapid opening of the canopy and a correspondent high availability of light leading to dense layers of early post-fire colonizers. The combination of both factors may delay successful beech regeneration for several years.

7.6 Changes in the protective capacity

The combination of the dieback of fire-injured trees and the relatively slow secondary growth of tree regeneration (DBH > 8 cm protects effectively against rockfall) affects the protective capacity of burned beech stands. Generally, the protective capacity of forest stands against rockfall highly depends on (i) species composition, (ii) stand structure, and (iii) the guarantee of sustainable forest regeneration (Motta & Haudemand, 2000; Dorren et al., 2004; Dorren & Berger, 2005). Disturbances such as forest fires abruptly and substantially change the forest structures, which may temporarily affect the protective capacity of the concerned forest stand (Dorren et al., 2004).

The results show that episodic surface fires in beech dominated stands cause little changes in the tree species composition. Beech

forests directly re-grows after single fire events, resulting in stable and locally adapted forests on the long-term (Dorren et al., 2004; Rigling & Schaffer, 2015). However, the post-fire vertical and horizontal stand structures, as well as the amount and timing of regeneration, depends strongly on the burn severity. The forest structure in low-severity burns is mostly comparable to those of the unburned forests (Keyser et al., 2008). The small, fire related changes in tree density, canopy layer, and regeneration dynamics do not seem to affect the overall protective effect. This contrasts to moderate and high-severity burns, where significant structural changes occur after fire, what may cause failures in the protective effectiveness against rockfall depending on the length of the forested slope, the mean slope gradient and the rock size.

Structural changes in moderate-severity burns are mostly due to the dieback of small- and intermediate-sized trees, which goes in line with post-fire observations in conifer stands (Keyser et al., 2008). Surviving tall trees maintain to some extent the protective capacity (Volkwein et al., 2011). The gradual canopy opening of the dominant tree layer leads to emerging beech regeneration, so that the forest protective effect increases again after 20 years post-fire. In the long-term, the mixture of surviving tall and emerging small- and intermediate-sized trees results in a multi-layer stand structure that may better meet the protective function standards than mono-layered stands (Dorren & Berger, 2005; O'Hara, 2006). Nevertheless, the temporary deficit in the protective effectiveness of the forests seem to occur between 10 and 35 years post-fire, especially in case of forested slopes limited in length.

Tree mortality in high-severity burns happens immediately and concerns all tree sizes. This is similar to crown fires in conifer stands (Keyser et al., 2008; Brown et al., 2013) and to windthrow areas, where most trees die immediately after the disturbance event. In those areas, snags and logs mostly maintain the forest protective effect (Frey & Thee, 2002; Schönenberger et al., 2005; Bebi et al., 2015), although their resistance decreases with time, as shown by tensile tests (Frey & Thee, 2002; Bebi et al., 2015). The dead wood

quantity and quality might be also lower in burns than in windthrow areas (Wohlgemuth et al. 2010; Priewasser et al. 2013), especially in case of tree species such as beech displaying a rapid decaying wood (see Chapter 6.1.1 on page 94). As shown by the results, the amount of dead wood consistently decreases from 15 years post-fire on, contributing little in the long-term to the forest protective capacity (Frey & Thee, 2002). Such a loss in protective capacity has to be compensated by the upcoming regeneration, which might be delayed due to a lack of seed providing trees and/or a thick layer of competing, fast growing early post-fire colonizers (Chapter 6.3.1 on page 119). At the same time the present results indicate significantly increase in the coverage of early post-fire colonizers and fallen dead branches, which may contribute to some extent to the protective capacity against falling rocks with volumes smaller than 0.2 m^3 in the first 20 years post-fire. However, to date their effective contribution is hard to quantify in process-orientated models.

7.7 Limits of the study

Limits in beech mortality models

The chronosequence approach used in this study accompanied by rapid post-fire beech mortality and wood decay may have caused a bias in the precision of assessing pre-fire stand characteristics. This is especially true for burns older than 10 years post-fire. Usually, logistic regressions 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 (Hély et al., 2003; Hood et al., 2007; Catry et al., 2010), and (iv) immediately damages on root, stem and foliage (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 the use of all these variables in the model, given the difficulty to assess them in all plots of the used chronosequence approach. 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 (Table 6.2 on page 101). In contrast, the control-model reached an explanatory power of 47%. In addition, it was not possible to precisely date the year in which an individual died. Therefore, the influence of harsh weather conditions during the post-fire period could not be taken into account. The presented mortality models give only a first hint in factors triggering beech mortality, but cannot provide mortality predicting curves.

Limites in beech regeneration models

The chronosequence approach used in this study might diminish temporal changes in post-fire tree communities regarding sites of different burn severities. Therefore, converge of succession may temporally differ between low-, moderate- and high-severity burns as indicated by the delayed beech regeneration in some high severity plots. Moreover, it was neither possible to quantify the burn intensity nor the fire behavior, which enables this study only to indirectly estimate their influences on beech regeneration.

Due to the focus on post-fire beech regeneration, the numbers of control plots were limited in the experimental design. In steep and partly inaccessible terrain, it was not always possible to establish control plots in all burns. In the end this made it impossible to calculate additionally to the burn-models also a control-model.

Limits in the approach to determine the protective capacity of burned forests

One of the aims of this study was to test the general protective capacity of beech forests exposed to fires of varying severity. Since surface fires cause structural changes in forests, the Rockfor.net model was chosen because of its particular sensitivity to structural forest parameters (Berger & Dorren, 2007).

The protective capacity of burned beech stands was calculated for standard conditions and therefore independent from local plot conditions (e.g. topography, soil type). This provides foresters with a tool for quickly estimate periods of lacking protection capacity based on the burn severity and average conditions of the concerned stands. A precise assessment of the probability of stopping falling rocks in a particular forest stand, however, has to be conducted by implementing detailed local site conditions (e.g. slope inclination, length of the forested slope) or by using a spatially explicit model with high resolution (e.g., Zinggeler et al. 1991; Bartelt et al. 2002; Dorren 2012). As the Rockfor.net model was selected to calculate the protection capacity of burned beech forests, it was not possible to consider brushwood and densities of early post-fire colonizers in the calculation. Due to their contribution in the surface unevenness, they might contribute to the protective capacity in the disturbed beech forests.

Chapter 8

Conclusion and outlook

The study demonstrated that beech is able to persist single fires of mixed-severity under current climatic conditions in the study area (900—1800 mm yr⁻¹, mean temperature 12°C). Beech forests disturbed by a single surface fire seems to recover to the pre-disturbance species composition within a short period of only 40 years. This contradicts the common perception that the species has no ability to cope with fire disturbances (Packham et al., 2012).

The observed mortality process in fire-disturbed beech stands started 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 only few surviving trees died. The major drivers of beech mortality in this study were related to a combination of the proportion of woody tissue damaged as a consequence of tree diameter and growth habit in relation to burn severity, and the likelihood that exposed woody tissue was colonized by active (fructifying) fungi.

The progressively dieback of fire-injured beech trees promotes the woody regeneration, which was mainly dominated by beech. Major driver for successful beech regeneration was the rapid *in situ* germination of seeds. Since beech seeds are limited in their dispersal

distance, regeneration densities were found to be highest close to seed-bearing trees. Apart from the availability of seeds, remnant trees provide intermediate light conditions and shelter from harsh weather conditions, such as late spring frosts (Agestam et al., 2003).

Closely linked to the light conditions on the forest floor is the chance for early post-fire colonizers to establish. Both beech seedlings and saplings can persist intermediate densities of early post-fire colonizers, but in case of rapid canopy opening, early post-fire colonizers build dense layers and may prevent the establishment of beech regeneration. The observed processes of beech regeneration appear to act independently of the precipitation gradient in the study area. Thus, episodic forest fires may not represent a major threat to the resilience of beech forests within this climatic range.

The cumulative effect of both, the dieback of fire-injured trees and the slow secondary growth of young trees, reduced the protective capacity of burned beech stands. In particular, burned beech forests affected by low severe fires provide nearly the same protective capacity as the unburned ones. In the case of moderate to high severe fires, forest stands may experience a temporary deficit up to 50% in their protective capacity between 10 to 30 years post-fire. Thereby the protective capacity depends on the effective burn severity, the rock sizes, the length and the mean inclination of the forested slope.

In consideration of the cost-benefit ratio the following practical consequences can be derived from the study results:

Practical consequences for forest management

The most important requisite for post-fire management decisions is the correct and rapid assessment of the burn severity class. Based on the present results, forest managers should be able to assess the burn severity class within the first three years post-fire (Figure 5.5 on page 75). Such assessment basically refers to the ratio between basal area of post-fire surviving beeches and the overall basal area in the pre-fire period. The related mortality processes should additionally be analyzed by evaluating the proportion of fire-injured bark with respect to the tree diameter of living beech and subsequent

evidences of fungi fruitbodies on exposed tissue. Once assessed, the burn severity class can be related to the stand dynamic, based on which management decisions can be made. In particular:

1. *Low-severity burns:*

- Burned beech forests hit by low severe fires display nearly similar forest structures as the unburned ones. Beech regeneration in the understory might be suppressed by lateral crown expansion of remnant beeches, making small-scale falling potentially necessary in order to improve light conditions for the establishment and growth of the beech regeneration. From the point of the forest protection capacity, silvicultural measures are generally not necessary. Nevertheless, the protective capacity has to be assessed on an individual basis.

2. *Moderate-severity burns:*

- Managers may take advantage of the positive fire effects in moderate-severity burns, such as the removal of litter and the input of ash and charcoal (increase soil pH-value and short-term nutrient release and availability; Delarze et al., 1992). Beech regeneration grows abundantly in the mid-term post-fire period, and foresters can apply (if requested) a business-as-usual approach to forest regeneration (i.e., shelterwood cutting in the winter of a mast year; Ascoli et al., 2013, 2015).

3. *High-severity burns:*

- Forest managers may pay particular attention to the stand dynamics in high-severity burns. Post-fire surviving beech trees, even if damaged, should be left on the burns in order to provide seeds and shelter for beech regeneration. In extended high-severity burns, where fire-injured beech

trees rapidly die and early post-fire colonizers build dense vegetation layers, weed control combined with artificial beech seed dispersal may reduce the inter-species competition and accelerate the establishment of a new beech generation.

4. *The role of dead wood in the forest protective capacity:*

- Dead wood plays an important role in the regeneration process of beech. Hence, snags and logs should generally be left on the burns— not only because they provide shade, moisture and nutrients for beech regeneration, but also because of their temporary contribution to the forest protective capacity against rockfall. In special cases, where beech stands serve as direct protection forest, accumulation of logs following tree collapse in moderate- and high-severity burns may increase the danger of natural hazards (especially in case of downhill shifting log piles). If so, timely directional tree fellings along the contour lines of the slopes before fungi compromise mechanical stability may be taken into account.
- Finally, technical measures may be necessary to improve the protective capacity, depending on the risk for humans and their assets in relation to the cost-benefit ratio. Beside the installation of rockfall nets or walls, small-scale felling of standing dying trees and obliquely positioning of the resulting logs offers a possibility to partially mitigate the loss in the protective capacity.

Due to the limitations of the study further research should concentrate on:

- *Differences in the geological bedrock*: The present study gives a revealing insight into the fire ecology of beech on crystalline bedrock. The water storage capacity of the soils and the nutrient availability in the study region may differ from those with other geological conditions. Since the water supply is beside temperature the most important factor driving beech productivity (Ellenberg & Leuschner, 2010), additional research is needed focusing on resistance and resilience processes in burned beech forests on various bedrocks and soil types.
- *Fire return interval*: The investigated post-fire beech regeneration processes concerned burns that experienced no additional fire at least within one beech generation. Such a long fire return interval enables beech to become nubile¹ and ensure the seed input for the post-fire regeneration processes. Potential of beech to regenerate in burns with shorter fire return intervals remain an open question. In particular, the resprouting capacity of young and non-nubile beech individuals should be assessed.
- *Wood decaying fungi*: The mortality models presented in this study revealed fungi as one important factor in driving beech mortality. Unfortunately, studying the specific ecology of the wood decaying fungi and the post-fire environmental factors facilitating their colonization processes on fire-injured beeches would have gone beyond the scope of the present study. Post-fire fungal ecology in beech forest may, however, represent a very promising field of study in the future.
- *Contribution of surface roughness to the forests protection capacity*: In the present study, the protective capacity of burned

¹Beech becomes nubile at the age of 40 years in open stands, and between 60–80 years in dense forest stands (Packham et al., 2012)

beech stands against rockfall has been assessed on standing and falling trees only. The contribution of dense layers of surface vegetation and large volumes of brushwood to the forest protection capacity should be also quantitatively assessed in the future, so that rockfall models for disturbed forests can be better calibrated.

- *Prescribed burning*: Initiating natural regeneration processes in mature beech stands in steep and rough terrain can be problematic due to technical and economic reasons. The successful, natural beech regeneration after forest fires of mixed severity may open new perspective of using prescribed burning activities or targeted burning of single individual beech trees for forcing natural beech regeneration.

Outlook

In conclusion, episodic forest fires may not represent a major threat to the resilience of beech forests under the current climate conditions in the study area. Indeed irregular fires even stimulate the prevalence of beech. However, this might change in the future when increase periods of droughts are expected to cause more intensive and frequent wildfires (Westerling et al., 2006). Thus, the resistance and resilience of beech forests after a fire might be exacerbated by periods of droughts in consecutive years. To understand factors driving post-fire beech recruitment under contrasting climatic conditions, it necessary to investigate factors influencing the germination and early recruitment of beech after forest fires in a broader climatic range (e.g. including the Mediterranean region) and on varying types of soil.

Appendices

Appendix A

Calculation of variation in tree stem densities with slope inclination

Slopes of the plots were measured in degree and implemented as explanatory variable in a mixed effect model with negative binomial distribution (Bolker et al., 2013). Stem densities served as response variable, and because of the high intra-class correlation burns were implemented as random effect in the model. The result shows that slope inclination was not significant at the 0.05-level, and thus it was possible to use standardized slope inclination in the Rockfor.net model. Against this background, the 1st (26.7°) and 3rd quantile (35°) as well as the mean (29.7°) was used as standardized slope inclinations.

Table A.1: Estimates and standard error of the mixed-effect model for stem densities modeled against slope inclination

Variable	Estimate	Standard error
Intercept	5.9	<0.0001
Slope	0.009	0.25
<i>Random intercept</i>	<i>Variance</i>	<i>StdDev.</i>
	0.33	0.6

Appendix B

Mortality curves

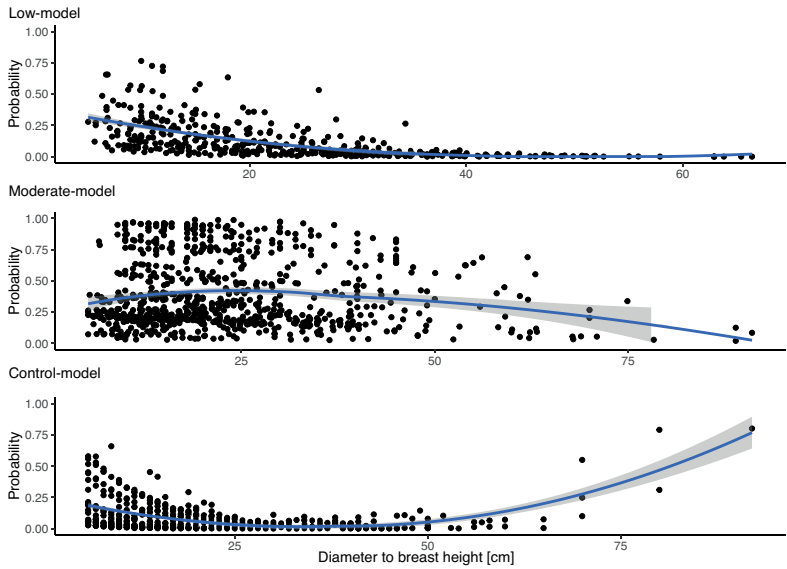


Figure B.1: Standard probability curves of beech mortality as a function of diameter to breast height separately for low- and moderate-severity burns and the unburned forest

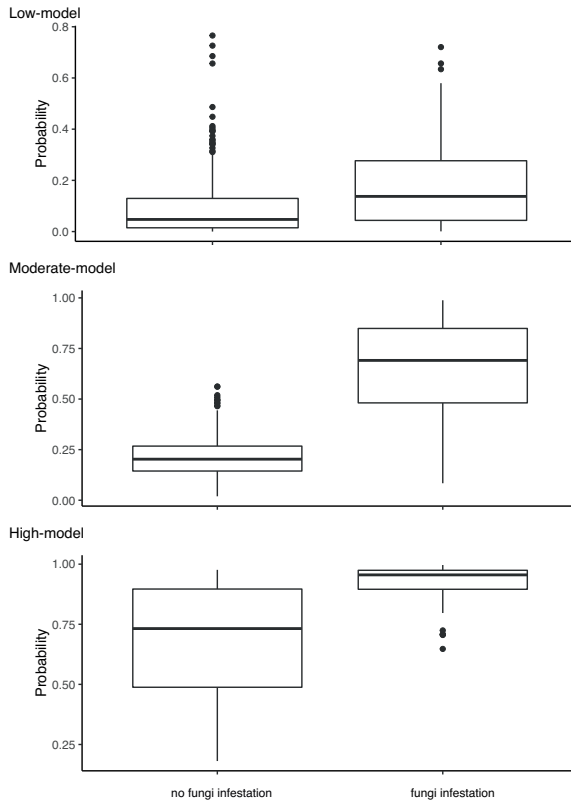


Figure B.2: Standard probability curves that a beech dies as a function of fungi infestation separately for low-, moderate- and high-severity burns

Appendix C

Logs in rockfall

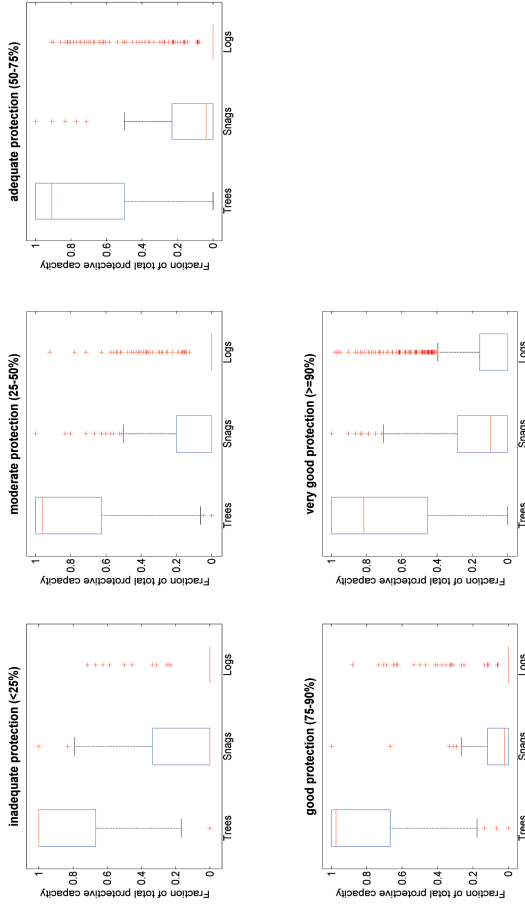


Figure C.1: The influence of logs, snags (standing dead) and trees (standing alive) in the total protective capacity against rockfall for the burned forests visualized separately for the five defined levels of protection ($\geq 90\%$ very good protection, 75–90% good protection, 50–75% adequate protection, 25–50% moderate protection, and $< 25\%$ inadequate protection)

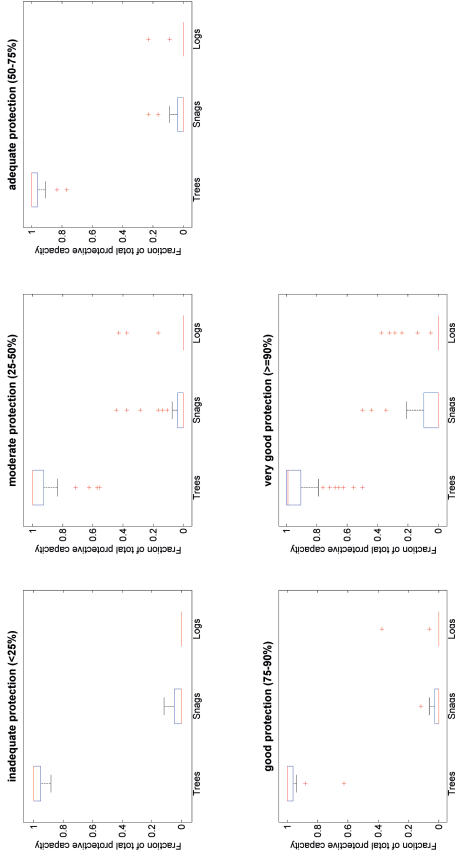


Figure C.2: The influence of logs, snags (standing dead) and trees (standing alive) in the total protective capacity against rockfall for the unburned forests visualized separately for the five defined levels of protection ($\geq 90\%$ very good protection, 75–90% good protection, 50–75% adequate protection, 25–50% moderate protection, and $< 25\%$ inadequate protection)

Appendix D

Vegetative regeneration on fire-injured trees

Table D.1: Average number of shoots sorted by pre-fire trees showing vegetative response.

Species	No. of shoots	Mean $[\pm \text{SE}]$	No. of trees with shoots
<i>Fagus sylvatica</i> L.	5.9	$[\pm 0.01]$	339
<i>Castanea sativa</i> Mill.	12.25	$[\pm 0.01]$	20
<i>Quercus petraea</i> (Matthuschka) Liebl.	3.5	$[\pm 0.04]$	9
<i>Betula pendula</i> Roth	9.25	$[\pm 0.05]$	8
<i>Sorbus aria</i> (L.) Crantz	3.6	$[\pm 0.06]$	7
<i>Fraxinus excelsior</i> L.	3	$[\pm 0]$	1
<i>Acer pseudoplatanus</i> L.	2	$[\pm 0]$	1

Appendix E

Single rockfall scenarios

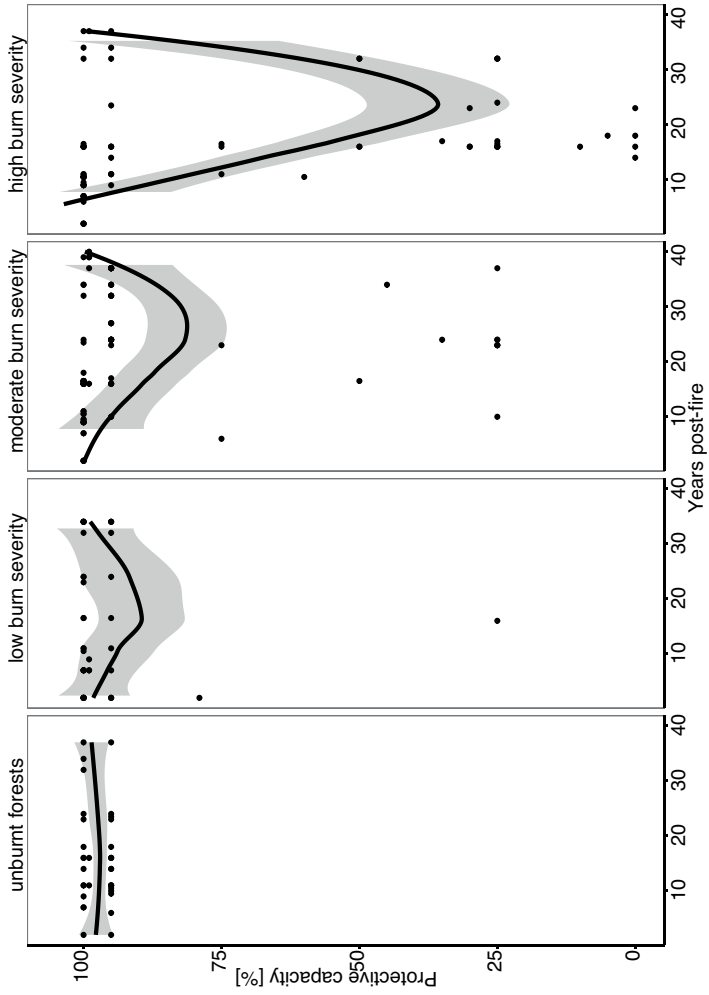


Figure E.1.: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of $0,05 \text{ m}^3$, on 75 m forested slopes and 27° slope inclination

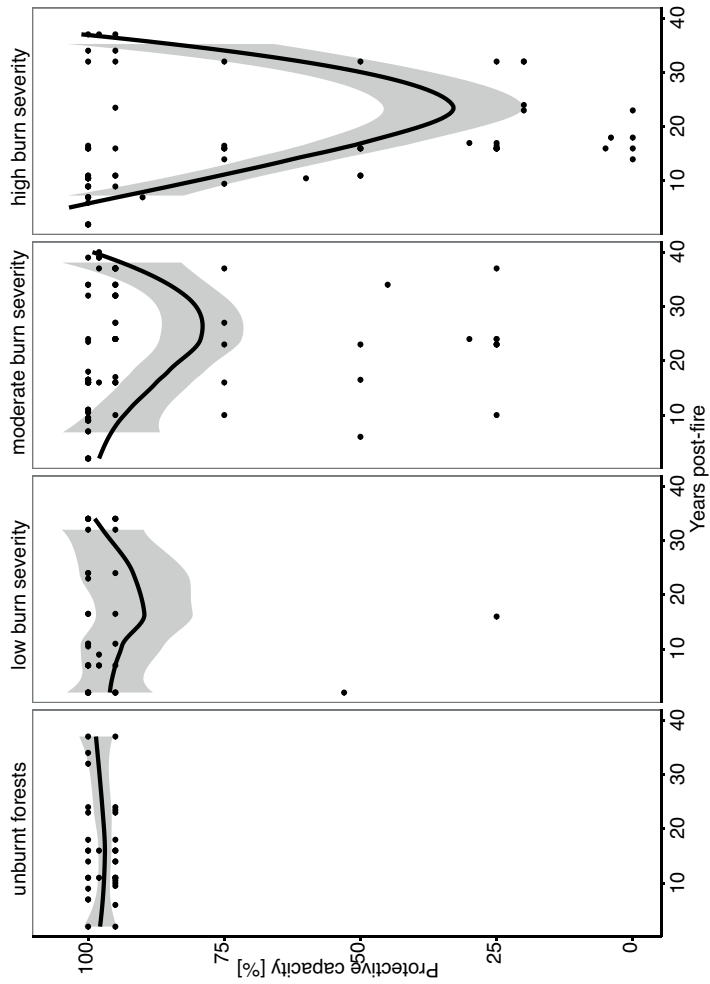


Figure E.2: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.05 m^3 , on 75 m forested slopes and 30° slope inclination

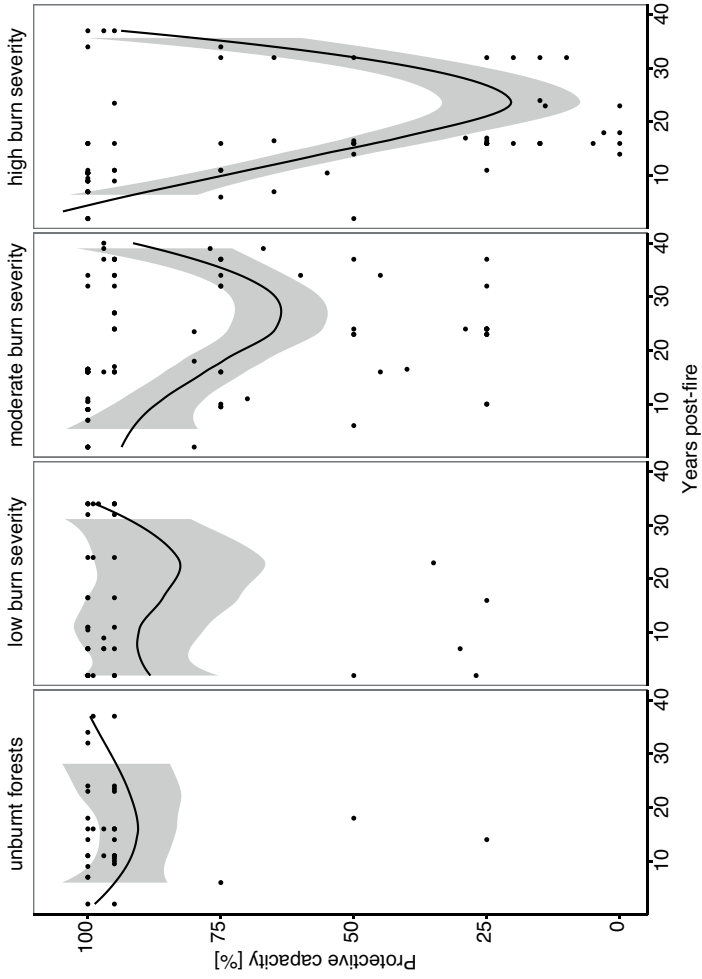


Figure E.3: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of $0,05 \text{ m}^3$, on 75 m forested slopes and 35° slope inclination

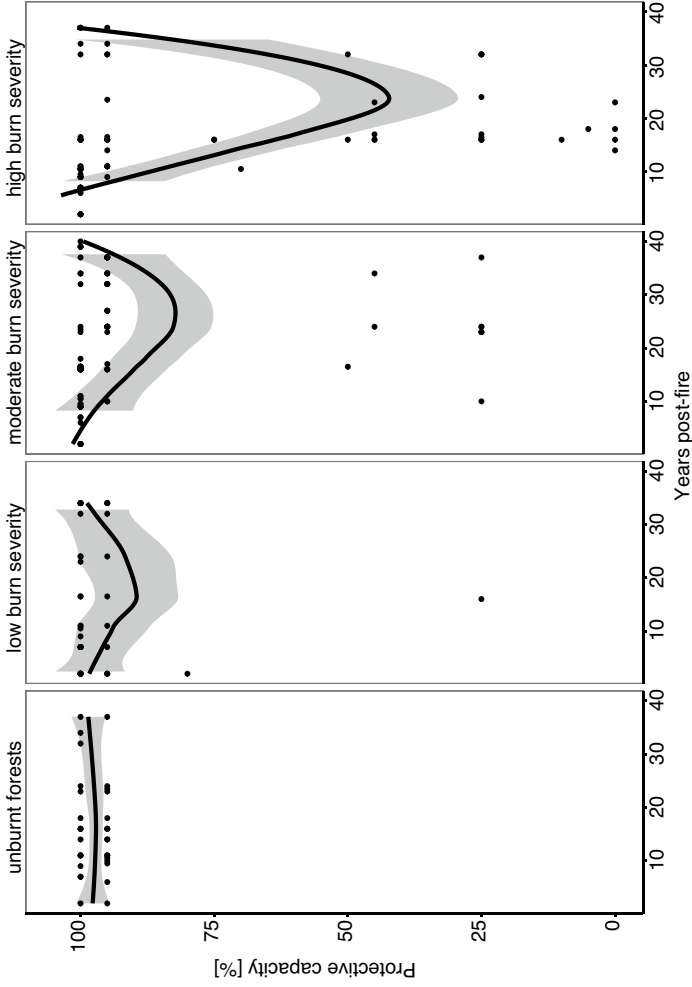


Figure E.4: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.05 m^3 , on 150 m forested slopes and 27° slope inclination

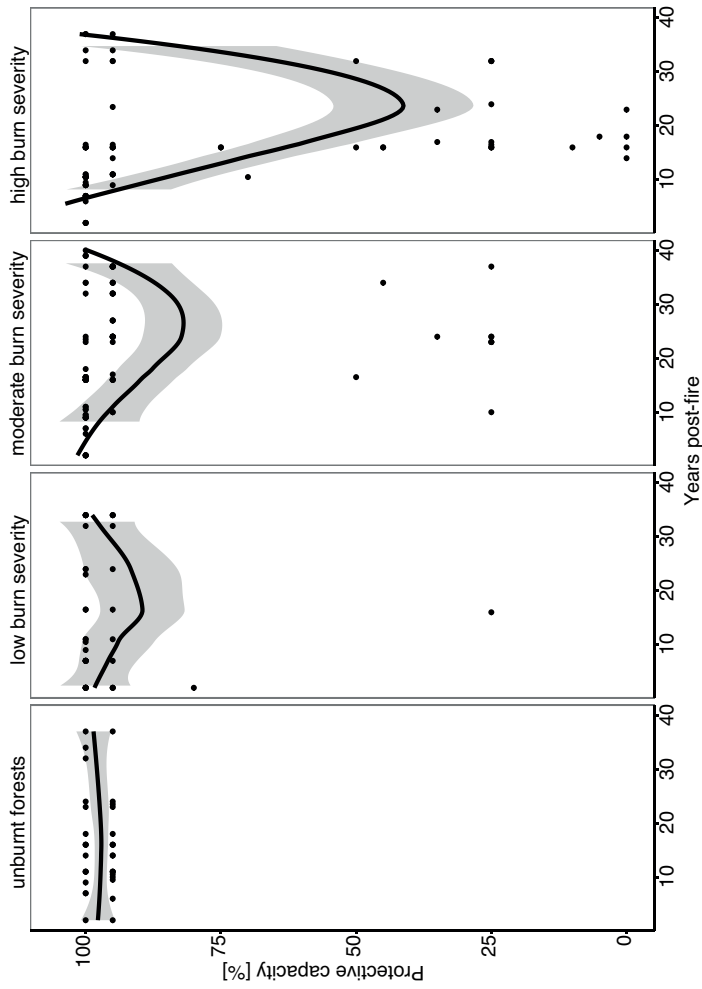


Figure E.5: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.05 m^3 , on 150 m forested slopes and 30° slope inclination

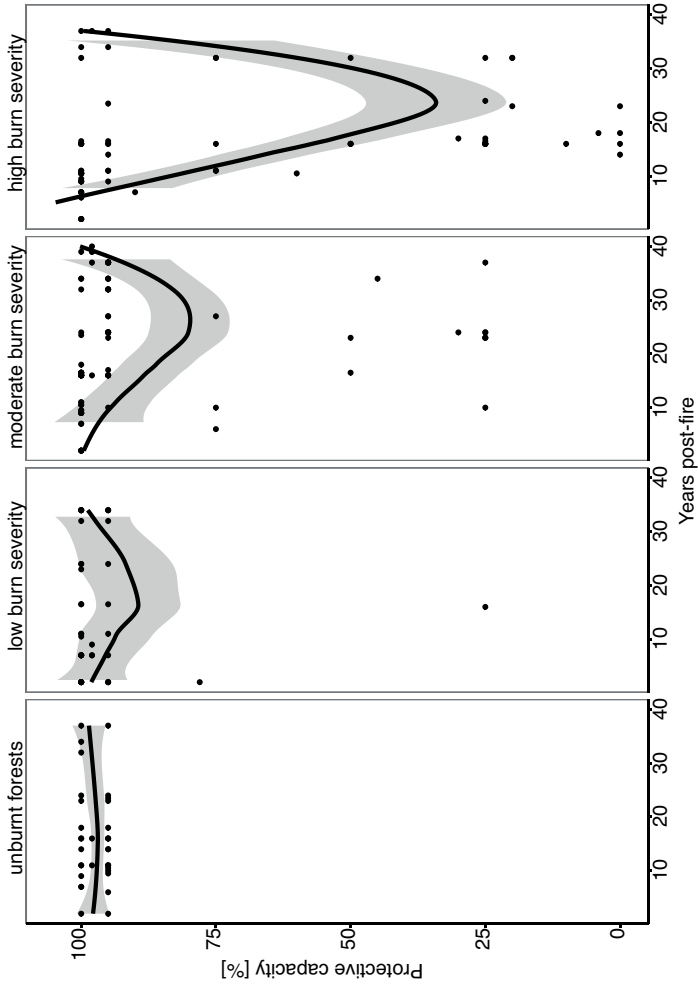


Figure E.6: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.05 m^3 , on 150 m forested slopes and 35° slope inclination

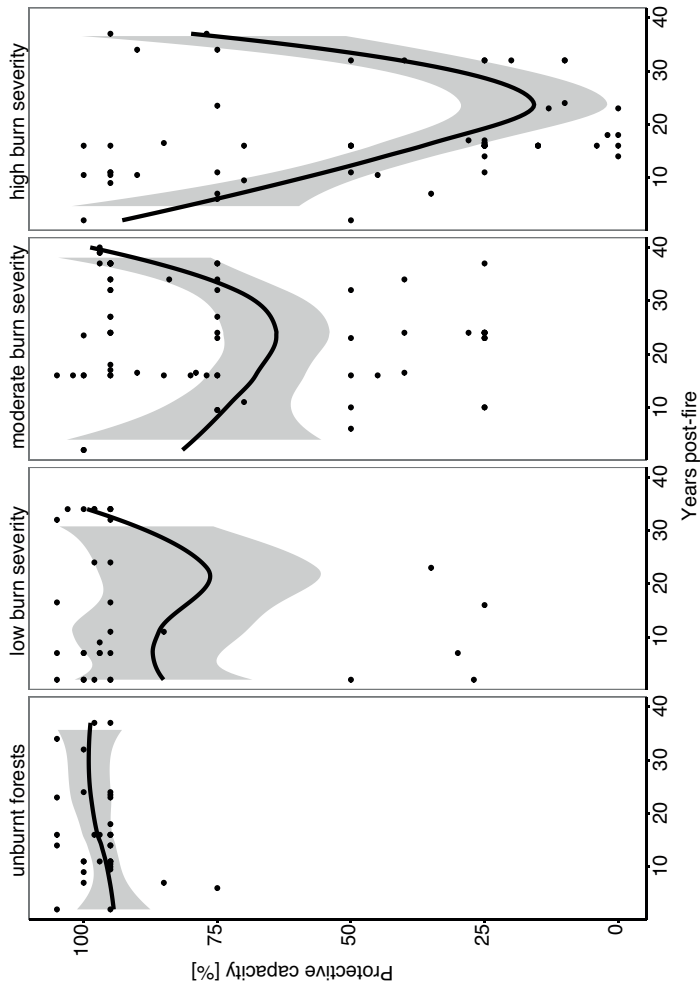


Figure E.7: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.2 m^3 , on 75 m forested slopes and 27° slope inclination

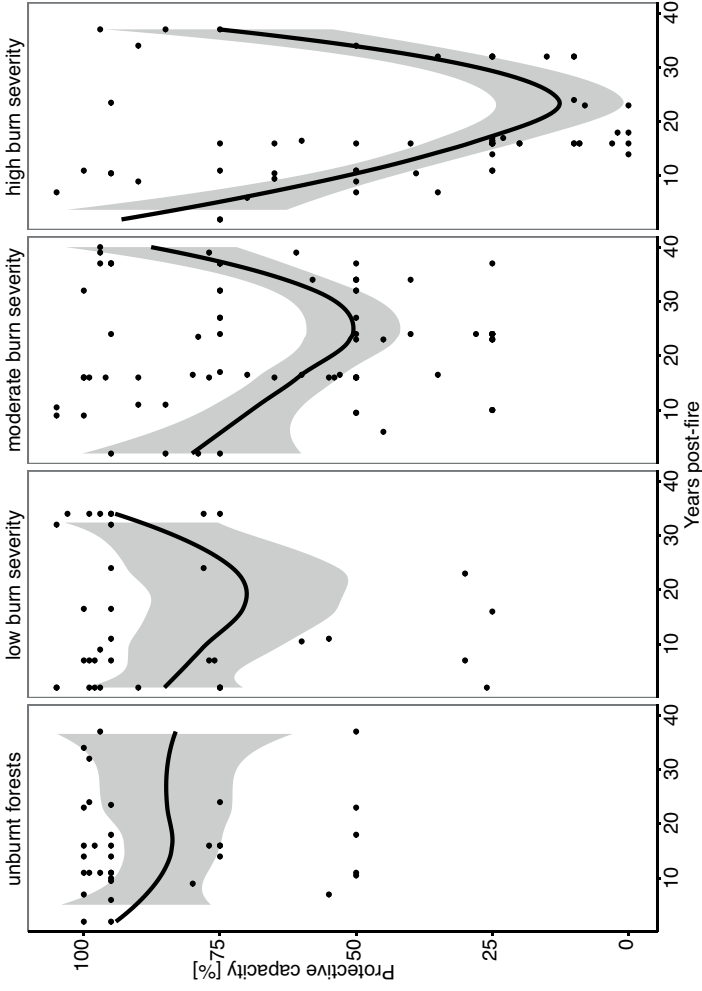


Figure E.8: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.2 m^3 , on 75 m forested slopes and 30° slope inclination

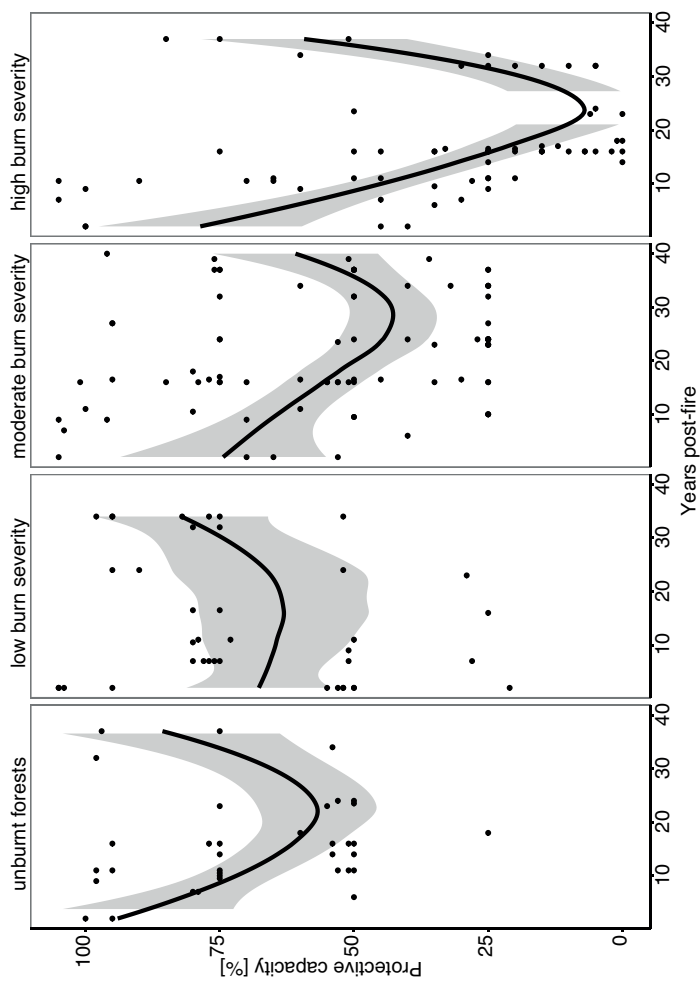


Figure E.9: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.2 m^3 , on 75 m forested slopes and 35° slope inclination

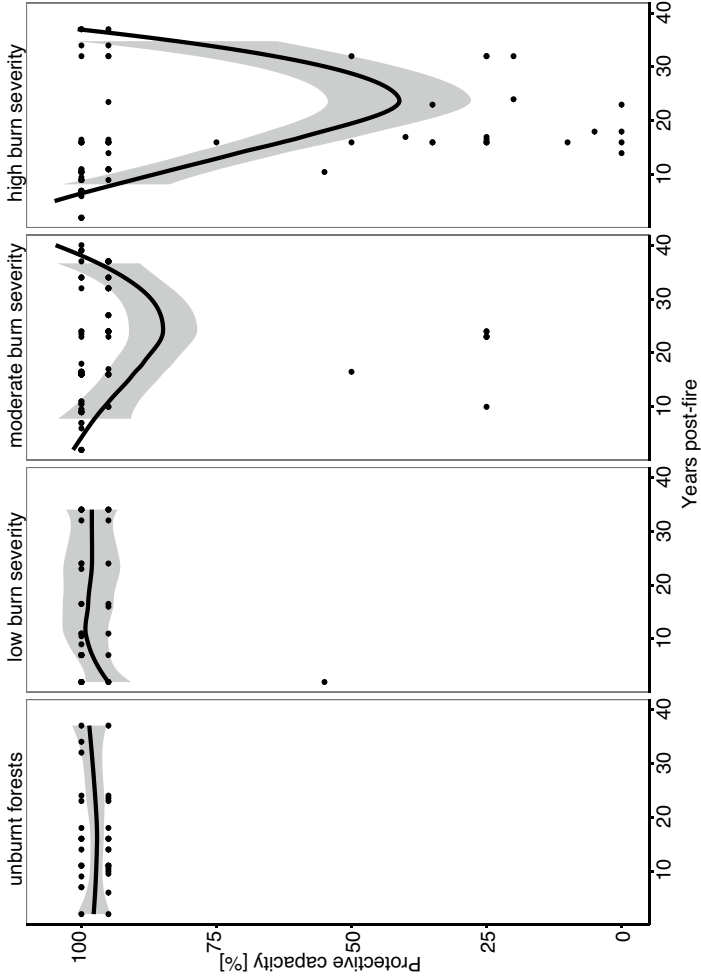


Figure E.10: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.2 m³, on 150 m forested slopes and 27° slope inclination

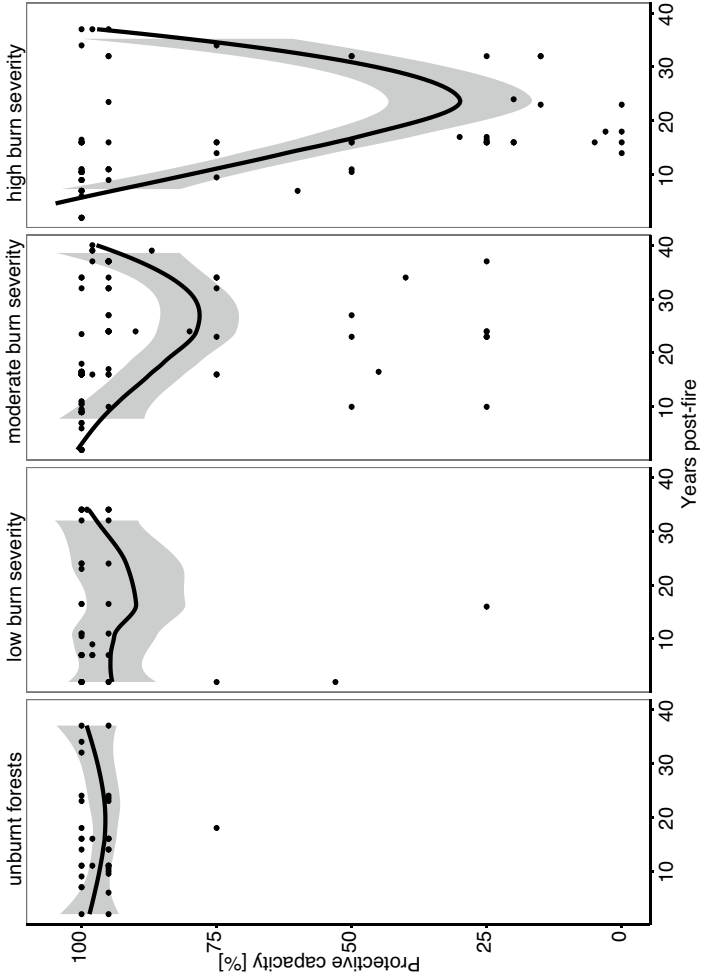


Figure E.11: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.2 m^3 , on 150 m forested slopes and 30° slope inclination

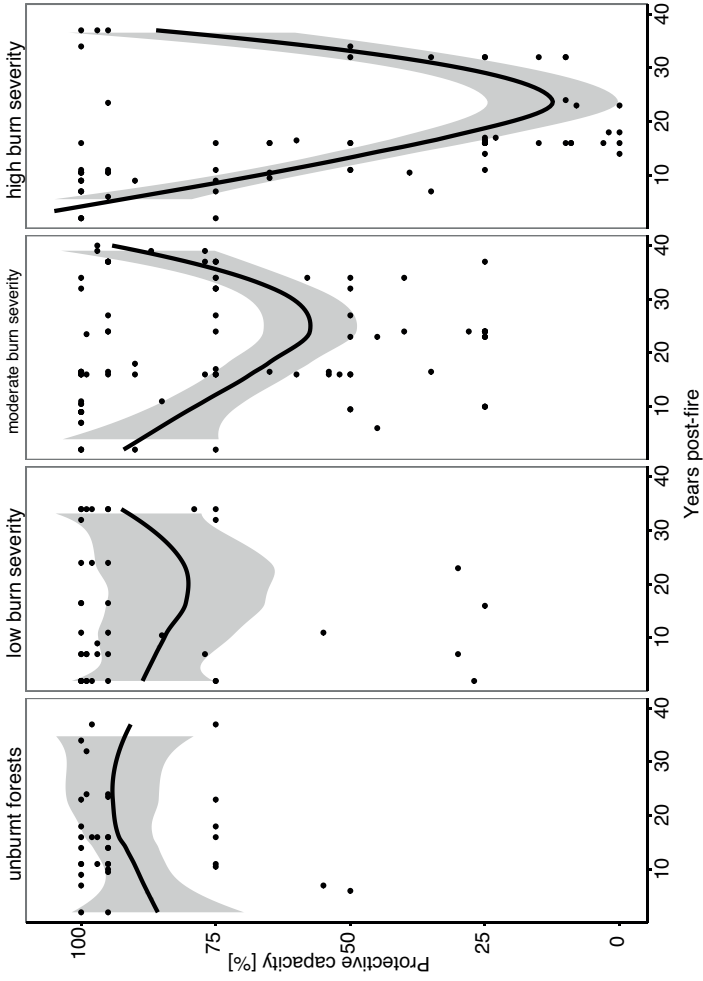


Figure E.12: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 0.2 m³, on 150 m forested slopes and 35° slope inclination

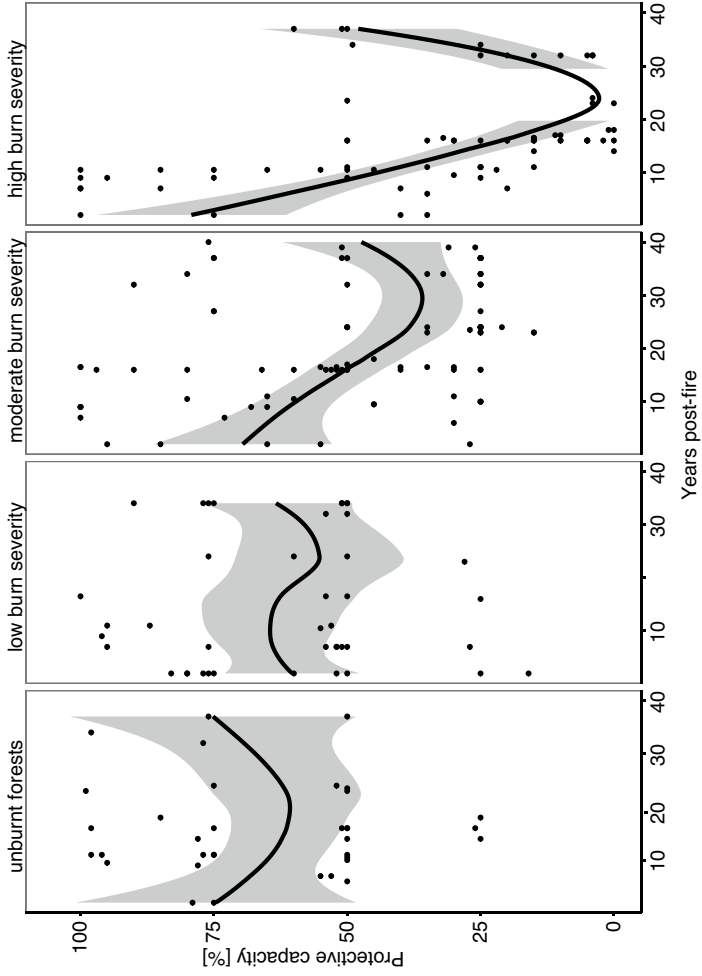


Figure E.13: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned forests against rocks of 1 m³, on 75 m forested slopes and 27° slope inclination

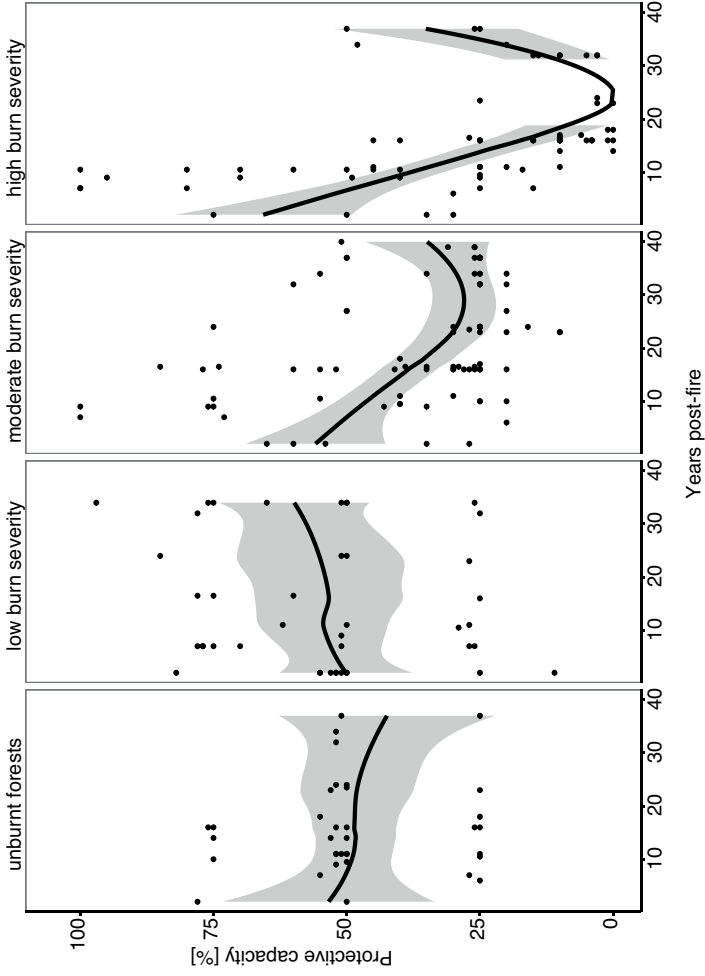


Figure E.14: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 1 m³, on 75 m forested slopes and 30° slope inclination

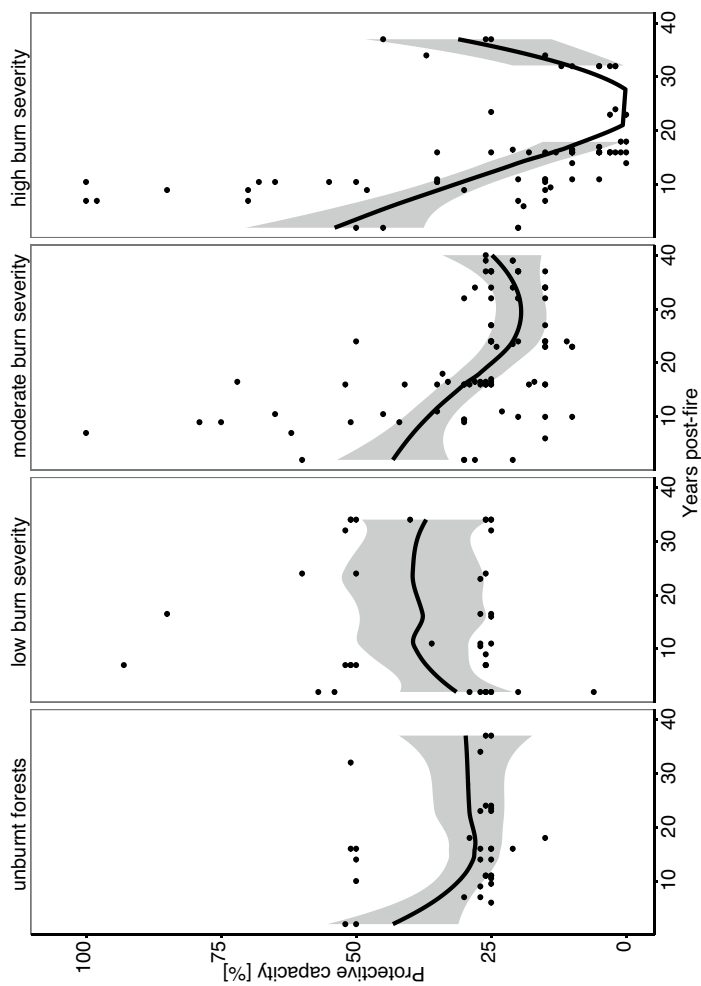


Figure E.15: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 1 m^3 , on 75 m forested slopes and 35° slope inclination

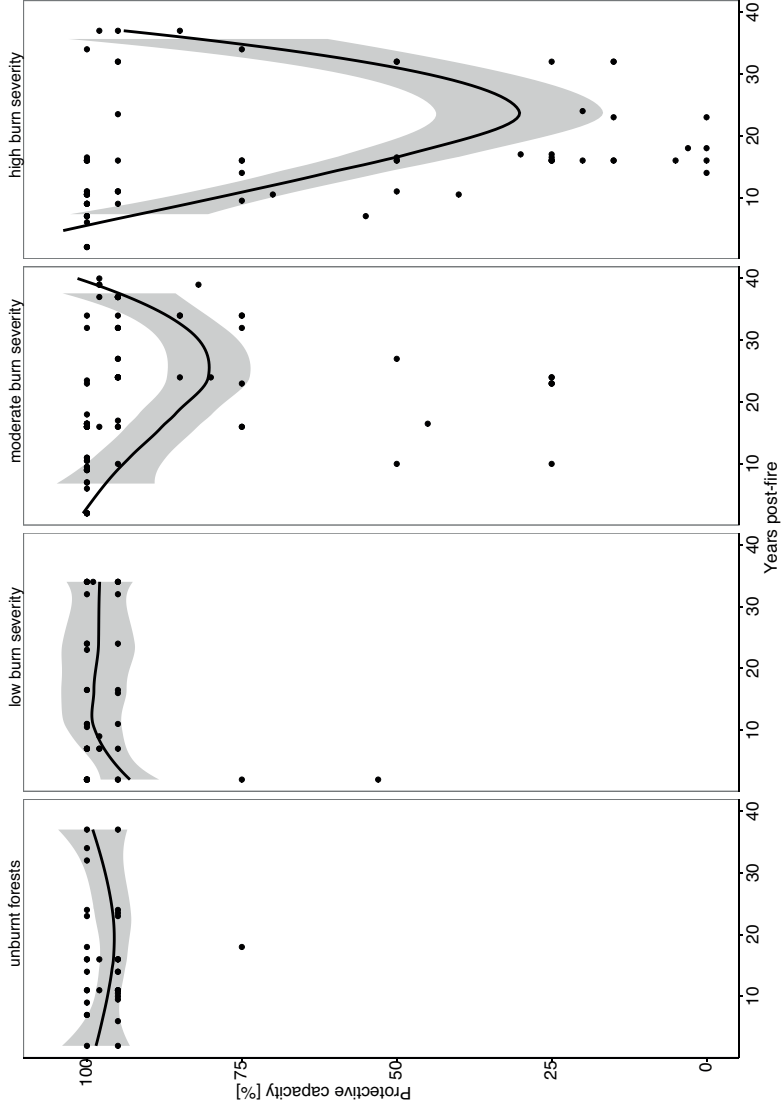


Figure E.16: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 1 m³, on 150 m forested slopes and 27° slope inclination

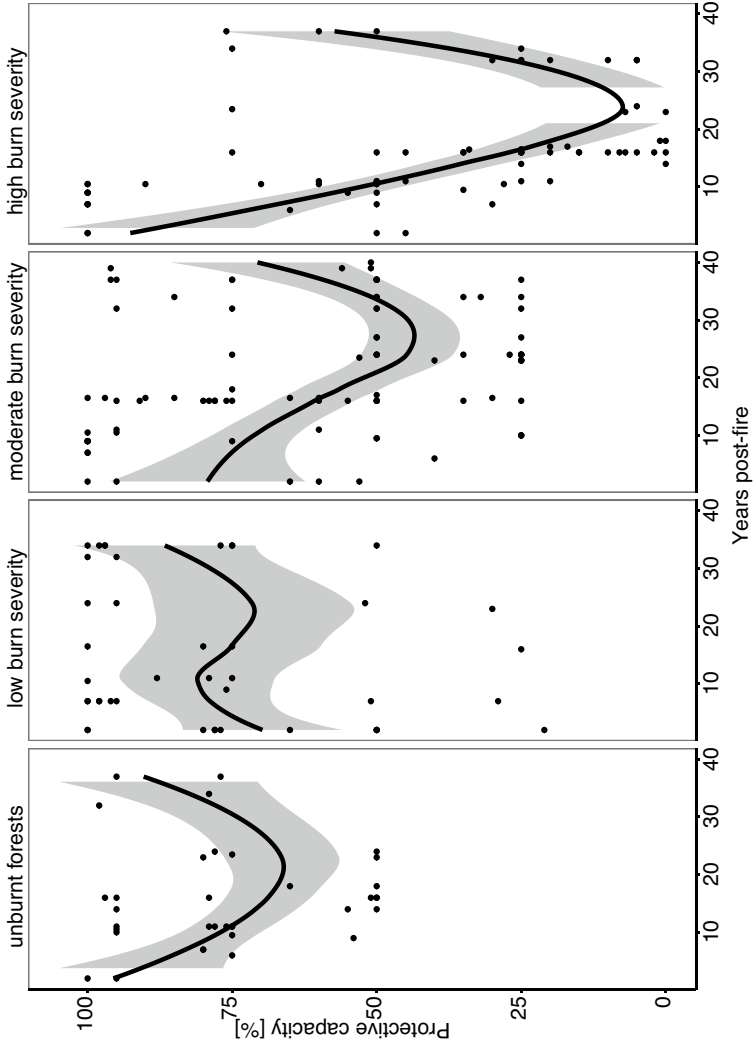


Figure E.17: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 1 m³, on 150 m forested slopes and 30° slope inclination

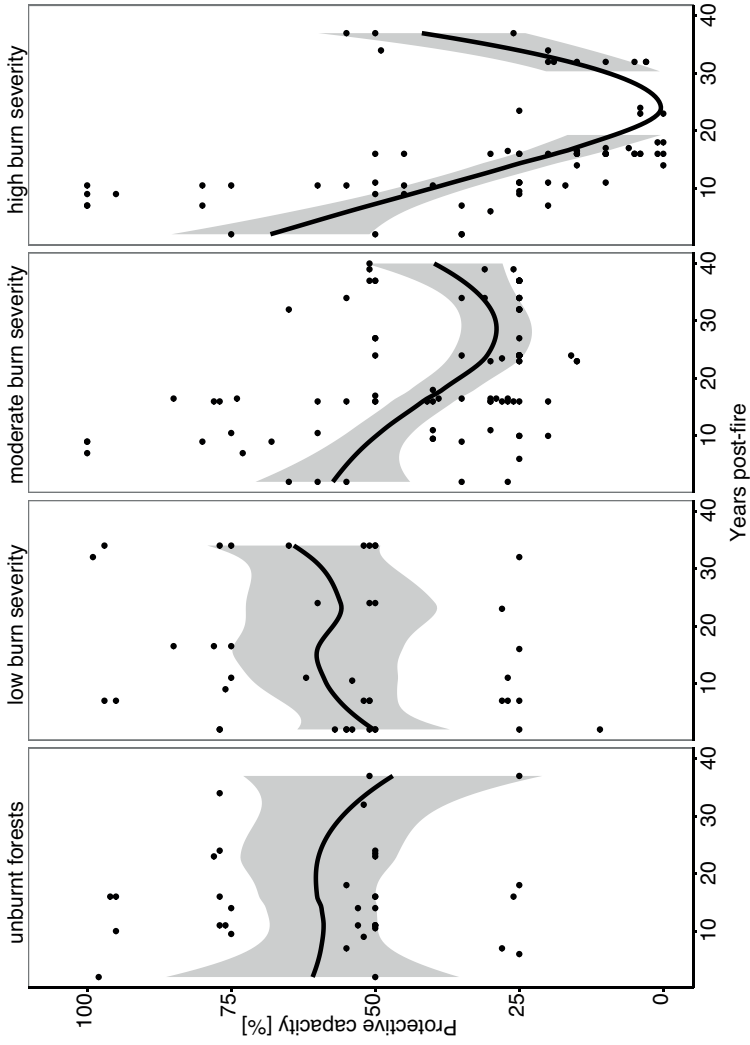


Figure E.18: Temporal trends in the protective capacity [%] of beech stands hit by low, moderate and high burn severity and the corresponding unburned beech forests against rocks of 1 m^3 , on 150 m forested slopes and 35° slope inclination

Appendix F

Model results of temporal trends in the forest protective capacity of burned and unburned beech forests

Table F.1: Results of the linear regression model for all 72 scenarios specification detecting temporal trends in the forest protective capacity.

Scenario	Stone size [m ³]	Slope length [m]	Slope inclination [°]	in-clination	Model	Intercept	AGE	AGE ²
0.05	75	27		Control	***	ns	ns	
				Sev1	+	**	ns	
				Sev2	+	•	ns	
0.05	150	27		Sev3	+	***	***	
				Control	+	***	ns	
				Sev1	+	***	ns	
0.05	75	30		Sev2	+	***	•	
				Sev3	+	***	•	
				Control	+	***	ns	
0.05	150	30		Sev1	+	***	ns	
				Sev2	+	***	•	
				Sev3	+	***	•	
0.05	75	35		Control	+	***	ns	
				Sev1	+	***	ns	
				Sev2	+	***	•	
0.05	150	35		Sev3	+	***	•	
				Control	+	***	ns	
				Sev1	+	***	ns	
0.05	75	35		Sev2	+	***	•	
				Sev3	+	***	•	
				Control	+	***	ns	

Scenario	Slope length [m]	Slope in-clination [°]	Model	Intercept	AGE	AGE ²
0.05	150	35	Control	(+)	ns	ns
			Sev1	(+)	ns	ns
			Sev2	(+)	(-)	(+)
			Sev3	(+)	(-)	(+)
0.2	75	27	Control	(+)	ns	ns
			Sev1	(+)	ns	ns
			Sev2	(+)	(-)	(+)
			Sev3	(+)	(-)	(+)
0.2	150	27	Control	(+)	ns	ns
			Sev1	(+)	ns	ns
			Sev2	(+)	(-)	(+)
			Sev3	(+)	(-)	(+)
0.2	75	30	Control	(+)	ns	ns
			Sev1	(+)	ns	ns
			Sev2	(+)	(-)	(+)
			Sev3	(+)	(-)	(+)
0.2	150	30	Control	(+)	ns	ns
			Sev1	(+)	ns	ns
			Sev2	(+)	(-)	(+)
			Sev3	(+)	(-)	(+)

Scenario	Stone size [m ³]	Slope length [m]	Slope inclination [°]	in-clination	Model	Intercept	AGE	AGE ²
0.2	75	35		Control	(+)	(-)	(-)	(+)
				Sev1	(+)	ns	ns	ns
				Sev2	(+)	(-)	(-)	(+)
0.2	150	35		Sev3	(+)	(-)	(-)	(+)
				control	(+)	ns	ns	ns
				Sev1	(+)	ns	ns	ns
1	75	27		Sev2	(+)	(-)	(-)	(+)
				Sev3	(+)	(-)	(-)	(+)
				Control	ns	ns	ns	ns
1	150	27		Sev1	ns	ns	ns	ns
				Sev2	(+)	(-)	(-)	(+)
				Sev3	(+)	(-)	(-)	(+)
1	75	30		Control	(+)	ns	ns	ns
				Sev1	(+)	(-)	(-)	(+)
				Sev2	(+)	(-)	(-)	(+)
1	75	30		Sev3	(+)	(-)	(-)	(+)
				Control	ns	ns	ns	ns
				Sev1	(+)	(-)	(-)	(+)

Scenario	Stone size [m ³]	Slope length [m]	Slope inclination [°]	Model	Intercept	AGE	AGE ²		
1	150	30	Control	(+)	***	(-)	***		
			Sev1	(+)	*	ns	ns		
			Sev2	(+)	***	(-)	**	(+)	**
			Sev3	(+)	***	(-)	***	(+)	***
1	75	35	Control	ns	ns	(-)	●		
			Sev1	(+)	**	ns	ns		
			Sev2	(+)	*	(-)	**	(+)	●
			Sev3	(+)	**	(-)	***	(+)	***
1	150	35	Control	ns	ns	ns	ns		
			Sev1	ns	ns	ns	ns		
			Sev2	(+)	*	(-)	**	(+)	●
			Sev3	(+)	***	(-)	***	(+)	***

Appendix G

Names of species

Table G.1: Tree species names in Latin, German and English

Species name	German	English
<i>Acer campestre</i> L.	Feld-Ahorn	Field maple
<i>Acer pseudoplatanus</i> L.	Berg-Ahorn	Sycamore maple
<i>Acer platanoides</i> L.	Spitzahorn	Norway maple
<i>Acer opulifolium</i> Chaix	Schneeball Ahorn	Italian maple
<i>Ailanthus altissima</i> (Mill.) Swingle	Götterbaum	Tree of heaven
<i>Alnus glutinosa</i> (L.) Gaertn.	Schwarz-Erle	Common alder
<i>Betula pendula</i> Roth.	Hänge-Birke	Silver birch
<i>Castanea sativa</i> Mill.	Eßkastanie	Sweet-chestnut
<i>Corylus avellana</i> L.	Hasel	Common hazel
<i>Cytisus scoparius</i>	Besenginster	Common broom
<i>Fagus sylvatica</i> L.	Rotbuche	European beech
<i>Fagus grandifolia</i> Ehrh.	Amerikanische Buche	American beech
<i>Fagus orientalis</i> Lipsky.	Orientalische Buche	Oriental beech
<i>Fraxinus excelsior</i> L.	Eberesche	Ash
<i>Frangula alnus</i> Mill.	Faulbaum	Alder buckthorn
<i>Ilex aquifolium</i> L.	Stechpalme	Holly
<i>Juglans regia</i> L.	Walnuss	Persian walnut
<i>Larix decidua</i> Mill.	Lärche	European larch
<i>Laburnum alpinum</i> J. Presl.	Goldregen	Scotch laburnum
<i>Molinia arundinacea</i>	Pfeifengras	Purple moor grass
<i>Paulownia tomentosa</i> Thunb.	Blauglockenbaum	Empress tree

Species name	German	English
<i>Populus nigra</i> L.	Schwarz-Pappel	Black poplar
<i>P. tremular</i> L.	Zitterpappel	Aspen
<i>P. alba</i> L.	Silberpappel	Silver poplar
<i>Prunus avium</i> L.	Vogel-Kirsche	Wild cherry
<i>Picea abies</i> L.	Gemeine Fichte	Norway spruce
<i>Pinus sylvestris</i> L.	Waldkiefer	Scotch pine
<i>P. strobus</i> L.	Weymouth-Kiefer	Eastern white pine
<i>Pteridium aquilinum</i>	Adlerfarn	Common bracken
<i>Quercus petraea</i> Mattuschka	Traubeneiche	Sessile oak
<i>Q. pubescens</i> Willd.	Flaumeiche	Downy oak
<i>Robinia pseudoacacia</i> L.	Gewöhnliche Robinie	Black locust
<i>Salix caprea</i> L.	Salweide	Goat willow
<i>Sorbus aucuparia</i> L.	Vogelbeere	Rowan
<i>Sorbus aria</i> L.	Echte Mehlbeere	Whitebeam
<i>Taxus baccata</i> L.	Europäische Eibe	European yew
<i>Tilia cordata</i> Mill.	Winterlinde	Small-leaved linden

Appendix H

Admission forms

Table H.1: Notes on the admission form

Abbreviation	Explanation
area code	First three letters of the municipality, fire date
plot ID	Continued implementation
N and E	GPS coordinates
tree cover 1.3—5.0 (%)	Crown cover in the height between 1.3-5.0 m above the ground
tree cover >5.0 (%)	Crown cover in the height >5.0 m above the ground
Monokot (%)	Cover of grasses
Dikot (%)	Cover of herbs
Pteridium (%)	Cover of Pteridium aquilinum
Cytisus (%)	Cover of Cytisus
Litter (%)	Cover of litter
Bare soil	Cover of bare soil
CWD	Cover of coarse woody debris
Date	Date of field assessment
Convex, plane, concave	Micro-topography
Dendroprobe	Number of saples for dendrochronological determination
Crown closure	See (Keller, 2005)
Species	Species name
Dead or alive	Vitality status
E	Logs
D	Standing tree
Wood.comp	Class of wood decay
DBH (cm)	Diameter to breast height in 1.3 m
Ddam.bark (%)	Porportion of damaged bark
Wound (m)	Fire scar height
Fungi	Fungi cover class
Height (m)	Height of the standing tree
Length (m)	Length of the log
Layer	Social position of the tree (US = sublayer, MS = medium layer, OB = upper layer)
Crown length (%)	Length of the tree crown in relation to the length of the whole tree
Lost habitus (%)	Porportion of lost in relation to the undisturbed tree
Foliage (%)	Porportion of leaves lost
Lop sided tree (°)	Relation to the vertical lead
Root (1–10)	Anchorage of the root on a 10-degree scale
Basal shoots	Number and height of basal shoots

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Acknowledgement

Many helping hands have supported this work and I would like to thank all of them. In the first place, I would like to thank Prof. Dr. Kaule for the support of my thesis and the constructive comments on my manuscript. I also thank my second examiner Prof. Dr. Schmidlein (Karlsruher Institute of Technology) for supporting my research. I appreciate our fruitful discussions.

When it came to this stage, that I had to write the acknowledgement, I went back in my memories and thought how everything started. It was in spring of 2009, when I attended an excursion under the leadership of Dr. Christophe Neff (Karlsruher Institute of Technology) to Ticino. Christophe Neff introduced me to Dr. Marco Conedera – the head of the WSL (Swiss Federal Institute for Forest, Snow and Landscape) in Bellinzona. During this excursion, we went to a large fire site close to the village of Cugnasco. And without any real wildfire I caught fire for the topic of fire ecology. Marco offered me a Diploma-Thesis and so I did my steps in the research field of fire ecology. After finishing my Diploma-Thesis, Marco pushed me to write my first paper based on the work I have done for the Diploma thesis. During this stage, he introduced me to Dr. Thomas Wohlgenuth (WSL- Birmensdorf), who taught me more about ecology, statistic and structured scientific writing. After one year my first scientific paper was published. But this was not the end of the story because we still had so many open questions.

The idea came to our minds that a project in beech fire ecology

would be nice, because we discovered so many interesting things in the fire site of Cugnasco. In the beginning we had no financial support for the project, but one thing led to another – I was employed by the Institute of Landscape Planning and Ecology and became a PhD-student. So I was able to start this part of the project, which is covered by my thesis. At this point, I would like to thank Dr. Hans-Georg Schwarz von Raumer, Dr. Susanne Kost and Christina Kölking, who always had an open ear for me. At the same time as I started my work in Stuttgart, Marco got some funding for the beech fire ecological project from the Swiss Federal Office for the Environment. Now we were able to start the field work and extend the research area.

Still my field work and thus my thesis was based on weak ground because my son was newly born. Luckily my mother-in-law and my husband spent all their holidays for taking care of him and Yolanda and Marco Conedera gave us a warm and comfortable home for two summers. Moreover I had great helpers, who assisted me during the field work. Thanks goes to Franco Fibbioli, Simone Giavi, Marianne Steffen, and Jordi Murgadas from the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Sven Hofmann from the University of Karlsruhe (Germany), Lisa Berghäuser from the University of Potsdam.

After the field work in Ticino, we planned to extend the research area to the neighboring region of Piedmont (Italy) and here Davide Ascoli made everything possible to investigate in another eight burns. We spent a summer working hard with incredible helpers in the field – and Davide opened my mind to the post-fire management perspective and to the topic of beech masting behavior. Thanks Davide, I really enjoyed and still enjoy our endless discussions on beech fire ecology.

After fieldwork it was time to analyze my data and I am thankful to Michael – my husband – who gave me technical support and made lots of things possible. It was a tough time and I was stuck in R-codes trying to find solutions and explanations for so many open questions. There was Tom Wohlgemuth again who told me: "Janet,

first you have to learn how to walk before you start doing races." This advice opened my mind— and the data analysis worked. I'm thankful for Tom's and Marco's time, who taught me with patience how to write papers. Additionally, they are the co-authors contributing to determine the fungi species (Dr. Nicolas Küffer) or helping in understanding rockfall models (Dr. Peter Bebi, Prof. Dr. Luuk Dorren).

Last but not least there were lots of friends and family members who supported me with their time and patience. And special thanks to Michael and Jacob.

Publications and picture credits

Prior publications

This thesis is based on the work reported in the following papers. The prior publications were authorized by the PhD Committee presided by Prof. Dr. J. Jessen.

Peer-reviewed papers

1. Maringer, J.; Conedera, M.; Ascoli, D.; Schmatz, D.R.; Wohlgemuth, T. (in press): Resilience of European beech forests (*Fagus sylvatica* L.) after fire in a global change context. *Journal of Wildland Fire*.
 - The contribution of Janet Maringer to this paper included the responsibility for the experimental design, the field work (under assistance of Franco Fibbioli, Simone Giavi, Marianne Steffen, Lisa Berghäuser, and Jordi Murgadas from the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), and Sven Hofmann from the University of Karlsruhe), and the data analysis. Thomas Wohlgemuth and Janet Maringer were responsible for the paper concept. Janet Maringer was corresponding author

and the main author responsible for writing the text with contributions from other authors.

2. Maringer, J.; Ascoli, D.; Küffer, N.; Schmidlein, S.; Conedera, M. (2016): What drives European beech (*Fagus sylvatica* L.) mortality after forest fires of varying severity? *Forest Ecology and Management* 368: 81-93.

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- The contribution of Janet Maringer to this paper included the responsibility for the experimental design, the field work (under assistance of Franco Fibbioli, Simone Giavi, Marianne Steffen, Lisa Berghäuser, and Jordi Murgadas from the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), and Sven Hofmann from the University of Karlsruhe), and the data analysis. Nicolas Küffer determined the fungi species. Janet Maringer was responsible for the paper concept, corresponding author and the main author responsible for writing the text with contributions from other authors.

3. Maringer, J.; Ascoli, D.; Dorren, L.; Bebi, P.; Conedera, M. (subm.): Temporal trends in the protective capacity of burned beech forests (*Fagus sylvatica* L.) against rockfall. *European Journal of Forest Research*.

- The contribution of Janet Maringer to this paper included the responsibility for the experimental design, the field work (under assistance of Franco Fibbioli, Simone Giavi, Marianne Steffen, Lisa Berghäuser, and Jordi Murgadas from the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), and Sven Hofmann from the University of Karlsruhe), and the data analysis. Luuk Dorren was responsible for calculate the protective capacity, and Janet Maringer for data processing in R (R

Development Core Team, 2014). Marco Conedera and Janet Maringer were responsible for the paper concept. The latter was corresponding author and the main author responsible for writing the text with contributions from other authors.

Conference papers:

- Maringer, J.; Ascoli, D.; Wohlgemuth, T.; Bovio, G.; Conedera, M. (2013): Fire effects and post-fire management on beech forests in the Southern Alps. [Abstract] In: Wohlgemuth, T.; Priewasser, K. (eds) ClimTree 2013. International Conference on Climate Change and Tree Responses in Central European Forests. Conference, 1 to 5 September 2013. Abstracts. Birnmensdorf, Swiss Federal Institute for Forest, Snow and Landscape WSL.
- Maringer, J.; Wohlgemuth, T.; Ascoli, D.; Neff, C.; Conedera, M. (2013): Wie regenerationsfähig sind Zentraleuropäische Buchenwälder (*Fagus sylvatica* L.) nach Waldbrand? 58. Deutscher Geographentag, 2.10-8.10.2013, Passau.

Further publications to the issue of fire ecology:

- Maringer, J.; Wohlgemuth, T.; Neff, C.; Pezzatti, G.B.; Conedera, M. (2012): Post-fire spread of alien plant species in a mixed broad-leaved forest of the Insubric region. *Flora* 207, 19-29.
- Ascoli, D.; Vacchiano, G.; Maringer, J.; Bovio, G.; Conedera, M. (2015): The synchronicity of masting and intermediate severity fire effects favors beech recruitment. *Forest Ecology and Management* 353, 126-135.

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