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Quantity and quality of coarse woody debris in mountainous Norway spruce forest reserves in Switzerland

Master thesis at the Chair of Forest Ecology, Department of Environmental Systems Sciences, ETH Zurich, and at the Research Unit Forest Resources and Forest Management, WSL Birmensdorf.

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SUMMARY

Dead wood of high quantities, different dimensions and decay stages provides a key habitat for a variety of forest species (e.g. fungi, lichens, bryophytes or beetles) and is acknowledged as a good indicator for a forest's naturalness. This master thesis focuses on the lying dead wood component. The purpose was to investigate for the first time the dead wood dynamic in seven Swiss mountainous Norway spruce (*Picea abies*) dominated forest reserves in a permanent plot inventory and to provide a first reference for the governmental biodiversity strategy in managed stands. Therefore, lying dead wood quantity and quality was assessed in field and statistically related to site, stand and climate conditions, past disturbances and former management regime. Furthermore, the spatial pattern of dead wood with respect to orientation and distribution was analyzed.

The investigated forest reserves featured on average lying dead wood volumes of 80 ± 23 m^3/ha, generally consisting of large dimensions and advanced decomposition stages, two quality features particularly important for saproxylic species. Statistical modeling by several environmental factors was limited to 24 investigated permanent plots only and the effect of the examined factors could only be partly understood. More study plots might alleviate this problem. Concerning spatial pattern analysis, hillside orientation, slope inclination and past wind disturbances were main drivers influencing the falling direction of logs. The results of spatial pattern analysis largely confirm that the spatial pattern of standing trees directly influences the spatial pattern of logs and that the stand age affects the spatial clustered or random distribution of dead wood.

The found values of dead wood quantity and quality are comparable to other coniferous forest reserves across Europe. Nevertheless, traces of former management are still partly visible, particularly in the diameter and spatial distribution of dead wood. The analyses suggest that the governmental biodiversity strategy well aims the implementation of a continuous temporal and spatial distribution of dead wood, but the targeted volumes are only partly sufficient to preserve the forest biodiversity. Moreover, important quality features such as for example large dimensions are not included in the biodiversity strategy.

ZUSAMMENFASSUNG

Totholz in grossen Mengen, unterschiedlichen Dimensionen und Zersetzungsstadien bietet ein wertvolles Habitat für eine Vielfalt von waldbewohnenden Arten (z.B. Pilze, Flechten, Moose oder Käfer). Zudem gilt Totholz als guter Indikator für die Naturnähe eines Waldes. Diese Masterarbeit legt den Fokus auf die liegende Totholzkomponente. Das Ziel war die erstmalige Untersuchung der Totholzdynamik in sieben Schweizer Fichten (*Picea abies*) dominierten Gebirgswaldreservaten auf Kernflächenebene sowie die Erarbeitung eines ersten Referenzwertes für die Biodiversitätsstrategie des Bundes in bewirtschafteten Wäldern. Dazu wurden Totholzquantität und –qualität im Feld erfasst und statistisch in Beziehung gesetzt zu Standort, Klima, früheren Störungen und einstiger Nutzung. Zudem wurden die räumliche Orientierung und Verteilung des Totholzes analysiert.

Die untersuchten Waldreservate wiesen ein durchschnittliches liegendes Totholzvolumen von 80 ± 23 m^3/ha auf, welches sich generell aus dicken Durchmessern und fortgeschrittenen Zersetzungsstadien zusammensetzte; zwei Qualitätseigenschaften, welche für totholzabhängige Arten besonders wichtig sind. Die statistische Analyse durch die verschiedenen Umweltfaktoren war durch die geringe Anzahl von nur 24 untersuchten Kernflächen limitiert und die Bedeutung der einzelnen untersuchten Faktoren konnte nur teilweise erklärt werden. Eine grössere Anzahl an Untersuchungsflächen könnte diesem Problem entgegenwirken. Exposition, Hangneigung und vergangene Windstörungen erwiesen sich als wichtige Einflussfaktoren bezüglich der Fallrichtung des Totholzes. Die Resultate bestätigen weitgehend dass die räumliche Anordnung der stehenden Bäume diejenige der liegenden toten Bäume beeinflusst und dass das Bestandesalter eine Auswirkung auf die räumliche aggregierte oder zufällige Verteilung des Totholzes hat.

Die Totholzquantität und –qualität in den untersuchten Waldreservaten sind vergleichbar mit anderen Nadelwaldreservaten in Europa. Allerdings sind die Spuren vergangener Holznutzung teilweise immer noch sichtbar, insbesondere in der Durchmesser- und räumlichen Verteilung des Totholzes. Diese Arbeit zeigt, dass die Biodiversitätsstrategie des Bundes eine kontinuierliche zeitliche und räumliche Totholzverteilung zielorientiert umsetzen will. Die anvisierten Volumina genügen jedoch nur teilweise zur Erhaltung der Artenvielfalt im Wald und wichtige Qualitätsmerkmale wie zum Beispiel dicke Durchmesser sind darin nicht berücksichtigt.

RÉSUMÉ

Le bois mort en grande quantité et de différentes dimensions et stade de décomposition offre un habitat fondamental à une grande variété d'espèces de la forêt (ex. champignons, lichens, mousses ou coléoptères) et est reconnu comme un bon indicateur de l'état naturel d'une forêt. L'accent majeur de ce travail de master porte sur le bois mort au sol. Le but était d'analyser pour la première fois la dynamique du bois mort dans sept réserves forestières dominées par l'épicéa (*Picea abies*) dans les montagnes suisses sur la base d'un inventaire des placettes permanentes et de fournir ainsi une première valeur de référence concernant la stratégie nationale pour la biodiversité des forêts exploitées. Pour cela, la quantité et la qualité du bois mort au sol étaient furent évaluées sur le terrain et ensuite mises en corrélation statistique avec le lieu, le climat, les perturbations passées et le mode d'exploitation précédente. En outre, l'orientation et la distribution spatiale du bois mort furent aussi analysées.

Les réserves forestières examinés présentaient en moyenne un volume de bois mort au sol de 80 ± 23 m^3/ha ; ce bois mort était en général de grosses dimensions et avait un niveau de décomposition avancé, deux caractéristiques qualitatives particulièrement importantes pour les espèces saproxyliques. L'analyse statistique des différents facteurs environnementaux fut limitée puisque seul 24 lieux furent étudiés. De ce fait l'effet des facteurs n'a pu être que partiellement compris. Un plus grand nombre de placettes pourrait parer à ce problème. Concernant le modèle spatial, l'exposition, la pente et les tempêtes passées ont principalement influencé la direction de chute des troncs. Les analyses confirment en grande partie que la disposition spatiale des arbres debout affecte directement celle des arbres tombés et que l'âge des peuplements a un effet sur la distribution spatiale groupée ou au hasard du bois mort.

La quantité et la qualité du bois mort examinées étaient comparables avec d'autres réserves forestières de conifères en Europe. Néanmoins, des traces de la gestion précédente étaient encore visibles dans certaines réserves forestières, particulièrement dans la variation des dimensions et de la distribution spatiale du bois mort. Les analyses suggèrent que la stratégie nationale pour la promotion de la biodiversité tien bien compte d'une distribution continue temporelle et spatiale mais les volumes présentés ne sont que partiellement suffisants pour la préservation de la biodiversité en forêt. De plus, des caractéristiques qualitatives importantes, comme par exemple la présence de bois mort de grosses dimensions, n'y sont pas mentionnées.

RIASSUNTO

Grandi quantità di legno morto di differenti dimensioni e in vari stati di decomposizione costituiscono un habitat fondamentale per la sopravvivenza di molte specie boschive (come ad esempio funghi, licheni, muschi e coleotteri) e sono riconosciute quale buon indicatore della naturalità del bosco. In questa tesi di master l'attenzione si è focalizzata sul legno morto al suolo. L'obbiettivo era di analizzare per la prima volta le dinamiche del legno morto in sette riserve forestali di montagna dominate dall'abete rosso (*Picea abies*) all'interno di aree di osservazione permanenti, e di fornire così dei primi valori di riferimento per la strategia nazionale per la promozione della biodiversità nel bosco. A tal fine sono state rilevate sul terreno quantità e qualità del legno morto, che sono poi state statisticamente correlate alla località geografica, alle associazioni forestali, alle condizioni climatiche, a perturbazioni passate e alla storia della precedente gestione forestale dei siti esaminati. È stato inoltre elaborato un modello spaziale prendendo in considerazione la direzione di caduta dei tronchi e la loro distribuzione al suolo.

I boschi esaminati presentavano mediamente 80 ± 23 m^3/ha di legno morto al suolo, costituiti in gran parte da alberi di grandi dimensioni e in avanzato stato di decomposizione, due caratteristiche particolarmente importanti per le specie saprofite. Il potere esplicativo dei modelli statistici si è rivelato limitato a causa delle sole 24 superfici analizzate; di conseguenza l'effetto dei fattori coinvolti ha potuto essere spiegato solo parzialmente. A questo problema si potrebbe potenzialmente ovviare prendendo in considerazione un maggior numero di località. Per quello che concerne il modello spaziale, l'esposizione del pendio e la sua inclinazione, unitamente a perturbazioni precedenti ad opera del vento, si sono rivelati fattori determinanti per la direzione di caduta dei tronchi. È stato pure confermato come nella maggior parte dei casi la disposizione topografica degli alberi eretti influenzi direttamente quella dei tronchi al suolo. Una maggiore età del bosco è correlata ad una distribuzione spaziale aggregata piuttosto che casuale del legno morto al suolo.

Il volume e la qualità del legno morto nei boschi esaminati sono risultati in linea con i valori di altre foreste primarie di conifere in Europa. Malgrado ciò, in alcuni casi erano ancora visibili tracce della precedente gestione, segnatamente nella composizione diametrica e nella distribuzione spaziale dei tronchi caduti al suolo. L'analisi suggerisce che la strategia nazionale per la promozione della biodiversità potrebbe essere adatta a raggiungere l'obbiettivo di una presenza spaziale e temporale continua di legno morto; malgrado ciò, i volumi auspicati sono solo parzialmente sufficienti a preservare la biodiversità del bosco nella sua integrità. Altri aspetti rilevanti, come ad esempio l'importanza di tronchi di grandi dimensioni, non vi sono menzionati.

LIST OF ABBREVIATIONS

AIC	Akaike Information Criteria
CWD	Coarse Woody Debris, lying dead wood with a minimum diameter of 7 cm and a minimum length of 2 m.
DBH	Diameter at Breast Height [cm], measured at a height of 1.3 m above ground.
ETH	Swiss Federal Institute of Technology, Zurich
FOEN	Swiss Federal Office of the Environment
ha	hectare: 100x100 m
MAAT	Mean Annual Air Temperature [°C], measured 2 m above ground
MAP	Mean Annual Precipitation sum [mm]
NFR	Natural Forest Reserve
PCA	Principal Component Analysis
PP	Permanent Plot
RDA	Redundancy Analysis
WSL	Swiss Federal Institute of Forest, Snow and Landscape Research, Birmensdorf

1 INTRODUCTION

In managed forests, dead wood is removed from the forest floor with the intention to avoid pest insect infestations, to reduce flammable material with respect to forest fires and to allow unhindered access for forestry operations (Montes and Cañellas 2006). However, standing and lying dead wood play significant roles in several ecological processes within the forest ecosystems. First, dead wood influences the forest microclimate as it provides long-term water and nutrient storage (Harmon et al. 1986). Second, coarse woody debris (CWD, i.e.: lying dead wood) serves as an important microsite for successful tree regeneration in higher elevations (Eichrodt 1969, Lachat et al. 2014). Third, dead wood stores carbon and thus contributes to the carbon sequestration of forest ecosystems in the global carbon cycle (Harmon 2001). In Swiss forests, about 2% (7 tons Carbon/ha) of the forest carbon stock is stored in dead wood (Rigling and Schaffer 2015). Lastly, dead wood is a key element for biodiversity in forests and provides a habitat for thousands of species depending on dead and down wood (Sverdrup-Thygeson et al. 2014). In Switzerland, about 6000 forest organisms (more than 20% of all forest species) require dead wood as a habitat and/or food resource (Rigling and Schaffer 2015). Examples of saproxylic (i.e. dead wood associated) species are fungi (Junninen et al. 2006), bryophytes (Ódor et al. 2006), lichens (Uliczka and Angelstam 2000) or beetles (Similä et al. 2003), several of them listed as endangered in national red lists (Sverdrup-Thygeson et al. 2014).

Besides the amount of dead wood (Müller and Bütler 2010), also its quality (Similä et al. 2003, Heilmann-Clausen and Christensen 2004, Lutz et al. 2012, Preikša et al. 2015) and its spatial distribution and continuity are decisive for the species diversity (Edman and Jonsson 2001, Grove 2002, Sverdrup-Thygeson et al. 2014). Quality features include the type of dead wood (lying or standing dead wood), the tree species, the decay stage and the dimension. Large dimensioned trees are particularly important for many species as they decay slower than small dimensioned trees, thus remain longer in the forest ecosystem and form a more continuous habitat (Lachat et al. 2014).

In Switzerland, natural forest dynamic is investigated systematically within the long-term forest reserves project, a collaboration project between the Swiss Federal Institute of Technology Zurich (ETH Zurich), the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL Birmensdorf) and the Swiss Federal Office of the Environment (FOEN, (Wunder et al. 2007)). The first natural forest reserve, Scatlè, was established in 1910 (Bugmann and Brang 2009). The origin of the natural forest reserve (NFR) network goes back to the late 1940s (Leibundgut 1957). Since then, the network has been steadily expanded and today consists of 49 NFRs (Heiri et al. 2011). Any management activity is prohibited and the forest reserve status is ensured by a longtime contract with the forest owner.

The purpose of research in NFRs is a deeper understanding of uninterrupted forest development for the most predominant forest types of Switzerland (Bugmann and Brang 2009). Furthermore, natural forest research should provide reference values for the governmental biodiversity policy and the related cantonal support measures in managed Swiss forests (e.g. increase of dead wood amounts for promotion of forest biodiversity, (Swiss Federal Office of the Environment 2013)) in order to compare unmanaged and managed with respect to species richness, structural diversity and forest dynamics.

Since the establishment of the network, the forest dynamics in Swiss NFRs are explored by means of periodic inventories so that today long-term datasets exist (partly more than 50 years) on the level of permanent plots (PP) or compartments (Heiri et al. 2011).

Traditionally, only data of standing trees (living and dead) were collected and data of lying dead trees were missing. However, all components of dead wood, but in particular lying dead wood, are important to biodiversity (Preikša et al. 2015). Moreover, lying dead wood usually makes up the larger part of total dead wood in virgin forests (Korpel' 1997). Thus, a major part of information concerning dead wood is lacking if only standing dead trees are inventoried. Since 2007 the monitoring methods in the NFR project are supplemented by sample plot inventories in which also lying dead wood is recorded systematically (Heiri et al. 2011). Sampling of lying dead wood on PP level is not performed systematically due to time and budget limitations. Nevertheless, Herrmann et al. (2012) undertook the effort and analyzed lying and standing dead wood quantity and quality in 44 PPs of deciduous and deciduous mixed NFRs. However, studies about dead wood on PP level in mountainous Norway spruce (*Picea abies* (L.) H. Karst.) forests, the second most important forest type in the NFR network, are lacking. This thesis will fill this gap by analyzing natural small-scaled forest dynamic of lying (logs with minimal diameter ≥7 cm and minimal length ≥2 m) and standing (snags with diameter at breast height (DBH) ≥4 cm) dead wood with respect to volumes, stem numbers, tree species composition, diameter distribution and decay classes. Lying and standing dead wood data in all Swiss forests is periodically investigated in sample plot inventories of the National Forest Inventory (Brändli 2010). However, this thesis will provide a first reference value for the governmental biodiversity measures from permanent plot inventories in presently unmanaged coniferous forests.

In earlier studies in unmanaged and managed European forests, dead wood quantity and quality were related to many environmental and geographical factors. For example, Hahn and Christensen (2005) described higher dead wood volumes in submontane beech-fir forests in Slovenia than in southern boreal Norway-spruce dominated stands. Other studies reported significantly higher dead wood volumes, larger dimensioned logs and/or higher shares of advanced decay stages in forests being left unmanaged for an extended time (Siitonen et al. 2000, Christensen et al. 2005, Burrascano et al. 2008, Vandekerkhove et al. 2009, Seidling et al. 2014) and in stands with high living tree volumes (Sippola et al. 1998), which was used as a proxy for site productivity. In a virgin beech forest in Slovakia, the highest dead wood volumes occurred during the break-down stage (Saniga and Schütz 2001). Moreover, recent major disturbances (e.g. wind-throw, insect attacks, extreme weather conditions) led to particularly high dead wood volumes (Hahn and Christensen 2005, Seidling et al. 2014). This thesis aims to examine whether and if to what extent the dead wood data from mountainous coniferous NFRs in Switzerland are related to several environmental factors.

In literature, position and falling direction of logs were analyzed to get information about past major disturbances such as storm events, insect attacks or fungal infection (Deal et al. 1991, Qinghong and Hytteborn 1991, Nagel and Diaci 2006). Fosberg (1986), Esseen (1994), Coates (1997) and Huggard et al. (1999) investigated susceptibilities to windthrow in unmanaged forests and in forests with preceding different intensities and types of management interventions. They concluded that, besides the forestry policy (e.g. selective logging (Huggard et al. 1999) and thinning (Fosberg 1986)), advanced stand age, taller trees, shallow-rooting tree species such as Norway spruce, moist soils and pure stands increased the risk of windthrow. The majority of damaged trees was uprooted rather than broken and the dominant falling direction corresponded with the dominant wind direction (Qinghong and Hytteborn 1991, Coates 1997). While storms initially weaken the fitness of trees, insect attacks or fungal infections are often direct results (Qinghong and Hytteborn 1991, Forster and Meier 2010). When major disturbances did not occur, log orientation is rather random than aligned (Deal et al. 1991).

Regarding spatial patterns, Larson et al. (2015) described random log distribution in young forests (small-scaled internal mortality mainly due to competition for light) and aggregated (clustered) log distribution in old-growth forests (mortality mainly due to disturbance factors like insects and wind). Besides stand age, Edman and Jonsson (2001) assumed that the spatial pattern of standing trees directly influences the spatial pattern of living trees, but they did not test this relationship. This thesis attempts to fill this knowledge gap. In addition, an integrative comparison of spatial patterns of logs in unmanaged forests associated to competition caused mortality, geographical factors (e.g. hillside exposition, slope inclination) and disturbances has to my knowledge not yet been conducted. Moreover, spatial analyses of downed logs do not exist for Norway spruce dominated stands of Central Europe, as most studies focus on forests in North America (Fosberg 1986, Deal et al. 1991, Coates 1997, Huggard et al. 1999) or Scandinavia (Qinghong and Hytteborn 1991). The third part of this thesis will fill this gap by mapping the lying dead wood position, running spatial cluster analysis for lying and standing trees and interpreting the spatial log orientation with respect to geographical factors and past disturbances.

The goals of this thesis are:

(i) To generally describe dead wood quantity and quality of Norway spruce forest reserves in Swiss mountainous regions, to compare these findings with results from other studies in unmanaged forests across Europe and to provide a first baseline for managed coniferous forests in Switzerland regarding the governmental biodiversity policy,

(ii) To assess the effects of forest history, stand and site characteristics, climate and external disturbances on the observed lying dead wood quantity and quality, and

(iii) To analyze the orientation and spatial distribution of dead wood and to find possible influencing factors related to the observed spatial pattern.

2 STUDY AREA

2.1 Natural forest reserves

In total, seven coniferous NFRs in Swiss mountainous regions were surveyed and investigated for dead wood quantities and qualities: Derborence, Scatlè, Bödmerenwald, Leihubelwald, Seeliwald, Schweizer National Park (Swiss National Park) and Combe Biosse (Figure 1). All NFRs in the Swiss NFR network were selected, which are (at least partly) dominated by Norway spruce and for which continuous inventory data on the PP level (not only random samples) are available.

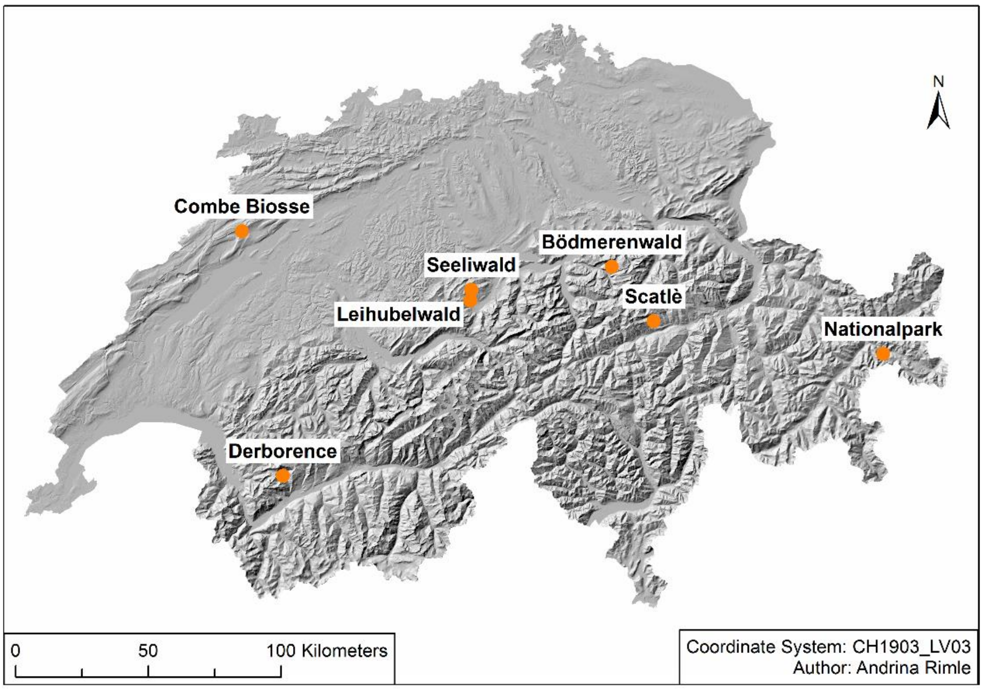

Figure 1. Geographical location of the seven investigated natural forest reserves. Relief based on DEM50 (WSL Birmensdorf).

All natural forest reserves except Scatlè belong to the Swiss federal inventory of landscapes and natural monuments of national importance (Swiss Federal Office of Environment 2015). The last timber harvest took place about 40 years (Combe Biosse) up to about 300 years ago (Derborence) and in Scatlè and Bödmerenwald, timber was probably never or only extensively extracted (Table 1).

Tree species composition

Derborence and Leihubelwald are mixed Norway spruce-silver fir (*Abies alba* Mill.) forests with some European larch (*Larix decidua* Mill.; Derborence) or European beech (*Fagus sylvatica* L.; Leihubelwald). Scatlè and Bödmerenwald are pure Norway spruce forest. Large areas of Seeliwald are peat bog, along its edges Norway spruce is growing together with mountain pine (*Pinus mugo* Turra ssp. mugo). The National Park is covered extensively by mountain pine, but Norway spruce interspersed with mountain pine, Swiss stone pine (Pinus cembra L.) and European larch dominates small areas. Combe Biosse is described as silver fir-beech forest (Heiri et al. 2012), but in several PPs, more than 45% of standing basal area consists of Norway spruce (Brang et al. 2008).

Geology

In Derborence, the parent rock is cretaceous limestone (Droz 1994). Scatlè lies on Verrucano hillside debris (Kral and Mayer 1969). Bödmerenwald is part of a large karst area with deep hollows and caves (Liechti et al. 2011) and Seeliwald and Leihubelwald lie on Schlierenflysch (Streit and Brang 2011, Streit and Heiri 2011). National Park is located on dolomite and in parts on Verrucano (Brang et al. 2011) and Combe Biosse on rubble slopes in the limestone landscape of the Jura (Swiss Federal Office of Topography 2015).

Climate

The seven natural forest reserves cover a climatic gradient from cold and dry (National Park) to cold and wet (Scatlè) and to extremely wet (Bödmerenwald) and an altitudinal gradient from uppermontane[1] (Combe Biosse) to subalpine[1] (Scatlè, Bödmerenwald, Seeliwald and National Park; Table 1).

The following section summarizes each natural forest reserve. A short description of important facts and personal impressions during field work is given, along with a characteristic photo of the reserve.

[1] Terms used according to the Swiss definitions “obermontan” and “subalpin”.

DERBORENCE

Figure 2. PP1, photo: Andrina Rimle, 30.07.2015

Derborence is one of the most pristine forests in Switzerland. Hurricane Vivian (1990) damaged and uprooted many trees (Heiri et al. 2011). Derborence is characterized by high lying dead wood volumes with many large diameter trees, a steep slope and an abundant amount of young growth of rowan (*Sorbus aucparia*), red elder (*Sambucus racemosa*) and honeysuckle (*Lonicera alpigena*) with young Norway spruces and silver firs underneath.

SCATLÈ

Figure 3. PP10, photo: Andrina Rimle, 13.10.2015

Scatlè is the first Swiss forest reserve established and is vaunted as one of few virgin forests in Switzerland (Heiri and Hallenbarter 2011). Huge boulders from a post-glacial rockslide characterize the steep slope in the forest of Scatlè. *Ptilium crista-castrensis*, *Spagnum* spp. or *Plagiothecium undulatum* occur in the moss layer and indicate cold and wet climate conditions. Many lying trunks of considerable dimensions serve as nurse logs.

BÖDMERENWALD

Figure 4. PP3, photo: Andrina Rimle, 25.06.2015

Bödmerenwald is the largest Norway spruce forest with virgin forest characteristics in the Swiss Alps and stands out for its high species diversity, especially of mosses and rare lichens (Bütler et al. 2015). Most trees are growing on mounds. The forest structure is open with dense ground vegetation consisting of ferns and *Adenostyles*. Large diameter logs are common.

LEIHUBELWALD

Figure 5. PP13, photo: Andrina Rimle, 04.07.2015

Leihubelwald is a dense forest with tall Norway spruces and silver firs of large diameters. Consequently, light is sparse on the forest floor, but shade-tolerant beech is common in the base layer. In the lying dead wood, large dimensioned logs are frequent. The storm Vivian (1990) and the following bark beetle infestation affected predominantly the southern edge of the forest reserve (Streit and Heiri 2011).

SEELIWALD

Figure 6. PP2, photo: Andrina Rimle, 05.08.2015

The nature forest reserve Seeliwald is part of the federal inventory of upland and peat moors of national importance (Object number 263, (Swiss Federal Office of Environment 2007)). Thus, European blueberries (*Vaccinia myrtillus*) and sphagnum moss (*Spagnum* spp.) dominate the ground vegetation. Lying dead wood volumes and stem numbers are low and the logs are widely dispersed.

NATIONAL PARK

Figure 7. PP18, photo: Andrina Rimle, 22.07.2015

The Swiss National Park in the Canton of Grisons is the only National Park in Switzerland and celebrated its 100th anniversary two years ago. Before its establishment, the area of the National Park was intensively clear cut (Parolini 1995). The highest volumes of little decomposed lying dead wood were found in this forest reserve.

COMBE BIOSSE

Figure 8. PP16, photo: Andrina Rimle, 10.08.2015

Among the selected forest reserves, Combe Biosse is the only one with a considerable amount of deciduous trees (*Fagus sylvatica*, *Acer pseudoplatanus*) in the standing and lying wood. The research plots are located in a deep, steep caldron, which has a southeast facing and a northwest facing side. Lying dead wood volumes are low.

Table 1. Detailed site information over the investigated forest reserves. MAAT=Mean Annual Air Temperature. MAP=Mean Annual Precipitation sum. VS=Valais. GR=Grisons. SZ=Schwyz. OW=Obwalden. NE=Neuchatel. The classification of forest communities is following Ellenberg and Klötzli (1972). If not stated differently, all information is extracted from various chapters in Brang et al. (2011). All information except the first four columns is related to the investigated permanent plots, whose selection and characteristics are presented in chapter 2.2.

Reserve	Canton	Foundation	Last management intervention	First/last inventory [a]	Elevation [m a.s.l.] [b]	Aspect [c]	MAAT [°C] [d]	MAP [mm] [d]	Investigated permanent plots		
									Numbers	Total Area [ha] [e]	Forest community
Derborence	VS	1955	before 1714 [f]	1981/2008	1430-1610	NW	4.2-5.2	1470-1590	1, 5, 8, 18	1.65	50, 67 [g]
Scatlè	GR	1910	Never [h]	1965/2006	1660	E	3.3	1560	10, 11	0.44	57 [g]
Bödmerenwald	SZ	1971	Never [i]	1973/2003	1500-1530	-	4-4.1	2380-2390	1, 3, 4	3.63	60
Leihubelwald	OW	1972	1920s [j]	1973/2011	1100-1190	E	6-6.4	1720-1790	1, 4, 10, 13	1.49	46, 49 [k]
Seeliwald	OW	1972	1960s [l]	1973/1996	1380-1520	NW	4.2-5	1860-1950	1, 2, 4, 5	2.91	57, 71 [m]
National Park	GR	1914	1914 [n]	1977/2012	1660-1860	N-NE	2.3-3.5	860-940	7, 18, 19	1.47	58 [o]
Combe Biosse	NE	1943 [p]	1972 [q]	1987/2010	1130-1260	S/W-NW	5.4-6.1	1350-1380	14, 16, 17, 19	1.86	18, 20 [o]

[a] NFR inventory data. Derborence: first inventory: PP1, PP5 and PP8: 1981; PP18: 1982; last inventory: PP1 and PP5: 2008; PP8: 2009; PP18: 2010. Seeliwald: last inventory: PP1 and PP2: 1996; PP4 and PP5: 1997. National Park: first inventory: PP7: 1977; PP18 and PP19: 1978.

[b] range in elevation of the investigated PPs (precise on 10 m). For details, see section “Fixed effects” (Climate) in chapter 3.3.4.1.

[c] derivation is presented in chapter 3.3.5.1.

[d] range in MAAT and MAP of the investigated PPs (MAAT precise on 0.1°C, MAP precise on 10 mm). For details, see section “Fixed effects” (Climate) in chapter 3.3.4.1.

[e] information about plot size has been extracted in ArcGIS from NFR inventory data (precise on 0.01 ha).

[f] Herrmann et al. (2012)

[g] Frehner and Burnand (2009): Derborence: PP1, PP8 and PP18: forest community 50 (*Adenostylo alliariae-Abieti-Piceetum typicum*); PP5: forest community 67 (*Erico-Pinetum montanae*).

[h] Klöti (1991)

[i] Due to its inaccessibility, the Bödmerenwald was never touched my man (Thee et al. 1987).

[j] Gross (1982)

[k] NFR inventory data: PP1 and PP13: forest community 49 (*Equiseto-Abieti-Piceetum typicum*); PP4 and PP10: forest community 46 (*Vaccinio myrtillii-Abieti-Piceetum typicum*).

[l] Gregor Jakober, personal communication, October 21, 2015

[m] Lienert et al. (1982): PP1 and PP2: forest community 71 (*Sphagno-Pinetum montanae*); PP4 and PP5: forest community 57S (*Homogyno-Piceetum sphagnetosum*).

[n] The last thinning took place 1931 in Champlönch (Parolini 1995).

[o] Brang et al. (2008): Combe Biosse: PP14 and PP16: forest community 18 (*Festuco-Abieti-Fagetum*); PP17 and PP19: forest community 20 (*Adenostylo alliariae-Abieti-Fagetum typicum*).

[p] foundation of the cantonal reserve (EcoConseil 2003), establishment in the frame of the NFR project was 1985.

[q] foundation of a “réserve forestière totale”, no timber harvest except some removal to reduce a bark beetle infestation in 1984 at the border of the reserve (EcoConseil 2003).

2.2 Permanent plots

A permanent plot in Swiss NFR research is defined as an area of "homogeneous forest community type, microtopography, state of development and stand structure" ((Wunder et al. 2007), p.2). A single PP has marked borders and geographically gauged edge points. Each individual tree within the PP borders above the callipering limit of DBH ≥4 cm is numbered and assessed in periodical inventories recording tree species, DBH in 1-cm classes, condition (alive or dead and standing or lying) and social position (Tinner et al. 2010). All data are stored in the NFR inventory database. For this thesis, in each of the seven NFRs two to four PPs were selected, applying the following three selection criteria:

1. Basal area of the live stand consisting of at least 50% of Norway spruce (preferably) and silver fir (monitoring data from Brang et al. (2008)), two tree species that often co-occur, apply similar competitive pressure and their wood has similar decomposition rates (Norway spruce: 0.039 year^{-1}; silver fir: 0.037 year^{-1} (Hütter 2011)) and thus may remain for an equal amount of time in the PP.
2. PPs that are still actively monitored after the re-evaluation of the reserve network in 2008.
3. Possible avoidance of PPs which were heavily affected by disturbances, e.g. storm or bark beetle infestation (assessment based on descriptions in various chapters in Brang et al. (2011)).

In Scatlè, two permanent plots (PP1 and PP2) with repeated inventories exist. As they are large (PP1: 3.47 ha; PP2: 2.89 ha) compared to the other selected PPs, I intended instead to investigate a square of 90x90 m with four sub-squares of 45x45 m in PP1, which had been established in a student exercise on the bachelor level at ETH Zurich in 2005. However, a field trip showed that the sub-squares were difficult to reconstruct as the wood poles acting as marking points were missing (probably already decomposed). Still, it was possible to reconstruct in field the two lower sub-squares (A and D), to measure the coordinates of the border points with a GPS (Trimble Geoexplorer 6000 series, Trimbe Navigation (Westminster, USA)) and to mark the boundary line. Although the two sub-squares are not exactly PPs, I will call them that for the purpose of this thesis to number consistently the PPs. The two newly constructed "PPs" in Scatlè will be denoted as PP10 (sub-square A) and PP11 (sub-square D).

In total, 24 permanent plots were selected. Their size varies between 0.21 and 1.65 ha (mean 0.56 ha; median: 0.52 ha). The selected PPs cover 4% (Seeliwald) up to 74% (Bödmerenwald) in relation to the research area of the NFRs (compartments or PPs), which is in some NFRs much smaller than the entire reserve perimeter (Derborence, Scatlè, Bödmerenwald, National Park). An overview of the selected PPs including information about selection criteria is given in Table 2.

Table 2. General site description over the investigated permanent plots per forest reserve. The last three columns refer to the selection criteria of the permanent plots. Information about plot size and focal point coordinates has been extracted in ArcGIS from NFR inventory data. Coordinates are in the coordinate system CH1903 LV03. Shares of Norway spruce and silver fir in standing basal area follow Brang et al. (2008). Information about past wind disturbances is assessed from various chapters in Brang et al. (2011) and relates to hurricane Vivian in February 1990.

Reserve	PP number	Area [ha]	PP's focal point coordinates		Share of Norway spruce in standing basal area [%]	Share of silver fir in standing basal area [%]	Past disturbance
			x	y			
Derborence	1	0.2520	583 392	125 400	77	0	yes
	5	0.2459	583 279	125 409	65	0	no
	8	0.6660	583 400	125 344	64	35	yes
	18	0.4880	582 788	124 800	65	26	yes
Scatlè	10	0.2074	722 832	183 434	100	0	no
	11	0.2371	722 829	183 479	100	0	no
Bödmerenwald	1	1.1274	707 068	204 614	100	0	no
	3	0.8446	707 132	204 607	100	0	no
	4	1.6541	707 181	204 790	100	0	no
Leihubelwald	1	0.2555	653 555	191 023	58	35	yes
	4	0.2499	653 890	191 122	50	44	no
	10	0.4880	653 701	191 002	55	43	yes
	13	0.5358	653 676	191 456	60	36	no
Seeliwald	1	0.5001	654 224	195 852	77	0	no
	2	0.8662	654 346	195 447	66	0	no
	4	0.6484	654 453	195 052	100	0	no
	5	0.8976	653 907	195 102	100	0	no
National Park	7	0.5567	812 215	171 515	52	0	no
	18	0.6770	808 524	171 545	65	0	no
	19	0.2389	808 395	171 580	69	0	no
Combe Biosse	14	0.6908	567 636	217 418	49	15	no
	16	0.5971	567 759	217 544	47	6	no
	17	0.3081	567 807	217 346	47	6	no
	19	0.2689	567 896	217 446	60	0	no

3 MATERIAL AND METHODS

3.1 Field work

To gather information about lying dead wood quantity and quality in the selected 24 PPs, a complete inventory of all lying dead wood pieces was carried out between 25th June and 14th October 2015 following the method proposed by Robin and Brang (2009). Hence, a piece was only recorded if its angle to the ground measured less than 50 gon, its thicker end was within the marked boundaries of the PP, at least 75% of the diameter were still present, its minimal diameter was at least 7 cm and its length at least 2 m (reduced to length ≥0.5 m if minimal diameter ≥36 cm). The diameter at both log ends (1 cm precision, 2 measures per side), its length (5 cm precision) and its decomposition stage were investigated. The decomposition stage was classified into five decay classes according to Table 3 and measured with a pocketknife at four locations on the log surface. In addition, the tree species and - if detectable - the original tree number from the NFR inventories were recorded. In case the tree species could not be identified but the original tree number was found, the species was determined by consulting the NFR inventory database. Otherwise, the dead wood piece was at least classified as coniferous or deciduous. Furthermore, the presence of a rootstock was recorded and its volume was estimated (accuracy of 0.1 m^3) in order to get potential information on past disturbance activities.

Table 3. Log decay classifications (I-V) following Robin and Brang (2009).

Decay class	Description	Penetration depth of pocketknife	
		Parallel along the wood fibers	Perpendicular against the wood fibers
Class I	Fresh wood	No	No
Class II	Hard wood	Little (maximum some mm)	Little (maximum some mm)
Class III	Soft decaying wood	Simple (maximum some cm)	Little (maximum some mm)
Class IV	Spongy decaying wood	Simple (maximum some cm)	Simple (maximum some cm)
Class V	Powder wood	Strongly decayed, powdery	Strongly decayed, powdery

Along with the recording process described above, data of the geographical location of both log ends were collected from set measurement points by using a boussole (Meridian-Wyssen-Kompass MI-4006, Spectros (Köniz, Schweiz)) for measuring the azimuth (angle to north; accuracy of 1 gon) and a vertex (Vertex IV, Haglöf (Långsele, Sweden), applying the “angle” tool to adjust for the slope) for measuring the distance (accuracy of 0.1 m). Set measurement points were boundary points or newly established points. Starting at an already gauged edge point of the PP (example from Seeliwald, PP4: point 84 in Figure 9), I determined new measurement points (points 101, 102, 103) in the PP to be able to cover the entire area, this because distance measurements with the vertex were limited or the view was obstructed due to topography. New points (e.g. point 103) were calibrated by taking azimuth and distance from the existing boundary points or formerly established measurement points (e.g. point 102).

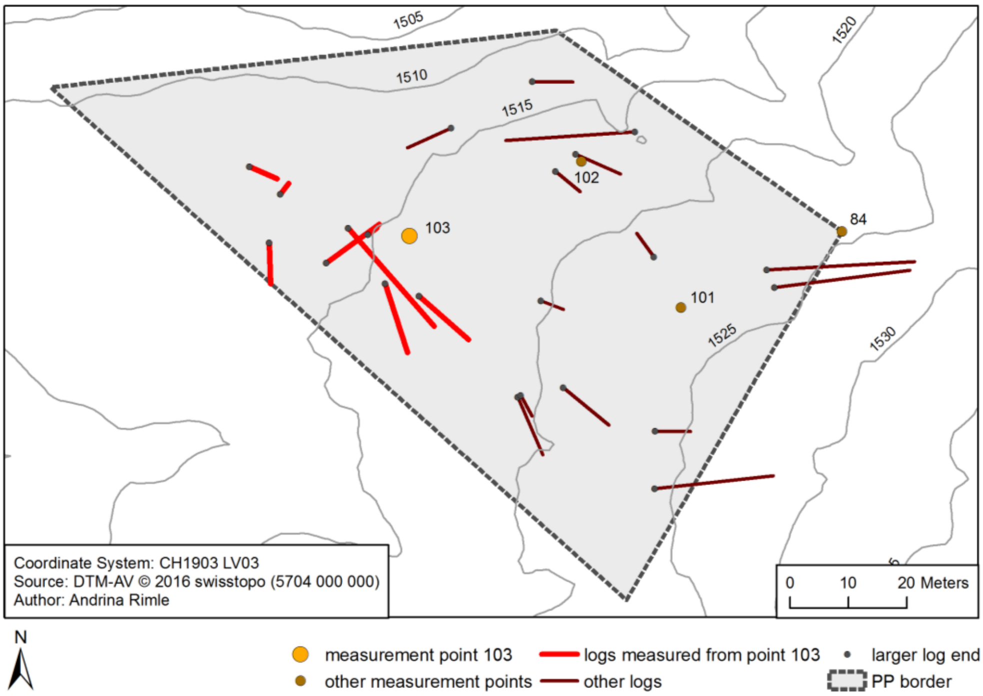

Figure 9. Methodical procedure to investigate the spatial distribution of lying dead wood pieces. Starting at the already gauged edge point (point 84), new measurement points were established (points 101, 102 and 103), whereby for instance the red colored logs were measured from point 103. Example from Seeliwald, PP4 (number of logs=22).

3.2 Volume calculations

3.2.1 Lying dead wood

The volume of each single lying dead wood piece was calculated assuming the volume of a cylinder (formula 1), following Herrmann et al. (2012) and Preikša et al. (2015).

$$V = \frac{g_1 + g_2}{2} \cdot L \tag{1}$$

with:

V: volume of the lying dead wood piece [m^3]

g_1: cross-section area at the large diameter end [m^2]. For radius, both measures of larger diameter were averaged and divided by two.

g_2: cross-section area at the small diameter end [m^2]. For radius, both measures of smaller diameter were averaged and divided by two.

L: length of the lying dead wood piece [m]

For the total dead wood volume per PP, the volumes of the single pieces were summed up, divided by the area of the PP and expressed as m^3/ha. However, two important facts have to be considered when applying the chosen volume calculation method.

First, it would have been an option to calculate the lying dead wood volumes with the formula of a truncated cone as it has been performed by Vandekerkhove et al. (2009). This would lead to 9% higher volumes on average and to maximally 12% higher volumes on PP level (Bödmerenwald, PP1) as with the cylinder formula, as a comparison of the two calculation methods showed. As my results should be comparable with dead wood data recorded in deciduous and deciduous mixed NFRs by Herrmann et al. (2012), the only existing study about dead wood on permanent plot level in Switzerland, calculating dead wood volumes with the formula of a truncated cone was not an option any more.

Second, the estimated rootstock volumes have been excluded from total CWD volume calculations, as the estimations have proven to be difficult, and thus, they are probably inaccurate. Totally, I found 178 rootstocks and estimated an average volume of 0.34 m^3 per rootstock. CWD volumes would increase by 6% on average and by maximally 22% (Bödmerenwald, PP1) if the rootstock estimations would be integrated. The numbers of rootstocks per hectare in each PP are presented in Appendix Table A2.

Furthermore, the chosen measurement threshold in this thesis (minimal diameter ≥7 cm) implies a lot of effort and time for data recording. However, the volume estimations are up to 28% higher compared to a threshold of ≥12 cm (Böhl and Brändli 2007). Moreover, small diameter trees are not negligible concerning biodiversity conservation as fine wood debris also host many species (Kruys and Jonsson 1999, Brin et al. 2011, Preikša et al. 2015). Therefore, the low measurement threshold is justifiable.

3.2.2 Standing dead wood and living trees

A standing dead tree is defined as a snag with a DBH ≥4 cm and an inclination angle to ground of more than 50 gon. Volumes and stem numbers of standing dead and living trees were extracted from the last recording in the NFR inventory data applying the coding for the condition live or standing dead (Tinner et al. 2010). The last inventory took place 4 years up to 20 years ago (Table 1). The stock-wood volume of each single standing dead or living trees was calculated in all forest reserves except in Derborence using the tariff model following Kaufmann (2000) which takes the individual tree species and region into account. This model (formula 2) is widely acknowledged in Switzerland and is used in the National Forest Inventory for volume estimations of the live stand (Brändli 2010).

$$V_k = e^{(b_{0k} + b_{1k} \cdot \ln(DBH) + b_{2k} \cdot ln^4(DBH) + \sum_{j=3}^{7} b_{jk} \cdot B_j)} \qquad (2)$$

with:

V:	stock-wood volume in bark [m^3]
k:	tariff number: dependent on tree species and region (e.g. Jura, Alps, Prealps)
$b_0 - b_7$:	model coefficients in dependency of the tariff number
DBH:	diameter at breast height [cm]
$B_3 - B_7$:	individual tree, stand or site characteristics
B_3:	site fertility: total productivity [kg dry substance/(year*ha)]
B_4:	indicator for development stage: averaged DBH of the hundred largest trees per hectare [cm]
B_5:	tree fork (0: no; 1: yes)
B_6:	altitude [m a.s.l.]
B_7:	layer of a tree (0: upper layer; 1: not upper layer)

According to WSL collaborator Mr. Andreas Zingg, who calculated all standing tree volumes for the purpose of this thesis, errors in the existing NFR inventory data in Derborence did not allow to apply formula (2). Hence, volumes of snags and living trees were calculated by applying the tariff model III of the Canton Lucerne, which is yearly published in the Swiss forestry calendar (Schweizer 2013).

Volumes of lying dead wood and standing dead and live trees were recorded at different times and calculated by different formulas. Therefore, I will renounce any comparison (e.g. ratios) between lying dead wood and live stand or a summation of the two dead wood components (standing or lying). A tree coded as living or standing dead in the last inventory might be recorded as lying dead during my field work and therefore be double-counted.

3.3 Data analysis

All calculations and analysis were performed using R (Version R-0.99.484, (R Core Team 2015)). Spatial operations and maps creations were carried out in the Geographical Information System (GIS) software (ArcGIS, Version 10.3.1.4959, (ESRI 2015)). The Swiss coordinate system CH1903 LV03 was utilized. Significance level for all tests is set at α=0.05.

It is important to know that errors in the NFR inventory database concerning the tree coding, the volume calculations and the coordinates of the single standing trees are possible, particularly in the first inventories. However, the data are property of WSL Birmensdorf and ETH Zurich and thus I did not make any modifications. Furthermore, in PP13 in Leihubelwald, which is located at the border of the NFR and close to a river, ten recorded logs were obviously washed ashore from higher ground during a heavy rainfall. Consequently, these logs did not belong to the natural forest dynamic in the PP and were excluded from all analysis.

3.3.1 Dead wood quantity

Dead wood quantity (stem densities and volumes) was analyzed for standing and lying dead wood separately. For stem densities per PP, absolute stem counts were summed up, divided by the area of the PP and expressed as stems per hectare (no./ha). For average values of dead wood volumes and stem numbers per forest reserve and in total, plot data were weighted by the PP's area size. In the result part, PPs from one NFR were summarized and labelled by the reserve name, although the presented values do not properly reflect the whole NFR, but only the results from the surveyed PPs, which are not randomly distributed within the reserve and selection based on three criteria (see chapter 2.2). The weighted standard error served as a measure of dispersion.

3.3.2 Dead wood quality

Lying dead wood volumes and stem numbers were stratified regarding dead wood quality (tree species, dimensions and decay stages). Standing dead wood was only examined concerning diameters as the lying dead wood component was the focus of this study.

In temperate broadleaf forests, Preikša et al. (2015) documented the highest species of rare cryptogams on European ash (*Fraxinus excelsior* L.), English oak (*Quercus robur* L.) and Norway spruce (*Picea abies* (L.) H. Karst). Also Jonsell et al. (1998) reported Norway spruce among the tree species to be hosting the most red-listed invertebrates in Sweden. However, a stratification regarding the tree species was only carried out for coniferous and deciduous trees and not for individual tree species for two reasons. First, the occurrence of the single species varied greatly between the reserves and the presence was partly in adequately small amounts (Appendix Table A4). Second, the tree species could not always be identified on the species level but only on the level of coniferous or deciduous trees.

With respect to dimensions, large diameter trees are defined in literature as dead wood with a larger diameter of more than 35 cm (Similä et al. 2003), 36 cm (Heiri et al. 2012) or even 100 cm (Lutz et al. 2012). In this thesis, a large dimensioned log is defined as a log with a larger diameter >30 cm according to Herrmann et al. (2012). Additionally to large and small dimensioned logs, I also stratified for extraordinarily large lying and standing dead trees (larger diameter or DBH ≥80 cm), called giant trees. In natural forest research, the amount of giant trees is a commonly used indicator for a forest's naturalness (Bütler et al. 2015) as large diameter trees are rare in managed forest because timber is usually harvested prematurely (Siitonen et al. 2000, Jonsson et al. 2005). Moreover, the number of logs and snags per hectare (on reserve level) was pooled in 4-cm diameter classes as in Heiri et al. (2009) in order to analyze diameter range and most abundant diameter classes.

Regarding the determination of the decay stage, the used method following Robin and Brang (2009) has the advantage that it is very simple to apply in the field. However, there are also some disadvantages. First, only the outermost layer of the log is considered, but the determined class is assigned to the whole log. This may lead to a bias particularly in the case of large dimensioned logs which may have a different decomposition stage in outer than inner layers. Second, specifications regarding tree species are missing, although they expose different wood properties and thus decomposition behaviors (Herrmann and Bauhus 2013). Third, the chemical composition of the log (e.g. ratio between lignin and cellulose content) is unknown, but probably important for many species.

As large diameter trees (larger log diameter >30 cm) and advanced decay stages (class IV+V) are especially important to a great variety of species (Hoiland and Bendiksen 1996, Grove 2002, Heilmann-Clausen and Christensen 2003, Ódor et al. 2006) and rare in managed Swiss forests (Rigling and Schaffer 2015), I will particularly focus on these two dead wood quality characteristics.

3.3.3 Statistical testing

To investigate whether total lying dead wood volumes and stem densities differed between reserves, a nested ANOVA (Analysis of Variance) was set up, whereby the data of the single PP were used as input and weighed according to plot size (Dormann and Kühn 2009). The nesting factor was the forest reserve. Nested ANOVA assumes a random sampling design. This was in reality not true, as PPs are not randomly distributed within a reserve, but facilitated statistical analysis. Further important assumptions of nested ANOVA are equal variances of residuals, independence of errors and normal distribution of errors (Crawley 2012), which could be fulfilled by log-transforming the dead wood data. As the nested ANOVA resulted in no differences of CWD volumes and stem densities between forest reserves (for details see chapter 4.1.1), a post-hoc test to evaluate between which particular reserves the differences occurred was not necessary.

3.3.4 Statistical modeling of dead wood quantity and quality

In order to explain the differences in observed dead wood data, total CWD volumes (quantity) and volumetric percentages of large dimensioned dead wood as well as of different decomposition stages (quality) were modeled in dependence of several factors (detailed description in chapter 3.3.4.1). These explanatory variables cover processes determining the dead wood accumulation (input) and the dead wood decomposition (output). Total CWD volumes and dimensions were modeled in a linear mixed effect model (chapter 3.3.4.1) and decay stages were examined in a multivariate analysis based on the five classes of decomposition stage (chapter 3.3.4.2).

3.3.4.1 Total CWD volume and dimensions

Choice of the model type

Given the nested sample design of several PPs located in one NFR (hierarchical structure), the linear mixed effect model was chosen as the appropriate model type (Zuur et al. 2009) applying the *nlme* R package (Pinheiro et al. 2012). Linear mixed effect models are based on two sorts of explanatory variables: random effects, which was the forest reserve itself, and fixed effects (Crawley 2012). The response variables and the fixed effects (reasons for their choice and derivation) are described in detail in the following section and the raw data of the fixed effects is summarized in Appendix Table A10.

Response variables

The linear mixed effect model was run twice with the following response variables: total CWD volumes (VOLUME_LYING_DEAD) and volumetric percentages of large (>30 cm) dimensioned logs in total CWD volume (VOLUME_LARGE_DIMENSIONS; raw data see Appendix Table A1). As volumetric percentages of large and small dimensioned logs complement one another to 100%, only one dimension component was modeled.

Fixed effects

Forest history

Literature study has revealed that the longer timber has not been harvested from a forest, the more dead wood can accumulate and the higher are the dead wood volumes (Christensen et al. 2005, Burrascano et al. 2008, Vandekerkhove et al. 2009, Seidling et al. 2014). Thus, the lack or rather the time since last forestry operations (MANAGEMENT) has been established as a widely used variable predicting dead wood volumes. Time since last management was classified into 20-50 years, 50-100 years and >100 years (Heiri et al. 2012) and data source is presented in Table 1.

Site productivity

In earlier studies site productivity was described by volume or basal area of the live stand (Sippola et al. 1998, Nilsson et al. 2002, Nordén et al. 2004, Seidling et al. 2014) or soil fertility (Vandekerkhove et al. 2009) and positively related to dead wood volumes. Data of the live stand were extracted from the last record in the NFR inventory database by extracting the trees coded as living (Tinner et al. 2010). Volumes (VOLUME_LIVING) were calculated as presented in chapter 3.2.2. Basal area (BASAL_AREA) was calculated as the sum of the circular area (measured at breast height) of all living trees divided by the plot area. Soil fertility data was not directly available, but a possible influence of the forest community on CWD volumes and decay stages is discussed in chapter 5.2.1 and 5.2.3.

In addition, Heiri et al. (2012) proposed as a productivity index the maximal average total site productivity following Keller (1978) (PRODUCTIVITY_KELLER), which was used as the third site productivity variable and calculated as follows (formula 3):

$$y = \frac{k}{x - c} + m + p \cdot x \tag{3}$$

with:

y: site productivity [kg dry substance/(ha*year)]

x: elevation of the focal point of each permanent plot (derivation see below in section "Climate") [m a.s.l.]

k, m, p, c: constants (k: [kg*m]; m: [kg]; p: [kg/m]; c: [m])

The derivation of the constants k, m, p and c require information of the region (e.g. Jura, Prealps or High Alps) where the study area was located, the geology (base-poor or base-rich), the exposition (north or south) and the steepness (e.g. slope, scarp, base of the hillside or plateau). The necessary data could be gathered from topographical and geological maps.

Past major disturbances

Past major disturbances like storm events, insect infestations or fires have been reported to increase the dead wood volumes to a high extent (Hahn and Christensen 2005, Seidling et al. 2014). As forest fires so far did not occur in the selected PPs and insect infestations are often direct consequences of storm events (Forster and Meier 2010), the presence or absence of past severe storms (WIND) was chosen as an appropriate variable describing disturbance regimes, whereby WIND refers hurricane Vivian in February 1990. Data were evaluated from various chapters in Brang et al. (2011).

Climate

Climate conditions mainly influence the activity of microorganisms responsible for decomposition and consequently the disintegration time of dead wood (Herrmann and Bauhus 2013). Warmer and wetter climate conditions enhance the decomposition process (Korpel' 1997) and might thus result in low CWD volumes given that the stand productivity (dead wood input) is also low (Hahn and Christensen 2005). Mean annual precipitation sum (PRECIPITATION) and mean air temperature in the vegetation period (TEMPERATURE; monthly average temperature >5°C) were selected as appropriate variables describing the climate conditions. Mean air temperature in the vegetation period was chosen instead of mean annual air temperature to probably better describe the mean temperature when microorganisms are actively decomposing dead wood.

For obtaining monthly average temperature or precipitation data at any location in Switzerland, daily values of MeteoSwiss (Federal Agency of Meteorology and Climatology) weather stations were interpolated using the daymet software presented by Thornton et al. (1997). The digital elevation data determining the location was of 100 m resolution and the research group of Land Use Dynamics at WSL Birmensdorf has processed the geographical and meteorological data. Coordinates in the Swiss coordinate system CH1903 LV03 defined the location for which climate data were demanded. For each PP, the coordinates of its focal point, extracted in ArcGIS from the area polygon, were used. Monthly average data over the reference period of 1981-2010 was summed up (PRECIPITATION) or averaged for the period from May to October, when monthly average temperature from daymet interpolation exceeded in the majority of permanent plots the value of 5°C (TEMPERATURE).

Hillside exposition

Næsset (1999) related aspect, which correlates with solar exposure and soil moisture, substantially to decomposition rate. Mean aspect of the hillside was calculated for each PP as described in chapter 3.3.5.1. Afterwards, aspect was transformed into northness (NORTHNESS) by taking the cosine, so that the aspect resulted in values between -1 (south) and 1 (north) whereby 0 indicated a hillside exposition to east or west.

Tree species composition

Tree species composition in the selected PPs and thus decomposition processes differ as decay rates are, among other parameters, dependent on the substrate and hence the tree species (Hahn and Christensen 2005). Deciduous trees (except oak, which however was not present in the study area) decompose generally faster than coniferous trees. For example, a beech log is decomposed on average to 95% within 25 years and a Norway spruce or silver fir log within 80 years (Lachat et al. 2014). Thus, the relative abundance of deciduous tree species in the basal area of the live stand (DECIDUOUS) was taken as the variable to describe tree species composition (evaluation data from Brang et al. (2008)).

Model preparation and development

In a first step, the nine fixed effects and the two response variables were checked visually for normal distribution using histograms. Hence, total CWD volume was log-transformed and volumetric percentages of large diameter trees as well as proportion of deciduous tree species in living basal area were arc-sine-transformed (Dormann and Kühn 2009). An overview over response variables and fixed and random effects with their corresponding transformation is given in Appendix Table A9. Secondly, Person correlation coefficients (R^2) were derived for every variable combination of fixed effects (Sachs 2013). The basal area and volume of the live stand as well as maximal average total site productivity following Keller (1978) and hillside exposition were highly correlated (Appendix Table A11). Consequently, volume of the live stand and site productivity following Keller (1978) were removed from the variable set due to higher correlations with the other variables. Finally, the full model contained seven fixed effects, which had a maximal correlation of $R^2=|0.62|$ to each other.

Starting from the full model, variables were continuously removed until Akaike Information Criteria (AIC) did not decrease anymore (Zuur et al. 2009). The application of the AIC selection criteria is a widely used method to find a set of variables best describing the variation in the response variable (Dormann and Kühn 2009, Zuur et al. 2009, Sachs 2013). However, AIC searches a model with as few parameters as possible in order to most adequately describe the data and thus important factors might be ignored (Sachs 2013). The final model was only considered appropriate if residuals showed constant variance and normal distribution (Zuur et al. 2009). The final variables should have a p-value <0.05, but this requirement could not always be fulfilled, particularly not for all levels of categorical variables (e.g. time since last management intervention), as a low AIC criterion was the primary criterion for the variable selection. For model presentation, the marginal R^2 describing the proportion of variance explained by the fixed effects only and the conditional R^2, which includes also the random effects, was calculated (Nakagawa and Schielzeth 2013).

3.3.4.2 Decomposition stages

To visualize the relative abundance of decomposition stages in CWD volumes in the different PPs, I performed a Principal Component Analysis (PCA, (Borcard et al. 2011)) with the help of the *vegan* R package (Oksanen et al. 2007). Input data were the volumetric proportions of the CWDs individual decay stages on PP level (absolute values in Appendix Table A1). To reduce errors caused by zero values (decay class I+II), Hellinger transformation on the abundance data as described in Legendre and Gallagher (2001) was applied.

Linear relationships between environmental factors and abundance of decomposition stages in CWD volumes were examined by a Redundancy Analysis (RDA, (Borcard et al. 2011)) using the *vegan* R package (Oksanen et al. 2007). The response variable was the abundance data of decay stages, again Hellinger transformed. All variables used in the linear mixed model as fixed effects were selected as explanatory variables. The time since last management intervention was expressed as a dummy variable and the proportion of deciduous tree species in living basal area was arcsine-transformed. A selection procedure both in forward and backward direction based on AIC selection criterion and permutation test (999 random permutations) was performed to seek for a final set of environmental factors that contribute significantly better to abundance of decomposition stages than a set of randomly chosen factors (Borcard et al. 2011). The final environmental variables were only considered as appropriate if the variance inflation factor assessing collinearity was less than 10 (Oksanen 2012). For plotting, scores of decay classes were scaled by eigenvalues (scaling type 2).

3.3.5 Spatial distribution of dead wood

3.3.5.1 Log orientation

For both log ends, coordinates were derived based on measured azimuth and distance. For each larger log end, slope and aspect of close surrounding was calculated in ArcGIS by including a square of 6x6 m (source: DTM-AV © 2016 swisstopo (5704 000 000)). Information of slope and aspect were imported in R again for further analysis. In a first step, the falling direction (oriented to north) of each single dead wood piece was computed. Secondly, the absolute difference between the falling direction of the log and the aspect of close log surrounding was calculated (0°: log and hillside faced the same direction; ±180°: log and hillside were oppositely oriented). Thirdly, the aspects (at larger log end) were averaged in each PP and so the mean angle of hillside orientation was calculated (Zar 1999).

Furthermore, significant uniform circular distribution of logs in each PP was verified by the Rayleigh test (Zar 1999). In addition, assuming that the differences between log and hillside orientation were normally distributed, the parametric Hotelling test for paired samples of angles was used in order to test the hypothesis whether log and hillside are oriented in the same direction or not (Zar 1999). Moreover, the proportion of logs falling in hillside direction was derived in order to assess whether the aspect of close log surrounding has an effect on the falling direction of logs. Based on my own definition, a log was falling in hillside direction if the difference between log and hillside orientation was less than 45°. This last analysis steps was conducted for all logs together and in the single PPs for (i) all logs, (ii) all large logs (larger diameter ≥12 cm), (iii) all large logs on steep slopes (larger diameter ≥12 cm and slope at larger log end ≥20°), (iv) all long logs (length ≥20 m), and (v) all short logs (length

<20 m). However, analysis was stopped if the number of logs in one of the five analyzed categories was less than 10 per plot in order to still get reliable results and thus not conducted for PP5 in Derborence at all (totally eight logs). Threshold values of larger diameter ≥12 cm, slope ≥20° and length ≥20 m were set to keep the number of stems as high as possible and additionally for the following reasons:

1. Windthrow risk increases with tree diameter and, more so, tree height (Lohmander and Helles 1987, Gardiner et al. 2000). Applying a threshold value of 12 cm for log diameter covered 87% of all investigated logs and was in accordance with the threshold used in the National Forest Inventory for lying dead wood assessments (Brändli 2010). Trees from the upper canopy are more susceptible to windthrow (Coates 1997, Gardiner et al. 2000). All logs with a length ≥20 m (11% of all logs) were analyzed separately as these logs may have reached the upper canopy layer as living and standing trees and therefore have been more heavily exposed to higher wind speeds than smaller trees (shorter logs) growing in lower layers.
2. When plotting the slope against the absolute differences between log and hillside orientation, a trend of higher density of small differences was observed above a slope of 20° (Appendix Figure A3), indicating that steeper slopes might cause more logs to fall in hillside direction (downslope).

3.3.5.2 Spatial pattern analysis

Spatial pattern of logs in the different PPs was examined using Ripley's K-function (Ripley 1981), implemented in the R package *spatstat* (Baddeley and Turner 2004). The Ripley's K-function $\widehat{K}(r)$ (formula 4) is a distance-based method counting the number of neighbors of each log located within a radius r (Baddeley 2008).

$$\widehat{K}(r) = \frac{A}{n^2} \cdot \sum_{i} \sum_{i \neq j} 1 \left\{ \left\| x_i - x_j \right\| \leq r \right\} \cdot e(x_i; x_j; r) \tag{4}$$

with:

$\widehat{K}(r)$:	estimated Ripley's K-function for the observed spatial pattern of the logs within the PP border [m^2]
r:	radius r, adapted on the observed area size and geometry [m]
A:	PP area [m^2]
n:	number of logs in the PP area A
$xi - xj$:	distance between logs i and j [m]
$e(x_i; x_j; r)$:	edge correction weight: needed to reduce bias arising from the unaccounted logs outside the PP border (Ripley 1988). In this thesis, the Ripley's isotropic correction for polygonal areas was used (Ripley 1988). [1/m]

The estimated Ripley's K-function was later compared with a homogeneous Poisson process $K_{pois}(r)$ (formula 5) describing complete spatial randomness of log distribution (Baddeley 2008).

$$K_{pois}(r) = \pi \cdot r^2 \tag{5}$$

To determine statistical significance, a confidence envelope based on 100 random simulations was derived (Edman and Jonsson 2001). Location of $\widehat{K}(r)$ above the confidence envelope suggested spatial clustering, below spatial regularity and within spatial regularity (Baddeley 2008). A representative example for spatial clustering and spatial randomness from the investigated PPs is provided in Figure 10a and Figure 10b, respectively.

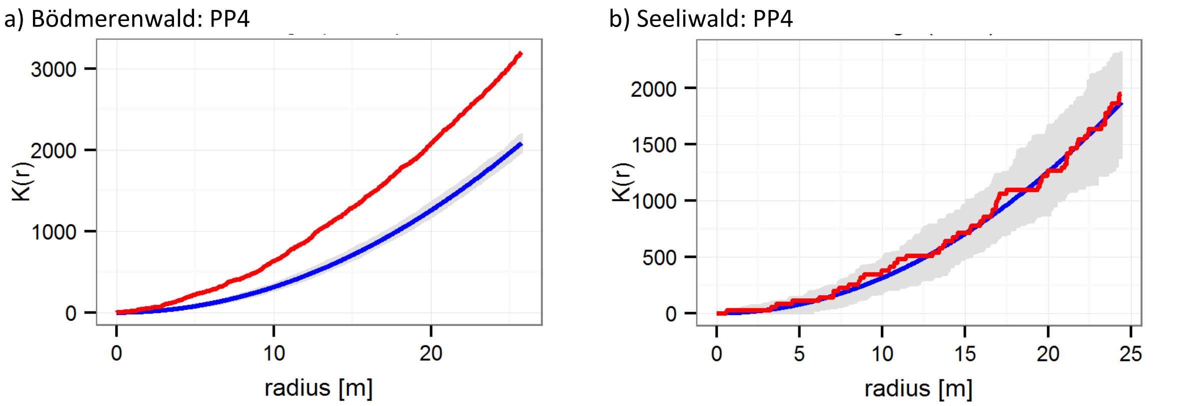

Figure 10 (a/b). Diagrams of the $K(r)$ function in Bödmerenwald, PP4 (a) suggesting spatial clustering and Seeliwald, PP4 (b) suggesting spatial randomness. Number of all logs within PP borders was 143 (Bödmerenwald, PP4) and 22 (Seeliwald, PP4). The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

Spatial patterns were analyzed for all logs as well as for both dimensions (large and small) and the five decay classes if their number in one of the inspected categories was at least 10 per plot. For fewer observations, Ripley's K-function provides an estimate only and is hardly interpretable (thus, PP5 in Derborence was not spatially analyzed). Furthermore, it has to be considered that Ripley's K-function analyzes the spatial pattern on a small scale, dependent on the size of the investigated area. Thus, the inspected radius varied between 12 m (Scatlè, PP10 and PP11) and 35 m (Combe Biosse, PP14).

In order to test the hypothesis whether the spatial pattern of standing trees directly influences the spatial pattern of logs as assumed but not tested by Edman and Jonsson (2001), spatial pattern analysis was also conducted for standing (live and dead) trees. However, coordinates of standing trees were only available for plots inventoried after 2007 (Derborence, Leihubelwald, National Park and Combe Biosse) and were extracted from the NFR inventory database.

Logs were reduced to their larger end and treated as points, as Ripley's K-function is a tool of point pattern analysis. The analyzed area was the shape of the PP, within whose border the larger log ends and the standing trees should be located based on the recording criteria. The acknowledgement of the exact PP shape is a great advantage of *spatstat* as it is also important to know where logs were not observed (e.g. outside PP border) and not only the smallest rectangle around the logs is taken into account. However, in a majority of PPs some logs and standing trees were placed outside the PP borders (partly up to 47% of all logs in Scatlè, PP11) due to measurement errors during the field work and thus excluded from spatial pattern analysis. These measurement errors, which are also visible in the maps depicting all logs (references in Table 7), might have occurred because of two reasons. First, the used method (measuring azimuth and distance to derive standing trees or logs coordinates) works best for flat areas but is limited for inclined areas, what most plots are. Second, each displacement from one measurement point to another was combined with errors, which increased with higher numbers of newly established measurement points.

4 RESULTS

In total, 1807 logs were recorded during the fieldwork, ranging from eight pieces per PP (Derborence, PP5, 0.25 ha) up to 218 pieces per PP (National Park, PP18, 0.68 ha). A log measured on average 28 cm at the larger diameter and 9.40 m in length and had a volume of 0.6 m^3. 15 different tree species were present in the lying dead wood (for stem numbers and amounts, see Appendix Table A4). 1690 logs (94%) were conifers, 117 (6%) deciduous. 1162 logs (64%) were of small dimensions (larger log diameter ≤30 cm), 645 (36%) of large dimensions, whereby 93% of all deciduous and 63% of all conifers belonged to small diameter trees. Decomposition stage class V was most frequent (691 logs, 39%) and class I least frequent (53 logs, 3%). 73% of large diameter logs consisted of advanced decay stages (class IV+V). Regarding tree species, 64% of conifers and 59% of deciduous trees belonged to advanced decomposition stages. For 500 lying dead trunks (28%), the original tree number could be assigned. The largest log held a volume of 11.2 m^3/ha (silver fir in PP8 in Derborence, 120 cm at the large diameter and 34.85 m in length), which corresponds to the combined volume of the 428 smallest logs.

4.1 Dead wood quantities

4.1.1 Lying dead wood

In the 24 investigated PPs, CWD volumes ranged from 1 m^3/ha (Derborence, PP5) to 343 m^3/ha (Derborence, PP18; Figure 11 and Appendix Table A1). Considering the reserves, two showed small (<25 m^3/ha) average lying dead wood volumes (Seeliwald and Combe Biosse) and four mean CWD volumes around 100 m^3/ha (Scatlè, Bödmerenwald, Leihubelwald and National Park; Table 4). Derborence had by far the highest CWD volumes (233 ± 106 m^3/ha). The average CWD volume over all PPs amounted to 80 ± 23 m^3/ha. In the undisturbed PPs (e.g. PPs not indicated to be wind damaged in Table 2) the mean CWD volume was 55 ± 13 m^3/ha.

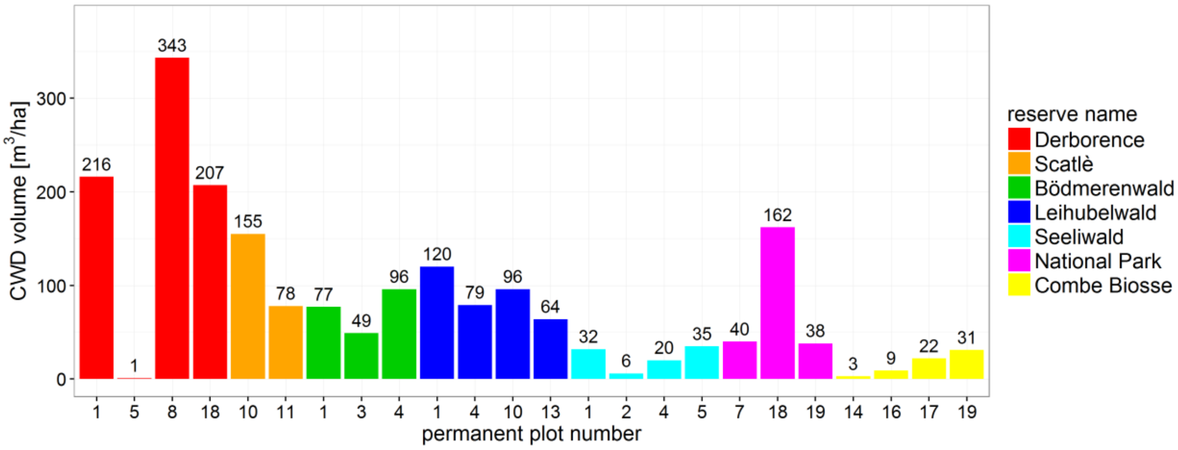

Figure 11. CWD volume in the different permanent plots ordered by forest reserve. Numbers above bars refer to CWD volume per hectare in the corresponding permanent plot.

Considering stem numbers, the picture was slightly different. The highest and lowest stem numbers still occurred in Derborence (PP1: 397 no./ha; PP5: 32 no./ha; Figure 12 and Appendix Table A2). On the reserve level however, National Park (271 ± 49 no./ha) showed the highest stem numbers, followed by Derborence and Scatlè (Table 4). Seeliwald and Bödmerenwald had the lowest stem numbers (and not Combe Biosse with the lowest CWD volumes). Over all reserves, 134 ± 27 stems per hectare were present on average in the lying dead wood.

Volumes and stem numbers fluctuated (partly considerably) within, but also between the reserves. However, CWD volumes and stem numbers did not differ significantly between the reserves (nested ANOVA, residuals=17, p=0.51 for volumes and p=0.31 for stem numbers).

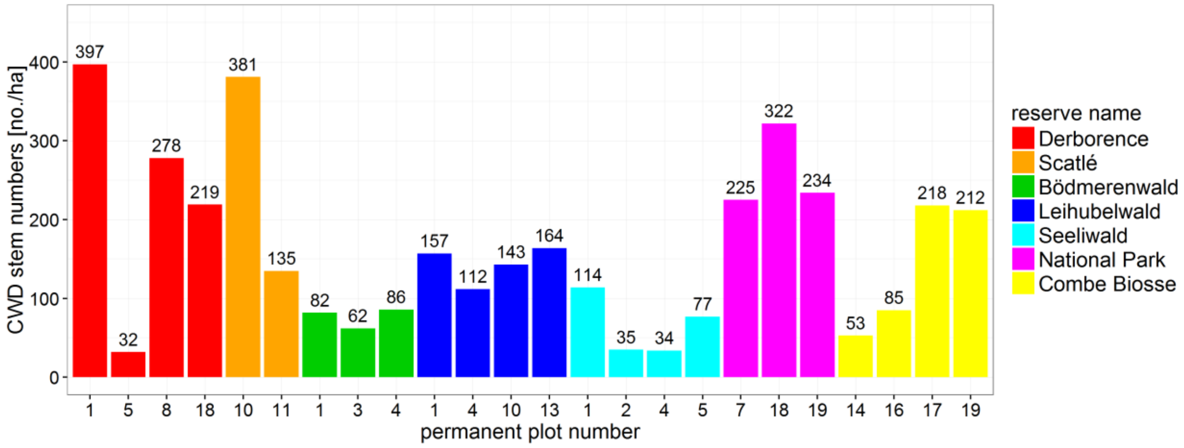

Figure 12. CWD stem numbers in the different permanent plots ordered by forest reserve. Numbers above bars refer to CWD stem numbers per hectare in the corresponding permanent plot.

Table 4. Average volumes and stem numbers of standing and lying dead wood over the investigated permanent plots per forest reserve and on average over all investigated permanent plots. Mean and standard error is weighted by the area size of the corresponding permanent plots. Average volumes and stem numbers of standing dead wood have to be regarded with care due to recording in different years.

Reserve	Number/total area [ha] of investigated PPs	Last inventory	Standing dead wood		Lying dead wood	
			Volume [m³/ha]	Stem number [no./ha]	Volume [m³/ha]	Stem number [no./ha]
Derborence	4/1.65	2008/09/10[1]	83 ± 44	111 ± 45	233 ± 106	242 ± 97
Scatlè	2/0.44	2006	38 ± 45[1]	43 ± 20	114 ± 82	250 ± 261[2]
Bödmerenwald	3/3.62	2003	30 ± 5	24 ± 3	79 ± 12	79 ± 6
Leihubelwald	4/1.49	2011	35 ± 20	100 ± 17	86 ± 19	148 ± 18
Seeliwald	4/2.91	1996/97[3]	10 ± 6	33 ± 9	23 ± 8	61 ± 21
National Park	3/1.47	2012	15 ± 10	35 ± 14	96 ± 64	271 ± 49
Combe Biosse	4/1.86	2010	37 ± 30	169 ± 76	12 ± 9	113 ± 60
Average			**32 ± 9**	**66 ± 18**	**80 ± 23**	**134 ± 27**

[1] PP1 and PP5: 2008; PP8: 2009; PP18: 2010.

[2] may occur with skewed distribution and/or few observations.

[3] PP1 and PP2: 1996; PP4 and PP5: 1997.

4.1.2 Standing dead wood

Standing dead wood data were extracted from NFR inventory database and correspond to the last inventory (recording 4-20 years ago). On plot level, snag volumes ranged between 2 m^3/ha (Seeliwald, PP2) and 124 m^3/ha (Derborence, PP1 and PP8) and stem numbers between 16 no./ha (Seeliwald, PP2) and 342 no./ha (Combe Biosse, PP19; Appendix Table A3). Regarding the temporal development, snag volumes have generally increased since the start of the inventory, but partly fluctuated greatly (Derborence, PP18). On the reserve level, Seeliwald showed the lowest snag volumes (10 ± 6 m^3/ha) and Derborence the highest (83 ± 44 m^3/ha), whereby the range in stem numbers was determined by Bödmerenwald (24 ± 3 no./ha) and Combe Biosse (169 ± 76 no./ha; Table 4). On average over all investigated PPs, snag volume was 32 ± 9 m^3/ha and stem number 66 ± 18 no./ha. In the plots not damaged by hurricane Vivian (Table 2), the mean snag volume amounted to 24 ± 7 m^3/ha.

The proportion of snags out of total stem number (standing living and dead trees, data recorded in the same year) was lowest in PP1 and PP2 of Seeliwald (2%) and highest in PP19 of Combe Biosse (33%; Appendix Table A3). On reserve level, this ratio varied between 4 ± 1% (Seeliwald) and 20 ± 6% (Combe Biosse) and was on average over all investigated permanent plots 10 ± 2%.

4.2 Dead wood qualities

4.2.1 Tree species

Conifers were very abundant in CWD volume and stem number and no deciduous trees in the lying dead wood at all were present in the entire investigated perimeter of Scatlè, Bödmerenwald, Seeliwald and National Park (Appendix Table A5). The highest volumes (4 ± 3 m^3/ha) and stem numbers (56 ± 29 no./ha) of deciduous trees were present in Combe Biosse, where 90% of all recorded deciduous logs were found. In two PPs in Combe Biosse, even more than 50% of CWD volumes (PP16) and stem numbers (PP16, PP17) consisted of deciduous wood (Appendix Table A1 and Table A2). On average over all PPs, deciduous wood had an amount of 1% in CWD volume and 6% in CWD stem number (Appendix Table A5).

4.2.2 Dimensions

4.2.2.1 Large and small diameter trees

In 16 of 24 PPs, CWD volumes consisted more of large (>30 cm) diameter than of small (≤30 cm) diameter trees (Figure 13). On PP level, volume of large diameter trees contributed between 0% (Derborence, PP5) and 97% (Leihubelwald, PP4) to total CWD volumes; in absolute numbers the CWD volumes of large diameter trees ranged between 0 m^3/ha and 331 m^3/ha (Derborence, PP5 and PP18; Appendix Table A1). On the reserve level, large dimensions were always more abundant in volume except in Combe Biosse (43% large diameter trees; Appendix Table A6) with highest abundance in Derborence (94%). Over all investigated PPs, large logs contributed with 88% and small logs with 12% to the mean CWD volume of 80 ± 23 m^3/ha.

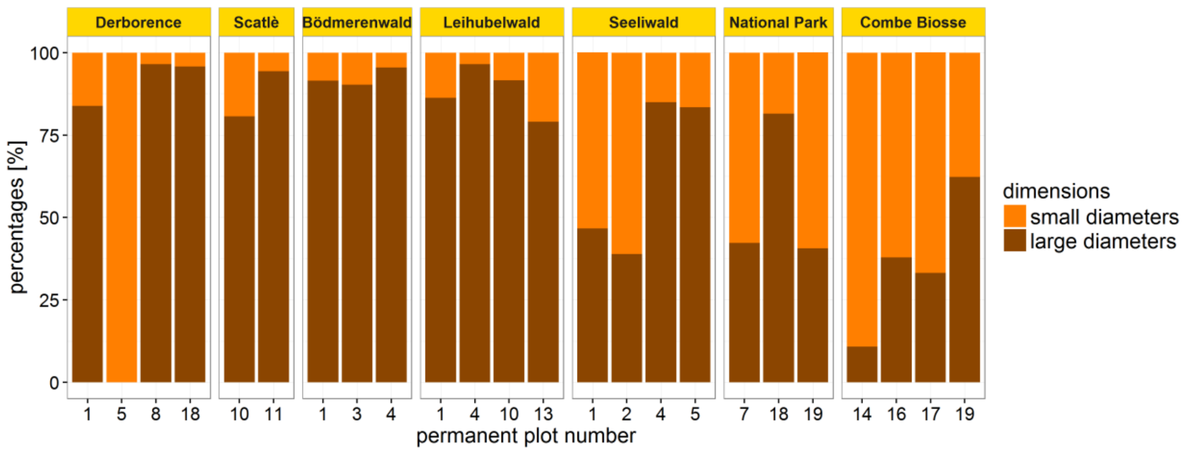

Figure 13. Shares of large (>30 cm) and small (≤30 cm) diameter trees in lying dead wood volumes in the different permanent plots ordered by forest reserve. Absolute values are presented in Appendix Table A1.

Concerning the stem numbers, the share of large diameter trees was not as high as that in volumes. Only in five PPs large logs were more abundant in stem counts than small logs, with the highest share in PP8 in Derborence (71%; Figure 14). Large diameter trees reached maximally 198 no./ha (Derborence, PP1) and small diameter trees 232 no./ha (Scatlè, PP10; Appendix Table A2). On the reserve level, only Derborence showed a majority of large dimensioned logs (62%; Appendix Table A6), what probably also resulted in the high total CWD volumes of 233 ± 106 m^3/ha. Overall, 86 ± 18 (64%) logs per hectare belonged to small dimensions and 48 ± 15 (36%) logs per hectare to large dimensions.

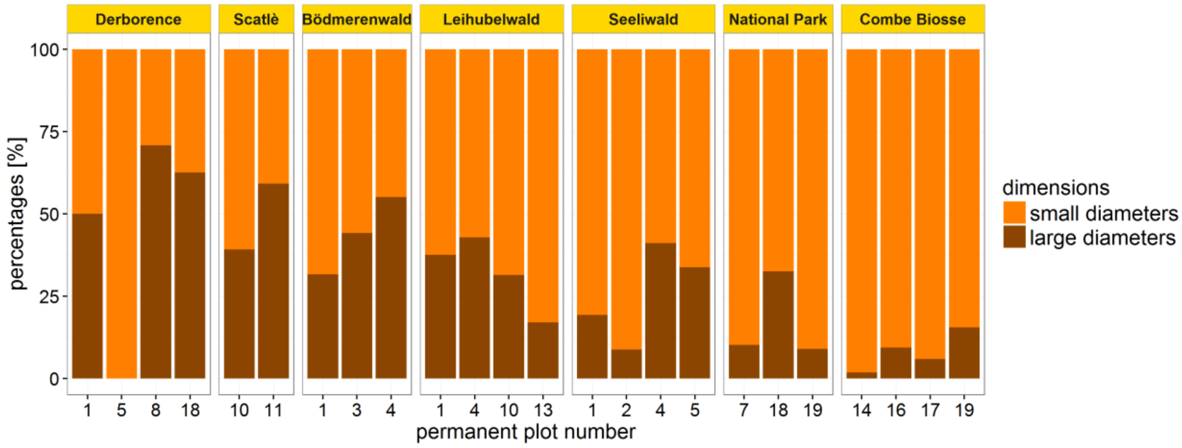

Figure 14. Share of large (>30 cm) and small (≤30 cm) diameter trees in lying dead wood stem number in the different permanent plots ordered by forest reserve. Absolute values are presented in Appendix Table A2.

4.2.2.2 Giant trees

In the lying dead wood, most giant trees (larger log diameter ≥80 cm) were found in PP8 in Derborence (9 giant trees per hectare), followed by 3 no./ha (Bödmerenwald, PP1), 2 no./ha (Bödmerenwald, PP1; Derborence, PP18) and 1 no./ha (Bödmerenwald, PP3; National Park, PP18). In the remaining PPs of Derborence, Bödmerenwald and National Park as well as in all the studied PPs of Scatlè, Leihubelwald, Seeliwald and Combe Biosse, giant trees were absent. In the standing dead wood giant trees were present in two PPs only: 9 no./ha in PP8 of Derborence and 1 no./ha in PP18 of National Park, whereby it is possible that a giant tree formerly recorded as standing dead was during the field work recorded as lying dead.

4.2.2.3 Diameter distribution

The diameter distribution of the lying dead trees showed differences on the NFR level. In Derborence for instance, the larger log diameter varied between 8 cm and 120 cm and did not show a clear peak in a certain diameter range (Figure 15a), similar to Bödmerenwald (Appendix Figure A1b), Seeliwald (Appendix Figure A2a) and partly Scatlè (Appendix Figure A1a). However, Bödmerenwald and Seeliwald had much lower stem numbers and Seeliwald a smaller diameter range. By contrast, the larger log diameter in Combe Biosse ranged only between 8 cm and 46 cm and showed a peak in stem counts at small diameters, with a rapid decline towards larger diameters (Figure 15b). A similar picture showed Leihubelwald (Appendix Figure A1c) and National Park (Appendix Figure A2b), but with different diameter ranges and stem counts.

Considering the standing dead trees (recorded in the last inventory), the diameter distribution of logs was well reflected in Bödmerenwald, Leihubelwald, Seeliwald and Combe Biosse. In Derborence, Scatlè and National Park, stem counts of snags was much lower and/or with a different diameter distribution.

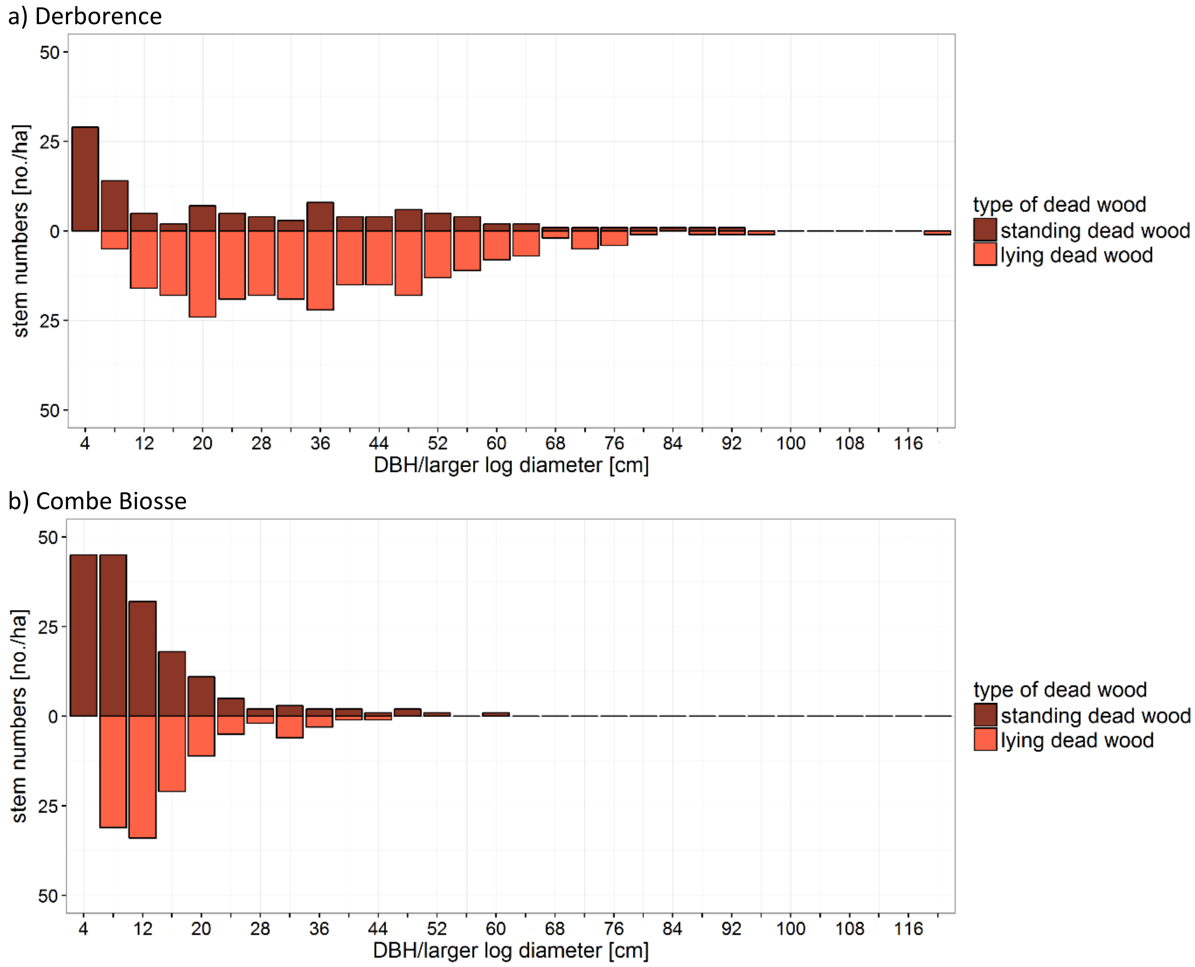

Figure 15 (a/b). Diameter distribution (in 4-cm classes) of standing (data from the last inventory record stored in the NFR inventory database) and lying dead wood in the forest reserves of Derborence (a) and Combe Biosse (b). X-values represent the minimum diameter value of each DBH class (standing dead wood) or each larger log diameter class (lying dead wood). Note that x-range and y-range are the same for all diameter distribution plots and are limited by Derborence (x-range) and National Park (y-range).

4.2.3 Decomposition stages

Decomposition class I was absent in ten PPs, class II+III in one PP and advanced decay stages (class IV+V) occurred in all PPs (Appendix Table A1). In 21 of 24 PPs, advanced decomposition stages were the most abundant decay classes with respect to CWD volumes (Figure 16). In the remaining PPs, class III (Leihubelwald, PP13; National Park, PP7) or class II (National Park, PP19) were most prevalent in volumes. Highest absolute volumes of the single decay stages were found in two PPs only: PP8 of Derborence (class I: 19 m^3/ha; class III: 43 m^3/ha; class IV: 92 m^3/ha; class V: 181 m^3/ha) and PP18 of National Park (class II: 25 m^3/ha). On the reserve level, decay class V dominated CWD volumes in all NFRs except Bödmerenwald and Leihubelwald (class IV; Appendix Table A7). Highest relative abundance of decay stage classes I+II was found in National Park, of class III in Scatlè and Bödmerenwald, of class IV in Leihubelwald and of class V in Seeliwald. On average, class IV (32%) and class V (39%) together accounted for 71% of CWD volumes.

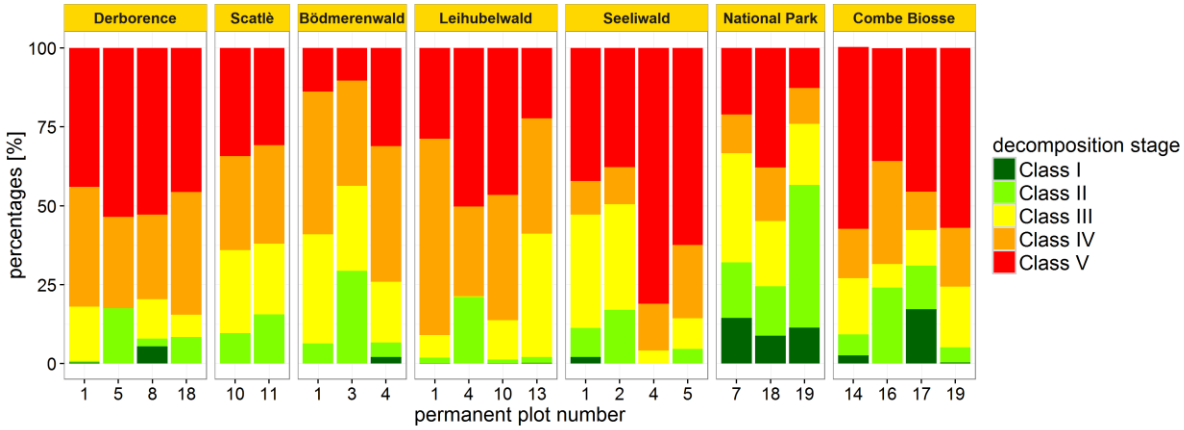

Figure 16. Shares of decomposition stage classes in lying dead wood volumes in the different permanent plots ordered by forest reserve. Absolute values are presented in Appendix Table A1.

With respect to stem numbers, class IV or class V were again most prevalent in 21 PPs, but not in PP11 of Scatlè (class II+III), in PP13 of Leihubelwald and PP19 of National Park (class III; Figure 17). On the reserve level, decay class V dominated stem numbers of all reserves except Leihubelwald (class IV; Appendix Table A8). Highest proportions of decay class I+II occurred in National Park, of class III in Scatlè, of class IV in Leihubelwald and of class IV in Seeliwald. In total, 63% of stem numbers consisted of advanced decay classes, with class V in higher proportions (38%).

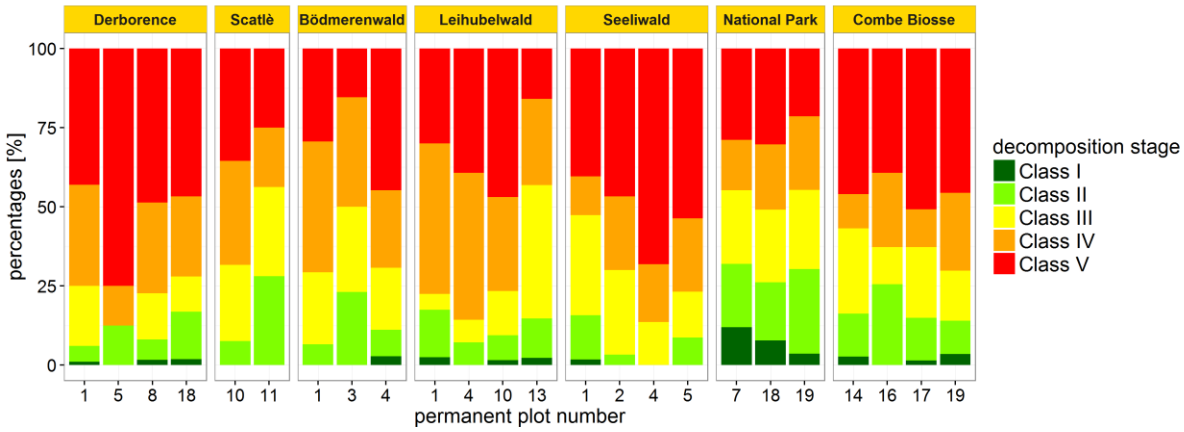

Figure 17. Shares of decomposition stages in lying dead wood stem number in the different permanent plots ordered by forest reserve. Absolute values are presented in Appendix Table A2.

Combining the two quality characteristics of large dimensions and advanced decay stages, CWD volumes ranged between 0 m^3/ha (Derborence, PP5; Seeliwald, PP2; National Park, PP19) and 265 m^3/ha (Derborence, PP8) and stem numbers between 0 no./ha and 166 no./ha (Derborence, PP1). Large dimensions and advanced decomposition stages maximally contributed to 85% of total CWD volumes (Seeliwald, PP4) and to 59% of total stem numbers (Derborence, PP8). On reserve level, proportions of volumes and stem numbers ranged between 31% and 90% respectively between 7% and 60%, with lowest values in Combe Biosse and highest in Derborence. Overall, 70% of total CWD volumes and 29% of lying stem numbers consisted of high quality lying dead wood.

4.3 Statistical modeling of dead wood quantity and quality

4.3.1 Total CWD volume

After the selection procedure for linear mixed effect models applying the AIC selection criteria, the final combination of variables best explaining the total CWD volumes in the 24 investigated PPs included as fixed effects time since last management, presence of wind, northness of the hillside and proportion of deciduous tree species in living basal area (Table 5). The first three factors were positively correlated with CWD volumes, the fourth negatively. The marginal R^2, which describes the proportion of variance explained by the fixed effects only, was 0.48 and the conditional R^2, including also the random effect, was 0.73, indicating that the reserve itself explained for 25% of total variance.

Table 5. Final linear mixed effect model explaining total CWD volume. The random effect (forest reserve) is marked in blue. A detailed explanation of the fixed effects is given in the section "Fixed effects" in chapter 3.3.4.1.

log(VOLUME_LYING_DEAD) ~ MANAGEMENT + WIND + NORTHNESS+ arcsine(DECIDUOUS) + RESERVE				
Coefficient	**Estimate**	**Standard Error**	**t-value**	**p-value**
Intercept	2.74	1.00	2.74	0.02
Last management 50-100 years	0.94	1.31	0.72	0.51
Last management >100 years	0.62	1.05	0.59	0.59
Wind	1.68	0.69	2.43	0.03
Northness	0.94	0.49	1.92	0.08
Deciduous tree species	-0.74	1.92	-0.39	0.71

4.3.2 Dimensions

Volumes of large (>30 cm) dimensioned logs were negatively correlated to the amount of deciduous tree species in basal area of the live stand (Table 6). Volumes of small dimensioned logs were therefore positively associated with deciduous tree species. The fixed effects explained 26% of total variance (marginal R^2) and both the fixed and the random effects 38% (conditional R^2).

Table 6. Final linear mixed effect model explaining the volumetric percentages of large (>30 cm) dimensioned logs in total CWD volume. The random effect (forest reserve) is marked in blue. A detailed explanation of the fixed effect is given in the section "Fixed effects" in chapter 3.3.4.1.

arcsine(VOLUME_LARGE_DIMENSIONS) ~ arcsine(DECIDUOUS) + RESERVE				
Coefficient	**Estimate**	**Standard Error**	**t-value**	**p-value**
Intercept	1.11	0.09	12.10	<0.001
Deciduous tree species	-0.77	0.32	-2.43	0.03

4.3.3 Decomposition stages

When visualizing the relative abundance of decay stages in CWD volumes in the 24 PPs, the first principal component (PCA1) of the PCA explained for 42% of total variance and the second principal component (PCA2) for 26% (Figure 18). The first axis distinguished between fresh and medium decomposition stages (class I+II+III) and advanced decay stages (class IV+V) and the second axis contrasted most between decay class II and decay class III. Permanent plots of National Park and Scatlè were rather well aggregated, whereby plots of Seeliwald and partly Combe Biosse showed a rather varied picture considering decay class distribution. Fresh decomposition stages (class I+II) characterized National Park and advanced decay stages Derborence, Leihubelwald and PP4 and PP5 of Seeliwald. Bödmerenwald and Scatlè consisted predominantly of medium decay stages (class III).

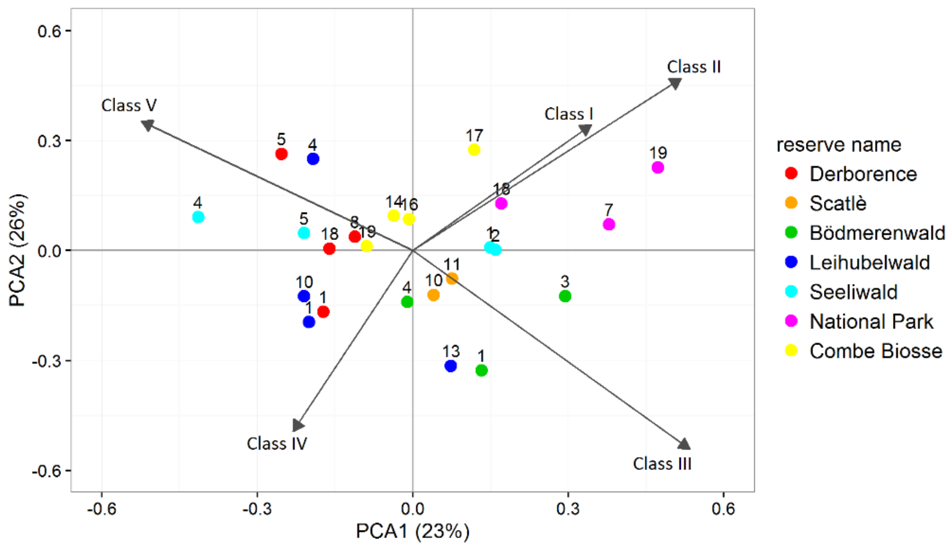

Figure 18. Principal Component Analysis (PCA) showing the differences in the relative abundances of decomposition stages in CWD volumes of the different permanent plots colored by forest reserve. Numbers above dots refer to permanent plot number. Vectors for decay stages are marked in black.

In the RDA, the final set of environmental variables best explaining the abundance of decomposition stages following the AIC selection criteria included time since last forestry operation of 20-50 years ago, past wind disturbance, precipitation and exposition of the hillside (northness). The first axis (RDA1) accounted for 24% of observed variation and the second axis (RDA2) for 13% (Figure 19). The adjusted R^2 was 0.33. The first axis is mainly shaped by wind presence/absence and the second axis by short/medium or long time since last management intervention. Decay stage composition in all plots of National Park were negatively correlated with past wind disturbance and precipitation, whereby most plots in Derborence and Leihubelwald were positively correlated with these two variables. Bödmerenwald and Scatlè were negatively associated with time since last management of 20-50 years ago and Seeliwald and Combe Biosse mainly positively.

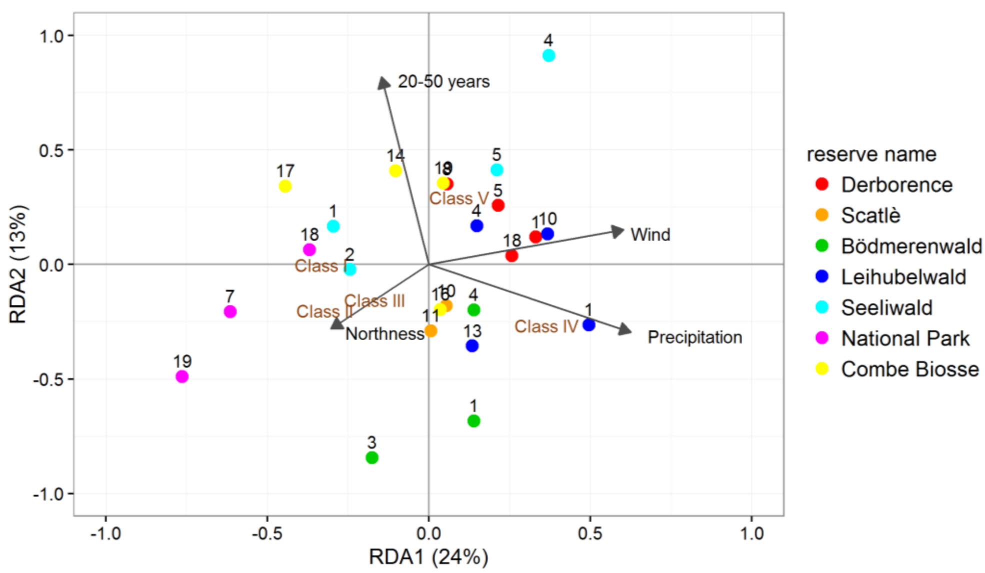

Figure 19. Redundancy Analysis (RDA) showing the relationships between the decay classes and environmental factors (black vectors) in the different permanent plots. Decay class names in brown indicate the decay stage's vector endpoints. Numbers above dots refer to permanent plot number.

4.4 Spatial distribution of lying dead wood

4.4.1 Log orientation

On average, 20% of all logs were falling in hillside direction. This percentage slightly increased on steeper slopes. Generally, log orientation peaked in direction of hillside gradient (if there was one). On PP level, the number of all logs falling in hillside direction ranged from 9% (Seeliwald, PP4) to 37% (Combe Biosse, PP17; Table 7). The proportion of logs falling in hillside direction of the inspected five categories (see chapter 3.3.5.1) varied greatly, from 6% (large logs on steep slopes, n=17, Leihubelwald, PP1) up to 39% (large logs on steep slopes, n=33, Combe Biosse, PP16) but a general pattern could not be identified. The Rayleigh test indicating a uniform log orientation was significant in Scatlè PP11 and Bödmerenwald PP3 (Table 7). The Hotelling test showing no differences between log and aspect of close log surrounding was significant in Bödmerenwald PP3 and Leihubelwald PP4.

A similar pattern in log orientation distribution suggested PP1, PP8 and PP18 of Derborence, PP1 and PP4 of Bödmerenwald and PP10 of Leihubelwald. In the 3 plots in Derborence, which are located on a steep slope, 17-25% of all logs were falling downslope (Table 7). However, another 40-45% was shifted by about 45° with respect to slope orientation (Derborence, PP1: Figure 20b). In Leihubelwald, PP10 is situated on a small plateau and more than 25% of all logs were oriented to northeast. In PP1 and PP4 of Bödmerenwald, which are located in a relatively flat area with small mounds, about 55% of all logs peaked in northeastern to southeastern direction, whereby the peak in PP1 was more pronounced. Common features of these six PPs were that particularly longer and larger logs showed a greater shift or peak into one direction than short and small logs, respectively, that a great majority of these logs were of decay class IV and, more so, class V and that all PPs exhibited spatial clustering (Table 7).

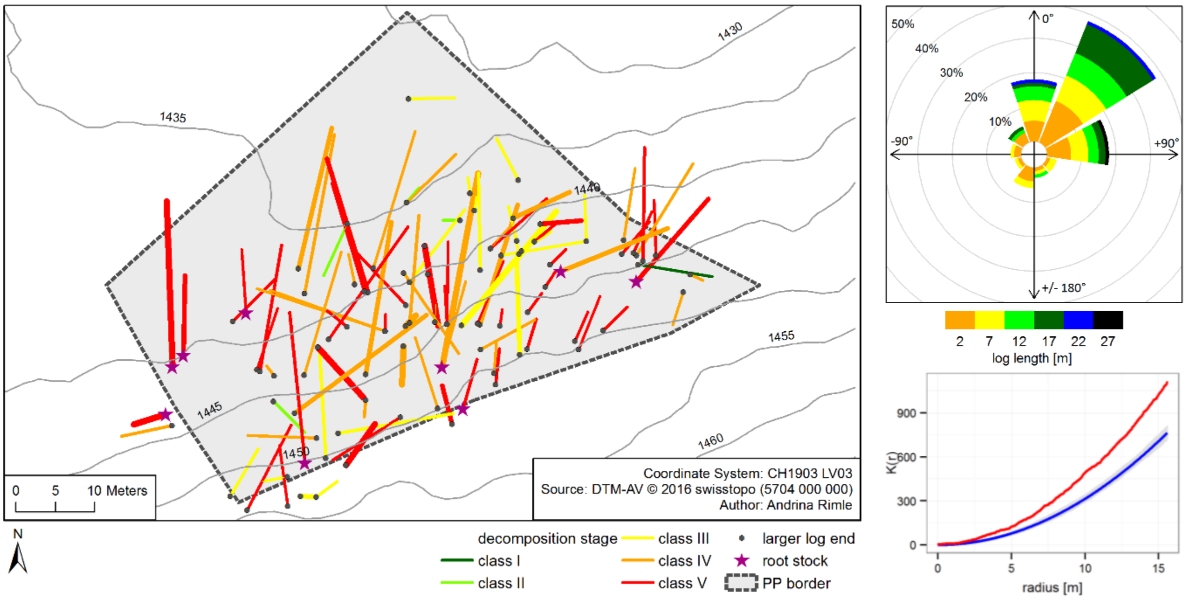

Figure 20 (a/b/c). Derborence, PP1 (n=100). Slope: NW/W, ~30°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of differences between log and hillside orientation in 45°-classes stratified by log length of 5 m classes. 0°: no differences between log and hillside direction; ± 180°: log and hillside are oppositely oriented. X-values in the legend represent minimum length value of each class. Lower right panel: Diagram of the $K(r)$ function of all logs within PP borders (n=90) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

Table 7. Results of spatial analysis of lying dead trees and standing (living and dead) trees in the different permanent plots ordered by forest reserve. Rayleigh's test indicates spatially uniform log orientation and Hotelling test examines whether mean angle of log orientation and mean aspect of close log surrounding are likewise oriented. Figure references refer to map depiction of all logs, log orientation plots and diagrams of $K(r)$ function of all logs within PP borders for each particular permanent plot. The spatial pattern of standing trees (results are presented in the last two columns) was analyzed if coordinates of standing trees were available in the NFR inventory database, which was only the case for inventories run after the year 2007. Spatial pattern in PP5 in Derborence was not analyzed because of eight logs only and no coordinates available for standing trees.

Reserve	PP number	Slope orientation (inclination)	Number of logs: all/all within PP borders	Significance of Rayleigh's test/ Hotelling test for all logs	Proportion of all logs falling in hillside direction [%]	Spatial pattern analysis for all logs within PP borders	Figure reference (A: Appendix)	Number of standing trees: all/all within PP borders	Spatial pattern analysis for all standing trees within PP borders
Derborence	1	N/NW (~30°)	100/90	no/no	20	clustered	Figure 20	248/248	varying
	5	-	8/8	-	-	-	Figure A4	-	-
	8	N/NW (~30°)	185/146	no/no	17	clustered	Figure A5	247/236	clustered
	18	NW (~30°)	107/105	no/no	25	clustered	Figure A6	172/167	clustered
Scatlè	10	E (~30°)	79/77	no/no	19	clustered	Figure A7	-	-
	11	E (~30°)	32/17	yes/no	28	random	Figure A8	-	-
Bödmerenwald	1	-	92/80	no/no	10	clustered	Figure A9	-	-
	3	-	52/44	yes/yes	15	clustered	Figure A10	-	-
	4	-	143/143	no/no	16	clustered	Figure A11	-	-
Leihubelwald	1	E (~20°)	40/39	no/no	15	random	Figure A12	215/210	clustered
	4	E/SE (~20°)	28/28	no/yes	19	clustered	Figure A13	302/293	clustered
	10	E/SE (~10°)	64/62	no/no	19	clustered	Figure A14	521/490	clustered
	13	NE (~10°)	88/82	no/no	15	clustered	Figure A15	430/405	clustered
Seeliwald	1	NW (~20°)	57/49	no/no	12	clustered	Figure A16	-	-
	2	NW (~15°)	30/30	no/no	17	varying	Figure A17	-	-
	4	W (~10°)	22/22	no/no	9	random	Figure A18	-	-
	5	N/NE (~10°)	69/68	no/no	13	clustered	Figure A19	-	-
National Park	7	N (~25°)	125/121	no/no	26	clustered	Figure A20	398/394	clustered
	18	NE (~20°)	218/195	no/no	24	clustered	Figure A21	571/564	clustered
	19	N (~20°)	56/51	no/no	18	random	Figure A22	273/272	clustered
Combe Biosse	14	S (~25°)	37/36	no/no	27	clustered	Figure A23	603/574	clustered
	16	S (~25°)	51/46	no/no	31	varying	Figure A24	347/333	varying
	17	NW (~35°)	67/64	no/no	37	varying	Figure A25	284/264	varying
	19	W (~35°)	57/56	no/no	12	random	Figure A26	281/269	random

4.4.2 Spatial pattern analysis

4.4.2.1 Lying dead wood

Concerning spatial pattern analysis, 15 PPs showed a clustered pattern of all logs within PP borders, five PPs a random pattern and spatial pattern of three PPs varied within the inspected radius (Table 7). A regular spatial pattern was not observed. On the reserve level, only all PPs of Derborence and Bödmerenwald suggested a clustered pattern. In the remaining reserves, PP's individual spatial pattern differed, but in general, a clustered pattern was more frequent than a random pattern. Besides in one PP (Seeliwald, PP4), the spatial pattern of all logs was not similarly reflected by the pattern of the diameter or decay classes, but a trend could not be identified.

4.4.2.2 Standing trees

Spatial pattern of standing (living and dead) trees could only be analyzed for plots in which the last inventory took place after the year 2007 (before, coordinates were not measured). Of 14 plots totally analyzed, ten PPs suggested spatial clustering of all standing trees within PP borders, one PP spatial randomness and three PPs spatial variation (Table 7). On the reserve level, all PPs in Leihubelwald and National Park indicated spatial clustering whereas in the remaining reserves (Derborence and Combe Biosse) the spatial pattern was not uniform over all investigated PPs. In 11 of 14 plots, the spatial pattern of logs corresponded with the spatial pattern of standing trees.

5 DISCUSSION

5.1 Dead wood quantity and quality

The purpose of the first part of this thesis is to generally describe dead wood quantity and quality of Norway spruce forest reserves in Swiss mountainous regions, to compare these findings with results from other studies in unmanaged forests across Europe (preferably *Picea abies* forests) and to provide a first baseline for managed coniferous forests in Switzerland regarding the governmental biodiversity policy.

5.1.1 Volumes

Lying dead wood volumes in the 24 investigated PPs amounted to 80 ± 23 m^3/ha on average (12-233 m^3/ha on reserve level, Table 4; 1-343 m^3/ha on plot level, Appendix Table A1). Standing dead wood volumes reached in the last inventory on average 32 ± 9 m^3/ha (10-83 m^3/ha on reserve level, Table 4; 2-124 m^3/ha on plot level, Appendix Table A3). When comparing lying and standing dead wood volumes in the investigated PPs with other European studies in unmanaged or old-growth forests of different tree species composition (Table 8), it has to be kept in mind that measurement thresholds differed with respect to diameter and length. Furthermore, dead wood volumes vary highly, depending for instance on forest type (Hahn and Christensen 2005), site conditions (Sippola et al. 1998), exceptional events such as storms or dry weather periods (Kirby et al. 1998), development stage (Saniga and Schütz 2001) or decomposition conditions (Korpel' 1997). Additionally, my findings of lying dead wood volumes are probably underestimated due to the calculation method and the omitting of root stock estimations (see chapter 3.2.1).

Table 8. Dead wood volumes of snags, logs and in total (without stumps or branches) in European forest reserves or old-growth forests of different tree species composition ordered by broadleaf forests, mixed coniferous and deciduous forests and coniferous forests. The measurement threshold was not always reported (-). Volume values are given for the mean ± standard error (a) or standard deviation (b) and (in parenthesis) the range over the investigated study plots.

Dominant tree species	Region	Measurement threshold for snag/log diameter [cm]	Dead wood volumes [m^3/ha]			Reference
			Snags	Logs	Total	
Fagus sylvatica	Europe	-/5	39 (1-282)	94 (3-456)	130 ± 103 [a] (6-550)	Christensen et al. (2005)
Fagus sylvatica	Central Italy	2.5/10	10 ± 16 [b]	12 ± 24 [b]	22	Burrascano et al. (2008)
Tilia cordata/ Carpinus betulus	Poland	-/5	-	(52-94)	-	Kirby et al. (1991)
Fagus sylvatica/ Abies alba	Switzerland	4/7	25 ± 4 [a] (13-38)	44 ± 12 [a] (20-100)	69 ± 13 [a] (49-129)	Herrmann et al. (2012)
Fagus sylvatica/ Abies alba/ Picea abies	Slovakia	-/-	(41-82)	(140-198)	(181-280)	Korpel' (1997)
Picea abies	Slovakia	-/-	(18-55)	(26-141)	(50-183)	Korpel' (1997)
Picea abies	Germany	-/-	56	28	84 (10-180)	Rauh and Schmitt (1991)
Picea abies	Southern Finland	10/10	33	77	110 ± 33 [b] (70-184)	Siitonen et al. (2000)
Picea abies	Finish Lapland	1/5	5	13	18	Sippola et al. (1998)

On average, my findings of lying and standing dead wood are comparable or even exceed volumes reported from unmanaged forests of different tree species composition across Europe. In managed Swiss forests, total dead wood (standing and lying) volumes amount to 34 m^3/ha, with highest values in the conifer dominated Northern Alps (46 m^3/ha) and lowest in the deciduous dominated Swiss Midlands (24 m^3/ha), whereby the measurement threshold for standing dead wood was 12 cm and the one for lying dead wood 7 cm (Brändli 2015).

The presented lying and standing dead wood volumes exceed in a majority of investigated PPs the recommended total dead wood volumes of 10 m^3/ha for a semi-natural silviculture (Kaufmann et al. 2010) and of 20 m^3/ha (Jura) respectively of 25 m^3/ha (Prealps, Alps) targeted in the national forest policy 2020 (Swiss Federal Office of the Environment 2013). Furthermore, they surpass the suggested habitat threshold of standing (18 m^3/ha) and of lying (15 m^3/ha) dead wood volumes for subalpine *Picea abies* forests, when the majority of dead wood associated species and particularly the three-toed woodpecker (*Picoides tridactylus*), an umbrella species, should be present (Bütler 2003). In addition, total dead wood volumes of 20-30 m^3/ha as recommended by Müller and Bütler (2010) for boreo-alpine pine-spruce forests are exceeded. Indeed, some species require volumes far above the suggested thresholds. For example the rare fungus *Antrodiella citrinella* living on Norway spruce dead wood requires volumes >134 m^3/ha (Bässler and Müller 2010). Although such precise volume data are probably difficult to evaluate in practice, they still indicate that some species are dependent on extraordinarily high dead wood amounts. In this thesis, CWD volumes of six single PPs and of two reserves on average exceeded 100 m^3/ha (Figure 11 and Table 4), amounts assumed to be common before European forests were intensively exploited by humans (Nilsson et al. 2002).

In summary, the standing and lying dead wood volumes in Norway spruce dominated NFRs presented in this thesis are comparable with values found in others unmanaged (pure) *Picea abies* forests across Europe and are higher than dead wood volumes in managed conifer stands of Switzerland. Recommended total dead wood volumes by the Swiss government are exceeded.

5.1.2 Stem numbers

Stem densities in the lying dead wood averaged to 134 ± 27 stems per hectare (61-271 no./ha on reserve level, Table 4; 32-397 no./ha on PP level, Appendix Table A2) and in the standing dead wood to 66 ± 18 stems per hectare (24-169 no./ha on reserve level, Table 4; 16-342 no./ha on PP level, Appendix Table A3). References concerning dead wood stem numbers from other studies in European unmanaged coniferous forests are rare as dead wood volumes were often the research focus. Nilsson et al. (2002) reported 80-230 lying dead trees per hectare respectively 30-180 standing dead trees per hectare (diameter threshold >10 cm) and Siitonen et al. (2000) described 354 standing dead trees per hectare (DBH >5 cm). Both studies were conducted in Scandinavian Norway spruce dominated old-growth forests.

5.1.3 Tree species

CWD volumes and stem numbers of deciduous trees were low except in Combe Biosse (Appendix Table A5), the only selected forest reserve with a considerable amount of deciduous tree species (*Fagus sylvatica*, *Acer pseudoplatanus*) in the live stand (Brang et al. 2008).

5.1.4 Dimensions

On average 88% of CWD volumes and 36% of CWD stem numbers in the studied NFR consisted of large diameter trees (>30 cm; Appendix Table A6). In comparison, Herrmann et al. (2012) documented in Swiss deciduous and deciduous mixed forest reserves 46% of lying dead wood to be consisting of large diameter trees (>30 cm). In addition, Sippola et al. (1998) reported from old-growth *Picea abies* forests in Finland 22% of total dead wood volumes and 2% of total dead wood stem numbers to be of large diameters (≥30 cm). In Swiss managed forests, large diameter trees (>30 cm) are underrepresented in total dead wood volumes with a proportion of 35% (Brändli 2010). In short, the investigated plots feature extraordinarily high lying dead wood volumes and stem numbers of large dimensions.

Regarding giant trees, a common used indicator for a forest's naturalness (Bütler et al. 2015), references from European forest reserves and Swiss managed forests could only be found for living but not for dead trees. In the investigated seven NFRs, Heiri et al. (2012) reported the amount of giant trees per hectare in the live stand to be none (Seeliwald and National Park), three (Combe Biosse), seven (Bödmerenwald), eight (Scatlè) or ten (Derborence and Leihubelwald). In the lying and standing dead wood, giant trees were absent in more reserves and if present, their number was lower. In beech dominated stands of Central Europe, Nilsson et al. (2002) documented 10-17 giant trees per hectare and Korpeľ (1995) reported 6-18 giant trees per hectare in *Picea abies* dominated stands in the Western Carpathians (Slovakia). In Swiss managed forests, 1-2 giant trees per hectare occur in the live stand (Brändli 2010). In brief, Swiss NFRs are regarding giant trees in the live stand not yet comparable with other unmanaged forests in Europe but in a more natural condition than Swiss managed forests.

With respect to the diameter distribution of standing and lying dead trees, smaller diameters were much more frequent than larger diameters in Leihubelwald, National Park and Combe Biosse (Appendix Figure A1c and Figure A2b; Figure 15b), whereby the diameter range in the first two listed reserves was wider than in the latter. Diameter distribution of standing and lying dead wood corresponded well to each other except in National Park (snags in much lower stem counts than logs). Such a diameter distribution (reversed J-shaped) is characteristic for rather young forests in early development stages (Linder 1998, Siitonen et al. 2000), what these three forests reserve are (Korpeľ 1995) as they were managed for the last time about 100 years ago (Table 1). Although National Park was earlier established as a forest reserve than Leihubelwald and Combe Biosse, the diameter distribution is still indicative for a young forest. A possible reason for that observation could be that the lower site productivity and the cold and dry climate conditions in National Park (Appendix Table A10) may have a decelerating effect on tree growth and thus on the development of large diameters. Furthermore, dead wood is also the slowest element in natural forests to recover after a management intervention (Siitonen et al. 2000), which was intensive in National Park (Parolini 1995).

In Derborence, Scatlè, Bödmerenwald and Seeliwald (Figure 15a and Appendix Figure A1a, Figure A1b and Figure A2a), the diameters were more evenly distributed and larger diameters were highly present (particularly in Derborence and Bödmerenwald). This type of diameter distribution is indicative for older forests with a small-scale pattern of different development stages next to each other (Linder 1998, Siitonen et al. 2000). The last forestry operation in Derborence took place more than 300 years ago and Scatlè and Bödmerenwald were never managed (Table 1). High stem counts of large diameter trees in the lying dead wood in Derborence could also be related to hurricane Vivian, as logs of large dimensions reaching the upper canopy layer as standing trees were rather downed during this heavy storm as they were more susceptible to windthrow than small diameter trees growing in lower canopy layers (Coates 1997). In Seeliwald however, a rather young reserve (Table 1), trees were extracted for the last time about 50 years ago, but management was always of low intensity (Gregor Jakober, personal communication, October 21, 2015), why few trees could probably still reach large diameters. The low stem counts may be related to the limited site productivity due to the location in a peat bog.

5.1.5 Decomposition stages

With respect to decay stages, 72% of CWD volumes in the studied coniferous NFRs belonged on average to advanced decomposition stages (class IV+V, Appendix Table A7) in contrast to 53% in deciduous and deciduous mixed NFRs in Switzerland (Herrmann et al. 2012). In old-growth *Picea abies* forests in Finnish Lapland, decay class III and IV are most present in lying dead wood volumes (Sippola et al. 1998). In Swiss forests, only about 10% of CWD volumes consist of advanced decomposition stages, but more than 70% of decay class I and II (Brändli 2010). In brief, the investigated PPs exhibit higher shares of advanced decomposition classes than other forest reserves or managed Swiss forests.

In Swiss forests dead wood of large dimensions and advanced decay stages is rare (Rigling and Schaffer 2015). Similar results are documented from managed Norway spruce dominated stands in Finland (Siitonen et al. 2000). In managed forests, primarily large diameter trees are harvested and logging waste (e.g. branches), which is left behind in the forest, is of small dimensions (Kirby et al. 1998). Advanced decomposition stages develop only after an extended time without any human interference or natural disasters such as storm events or bark beetle infestations (Jonsson et al. 2005). However, these two quality characteristics, found in high shares in the investigated forest reserves, have been identified to host a great diversity of beetles (Jonsell et al. 1998, Similä et al. 2003, Brin et al. 2011), fungi (Hoiland and Bendiksen 1996, Ódor et al. 2006), bryophytes (Ódor et al. 2006) and lichens (Uliczka and Angelstam 2000). Not all of the species investigated in the mentioned studies occur on Norway spruce logs, but many of them are listed in the national red list of Switzerland and other countries. For example, the moss *Jungermannia leiantha*, acknowledged to be a good indicator for old-growth forests, occurs preferably on beech logs of large diameters and of intermediate and advanced decay stages (Ódor et al. 2006) and is listed as a vulnerable species in the Swiss national list of high priority species (Swiss Federal Office of Environment 2011).

5.1.6 References for forest management and biodiversity conservation

To improve the conditions for dead wood associated organisms in Swiss mountainous coniferous regions, it is important to have a natural reference. CWD volumes of 80 ± 23 m^3/ha and snag volumes of 32 ± 9 m^3/ha, recorded in a complete enumeration on plot level, provide a first baseline of volumes which can be obtained today under unmanaged conditions. However, dead wood volumes fluctuate also in pristine forests (Korpel' 1997), depending for instance on development stage (Saniga and Schütz 2001) or the type and frequency of disturbances (Kirby et al. 1998). Thus, a volume range may be more appropriate. The presented volume values may be still too high as a practicable guideline in managed stands. From a management technical perspective, the total dead wood volumes of 20 m^3/ha (Jura) and 25 m^3/ha (Prealps and Alps) for managed forests targeted in the national forest policy 2020 (Swiss Federal Office of the Environment 2013) may be more adequate because secured working conditions for forestry workers are of high priority but can be negatively affected by high dead wood volumes (Imesch et al. 2015). However, from a biological point of view, I only partly approve the governmental recommendations regarding dead wood volumes. First, specifications about lying and standing dead wood, one of the most important quality characteristic (Christensen et al. 2005), are missing. Second, the total dead wood volumes of 33 m^3/ha suggested by Bütler (2003), when the majority of dead wood associated species in subalpine *Picea abies* forests should be present, are not met. In addition, also the recommended values by Bütler (2003) do not fulfill the requirements of all species as some (e.g. *Antrodiella citronella*) require much higher dead wood volumes (see chapter 5.1.1). Nevertheless, the consideration of the requirements of such specialized species may be, certainly on a large scale, difficult to realize in managed forests and it may be better to promote at least the majority of saproxylic species to preserve and promote forest biodiversity. Consequently, forest reserves are particularly valuable as they can feature these high volumes required by rare species as could be demonstrated in this thesis (Figure 11) and in studies in other unmanaged forests (Table 8).

Besides a first baseline about volumes, also a variety of different quality features is necessary for many of saproxylic species. Higher amounts of lying than standing dead wood (Christensen et al. 2005), a broad diameter distribution (especially large diameters; (Nilsson et al. 2002)), different decay stages (especially advanced; (Hoiland and Bendiksen 1996)), uprooted trees (Heilmann-Clausen and Christensen 2003) and an extensive spatial distribution as well as temporal continuity (Grove 2002, Sverdrup-Thygeson et al. 2014) are important for a high species richness. The dead wood quantity and quality in the seven investigated NFRs cover on average all mentioned requirements. However, spatial distribution was only examined once (for the purpose of this thesis) and on a small scale (for details see chapter 5.3.2). Long-term data about temporal continuity on plot level is only available for snags and not for logs, but showed a continuous presence, partly with high fluctuations (Appendix Table A3).

Regarding dead wood quality, the national forest policy 2020 aims to designate 3-5 so-called habitat trees per hectare (DBH>70 cm for conifers) in managed forests until 2030 (Swiss Federal Office of the Environment 2013). However, a habitat tree has not necessarily dead components because e.g. a nest of a bird of prey already suffices as selection criterion. Nevertheless, the set amount seems promising from my point of view, compared to the recorded amount of living giant trees in the selected forest reserves (see chapter 5.1.4). Furthermore, the spatial continuity of dead wood, important for the species network, is in my opinion well supported by the maintenance and new-establishment of forest reserves (larger areas) and by stepping stones such as old-growth islands and habitat trees. The temporal continuity is taken into account as forest reserves are usually contractual protected over 50 years, which is however only efficient on the long-term if the contract is renewed several times. Regrettably, precise specifications about the dimensions are lacking. Large dimensioned dead wood is rare in managed forests, but particularly important for many species as it forms a continuous habitat (Lachat et al. 2014). Thus, large diameter trees should be prioritized for forest biodiversity promotion and be left in the forest so that all decay classes (especially advanced) can develop.

In summary, the investigated plots in the mountainous coniferous forest reserves in Switzerland feature higher dead wood volumes of better quality (larger dimensions and of more advanced decomposition stages) than Swiss managed forests (Brändli 2010, Rigling and Schaffer 2015) and are comparable to unmanaged coniferous forests across Europe with respect to dead wood quantity and quality. In a majority of plots, volumes recommended for a semi-natural silviculture (Kaufmann et al. 2010) or for a high species diversity (Bütler 2003) and targeted in the national forest policy (Swiss Federal Office of the Environment 2013) are exceeded. The frequent large diameter and advanced decomposed logs form an excellent substrate for a variety of species, many of them endangered. Therefore, the examined forest reserves are highly important to achieve the objectives of the national forest policy 2020 as they incorporate already many characteristics of a natural forest dynamic and are valuable with regard to a high forest biodiversity and the preservation of threatened species.

5.2 Statistical modeling of lying dead wood quantity and quality

The aim of the second part of this thesis is to assess the effects of different environmental factors such as forest history, stand characteristics, site conditions, climate and external disturbances on the observed lying dead wood quantity and quality with the help of statistical modeling.

It has to be taken into account that the capacity of statistical modeling of lying dead wood quantity and quality could not be exploited efficiently due to the low number of 24 investigated PPs only. Furthermore, there is a high probability of extraordinarily high or low values because of a local random effect as plot size was relatively small (between 0.21 ha and 1.65 ha). A great variety of explanatory variables reported to be important for dead wood dynamics in literature could not be included in the final due to the problem of over-fitting the model or due to exclusion during the selection process by applying the AIC criterion (Sachs 2013). Although the presented final sets of variables best explained the observed dead wood data, they have to be regarded with care, as with a higher number of investigated plots or less extreme values, they may be different.

Regrettably, the large data set of high quantity (1807 recorded logs) and high quality was strongly reduced to 24 observations for modeling. Another recording method (e.g. on sample plot instead permanent plot level) may result in more observations per forest reserve. Furthermore, the research plots would be more regularly distributed within the research perimeter of the forest reserve and the effect of extreme values on the modeling process could be reduced.

5.2.1 Total CWD volume

Higher total CWD volumes were positively associated with a longer time since last forestry operation, the presence of wind and the increasing northness of a hillside, but negatively with an increasing amount of deciduous tree species in the living basal area (Table 5). These four factors are discussed in the following section. Still, it has to be kept in mind that although the forest reserve explained 25% of total variance in the final linear mixed effect model, CWD volumes between reserves were not significantly different in the nested ANOVA test and modeling CWD volumes may only capture trends.

Time since last management intervention

Also Christensen et al. (2005), Burrascano et al. (2008) and Bütler and Lachat (2009) observed dead wood volumes to increase with progressive time since last management intervention. This relation could be generally verified in the investigated forest reserves, whereby extraordinarily high CWD volumes in Derborence may not only be related to a long time since last forestry operation, but also to a high dead wood input caused by hurricane Vivian (Heiri et al. 2011). Seeliwald and Combe Biosse showed the lowest CWD volumes (Figure 11), a result that corresponds with the fact that in these two forest reserves the time since the last cutting was shortest compared to the other selected NFRs (Table 1) and large diameter trees containing high volumes could not yet develop (Figure 14).

A factor not considered in the set of explanatory variables as difficult to determine due to small-scale occurrence particularly in old-growth forests and due to many intermediate forms and overlaps is closely linked to the time since the last forestry operation: development stage. The entire cycle of development stages starts with tree recruitment, which is followed by a growing-up stage, an optimum and a break-down stage and lasts in Norway spruce virgin forests about 350 years (Korpeľ 1995), whereas the duration may vary dependent on site and climatic conditions. Management interventions restart (after clear cutting) or interrupt this cycle on a small scale like the PPs. The optimum stage with generally low CWD volumes (Saniga and Schütz 2001) dominates in most Swiss NFRs (Heiri et al. 2011), but much higher CWD volumes were reported in the break-down stage (Saniga and Schütz 2001).

Therefore, an increase in CWD volumes may be expected in future decades in Leihubelwald, Seeliwald, National Park and Combe Biosse, which face a relatively short time since last management intervention and/or a diameter distribution characteristic for younger forests (see chapter 5.1.4) and may be in a late grow-up or early optimum stage. But also in old-growth and never managed forests with a rather small-scaled pattern of different development stages next to each other, lying dead wood volumes fluctuate (Korpel' 1997). In Bödmerenwald for instance, Liechti et al. (2005) documented in a sample plot inventory (measurement threshold ≥16 cm) conducted in the year 2004, which covered however a larger area than the one of the investigated PPs, CWD volumes of 37 m^3/ha (in comparison to recorded 79 ± 12 m^3/ha ten years later in this thesis). In Derborence, I personally do not expect a prospective tremendous dead wood increase because Vivian has already felled many large diameter trees containing high volumes and lying dead wood volumes already exceed CWD volumes found in other European coniferous NFRs and old-growth forests (Table 8).

Past wind disturbance

Wind as a major catastrophic and random event leads to a dead wood input of great extent (Hahn and Christensen 2005, Seidling et al. 2014). This effect could be confirmed by dead wood data from the examined PPs. The plots PP1, PP8 and PP18 in Derborence, in which in February 1990 hurricane Vivian caused many trees to be uprooted or damaged (Heiri et al. 2011), showed the highest CWD volumes over all investigated PPs (Figure 11). Also in the two wind affected plots (PP1 and PP10) in Leihubelwald (Streit and Heiri 2011), total CWD volumes were higher than in the undisturbed plots PP4 and PP13. In addition, dispersed Vivian-related wind damages were reported in PP1 and PP4 of Bödmerenwald (Liechti et al. 2011), in which higher volumes were found than in the less disturbed PP3.

Hillside exposition

The final model suggested that the more north oriented the slope is, the higher are the dead wood volumes. To my knowledge however, northness of a hillside was never directly related to lying dead wood volumes in earlier studies, but rather to decomposition rates (Næsset 1999). The author stated enhanced decomposition processes on sites where solar exposure is limited (e.g. north and east oriented slopes) and related this effect to the higher soil moisture due to restricted evaporation. However, there may occur an opposite effect, namely that on north and east oriented slopes, the temperature is also lower than on sunnier west and south oriented slopes and consequently, the microbiological activity is reduced and the decomposition process decelerated (Korpel' 1997, Herrmann and Bauhus 2013). On a south oriented slope, it would be vice versa: higher temperatures accelerate decomposition, while dryer conditions reduce decomposition. In a south oriented forest reserve in southwestern Germany with *Fagus sylvatica*, *Abies alba* and *Picea abies*, Herrmann and Bauhus (2013) reported that decay rate was rather temperature than moisture controlled. If this result could be transformed to north oriented slopes, the results by Næsset (1999), which analyzed decomposition rates after clear cuttings in southeastern Norway, would be refuted.

The controlling of the decomposition process by either temperature or moisture with respect to hillside orientation seems to be difficult to determine. In addition, also the tree species, the log size or the log contact with the forest floor influence the velocity of the decomposition process (Næsset 1999, Herrmann and Bauhus 2013), and an enhanced decomposition leads only to low CWD volumes if the dead wood input is low (Hahn and Christensen 2005). Dead wood input however is significantly positively related to site productivity (Sippola et al. 1998, Nilsson et al. 2002, Nordén et al. 2004) on average and to intermittent past disturbances (Seidling et al. 2014), two factors which may also vary with different expositions. For example, strong winds or storms in Switzerland predominantly blow from the west (Swiss Federal Office of Meteorology 2015) and thus, windthrow damages causing high dead wood inputs are likely to be most frequent on western oriented slopes. In short, there are many factors influencing dead wood volumes and the determination of the single effects are a challenge. Northness was probably only included as a final variable as Derborence with extraordinarily high CWD volumes is located on rather north oriented slopes. Such extreme values greatly influence a model output, particularly if the number of examined plots is small.

Tree species composition

The amount of deciduous tree species was negatively correlated with CWD volumes, but was regarding the p-value not significant. Combe Biosse is the only studied reserve with a considerable amount of deciduous trees (Appendix Table A5), but the combined effect of other characteristics of this reserve may well be responsible for the low total CWD volumes. For example, the recorded logs were primarily of small diameters and thus of low volumes (Figure 14). This effect however can be related to the short time since last silvicultural intervention (Christensen et al. 2005) or to the rather young development stage (Saniga and Schütz 2001). Furthermore, deciduous logs were in Combe Biosse but also in general of smaller diameters than coniferous logs. As the focus of this master thesis lies on coniferous forest reserves, conifers may dominate over deciduous trees and do, thanks to a better adaptation to the current climate and site conditions, get more light and resources and thus develop larger diameters.

An additional variable probably influencing dead wood dynamic but not included in the modeling due to already three variables related to site productivity is the forest community. Varying forest communities within one reserve generally resulted in different volumes or decay stages. For example, PP5 in Derborence with considerable low CWD volumes was not affected by Vivian, but is also mapped as another forest community type as the other three PPs, namely as the low productive forest community *Erico-Pinetum montanae* (Frehner and Burnand 2009). Similar results showed Combe Biosse, where volumes on PP level differed with varying forest community. In Leihubelwald and Seeliwald, differences in CWD volumes could not be observed with respect to forest community, but rather differences in the decomposition stage composition (Figure 18, discussion see chapter 5.2.3).

5.2.2 Dimensions

Volumes of large (>30 cm) diameter trees were negatively correlated with the share of deciduous tree species in the live stand (and small diameter trees positively, Table 6). As considerations are similar to total CWD volumes (large diameter trees contain high volumes), see discussion above (chapter 5.2.1).

5.2.3 Decomposition stages

The Redundancy Analysis (RDA) resulted in four final variables associated to decay stages: time since last management of 20-50 years, past wind disturbance referring to hurricane Vivian, precipitation and the hillside exposition (Figure 19). It has to be taken into account that the abundance of decay stages in CWD volume was taken as a response variable, whereby large diameter trees with high volumes mainly determine the proportions of each single decay stages and therefore the outcome of the RDA and the position of the PPs in the PCA plot (Figure 18). The following discussion part is structured by forest reserves as most of them were characterized by a similar decay stage composition.

National Park

The investigated plots in National Park were well aggregated in the RDA (Figure 19) and showed a relatively high abundance of fresh decay stages (class I+II) compared to the other investigated forest reserves. The area of National Park was intensively clear cut before the establishment as a forest reserve in 1914 (Parolini 1995). In the year 1850, the forest in Il Fuorn (area of PP7) and Praspöl (area of PP18 and PP19) was almost completely cleared, wood was also extracted afterwards and in Il Fuorn the last woodcutting took place in 1911 (Parolini 1995). Since then, a natural forest dynamic could develop there. In National Park, trees are growing relatively slowly (low site productivity, cold and dry climate) and logs of large diameters are not yet abundant (Appendix Figure A2b). As a result, large diameter trees with high volumes may not be dead for many decades and thus feature rather fresh decay stages. Another reason for the relatively high amount of less decomposed logs could be that because of absent windthrow, usually responsible for mechanical damages or uprooting (Coates 1997), trees may remain standing dead for a long time, where decomposition is slower than when lying on the forest floor (Hahn and Christensen 2005). When snags topple, they decompose slowly due to the substrate type (Norway spruce, but particularly European larch (Hahn and Christensen 2005)) and even more due to the microbiological decomposition process decelerated by dry and cold climate (Korpel' 1997, Herrmann and Bauhus 2013).

Derborence and Leihubelwald

Derborence and Leihubelwald were mainly characterized by decay stage V and to a less extent by decay stage IV (Figure 18). Three plots in Derborence (PP1, PP8 and PP18) and PP10 in Leihubelwald were, partly extensively, affected by wind damages caused by hurricane Vivian in winter 1990 (Heiri et al. 2011, Streit and Heiri 2011). A majority of damaged trees may have skipped the snag stage, turned directly into logs as storms mainly cause uprooting rather than snapping (Coates 1997) and were decomposed for the past 26 years. In comparison, Norway spruce logs in Finland required on average 27 years to reach decay class V (Mäkinen et al. 2006), in mid-northern Sweden 40 years (Kruys et al. 2002) and in Northern Finland and Northern Russia 43-84 years (Aakala 2010). However, decomposition rate is dependent on climate (Næsset 1999, Kruys et al. 2002, Herrmann and Bauhus 2013). Decomposition processes of Norway spruce (and also silver fir, the second important tree species in these two reserves, with a similar decomposition rate constant (Hütter 2011)) in Central Europe are faster than in high northern latitudes (Hahn and Christensen 2005). Consequently, logs nowadays in decay stage V may be related to hurricane Vivian, which caused windthrow of the - at that time standing - trees 26 years ago, long enough to establish advanced decay stages under the present climate conditions. This relation may be supported by the fact that particularly large diameter trees with high volumetric content (affect the RDA output more than small diameter trees) were downed by Vivian due to a higher susceptibility to windthrow as growing in upper canopy layers (Coates 1997).

The high amount of decay class IV may be related to the trees that died shortly after Vivian because of the following bark beetle infestation (Heiri et al. 2011, Streit and Heiri 2011). Fresh decay stages (class I+II) were rare probably for two reasons. Firstly, residence time of logs in decay class I is shortest, but longest for decay class V (Herrmann et al. 2015). Consequently, only trees that died recently were assigned to fresh decay stages. Secondly, many large diameter trees already died in Vivian or shortly afterwards. More recently, rather small diameter trees containing low volumes died and thus less influencing the RDA output. A heavy storm event such as Vivian is a random event. In the wind-damaged plots of Derborence and Leihubelwald, advanced decay classes (and CWD volumes) have probably an unnaturally high presence. Would Vivian have occurred only two years ago, fresh decay stages might be much more frequent. In comparison, the undisturbed plots PP13 in Leihubelwald for example showed a higher abundance of less decomposed logs (Figure 18).

Seeliwald and Combe Biosse

Decay classes in Seeliwald and Combe Biosse were positively correlated with a short time span since last forestry operation (Figure 19). The high abundance of advanced decay stages may be related to a first wave of tree die-off after the last cuttings. A development towards a more balanced forest structure is still running, as also the low presence of large diameter trees indicates (Figure 14).

In addition, PP4 and PP5 of Seeliwald consisted of more advanced decay stages than PP1 and PP2. This effect may be related to the location of the PPs in the peat bog and the associated forest community. PP1 and PP2 lie close to the center of the peat bog and are mapped as the low productive *Sphagno-Pinetum montanae* forest community, in contrast to PP4 and PP5, which are situated rather on the edge of the moor and mapped as the more productive *Homogyno-Piceetum sphagnetosum* forest community (Lienert et al. 1982). The higher site productivity in PP4 and PP5 has probably led to more trees of larger diameters (Figure 14) and thus to an earlier tree die-off with respect to time since last management intervention, meaning a longer decomposition span and therefore more advanced decay stages today. The acidity gradient in Seeliwald from the center to the edge of the peat bog may provoke due to a high internal small-scale variability in soil conditions an unevenly spread distribution in decay classes (Figure 18), but not large differences in volumes (Figure 11).

Scatlè and Bödmerenwald

Scatlè and Bödmerenwald were negatively correlated with a short time since last forestry operation (Figure 18) as these two forest reserves were never managed (Table 1). The distribution of decay classes showed highest abundance of decay class III and IV and was rather balanced in comparison to the young forest reserves (Seeliwald and Combe Biosse) and to the wind-damaged plots in Derborence and Leihubelwald (Appendix Table A7). A rather balanced distribution of decay classes and particularly diameter classes are characteristic for old-growth forests (Siitonen et al. 2000).

In conclusion, statistical modeling of dead wood quantity and quality in mountainous coniferous forest reserves by several environmental factors (e.g. forest history, stand and site characteristics, climate conditions and disturbance regime) was limited due to the relatively small number of only 24 investigated permanent plots. The extreme values of some plots may greatly influence the selection of the final variables. Although some factors such as time since last management intervention and external disturbances were (in congruence with other studies) significantly related to dead wood, the effects of for example the climate gradient, which the investigated forest reserves cover, or site and stand conditions could not be completely understood. The determination of the effect of a single variable on dead wood dynamic is challenging, as there are many factors and interactions playing a role. Therefore, a higher number of observation plots, which are more evenly distributed within a forest reserve or cover other site conditions than the one studied, may be helpful. In the seven forest reserves, preferably Norway spruce dominated permanent plots were selected, but in about 15 silver fir dominated plots (particularly in Derborence), lying dead wood records are missing and could be conducted in future studies. Additional plots covering a broader range of site and climate conditions than examined in this study may be located in newly established forest reserves or in forests left unmanaged for several decades, as they are abundant in the Alps and especially the southern side of the Alps (Brändli 2010).

5.3 Spatial distribution of lying dead wood

The goal of the third part of this thesis is to analyze the orientation and spatial distribution of dead wood and to find possible influencing factors related to the observed spatial pattern.

5.3.1 Log orientation

Given that in only two PPs logs were randomly oriented, there may be some factors other than randomness discussed in this section influencing the falling direction of logs. In eight plots, more than 20% of all logs were falling in hillside orientation (Table 7). However, the definition of a log falling in hillside direction is quite tight. Log orientation plots indicated that for example in PP16 of Combe

Biosse, more than 60% of all logs (n=51) were falling to the south, southeast or southwest on the south oriented slope, but only 31% were falling downslope based on my own definition (see chapter 3.3.5.1). Moreover, the proportion of logs falling downslope generally increased with steeper slopes (Appendix Figure A3). These results suggest that hillside exposition and steepness of slope have an effect on the falling direction of logs. Nicoll et al. (2005) showed that on a 30° slope less force was needed to uproot trees downslope than upslope. According to them, mechanical anchorage is more adapted to resist winds blowing upslope than downslope, as wind speeds are more intense on the luv side of a hill, and therefore trees fall more easily downslope. During the field work however I observed tree crowns to grow asymmetrically and being more developed downslope than upslope (probably due to more space and light). In stormy weather and/or with heavy snow cover, the higher mass of the tree crown pulling downslope might cause a failure of root anchorage and therefore leading to trees falling rather downslope than upslope. However, a low number of logs like in many plots in Scatlè, Seeliwald and Combe Biosse may have a big influence on result interpretations from log orientation analysis and should be regarded with care.

Hillside exposition and slope inclination are not the only factors possibly influencing spatial patterns. In Derborence (PP1, PP8 and PP18), Bödmerenwald (PP1 and PP4) and Leihubelwald (PP10), all plots with more than 60 logs and thus regarded as trustworthily interpretable, the log orientation indicated a clear peak (Figure 20 and Appendix Figure A5, Figure A6, Figure A9, Figure A11 and Figure A14). In PPs located on a slope (Derborence), this peak was primarily not congruent with hillside exposition. Referred PPs in Bödmerenwald and Leihubelwald were not located on a slope. This peak in log orientation can probably be related to hurricane Vivian (Heiri et al. 2011, Liechti et al. 2011, Streit and Heiri 2011). At close-by MeteoSwiss weather stations (Sion: 591 630/118 575, 480 m a.s.l.; Pilatus: 661 910/203 410, 2106 m a.s.l.), westerly wind gusts of 100-137 km/h were measured at that time (Z'graggen and Hostettler 2007), values far above the critical wind speeds of 50-60 km/h required to break or uproot a Norway spruce tree (Qinghong and Hytteborn 1991, Gardiner et al. 2000). In fact, a high number of uprooted trees was recorded in the field in these six PPs (Appendix Table A2).

In Derborence, the peak in falling direction of logs was not always congruent with predominantly western wind directions during hurricane Vivian (Z'graggen and Hostettler 2007). However, turbulences along mountain ridges and the relatively steep slope (~30°) may have played a counteracting role. In contrast, the western wind direction in Bödmerenwald (Sidler 2001) and the southwestern wind direction in Leihubelwald (Schüepp 1995) are in correspondence with the observed eastern and north-eastern oriented logs, respectively. In Bödmerenwald, logs in PP1 showed a clearer peak towards the east than in PP4. As PP1 is, due to its location, more exposed to west winds and PP4 is “hidden” behind PP2, the plot in which storm damages were most extensive (Liechti et al. 2011), dispersed storm damages might be higher in PP4. In contrast, log orientation in PP3, which was probably in the lee of PP1, did not peak in one direction and was even significantly uniform (Table 7). Moreover, PP3 showed lower lying dead wood volumes than PP1 and PP4 (Figure 11), an additional reference that PP3 was less wind-disturbed.

Beside a clear peak in falling direction, a second common feature of these six plots was that particularly long and large diameter trees of decay class IV and mainly decay class V formed this peak. These two characteristics are an additional indicator for Vivian (discussion in chapter 5.2.3). Small and short trees did not exhibit a dominant falling direction but rather a chaotic distribution pattern, suggesting they perished for competitive reasons rather than external impacts such as storms or pests (Deal et al. 1991). The still considerable amount of logs falling downslope in Derborence may be related to the trees that died standing some years after Vivian due to the subsequent bark beetle infestation (Heiri et al. 2011) and the first factors presented (hillside orientation and steepness of slope) were probably the main drivers influencing the falling direction of logs. However, neither hillside exposition, slope inclination, past storm events nor internal competition may cover all processes of natural forest dynamic relevant for log orientation. Soil conditions such as the base of the topsoil or the moisture may have an influence, but were not investigated in this study. This gap could be filled by further research.

In conclusion, it can be said that log orientation in about a quarter of investigated PPs was affected by hurricane Vivian, whereby large and long logs were falling predominantly in wind direction. In the remaining plots, especially the steep ones, the falling direction of logs was mainly congruent with the exposition of the hillside and logs were falling downslope. In rather flat undisturbed plots logs tended to be randomly oriented.

5.3.2 Spatial pattern analysis

Spatial pattern analysis suggested for each plot either a random or clustered log distribution (Table 7). In this thesis, I could confirm in 11 of 14 PPs the hypothesis from Edman and Jonsson (2001), namely that the spatial pattern of logs is directly influenced by the spatial pattern of standing trees, whose growth is, particularly in mountainous regions, limited to suitable sites (Kenkel 1988, Szwagrzyk and Czerwczak 1993). Also in Bödmerenwald, where the pattern of standing trees was not analyzed because of missing coordinates, I could observe that phenomenon. The growth of living trees is restricted to the small mounds scattered in the forest. Only the mounds with their existing soil layer offer favorable conditions for young growth, while the ground in the hollows is often bare and the temperature possibly too low. This peculiar topography influences the distribution of the living trees and thus the significantly clustered pattern of the lying dead trees in all plots in Bödmerenwald.

In addition to the spatial aggregation of the living trees, also the stand age and the related mortality patterns influence the spatial log distribution. Larson et al. (2015) described that in young coniferous forests (<60 years), logs tend to random distribution due to density-dependent competitive mortality when trees die intact and standing and not because of an external disturbance. Also Lutz and Halpern (2006) described in young forests rather mortality by suppression than by mechanical damages (e.g. uprooting or stem snapping) caused by disturbances. In this study, permanent plots facing either a short, medium or long time since last management intervention, a variable which could be used as a proxy for stand age, exhibited spatial randomness (also in the older forest reserves National Park and Scatlè). In the National Park, the time span since last cuttings may not be enough to establish spatial clustering in all three PPs as it is characteristic for old-growth forests, which Larson et al. (2015) defined as forests with a stand age >300 years. In PP11 of Scatlè, which suggested a random spatial pattern, only about half of all logs was analyzed. The remaining logs were excluded from spatial pattern analysis, as they were located outside the PP borders. It is therefore possible that all logs together would be clustered, particularly as the neighboring plot PP10 showed spatial clustering and Scatlè is an old-growth forest and has never been cut (Table 1). In any case it has to be considered that the size of the permanent plots is rather small (0.21-1.65 ha) and that only small-scale spatial patterns could be captured, but not processes on the stand or the landscape level. For that, studies in larger plots of several hectares would be necessary.

In contrast, old-growth forests (>300 years) tend to spatially clustered structures (Larson et al. 2015) caused by density-independent agents such as snow pressure, storm events and insect attacks (Larson and Franklin 2010). Snow breakage rarely takes place in the investigated forest reserves as it occurs most likely in deciduous forests below 1000 m a.s.l., where trees are not adapted to heavy snow loads (Rottmann 1985, Nykänen et al. 1997). In the storm- and partly insect-affected plots in Derborence, Bödmerenwald and Leihubelwald the logs were in fact clustered (Table 7) and Derborence and Bödmerenwald are old-growth forests (Table 1). Especially in Bödmerenwald, the clustering was strongly significant, probably also because of the aggregation of living trees on mounds (see above). In young and undisturbed forest reserves like Seeliwald or Combe Biosse, some plots also exhibited spatial clustering. In Seeliwald, a small-scale disturbance may have occurred, as the number of rootstocks in PP5 indicates. In Combe Biosse, the clustering was of little significance

As a conclusion of the spatial analysis, it can be said that hillside orientation, steepness of slope and wind were important drivers with respect to the observed pattern of log orientation. Furthermore, it could be confirmed that the spatial pattern of standing trees mainly influences the spatial pattern of lying trees. In addition, the spatial pattern of logs could not be consistently related with time since last management intervention used as a proxy for stand age. Nevertheless, young reserves exhibited rather spatially random distributed logs and older reserves rather spatially clustered distributed logs, as it was reported by Larson et al. (2015).

6 CONCLUSION

This master thesis examines in a permanent plot inventory the dead wood dynamic in seven mountainous *Picea abies* dominated forest reserves in Switzerland with a focus on the lying dead wood component. Dead wood of high quantities and different quality characteristics provides a habitat for a great variety of forest species, many of them endangered, and is acknowledged to be a good indicator for a forest's naturalness. My results suggest that:

(1) The investigated forest reserves feature high dead wood volumes of good quality (large dimensions and advanced decay stages) and are thus valuable for the preservation and promotion of a high forest biodiversity. The observed values are comparable to other coniferous unmanaged forests across Europe, higher than in Swiss managed stands and exceed the dead wood volumes targeted in managed forests by the national forest policy 2020.

(2) The governmentally demanded dead wood volumes may be adequate from a management technical perspective, but do not meet the requirements of a majority of saproxylic species. The aims considering the spatial and temporal continuity of dead wood are satisfying. However, not all quality features such as large dimensions required for a high species richness are incorporated in the strategy.

(3) Time since last management intervention and past wind disturbances were significantly related to lying dead wood but overall, statistical modeling was limited due to a low number of observations. The effect of for example climate conditions, site productivity and stand characteristics could not be completely understood. A bigger data set may help solving this problem.

(4) Regarding the spatial log orientation, past storm events are an important influencing factor for the falling direction of logs. Without any external disturbance, logs preferably fall downslope on inclined areas and are rather chaotically distributed in flat areas.

(5) My data support the hypothesis that the spatial pattern of logs is mainly influenced by the spatial pattern of standing trees. Furthermore, it could be largely confirmed that forest reserves with a rather high stand age exhibit spatial clustering of logs whereby younger forest reserves tend to show spatial randomness.

As only small-scaled dead wood dynamic was investigated, larger study areas may be necessary to study dead wood dynamic on stand or landscape level. In addition, most of the investigated forest reserves still show traces of past management and do not represent virgin forests. Nevertheless, the observed values of dead wood quantity and quality provide a first baseline for managed forests and indicate what values can be obtained today in Swiss mountainous regions under unmanaged conditions.

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9 APPENDIX

9.1 Appendix A: Dead wood quantities and qualities

Table A1. Volumes of lying dead wood in total and in different categories (tree species, dimension, decomposition stage) in the 24 different permanent plots ordered by forest reserve. Unit for all columns except the first three is m³/ha. Volumes smaller 1 m³/ha but not zero are indicated by <1.

Reserve	PP number	Area [ha]	Total	Trees species		Dimension		Decomposition stage				
				Conifers	Deciduous	Large (>30 cm)	Small (≤30 cm)	Class I	Class II	Class III	Class IV	Class V
Derborence	1	0.2520	216	216	<1	181	35	1	1	37	82	95
	5	0.2459	1	<1	<1	0	1	0	0	0	0	1
	8	0.6660	343	343	0	331	12	19	9	43	92	181
	18	0.4880	207	207	<1	199	9	0	17	14	81	95
Scatlè	10	0.2074	155	155	0	125	30	0	15	41	46	53
	11	0.2371	78	78	0	74	4	0	12	17	24	24
Bödmerenwald	1	1.1274	77	77	0	70	7	0	5	26	35	11
	3	0.8446	49	49	0	44	5	0	14	13	16	5
	4	1.6541	96	96	0	91	4	2	4	18	41	30
Leihubelwald	1	0.2555	120	112	8	104	16	0	2	9	75	35
	4	0.2499	79	79	0	76	3	0	17	0	22	40
	10	0.4480	96	91	5	88	8	0	1	12	38	45
	13	0.5358	64	64	<1	51	14	0	1	25	23	14
Seeliwald	1	0.5001	32	32	0	15	17	1	3	12	3	14
	2	0.8662	6	6	0	2	4	0	1	2	1	2
	4	0.6484	20	20	0	17	3	0	0	1	3	16
	5	0.8976	35	35	0	29	6	0	2	3	8	22
National Park	7	0.5567	40	40	0	17	23	6	7	14	5	8
	18	0.6770	162	162	0	132	30	14	25	34	28	62
	19	0.2389	38	38	0	16	23	4	17	7	4	5
Combe Biosse	14	0.6908	3	3	<1	0	3	0	0	1	1	2
	16	0.5971	9	1	8	3	5	0	2	1	3	3
	17	0.3081	22	14	8	7	15	4	3	3	3	10
	19	0.2689	31	28	3	19	12	0	1	6	6	17

Table A2. Stem numbers of lying dead wood in total and in different categories (tree species, dimension, decomposition stage) in the 24 different permanent plots ordered by forest reserve. Furthermore, numbers of rootstocks per hectare estimated to contain at least a volume of 0.1 m³/ha are presented. Units for all columns except the first three is no./ha. Stem numbers are rounded to zero decimal places.

Reserve	PP number	Area [ha]	Total	Tree species		Dimension		Decomposition stage					Rootstocks
				Conifers	Deciduous	Large (>30 cm)	Small (≤30 cm)	Class I	Class II	Class III	Class IV	Class V	
Derborence	1	0.2520	397	393	4	198	199	4	20	75	127	171	36
	5	0.2459	32	20	12	0	32	0	4	0	4	24	0
	8	0.666	278	278	0	197	81	5	18	41	80	135	27
	18	0.488	219	217	2	137	82	4	33	25	55	102	37
Scatlè	10	0.2074	381	381	0	149	232	0	29	92	125	135	24
	11	0.2371	135	135	0	80	55	0	38	38	25	34	13
Bödmerenwald	1	1.1274	82	82	0	26	56	0	5	19	34	24	17
	3	0.8446	62	62	0	27	35	0	14	17	21	9	8
	4	1.6541	86	86	0	48	38	2	7	17	21	39	18
Leihubelwald	1	0.2555	157	145	12	59	98	4	23	8	74	47	31
	4	0.2499	112	112	0	48	64	0	8	8	52	44	4
	10	0.448	143	136	7	45	98	2	11	20	42	67	4
	13	0.5358	164	162	2	28	136	4	21	69	45	26	17
Seeliwald	1	0.5001	114	114	0	22	92	2	16	36	14	46	8
	2	0.8662	35	35	0	3	32	0	1	9	8	16	6
	4	0.6484	34	34	0	14	20	0	0	5	6	23	5
	5	0.8976	77	77	0	26	51	0	7	11	18	41	12
National Park	7	0.5567	225	225	0	23	202	27	45	52	36	65	7
	18	0.677	322	322	0	105	217	25	59	74	66	97	25
	19	0.2389	234	234	0	21	213	8	63	59	54	50	13
Combe Biosse	14	0.6908	54	33	20	1	53	1	7	14	6	25	0
	16	0.5971	85	18	67	8	77	0	22	10	20	33	3
	17	0.3081	218	101	117	13	204	3	29	49	26	110	0
	19	0.2689	212	156	56	33	179	7	22	33	52	97	0

Table A3. Volume and stem numbers of standing dead wood extracted from NFR inventory data in the 24 different permanent plots ordered by forest reserve. No data (-) indicates plots in which standing dead wood was not present or not recorded. In Scatlè, standing dead wood in the origin plot PP1 was recorded, but reconstruction of tree numbers until 1965 was not possible anymore for the smaller selected plots PP10 and PP11. Ratio refers to the proportion of snag stem number to total (standing living and dead) stem number in the last inventory. Volumes smaller than 1 m^3/ha but not zero are indicated by <1. Stem numbers are rounded to zero decimal places.

Reserve	PP number	1st inventory			2nd inventory			3rd inventory			4th inventory			Ratio [%]
		Year	Volume [m^3/ha]	Stem number [no./ha]	Year	Volume [m^3/ha]	Stem number [no./ha]	Year	Volume [m^3/ha]	Stem number [no./ha]	Year	Volume [m^3/ha]	Stem number [no./ha]	
Derborence	1	1981	<1	67	1990	13	48	2008	124	155				15
	5	1981	<1	138	1991	3	183	2008	5	207				10
	8	1981	<1	29	1990	69	84	2009	124	90				13
	18	1982	<1	27	1991	221	139	2010	46	68				7
Scatlè	10	1965	-	-	1977	-	-	1989	-	-	2006	61	53	18
	11	1965	-	.	1977	-	-	1989	-	-	2006	18	34	12
Bödmerenwald	1	1973	-	-	1988	-	-	2003	27	20				7
	3	1973	-	-	1988	-	-	2003	18	20				6
	4	1973	-	-	1988	-	-	2003	38	28				10
Leihubelwald	1	1973	-	-	1983	-	-	1995	56	70	2011	42	70	11
	4	1973	-	-	1983	-	-	1995	68	132	2011	77	132	13
	10	1983	-	-	1995	-	-	2011	33	98				11
	13	1983	-	-	1995	-	-	2011	15	101				14
Seeliwald	1	1973	-	-	1984	-	-	1996	5	26				2
	2	1973	-	-	1984	-	-	1996	2	16				2
	4	1973	-	-	1985	-	-	1997	24	42				6
	5	1973	-	-	1985	-	-	1997	9	46				6
National Park	7	1977	-	-	1992	-	-	2012	4	18				4
	18	1978	-	-	1993	-	-	2012	25	44				8
	19	1978	-	-	1993	-	-	2012	15	50				5
Combe Biosse	14	1987	18	130	2010	16	158							18
	16	1987	7	82	2010	19	75							13
	17	1987	16	253	2010	45	227							25
	19	1987	49	376	2010	119	342							33

9.1.1 Appendix A1: Tree species

Table A4. Absolute stem numbers and their amounts of totally 1807 logs, divided into coniferous and deciduous tree species. Percentages smaller than 1 but not zero are indicated by <1.

Coniferous tree species			Deciduous tree species		
Name	**Stem number**	**%**	**Name**	**Stem number**	**%**
Picea abies H. Karst	1045	58	*Fagus sylvaticea* L.	33	2
Abies alba Mill.	108	6	*Fraxinus excelsior* L.	10	<1
Pinus sylvestris L.	3	<1	*Acer pseudoplatanus* L.	9	<1
Pinus mugo ssp. mugo	70	4	*Populus nigra* L.	1	<1
Pinus cembra L.	14	<1	*Betula pendula* Roth	1	<1
Larix decidua Mill.	54	3	*Salix caprea* L.	2	<1
unidentified	296	22	*Sorbus aria* Crantz	6	<1
			Sorbus aucuparia L.	5	<1
			Sorbus hyprida L.	1	<1
			unidentified	49	3
Total	**1690**	**94**	**Total**	**117**	**6**

Table A5. Average CWD volumes, stem numbers and corresponding share of coniferous and deciduous wood over the investigated permanent plots per forest reserve and on average over all investigated permanent plots. Mean and standard error is weighted by the area size of the corresponding permanent plots. Volumes and percentages smaller than 1 (m^3/ha) but not zero are indicated by <1.

Reserve	Coniferous wood				Deciduous wood			
	Volume [m^3/ha]	%	Stem number [no./ha]	%	Volume [m^3/ha]	%	Stem number [no./ha]	%
Derborence	233 ± 107	>99	239 ± 99	99	<1 ± <1	<1	3 ± 4	1
Scatlè	114 ± 82	100	250 ± 261	100	0	0	0	0
Bödmerenwald	79 ± 12	100	79 ± 6	100	0	0	0	0
Leihubelwald	83 ± 17	97	143 ± 17	97	3 ± 3	3	5 ± 4	3
Seeliwald	23 ± 8	100	61 ± 21	100	0	0	0	0
National Park	96 ± 64	100	271 ± 49	100	0	0	0	0
Combe Biosse	8 ± 8	64	57 ± 43	50[1]	4 ± 3	36	56 ± 29	50[1]
Average	**80 ± 23**	**99**	**126 ± 27**	**94**	**<1 ± <1**	**1**	**9 ± 6**	**6**

[1] slightly more coniferous wood

9.1.2 Appendix A2: Dimensions

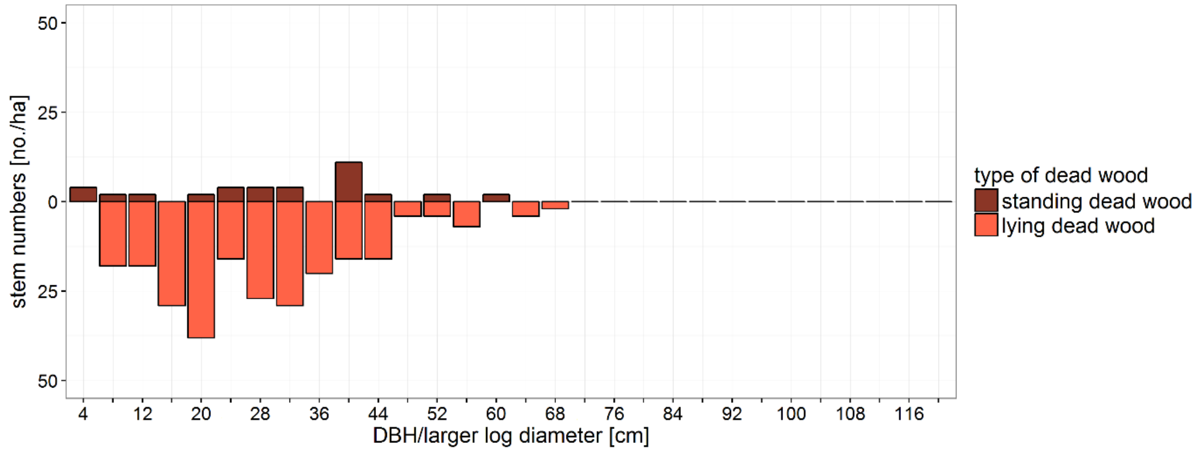
9.1.2.1 *Large and small diameter trees*

Table A6. Average CWD volumes, stem numbers and corresponding share of large (>30 cm) and small (≤30 cm) diameter trees over the investigated permanent plots per forest reserve and on average over all investigated permanent plots. Mean and standard error is weighted by the area size of the corresponding permanent plots.

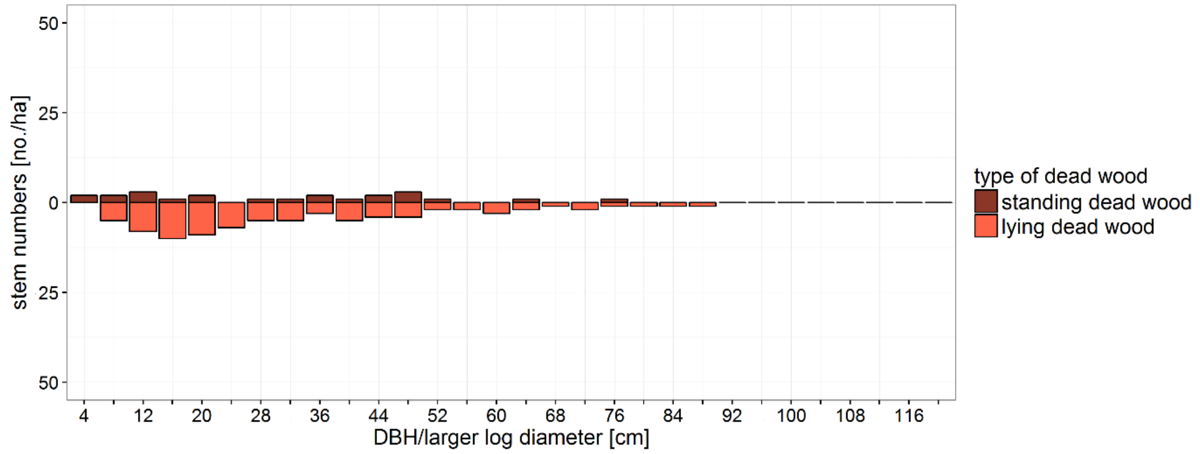
Reserve	Large diameters (>30 cm)				Small diameters (≤30cm)			
	Volume [m^3/ha]	%	Stem number [no./ha]	%	Volume [m^3/ha]	%	Stem number [no./ha]	%
Derborence	22 ± 104	94	150 ± 63	62	13 ± 9	6	92 ± 45	38
Scatlè	98 ± 55	86	112 ± 73	45	16 ± 27	14	137 ± 187	55
Bödmerenwald	73 ± 12	94	36 ± 7	46	5 ± 1	6	43 ± 6	54
Leihubelwald	75 ± 19	88	42 ± 11	29	11 ± 4	12	106 ± 25	71
Seeliwald	16 ± 7	71	16 ± 6	26	7 ± 3	29	45 ± 17	74
National Park	70 ± 61	73	60 ± 43	22	26 ± 4	27	210 ± 8	78
Combe Biosse	5 ± 5	43	10 ± 9	9	7 ± 4	57	103 ± 53	91
Average	**70 ± 22**	**88**	**48 ± 15**	**36**	**10 ± 2**	**12**	**86 ± 18**	**64**

9.1.2.2 *Diameter distribution*

a) Scatlè



b) Bödmerenwald



c) Leihubelwald

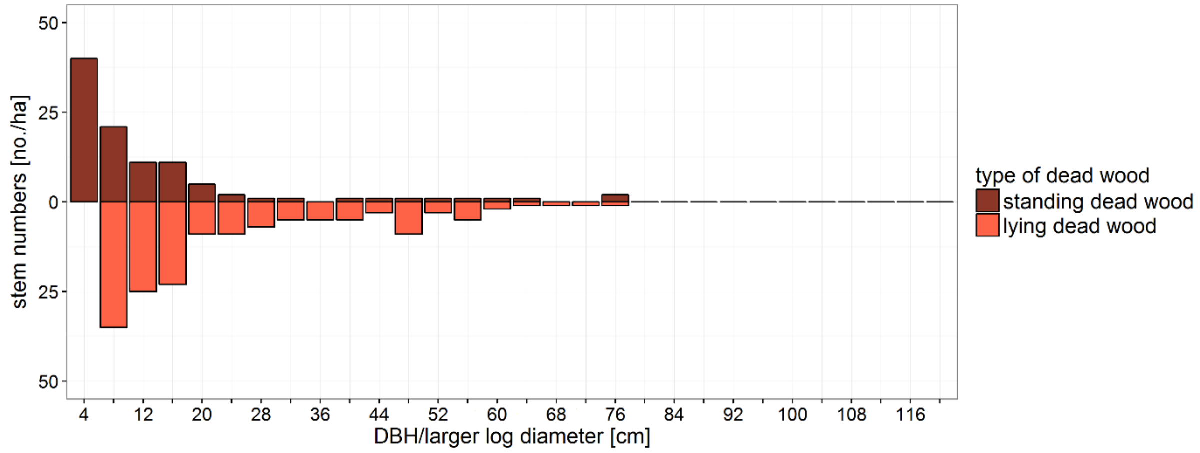


Figure A1. (a/b/c). Diameter distribution (in 4-cm classes) of standing (data from the last inventory record stored in the NFR inventory database) and lying dead wood in the forest reserves of Scatlè (a), Bödmerenwald (b) and Leihubelwald (c). X-values represent the minimum diameter value of each DBH class (standing dead wood) or each larger log diameter class (lying dead wood). Note that x-range and y-range are the same for all diameter distribution plots and are limited by Derborence (x-range) and National Park (y-range).

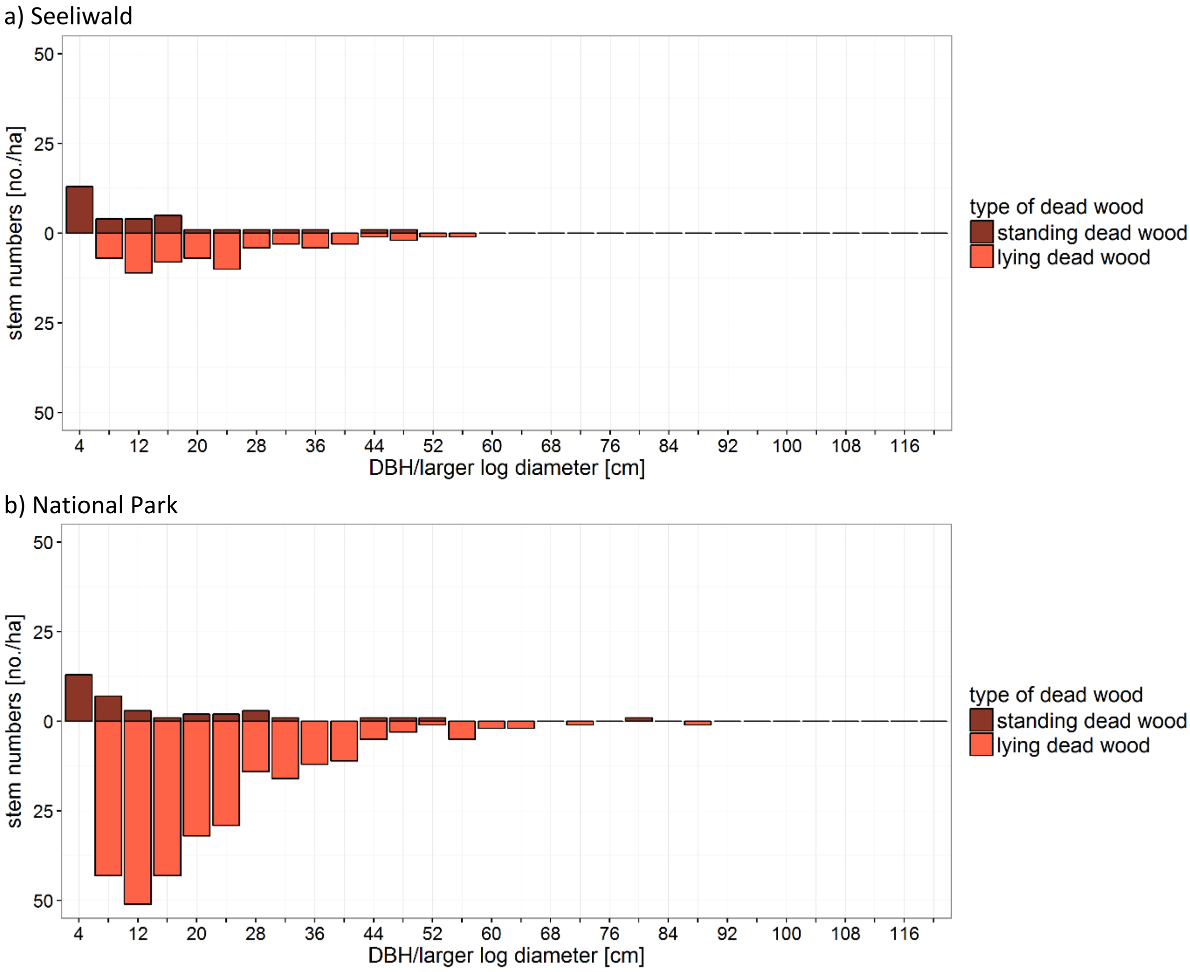


Figure A2 (a/b). Diameter distribution (in 4-cm classes) of standing (data from the last inventory record stored in the NFR inventory database) and lying dead wood in the forest reserves of Seeliwald (a) and National Park (b). X-values represent the minimum diameter value of each DBH class (standing dead wood) or each larger log diameter class (lying dead wood). Note that x-range and y-range are the same for all diameter distribution plots and are limited by Derborence (x-range) and National Park (y-range).

9.1.3 Appendix A3: Decomposition stages

Table A7. Average CWD volumes and corresponding share of decomposition stages over the investigated permanent plots per forest reserve and on average over all investigated permanent plots. Mean and standard error is weighted by the area size of the corresponding permanent plots. Volumes and percentages smaller than 1 (m^3/ha) but not zero are indicated by <1.

Reserve	**Decomposition stage**									
	Class I		**Class II**		**Class III**		**Class IV**		**Class V**	
	Volume [m^3/ha]	**%**	**Volume [m^3/ha]**	**%**	**Volume [m^3/ha]**	**%**	**Volume [m^3/ha]**	**%**	**Volume [m^3/ha]**	**%**
Derborence	8 ± 8	3	9 ± 6	4	27 ± 15	12	73 ± 29	31	116 ± 58	50
Scatlè	0	0	14 ± 3	12	28 ± 25	25	35 ± 23	30	38 ± 31	33
Bödmerenwald	<1 ± <1	1	7 ± 3	9	20 ± 3	25	33 ± 6	42	18 ± 7	23
Leihubelwald	<1 ± <1	<1	4 ± 5	5	14 ± 9	16	36 ± 18	43	31 ± 13	36
Seeliwald	<1 ± <1	<1	1 ± 1	6	4 ± 3	17	4 ± 2	18	13 ± 5	59
National Park	10 ± 5	10	17 ± 4	18	22 ± 12	23	15 ± 12	16	32 ± 28	33
Combe Biosse	<1 ± <1	6	1 ± <1	12	2 ± 2	14	2 ± 1	19	6 ± 5	49
Average	**2 ± 1**	**3**	**6 ± 12**	**8**	**15 ± 3**	**18**	**26 ± 7**	**32**	**31 ± 12**	**39**

Table A8. Average CWD stem numbers and corresponding share of decomposition stages over the investigated permanent plots per forest reserve and on average over all investigated permanent plots. Mean and standard error is weighted by the area size of the corresponding permanent plots.

Reserve	**Decomposition stage**									
	Class I		**Class II**		**Class III**		**Class IV**		**Class V**	
	Stem number [no./ha]	**%**	**Stem number [no./ha]**	**%**	**Stem number [no./ha]**	**%**	**Stem number [no./ha]**	**%**	**Stem number [no./ha]**	**%**
Derborence	4 ± 1	2	21 ± 9	9	35 ± 20	14	68 ± 33	28	114± 40	47
Scatlè	0	0	34 ± 10	14	63 ±57	25	72 ± 106[1]	29	81 ± 107[1]	32
Bödmerenwald	1 ± 1	1	8 ± 2	10	17 ± 1	22	25 ± 4	32	27 ± 8	34
Leihubelwald	3 ± 1	2	16 ± 6	11	34 ± 26	23	50 ± 11	34	45 ± 16	30
Seeliwald	0 ± 1[2]	0	5 ± 4	8	13 ± 7	21	12 ± 3	20	31 ± 8	51
National Park	23 ± 7	9	54 ± 8	20	63 ± 11	23	53 ± 15	20	77 ± 20	28
Combe Biosse	2 ± 2	2	18 ± 7	16	21 ± 12	18	20 ± 13	18	52 ± 31	46
Average	**4 ± 2**	**3**	**17 ± 4**	**13**	**28 ± 6**	**21**	**34 ± 6**	**25**	**51 ± 11**	**38**

[1] may occur with skewed distribution and few observations

[2] may happen when rounding the numbers

9.2 Appendix B: Statistical modeling of dead wood quantity and quality

Table A9. Explanatory (in red) and response variables (random effect: in orange; fixed effects: in white) in the linear mixed effect model. Total lying dead wood volume was used as a response variable for explaining dead wood quantity. Volumetric percentage of large dimensioned logs was used as a response variable for explaining variations in dead wood quality (dimensions). A detailed description of the fixed effects is given in the section “Fixed effects” in chapter 3.3.4.1.

Variable	**Description**	**Unit**	**Scale level**	**Transformation**
VOLUME_LYING_DEAD	Total lying dead wood volume	m^3/ha	numerical	logarithmic
VOLUME_LARGE_ DIMENSIONS	Volumetric percentage of large (>30 cm) dimensioned logs on total CWD volume	%	numerical	arcsine
RESERVE	Nested effect of the forest reserve	-	categorical	
MANAGEMENT	Time since last forestry operation (20-50, 50-100, >100 years)	years	categorical	-
BASAL_AREA	Basal area of the live stand	m^2/ha	numerical	-
VOLUME_LIVING	Volume of the live stand	m^3/ha	numerical	-
PRODUCTIVITY_KELLER	Maximal average total site productivity following Keller (1978)	kg/(ha*year)	numerical	-
WIND	Presence or absence of past storm events	-	categorical	-
PRECIPITATION	Mean annual precipitation sum (reference period 1981-2010)	mm	numerical	-
TEMPERATURE	Mean temperature in vegetation period (May-October; reference period 1981-2010)	°C	numerical	-
NORTHNESS	Cosine of plot exposition (-1, 1) , derived from aspect calculations on larger log end in ArcGIS	-	numerical	
DECIDUOUS	Percentage share of deciduous trees in basal area of live stand	%	numerical	arcsine

Table A10. Explanatory variables in the linear mixed effect model (only fixed effects) and in the multivariate analysis (Redundancy Analysis, RDA). Basal area and volume of the live stand and site productivity following Keller (1978) were used as a proxy for site productivity. Mean air temperature in the vegetation period and precipitation cover the climate conditions. A detailed description of the variables is presented in the section “Fixed effects” in chapter 3.3.4.1.

Reserve	PP number	Time since last management intervention [years]	Basal area of live stand [m²/ha]	Volume of live stand [m³/ha]	Maximal average total site productivity following Keller (1978) [kg/(ha*year)]	Past disturbance	Mean air temperature in the vegetation period [°C]	Precipitation [mm]	Northness [-]	Proportion of deciduous tree species in living basal area [%]
Derborence	1	>100	66	748	2244	yes	10.45	1481	0.93	0
	5	>100	38	394	2232	no	10.54	1475	-0.05	5
	8	>100	50	594	2200	yes	10.03	1524	0.94	0
	18	>100	48	567	1928	yes	9.50	1589	0.82	0
Scatlè	10	>100	62	644	2711	no	8.73	1564	0.07	0
	11	>100	40	418	2692	no	8.79	1562	0.03	0
Bödmerenwald	1	>100	55	590	332	no	9.35	2391	0.97	0
	3	>100	59	634	328	no	9.35	2391	0.97	0
	4	>100	42	433	430	no	9.53	2376	0.77	0
Leihubelwald	1	50-100	40	496	2531	yes	11.40	1785	0.28	4
	4	50-100	68	883	4134	no	11.89	1722	-0.28	6
	10	50-100	76	1004	4037	yes	11.55	1764	-0.24	0
	13	50-100	57	700	2614	no	11.49	1766	0.48	4
Seeliwald	1	20-50	35	389	1854	no	10.29	1857	0.54	0
	2	20-50	21	174	1601	no	9.86	1908	0.83	0
	4	20-50	55	641	1290	no	9.47	1953	0.62	0
	5	20-50	57	653	1502	no	9.76	1925	0.95	0
National Park	7	>100	31	297	1344	no	8.19	939	1.00	0
	18	>100	59	584	1802	no	9.28	872	0.63	0
	19	>100	60	567	1821	no	9.39	865	0.93	0
Combe Biosse	14	20-50	54	679	4198	no	11.39	1345	-0.87	34
	16	20-50	56	709	3885	no	11.05	1364	-1.00	45
	17	20-50	59	607	1448	no	10.72	1379	0.71	45
	19	20-50	72	785	1377	no	10.65	1383	0.17	37

Table A11. Pearson correlation coefficients (R^2) between fixed effects, which are described in detail in the section „Fixed effects" in chapter 3.3.4.1. Red colored are the variables excluded from the full model due to high correlations with other variables. The variable DECIDUOUS has already been arcsine-transformed.

Variable	MANAGEMENT	BASAL_AREA	VOLUME_LIVING	PRODUCTIVITY_KELLER	WIND	PRECIPITATION	TEMPERATURE	NORTHNESS
BASAL_AREA	0.019							
VOLUME_LIVING	-0.14	0.93						
PRODUCTIVITY_KELLER	-0.23	0.27	0.46					
WIND	0.25	0.24	0.26	0.23				
PRECIPITATION	-0.069	-0.093	0.0029	-0.36	-0.0048			
TEMPERATURE	-0.49	0.33	0.54	0.62	0.25	0.053		
NORTHNESS	0.36	-0.57	0.38	-0.82	0.11	0.18	-0.57	
DECIDUOUS	-0.57	0.21	0.28	0.36	-0.22	-0.27	0.56	-0.61

9.3 Appendix C: Spatial log distribution

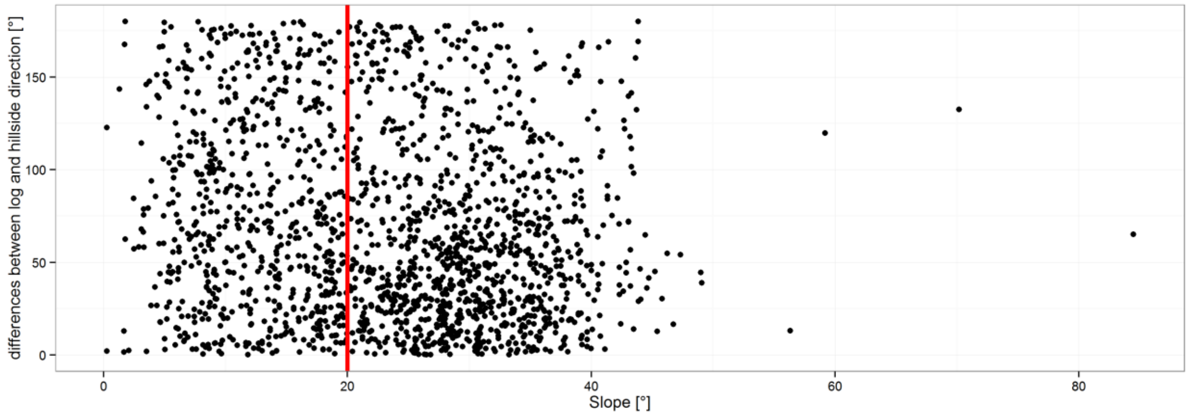


Figure A3. Plot of slope against absolute differences between log and hillside orientation (n=1807). The four outliers with steep slopes occur from PP4 in Bödmerenwald (Slopes of 59°, 70° and 84°) and from PP17 in Combe Biosse (Slope of 56°). In Bödmerenwald, there are various mounds with nearly vertical sides. As slope calculations considered only a square of 6x6m, steep slopes might be a result. In Combe Biosse, the upper part of PP17 is in fact steep.

9.3.1 Appendix C1: Log positon, orientation and spatial pattern analysis

9.3.1.1 Derborence

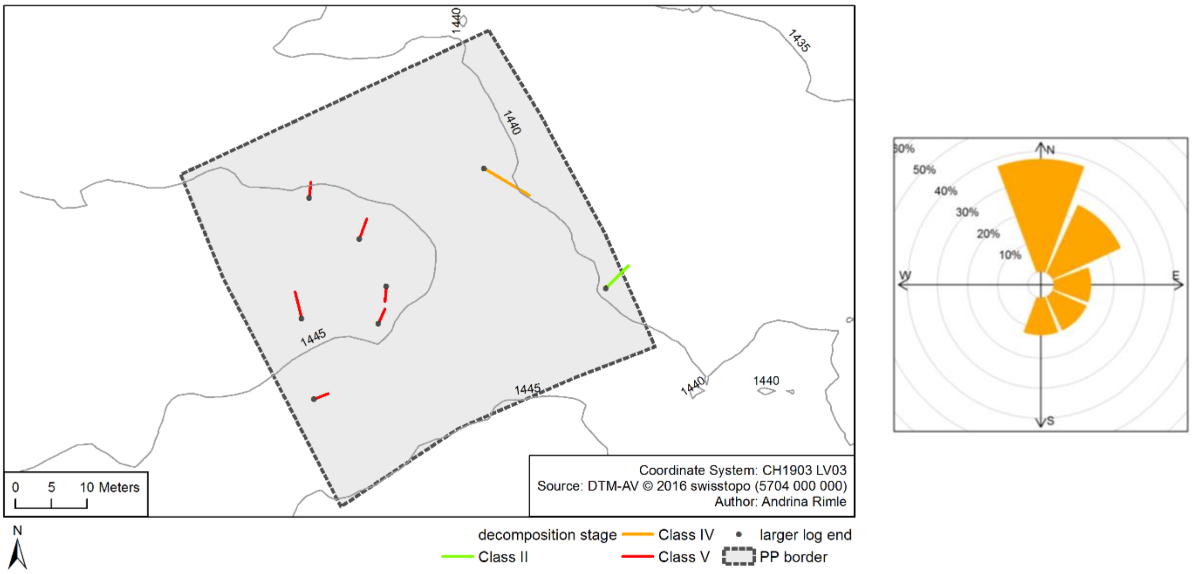


Figure A4. Derborence, PP5 (n=8). Slope: -. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Right: Relative frequency of log orientation in 45°-classes.

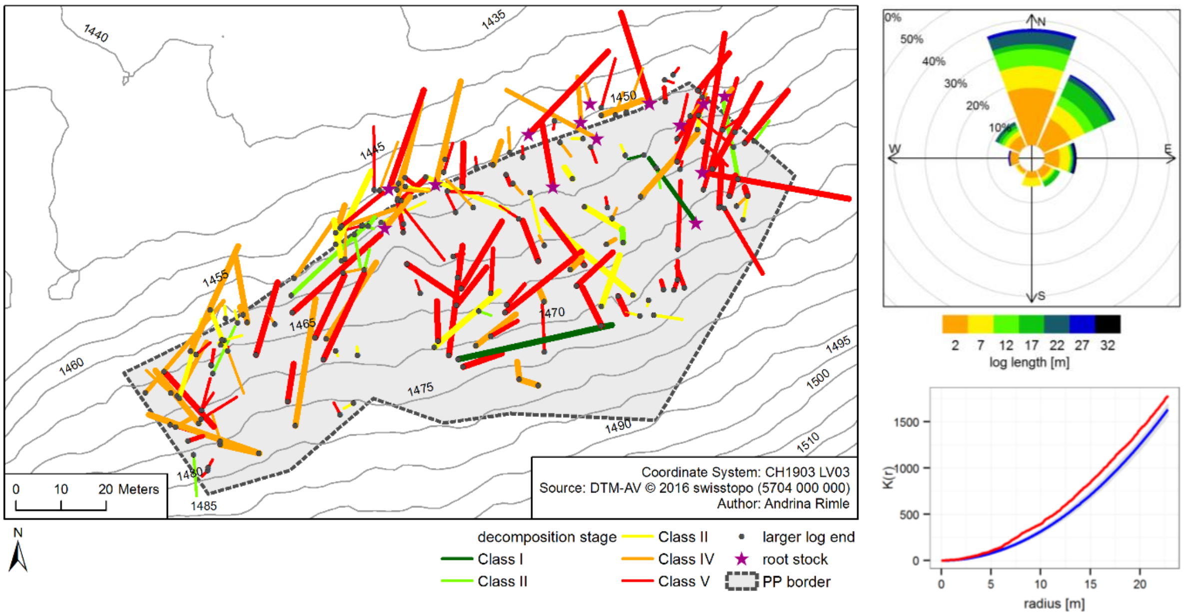


Figure A5. Derborence, PP8 (n=185). Slope: N/(NW), ~30°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by log length of 5 m classes. X-values in the legend represent minimum length value of each class. Lower right panel: Diagram of the K(r) function of all logs within PP borders (n=146) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

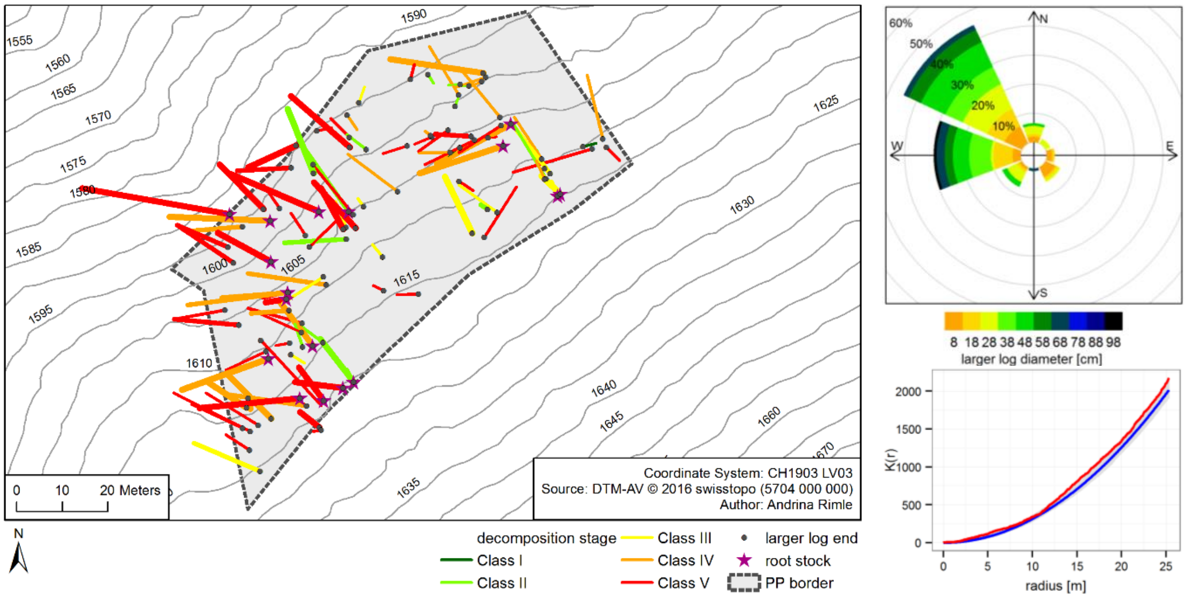


Figure A6. Derborence, PP18 (n=107). Slope: NW, ~30°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent minimum diameter value of each class. Lower right panel: Diagram of the $K(r)$ function of all logs within PP borders (n=105) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

9.3.1.2 Scatlè

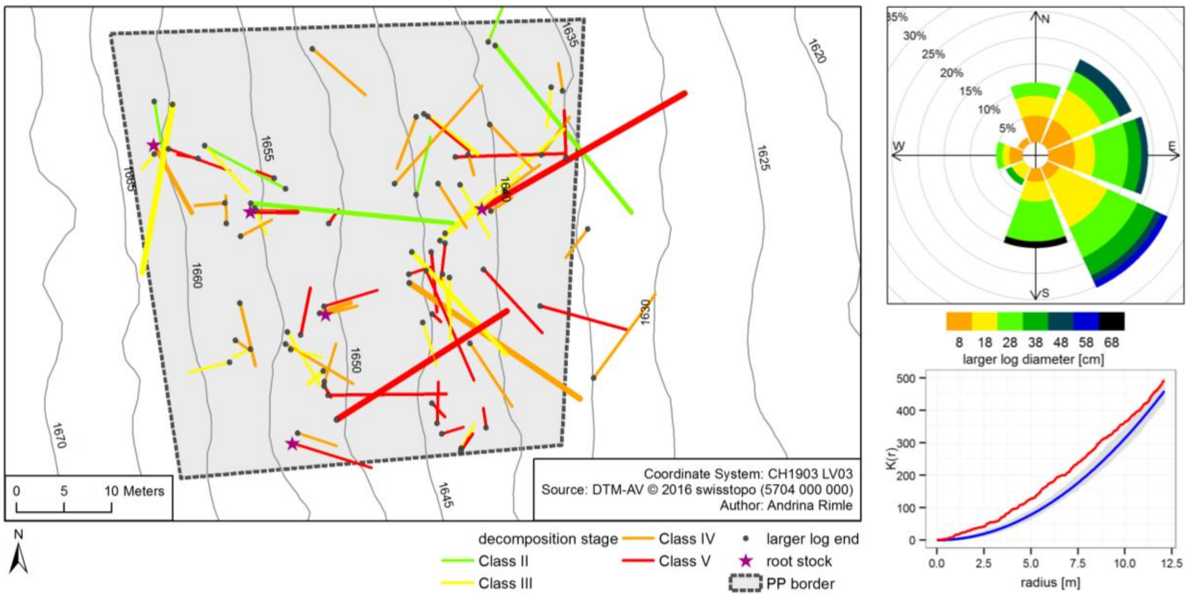


Figure A7. Scatlè, PP10 (n=79). Slope: E, ~30°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent minimum diameter value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=77) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

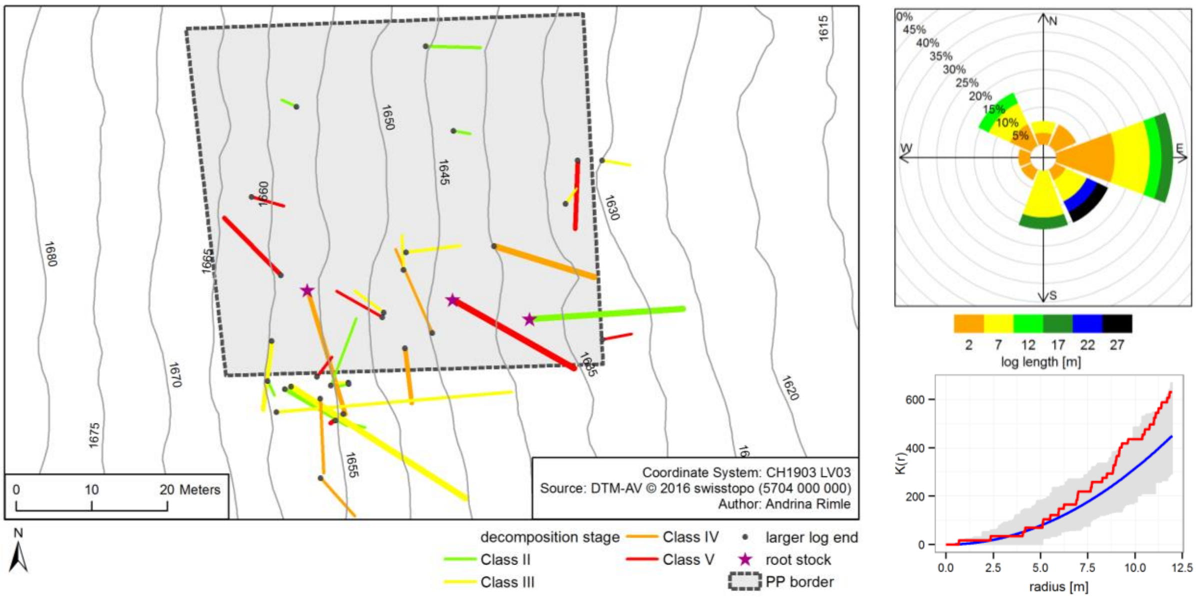


Figure A8. Scatlè, PP11 (n=32). Slope: E, ~35°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by log length of 5 m classes. X-values in the legend represent minimum length value of each class. Lower right panel: Diagram of the K(r) function for all logs within PP borders (n=17) indicating spatial randomness. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

9.3.1.3 Bödmerenwald

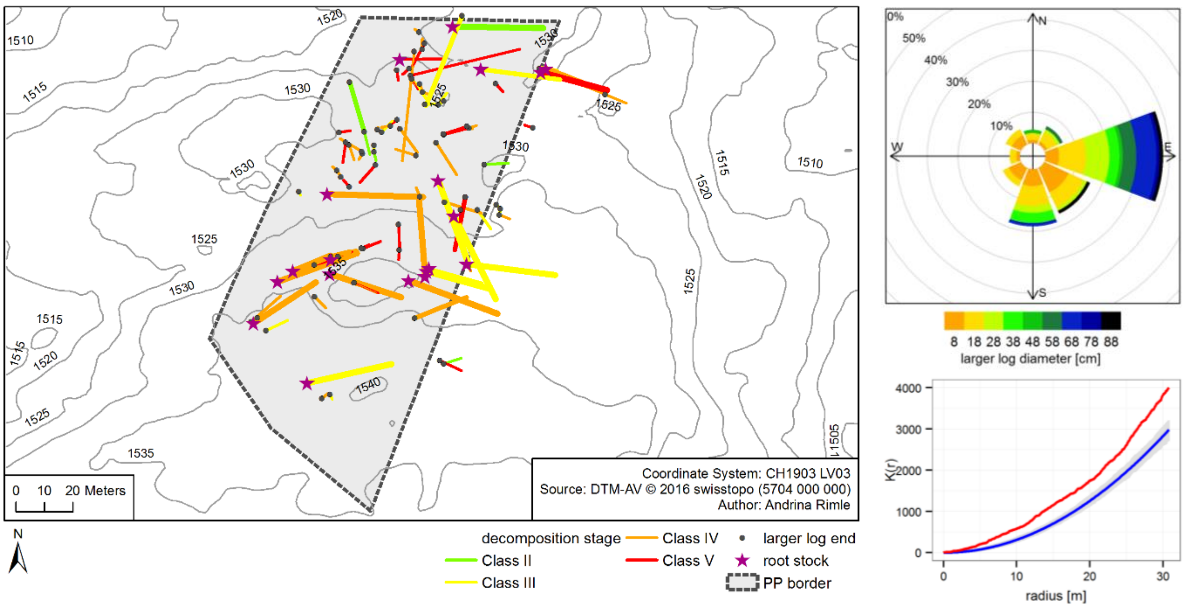


Figure A9. Bödmerenwald, PP1 (n=92). Slope: -. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent minimum diameter value of each class. Lower right panel: Diagram of the K(r) function for all logs within PP borders (n=80) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

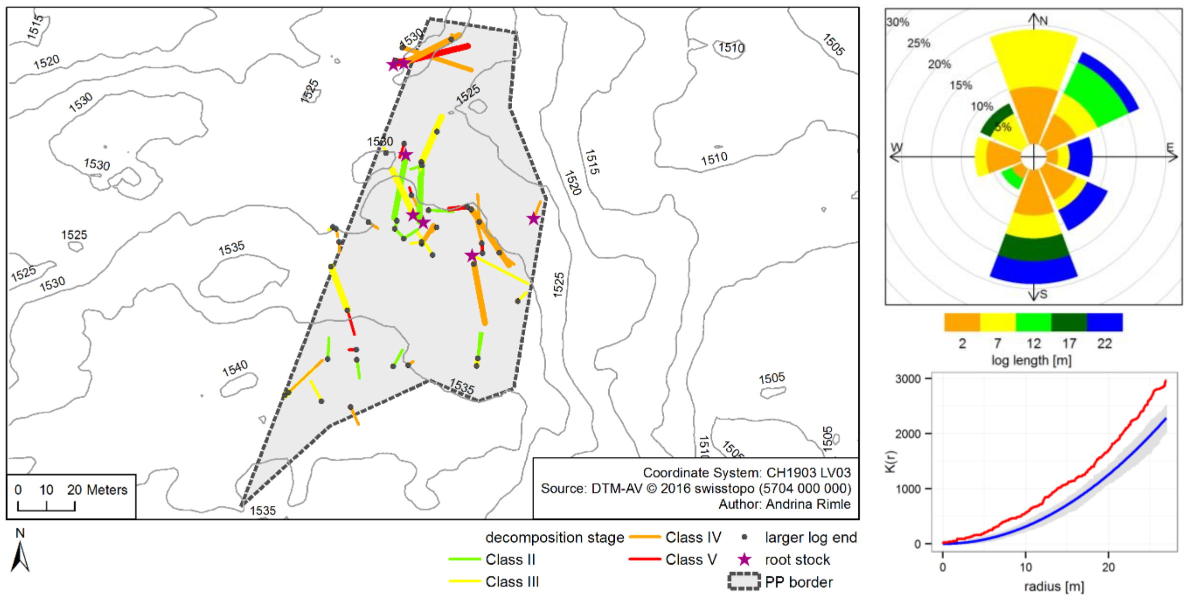


Figure A10. Bödmerenwald, PP3 (n=52). Slope: -. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by log length of 5 m classes. X-values in the legend represent minimum length value of each class. Lower right panel: Diagram of the $K(r)$ function of all logs within PP borders (n=44) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

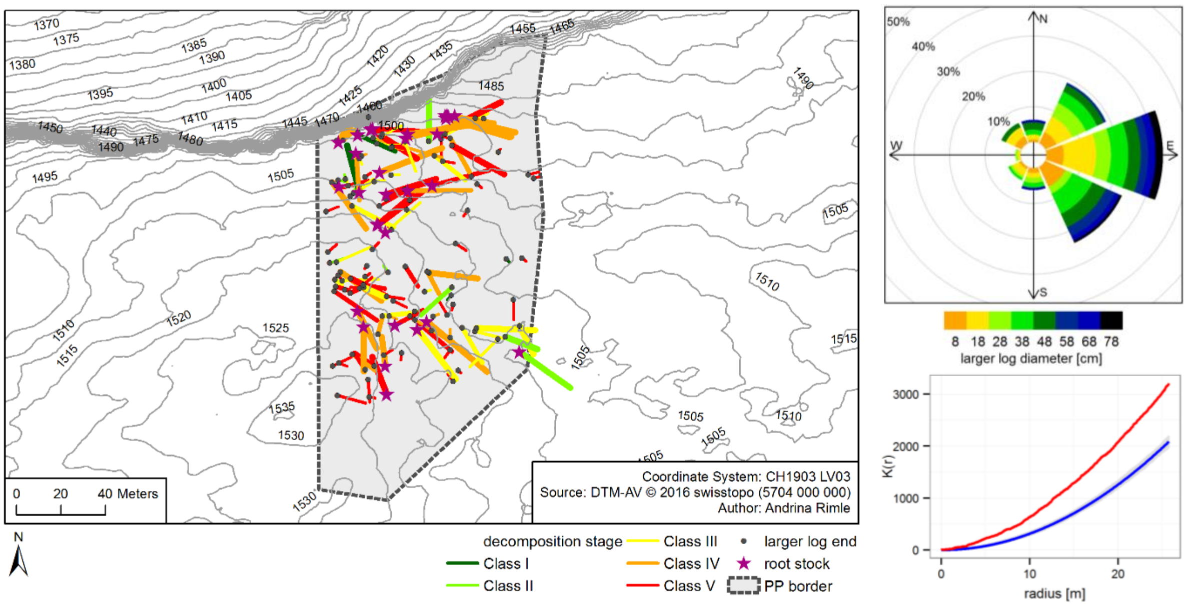


Figure A11. Bödmerenwald, PP4 (n=143). Slope: -. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent minimum diameter value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=143) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

9.3.1.4 *Leihubelwald*

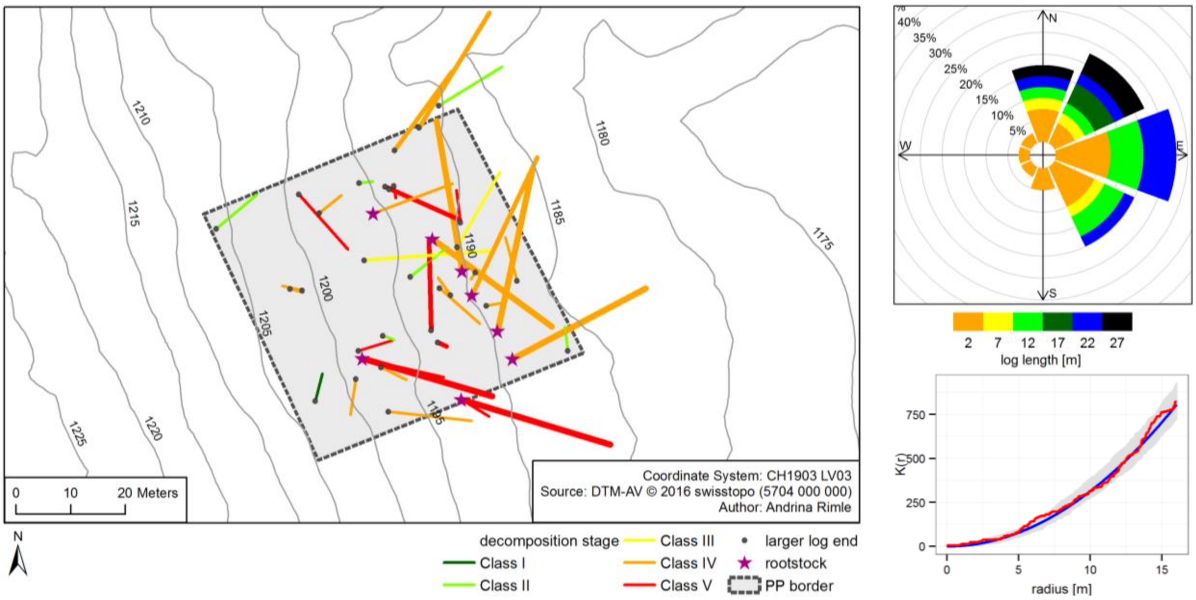


Figure A12. Leihubelwald, PP1 (n=40). Slope: E, ~20°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right pane: Relative frequency of log orientation in 45°-classes stratified by log length of 5 m classes. X-values in the legend represent minimum length value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=39) indicating spatial randomness. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

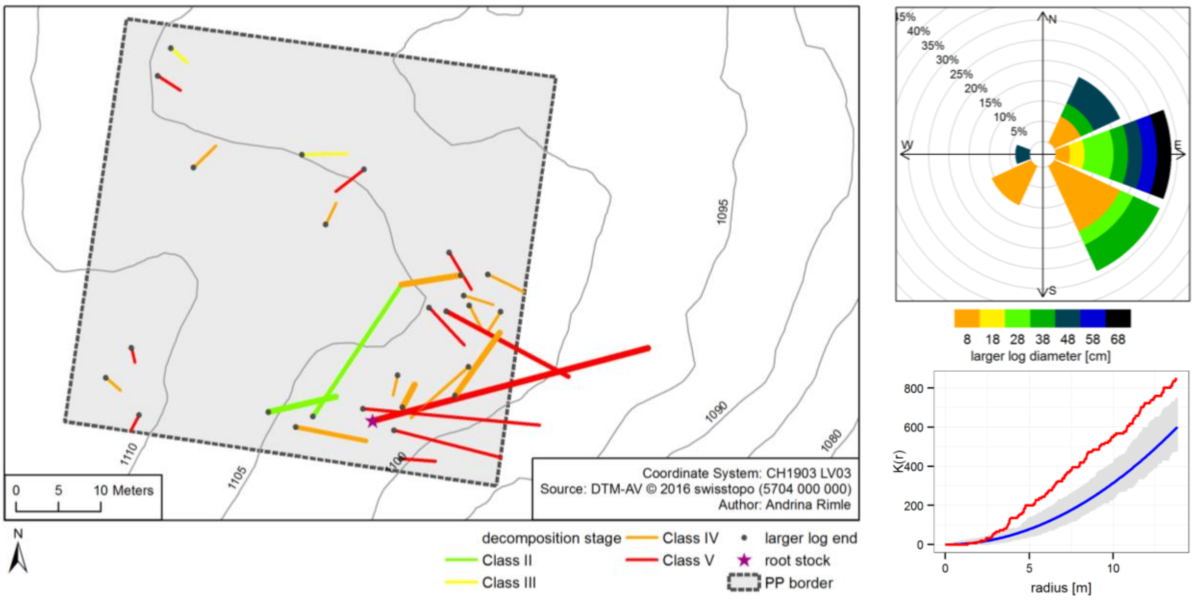


Figure A13. Leihubelwald, PP4 (n=28). Slope: E/SE, ~20°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent minimum diameter value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=28) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

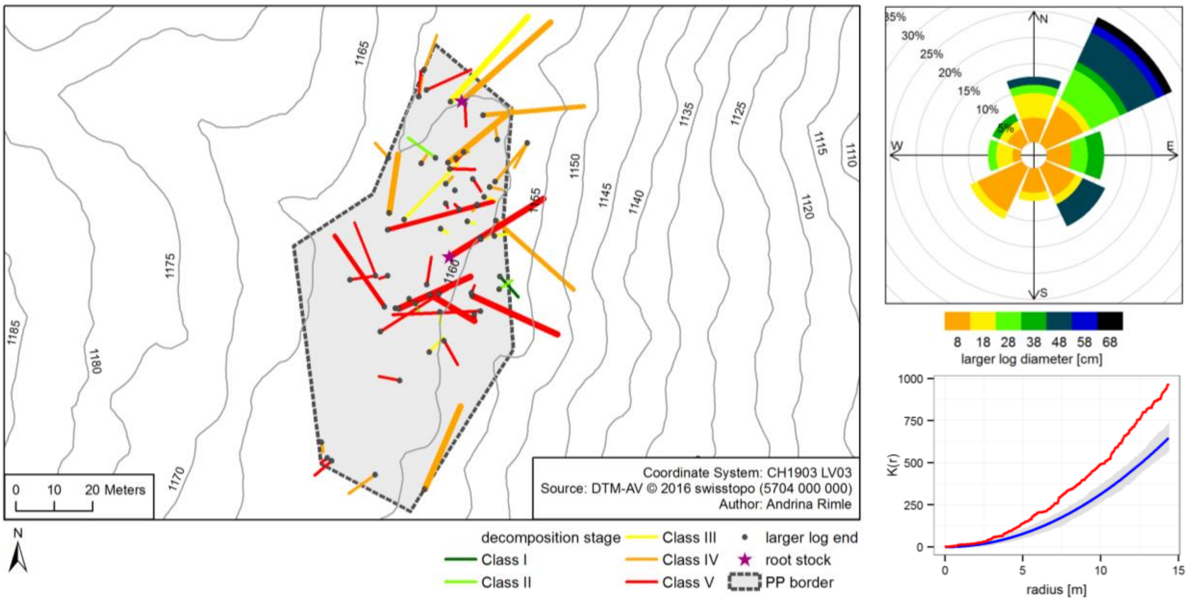


Figure A14. Leihubelwald, PP10 (n=64). Slope: E/SE, ~10°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent minimum diameter value of each class. Lower right panel: Diagram of the $\mathrm{K(r)}$ function for all logs within PP borders (n=62) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

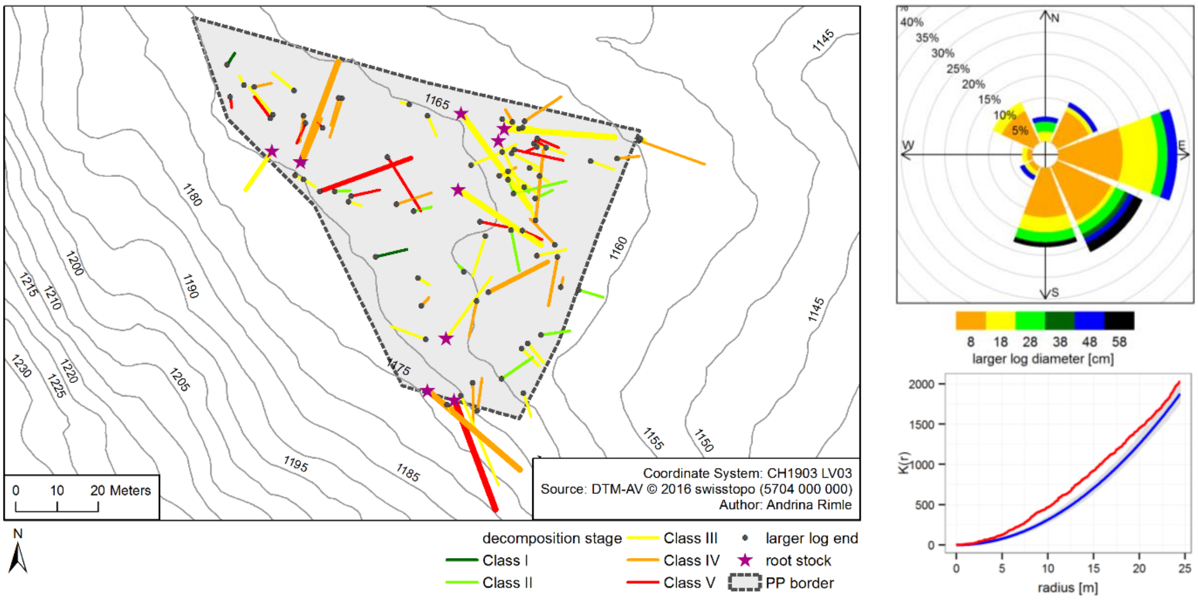


Figure A15. Leihubelwald, PP13 (n=88). Slope: NE, ~10°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent minimum diameter value of each class. Lower right panel: Diagram of the $\mathrm{K(r)}$ function for all logs within PP borders (n=82) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

9.3.1.5 Seeliwald

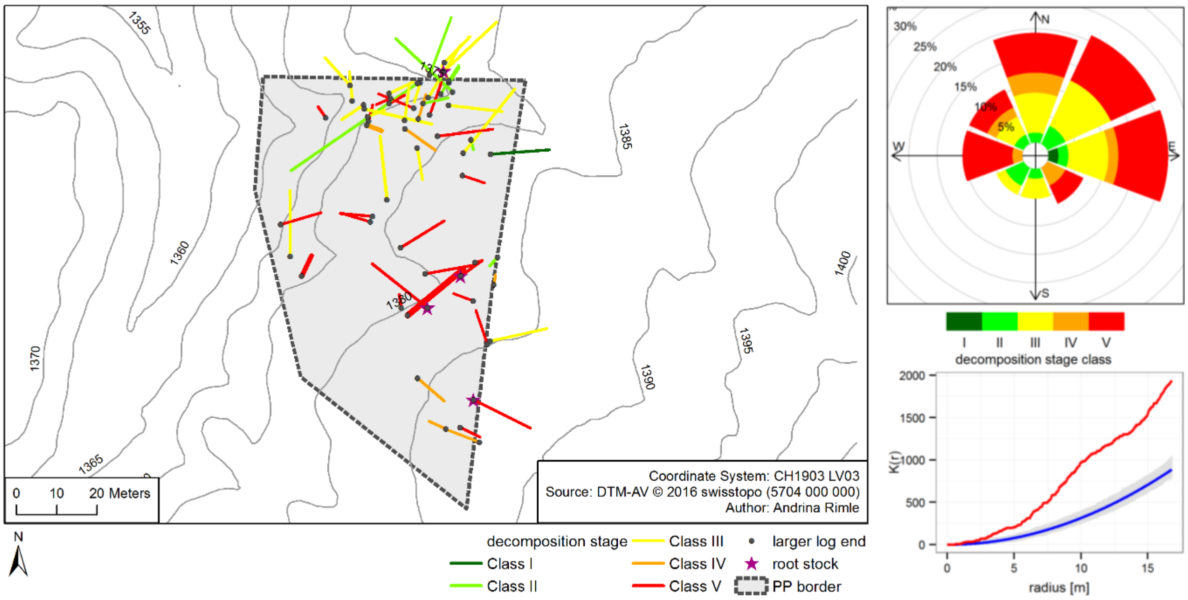


Figure A16. Seeliwald, PP1 (n=57). Slope: NW, ~20°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by decomposition stage classes. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=49) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

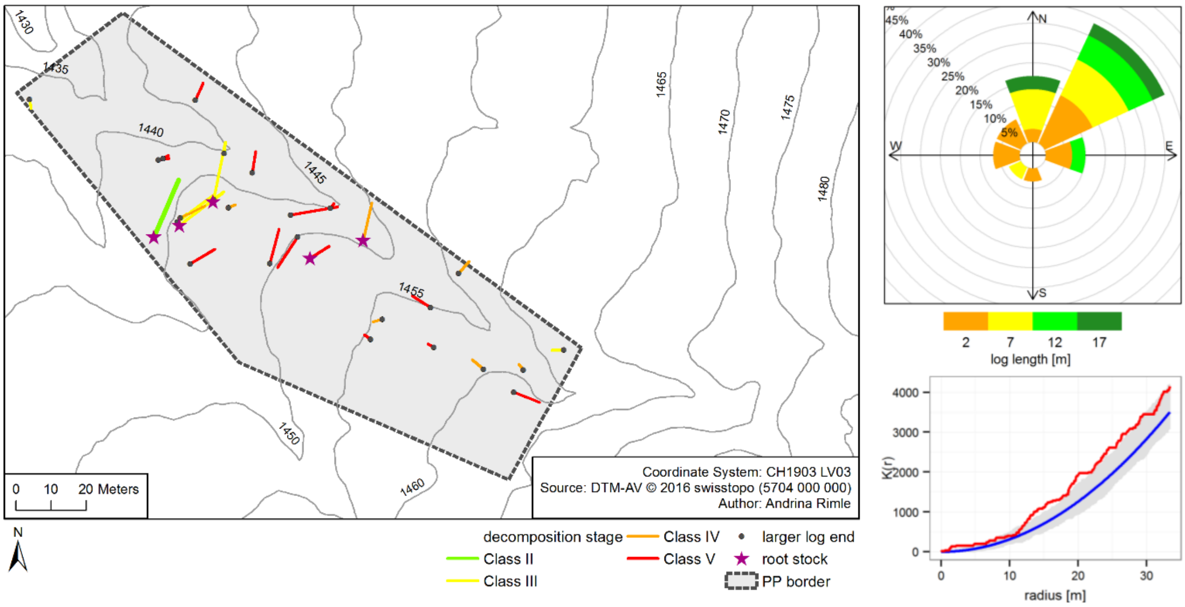


Figure A17. Seeliwald, PP2 (n=30). Slope: NW, ~15°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by log length of 5 m classes. X-values in the legend represent minimum length value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=30) indicating spatial variation. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

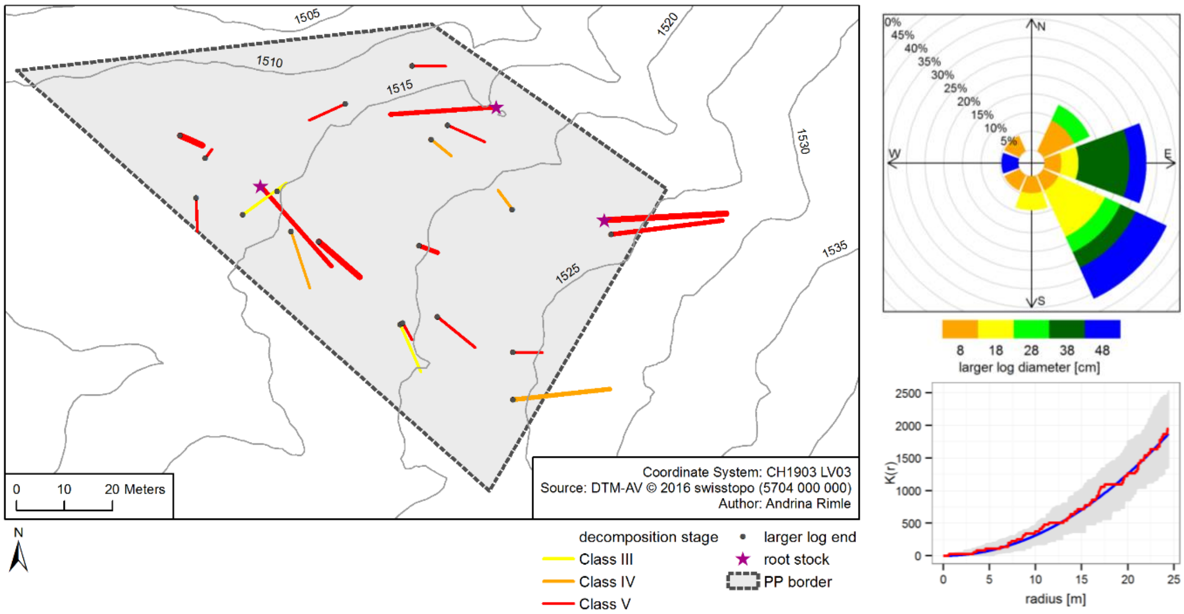


Figure A18. Seeliwald, PP4 (n=22). Slope: W, ~10°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent minimum diameter value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=22) indicating spatial randomness. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

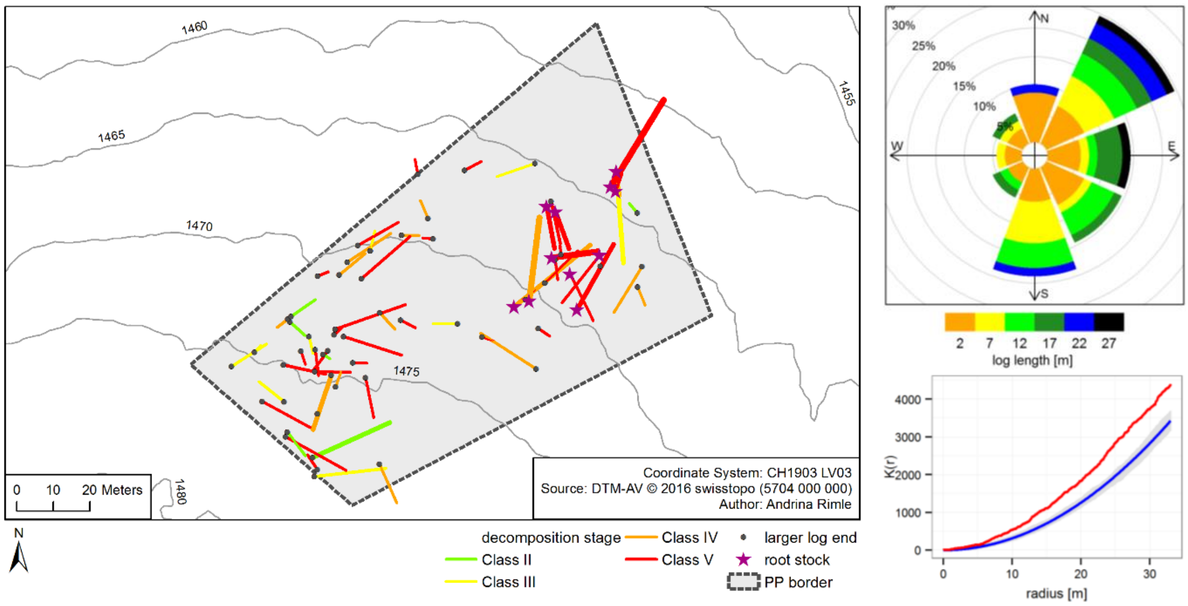


Figure A19. Seeliwald, PP5 (n=69). Slope: N/NE, ~10°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by log length of 5 m classes. X-values in the legend represent minimum length value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=68) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

9.3.1.6 National Park

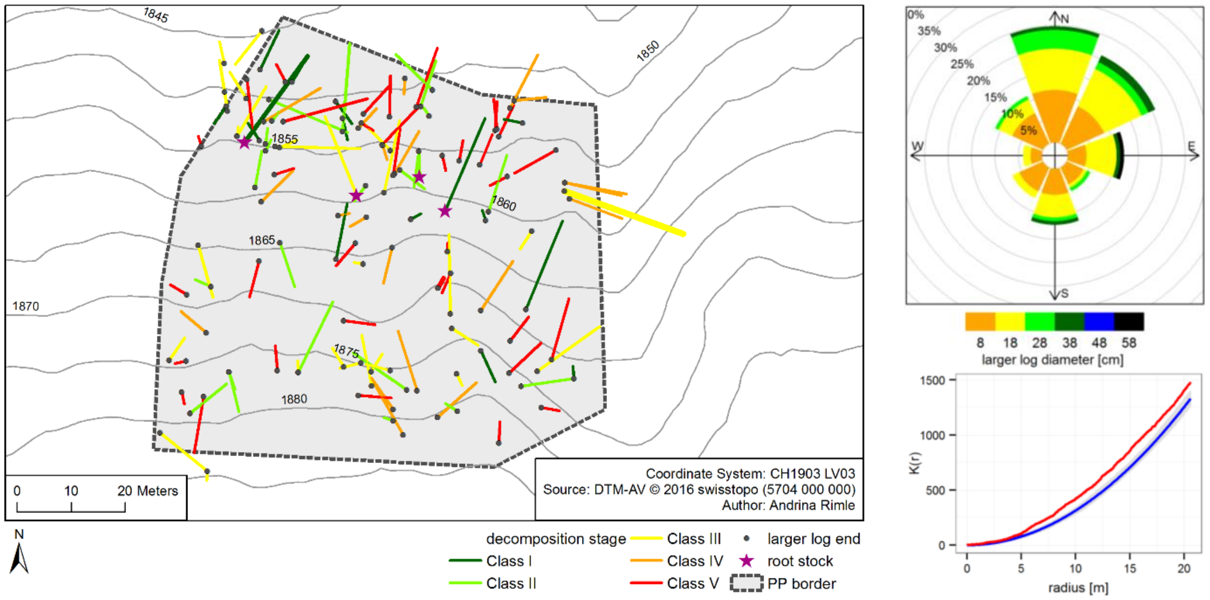


Figure A20. National Park, PP7 (n=125). Slope: N, ~25°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent minimum diameter value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=121) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

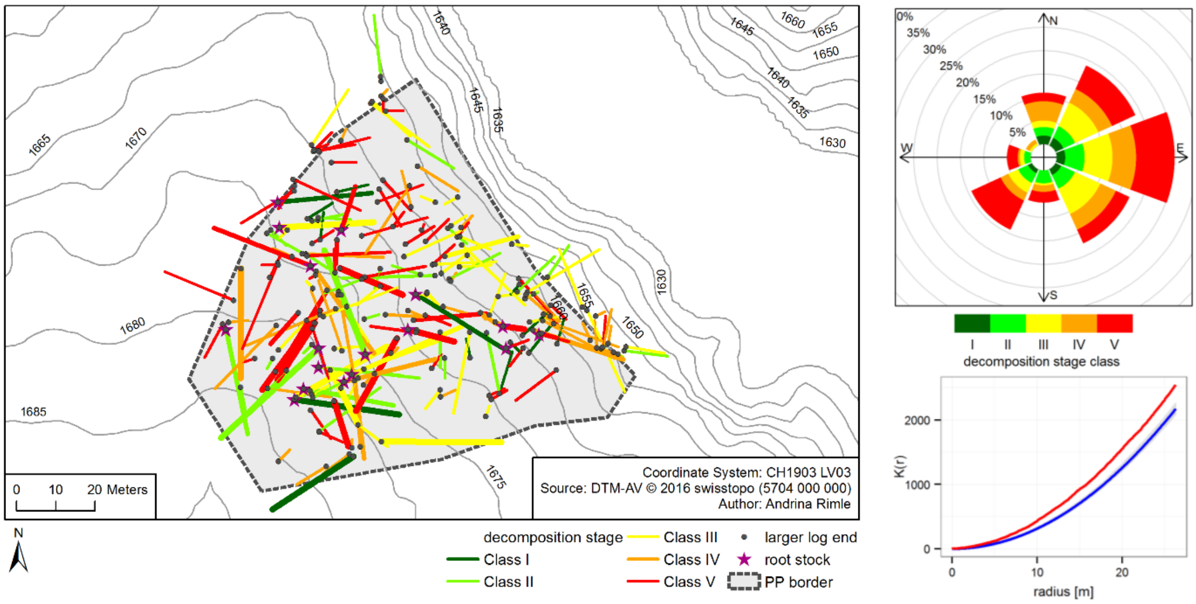


Figure A21. National Park, PP18 (n=218). Slope: NE, ~20°. Left: Spatial depiction. The flat area in the upper right corner is reservoir Lai da Ova Spin. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by decomposition stage classes. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=195) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

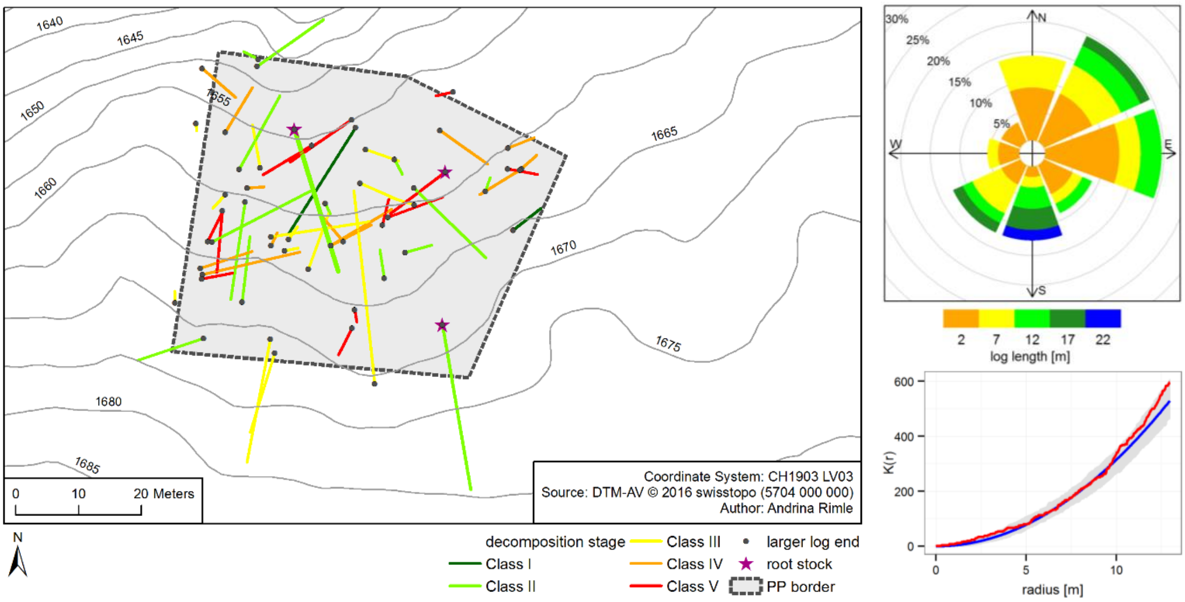


Figure A22. National Park, PP19 (n=56). Slope: N, ~20°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by log length of 5 m classes. X-values in the legend represent minimum length value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=51) indicating spatial randomness. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

9.3.1.7 Combe Biosse

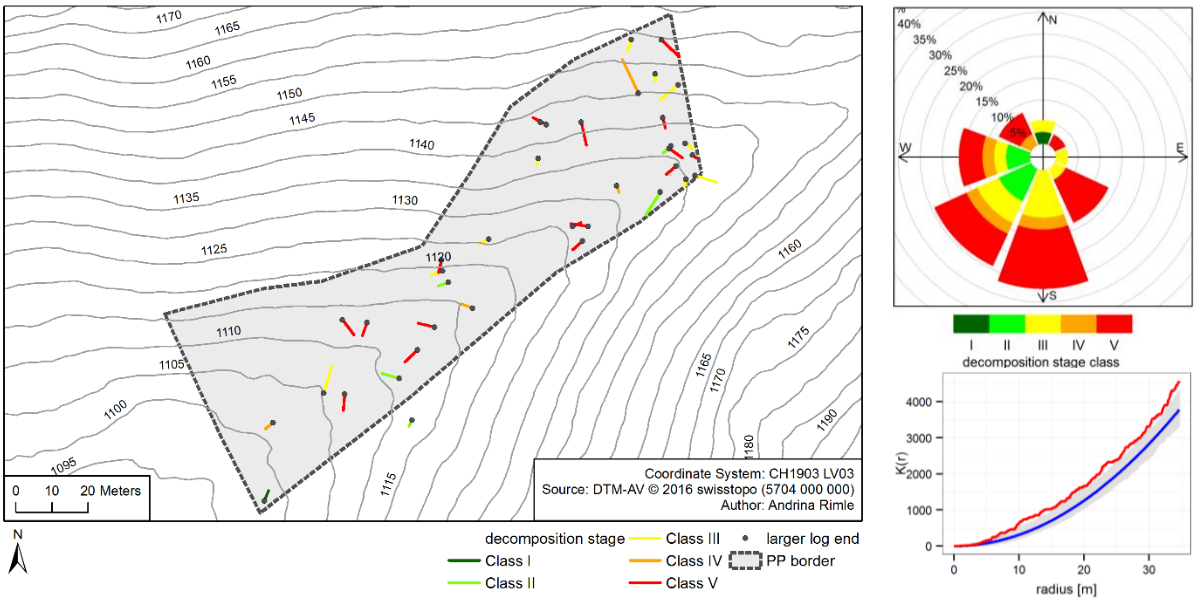


Figure A23. Combe Biosse, PP14 (n=37). Slope: S,, ~25°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by decomposition stage classes. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=36) indicating spatial clustering. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

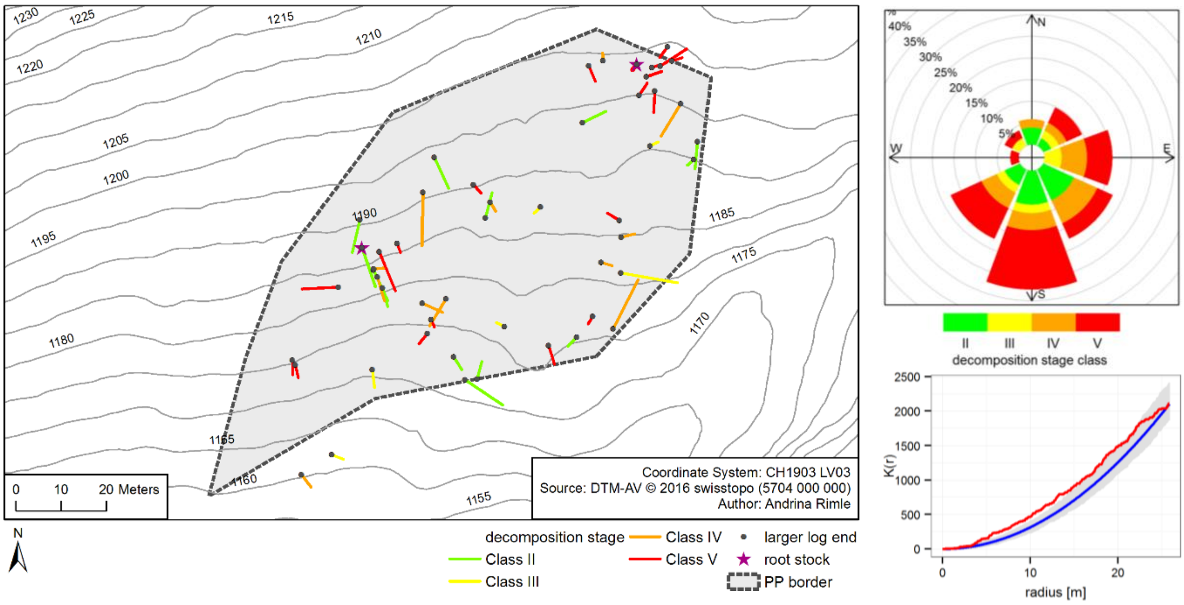


Figure A24. Combe Biosse, PP16 (n=51). Slope: S, ~25°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by decomposition stage classes. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=46) indicating spatial variation. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

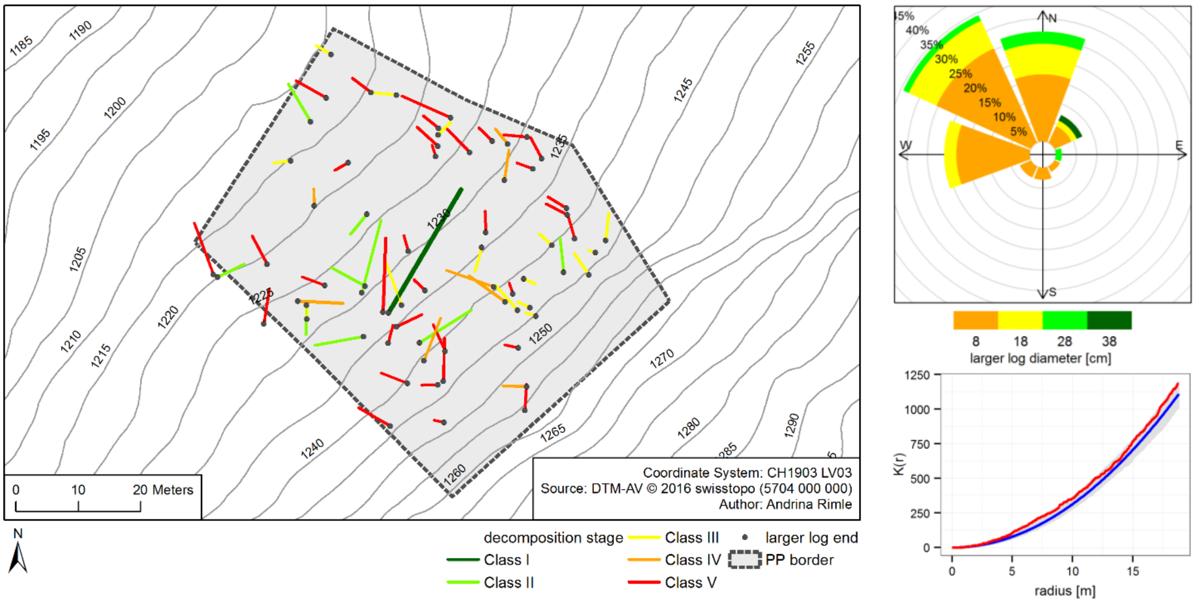


Figure A25. Combe Biosse, PP17 (n=67). Slope: NW, ~35°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by larger log diameter of 10 cm classes. X-values in the legend represent the minimum diameter value of each class. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=64) indicating spatial variation. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

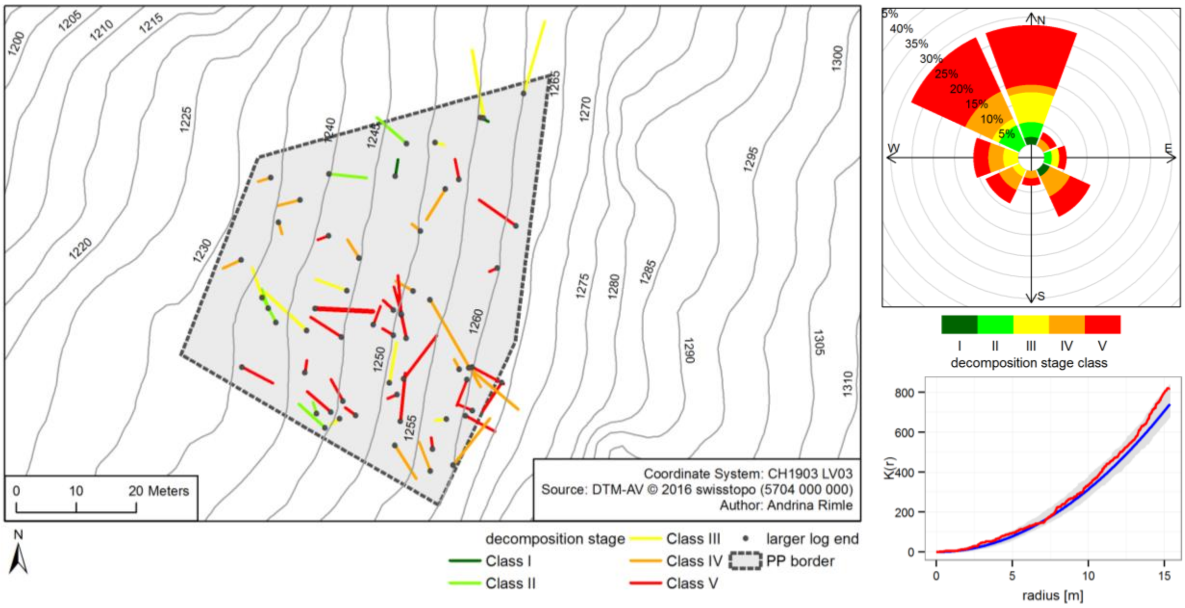


Figure A26. Combe Biosse, PP19 (n=57). Slope: W, ~35°. Left: Spatial depiction. Log thickness corresponds to diameter classes of <20 cm, 20-30 cm, 30-40 cm, 40-50 am and >50 cm, with larger log diameter as reference. Upper right panel: Relative frequency of log orientation in 45°-classes stratified by decomposition stage classes. Lower right panel: Diagram of the $K(r)$ function for all logs within PP borders (n=77) indicating spatial randomness. The blue line represents the theoretical random distribution (homogeneous Poisson process) and the red line the observed distribution (Ripley's K-function). The grey area limits the confidence envelope based on 100 random simulations.

9.4 Appendix D: Declaration of originality

Declaration of originality

This signed "Declaration of originality" is a required component of any written work (including any electronic version) submitted by a student during the course of studies in Environmental Sciences. For Bachelor and Master theses, a copy of this form is to be attached to the request for diploma.

I hereby declare that this written work is original work which I alone have authored and written in my own words, with the exclusion of proposed corrections.

Title of the work

Quantity and quality of coarse woody debris in mountainous Norway spruce forest reserves in Switzerland

Author(s)

Last name	First Name
Rimle	**Andrina**

With my signature, I hereby declare:

- I have adhered to all rules outlined in the form on „Citation etiquette", www.ethz.ch/students/exams/plagiarism_s_en.pdf.
- I have truthfully documented all methods, data and operational procedures.
- I have not manipulated any data.
- I have identified all persons who have substantially supported me in my work in the acknowledgements.
- I understand the rules specified above.

I understand that the above written work may be tested electronically for plagiarism.

Zürich, 01.02.2016 A.Rim

Place, Date Signature*

* The signatures of all authors are required for work submitted as a group. The authors assert the authenticity of all contents of the written work submitted with their signatures.