Sustainable management of naturally disturbed forests

Nachhaltiges Management von natürlichen Störungen in Wäldern

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Summary

Owing to climate change, natural forest disturbances and consecutive salvage logging are drastically increasing worldwide, consequently increasing the importance of understanding how these disturbances would affect biodiversity conservation and provision of ecosystem services.

In chapter II, I used long-term water monitoring data and mid-term data on α-diversity of twelve species groups to quantify the effects of natural disturbances (windthrow and bark beetle) and salvage logging on concentrations of nitrate and dissolved organic carbon (DOC) in streamwater and α-diversity. I found that natural disturbances led to a temporal increase of nitrate concentrations in streamwater, but these concentrations remained within the health limits recommended by the World Health Organization for drinking water. Salvage logging did not exert any additional impact on nitrate and DOC concentrations, and hence did not affect streamwater quality. Thus, neither natural forest disturbances in watersheds nor associated salvage logging have a harmful effect on the quality of the streamwater used for drinking water. Natural disturbances increased the α-diversity in eight out of twelve species groups. Salvage logging additionally increased the α-diversity of five species groups related to open habitats, but decreased the biodiversity of three deadwood-dependent species groups.

In chapter III, I investigated whether salvage logging following natural disturbances (wildfire and windthrow) altered the natural successional trajectories of bird communities. I compiled data on breeding bird assemblages from nine study areas in North America, Europe and Asia, over a period of 17 years and tested whether bird community dissimilarities changed over time for taxonomic, functional and phylogenetic diversity when rare, common and dominant species were weighted differently. I found that salvage logging led to significantly larger dissimilarities than expected by chance and that these dissimilarities persisted over time for rare, common and dominant species, evolutionary lineages, and for rare functional groups. Dissimilarities were highest for rare, followed by common and dominant species.

In chapter IV, I investigated how β-diversity of 13 taxonomic groups would differ in intact, undisturbed forests, disturbed, unlogged forests and salvage-logged forests 11 years after a windthrow and salvage logging. The study suggests that both windthrow and salvage logging drive changes in between-treatment β-diversity, whereas windthrow alone

seems to drive changes in within-treatment β-diversity. Over a decade after the windthrow at the studied site, the effect of subsequent salvage logging on within-treatment β-diversity was no longer detectable but the effect on between-treatment β-diversity persisted, with more prominent changes in saproxylic groups and rare species than in non-saproxylic groups or common and dominant species.

Based on these results, I suggest that salvage logging needs to be carefully weighed against its long-lasting impact on communities of rare species. Also, setting aside patches of naturally disturbed areas is a valuable management alternative as these patches would enable post-disturbance succession of bird communities in unmanaged patches and would promote the conservation of deadwood-dependent species, without posing health risks to drinking water sources.

Zusammenfassung

In Folge des Klimawandels treten in Wäldern vermehrt natürliche Störungen auf, wodurch wiederum die Zahl an nachfolgenden Sanitärhieben (Räumungen) drastisch gestiegen ist. Wie sich natürliche Störungen und Sanitärhiebe auf die biologische Vielfalt und die Bereitstellung von Ökosystemleistungen auswirken können, ist bisher jedoch nur unzureichend bekannt.

In Kapitel II nutzte ich langfristige Wassermonitoringdaten und mittelfristige Biodiversitätsdaten über zwölf Artengruppen, um die Effekte von natürlichen Störungen (Windwurf und Borkenkäfer) und Sanitärhieben auf die Konzentrationen von Nitraten und gelöster organischer Kohlenstoffe (GOK) in Bächen und Artenzahl zu quantifizieren. Die Ergebnisse zeigen, heraus, dass natürliche Störungen zu einer temporären Erhöhung der Nitratwerte führen, welche dennoch laut Angaben der Weltgesundheitsorganisation immer noch als unbedenklich eingestuft werden können. Die Sanitärhiebe hatten keinen zusätzlichen Einfluss auf die Nitrat- und GOK-Konzentrationen und daher keinen Einfluss auf die Wasserqualität. Daraus lässt sich schließen, dass sich weder natürliche Waldstörungen in Wassereinzugsgebieten noch die damit verbundenen Sanitärhiebe auf die Trinkwasserqualität aus auswirken. Natürliche Störungen erhöhten die Artenzahlen in acht von zwölf Artengruppen. Zusätzlich erhöhten die Sanitärhiebe die Artenzahlen von fünf Artengruppen, welche auf offene Lebensräume angewiesen sind, verringerte jedoch die Artenzahlen von drei xylobionte Artengruppen.

In Kapitel III habe ich untersucht, ob Sanitärhiebe nach natürlichen Waldstörungen zu sukzessiven Veränderungen der Vogelgemeinschaften führen. Hierzu habe ich die taxonomische, funktionelle und phylogenetische Diversität von Brutvogelgemeinschaften aus neun Untersuchungsregionen in Nordamerika, Europa und Asien über die Zeit von 17 Jahren verglichen und analysiert, ob sich das jeweilige Diversitätsmaß verändert, wenn seltene, häufige und dominante Arten unterschiedlich gewichtet werden. Ich konnte zeigen, dass Sanitärhiebe zu signifikant größeren Unterschieden geführt haben als zufällig zu erwarten gewesen sind und dass diese Unterschiede über die Zeit sowohl für seltene, häufige und dominante Arten, als auch für evolutionäre Linien, und funktionelle Gruppen fortdauern. Diese Unterschiede waren am größten für seltene, gefolgt von häufigen und dominanten Arten.

In Kapitel IV untersuchte ich wie sich die β-Diversität von 13 taxonomischen Gruppen zwischen ungestörten Wäldern, gestörten und ungeräumten Wäldern sowie gestörten und geräumten Wäldern 11 Jahre nach Windwurf und anschließender Räumung unterscheidet. Die Ergebnisse deuten darauf hin, dass sowohl Windwurf als auch Räumung Änderungen in der β-Diversität bewirken. Windwurf allein jedoch scheint diese Änderungen in der β-Diversität innerhalb der Behandlung bewirken zu können. Über ein Jahrzehnt nach dem Windwurf war der Effekt des Sanitärhiebes auf die β-Diversität innerhalb der Behandlung nicht mehr nachweisbar. Der Effekt auf die β-Diversität zwischen den Behandlungen blieb jedoch bestehen, wobei sich die xylobionten Gruppen und seltenen Arten stärker veränderten als die nicht-xylobionten Gruppen oder häufigen und dominanten Arten.

Basierend auf diesen Ergebnissen schlage ich vor, dass der Einsatz von Sanitärhieben sorgfältig gegen ihre langfristigen Auswirkungen auf Gemeinschaften seltener Arten abgewogen werden muss. Zusätzlich, besteht mit dem Belassen von natürlich gestörten Waldgebieten eine wertvolle Managementalternative, da diese Flächen eine natürliche Entwicklung von Vogelgemeinschaften ermöglichen und xylobionte Arten fördern, ohne dass die Trinkwasserqualität negativ beeinträchtigt wird.

Chapter I: General introduction

Forests are among the most important ecosystems on the planet, as they cover approximately 30% of the earth's terrestrial surface (Keenan et al., 2015). Forests hold a considerable part of the terrestrial biodiversity and sustain numerous ecosystem services, such as regulation of climate and rainfall, provision of drinking water and raw materials, and many others (FAO et al., 2020). Forested area in temperate regions is constantly growing (Keenan et al., 2015), leading to an increase of growing stock that makes forests an important carbon sink (Ciais et al., 2008). However, there are signs that forests may lose their importance as carbon sink because of the increase of carbon releasing events such as natural disturbances (Nabuurs et al., 2013).

Natural forest disturbances, such as wildfires, windthrows and insect outbreaks, are a major driver of ecosystem dynamics in forests. Natural disturbances are commonly defined as discrete events that kill groups of trees or entire forest stands (Pickett et al., 1985). Disturbances have important characteristics like size, frequency of occurrence and intensity, which all define the disturbance regime of a particular forest ecosystem. Disturbances range from small gap-forming perturbations that create canopy openings only a few hectares in size, to large-scale stand-replacing disturbances that perish hundreds or even thousands of hectares of forest (Lindenmayer et al., 2008). Gap-forming disturbances usually have low intensities and occur more frequently, while high-intensity, stand-replacing disturbances occur less frequently (Lindenmayer et al., 2008). In this thesis the main focus is on intensive, infrequent, stand-replacing disturbances. These disturbances cause by far the most economic damage hence they are most relevant from forest management perspective.

Natural disturbances create high structural heterogeneity as a result of diverse biological legacies left after a disturbance (Swanson et al., 2011). Forest disturbances create a resource pulse of deadwood over a short period of time (Kulakowski et al., 2017), increase light availability and change microclimatic conditions (Swanson et al., 2011; Wohlgemuth et al., 2019). Natural disturbances can affect the provision of water by altering hydrological regimes and by increasing soil erosion and leaching of soil nutrients into streams (Mikkelson et al., 2013). Disturbances affect biodiversity by increasing species richness of pioneer, open-land species and taxonomic groups that utilize deadwood resources (Thorn et al., 2018). Thus, natural disturbances can affect human well-being by altering or even disrupting the provision of ecosystem services on one side, but can facilitate biodiversity by creating valuable habitats on the other side (Thom et al., 2016).

Global warming is predicted to increase the area, frequency and duration of droughts in Europe (Samaniego et al., 2018), which will also impact disturbance regimes. Higher average temperatures are likely to simultaneously lower winter mortality and increase voltinism of the European spruce bark beetle (*Ips typographus* L.) (Jönsson et al., 2009). In addition, weather extremes facilitate interactions between different disturbance types, such as drought, wildfire, windthrow and insect outbreaks (Seidl et al., 2017), which has resulted in a temporal synchronization of disturbances throughout European temperate forests for the period 1986–2016 (Senf & Seidl, 2018). During the same period canopy mortality has doubled in temperate European forests (Senf, Pflugmacher, et al., 2018) and the frequency of stand-replacing forest disturbances has steadily increased (Senf et al., 2021). In other regions, such as the USA, the frequency and severity of wildfires have also increased since 1970 (James et al., 2018). North America, especially the Pacific Northwest and boreal forests, suffer from unprecedented waves of insect outbreaks that last for decades and kill millions of hectares of forest (Raffa et al., 2008).

In Europe, windstorms are the most important disturbance agents, responsible for 53% of the total damage in forests over the period of 1950–2000 (Schelhaas et al., 2003). By increasing the amount of available deadwood, windstorms create favorable conditions for the development of bark beetle populations (Biedermann et al., 2019). Over the period 1958–2001, such interactions have led to a drastic increase of forest damage of 12.59% per year for wind disturbances, 14.23% per year for wildfire, and 15.31% per year for bark beetles (Schelhaas et al., 2003).

To understand the reasons for forest damage, one has to consider all interactions between tree biology, species composition, forest management and climate change (Seidl et al., 2017). Coniferous forests in the boreal and temperate zone are naturally prone to large-scale natural disturbances such as windthrows and bark beetle outbreaks (Morris et al., 2018). However, by increasing the area of even-aged coniferous plantations and implementing fire suppression policies, forest management has led to an increase in the growing stock in coniferous forests in Europe (Ciais et al., 2008), increasing the susceptibility to natural disturbances (Schelhaas et al., 2003). Another proof of the increased susceptibility of coniferous forests to natural disturbances is the positive relationship between growing stock and storm damage in central European forests

(Wohlgemuth et al., 2019). Given all these facts, management of naturally disturbed forests may potentially become a central topic in forest management in many temperate and boreal regions.

I.1 Management of natural disturbances

The increase of natural disturbances has triggered unprecedented levels of post-disturbance salvage logging in both, managed and protected forests worldwide (Leverkus, Lindenmayer, et al., 2018; Müller et al., 2019). Salvage logging is the most common post-disturbance management practice, during which disturbance-affected trees are felled and removed from affected sites (Lindenmayer et al., 2008). In Europe, recouping economic value of timber, pest control and safety are the most important motivations for performing salvage logging in unprotected areas, while pest control and timber value are the main justification in protected areas (Müller et al., 2019). Timber value of infested trees decreases rapidly with time due to fast-spreading fungi and insects that colonize the trees after a disturbance (Akay et al., 2007). As result of that, salvage logging is usually conducted during the first or the second year, at the latest, after a natural disturbance (James et al., 2018). Because it is conducted in already disturbed ecosystems, salvage logging can act as an additional anthropogenic disturbance and its effects on forests ecosystems and forest biodiversity have to be taken into account (Lindenmayer et al., 2006).

Salvage logging can alter the structural complexity of forests, ecosystem processes and functions (Noss et al., 2006). Salvage logging differs from the conventional logging of commercial forests, termed as green-tree logging, in a number of ways. As opposed to green-tree logging, salvage logging takes place in forests that have already experienced a dual stress of drastic changes in environmental conditions prior to the natural disturbance followed by the stress of the disturbance itself (Lindenmayer et al., 2008). In addition, Leverkus et al. (2018b) describe three main differences between salvage logging and green-tree logging. First, when a natural disturbance affects young stands, salvage logging may lead to logging of these stands that would otherwise be deemed too young for logging. Second, salvage logging tends to be more intense than green-tree logging. This often happens during the so called “bycatch”, when surviving trees are logged unselectively together with dead and damaged trees (Lindenmayer et al., 2008). Third, in cases when a natural disturbance affects large areas, then salvage clearcuts can be much larger than green-tree clearcuts (Sullivan et al., 2010). Due to a rarely considered complex socioecological interaction between natural disturbances and logging, forests have higher probability to be logged if they are disturbed, regardless of their legal protection status (Leverkus, Lindenmayer, et al., 2018). Also, salvage logging can even occur in stands that are usually excluded from logging or are part of protected areas (Müller et al., 2019).

A major knowledge gap in the research about salvage logging is that there is a worldwide underrepresentation of studies investigating its effects on biodiversity after the first 5 years post-disturbance (Leverkus, Gustafsson, et al., 2020; Thorn et al., 2018). However, as both natural disturbances and post-disturbance management may have important long-lasting effects on ecosystems and biodiversity (Hobson et al., 1999), there is a need for more mid- to long-term studies.

I.2 Effects on biodiversity

I.2.1 Taxonomic, functional and phylogenetic diversity

Biological diversity encompasses all biotic variation ranging from genes to ecosystems (Purvis et al., 2000). Taxonomic diversity, mostly measured as species richness, is one of the most commonly used metrics in ecology (Jarzyna et al., 2016). However, taxonomic diversity measures do not provide information on ecosystem functioning and community evolutionary history (Cardoso et al., 2014). There is increasing evidence that functionally and phylogenetically diverse communities are necessary for the provision of ecosystem services and for increasing ecosystem stability (Cadotte et al., 2012; Loreau et al., 2013). Also, the response of functional diversity and phylogenetic diversity to environmental perturbations must not mandatorily match those of taxonomic diversity (Cisneros et al., 2015; Dehling et al., 2014; Devictor et al., 2010). For example, Gerisch et al. (2012) found that higher disturbance intensity (flooding) is associated with increasing of taxonomic diversity and reduction of functional diversity of ground beetles. This mismatch in responses impedes the straightforward development of strategies for the conservation of functional and phylogenetic diversities (Thuiller et al., 2015). However, empirical tests of how different types of diversities are affected by natural disturbances and salvage logging are scarce.

According to the successional trajectory theory, disturbed communities are expected to recover to their pre-disturbance condition with time (Holling, 1996). Stand-replacing natural disturbances can affect communities by prolonging the time they need to return to pre-disturbance state (Turner, 2010). However, the effect of salvage logging in this matter have been barely investigated.

I.2.2 Effects on α- and β-diversity

Salvage logging impact biodiversity differently depending on its association with the resources that these disturbances alter. The most prominent ecological consequence of salvage logging is the reduction of biological legacies, such as large damaged or dying trees, snags and logs and pit-and-mounds (Lindenmayer et al., 2008). Because of the changes in forest structure and reduction of biological legacies, salvage logging affects negatively the α-diversity of saproxylic taxonomic groups, which are deadwood-dependent (Thorn et al., 2018). Contrary, however, salvage logging can also facilitate the α-diversity of species and taxonomic groups that are associated with open habitats (Thorn et al., 2018).

The number of species found at certain locations, i.e. α-diversity, is the most widespread measure of biodiversity in ecological studies as it is easy to record or observe (Martinez, 1996). Even though, α-diversity is the most commonly used metric of biodiversity, investigating only the number of species locally may not show the entire picture of biodiversity responses to environmental change (Hillebrand et al., 2018). This is evident from a global analysis, which showed a lack of systematic α-diversity loss over time, but found systematic temporal loss of β-diversity (Dornelas et al., 2014). It has been argued that β-diversity, the spatiotemporal compositional change of α-diversity between local communities, provides an opportunity to better capture the response of biodiversity to intensive land-use, urbanization, logging and environmental changes (Socolar et al., 2016). Loss of β-diversity can negatively affect ecosystem functioning (i.e., productivity, nutrient cycling and decomposition) and stability (Cardinale et al., 2012). In addition, β-diversity studies have been used to quantify the homogenization of biotic communities, which is the process by which biological communities become increasingly similar over time or space (Olden et al., 2006). For example, human-induced decrease in environmental heterogeneity can result in an increase of similarity between local communities in space and time, causing community homogenization (Mori et al., 2018).

Not only human but also natural disturbances and salvage logging can affect β-diversity by either changing community composition or community homogenization. For example, different natural disturbances can reduce β-diversity between disturbed sites, resulting in an increased homogenization of communities (Arnan et al., 2020; Burkle et al., 2015). Windthrows can also change community compositions but do not lead to community homogenization of pollinators and saproxylic beetles (Wermelinger et al., 2017). In contrast, post-fire salvage logging changes bees and flowers community composition and homogenizes bees communities (Heil et al., 2018). Even though, post-windthrow salvage logging does not seem to affect community homogenization of arthropods (Wermelinger et al., 2017), our knowledge is rather incomplete and rigorous statistical tests are missing. As salvage logging is considered an additional anthropogenic disturbance (Lindenmayer et al., 2006), it is also important to understand whether its effects on β-diversity superimpose on the effects of natural disturbances. It is also important to understand whether and how natural and anthropogenic disturbance change the β-diversity communities found in undisturbed forests. However, studies about salvage logging and β-diversity that compare naturally disturbed and salvage logged-sites with undisturbed forests are scarce (but see Wermelinger et al., 2017).

I.2.4 Hill numbers and species relative abundance

One of ecology's universal laws states that species in biological communities are not equally abundant and communities consist of many rare and few common species (McGill et al., 2007). Species responses to environmental change may strongly depend on ecological specialization and their respective population sizes (Clavel et al., 2011). For example, natural disturbances like hurricanes can negatively affect the diversity of rare species (Vandecar et al., 2011). On the other side, human-induced disturbances can also lead to a reduction of specialized species and/or increase of generalist species (Gossner et al., 2016). Also, intense disturbances can strongly affect functional diversity, changing the composition of different functional groups (Fukami et al., 2005). These findings suggest that rare species, rare evolutionary lineages, and rare functional groups might be more susceptible to disturbances than common species.

Another important question is, how the loss of rare species and/or the gain of common species contributes to changes in β-diversity along environmental or disturbance gradients (reviewed in Mori et al. (2018)). As β-diversity reflects how species' dominance and identity shift in communities over space and time (Socolar et al., 2016), using a statistical framework like Hill numbers that incorporates species relative abundances in quantifying β-diversity (Gotelli et al., 2013) can help to understand how accumulating natural and anthropogenic disturbances may affect the process of community homogenization.

I.3 Effects on water quality

Forested watersheds play a crucial role in sustaining freshwater supplies and providing clean drinking water (Bonan, 2008). Stand-replacing disturbances in forested watersheds can affect water quality. For example, high tree mortality is followed by deadwood decomposition that increases the organic content in soils, which can result in leaching of nutrients, such as nitrogen and carbon into streams (Mikkelson et al., 2013). Increased nitrogen concentrations in drinking water can cause methemoglobinemia, a serious metabolic disorder for bottle-fed infants (Fossen Johnson, 2019). An increase of dissolved organic carbon (DOC) in drinking water is also problematic, because DOC can reduce water pH, bind and transport heavy metals and increase organic contaminants in water (Kaplan et al., 2000). Salvage logging can also affect water quality by creating additional soil compaction, increased water discharge, erosion, turbidity and an export of solutes and nutrients to streamwater (Malvar et al., 2017; Silins et al., 2014; Smith et al., 2012). However, as the effects on water quality are rather well known for post-fire salvage logging, little is known about the effects after windthrow and bark beetles (Leverkus, Gustafsson, et al., 2020).

Since natural disturbances and salvage logging are increasing, as discussed above, this might affect the probability of leaching of nutrients in water reservoirs used for drinking water. Therefore, it is important to understand how these disturbances would affect nitrate and DOC concentration in streamwater. Also, mid- to long-term studies about the effects of salvage logging on water quality are scarce (Leverkus, Gustafsson, et al., 2020).

I.4 Objectives of the thesis

The main objective of the thesis is to expand our understanding about the mid- to long-term effects of natural disturbances and salvage logging on different facets of biodiversity and additionally on water quality as a an important ecosystem service.

Specific objectives of the thesis are:

- ✓ Investigating how the combination of natural disturbances, such as windthrow and bark beetle infestations, and salvage logging affect water quality and α-diversity of different taxonomic groups (chapter II).
- ✓ Exploring the taxonomic, functional and phylogenetic dissimilarity among bird communities that are affected by natural disturbances, such as wildfire and windthrow, and salvage logging (chapter III).
- ✓ Investigating how windthrow and salvage logging change β-diversity of different taxonomic groups (chapter IV).
- ✓ Exploring how changes in species relative abundance affect taxonomic, functional and phylogenetic diversity and β-diversity in general, and testing whether rare species in a community are more strongly impacted by natural disturbances and salvage logging than common and dominant species (chapter III and IV).

I.5 Study areas and data sets

I.5.1 Study areas

In chapter III, I re-analyzed raw data from published studies that covered nine different areas in North America, Europe and Asia (Fig. III-1). Basis for the analyses in chapter II and IV was a study conducted in the Bavarian Forest National Park, south-eastern Germany (49°070 N, 13°310 E). The park is dominated by subalpine forests of Norway spruce (*Picea abies* (L.) H. Karst). Annual precipitation ranges from 1300 to 1800 mm and the annual mean air temperature is 3.0–4.0°C in the valleys and summit areas and 8°C in medium slopes areas (Bässler et al., 2010, updated in 2019). In January 2007, the windstorm referred to as ‘Kyrill’ struck the Bavarian Forest National Park, with intensities ranging from single tree felling to the downing of complete stands (Thorn et al., 2017). From the total amount of ~1000 ha wind-felled forests, park managers left four larger patches (totaling ~200 ha) unlogged. On the remaining ~800 ha, wind-felled trees were removed by salvage logging, which continued until August 2007. During logging operations, branches were cut off the trunk and left on the ground, and the main trunk was removed. On unlogged and logged patches, park authorities initiated a long-term monitoring program by establishing plots for biodiversity surveys (Fig. IV-1).

I.5.2 Data sets

In chapter III, I re-analyzed raw bird assemblage data from nine published studies (Table III-1). The studies were chosen from a database compiled by two reviews about the effect of salvage logging on biodiversity and ecosystem services (Leverkus, Benayas, et al., 2018; Thorn et al., 2018). The study selection followed a systematic review protocol to warrant high standards in data selection (Leverkus et al., 2015). In addition to the use of the raw data from the published studies (see Table III-1 and III.9 Data sources section), the time series for the present work was extended by expanding three of the published studies (Hutto et al., 2002; Thorn, Bässler, et al., 2016; Zmihorski, 2010) by additional surveys, adhering in each case to the original sampling design. I conducted a bird survey in the Bavarian Forest National Park in 2018 (see below), which extended the existing time series data of Thorn et al. (2016a) to 11 years after the natural disturbance. This time series data was then used for the analysis in chapters II and IV.

The biodiversity data for chapters II and IV were collected during the long-term monitoring program of the Bavarian Forest National Park that was initiated after the windstorm ‘Kyrill’ in 2007. The main aim of the monitoring program was to collect representative biodiversity data in disturbed, unlogged plots and disturbed, salvage-logged plots. The study plots were placed in the northern part of the national park (Fig. II-1, Fig. IV-1). For the period 2007–2014, the monitoring program covered eight taxonomic groups: saproxylic beetles, wood-inhabiting fungi, epigeic and epixylic lichens, epigeic and epixylic bryophytes, vascular plants and birds. In 2018, the monitoring program was extended by adding plots in undisturbed, intact forests. In 2018, all eight taxonomic groups covered until 2014 were surveyed again, plus additionally five new taxonomic groups were surveyed: epigeic spiders, ants, bees and wasps, non-saproxylic beetles, epigeic beetles.

During the years a maximum of 76 plots were surveyed: 32 logged plots, 20 unlogged plots, and 24 plots of intact forest not affected by the windthrow (Fig. II-1, Fig. IV-1). However, the number of plots differed slightly among the studied taxa and during the different years (for details, see Table IV-S1).

For chapter II, the entire data set covering 12 taxonomic groups in logged, unlogged and intact forest plots for all studied years between 2007 and 2018 was used in the analysis of species numbers. For the analysis of β-diversity in chapter IV, the data set comprised of data for all 13 taxonomic groups studied during 2018 on logged, unlogged and intact forest plots. The data set covered only 2018 because this was the only year when intact forest plots were surveyed.

I.5.3 Water monitoring

To analyze the effects of natural disturbances and salvage logging on streamwater water quality (chapter II), I used water chemistry data that was collected during a long-term monitoring program of the Bavarian Forest National Park. The chemical composition of the streamwater was determined within five watersheds (Fig. II-1), which were dominated by Norway spruce. The water monitoring for the watersheds started in 1985 for two watersheds, for one watershed in 1987, and for another two data collection started in 2000. Forests in all watersheds were not affected by stand-replacing natural disturbances before the beginning of the water monitoring. During the years different parts of the watersheds were affected by windthrows and bark beetle infestations, and part of the affected forest patches were either salvage-logged or left unlogged.

Chapter II: Water quality and α-diversity

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II.1 Abstract

Forests host most terrestrial biodiversity and provide important ecosystem services, including the provision of drinking water. Increasing frequency and intensity of natural disturbances and subsequent salvage logging may impact both biodiversity and drinking-water quality. However, empirical evidence and particularly that generated from long-term studies, is scarce. Using data obtained from the monitoring of streamwater between 1985–2018 and mid-term data on biodiversity of twelve species groups, we quantified the combined effects of natural disturbances and salvage logging. We used generalized additive models to test the effects of cumulative disturbed and salvage-logged areas on annual maximum nitrate and dissolved organic carbon (DOC) concentrations. We used generalized mixed-effects models to test the effect of management (disturbed unlogged, disturbed logged and undisturbed, intact forest) on species numbers of studied taxa. We found that forest disturbances led to a temporal increase of nitrate concentration in streamwater, yet remaining far below 50 mg L^{-1}, the limits recommended by the World Health Organization. Salvage logging did not exert any additional impact on nitrate and DOC concentrations, and hence did not affect streamwater quality. Natural disturbances increased the biodiversity in eight out of twelve species groups. Salvage logging additionally increased the biodiversity of five species groups related to open habitats, but decreased the biodiversity of three deadwood-dependent species groups. We conclude that neither natural forest disturbances in watersheds nor associated salvage logging have a harmful effect on

the quality of the streamwater, which is used for drinking water. Setting aside naturally disturbed areas would promote the conservation of deadwood-dependent species.

II.2 Introduction

The world's forests store vast amounts of carbon, provide important ecosystem services to humans and host a considerable part of the planet's terrestrial biodiversity (FAO et al., 2020). In recent decades, natural disturbances, such as wildfire, windstorms and insect outbreaks, have severely disrupted large areas of the world's forests at an unprecedented rate (Seidl, Schelhaas, et al., 2014). Natural disturbances can cause a decreased interception, increased surface runoff, soil moisture, erosion and leaching of soil nutrients into streams (Mikkelson et al., 2013; Moore et al., 2012). In terms of biodiversity, however, species richness, habitat quality and other diversity indices mostly increase in disturbance-affected forests (Beudert et al., 2015; Thom et al., 2016).

In Europe, windstorms are the most important disturbance agents, responsible for 53% of the total damage in forests between 1950 and 2000 (Schelhaas et al., 2003). Forest stands affected by windstorms often enable the rapid growth of bark beetle populations (Seidl, Schelhaas, et al., 2014), which accounted for 8% of the total damage in European forests between 1950 and 2000 (Schelhaas et al., 2003). Although the interactions between windthrow and bark beetle outbreaks are well understood (Kulakowski et al., 2017), those between windthrow and post-disturbance logging have been rarely investigated, especially through the use of long time series (Leverkus, Lindenmayer, et al., 2018).

Despite its detrimental effects on biodiversity (Thorn et al., 2018), salvage logging is the most common post-disturbance management practice (Müller et al., 2019). As the extent, frequency and intensity of natural disturbances increases worldwide due to climate change (Seidl et al., 2017), the area of salvage logging in both managed and protected forests has increased as well (Leverkus, Lindenmayer, et al., 2018; Müller et al., 2019). The main justifications for salvage logging are the recovery of economic value from disturbance-affected timber as well as recovering the provision of ecosystem services (Müller et al., 2019). The effects of salvage logging on biodiversity have been examined, but the majority of studies compared salvage-logged with unlogged (no intervention) plots rather than using intact forest stands as the control treatment (Fontaine et al., 2009; Zmihorski, 2010). In addition, while the response of biodiversity to salvage logging during the first 5 years after the disturbance has been investigated (Thorn et al., 2018), studies of longer time series are scarce (Thorn, Chao, Georgiev, et al., 2020).

Natural disturbances and subsequent salvage logging promote the mineralization of organic matter and nitrification in soils under humid and seasonal warm climate conditions (Vitousek et al., 1979), leading to higher availabilities of dissolved nitrogen (as NH_4^+ and NO_3^-) and dissolved organic carbon (DOC) in soils. The reduction of canopy cover that follows a natural disturbance not only drastically reduces nutrient uptake by plants, it also decreases evapotranspiration losses, leading to higher soil water flows (Andréassian, 2004) and increased leaching of nitrates and DOC into streams (Laudon et al., 2009; Strohmeier et al., 2013). When nitrate concentrations in drinking water exceed 50 mg L^{-1}, water becomes a major source of total nitrate intake for human consumers, which in bottle-fed infants may result in fatal disorders (World Health Organization, 2016). DOC is also an important water quality parameter, it has the potential to reduce soil water pH, transport metals and organic contaminants as well as nutrients into streams (Ågren et al., 2010; Kaplan et al., 2000), and may induce the formation of cancerogenic disinfection by-products in drinking water (Mikkelson et al., 2013). In fact, increasing DOC concentrations in many streams and lakes in the boreal forests in Europe and North America have recently been measured (Garmo et al., 2014; Monteith et al., 2007).

The amount and type of soil disturbance can cause changes in water regimes and water quality in mountainous watersheds. For instance, severe wildfires reduce natural soil water repellency by scorching the surface soil layer (Martins et al., 2020). Furthermore, post-fire salvage logging additionally compacts burned soils (Malvar et al., 2017), resulting in a greater water discharge, increased erosion, turbidity, export of solutes and nutrients to streamwater (Silins et al., 2014; Smith et al., 2012). However, the impact of salvage logging on water quality after windthrow and bark beetles are poorly understood as majority of the studies concern post-fire salvage logging (Leverkus, Gustafsson, et al., 2020). In addition there is a lack of mid- to long-term studies about salvage logging effects on water quality (Leverkus, Gustafsson, et al., 2020).

In general, biodiversity response to forest disturbances and salvage logging is largely determined by changes in insolation and deadwood amounts (Thorn et al., 2018). Compared to intact forests, windthrow increases deadwood amount and insolation, whereas salvage logging reduces deadwood amount and may increase additionally insolation and surface temperatures (Fontaine et al., 2010). As result, the species richness of deadwood-dependent (i.e. saproxylic) taxa, such as saproxylic beetles, wood-inhabiting fungi, epixylic lichens and bryophytes, can increase following disturbances (Beudert et al., 2015), but may decrease following salvage logging (Thorn et al., 2018). On the other side, species groups that do not rely on deadwood but benefit from increased insolation, such as vascular plants, epigeic spiders, lichens and bryophytes, have higher species richness in disturbed forests and salvage-logged forest as well (Thorn et al., 2018).

We analyzed data from long-term streamwater monitoring conducted in five watersheds and associated mid-term biodiversity data of 12 species groups with largely differing relation to deadwood and insolation. Our aim was to examine the effects of natural disturbances and salvage logging on: i) maximum concentrations of nitrate and dissolved organic carbon (DOC) in the runoff that provides drinking water and ii) species diversity within 12 species groups.

We expected that nitrate and DOC concentrations would increase within several years after the natural disturbances. A reduction in nitrate and DOC concentrations in salvage-logged watersheds would mean that deadwood extraction would effectively reduce leaching, affecting water quality positively. An increase in nitrates and DOC in salvage-logged watersheds would mean that possibly due to soil disturbance salvage logging operations would affect water quality negatively. In terms of biodiversity effects, we expected that natural disturbance would increase species numbers of deadwood-dependent groups and groups related to open habitats. Salvage logging would decrease species numbers in deadwood-dependent groups but would additionally facilitate open-land groups.

II.3 Materials and methods

II.3.1 Study area

The study was conducted in the Bavarian Forest National Park (Fig. II-1), south-eastern Germany (49°070 N, 13°310 E). The park is dominated by subalpine forests of Norway spruce (*Picea abies* (L.) H. Karst). Annual precipitation ranges from 1300 to 1800 mm and the annual mean air temperature is 3.0–4.0°C in the valleys and summit areas and 8°C in medium slopes areas (Bässler et al., 2010, updated in 2019).

In January 2007, the windstorm referred to as ‘Kyrill’ struck Central Europe. The storm hit the entire park, including the studied catchment areas, with intensities ranging from single tree felling to the downing of complete stands (Thorn et al., 2017). From the 1000 ha of mature Norway spruce forests felled by the winds, park managers left four larger patches, totaling ~200 ha, unlogged to establish study plots for biodiversity surveys. On the remaining 800 ha, storm-felled trees were removed by post-disturbance logging, which continued until August 2007. During logging operations, branches were cut off the trunk and left on the ground, and the main trunk was removed. Logging reduced the deadwood amount in all logged areas from ~300 m³/ha to ~50 m³/ha (Thorn et al., 2014, 2015).

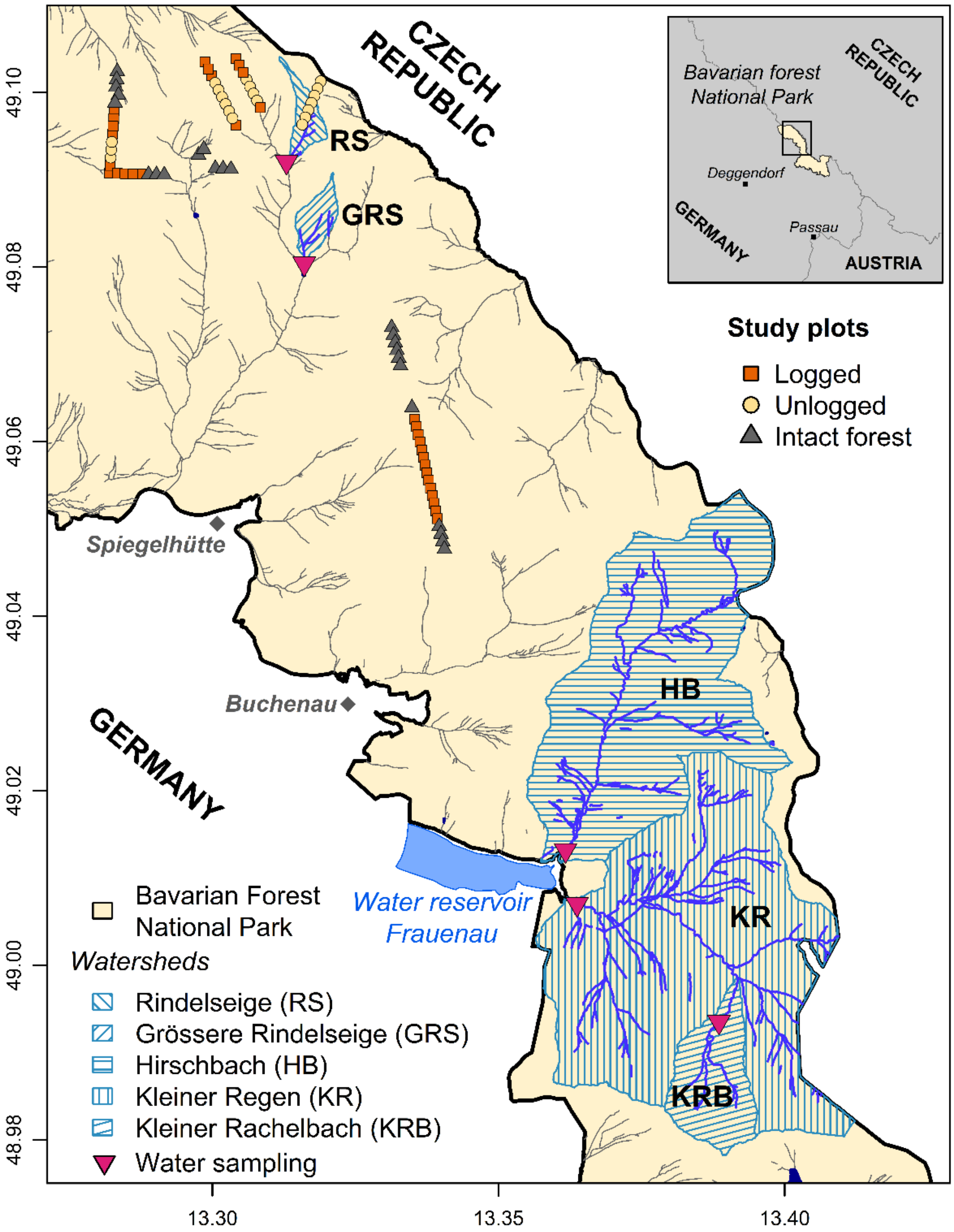

Figure II-1: Watersheds and sampling plots in the Bavarian Forest National Park. The contour lines represent the elevation above sea level, and the blue lines the streams of the studied watersheds.

II.3.2 Forest cover monitoring

The amount of disturbed and salvage-logged area within the watersheds was estimated by identifying bark beetle infested and wind-thrown spruce trees on annually recorded color-infrared images (Lausch et al., 2011). Afterwards, the percentage of disturbed and salvage-logged area for every single watershed was plotted as accumulated totally disturbed area over time (Fig. II-2, Fig. II-3).

II.3.3 Water monitoring

Data for water chemistry were collected during a long-term monitoring program of the Bavarian Forest National Park. The chemical composition of the streamwater was determined within five watersheds: Rindelseige, Grössere Rindelseige, Hirschbach, Kleiner Regen and Kleiner Rachelbach (Fig. II-1, Table II-1), all of which were dominated by Norway spruce. The water monitoring for the watersheds Hirschbach and Kleiner Regen started in 1985, for Kleiner Rachelbach in 1987, and for Rindelseige and Grössere Rindelseige in 2000. Forests in all watersheds were not affected by stand-replacing natural disturbances before the beginning of the water monitoring. Forests in the national park are important for water provision in the region, for instance, the Frauenau drinking water reservoir (Fig. II-1) is almost entirely fed by the Hirschbach and Kleiner Regen watersheds. Mean modeled annual precipitation (mm) and runoff (mm) from 1981 to 2015 for the five watersheds was as follows: Ringelseige (1875 mm / 1340 mm), Grössere Rindelseige (1552 mm / 991 mm), Hirschbach (1635 mm / 1079 mm), Kleiner Regen (1637 mm / 1106 mm), Kleiner Rachelbach (1741 mm / 1292 mm) (Klöcking, 2019). Water samples were taken manually in 1- or 2-week intervals at or near the catchment outlets (for exact locations see Fig. II-1). Sampling as well as sample storage and preparation strictly followed international instructions (ICP-Forests, 2010; ICP-Integrated-Monitoring, 2010). Chemical components were analyzed by certified laboratories of state institutes using ion chromatography for nitrates (DIN EN ISO 10304-1, 1992) and elemental analysis after UV oxidation for dissolved organic carbon (DIN EN 1484-H3:1997-8, 1997). The hydrochemical data of Hirschbach, Kleiner Regen and Kleiner Rachelbach were provided from the Bavarian Environment Agency (LFU) those of Rindelseige and Grössere Rindelseige by the Bavarian Forest National Park.

II.3.4 Biodiversity sampling

Biodiversity sampling was part of a long-term monitoring program of the Bavarian Forest National Park that was initiated after the windstorm “Kyrill” in 2007. The main aim of the monitoring program was to collect representative biodiversity data in disturbed unlogged areas and disturbed salvage-logged areas. In 2018, the monitoring program was extended by adding plots in intact forests. The study plots were placed in the northern part of the national park and covered representatively logged, unlogged and intact forests in the study area (Fig. II-1). The number of plots differed slightly among the studied taxa (for details, see Table II-S1). Twelve species groups were sampled in the study: epigeic spiders, ants, bees and wasps, saproxylic beetles (i.e. beetles dependent on or associated with living as well as dead trees; Alexander 2008), non-saproxylic beetles, wood-inhabiting fungi, epigeic bryophytes, epigeic lichens, epixylic bryophytes, epixylic lichens, vascular plants and birds. Bees and wasps, saproxylic beetles and non-saproxylic beetles were trapped using flight-interception traps placed at the center of every study plots (Thorn et al., 2014). Epigeic spiders and ants were trapped using two pitfall traps per plot. The two pitfall traps were placed within a 10 m buffer around the center of each plot, at least 10 m apart from each other. Bryophytes and lichens were mapped on deadwood objects (i.e. epixylic) and on the ground (i.e. epigeic) separately. Wood-inhabiting fungi, epixylic bryophytes and epixylic lichens were sampled on five deadwood objects that were randomly selected in a 20 m radius around the center of each plot (Thorn, Bässler, et al., 2016). The deadwood objects we selected in 2007 for logged and unlogged plots, and in 2018 for intact forest plots. Over the years, some objects on logged and unlogged plots decomposed, hence their sampling number varied over years for these two treatments. In 2018, a total of 138 deadwood objects on logged and unlogged and 100 object on forest plots were surveyed. Vascular plants, epigeic mosses and lichens were sampled on circular plots (relevees) of 200 m^2 around each plot’s center. Birds were surveyed five times during the breeding season by applying fixed-radius (50 m radius) point-counts with 5-min count intervals per plot (Thorn, Werner, et al., 2016). All bird counts were conducted during the morning hours in good weather conditions. The biodiversity data were aggregated to the plot level for each year for subsequent analyses. Due to financial and personnel constraints, not all treatment types were sampled in all years, except birds. However, 11 years after the disturbance all 12 species groups in all habitat types were examined in a comprehensive assessment.

II.3.5 Data analysis

The analyses were carried out in R 4.0.1 (R Development Core Team, 2020). Generalized additive models (GAM) were applied to test the effects of annual and cumulative disturbed and salvage-logged areas on annual maximum nitrate and DOC concentrations for the five watersheds (Wood, 2006). The explanatory variables were the percentages of disturbed and salvage-logged area, as the linear terms, and the proportional annual increase in disturbed area (%), as well as, when applicable, the proportional annual increase in salvage-logged area (%) as smooth terms. Because the peaks in maximum nitrate and DOC concentrations were time-delayed, an additional explanatory time-lagged variable was included. For the percentages of disturbed and salvage-logged areas, 10 time lags were created, i.e. each of the original values was lagged between 1 and 10 years. The best fitting time lag was determined by re-running the model, replacing every one of the ten time-lagged variables while keeping the remaining variables constant. The final model was selected based on the highest adjusted r^2, with the corresponding time-lagged variables (Table II-S2). Time-lagged variables were not used for watersheds Rindelseige (RS) and Grössere Rindelseige (GRS) as the models were unstable. Following an analysis of the temporal correlation structure of the model residuals, using the autocorrelation function (*acf*) and the partial autocorrelation function (*pacf*; package '*stats*'), we included a first-order autocorrelation as the correlation structure in the GAMs (Fig. II-S2).

Changes in the number of species were modeled using linear mixed-effects models with a Poisson error distribution (function *glmer* from *lme4* package; Bates et al., 2015). Separate models were fitted for all species groups (Table III-S3), with the number of species as the response variable and the treatment (disturbed, logged, forest) as the explanatory variable. For each group with more than one study year, the effects of disturbances and salvage logging were tested separately for each year by including an interaction term between study year and treatment as an additional explanatory variable. To account for possible spatial autocorrelations, a spatial autocovariate term of the geographical coordinates of the plots was included as a fixed effect in all models (function *autocov_dist*; package *spdep*; Bivand et al., 2013). Differences across the study plots and repetitive sampling within these plots were accounted for using plot identity as a random effect. This was followed by pairwise-comparisons based on general linear hypothesis tests with simultaneous adjustment of the p-values (function *glht*, package *multcomp*; Hothorn et al., 2008), to test for differences between single treatments during every studied year. The general linear hypothesis tests are used to control the overall type I error rate when multiple null hypothesizes are tested simultaneously (Hothorn et al., 2008). Only significant differences ($p < 0.05$) are shown, indicated as superscript letters above the boxplots (Fig. II-3).

A possible mass effect influencing the number of saproxylic beetles was taken into account by standardizing the number of sampled plots—as a proxy for deadwood resources—by extrapolating the species number to 40 plots within all treatments, using rarefaction and extrapolation curves (*iNEXT* package; Hsieh et al., 2016).

II.4 Results

II.4.1 Effects on water quality

The studied watersheds (Fig. II-1) were affected to different degrees by natural disturbances, with the overall largest proportion of cumulative forest dieback in the Rindelseige watershed (98.7%), followed by the Kleiner Rachelbach (89.5%), Grössere Rindelseige (28.9%), Hirschbach (26%) and Kleiner Regen (25%) watersheds.

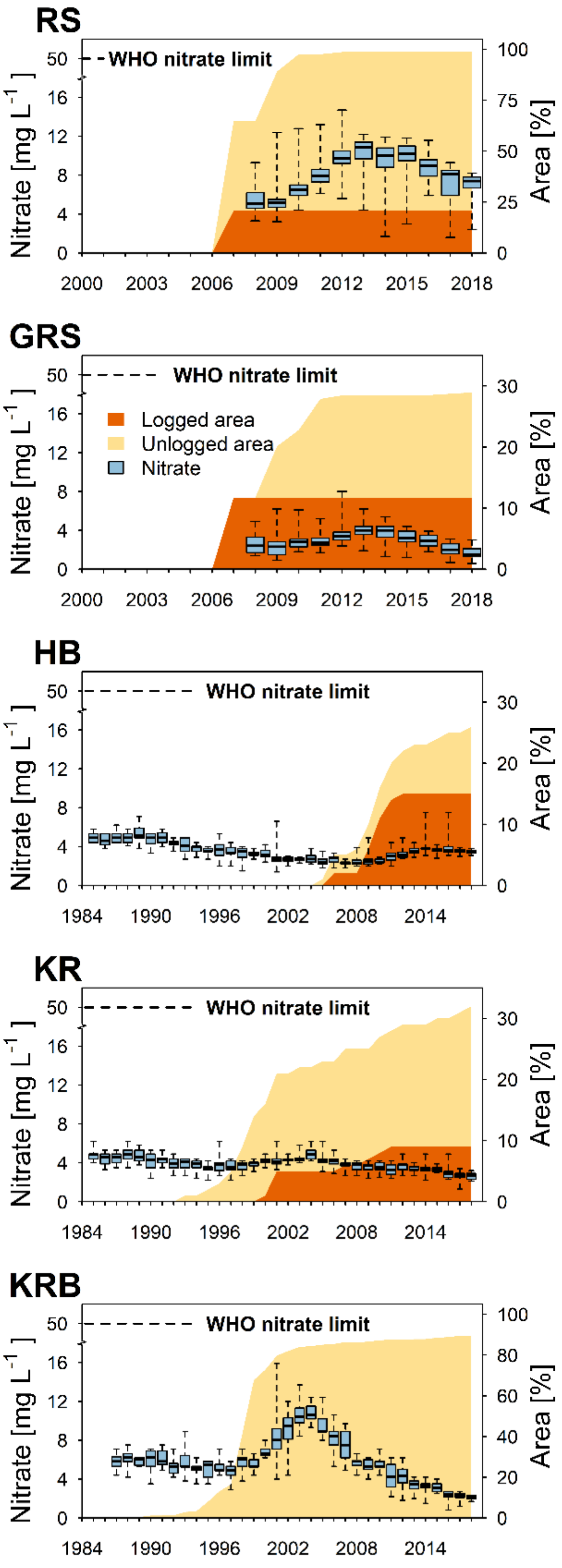

Figure II-2: Concentrations of nitrate in the streamwater of five watersheds in the Bavarian Forest National Park: RS: Rindelseige, GRS: Grössere Rindelseige, HB: Hirschbach, KR: Kleiner Regen, KRB: Kleiner Rachelbach. Note the differences in the y-axis.

Annual maximum nitrate concentrations increased steadily following a disturbance, with a time-delayed peak (Fig. II-2). The modeling results showed that the maximum nitrate concentration increased markedly in the most severely affected watersheds but the increase was significantly related only to the percent increase of annually disturbed area in the Kleiner Rachelbach watershed and to the 6-year-lagged percent of disturbed area for the Kleiner Regen and Kleiner Rachelbach watersheds (Table II-S2). Nonetheless, in none of the watersheds did the maximum nitrate concentration exceed 16 mg L^{-1}, a value far below the World Health Organization limit of 50 mg L^{-1}. According to this result, general water quality did not suffer from a natural disturbance (windthrow and bark beetles) or salvage logging. The percent of salvage-logged area was not significantly associated with the maximum nitrate concentration for any of the studied watersheds (Table II-S2).

Unlike nitrates, there were no distinct peaks in the maximum DOC concentration, irrespective of the forested area affected by natural disturbance and subsequent salvage logging (Fig. II-3). The modeling results showed that the annual maximum DOC concentrations were significantly associated only with the increase in the annual disturbed area for the Hirschbach watershed as well as the percent disturbed area and the 1-year-lagged percent disturbed area of the Kleiner Rachelbach watershed (Table II-S2). There was no significant association between the salvage-logged area and the maximum concentrations of DOC in streamwater.

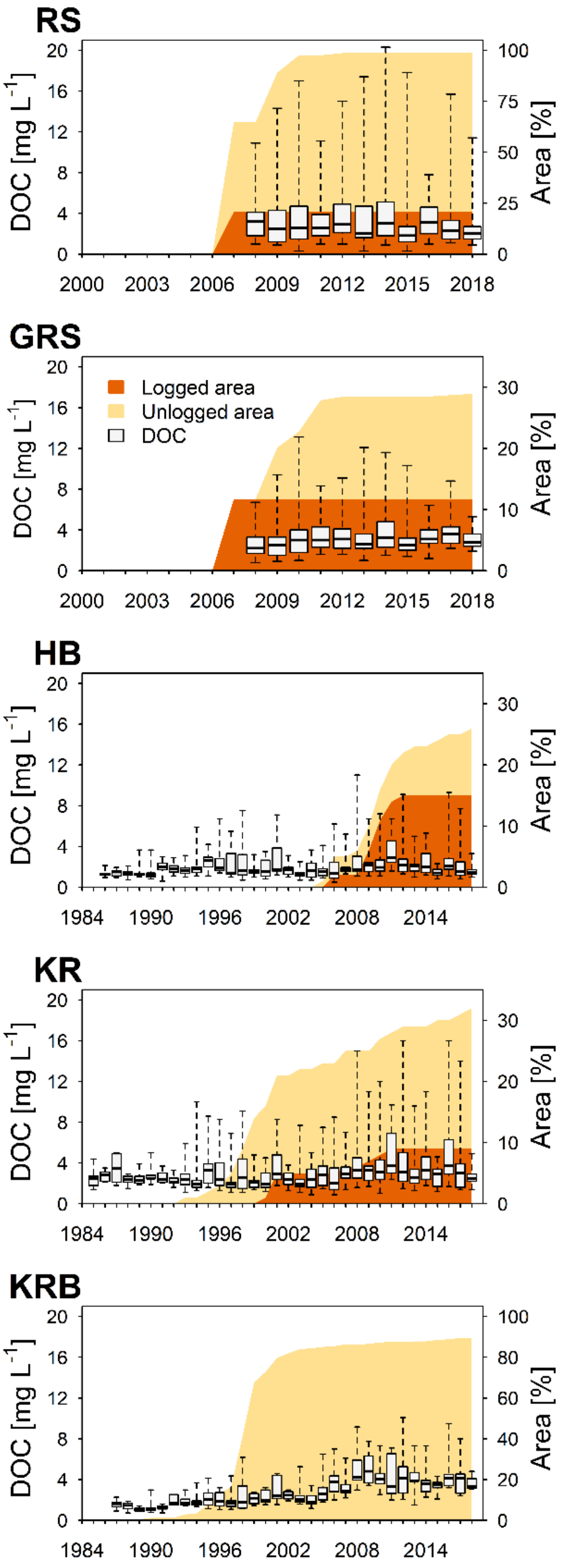

Figure II-3: Concentrations of dissolved organic carbon (DOC) in the streamwater of five watersheds in the Bavarian Forest National Park: RS: Rindelseige, GRS: Grössere Rindelseige, HB: Hirschbach, KR: Kleiner Regen, KRB: Kleiner Rachelbach. Note the differences in the y-axis.

II.4.2 Effects on biodiversity

The 12 species groups sampled in this study represented 1341 species. Non-saproxylic beetles (n = 332) were the most species-rich group followed by saproxylic beetles (n = 259), wood-inhabiting fungi (n = 155), and epigeic spiders (n = 138) (Fig. II-4). Epigeic lichens (n = 15), and ants (n = 13) had the fewest number of species.

Forest dieback caused by natural disturbances significantly affected most species groups, such that the species numbers of plants, bees and wasps, ants, epigeic spiders and non-saproxylic beetles were higher on unlogged than on forested plots (Fig. II-4I–L, Table II-S3). However, the removal of deadwood resources during salvage logging significantly altered the effects of a preceding natural disturbance, as with few exceptions consistently higher numbers of species from saproxylic groups, i.e. epixylic lichens, wood-inhabiting fungi and saproxylic beetles, were detected on unlogged than on salvage-logged plots (Fig. III-4). Conversely, the number of species in the non-saproxylic groups, i.e. epigeic bryophytes, epigeic lichens, ants, spiders and non-saproxylic beetles, was higher on logged plots (Fig. II-4). Nonetheless, these differences for the non-saproxylic groups were only significant 11 years after the disturbance. Bird species numbers varied the most between treatments and years, with undisturbed forested plots consistently hosting the largest number of species throughout the 11-year study period (Fig. II-4H).

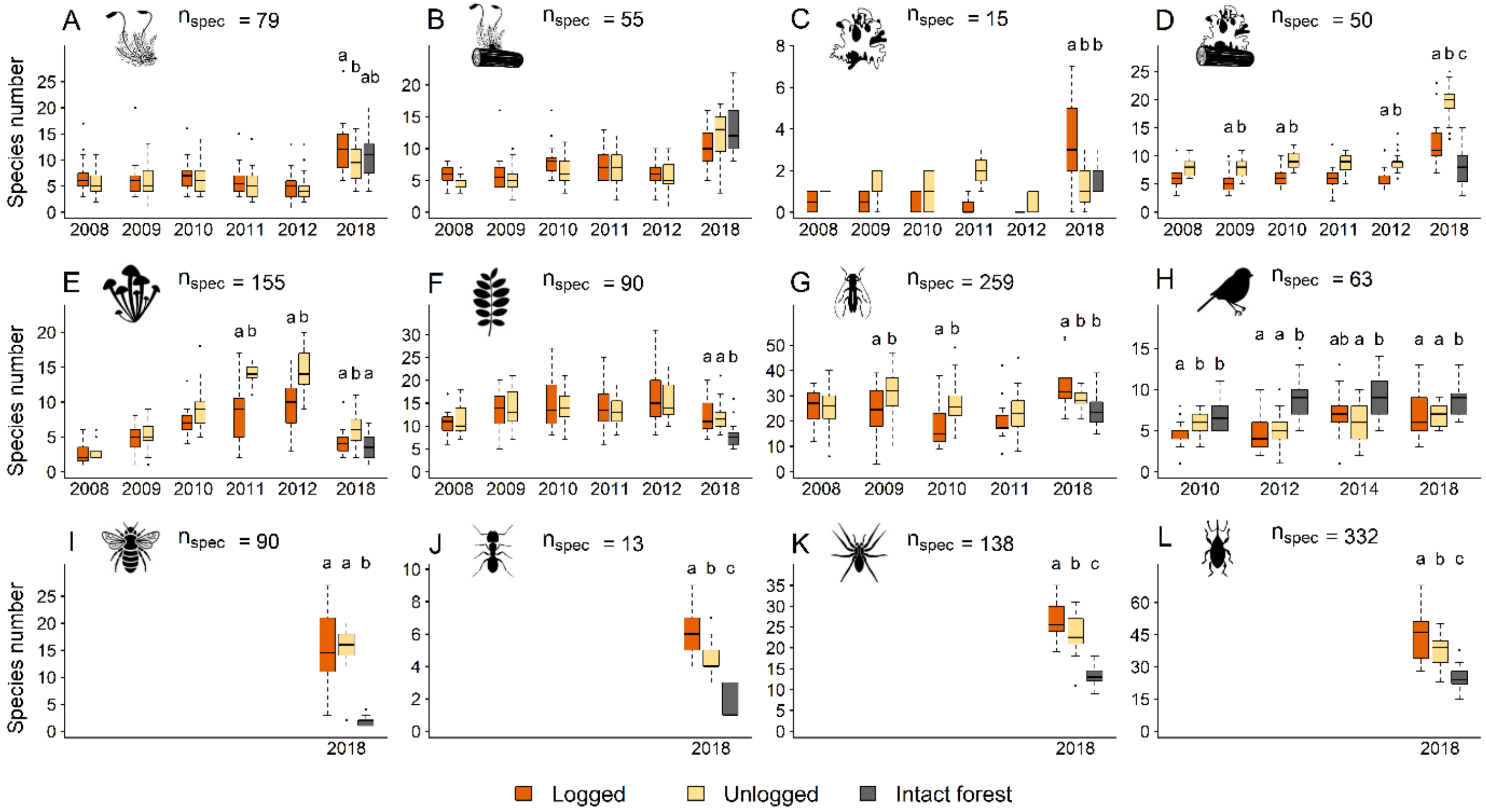

Figure II-4: Species numbers of 12 taxa sampled in salvage-logged disturbed forest (logged), unlogged disturbed forest (unlogged) and undisturbed mature spruce forest (intact forest) plots in the Bavarian Forest National Park. A) Epigeic bryophytes, B) epixylic bryophytes, C) epigeic lichens, D) epixylic lichens, E) fungi, F) plants, G) saproxylic beetles, H) birds, I) bees and wasps, J) ants, K) epigeic spiders and L) non-saproxylic beetles. n_{spec} indicates the total number of sampled species. Superscripts above the boxplots denote significant differences ($p < 0.05$) in species

II.5 Discussion

Using long-term water monitoring data, we demonstrated that an increase in naturally disturbed areas was followed by a temporal increase in the annual maximum concentrations of nitrates (Fig. II-2) and, to a lesser extent, of DOC in streamwater (Fig. II-3). Salvage logging did not significantly change the maximum concentrations of nitrates or DOC (Table II-S2) but it did lead to contrasting responses of biodiversity. We registered an increase of species numbers in non-saproxylic, open-land species groups but also a considerable decline in species numbers of saproxylic species groups (Fig. II-4).

The maximum nitrate concentrations did not exceed the WHO drinking water limit of 50 mg L^{-1} in any of the studied watersheds. These results support the findings from studies in bark-beetle-killed (Beudert et al., 2015), burned (Smith et al., 2012) and wind-felled (Hartmann et al., 2016) forests, in which maximum nitrate concentrations did not exceed the WHO health limit. Thus, the main natural-disturbance agents across the Northern Hemisphere seem to have few overall effects on water quality (Leverkus, Gustafsson, et al., 2020).

The peak in maximum nitrate concentrations 3–5 years after the disturbance event (Fig. II-2) is in agreement with the findings of Hartmann et al. (2016), who registered peaks of dissolved inorganic nitrogen (mainly nitrate) ~4 years after a windthrow. In our study, in the Kleiner Regen and Kleiner Rachelbach watersheds the peak in nitrates was best explained by the 6-year lag in the percent disturbed area (Table II-S2), which is an independent lagged variable. While not reaching significant levels, the maximum nitrate concentrations for the Rindelseige watershed also had a time lag of 6 years (Fig. II-2). These results indicate that the maximum concentration of nitrates in those watersheds depended on the percent of annually disturbed area 6 years earlier. A return to the pre-disturbance level of nitrates occurred ~10 years after the disturbance event (Fig. II-2), which is similar to the findings from other watersheds in the Bavarian Forest National Park (Beudert et al., 2015; Huber, 2005). A number of processes are responsible for the time-delayed increase of nitrates after the disturbance and the return to pre-disturbance nitrate levels. During the first years after a disturbance the sparse understory vegetation is unable to take up and assimilate the surplus of nitrogen in the soil, resulting in the lateral transport of nitrates through near-surface soil layers into streams as well as vertical transport towards aquifers. This is the reason for the time-delayed increase of nitrates. The nitrate concentrations return to their pre-disturbance level when regeneration of the disturbed stand progresses, the nitrogen cycle is again controlled by vegetation uptake, which reduces the leaching losses of nitrates such that their concentrations in groundwater and streams fall to and below pre-disturbance levels (Likens et al., 1978).

Compared to undisturbed forests, an increase of DOC concentrations in surface water has been reported after clear-cut logging in European boreal forests (Laudon et al., 2009) as well as after wildfire and consecutive salvage logging in Canadian boreal forests (Emelko et al., 2011). By contrast, we found no evidence of a significant relationship between the annual salvage-logged area and the maximum annual DOC concentration in streamwater (Table II-S2), indicating that salvage logging did not affect DOC. These diverging results can be explained by the generally deeper (≥ 1 m) soils in our study region than in boreal regions. Deeper soils allow the more effective sorption and stabilization of DOC in mineral soil (Kalbitz et al., 2000; Kalks et al., 2020) such that less DOC leaches into aquifers and streams.

However, maximum DOC concentrations increased significantly with the annual increase of disturbed area in the Hirschbach watershed as well as in response to increases in the percent disturbed area and the 1-year lag in disturbed area in the Kleiner Rachelbach watershed (Table II-S2). While the results for these two watersheds were significant, they deviated only slightly from the general DOC trend, which was similar in all studied watersheds irrespective of the percentage of disturbed area in each one (Fig. II-3). Thus, the cumulative area of naturally disturbed forest seems to have little effect on the maximum DOC concentration.

DOC is composed of thousands of compounds, some of which can form harmful disinfection-by-products during chlorination, such as during water treatment (Mikkelson et al., 2013). Although there are no thresholds for DOC concentrations, water treatment generally becomes more expensive when the concentration surpass 4 mg L^{-1} (Emelko et al., 2011). In the watersheds in our study, DOC concentrations in streamwater were lower (2.39 mg L^{-1} on average) than in the streams of the Grosse Ohe catchment, located south of our study area, especially when the percentage of wet soils in their catchments was high (Beudert et al., 2012).

The inclusion of intact forest stands in our study revealed significant differences in species numbers between forested plots and logged as well as unlogged plots for most studied taxa (Fig. II-4, Table II-S3). With the exception of birds, which had higher species numbers in forest areas, the species numbers for all taxa were significantly lower on forested plots (Fig. II-4). These results highlight the importance of early successional forests as species-rich habitats (Swanson et al., 2011).

During most of the studied years, the species numbers of wood-inhabiting fungi, epixylic lichens and saproxylic beetles were significantly higher on unlogged than on logged plots (Fig. III-4). For these deadwood-dependent species groups, the amount of deadwood is a major driver of species richness (Bässler et al., 2016). However, 11 years after the disturbance the number of species of saproxylic beetles was higher on logged than on unlogged plots, in contrast to the early years after the disturbance (Fig. II-4G). In coniferous tree species, the abundance of saproxylic beetles typically decreases with increasing wood decay (Saint-Germain et al., 2007), as the reduced amount of nutrients in the later decay stages of deadwood attracts fewer saproxylic species over time (Kopf et al., 1998). In our study, the dieback after a windthrow caused a pulsed release of deadwood, resulting in a mass effect of coarse woody debris that most likely accounted for the higher species numbers on the unlogged plots. Support for this sequence of events is the fact that the differences between the three treatments became smaller when the species number was standardized by the number of investigated plots for the eleventh year after the disturbance (Fig. II-S1).

Species numbers of non-saproxylic groups (non-saproxylic beetles, bees and wasps, ants, epigeic spiders, plants, epigeic bryophytes and lichens) were significantly higher on logged plots 11 years after the disturbance (Fig. II-4), most likely due to the increase in resource availability. Windthrow and associated bark beetle infestations increase both the availability of light and the amount of deadwood (Wohlgemuth et al., 2019), while salvage logging typically reduces the amount of deadwood (Lindenmayer et al., 2008). Thus, on logged plots epigeic groups such as ants benefit from the higher insolation that increases the surface temperature, thereby facilitating species richness (Grevé et al., 2018; Kumischick et al., 2009). Similarly, the presence of epigeic bryophytes in the Bavarian Forest National Park is associated with open habitats, mainly due to their higher ground-surface temperatures (Raabe et al., 2010).

II.6 Conclusions

Our study showed that leaching of nitrates and DOC from disturbed watersheds does not pose a health risk to humans and conducting salvage logging does not change nitrate and DOC leaching into drinking water. However, the study also showed that natural disturbances in watersheds increase biodiversity of eight out of twelve species groups, mainly deadwood-dependent and species groups related to open habitats. Salvage logging additionally increased the biodiversity of five species groups related to open habitats, but decreased the biodiversity of three deadwood-dependent species groups. We conclude that neither natural forest disturbances in watersheds nor associated salvage logging have a harmful effect on the quality of the streamwater, which is used for drinking water. Setting aside naturally disturbed areas would promote the conservation of deadwood-dependent species.

II.7 Acknowledgements

We thank all taxonomic experts involved in the species identifications – Boris Büche, Oliver Dürhammer, Christoph Hahn, Heinrich Holzer, Jan Eckstein, Rainer Cezanne and Marion Eichler. We also thank the Bavarian Environment Agency (LFU) and the Bavarian Forest National Park (NP BW) for kindly providing the hydrochemical data for all five watersheds.

II.8 Supporting Information

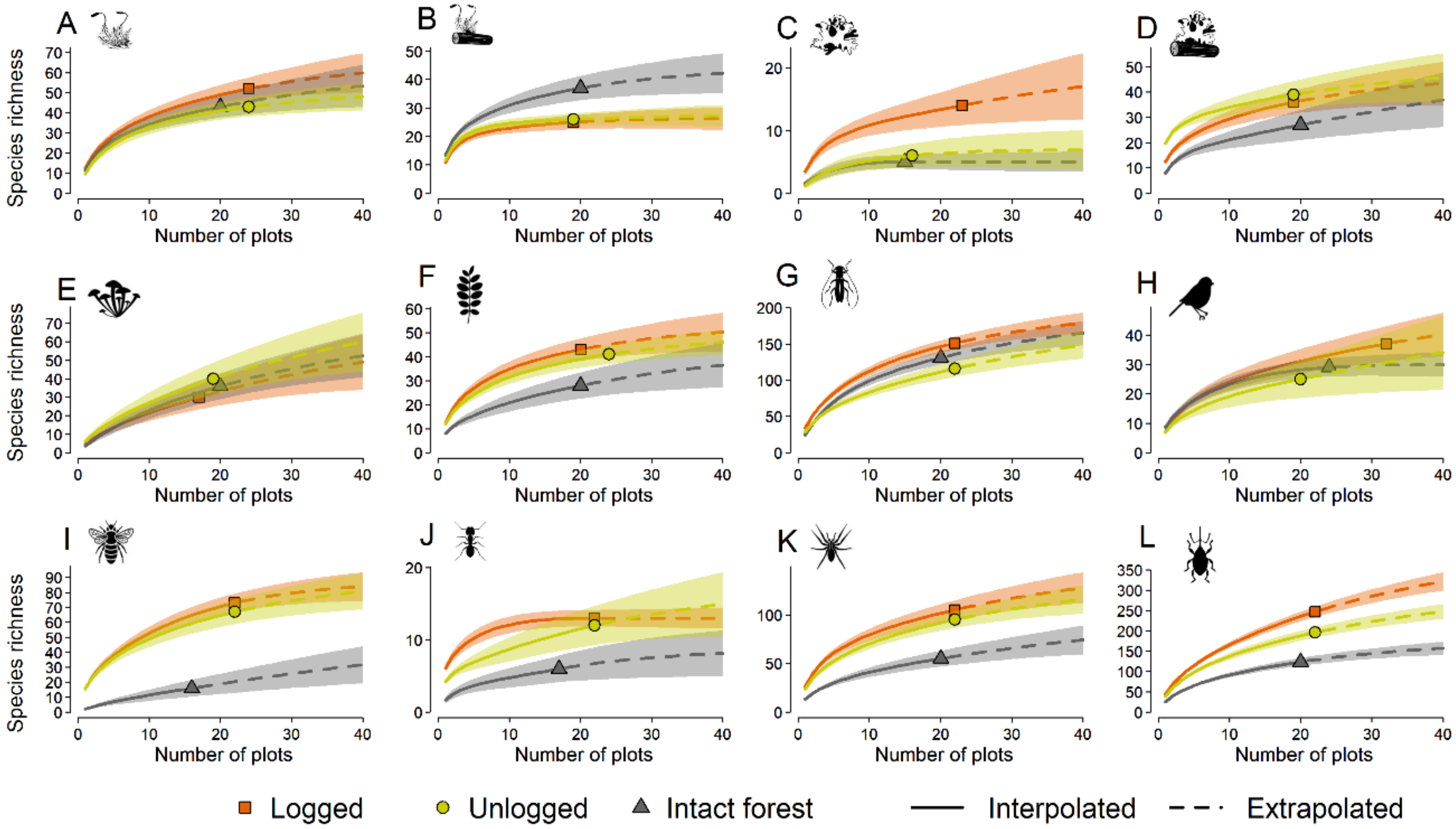

Figure II-S1: Estimated number of species for year 2018 in undisturbed mature spruce forests (intact forest), salvage-logged disturbed forest (logged) and unlogged disturbed forest (unlogged) plots. The estimation was performed with species accumulation curves (iNEXT R-package) by extrapolating the number of species to 40 studied plots.

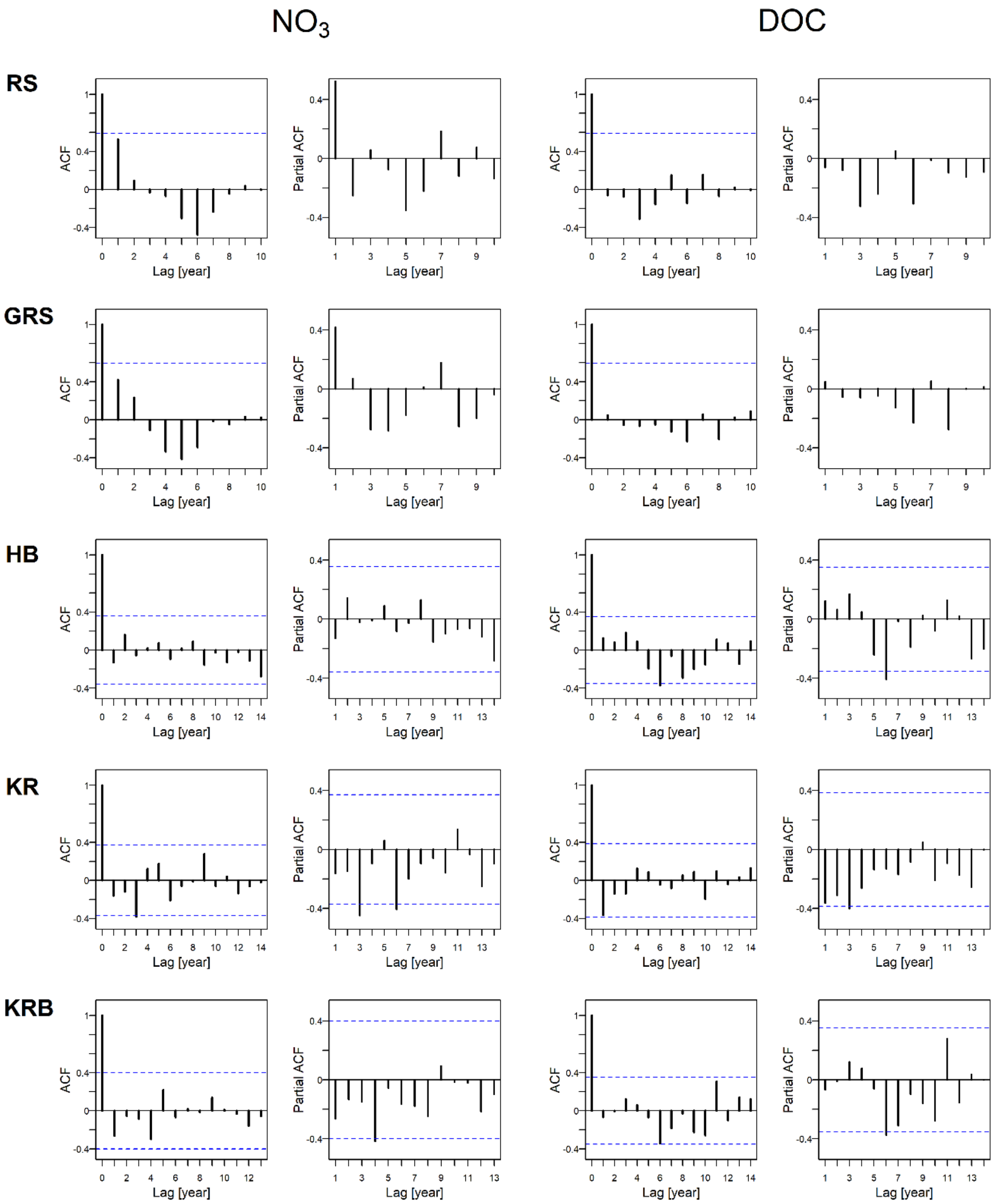

Figure II-S2: Estimates of the autocorrelation function (ACF) and partial autocorrelation function (partial ACF), for maximum concentrations of nitrate (NO3) and dissolved organic carbon (DOC). The blue lines depict the threshold beyond which the autocorrelation is significant. The abbreviation depict the names of the water catchments (for details Fig. II-1).

Table II-S1: Number of plots and survey details for twelve study species groups used to study the effects of natural disturbance and salvage logging on biodiversity, eleven years following a major windthrow.

Taxonomic group	**Plots**			**No. traps/deadwood objects**	**Sampling interval**	**Sampling frequency**	**Method**	**Reference**
	Logged	**Unlogged**	**Intact forest**					
Bees and wasps	22	22	20	64	May–Sept	Monthly trap emptying	Flight interception traps	(Achterberg et al., 2010)
Saproxylic beetles	22	22	20	64	May–Sept	Monthly trap emptying	Flight interception traps	(Achterberg et al., 2010)
Non-saproxylic beetles	22	22	20	64	May–Sept	Monthly trap emptying	Flight interception traps	(Achterberg et al., 2010)
Epigeic Spiders	22	22	20	128	May–Sept	Monthly trap emptying	Pitfall traps	(Abraham, 2013)
Ants	22	22	20	128	May–Sept	Monthly trap emptying	Pitfall traps	(Abraham, 2013)
Wood-inhabiting fungi	17	19	20	238 (4-5 deadwood per plot)	July–Sept	Single survey per season	Survey of deadwood objects	(Bässler et al., 2012)
Epigeic bryophytes	24	24	20	na	Sept–Oct	Single survey per season	Survey in 200 m^2 relevees	(Bässler et al., 2012)
Epigeic lichens	23	16	20	na	Sept–Oct	Single survey per season	Survey in 200 m^2 relevees	(Bässler et al., 2012)
Epixylic bryophytes	19	19	20	238 (4-5 deadwood per plot)	Sept–Oct	Single survey per season	Survey of deadwood objects	(Bässler et al., 2012)

Taxonomic group	**Plots**			**No. traps/deadwood objects**	**Sampling interval**	**Sampling frequency**	**Method**	**Reference**
	Logged	**Unlogged**	**Intact forest**					
Epixylic lichens	19	19	20	238 (4-5 deadwood per plot)	Sept–Oct	Single survey per season	Survey of deadwood objects	(Bässler et al., 2012)
Vascular plants	24	20	20	na	July–Sept	Single survey per season	Survey in 200 m^2 relevees	(Bässler et al., 2012)
Birds	32	24	20	na	March-June	5 counts per season	Point-count sampling	(Bibby et al., 2000)

Table II-S2: Results of generalized additive models with first order autocorrelation testing the effect of disturbed and salvaged-logged area on annual maximum concentrations of nitrates and dissolved organic carbon in streamwater in five water catchments in the Bavarian Forest National Park. Increase of annual disturbed area (%) represents the annual increase in the proportion of naturally disturbed area. Increase of annual logged area (%) represents the annual increase of salvage-logged area as a fraction of the yearly disturbed area. X-years lag of disturbed/logged area (%) represent the number of years with which the values of the respective variable were lagged.

Catchments	**Predictors**	**Annual maximum nitrate concentration**				**Annual maximum concentration of dissolved organic carbon (DOC)**			
		Estimate	CI	t-Value	p-Value	Estimate	CI	t-Value	p-Value
Rindelseige (RS)	Intercept	4.76	-7.81 – 17.33	0.874	0.408	2.9	-22.76 – 28.56	0.261	0.801
	Disturbed area (%)	7	-6.80 – 20.80	1.169	0.276	12.06	-16.11 – 40.23	0.987	0.352
	Logged area (%)	0.99	-1.62 – 3.60	0.874	0.408	0.6	-4.73 – 5.93	0.261	0.801
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	1	1	0.782	0.402	1	1	0.115	0.743
Grössere Rindelseige (GRS)	Intercept	5.59	-0.08 – 11.26	2.272	0.053	7.28	-2.44 – 16.99	1.728	0.122
	Disturbed area (%)	-2.1	-24.09 – 19.88	-0.221	0.831	7.06	-30.59 – 44.71	0.432	0.677
	Logged area (%)	0.66	-0.01 – 1.32	2.272	0.053	0.85	-0.29 – 1.99	1.728	0.122
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	1	1	0.668	0.437	1	1	0.146	0.712
Hirschbach (HB)	Intercept	**5.81**	**3.36 – 8.25**	**4.96**	**<0.001**	**-5.24**	**-10.25 – -0.24**	**-2.19**	**0.041**
	Disturbed area (%)	-52.22	-134.06 – 29.61	-1.33	0.2	62.6	-181.17 – 306.37	0.54	0.6
	Logged area (%)	58.21	-60.87 – 177.29	1.02	0.32	153.2	-230.44 – 536.84	0.83	0.41
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	4	4	0.23	0.91	**4.75**	**4.94**	**2.71**	**0.049**

Catchments	**Predictors**	**Annual maximum nitrate concentration**				**Annual maximum concentration of dissolved organic carbon (DOC)**			
		Estimate	CI	t-Value	p-Value	Estimate	CI	t-Value	p-Value
	Increase of annual logged area (%)	1	1	0.13	0.72	1	1	0.07	0.8
	3-years lag of disturbed area (%)	1	1	0.31	0.59	1	1	0.04	0.85
	4-years lag of logged area (%)	1.08	1.16	0.03	0.92				
	2-years lag of logged area (%)					1.88	1.98	3.6	0.057
Kleiner Regen (KR)	Intercept	**4.73**	**3.20 – 6.26**	**6.53**	**<0.001**	**11.9**	**5.90 – 17.91**	**4.2**	**0.001**
	Disturbed area (%)	-2.35	-13.22 – 8.53	-0.46	0.65	-19.72	-82.54 – 43.10	-0.67	0.51
	Logged area (%)	9.43	-27.97 – 46.83	0.53	0.6	17.96	-239.11 – 275.03	1.49	0.88
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	4.42	4.66	0.6	0.72	1	1	0.01	0.98
	Increase of annual logged area (%)	1	1	1.17	0.68	2.99	3	0.66	0.58
	6-years lag of disturbed area (%)	**2.21**	**2.53**	**7.95**	**0.004**				
	8-years lag of disturbed area (%)					2.03	2.52	2.86	0.2
	2-years lag of logged area (%)	1	1	1.81	0.2				
	8-years lag of logged area (%)					1	1	0.02	0.89
Kleiner Rachelbach (KRB)	Intercept	**6.54**	**3.62 – 9.46**	**5.06**	**<0.001**	**2.88**	**1.84 – 3.92**	**5.68**	**<0.001**
	Disturbed area (%)	1.27	-2.66 – 5.20	0.73	0.48	**3.93**	**2.26 – 5.60**	**4.83**	**<0.001**
	Smooth terms	*edf*	*Ref.df*	*F*	*p-Value*	*edf*	*Ref.df*	*F*	*p-Value*
	Increase of annual disturbed area (%)	**5.03**	**5.46**	**7.83**	**0.005**	1	1	0.32	0.57
	6-years lag of disturbed area (%)	**7.93**	**8.55**	**43.01**	**<0.001**				
	1-year lag of disturbed area (%)					**2.98**	**3.74**	**5.07**	**0.016**

Table II-S3: Results of generalized linear mixed models followed by multiple simultaneous comparisons of species numbers between undisturbed mature spruce forest (intact forest), salvage-logged disturbed forest (logged), and unlogged disturbed forest (unlogged), between one and eleven years following a major windstorm in the Bavarian Forest National Park.

Taxa	**Year after disturbance**	**Simultaneous comparisons**								
		salvaged–unsalvaged			**salvaged–forest**			**forest–unsalvaged**		
		Estimate	**t-Value**	**p-Value**	**Estimate**	**t-Value**	**p-Value**	**Estimate**	**t-Value**	**p-Value**
Bees and wasps	11	0.03 ± 0.108	0.274	0.784	**2.037 ± 0.208**	**9.793**	**>0.001**	**-2.008 ± 0.231**	**-8.686**	**>0.001**
Saproxylic beetles	1	0.08 ± 0.086	0.935	0.35						
	2	**-0.225 ± 0.085**	**-2.658**	**0.008**						
	3	**-0.336 ± 0.089**	**-3.766**	**>0.001**						
	4	-0.136 ± 0.09	-1.515	0.13						
	11	**0.267 ± 0.081**	**3.281**	**>0.001**	**0.329 ± 0.087**	**3.769**	**>0.001**	-0.062 ± 0.112	-0.552	0.581
Non-saproxylic beetles	11	**0.159 ± 0.062**	**2.566**	**0.01**	**0.567 ± 0.072**	**7.874**	**>0.001**	**-0.408 ± 0.085**	**-4.813**	**>0.001**
Epigeic Spiders	11	**0.143 ± 0.064**	**2.237**	**0.025**	**0.667 ± 0.082**	**8.115**	**>0.001**	**-0.524 ± 0.095**	**-5.539**	**>0.001**
Ants	11	**0.354 ± 0.137**	**2.582**	**0.01**	**1.318 ± 0.231**	**5.707**	**>0.001**	**-0.964 ± 0.248**	**-3.885**	**>0.001**
Wood-inhabiting fungi	1	-0.089 ± 0.248	-0.358	0.72						
	2	-0.195 ± 0.168	-1.158	0.247						
	3	-0.243 ± 0.143	-1.702	0.089						
	4	**-0.611 ± 0.132**	**-4.646**	**>0.001**						
	5	**-0.475 ± 0.127**	**-3.74**	**>0.001**						
	11	**-0.377 ± 0.169**	**-2.232**	**0.026**	0.271 ± 0.178	1.523	0.128	**-0.648 ± 0.191**	**-3.385**	**0.001**
Epigeic bryophytes	1	0.195 ± 0.144	1.353	0.176						
	2	0.04 ± 0.143	0.28	0.78						
	3	0.108 ± 0.14	0.771	0.441						

Taxa	**Year after disturbance**	**Simultaneous comparisons**								
		salvaged–unsalvaged			**salvaged–forest**			**forest–unsalvaged**		
		Estimate	**t-Value**	**p-Value**	**Estimate**	**t-Value**	**p-Value**	**Estimate**	**t-Value**	**p-Value**
	4	0.121 ± 0.148	0.82	0.412						
	5	0.033 ± 0.156	0.214	0.831						
	11	**0.241 ± 0.123**	**1.961**	**0.05**	0.008 ± 0.146	0.055	0.956	0.233 ± 0.143	1.624	0.104
Epigeic lichens	1	-0.734 ± 0.768	-0.956	0.339						
	2	-1.006 ± 1.119	-0.899	0.369						
	3	-0.538 ± 0.709	-0.759	0.448						
	4	-1.841 ± 1.065	-1.728	0.084						
	5	-27.452 ± 639668.107	0	1						
	11	**1.042 ± 0.259**	**4.025**	**>0.001**	**0.736 ± 0.276**	**2.662**	**0.008**	0.306 ± 0.326	0.939	0.348
Epixylic bryophytes	1	0.223 ± 0.166	1.343	0.179						
	2	0.176 ± 0.159	1.107	0.268						
	3	0.262 ± 0.147	1.786	0.074						
	4	0.097 ± 0.146	0.665	0.506						
	5	0.073 ± 0.157	0.464	0.643						
	11	-0.071 ± 0.126	-0.561	0.575	-0.191 ± 0.136	-1.4	0.161	0.12 ± 0.151	0.795	0.426
Epixylic lichens	1	-0.229 ± 0.142	-1.611	0.107						
	2	**-0.292 ± 0.144**	**-2.031**	**0.042**						
	3	**-0.327 ± 0.136**	**-2.407**	**0.016**						
	4	-0.238 ± 0.137	-1.741	0.082						
	5	**-0.351 ± 0.138**	**-2.542**	**0.011**						
	11	**-0.372 ± 0.105**	**-3.554**	**>0.001**	**0.407 ± 0.112**	**3.643**	**>0.001**	**-0.779 ± 0.131**	**-5.953**	**>0.001**

Taxa	Year after disturbance	Simultaneous comparisons								
		salvaged–unsalvaged			salvaged–forest			forest–unsalvaged		
		Estimate	t-Value	p-Value	Estimate	t-Value	p-Value	Estimate	t-Value	p-Value
Vascular plants	1	-0.008 ± 0.122	-0.065	0.948						
	2	0.037 ± 0.114	0.327	0.743						
	3	0.085 ± 0.112	0.757	0.449						
	4	0.037 ± 0.114	0.327	0.744						
	5	0.117 ± 0.11	1.065	0.287						
	11	0.073 ± 0.117	0.622	0.534	**0.382 ± 0.135**	**2.836**	**0.005**	**-0.31 ± 0.154**	**-2.011**	**0.044**
Birds	3	**-0.271 ± 0.135**	**-2.003**	**0.045**	**-0.364 ± 0.137**	**-2.655**	**0.008**	0.093 ± 0.128	0.727	0.467
	5	-0.079 ± 0.142	-0.561	0.575	**-0.646 ± 0.129**	**-4.986**	**>0.001**	**0.566 ± 0.126**	**4.482**	**>0.001**
	7	0.19 ± 0.121	1.568	0.117	-0.211 ± 0.113	-1.864	0.062	**0.401 ± 0.119**	**3.362**	**0.001**
	11	0.005 ± 0.108	0.047	0.962	**-0.21 ± 0.096**	**-2.178**	**0.029**	**0.215 ± 0.11**	**1.957**	**0.05**

Chapter III: Taxonomic, phylogenetic and functional diversity

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III.1 Abstract

Salvage logging following natural disturbances may alter the natural successional trajectories of biological communities by affecting the occurrences of species, functional groups and evolutionary lineages. However, few studies have examined whether dissimilarities between bird communities of salvaged and unsalvaged forests are more pronounced for rare species, functional groups, and evolutionary lineages than for their more common counterparts. Data on breeding bird assemblages were compiled from nine study areas in North America, Europe and Asia, covering a 17-year period following wildfire or windstorm disturbances and subsequent salvage logging. We tested whether dissimilarities based on non-shared species, functional groups and evolutionary lineages 1) decreased or increased over time and 2) the responses of rare, common and dominant species varied, by using a unified statistical framework based on Hill numbers and null models. We found dissimilarities between bird communities caused by salvage logging persisted over time for rare, common and dominant species, evolutionary lineages, and for rare functional groups. Dissimilarities of common and dominant functional groups increased fourteen years post-disturbance. Salvage logging led to significantly larger dissimilarities than expected by chance. Functional dissimilarities between salvaged and unsalvaged sites were lower compared to taxonomic and phylogenetic dissimilarities. In general, dissimilarities were highest for rare, followed by common and dominant species.

Synthesis and application: Salvage logging did not decrease dissimilarities of bird communities over time and taxonomic, functional, and phylogenetic dissimilarities persisted for over a decade. We recommend resource managers and decision makers to reserve portions of disturbed forest to enable unmanaged post-disturbance succession of

bird communities, particularly to conserve rare species found in unsalvaged disturbed forests.

III.2 Introduction

Naturally occurring disturbances (i.e. wildfires, windthrows and insect outbreaks) are an integral part of natural forest dynamics (Pickett et al., 1985). Disturbances can cause abrupt but long-lasting changes in forests by altering biophysical and environmental features, resource availability and ecosystem processes (Turner, 2010). Generally, forests are resilient to historic disturbance regimes and, given sufficient time, typically recover their pre-disturbance state (Gunderson, 2000). Within disturbance-affected communities, taxonomic diversity, i.e. the identity and richness of species, can gradually recover to a pre-disturbance state (Purvis et al., 2000). However, the extent, frequency and intensity of natural disturbances have increased globally and are expected to continue to increase in the near future (Seidl et al., 2017), with possible effects on community recovery. Functionally and phylogenetically diverse species communities may hence be necessary for the provision of ecosystem services and for maintaining ecosystem stability (Cadotte et al., 2012; Loreau et al., 2013). Also, evolutionarily distinct avian species are more likely to become extinct in anthropogenically disturbed forests (Frishkoff et al., 2014). While the loss of a single species could lead to a negligible reduction of taxonomic diversity, it might represent the loss of an entire evolutionary lineage or distinct functional group (Cadotte et al., 2010; Faith, 2015). The increasing amount of natural disturbances has also led to an increase of salvage logging, i.e. the removal of trees affected by disturbances, conducted in managed and protected forests worldwide (Leverkus, Lindenmayer, et al., 2018). It has hence become increasingly important to understand whether and how the recovery of forest biodiversity is altered by the combined effects of natural and anthropogenic disturbances.

Besides economic reasons, salvage logging is commonly justified on the basis that it contributes to forest structural restoration (reviewed in Müller et al., 2019). For instance, following a major drought and bark beetle outbreak in 2018/19, the Federal Ministry for Food and Agriculture of Germany called for a ‘clear-up followed by reforestation strategy’ to support the recovery of disturbed forest stands (Thorn et al., 2019). Because salvage logging immediately follows the natural disturbance (i.e. up to 3 years), it acts as an additional disturbance (Lindenmayer et al., 2018; Morissette et al., 2002), with possible negative effects on species richness, community recovery of various species groups (Thorn et al., 2018) and ecosystem services (Leverkus, Gustafsson, et al., 2020).

Naturally occurring disturbance and salvage logging can have long-lasting effects on forest structures (Donato et al., 2012) and forest bird communities (Thorn et al., 2018). For instance, the species richness and community composition of birds in boreal stands affected by wildfire or green-tree harvesting differed significantly during the first years after these disturbances, and differences may persist for more than 25 years (Hobson et al., 1999), or even 60–70 years (Zhao et al., 2013). However, in contrast to the many studies investigating community convergence in disturbed vs. green-tree-logged stands, there have been very few comparisons of disturbed and salvage-logged stands (reviewed in Thorn et al., 2018).

Anthropogenic disturbances, such as salvage logging, may result in the reduction of specialized species and/or increases of generalist species (Gossner et al., 2016) but also the potential extinction or extirpation of rare species (Leitão et al., 2016). Specialist bird species often respond negatively to landscape fragmentation and disturbance than generalists (Devictor et al., 2008). These changes in specialist and generalist species may also apply to rare functional groups or rare evolutionary lineages (Olden, 2006). However, empirical tests of whether the strength of community response to salvage logging varies depending on the relative contribution of dominant vs. rare (for abundance data) or common vs. rare (for occurrence data) species are lacking.

We compiled a large dataset of breeding bird assemblages sampled in salvaged and unsalvaged naturally disturbed forests in North America, Europe and Asia. We extended incidence-based dissimilarity metrics based on Hill numbers to include dissimilarities in species life-history traits and evolutionary ancestries (Chao et al., 2015, 2019) to test: 1) whether compositional differences between communities of salvage-logged and unsalvaged forests decrease or increase over time and 2) whether those trends differ for rare, common and dominant species. We expected that dissimilarities of non-shared species, functional groups and evolutionary lineages would decline with increasing time after the disturbance and that dissimilarities would be more pronounced for rare than for common and dominant species.

III.3 Materials and methods

III.3.1 Bird data

Data on breeding bird assemblages were compiled from nine study areas in North America (n = 3), Europe (n = 4) and Asia (n = 2) (Fig. III-1; Table III-1), by extending the databases compiled by two reviews on the effect of salvage logging on biodiversity and ecosystem services (Leverkus, Benayas, et al., 2018; Thorn et al., 2018). The data compilation followed a systematic review protocol to warrant high standards in data selection (Leverkus et al., 2015). We retained only datasets based on field-surveys and excluded modelling studies. Studies provided comparisons between completely salvage logged plots and completely unsalvaged control plots, i.e. more than 75% of the trees were affected by a natural disturbance and then completely salvage logged. Salvage logged plots were of similar size, surveyed with the same sampling effort as unsalvaged control plots (Thorn et al., 2018). In addition to the use of the raw data from published studies (see Table III-1 and III.9 *Data sources* section), the time series for the present work was extended by expanding three of the studies (Hutto et al., 2002; Thorn, Werner, et al., 2016; Zmihorski, 2010) by additional surveys, adhering in each case to the original sampling design.

Table III-1: Datasets used to investigate the effect of additional disturbance on the successional trajectories of bird communities.

No.	Country	Disturbance type	Number of years sampled	Study plots	Recorded species	Recorded individuals	Reference
1	USA	Wildfire	1	122	49	979	Fontaine et al. (2009)
2	USA	Wildfire	2	20	34	363	(Cahall and Hayes, 2009)
3	USA	Wildfire	17	4100	145	42,091	(Hutto and Young, 2002)
4	Spain	Wildfire	2	27	44	724	Castro et al. (2010)
5	Spain	Wildfire	3	58	55	971	Rost et al. (2012)
6	South Korea	Wildfire	1	38	24	105	Choi et al. (2007)
7	South Korea	Wildfire	2	48	42	689	Lee et al. (2011)
8	Germany	Windstorm	4	42	52	1,912	Thorn et al. (2016)
9	Poland	Windstorm	3	109	76	4,225	Zmihorski (2010)

The forests in the studied areas were affected first by wildfires or windstorms and then by salvage logging. Bird surveys were standardized to a specific plot area by using standardized fixed-radius point counts or fixed-width transect counts (Bibby et al., 2000). Bird surveys were conducted only on days without rain, with low wind speed and with clear or slightly overcast skies (Bibby et al., 2000). Our final dataset consisted of 668 salvage-logged plots (hereafter salvaged plots) and 3896 disturbed (control) plots without post-disturbance logging (hereafter unsalvaged plots) and covered studies with survey duration ranging from one to 17 consecutive sampling years after the natural disturbance (Table III-1).

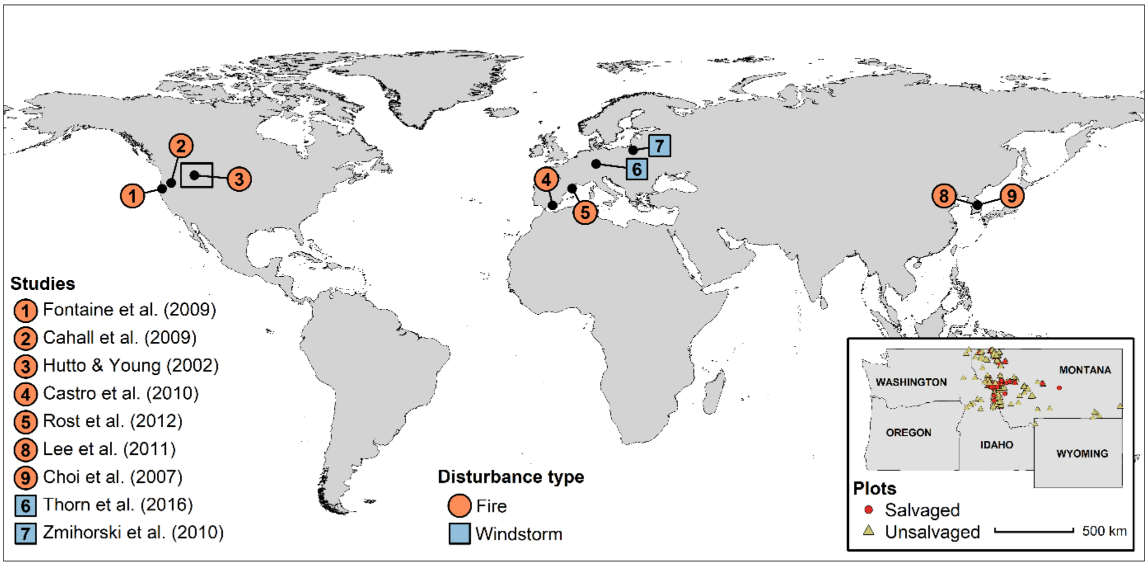

Figure III-1: General locations of the breeding birds surveyed to investigate the effects of salvage logging on bird communities. The inset map shows the extent of the sampling plots in the study of (Hutto et al., 2002).

III.3.2 Functional traits and phylogeny

We followed Calba et al. (2014) in the selection of 22 ecological traits reflecting avian resource and habitat use. Body mass and clutch size were continuous variables. Binary classifications were used for the main dietary component (plants, vertebrates, invertebrates), the main foraging method (pursuit, gleaning, pouncing, grazing, digging, scavenging, probing), the main foraging substrate (water, mud, ground, vegetation, air), the main foraging period (nocturnal) and the migratory status. Nest location was classified as one categorical variable (canopy, ground and hole). All traits were classified using the Cornell Laboratory of Ornithology (www.allaboutbirds.org; accessed at 16 Aug 2019) and the Handbook of Birds of the World (www.hbw.com; accessed at 16 Aug 2019). For a full list of the traits, see section III.8 Supporting information (Table III-S2). We did not account for possible regional differences in the species migratory status, since the majority of our studies were located on a similar latitude in the Northern Hemisphere (Fig. III-1).

Phylogenetic trees were constructed separately for the species pool in each study area by combining a relaxed molecular clock of trees containing well-supported avian clades and a fossil-calibrated backbone that included representatives from each clade (Hackett et al., 2008). For each study area, 4000 bootstrap replicate trees were mined from the online tool at www.birdtree.org, which first trims to a subset and then samples trees from a chosen pseudo-posterior distribution (Jetz et al., 2012). The bootstrap replicates were then condensed into a dated consensus tree using TreeAnnotator 1.8.2 (http://beast.community/treeannotator). All subsequent analyses were based on these consensus trees (phylogenetic trees may be found in Fig. III-S9–III-S17).

III.3.3 Quantifying dissimilarity

Dissimilarities between the bird communities of salvaged and unsalvaged plots were quantified by treating each sampled plot within each year as a sampling unit and then extracting the species incidence (presence/absence) to obtain a count of the occurrence (i.e. the incidence-based frequency) for each species. This procedure yielded a species-incidence-based frequency vector for salvaged and unsalvaged plots for each sampling year. The number of occurrences among multiple plots of each species was treated as a proxy of the abundance of that species. As shown by Colwell et al. (2012), such incidence-based occurrence records are able to account for spatial aggregation or clustering in the data. Moreover, incidence-based data support statistical approaches to diversity inferences that are just as powerful as the corresponding abundance-based approaches.

We used Hill numbers (i.e. the effective number of species; Hill 1973), based on species proportional incidence frequencies, to quantify and decompose diversity measures. Hill numbers differ by a parameter q that reflects their respective sensitivity to the relative frequency of a species. A main advantage of using Hill numbers is that they obey the replication principle (Chao, Gotelli, et al., 2014) and can thus be decomposed into independent components of alpha- and beta-diversity. The resulting beta-diversity is then transformed to obtain two general classes of dissimilarity measures, the Jaccard-type and the Sørensen-type (Chao, Chiu, et al., 2014). The Jaccard-type taxonomic dissimilarity index quantifies the effective proportion of non-shared species in salvaged and unsalvaged plots pooled, whereas the Sørensen-type index quantifies the effective average proportion of non-shared species in individual plots. These two types of dissimilarity measures include most of the commonly used dissimilarity indices.

We used Jaccard-type taxonomic dissimilarity measures (Chao, Chiu, et al., 2014) to quantify the temporal change in the dissimilarity of unsalvaged vs. salvaged plots. Fig. III-S1–III-S8 in section II.8 Supporting information show that the dissimilarity patterns for the Sørensen-type indices were generally consistent except for differences in magnitude. Setting $q = 0$ in the class of Jaccard-type measures yields the classic richness-based Jaccard index, which weights all species equally; setting $q = 1$ yields the Shannon-entropy-based Horn index, which weights all incidences equally, i.e. each species is weighted according to its incidence frequency; setting $q = 2$ yields the regional non-overlap index, which is very sensitive to dominant species but gives little weight to rare species (Chiu et al., 2014). Special cases of Sørensen-type measures are described in Chao et al. (2014). Because of the different weighting of the species, dissimilarity measure of $q = 0$ is disproportionally sensitive to rare species (i.e. infrequently detected species for incidence data), $q = 1$ to common species (i.e. frequently detected species for incidence data) and $q = 2$ to dominant species (i.e. highly frequently detected species for incidence data). Since our analysis is based on incidence frequencies, the classification of the species as rare (q=0), common (q=1), or dominant (q=2) was based on each local dataset and was not linked to their global abundance. Here, “rare” species refer to those species whose occurrence rates are relatively low in any plot.

Another advantage of using Hill numbers is that they enable a unified approach to generalizing the Jaccard- and Sørensen-type taxonomic dissimilarity measures to include species differences based on species evolutionary ancestries (i.e. phylogenetic trees; Chiu et al., 2014) or on species traits (Chao et al., 2019). In our study, the dendrogram-based approach of Chao et al. (2014) was applied to quantify phylogenetic dissimilarity between salvaged and unsalvaged plots. This approach takes all species inter-relations into account, incorporating species relations not only for species pairs but also for every possible combination of any subset of species. For functional dissimilarity, we followed the approach of Chao et al. (2019), which is based on species pairwise-distances. For species traits, these distances were obtained by Gower distances (Gower, 1971). All plausible threshold levels of functional distinctiveness between any two species were considered.

Interpretation of the Jaccard- and Sørensen-type phylogenetic and functional dissimilarity indices is similar to that of their taxonomic versions. For example, the Jaccard-type phylogenetic and functional dissimilarity measures quantified, respectively, the effective proportion of non-shared evolutionary lineages (for phylogenetic dissimilarity) and non-shared functional groups (for functional dissimilarity) in salvaged and unsalvaged plots.

III.3.4 Data analysis

All analyses were carried out in R 3.4.2 (R Development Core Team, 2017). Null models were used to compare the expected dissimilarities within unsalvaged plots (i.e. within the control treatment), to the dissimilarities between salvaged and unsalvaged plots (i.e. among treatments). Therefore, the dissimilarities of 999 randomly assembled communities ('simulated dissimilarities') recruited from unsalvaged plots were calculated and compared to the observed dissimilarities between salvaged and unsalvaged plots. Randomization was achieved using the independent swap algorithm (function *randomizeMatrix* from *picante* package; Kembel et al., 2010), in which species occurrences, frequencies, and species richness of the sample are held constant during the randomization process (Gotelli, 2000). Since, during randomization, every species can be randomly assigned to any unsalvaged plot, the results from the null model depicted the mean dissimilarities between any pair of unsalvaged plots occurring by chance.

For every study region and year after the disturbance, the mean dissimilarity value for every $q = \{0, 1, 2\}$ and every respective dissimilarity (taxonomic, functional and phylogenetic) was calculated. Changes in the mean dissimilarity in a given year between salvaged and unsalvaged plots over the course of succession were identified by fitting general additive mixed-effects models (Gaussian error distribution, function *gamm4* from *gamm4* package; (Wood et al., 2017). Separate models were fitted for all types of dissimilarities (taxonomic, functional and phylogenetic) and q numbers ($q = 0$, $q = 1$, $q = 2$), resulting in nine models (Table III-S1). To each of those models, we included the year after the disturbance as smoothed effect, fitted for observed and simulated communities separately, to test if successional trends in dissimilarities differ. Additionally, the null model (observed vs. simulated) was included as a fixed effect to test for differences between the observed and simulated dissimilarities. The study identity was specified as random effect to account for differences across the study sites and repetitive sampling within these sites.

The data provided by Hutto and Young (2002) covered 90% of all studied plots and 81% of all surveyed individuals in our final dataset (Table III-1). To assess the effect of this study on the overall results, we repeated our analysis by excluding the data of Hutto and Young (2002). However, our results and trends were mostly similar, with overall few exceptions (Fig. III-S5–III-S8). Also, we repeated the analysis by excluding the year 17, to evaluate the robustness of our results to this possible outlier. We found the same significant trends as in Fig. III-3 and III-S2, with the exception that the increasing trends in dissimilarity after year 14 either disappeared or became very small (Fig. III-S3 and III-S4).

III.4 Results

Our final dataset consisted of 299 species, represented by 51,813 individuals. The analysis showed that, observed and simulated bird communities differed significantly for non-shared species (taxonomic dissimilarity), evolutionary lineages (phylogenetic dissimilarity) and functional groups (functional dissimilarity) (Fig. III-2 and III-S1). The dissimilarities varied when the species were weighted according to their relative abundance. The largest dissimilarities occurred when all species, all evolutionary lineages and all functional groups were weighted equally (q = 0). The mean dissimilarity decreased when weighting of the species was shifted toward common (q = 1) and dominant (q = 2) species (Fig. III-2 and III-S1).

Over the course of 17 years, there was no significant increase or decrease in the observed community dissimilarity between salvaged and unsalvaged plots (Fig. III-3 and III-S2). Significant non-linear trends in the observed community dissimilarity were found only for: 1) common (q = 1) and dominant (q = 2) functional groups (Jaccard-type; Fig. III-3B); and 2) for dominant (q = 2) non-shared species (Sørensen-type; Fig. III-S2A), as well as for common (q = 1) and dominant (q = 2) functional groups (Sørensen-type; Fig. III-S2B). For all of these trends, the observed community dissimilarity followed a decrease between year 1 and year 12, followed by an increase after year 14 (Fig. III-3 and III-S2).

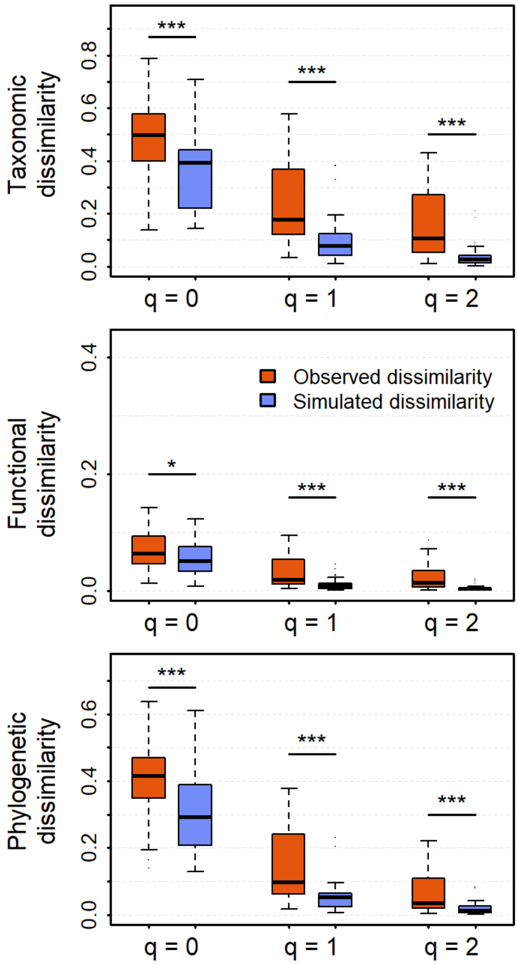

Figure III-2: Effective proportion (Jaccard-type) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). Boxplots show the dissimilarity for rare ($q = 0$), common ($q = 1$) and dominant ($q = 2$) species. Pairwise comparisons between observed and simulated dissimilarities are based on general additive mixed-effects models. Significance codes used: 0.001 – ‘***’, 0.05 – ‘*’.

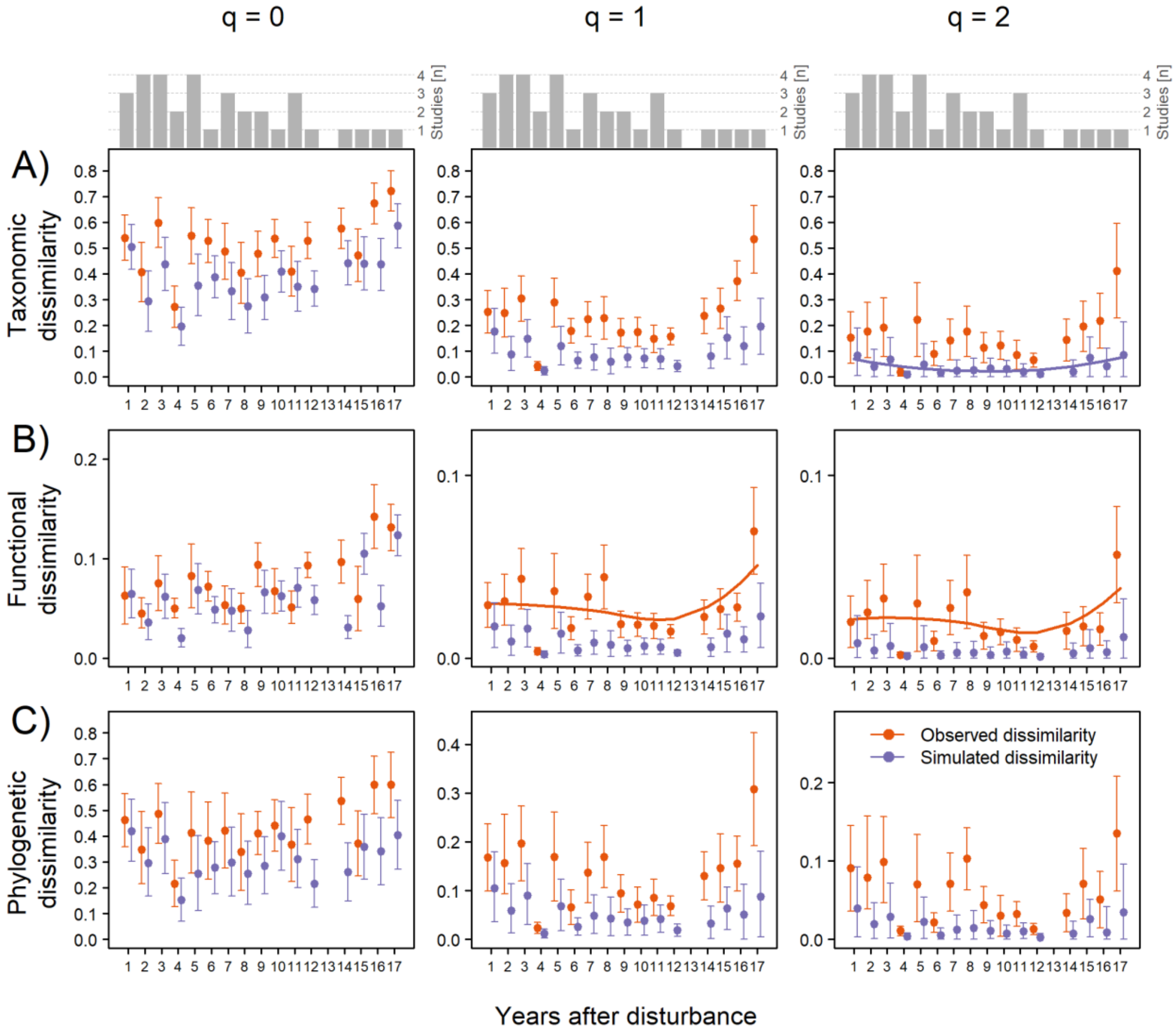

Figure III-3: Effective proportion (Jaccard-type; mean ± SD) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity), and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots over the studied years (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). (A) Taxonomic dissimilarity, (B) functional dissimilarity and (C) phylogenetic dissimilarity are shown. The columns represent the dissimilarities for rare ($q = 0$), common ($q = 1$) and dominant ($q = 2$) species. Significant ($p < 0.05$) trends are drawn as solid lines, showing the average dissimilarity, based on general additive mixed-effects models. Top-row bar plots indicate the number of studies used to calculate the mean dissimilarity within every single year. Note the different scales of the y-axes.

For simulated communities we found a significant trend of slight decrease followed by a slight increase only for dominant species (*q* = 2; taxonomic dissimilarity) (Fig. III-3A). However, the magnitude of changes in dissimilarities was very small (<5%).

The average dissimilarity of simulated communities was significantly lower ($p < 0.001$) than the observed dissimilarities (Table III-S1). Thus, the average dissimilarities between salvaged and unsalvaged plots were higher than the average dissimilarity that occurred within the unsalvaged plots by chance during the course of post-disturbance forest succession.

III.5 Discussion

Analyzing data from nine studies covering a post-disturbance period of 17 years, we demonstrated that dissimilarities persisted or showed a u-shaped pattern. These differences exceeded the changes expected by chance, i.e. without salvage logging, and were strongest for taxonomic, followed by phylogenetic and functional dissimilarity.

Comparisons of observed and simulated dissimilarities revealed that dissimilarities caused by salvage logging were higher than expected by chance (Table III-S1, Fig. III-2 and III-S1). Bird communities following naturally occurring disturbances are thought to undergo a gradual recovery, from disturbed-forest to mature-forest communities (Fontaine et al., 2009). Our results suggested that the differences between the bird communities of salvaged and unsalvaged sites persisted within the first 17 years after a natural disturbance. It may be that 17 years is much shorter than the time required by a disturbed forest to recover. For example, differences in species richness and community composition can be detected for >60–70 years in the bird communities of boreal forests affected by wildfire and clear cutting (Zhao et al., 2013). Hence, it may be that the differences in bird communities caused by salvage logging also last for several decades.

Our results showed that dissimilarities between bird communities of salvaged and unsalvaged plots were larger for rare (*q* = 0) than for common (*q* = 1) or dominant (*q* = 2) species (Fig. III-2 and III-S1). Moreover, the highest taxonomic, functional and phylogenetic dissimilarities for observed and simulated communities were those of rare species (Fig. III-3 and III-S2). These results confirm the findings of Magurran and Henderson (2003), who in temporal studies showed that species with a low relative abundance persist only few years in the assemblage. Rare species (*q* = 0) can be habitat specialists that rely on ephemeral resources and thus occur only on a limited number of plots for short periods. A main characteristic of salvage logging is that it diminishes the structural heterogeneity caused by the natural disturbance (Swanson et al., 2011). In our case, this reduction in heterogeneity resulted in the short occurrence of rare and/or specialist species on either salvaged or unsalvaged plots, increasing the dissimilarity for rare ($q = 0$) species. For example, the corn crake (*Crex crex*) likely benefited from grass-dominated post-storm salvaged stands and was found only on few salvaged plots in Poland. In contrast, the common redstart (*Phoenicurus phoenicurus*), which preferred remnant snags with cavities, was almost exclusively found on unsalvaged wind-disturbed plots in Germany. Conversely, common ($q = 1$) and dominant ($q = 2$) species consisted mainly of generalists that because of their broad habitat requirements and higher abundances were able to colonize salvaged and unsalvaged plots with similar success, resulting in a lower dissimilarity between the two site types.

Over the studied period, years 1–12 were characterized by a linear decrease in dissimilarity, followed after year 14 by an increase in dissimilarity for functional groups ($q = 1$ and $q = 2$; Fig. III-3). However, a more-detailed analysis of the included studies showed differences in the trends. For instance, after excluding Hutto and Young (2002) from the analysis no trend of increasing or decreasing dissimilarity was found, indicating that compositional differences persisted over the years (Fig. III-S7 and III-S8). This result might be attributed to the sensitivity of the bird communities to salvage logging among different regions. For example, post-fire salvage logging in the Rocky Mountains can have greater impact on bird communities than in the Mediterranean Basin because it affects a higher proportion of the bird community that occurs in burned forests (Rost et al., 2013). Also, in the Rocky Mountains salvage logging has detrimental effects to fire specialists, like the Black-backed Woodpecker (*Picoides arcticus*) or the American Three-toed Woodpecker (*Picoides tridactylus*), while in the Mediterranean Basin salvage logging affects only common forest birds species with wide distributions across European forests (Rost et al., 2013).

The dissimilarities between bird communities of salvaged and unsalvaged plots were lowest for functional groups (Fig. III-2 and III-S1). This suggests that bird communities of salvaged and unsalvaged plots share most functional groups but relatively smaller proportion of their species and evolutionary lineages. As salvage logging diminishes structural heterogeneity by reducing biological legacies (Swanson et al., 2011), communities of salvaged plots may have a high functional redundancy, in contrast to the low functional redundancy of the communities of unsalvaged plots. Although communities of salvaged plots may consist of functionally different groups (Azeria et al., 2011), we found a high similarity of rare, common and dominant functional groups in bird communities of salvaged and unsalvaged plots (Fig. III-2 and III-S1). Gerisch et al. (2012) showed that a high taxonomic diversity was not associated with a high functional diversity. We suggest that the observed pattern of functional, taxonomic and phylogenetic dissimilarity was driven by common or dominant species from genera like *Sylvia*, *Phylloscopus* and *Setophaga*, which while taxonomically and phylogenetically distant are functionally similar. These species are mainly generalists that colonize both unsalvaged and salvaged plots. It is thus likely that these genera drive not only the determined taxonomic and phylogenetic dissimilarity but also the high functional redundancy between communities. Indeed, larger difference can be detected when comparing salvaged and unsalvaged plots to undisturbed forests (Thorn, Werner, et al., 2016; Zmihorski, 2010), where phylogenetic and functionally distantly related genera occur with higher frequency.

Current knowledge about the effects of salvage logging has mainly come from local, short-term (1–5 years) studies (reviewed in Thorn et al., 2018). Our study, conducted at a wider spatial and temporal scale, provides a mid-term comparison of disturbed and salvage-logged forests but it is still relatively short compared to the time a forest needs to recover. Hence, future studies might address whether initial changes in successional trajectories persist to later stages and how these changes vary across changing and interacting disturbance regimes (Leverkus, Lindenmayer, et al., 2018; Seidl et al., 2017).

III.6 Conclusions

Our study provides evidence that salvage logging leads to short- to mid-term changes in bird community composition that are significantly greater than those occurring over the course of natural succession. Our results therefore demonstrate that salvage logging can lead to changes in community composition for non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity). In addition, because of the reduction of structural heterogeneity that salvage logging causes, it affects rare and/or specialized the most. The global increase in natural disturbances caused by climate change will trigger high levels of salvage logging worldwide. Hence, we argue that salvage logging may lead to widespread changes in the successional trajectories of forest bird community. Therefore, we recommend resource managers and decision makers to reserve portions of disturbed forest to enable unmanaged post-disturbance succession of bird communities, particularly to conserve rare species found in unsalvaged disturbed forests.

III.7 Acknowledgements

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III.8 Supporting Information

Table III-S1: Results of nine general additive mixed-effects models comparing the observed and null model dissimilarities (Jaccard-type) between the bird communities of salvaged and unsalvaged plots. The models were computed using the function *gamm4* from the R package *gamm4* (Wood et al., 2017).

Variables	**Dissimilarity**			
	Estimate	**Standard error**	**t-value**	**p-value**
Taxonomic diversity **q = 0 (rare species)**				
Intercept	**0.654**	**0.038**	**17.159**	**<0.001**
Model type = null model	**-0.101**	**0.021**	**-4.862**	**<0.001**
s(year) : observed model	0.010	0.016	0.610	0.542
s(year) : null model	0.003	0.042	0.074	0.941
q = 1 (common species)				
Intercept	**0.490**	**0.046**	**10.669**	**<0.001**
Model type = null model	**-0.162**	**0.023**	**-7.098**	**<0.001**
s(year) : observed model	0.111	0.064	1.740	0.0818
s(year) : null model	0.040	0.036	1.132	0.2575
q = 2 (dominant species)				
Intercept	**0.403**	**0.044**	**9.088**	**<0.001**
Model type = null model	**-0.180**	**0.021**	**-8.374**	**<0.001**
s(year) : observed model	0.138	0.071	1.939	0.0525
s(year) : null model	**0.034**	**0.017**	**1.993**	**0.0463**

Variables	**Dissimilarity**			
	Estimate	**Standard error**	**t-value**	**p-value**
Functional diversity **q = 0 (rare species)**				
Intercept	**0.244**	**0.014**	**16.842**	**<0.001**
Model type = null model	**-0.028**	**0.012**	**-2.240**	**0.0251**
s(year) : observed model	0.022	0.015	1.468	0.142
s(year) : null model	0.014	0.010	1.374	0.169
q = 1 (common species)				
Intercept	**0.178**	**0.020**	**8.868**	**<0.001**
Model type = null model	**-0.066**	**0.009**	**-6.920**	**<0.001**
s(year) : observed model	**0.023**	**0.011**	**2.111**	**0.035**
s(year) : null model	0.017	0.011	1.430	0.153
q = 2 (dominant species)				
Intercept	**0.727**	**0.040**	**17.99**	**<0.001**
Model type = null model	**-0.148**	**0.013**	**-11.21**	**<0.001**
s(year) : observed model	**0.016**	**0.008**	**2.103**	**0.035**
s(year) : null model	0.013	0.008	1.737	0.082
Phylogenetic diversity **q = 0 (rare species)**				
Intercept	**0.595**	**0.037**	**16.27**	**<0.001**
Model type = null model	**-0.090**	**0.019**	**-4.819**	**<0.001**
s(year) : observed model	0.018	0.016	1.146	0.252
s(year) : null model	-0.014	0.034	-0.413	0.680
q = 1 (common species)				
Intercept	**0.387**	**0.039**	**9.834**	**<0.001**
Model type = null model	**-0.128**	**0.018**	**-6.994**	**<0.001**
s(year) : observed model	0.080	0.047	1.690	0.090
s(year) : null model	0.026	0.014	1.789	0.074
q = 2 (dominant species)				
Intercept	**0.265**	**0.029**	**8.994**	**<0.001**
Model type = null model	**-0.110**	**0.015**	**-7.175**	**<0.001**
s(year) : observed model	0.044	0.033	1.321	0.186
s(year) : null model	0.021	0.014	1.497	0.134

Values in bold are significant ($p < 0.05$).

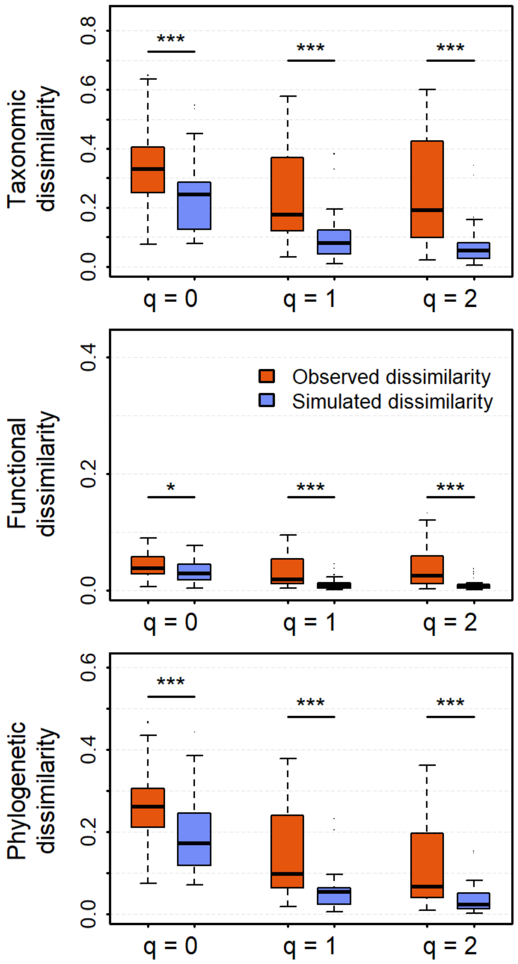

Figure III-S1: Effective proportion (Sørensen-type) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). Boxplots show the dissimilarity for rare (q = 0), common (q = 1) and dominant (q = 2) species. Pairwise comparisons between observed and simulated dissimilarities are based on general additive mixed-effects models. Significance codes used: 0.001 – ‘***’, 0.05 – ‘*’.

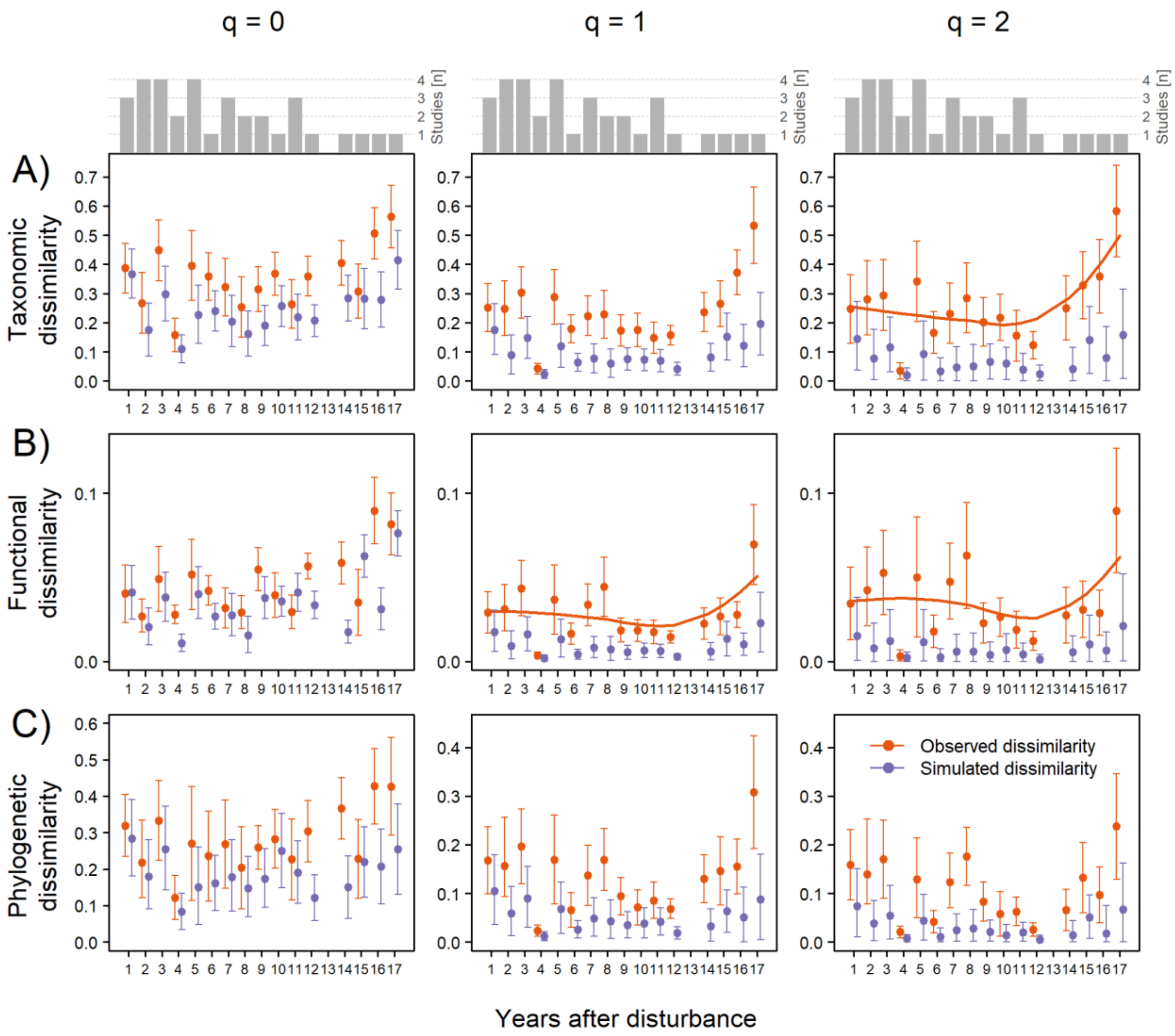

Figure III-S2: Effective proportion (Sørensen-type; mean ± SD) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity), and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots over the studied years (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). (A) Taxonomic dissimilarity, (B) functional dissimilarity and (C) phylogenetic dissimilarity are shown. The columns represent the dissimilarities for rare ($q = 0$), common ($q = 1$) and dominant ($q = 2$) species. Significant ($p < 0.05$) trends are drawn as solid lines, showing the average dissimilarity, based on general additive mixed-effects models. Top-row bar plots indicate the number of studies used to calculate the mean dissimilarity within every single year. Note the different scales of the y-axes.

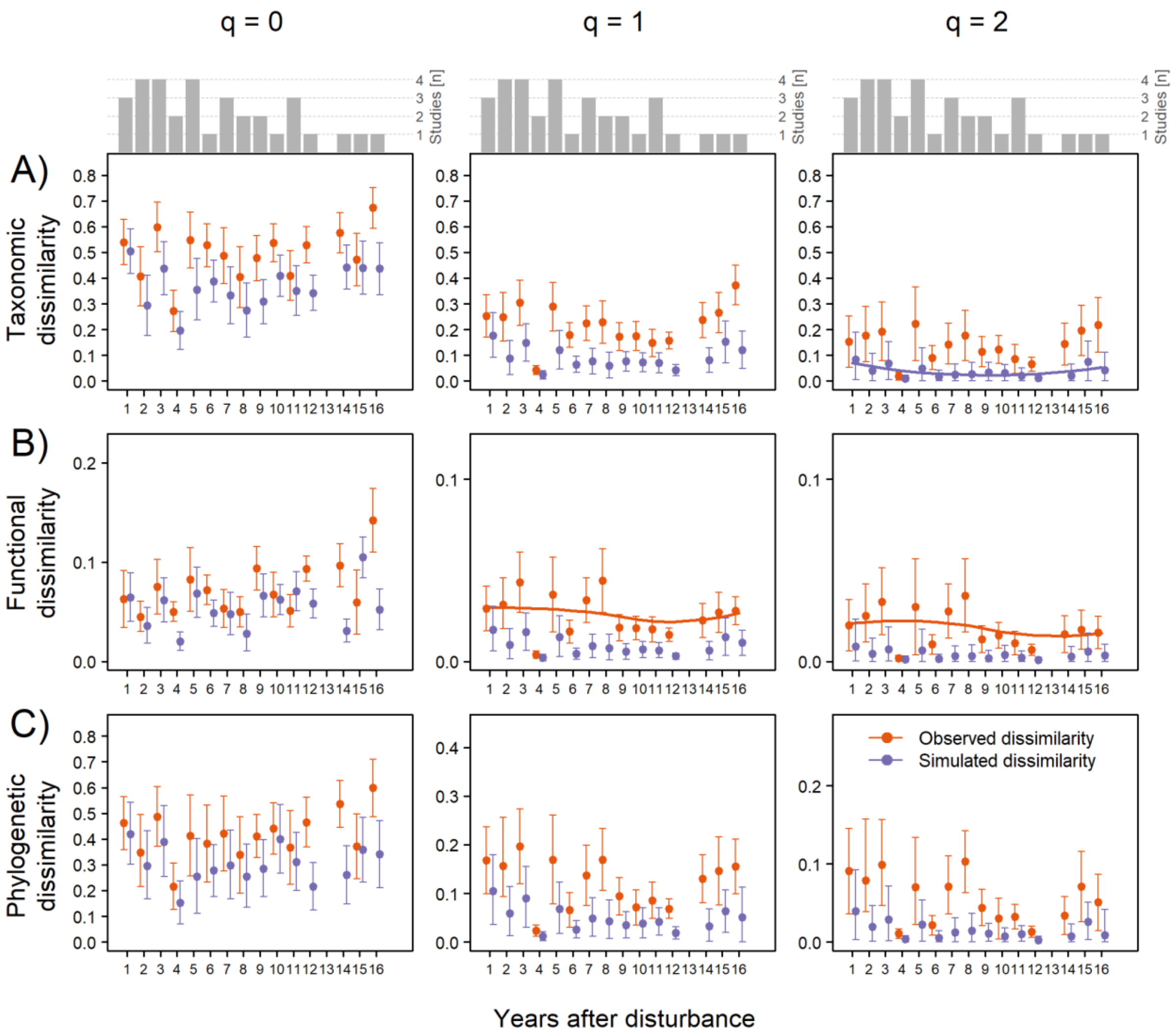

Figure III-S3: Effective proportion (Jaccard-type; mean ± SD) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity), and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots over the first 16 years (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). (A) Taxonomic dissimilarity, (B) functional dissimilarity and (C) phylogenetic dissimilarity are shown. The columns represent the dissimilarities for rare (q = 0), common (q = 1) and dominant (q = 2) species. Significant ($p < 0.05$) trends are drawn as solid lines, showing the average dissimilarity, based on general additive mixed-effects models. Top-row bar plots indicate the number of studies used to calculate the mean dissimilarity within every single year. Note the different scales of the y-axes.

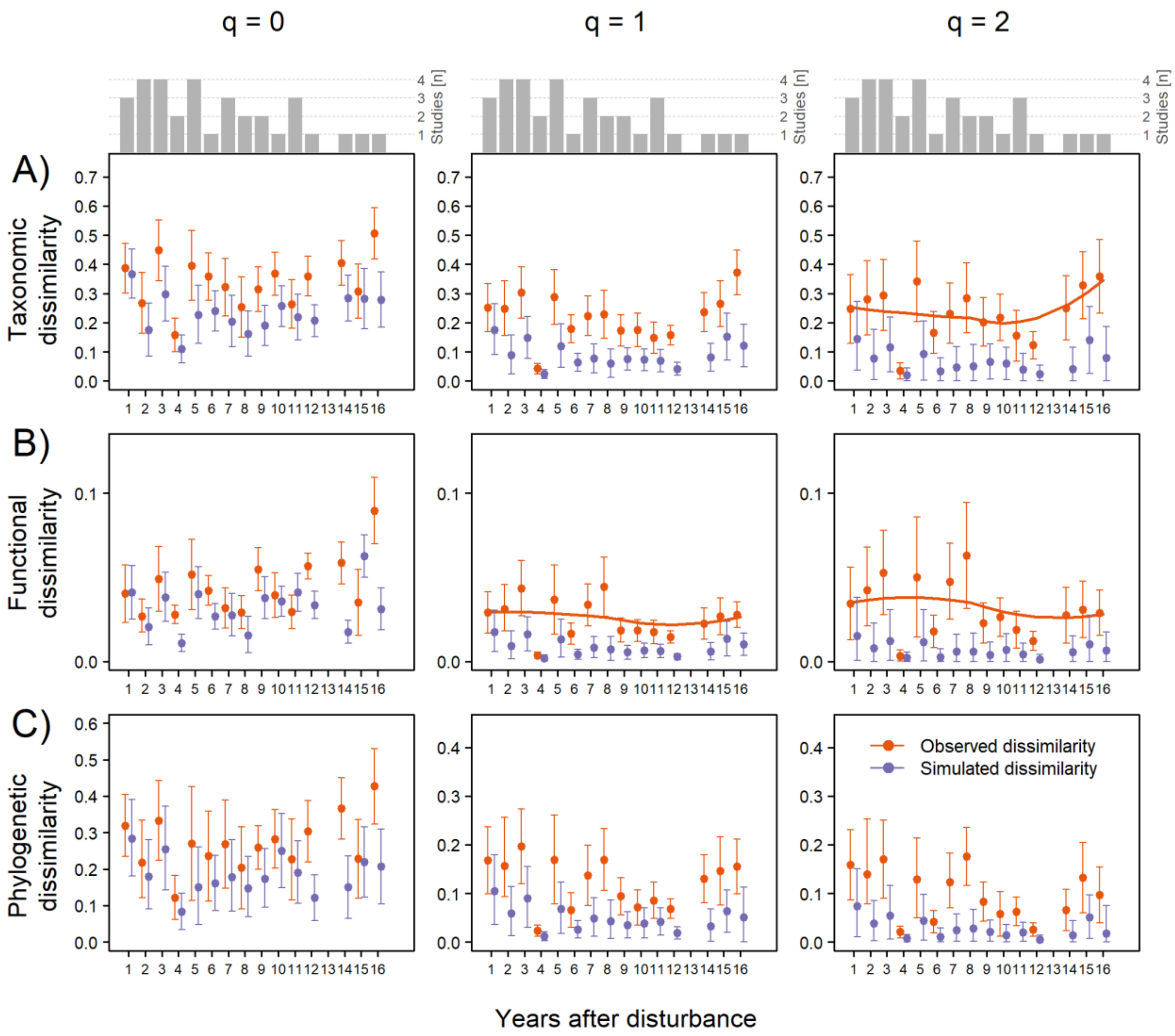

Figure III-S4: Effective proportion (Sørensen-type; mean ± SD) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity), and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots over the first 16 years (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). (A) Taxonomic dissimilarity, (B) functional dissimilarity and (C) phylogenetic dissimilarity are shown. The columns represent the dissimilarities for rare (*q* = 0), common (*q* = 1) and dominant (*q* = 2) species. Significant ($p < 0.05$) trends are drawn as solid lines, showing the average dissimilarity, based on general additive mixed-effects models. Top-row bar plots indicate the number of studies used to calculate the mean dissimilarity within every single year. Note the different scales of the y-axes.

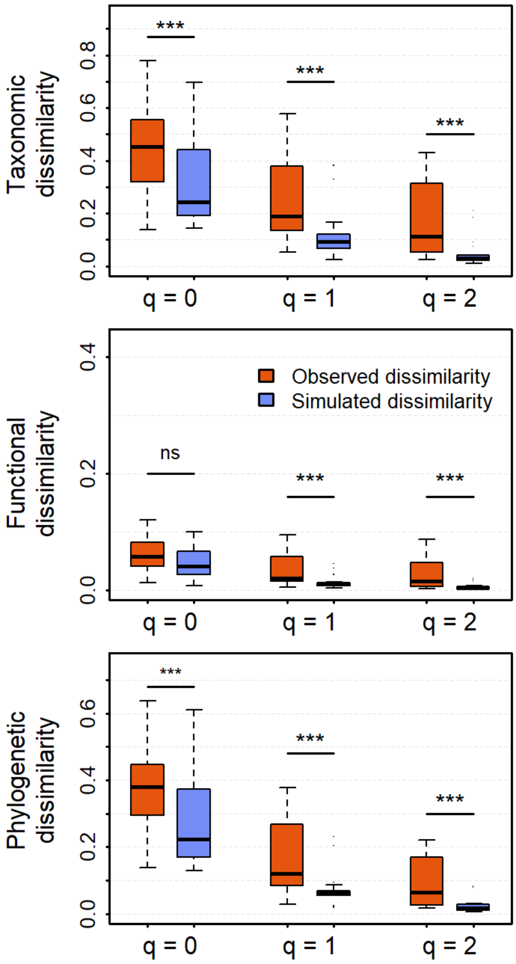

Figure III-S5: Effective proportion (Jaccard-type) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). The graph summarises the dissimilarities for all studies, except the study of Hutto and Young (2002) (for details see Table III-1). Boxplots show the dissimilarity for rare (q = 0), common (q = 1) and dominant (q = 2) species. Pairwise comparisons between observed and simulated dissimilarities are based on general additive mixed-effects models. Significance codes used: 0.001 – '***', 'ns' – not significant.

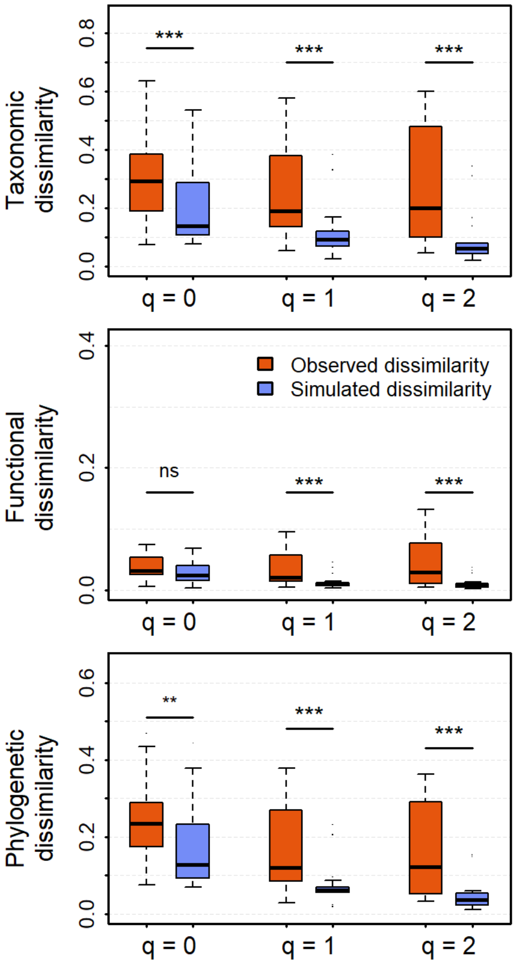

Figure III-S6: Effective proportion (Sørensen-type) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). The graph summarises the dissimilarities for all studies, except the study of Hutto and Young (2002) (for details see Table III-1). Boxplots show the dissimilarity for rare (*q* = 0), common (*q* = 1) and dominant (*q* = 2) species. Pairwise comparisons between observed and simulated dissimilarities are based on general additive mixed-effects models. Significance codes used: 0.001 – ‘***’, 0.01 – ‘**’, ‘ns’ – not significant.

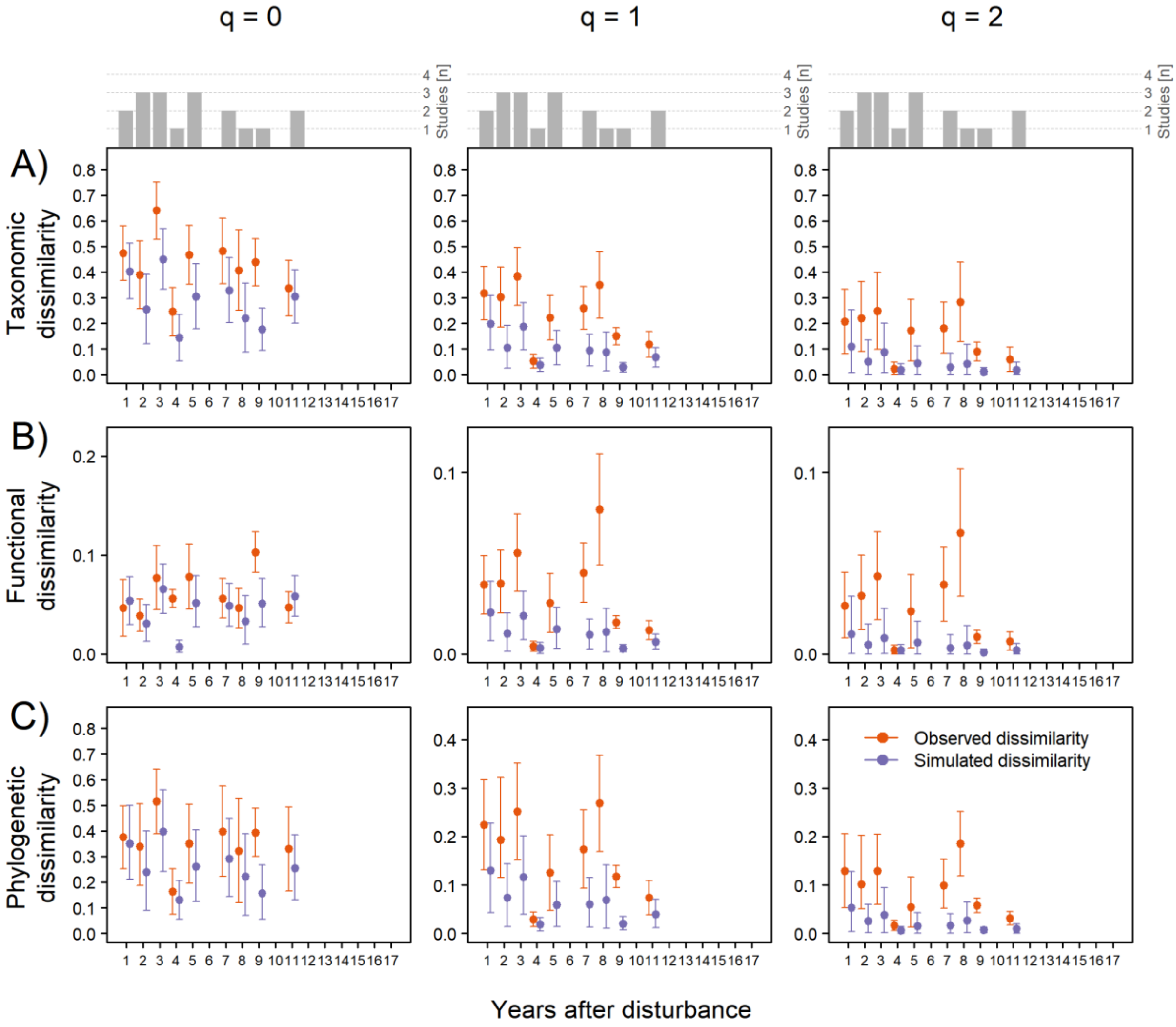

Figure III-S7: Effective proportion (Jaccard-type; mean ± SD) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots over the studied years (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). The graph summarises the results for all studies, except the study of Hutto and Young (2002) (Table III-1). (A) Taxonomic dissimilarity, (B) functional dissimilarity and (C) phylogenetic dissimilarity are shown. The columns represent the dissimilarities for rare (q = 0), common (q = 1) and dominant (q = 2) species. No significant trends ($p < 0.05$) were found after fitting general additive mixed-effects models. Top-row bar plots indicate the number of studies used to calculate the mean dissimilarity within every single year. Note the different scales of the y-axes.

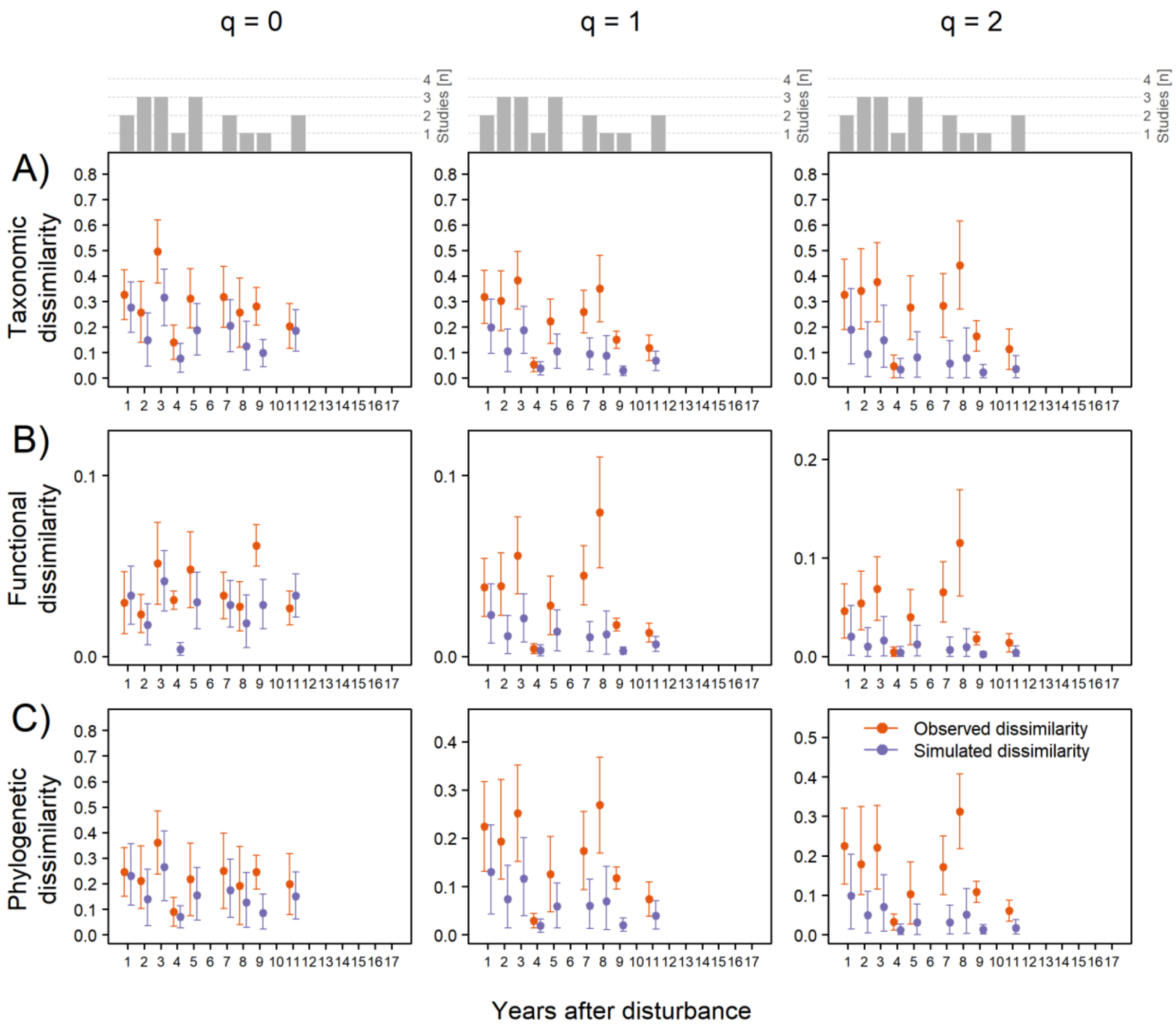

Figure III-S8: Effective proportion (Sørensen-type; mean ± SD) of non-shared species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity) between communities found in salvaged and unsalvaged plots over the studied years (orange) and expectations from unsalvaged plots based on a null model with 999 simulations (blue). The graph summarises the results for all studies, except the study of Hutto and Young (2002) (Table III-1). (A) Taxonomic dissimilarity, (B) functional dissimilarity and (C) phylogenetic dissimilarity are shown. The columns represent the dissimilarities for rare (*q* = 0), common (*q* = 1) and dominant (*q* = 2) species. No significant trends ($p < 0.05$) were found after fitting general additive mixed-effects models. Top-row bar plots indicate the number of studies used to calculate the mean dissimilarity within every single year. Note the different scales of the y-axes.

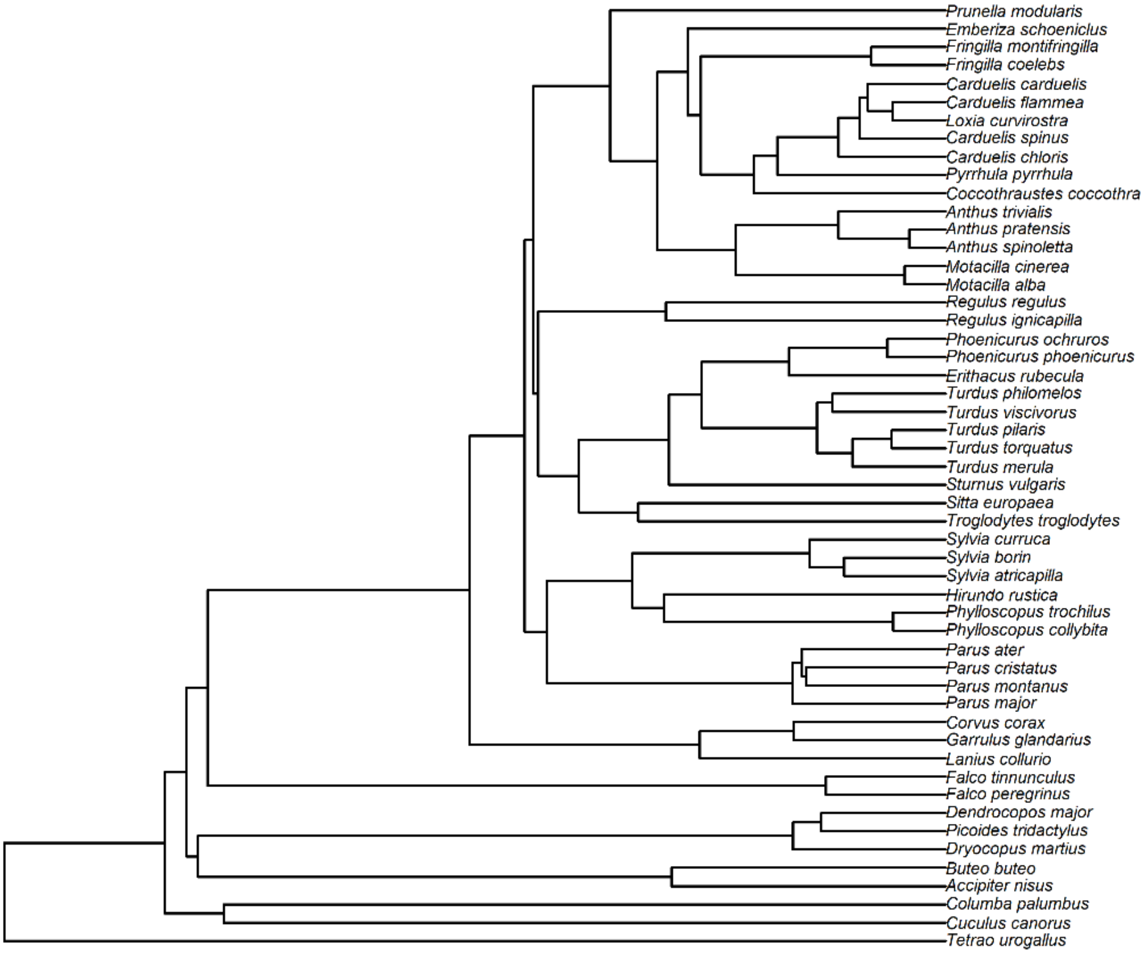

Figure III-S9: Phylogeny of bird species recorded by Thorn et al. (2016) included in the present analysis.

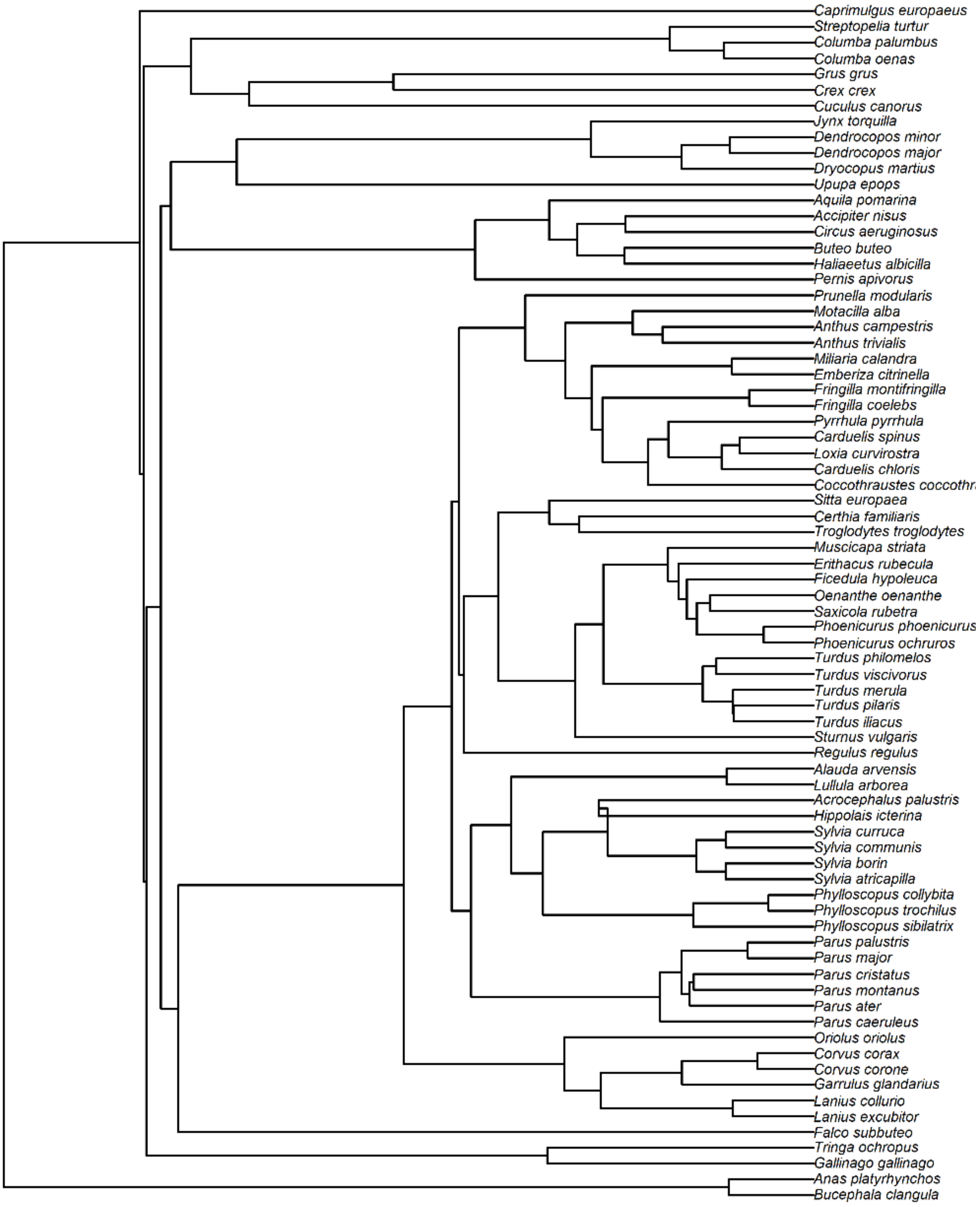

Figure III-S10: Phylogeny of bird species recorded by Zmihorski (2010) included in the present analysis.

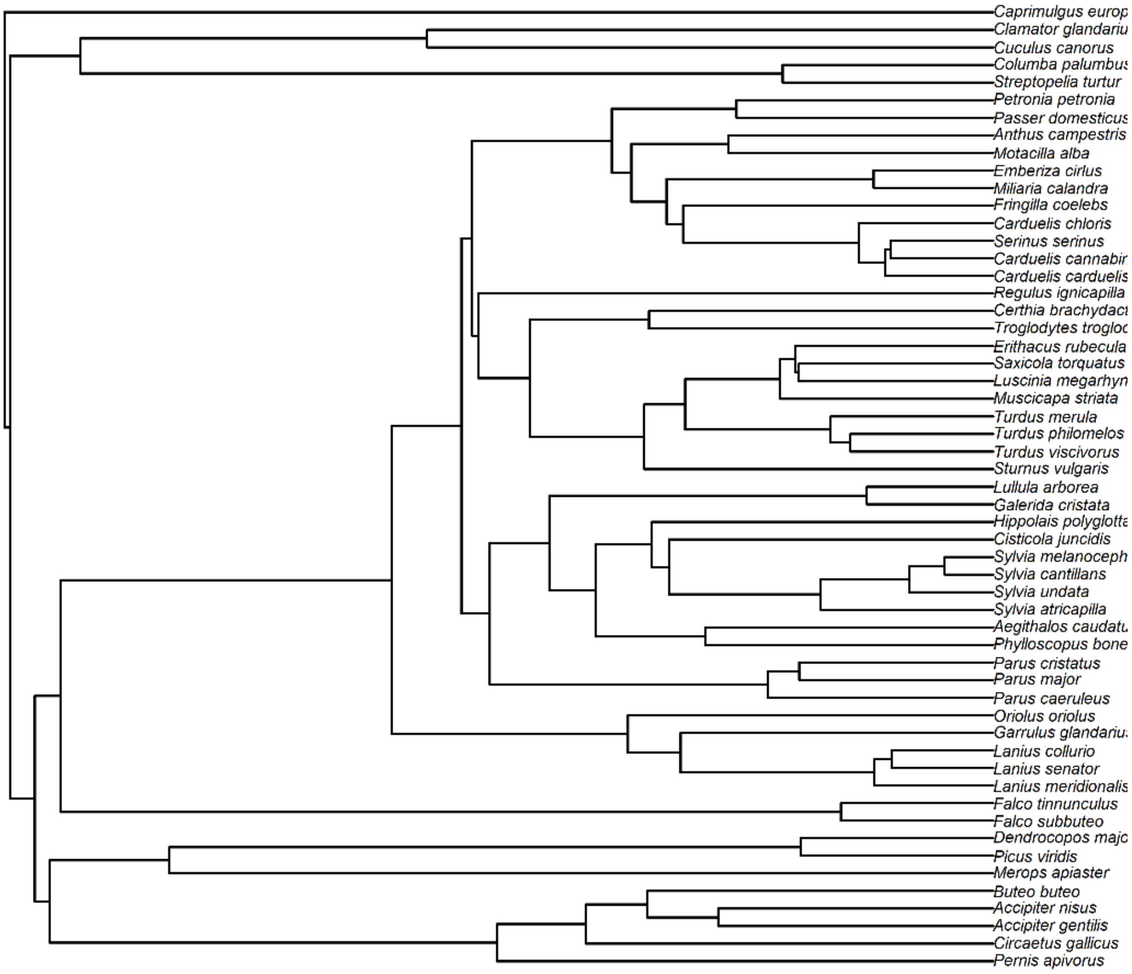

Figure III-S11: Phylogeny of bird species recorded by Rost et al. (2012) included in the present analysis.

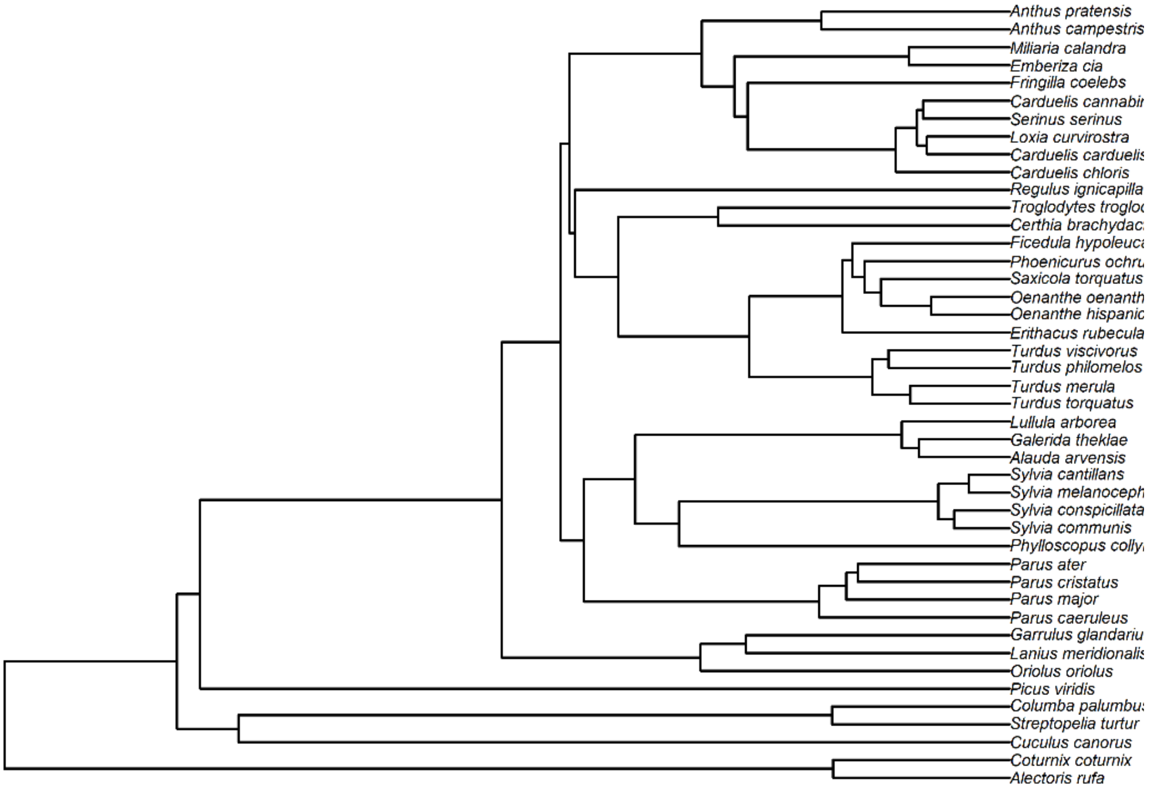

Figure III-S12: Phylogeny of bird species recorded by Castro et al. (2010) included in the present analysis.

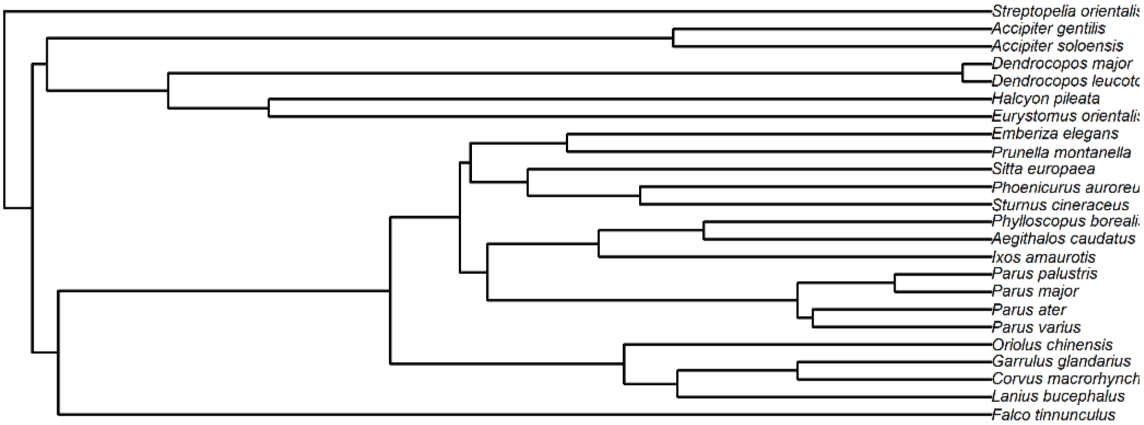

Figure III-S13: Phylogeny of bird species recorded by Choi et al. (2007) included in the present analysis.

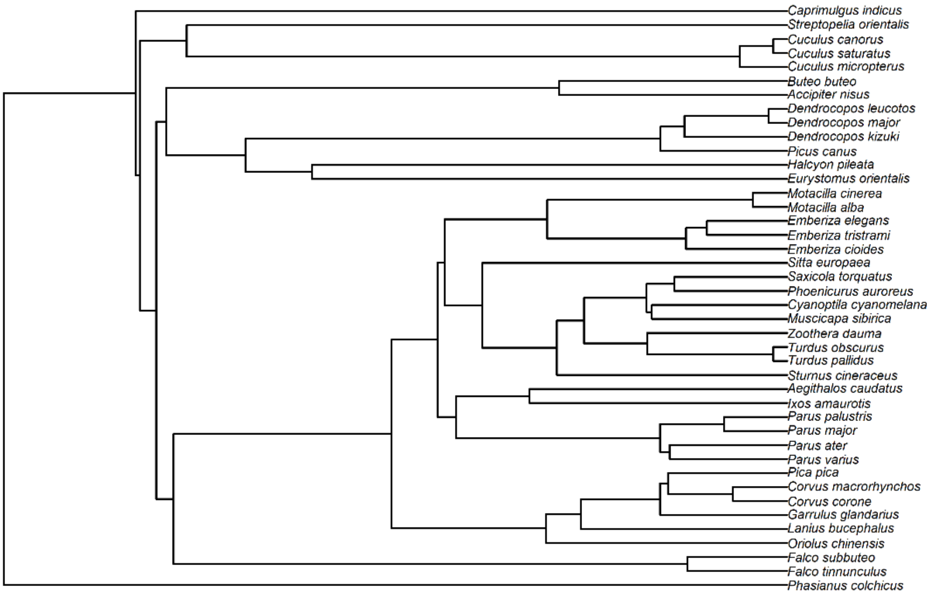

Figure III-S14: Phylogeny of bird species recorded by Lee et al. (2011) included in the present analysis.

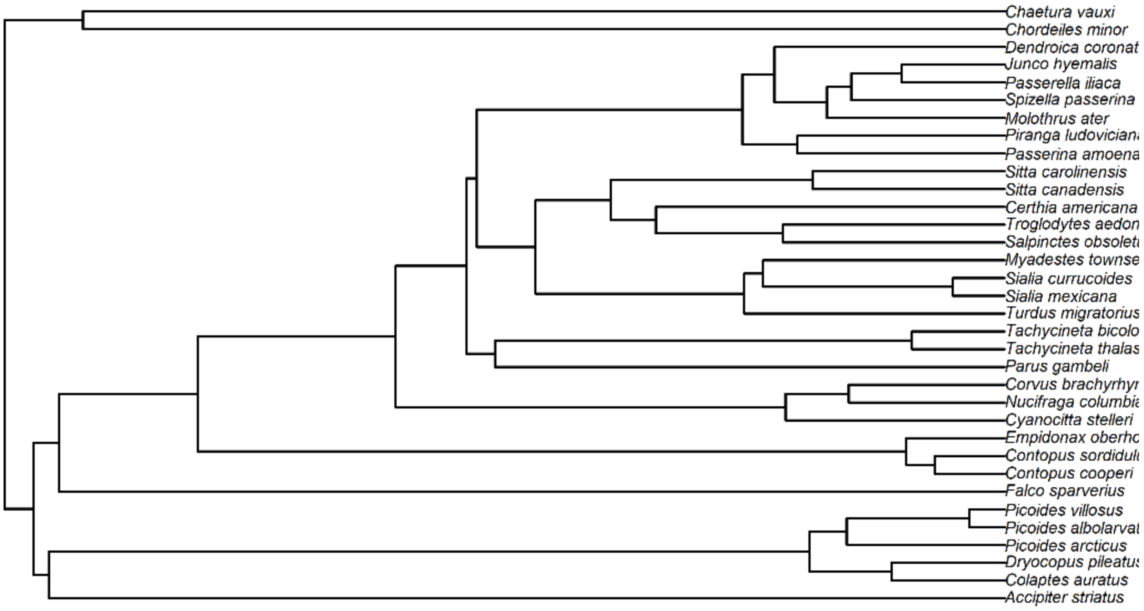

Figure III-S15: Phylogeny of bird species recorded by Cahall and Hayes (2009) included in the present analysis.

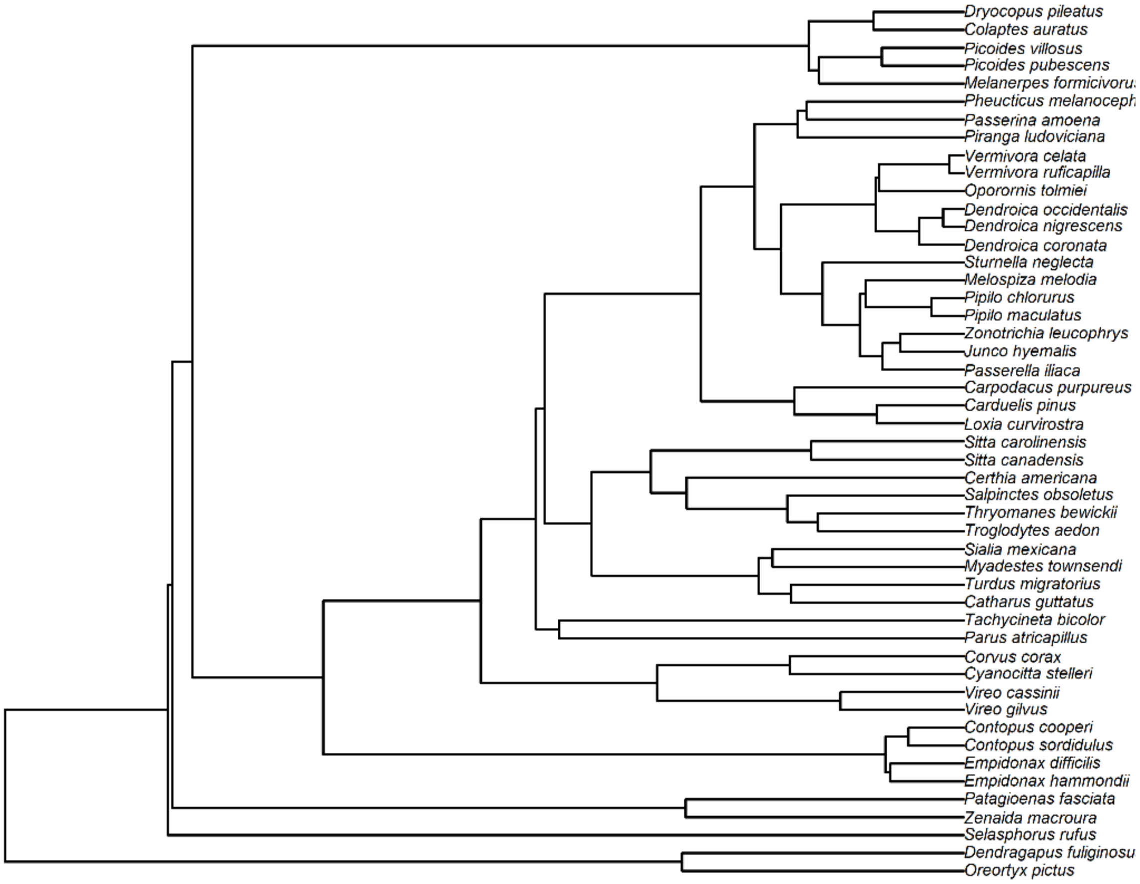

Figure III-S16: Phylogeny of bird species recorded by Fontaine et al. (2009) included in the present analysis.

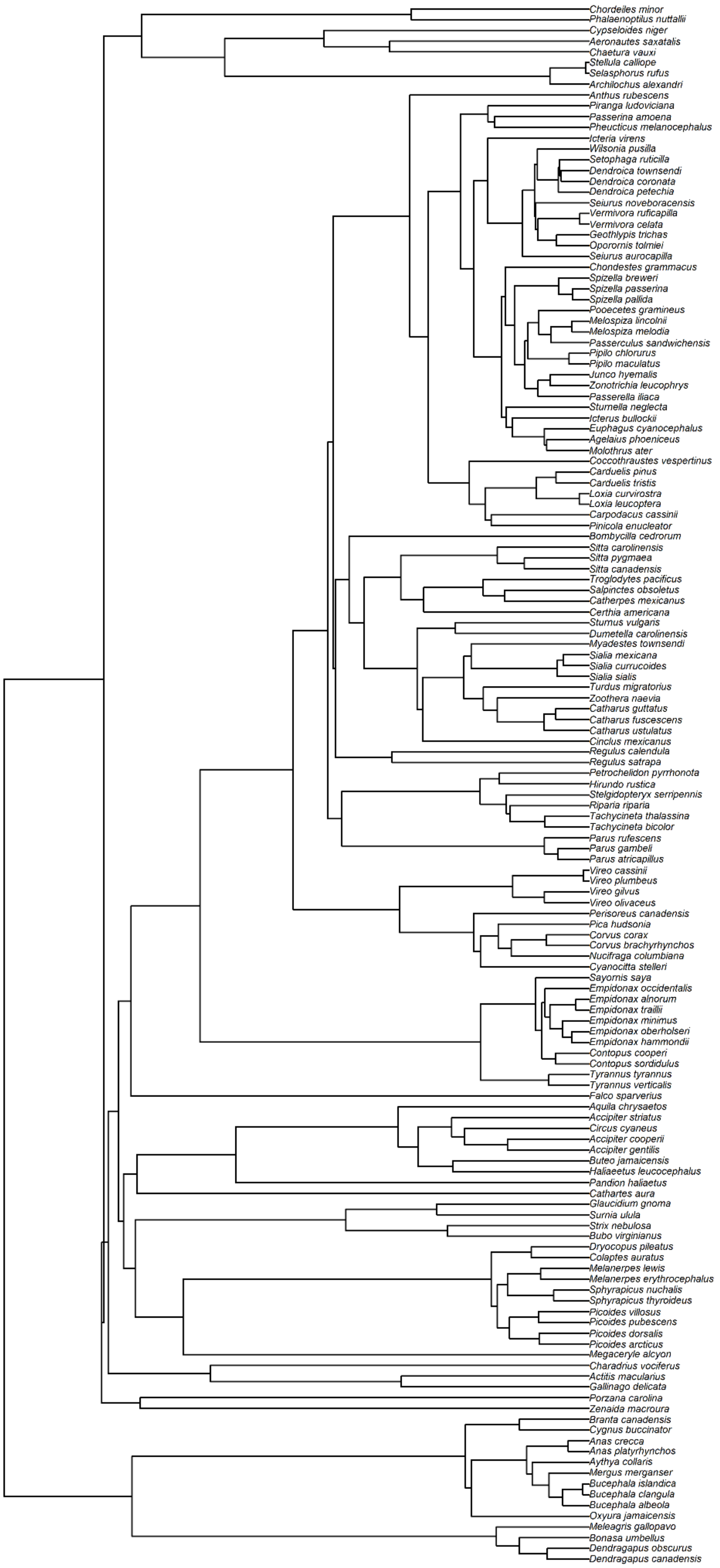

Figure III-S17: Phylogeny of bird species recorded by Hutto and Young (2002) included in the present analysis.

Table III-S2: List of species traits used to quantify functional dissimilarity.

No.	Species	Weight mean (g)	Clutch size mean	Nest position	Migration*	Nocturnal foraging**	Foraging substrate	Foraging method	Diet
1	*Accipiter cooperii*	488.5	4	canopy	1	0	air	pursuit,pouncing	vertebrates
2	*Accipiter gentilis*	808	3	canopy	0	0	ground,air	pursuit,pouncing,scavenging	vertebrates
3	*Accipiter nisus*	227	5	canopy	0	0	air	pursuit,pouncing	vertebrates
4	*Accipiter soloensis*	155	3.5	canopy	1	0	ground,air	pursuit,pouncing	vertebrates
5	*Accipiter striatus*	150	5	canopy	1	0	air	pursuit,pouncing	vertebrates
6	*Acrocephalus palustris*	12	4.5	canopy	1	0	vegetation	gleaning	invertebrates
7	*Actitis macularius*	47.25	4	ground	1	0	water,mud,ground	gleaning,probing	invertebrates
8	*Aegithalos caudatus*	8.3	10	canopy	0	0	trunk,vegetation	gleaning	invertebrates
9	*Aeronautes saxatalis*	33.25	4	ground	1	0	air	pursuit	invertebrates
10	*Agelaius phoeniceus*	52.5	3.5	canopy	1	0	ground,vegetation,air	gleaning,pouncing,digging	plants,invertebrates
11	*Alauda arvensis*	40	4	ground	1	0	ground	gleaning	plants,invertebrates
12	*Alectoris rufa*	465.5	13	ground	0	0	ground	gleaning,grazing,digging	plants,invertebrates
13	*Anas crecca*	325	9	ground	1	0	water	gleaning,grazing	plants,invertebrates
14	*Anas platyrhynchos*	1100	10	ground	1	0	water,mud,ground	gleaning,grazing	plants,vertebrates,invertebrates
15	*Anthus campestris*	28.75	5	ground	1	0	ground,vegetation	gleaning	invertebrates
16	*Anthus pratensis*	19	4.5	ground	1	0	ground,vegetation	gleaning	invertebrates
17	*Anthus rubescens*	21	5	ground	1	0	ground	gleaning	invertebrates

No.	Species	Weight mean (g)	Clutch size mean	Nest position	Migration*	Nocturnal foraging **	Foraging substrate	Foraging method	Diet
18	*Anthus spinoletta*	20.5	5	ground	1	0	ground,vegetation	gleaning	invertebrates
19	*Anthus trivialis*	24.4	6	ground	1	0	ground,vegetation	gleaning	invertebrates
20	*Aquila chrysaetos*	4752	2	ground	0	0	ground	pursuit,pouncing,scavenging	vertebrates
21	*Aquila pomarina*	1500	2	canopy	1	0	ground	pursuit,pouncing,scavenging	vertebrates
22	*Archilochus alexandri*	3.7	2	canopy	1	0	vegetation,air	gleaning	plants,invertebrates
23	*Aythya collaris*	700	9	ground	1	0	water	gleaning,grazing	plants,invertebrates
24	*Bombycilla cedrorum*	32	4	canopy	0	0	vegetation	gleaning	plants
25	*Bonasa bonasia*	367.5	5.5	ground	0	0	ground,vegetation	gleaning,grazing,digging	plants
26	*Bonasa umbellus*	667.5	11.5	ground	0	0	ground,vegetation	gleaning,grazing	plants
27	*Branta canadensis*	3916	6.5	ground	1	0	water,ground	grazing	plants
28	*Bubo virginianus*	1744	2.5	canopy	0	1	ground	pouncing	vertebrates
29	*Bucephala albeola*	415	9	hole	1	0	water	gleaning,digging,probing	invertebrates
30	*Bucephala clangula*	1147	6.5	hole	1	0	water	gleaning,grazing	invertebrates
31	*Bucephala islandica*	1012.5	9	hole	0	0	water	gleaning,digging,probing	invertebrates
32	*Buteo buteo*	893.5	3.5	canopy	0	0	ground	pursuit,pouncing,scavenging	vertebrates
33	*Buteo jamaicensis*	1075	3.5	canopy	0	0	ground	pursuit,pouncing,scavenging	vertebrates
34	*Caprimulgus europaeus*	75	2	ground	1	1	air	pursuit	invertebrates
35	*Caprimulgus indicus*	84	2	ground	1	1	air	pursuit	invertebrates
36	*Carduelis cannabina*	20.5	5.5	canopy	0	0	ground,vegetation	gleaning	plants

No.	**Species**	**Weight mean (g)**	**Clutch size mean**	**Nest position**	**Migration***	**Nocturnal foraging****	**Foraging substrate**	**Foraging method**	**Diet**
37	*Carduelis carduelis*	16.5	5	canopy	0	0	ground,vegetation	gleaning	plants
38	*Carduelis chloris*	25.5	4.5	canopy	0	0	ground,vegetation	gleaning	plants
39	*Carduelis flammea*	13.5	5	canopy	0	0	vegetation	gleaning	plants
40	*Carduelis pinus*	14.5	4	canopy	0	0	vegetation	gleaning	plants
41	*Carduelis spinus*	13.5	4	canopy	0	0	vegetation	gleaning	plants
42	*Carduelis tristis*	11.5	4.5	canopy	1	0	vegetation	gleaning	plants
43	*Carpodacus cassinii*	29	4.5	canopy	1	0	ground,vegetation	gleaning	plants
44	*Carpodacus purpureus*	23	4.5	canopy	0	0	vegetation	gleaning	plants
45	*Cathartes aura*	925	2	ground	1	0	ground	scavenging	vertebrates, invertebrates
46	*Catharus fuscescens*	34	4	canopy	1	0	ground	gleaning	plants,invertebrates
47	*Catharus guttatus*	28	4.5	ground	1	0	ground	gleaning	invertebrates
48	*Catharus ustulatus*	35	3.5	canopy	1	0	ground	gleaning	plants,invertebrates
49	*Catherpes mexicanus*	13.5	5	ground	0	0	ground	gleaning	invertebrates
50	*Certhia americana*	8.5	4.5	hole	0	0	trunk,vegetation	gleaning	plants,invertebrates
51	*Certhia brachydactyla*	9.2	5	hole	0	0	trunk,vegetation	gleaning	plants,invertebrates
52	*Certhia familiaris*	8.5	5	hole	0	0	trunk,vegetation	gleaning	plants,invertebrates
53	*Chaetura vauxi*	18.5	5.5	canopy	1	0	air	pursuit	invertebrates
54	*Charadrius vociferus*	96	4	ground	1	0	mud	gleaning	plants,invertebrates
55	*Chondestes grammacus*	29	4.5	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
56	*Chordeiles minor*	76.5	2	ground	1	1	air	pursuit	invertebrates

No.	**Species**	**Weight mean (g)**	**Clutch size mean**	**Nest position**	**Migration***	**Nocturnal foraging** **	**Foraging substrate**	**Foraging method**	**Diet**
57	*Cinclus mexicanus*	57.5	5	ground	0	0	water,ground	gleaning	invertebrates
58	*Circaetus gallicus*	1750	1	canopy	1	0	ground	pouncing,scavenging	vertebrates
59	*Circus aeruginosus*	682.5	4.5	ground	1	0	ground,air	pursuit,pouncing,scavenging	vertebrates
60	*Circus cyaneus*	504	6	ground	1	0	ground	pursuit,pouncing	vertebrates
61	*Cisticola juncidis*	9.5	4.5	ground	0	0	ground,vegetation	gleaning	invertebrates
62	*Clamator glandarius*	124	5.5	canopy	1	0	ground,vegetation	gleaning	vertebrates, invertebrates
63	*Coccothraustes coccothraustes*	59	4.5	canopy	0	0	ground,vegetation	gleaning	plants
64	*Coccothraustes vespertinus*	54.9	3	canopy	1	0	ground,vegetation	gleaning	plants
65	*Colaptes auratus*	135	4	hole	0	0	ground,trunk,vegetation	gleaning,probing	invertebrates
66	*Columba oenas*	325.5	3.5	hole	1	0	ground,vegetation	gleaning	plants
67	*Columba palumbus*	487	2	canopy	1	0	ground,vegetation	gleaning	plants
68	*Contopus cooperi*	34.5	3	canopy	1	0	vegetation,air	pursuit,gleaning,pouncing	invertebrates
69	*Contopus sordidulus*	13	3	canopy	1	0	vegetation,air	pursuit,gleaning,pouncing	invertebrates
70	*Corvus brachyrhynchos*	412.5	4.5	canopy	1	0	ground	gleaning,pouncing,digging,scavenging	plants,vertebrates,invertebrates
71	*Corvus corax*	1292.5	4.5	canopy	0	0	ground	pouncing,digging,scavenging	plants,vertebrates,invertebrates
72	*Corvus corone*	499	4	canopy	0	0	ground	gleaning,digging,scavenging	plants,vertebrates,invertebrates

No.	Species	Weight mean (g)	Clutch size mean	Nest position	Migration*	Nocturnal foraging **	Foraging substrate	Foraging method	Diet
73	*Corvus macrorhynchos*	725	4	canopy	0	0	ground	gleaning,digging,scavenging	plants,vertebrates,invertebrates
74	*Coturnix coturnix*	112.5	9	ground	1	0	ground	gleaning,digging	plants,invertebrates
75	*Crex crex*	169.5	10	ground	1	0	ground	gleaning,digging	invertebrates
76	*Cuculus canorus*	119.5	10	canopy	1	0	ground,vegetation	gleaning	invertebrates
77	*Cuculus micropterus*	119	10	canopy	1	0	ground,vegetation	gleaning	invertebrates
78	*Cuculus saturatus*	106	10	canopy	1	0	ground,vegetation	gleaning	invertebrates
79	*Cyanocitta stelleri*	121	4	canopy	0	0	ground,trunk,vegetation	gleaning	plants,invertebrates
80	*Cyanoptila cyanomelana*	25	5	hole	1	0	vegetation,air	pursuit,gleaning,pouncing	invertebrates
81	*Cygnus buccinator*	10300	5	ground	0	0	water	gleaning,grazing	plants,invertebrates
82	*Cypseloides niger*	40	1	ground	1	0	air	pursuit	invertebrates
83	*Dendragapus canadensis*	590	7	ground	0	0	ground	gleaning,grazing	plants,invertebrates
84	*Dendragapus falcipennis*	660	4	ground	0	0	ground,vegetation	gleaning,grazing	plants
85	*Dendragapus fuliginosus*	1037	7	ground	0	0	ground,vegetation	gleaning,grazing	plants
86	*Dendragapus obscurus*	1135	7	ground	0	0	ground,vegetation	gleaning,grazing	plants
87	*Dendrocopos kizuki*	22	6	hole	0	0	trunk,vegetation	gleaning,probing	invertebrates
88	*Dendrocopos leucotos*	105	4	hole	0	0	trunk	probing	invertebrates
89	*Dendrocopos major*	84	5	hole	0	0	trunk,vegetation	gleaning,probing	invertebrates
90	*Dendrocopos minor*	22	6	hole	0	0	trunk,vegetation	gleaning,probing	invertebrates

No.	**Species**	**Weight mean (g)**	**Clutch size mean**	**Nest position**	**Migration***	**Nocturnal foraging****	**Foraging substrate**	**Foraging method**	**Diet**
91	*Dendroica coronata*	13	4	canopy	1	0	trunk,vegetation	gleaning	invertebrates
92	*Dendroica nigrescens*	8.5	4	canopy	1	0	vegetation	gleaning	invertebrates
93	*Dendroica occidentalis*	10.5	4.5	canopy	1	0	vegetation	gleaning	invertebrates
94	*Dendroica petechia*	11	4	canopy	1	0	vegetation	gleaning	invertebrates
95	*Dendroica townsendi*	8.8	4.5	canopy	1	0	vegetation	gleaning	invertebrates
96	*Dryocopus martius*	310	5	hole	0	0	trunk	probing	plants,invertebrates
97	*Dryocopus pileatus*	300	4	hole	0	0	trunk	probing	plants,invertebrates
98	*Dumetella carolinensis*	39.5	4	canopy	1	0	ground	gleaning	plants,invertebrates
99	*Emberiza cia*	23	4	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
100	*Emberiza cioides*	21.5	4	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
101	*Emberiza cirlus*	24.5	3.5	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
102	*Emberiza citrinella*	27.5	4	ground	0	0	ground,vegetation	gleaning	plants
103	*Emberiza elegans*	22	3.5	ground	0	0	ground,vegetation	gleaning	plants,invertebrates
104	*Emberiza schoeniclus*	18	5.5	ground	1	0	ground,vegetation	gleaning	plants
105	*Emberiza tristrami*	17.5	5	canopy	1	0	ground,vegetation	gleaning	plants,invertebrates
106	*Empidonax alnorum*	13	3.5	canopy	1	0	vegetation,air	gleaning	invertebrates
107	*Empidonax difficilis*	10.5	4	canopy	1	0	vegetation,air	pursuit,gleaning	invertebrates
108	*Empidonax hammondii*	10	4	canopy	1	0	vegetation,air	pursuit,gleaning	invertebrates

No.	**Species**	**Weight mean (g)**	**Clutch size mean**	**Nest position**	**Migration***	**Nocturnal foraging****	**Foraging substrate**	**Foraging method**	**Diet**
109	*Empidonax minimus*	10.5	4	canopy	1	0	vegetation,air	pursuit,gleaning	invertebrates
110	*Empidonax oberholseri*	10	3.5	canopy	1	0	vegetation,air	pursuit,gleaning	invertebrates
111	*Empidonax occidentalis*	11	3.5	canopy	1	0	vegetation,air	pursuit,gleaning	invertebrates
112	*Empidonax traillii*	13.5	4	canopy	1	0	vegetation,air	pursuit,gleaning	invertebrates
113	*Erithacus rubecula*	17.6	5	ground	0	0	ground,trunk,vegetation	gleaning	plants,invertebrates
114	*Euphagus cyanocephalus*	61.8	5	canopy	1	0	ground	gleaning,digging	plants,invertebrates
115	*Eurystomus orientalis*	147.5	3.5	hole	0	0	air	pursuit,pouncing	invertebrates
116	*Falco peregrinus*	1005	3.5	canopy	0	0	air	pursuit,pouncing	vertebrates
117	*Falco sparverius*	123	5	canopy	0	0	ground,air	pursuit,pouncing	vertebrates, invertebrates
118	*Falco subbuteo*	235	3	canopy	1	0	ground,air	pursuit,pouncing	vertebrates, invertebrates
119	*Falco tinnunculus*	225	5	canopy	0	0	ground	pursuit,pouncing	vertebrates, invertebrates
120	*Ficedula hypoleuca*	16	6.5	hole	1	0	trunk,vegetation,air	pursuit,gleaning,pouncing	invertebrates
121	*Fringilla coelebs*	23	4.5	canopy	1	0	ground,trunk,vegetation	gleaning	plants,invertebrates
122	*Fringilla montifringilla*	23.5	6.5	canopy	1	0	trunk,vegetation	gleaning	plants,invertebrates
123	*Galerida cristata*	46	4	ground	1	0	ground	gleaning	plants
124	*Galerida theklae*	35	4	ground	0	0	ground	gleaning	plants,invertebrates
125	*Gallinago delicata*	112.5	4	ground	1	0	water,mud,ground	digging,probing	invertebrates

No.	Species	Weight mean (g)	Clutch size mean	Nest position	Migration*	Nocturnal foraging **	Foraging substrate	Foraging method	Diet
126	*Gallinago gallinago*	126.5	4	ground	1	0	water,mud,ground	digging,probing	invertebrates
127	*Garrulus glandarius*	163	5	canopy	0	0	ground,trunk,vegetation	gleaning	plants,invertebrates
128	*Geothlypis tolmiei*	11	4	canopy	1	0	ground,vegetation	gleaning	invertebrates
129	*Geothlypis trichas*	11.5	4	canopy	1	0	vegetation,air	pursuit,gleaning	invertebrates
130	*Glaucidium gnoma*	60.5	3.5	hole	0	0	air	pursuit,pouncing	vertebrates
131	*Grus grus*	5300	2	ground	1	0	water,mud,ground	gleaning,pouncing,digging	plants,vertebrates,invertebrates
132	*Halcyon pileata*	79	4.5	ground	1	0	water,air	pursuit,pouncing	vertebrates, invertebrates
133	*Haliaeetus albicilla*	4793	2	ground	0	0	water,mud,ground,air	pursuit,gleaning,pouncing,grazing,scavenging	vertebrates, invertebrates
134	*Haliaeetus leucocephalus*	4700	2	canopy	0	0	water,ground, air	pursuit,pouncing,scavenging	vertebrates
135	*Hippolais icterina*	13	4	canopy	1	0	vegetation	gleaning	invertebrates
136	*Hippolais polyglotta*	12	4	canopy	1	0	vegetation	gleaning	invertebrates
137	*Hirundo rustica*	19	4.5	hole	1	0	air	pursuit,pouncing	invertebrates
138	*Icteria virens*	27	3.5	canopy	1	0	vegetation	gleaning	plants
139	*Icterus bullockii*	37.7	4.5	canopy	1	0	vegetation,air	pursuit,gleaning	plants,invertebrates
140	*Ixos amaurotis*	75.3	4.5	canopy	1	0	trunk,vegetation	gleaning	plants,invertebrates
141	*Junco hyemalis*	19.8	4.5	ground	1	0	ground	gleaning	plants,invertebrates
142	*Jynx torquilla*	40	8	hole	1	0	ground,trunk	gleaning,probing	invertebrates

No.	Species	Weight mean (g)	Clutch size mean	Nest position	Migration*	Nocturnal foraging**	Foraging substrate	Foraging method	Diet
143	*Lanius bucephalus*	43	5.5	canopy	1	0	ground,vegetation	gleaning,pouncing	vertebrates, invertebrates
144	*Lanius collurio*	28.3	5.5	canopy	1	0	ground,vegetation	gleaning,pouncing	vertebrates, invertebrates
145	*Lanius excubitor*	64.5	6	canopy	1	0	ground,vegetation	gleaning,pouncing	vertebrates, invertebrates
146	*Lanius meridionalis*	70.5	5	canopy	0	0	ground,vegetation	gleaning,pouncing	vertebrates, invertebrates
147	*Lanius senator*	40	5	canopy	1	0	ground,vegetation	gleaning,pouncing	vertebrates, invertebrates
148	*Loxia curvirostra*	38	4	canopy	0	0	trunk,vegetation	gleaning	plants
149	*Loxia leucoptera*	32.5	3	canopy	0	0	vegetation	gleaning	plants
150	*Lullula arborea*	29	3.5	ground	1	0	ground	gleaning	invertebrates
151	*Luscinia megarhynchos*	26.5	4.5	ground	1	0	vegetation	gleaning	invertebrates
152	*Megaceryle alcyon*	145.5	6.5	ground	1	0	water,air	pouncing	vertebrates
153	*Melanerpes erythrocephalus*	76.5	5	hole	0	0	trunk	probing	invertebrates
154	*Melanerpes formicivorus*	73.5	4	hole	0	0	trunk,vegetation	gleaning,probing	plants,invertebrates
155	*Melanerpes lewis*	115	6.5	hole	1	0	trunk	probing	plants,invertebrates
156	*Meleagris gallopavo*	7300	11	ground	0	0	ground	gleaning	plants,invertebrates
157	*Melospiza lincolnii*	19.2	4.5	ground	1	0	ground,trunk,vegetation	gleaning	plants,invertebrates
158	*Melospiza melodia*	19.1	4	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
159	*Mergus merganser*	1500	9.5	ground	1	0	water	pursuit,gleaning	vertebrates, invertebrates

No.	Species	Weight mean (g)	Clutch size mean	Nest position	Migration*	Nocturnal foraging **	Foraging substrate	Foraging method	Diet
160	*Merops apiaster*	32.5	5.5	ground	1	0	air	pursuit,gleaning	invertebrates
161	*Miliaria calandra*	48.2	4.5	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
162	*Molothrus ater*	44	10	canopy	1	0	ground	gleaning	plants,invertebrates
163	*Motacilla alba*	21.1	5.5	ground	1	0	ground	gleaning	plants,invertebrates
164	*Motacilla cinerea*	17.5	4.5	ground	1	0	ground	gleaning	plants,invertebrates
165	*Muscicapa sibirica*	10.2	3.5	hole	1	0	vegetation,air	pursuit	invertebrates
166	*Muscicapa striata*	17	5	hole	1	0	air	pursuit	invertebrates
167	*Myadestes townsendi*	27.5	3.5	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
168	*Nucifraga columbiana*	141	3	canopy	0	0	vegetation	gleaning	plants,invertebrates
169	*Oenanthe hispanica*	17.2	4.5	ground	1	0	ground	gleaning	invertebrates
170	*Oenanthe oenanthe*	25.5	5.5	ground	1	0	ground	gleaning	plants,invertebrates
171	*Oporornis tolmiei*	10.6	4	canopy	1	0	ground,trunk,vegetation	gleaning	invertebrates
172	*Oreortyx pictus*	239.5	10	ground	0	0	ground,vegetation	gleaning	plants
173	*Oriolus chinensis*	82.5	3	canopy	1	0	vegetation	gleaning	plants
174	*Oriolus oriolus*	72	4	canopy	1	0	vegetation	gleaning	plants,invertebrates
175	*Oxyura jamaicensis*	552.5	7.5	ground	1	0	water,mud	gleaning,grazing,digging	plants,invertebrates
176	*Pandion haliaetus*	1520	3	canopy	1	0	water,air	pursuit	vertebrates
177	*Parus ater*	9.5	9	hole	0	0	vegetation	gleaning	invertebrates
178	*Parus atricapillus*	11.5	7	hole	0	0	vegetation	gleaning	invertebrates

No.	Species	Weight mean (g)	Clutch size mean	Nest position	Migration*	Nocturnal foraging **	Foraging substrate	Foraging method	Diet
179	*Parus caeruleus*	11.1	16	hole	0	0	vegetation	gleaning	plants,invertebrates
180	*Parus cristatus*	12.75	12.5	hole	0	0	vegetation	gleaning	invertebrates
181	*Parus gambeli*	10.5	8	hole	0	0	vegetation	gleaning	plants,invertebrates
182	*Parus major*	17	11	hole	0	0	vegetation	gleaning	plants,invertebrates
183	*Parus montanus*	11.5	8.5	hole	0	0	vegetation	gleaning	plants,invertebrates
184	*Parus palustris*	11.5	8	hole	0	0	vegetation	gleaning	invertebrates
185	*Parus rufescens*	11	6	hole	0	0	vegetation	gleaning	plants,invertebrates
186	*Parus varius*	16.5	6.5	hole	0	0	vegetation	gleaning	plants,invertebrates
187	*Passer domesticus*	28.5	5	hole	0	0	ground	gleaning	plants,invertebrates
188	*Passerculus sandwichensis*	22.75	4	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
189	*Passerella iliaca*	37.9	4	ground	0	0	ground,vegetation	gleaning	plants,invertebrates
190	*Passerina amoena*	16.1	4	ground	1	0	ground,vegetation	gleaning	invertebrates
191	*Patagioenas fasciata*	343	2	canopy	1	0	ground,vegetation	gleaning	plants
192	*Perisoreus canadensis*	67.5	3	canopy	0	0	vegetation	gleaning	plants,invertebrates
193	*Pernis apivorus*	705	2	canopy	1	0	ground,vegetation	pursuit,gleaning,scavenging	vertebrates, invertebrates
194	*Petrochelidon pyrrhonota*	22	4.5	ground	1	0	air	pursuit	invertebrates
195	*Petronia petronia*	32.5	4.5	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
196	*Phalaenoptilus nuttallii*	44.5	2	ground	1	0	air	pursuit	invertebrates

No.	**Species**	**Weight mean (g)**	**Clutch size mean**	**Nest position**	**Migration***	**Nocturnal foraging ****	**Foraging substrate**	**Foraging method**	**Diet**
197	*Phasianus colchicus*	1267.5	10	ground	0	0	ground	gleaning,pouncing	plants,invertebrates
198	*Pheucticus melanocephalus*	42	3.5	canopy	1	0	vegetation	gleaning	plants,invertebrates
199	*Phoenicurus auroreus*	15.5	4.5	hole	1	0	ground,air	pursuit,gleaning	plants,invertebrates
200	*Phoenicurus ochruros*	16	5	hole	1	0	ground	gleaning	plants,invertebrates
201	*Phoenicurus phoenicurus*	17	6	hole	1	0	ground,vegetation	pursuit,gleaning	plants,invertebrates
202	*Phylloscopus bonelli*	9.25	5.5	ground	1	0	vegetation	gleaning	invertebrates
203	*Phylloscopus borealis*	11.25	6	ground	1	0	vegetation	gleaning	invertebrates
204	*Phylloscopus collybita*	8.5	6.5	ground	1	0	vegetation	gleaning	plants,invertebrates
205	*Phylloscopus sibilatrix*	11.2	6	ground	1	0	vegetation	gleaning	invertebrates
206	*Phylloscopus trochilus*	10.5	6	ground	1	0	vegetation	gleaning	invertebrates
207	*Pica hudsonia*	177.5	6	canopy	0	0	ground,vegetation	gleaning,scavenging	plants,vertebrates,invertebrates
208	*Pica pica*	226.5	6.5	canopy	0	0	ground,vegetation	gleaning,scavenging	plants,vertebrates,invertebrates
209	*Picoides albolarvatus*	64.5	4.5	hole	0	0	trunk	probing	invertebrates
210	*Picoides arcticus*	74.5	3.5	hole	0	0	trunk	probing	invertebrates
211	*Picoides dorsalis*	55.75	5	hole	0	0	trunk	probing	plants,invertebrates
212	*Picoides pubescens*	25.5	4.5	hole	0	0	trunk	probing	plants,invertebrates
213	*Picoides tridactylus*	64.5	3.5	hole	0	0	trunk	probing	invertebrates

No.	**Species**	**Weight mean (g)**	**Clutch size mean**	**Nest position**	**Migration**[*]	**Nocturnal foraging** [**]	**Foraging substrate**	**Foraging method**	**Diet**
214	*Picoides villosus*	69.5	4	hole	0	0	trunk,vegetation	probing	invertebrates
215	*Picus canus*	158	8	hole	0	0	trunk	probing	invertebrates
216	*Picus viridis*	194	5	hole	0	0	ground,trunk,vegetation	gleaning,probing	invertebrates
217	*Pinicola enucleator*	59.5	4	canopy	0	0	vegetation	gleaning	plants
218	*Pipilo chlorurus*	30.5	6	canopy	1	0	ground,vegetation	gleaning	plants
219	*Pipilo maculatus*	39.8	4	ground	1	0	ground,vegetation	gleaning	invertebrates
220	*Piranga ludoviciana*	30	4	canopy	1	0	vegetation,air	pursuit,gleaning	plants,invertebrates
221	*Pooecetes gramineus*	24	4	ground	1	0	ground	gleaning	plants,invertebrates
222	*Porzana carolina*	85	11	ground	1	0	water,mud,ground	gleaning,grazing,probing	plants,invertebrates
223	*Prunella modularis*	19.5	4	ground	0	0	ground,vegetation	gleaning	plants,invertebrates
224	*Prunella montanella*	17.5	5	ground	1	0	ground,vegetation	gleaning	plants,invertebrates
225	*Pyrrhula pyrrhula*	29.5	4.5	canopy	0	0	vegetation	gleaning	plants,invertebrates
226	*Regulus calendula*	6	8	canopy	1	0	vegetation,air	gleaning	plants,invertebrates
227	*Regulus ignicapilla*	6	8	canopy	1	0	vegetation,air	gleaning	invertebrates
228	*Regulus regulus*	5.85	9	canopy	1	0	vegetation,air	gleaning	invertebrates
229	*Regulus satrapa*	7.5	8	canopy	1	0	vegetation,air	gleaning	plants,invertebrates
230	*Riparia riparia*	14.5	4.5	ground	1	0	air	pursuit	invertebrates
231	*Salpinctes obsoletus*	16.5	5	ground	1	0	ground	gleaning,digging,probing	vertebrates,invertebrates

No.	**Species**	**Weight mean (g)**	**Clutch size mean**	**Nest position**	**Migration***	**Nocturnal foraging****	**Foraging substrate**	**Foraging method**	**Diet**
232	*Saxicola rubetra*	19.5	5.5	ground	1	0	ground,vegetation	gleaning,pouncing	invertebrates
233	*Saxicola torquatus*	15	4	ground	1	0	ground,vegetation	gleaning,pouncing	invertebrates
234	*Sayornis saya*	18.25	4	ground	1	0	air	pursuit	invertebrates
235	*Seiurus aurocapilla*	21	4.5	ground	1	0	ground	gleaning	plants,invertebrates
236	*Seiurus noveboracensis*	18.7	4.5	ground	1	0	ground,vegetation	gleaning,digging	invertebrates
237	*Selasphorus rufus*	3.5	2	canopy	1	0	vegetation,air	gleaning	plants
238	*Serinus serinus*	11.25	4	canopy	1	0	ground,vegetation	gleaning	plants
239	*Setophaga ruticilla*	9.25	3.5	canopy	1	0	vegetation,air	pursuit,gleaning,pouncing	invertebrates
240	*Sialia currucoides*	30	4.5	hole	1	0	ground,vegetation,air	pursuit,gleaning,pouncing	plants,invertebrates
241	*Sialia mexicana*	29	5	hole	1	0	ground,vegetation	gleaning,pouncing	plants,invertebrates
242	*Sialia sialis*	30.5	4	hole	1	0	ground	gleaning,pouncing	plants,invertebrates
243	*Sitta canadensis*	10.5	6	hole	1	0	trunk,vegetation	gleaning,probing	plants,invertebrates
244	*Sitta carolinensis*	21.5	5	hole	0	0	trunk,vegetation	gleaning,probing	plants,invertebrates
245	*Sitta europaea*	22.5	5	hole	0	0	trunk,vegetation	gleaning,probing	plants,invertebrates
246	*Sitta pygmaea*	10.5	7	hole	0	0	trunk,vegetation	gleaning,probing	plants,invertebrates
247	*Sphyrapicus nuchalis*	52.4	4.5	hole	1	0	trunk	gleaning,probing	plants,invertebrates
248	*Sphyrapicus thyroideus*	54	2.5	hole	0	0	trunk	gleaning,probing	plants,invertebrates
249	*Spizella breweri*	11.5	4	canopy	1	0	ground,vegetation	gleaning	plants,invertebrates
250	*Spizella pallida*	12	4	ground	1	0	ground,vegetation	gleaning	plants,invertebrates

No.	**Species**	**Weight mean (g)**	**Clutch size mean**	**Nest position**	**Migration****	**Nocturnal foraging** **	**Foraging substrate**	**Foraging method**	**Diet**
251	*Spizella passerina*	12.9	4	canopy	1	0	ground,vegetation	gleaning	plants,invertebrates
252	*Stelgidopteryx serripennis*	14.3	6	ground	1	0	air	pursuit	invertebrates
253	*Stellula calliope*	3.15	4.5	canopy	1	0	vegetation	gleaning	plants
254	*Streptopelia orientalis*	219.5	2	canopy	1	0	ground,vegetation	gleaning	plants,invertebrates
255	*Streptopelia turtur*	134	2	canopy	1	0	ground	gleaning	plants,invertebrates
256	*Strix nebulosa*	839	4	canopy	0	1	ground	pouncing	vertebrates
257	*Sturnella neglecta*	97.7	4.5	ground	1	0	ground	gleaning,probing	plants,invertebrates
258	*Sturnus cineraceus*	81.5	6.5	hole	1	0	ground,vegetation	gleaning	invertebrates
259	*Sturnus vulgaris*	77.5	5.5	hole	0	0	ground,trunk,vegetation	gleaning	plants,invertebrates
260	*Surnia ulula*	329	7	canopy	0	1	ground,trunk,vegetation,air	pursuit,pouncing	vertebrates
261	*Sylvia atricapilla*	20	5	canopy	1	0	vegetation	gleaning	plants,invertebrates
262	*Sylvia borin*	19	5	canopy	1	0	vegetation,air	pursuit,gleaning	plants,invertebrates
263	*Sylvia cantillans*	11.5	5	canopy	1	0	vegetation	gleaning	plants,invertebrates
264	*Sylvia communis*	1615.5	5	canopy	1	0	vegetation	gleaning	plants,invertebrates
265	*Sylvia conspicillata*	10.5	4.5	canopy	1	0	vegetation	gleaning	invertebrates
266	*Sylvia curruca*	13.75	5	canopy	1	0	vegetation	gleaning	invertebrates
267	*Sylvia melanocephala*	18.5	4.5	canopy	1	0	vegetation	gleaning	plants,invertebrates
268	*Sylvia undata*	8.5	4	canopy	0	0	vegetation	gleaning	plants,invertebrates
269	*Tachycineta bicolor*	19	4	hole	1	0	air	pursuit,gleaning,pouncing	invertebrates

No.	Species	Weight mean (g)	Clutch size mean	Nest position	Migration*	Nocturnal foraging **	Foraging substrate	Foraging method	Diet
270	*Tachycineta thalassina*	15	5	hole	1	0	air	pursuit,gleaning,pouncing	invertebrates
271	*Tetrao urogallus*	2900	7	ground	0	0	ground,vegetation	gleaning,grazing	plants,invertebrates
272	*Thryomanes bewickii*	9	5	hole	0	0	ground,vegetation	gleaning	invertebrates
273	*Tringa ochropus*	86	3	ground	1	0	water,mud,ground	gleaning,probing	invertebrates
274	*Troglodytes aedon*	11.5	6	hole	1	0	ground,trunk,vegetation	gleaning	invertebrates
275	*Troglodytes pacificus*	10	6	hole	1	0	ground,trunk,vegetation	gleaning	invertebrates
276	*Troglodytes troglodytes*	9	6	hole	1	0	ground,trunk,vegetation	gleaning	invertebrates
277	*Turdus iliacus*	63	5	ground	1	0	ground,trunk,vegetation	gleaning	plants,invertebrates
278	*Turdus merula*	95	4	canopy	0	0	ground,vegetation	gleaning,digging	plants,invertebrates
279	*Turdus migratorius*	76.5	4	canopy	1	0	ground,vegetation	gleaning	plants,invertebrates
280	*Turdus obscurus*	89	5	canopy	1	0	ground,vegetation	gleaning	plants,invertebrates
281	*Turdus pallidus*	77	4.5	canopy	1	0	ground,vegetation	gleaning	plants,invertebrates
282	*Turdus philomelos*	78.5	5	canopy	1	0	ground,vegetation	gleaning,digging	plants,invertebrates
283	*Turdus pilaris*	111	5.5	canopy	1	0	ground,vegetation	gleaning,digging	plants,invertebrates
284	*Turdus torquatus*	114	4	canopy	1	0	ground,vegetation	gleaning	plants,invertebrates
285	*Turdus viscivorus*	130	4	canopy	0	0	ground,vegetation	gleaning,digging	plants,invertebrates
286	*Tyrannus tyrannus*	41	3.5	canopy	1	0	air	pursuit,pouncing	invertebrates
287	*Tyrannus verticalis*	38.5	4	canopy	1	0	air	pursuit	invertebrates

No.	**Species**	**Weight mean (g)**	**Clutch size mean**	**Nest position**	**Migration**[*]	**Nocturnal foraging**[**]	**Foraging substrate**	**Foraging method**	**Diet**
288	*Upupa epops*	67.5	6	hole	1	0	ground	gleaning,digging	invertebrates
289	*Vermivora celata*	9.5	5	ground	1	0	vegetation	gleaning	invertebrates
290	*Vermivora ruficapilla*	10.3	4.5	ground	1	0	vegetation	gleaning	invertebrates
291	*Vireo cassinii*	15.5	3.5	canopy	1	0	vegetation	gleaning	invertebrates
292	*Vireo gilvus*	14.7	4	canopy	1	0	vegetation	gleaning	invertebrates
293	*Vireo olivaceus*	17	4	canopy	1	0	vegetation	gleaning	invertebrates
294	*Vireo plumbeus*	14.15	4	canopy	1	0	vegetation	gleaning	invertebrates
295	*Wilsonia pusilla*	7.5	5	ground	1	0	vegetation	gleaning	invertebrates
296	*Zenaida macroura*	130.5	2	canopy	0	0	ground,vegetation	gleaning	plants
297	*Zonotrichia leucophrys*	29.75	4.5	ground	1	0	ground,vegetation	gleaning	invertebrates
298	*Zoothera dauma*	109	4	canopy	0	0	ground,vegetation	gleaning	plants,invertebrates
299	*Zoothera naevia*	82.5	4	canopy	1	0	ground,vegetation	gleaning	invertebrates

[*] 1 indicates a migratory species, while 0 means a non-migratory one.

[**] 1 indicates a species actively foraging at night, while 0 represents a species without nocturnal foraging activities.

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Chapter IV: Effects on β-diversity

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Georgiev, K.B., Bässler, C., Feldhaar, H., Heibl, C., Karasch, P., Müller, J., Perlik, M., Weiss, I., Thorn, S. (submitted). Windthrow and salvage logging cause long-lasting changes in the β-diversity of multiple species groups

IV.1 Abstract

The response of biodiversity to natural and anthropogenic disturbances is a central topic in applied ecology. Climate change has altered forest disturbance regimes, resulting in global increases in stand-replacing disturbances that subsequently include the removal of trees (salvage logging). Yet, the mid- to long-term effects of these disturbances on β-diversity are unclear, as is how potential differences are governed by differences in species relative abundances. We compared the β-diversity of 13 taxonomic groups in intact forest plots, disturbed unlogged plots, and salvage-logged plots 11 years after a windthrow. Hill numbers were used to quantify differences in between-treatment β-diversity and the degree of within-treatment β-diversity for rare, common, and dominant species. Permutational multivariate analyses of variance based on 1660 species revealed that the between-treatment β-diversity of all groups of saproxylic (dependent on deadwood) organisms differed significantly between logged, unlogged, and intact forest plots, for rare, common, and dominant species. For all non-saproxylic groups, between-treatment β-diversity differed between intact forest and both logged and unlogged plots, while for rare species differences in only three groups were detected between logged and unlogged plots. Compared to intact forests, both natural disturbance and salvage logging reduced within-treatment β-diversity, causing community homogenization for most saproxylic groups and half of the non-saproxylic groups. However, within-treatment β-diversity between disturbed unlogged and salvage-logged plots differed only for three groups. Difference in between- and within-treatment β-diversity were more pronounced for rare species than for common and dominant ones.

Synthesis and applications: Our study suggests that both windthrow and salvage logging drive changes in between-treatment β-diversity, whereas windthrow alone seems to drive changes in within-treatment β-diversity. Over a decade after the windthrow at the studied site, the effect of subsequent salvage logging on within-treatment β-diversity was no longer

detectable but the effect on between-treatment β-diversity persisted, with more prominent changes in saproxylic groups and rare species than in non-saproxylic groups or common and dominant species. Hence, salvage logging needs to be carefully weighed against its long-lasting impact on communities of rare species.

IV.2 Introduction

Human activities have led to global declines of biodiversity at unprecedented rates (Dirzo et al., 2014). However, studies that rely on local species richness (α-diversity) as a measure of biodiversity decline may not capture the multiple responses of biodiversity to environmental change (Hillebrand et al., 2018; Lyashevska et al., 2012). A more informative approach is to assess the compositional differences across sites, i.e., β-diversity (Socolar et al., 2016). By exploring compositional differences between local assemblages, β-diversity studies have revealed a global increase in the compositional similarity of biological communities (Mori et al., 2018). A loss of β-diversity has negative effects on ecosystem functioning (i.e., productivity, nutrient cycling and decomposition) and stability and therefore on the provision of ecosystem services as well (Cardinale et al., 2012).

Forests cover ~30% of the Earth's terrestrial surface (Keenan et al., 2015), sustain ecosystem services, regulate climate and rainfall, and host the majority of terrestrial biodiversity (FAO et al., 2020). Natural disturbances, such as wildfire, windthrow, and insect outbreaks, are a key component of forest ecosystems and forest life cycles (Turner, 2010; Wohlgemuth et al., 2019). Disturbances can create habitats with high structural diversity that host species-rich communities (Swanson et al., 2011). Furthermore, forest stands with high structural diversity are more resilient against possible future disturbances (Dymond et al., 2014; Seidl, Rammer, et al., 2014). However, climate change has led to a strong increase of stand-replacing forest disturbances, changing disturbances regimes (Senf et al., 2021; Westerling et al., 2006).

Natural disturbances have multiple positive effects on biodiversity (Thom et al., 2016) but influence β-diversity in different ways. For instance, high-severity wildfires can create more homogeneous communities, thus reducing β-diversity, as they foster disturbance-tolerant or rapidly colonizing species. By contrast, low-severity wildfires may increase β-diversity by creating heterogeneous habitats that promote heterogeneous species communities (Burkle et al., 2015). Windthrows, as another example, lead to changes in community composition for pollinators and saproxylic beetles but do not result in community homogenization per se (Wermelinger et al., 2017).

Following a natural forest disturbance, the most common management strategy employed worldwide is salvage logging (Lindenmayer et al., 2008). However, this practice diminishes most of the disturbance-created heterogeneity and largely undermines the positive effects of natural disturbances on ecosystem services (Leverkus, Gustafsson, et al., 2020) and biodiversity (Thorn et al., 2018). The adverse effects of salvage logging include changes of the community composition of saproxylic taxa (Thorn et al., 2018), as well as flowers and pollinators after wildfire, and decrease in β-diversity of pollinators within a decade post-fire (Heil et al., 2018). Following a windthrow, the β-diversity of the arthropod communities of logged and unlogged disturbed sites does not differ (Wermelinger et al., 2017), but rigorous statistical tests are still missing.

Biological communities consist of many rare and a few common species, evidenced by differences in species abundance distributions (McGill et al., 2007). β-diversity reflects how the dominance and identity of species in communities shift over space and time (Socolar et al., 2016). To quantify these changes in β-diversity, a statistical framework based on Hill numbers can be applied that takes into account the differences in species relative abundances (Gotelli et al., 2013). A recent study applying this approach has demonstrated that changes in community dissimilarities caused by salvage logging become more pronounced for rare species over time (Thorn, Chao, Bernhardt-Römermann, et al., 2020). Whether the effects of natural forest disturbance and associated salvage logging on β-diversity differ as a function of species relative abundances is still unclear.

This study investigated the effects of windthrow disturbance and subsequent salvage logging on the β-diversity of 13 taxonomic groups 11 years after a major windthrow. Specifically, a framework based on Hill numbers was used to test: i) whether windthrow disturbance and/or salvage logging lead to a between-treatment β-diversity different from that of intact forest; ii) whether windthrow disturbance and/or salvage logging lead to differences in within-treatment β-diversity; and iii) whether the effects of β-diversity differ depending on species relative abundance. Salvage logging is conducted in forests that have already been disturbed, therefore increasing the overall level of disturbance and possibly acting as an environmental filter (Buma et al., 2011). We hypothesized that within-treatment β-diversity should decrease with increasing degree of disturbance. Thus, we expected that the highest β-diversity, respectively the lowest community homogenization, would be in intact forests, followed by disturbed unlogged forests and salvage-logged forests, in which within-treatment β-diversity would be the lowest and community homogenization the highest. Since only a few specialized species are likely to persist in sites subjected to natural and anthropogenic disturbances, we expected that changes in between- and within-treatment β-diversity would be most pronounced for rare species.

IV.3 Materials and methods

IV.3.1 Study area and experimental design

The study was conducted in the Bavarian Forest National Park (BFNP) (Fig. IV-1), southeastern Germany (49°070 N, 13°310 E). The vegetation in the park is dominated by subalpine Norway spruce (*Picea abies* (L.) H. Karst) forests. Annual precipitation ranges from 1300 to 1800 mm, and the annual mean air temperature from 3.0 to 4.0°C in valleys and summit areas but 8°C in medium slopes areas (Bässler et al., 2010, updated to 2019).

The windstorm Kyrill struck the BFNP on January 16, 2007, felling ~1000 ha of mature Norway spruce forest (Thorn et al., 2017). Post-disturbance logging operations were conducted until August 2007 and removed ~800 ha of the wind-felled trees. The rest of the windthrow, ~200 ha, was left unlogged and was used to establish study plots for biodiversity surveys. During the logging operations, branches were cut off the trunks and left on the ground, and the main trunks were removed. The amount of deadwood in all logged areas was reduced from around 300 m^3/ha to around 50 m^3/ha (details in Thorn et al., 2015, 2014).

Seventy-six study plots were included in this study: 32 logged plots, 20 unlogged plots, and 24 plots of intact forest not affected by the windthrow (Fig. IV-1).

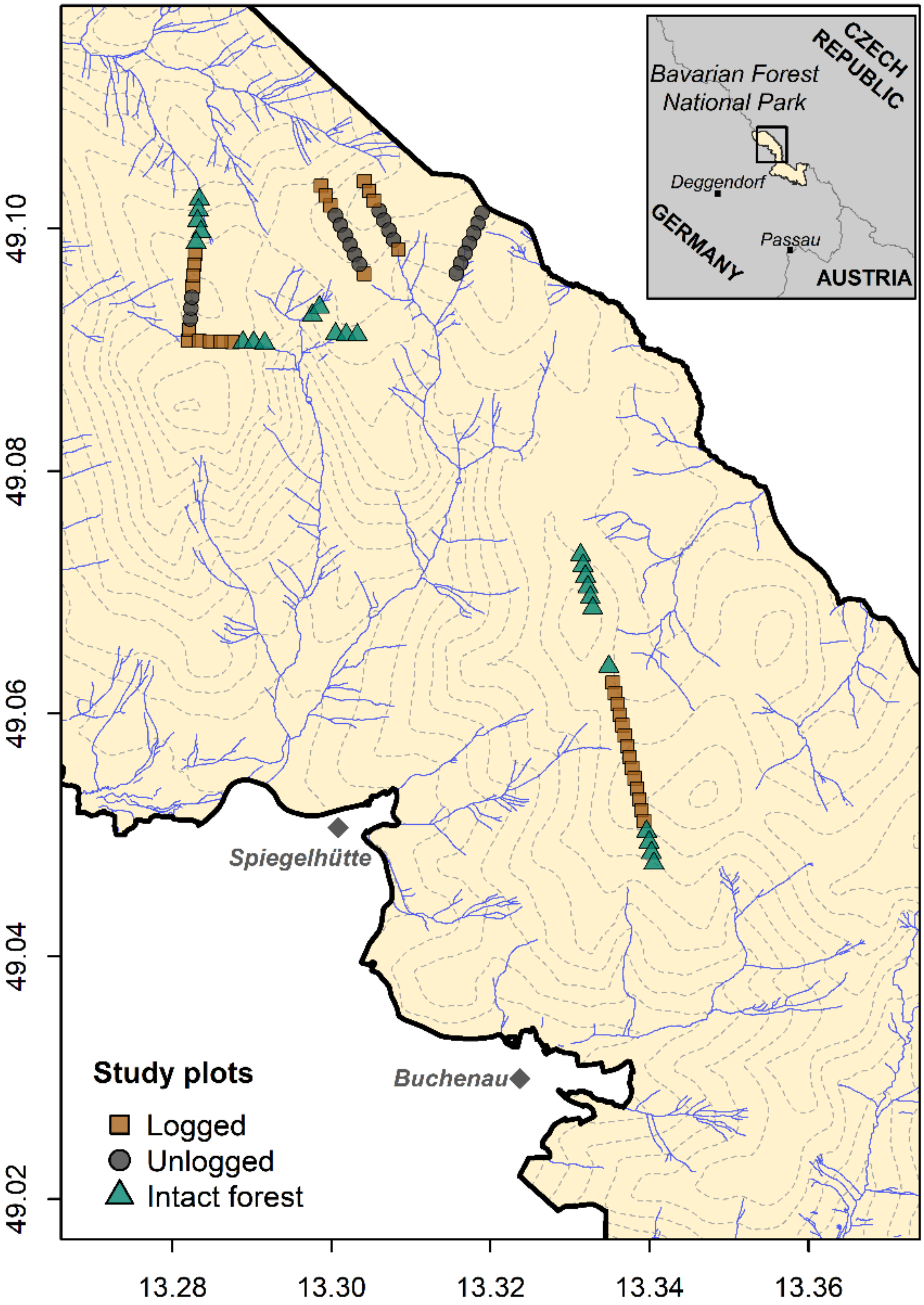

Figure IV-1: Study area and sampling plots in the Bavarian Forest National Park. The contour lines represent 50-m differences in elevation above sea level; the blue lines represent streams.

IV.3.2 Biodiversity sampling

Biodiversity data were collected 11 years after the disturbance, in 2018. Thirteen taxonomic groups were sampled: epigeic bryophytes, epigeic lichens, epixylic bryophytes, epixylic lichens, vascular plants, epigeic spiders, ants, bees, and wasps, epigeic beetles, saproxylic beetles (i.e., beetles involved in or dependent on the fungal decay of wood; Alexander, 2008), non-saproxylic beetles, wood-inhabiting fungi, and birds. Bees and wasps, saproxylic beetles, and non-saproxylic beetles were trapped using flight-interception traps placed at the centroid of the study plots (Thorn et al., 2014). Epigeic beetles, epigeic spiders, and ants were trapped using two pitfall traps per plot. Bryophytes and lichens on deadwood and on the ground were mapped separately as epixylic and epigeic, respectively. Wood-inhabiting fungi, epixylic bryophytes, and epixylic lichens were sampled on the same five randomly selected deadwood objects around each plot centroid (Thorn, Bässler, et al., 2016). Vascular plants, epigeic mosses, and lichens were sampled on circular plots (relevees) of 200 m^2 around each plot centroid. Birds were surveyed five times during the breeding season by applying fixed-radius (50-m) point-counts with 5-min count intervals per plot (Thorn, Werner, et al., 2016). All bird counts were conducted during the morning hours under good weather conditions. Sampling details are provided in Table IV-S1.

IV.3.3 Data analysis

Statistical analyses were carried out using R statistical software version 4.0.1 (R Development Core Team, 2020). Venn diagrams were used to visualize γ-diversity and the number of unique and shared species on logged, unlogged, and intact forest plots (Fig. IV-2). Differences in β-diversity between the three treatments were quantified using a statistical framework based on Hill numbers (Hill, 1973). Hill numbers are defined by a parameter q that reflects the sensitivity to a species relative occurrence probability. Setting $q = 0$ yields the richness-based Sørensen index, in which all species are weighted equally and a relatively large weight is assigned to rare species. Setting $q = 1$ yields the Horn index, which weights all occurrences equally, i.e., each species is weighted according to its incidence-based frequency; as a result, this index is sensitive to common species. Setting $q = 2$ yields the frequency-based Morisita-Horn index, which is sensitive to dominant species and assigns little weight to common and rare species. Therefore, different parameters of q reflect patterns of β-diversity, emphasizing rare ($q = 0$), common ($q = 1$), and dominant species (q = 2) in the dataset. According to this classification, in our analysis rare species were those with only a few observations on the study plots.

For each taxonomic group, pairwise dissimilarities between plots were calculated for q ={0, 1, 2} using the 'SpadeR' package (Chao et al., 2016). The obtained dissimilarity matrices were subjected to a permutational multivariate analysis of variance (PERMANOVA), with 999 permutations, as provided by the '*adonis'* function in the 'vegan' package (Oksanen et al., 2018). This procedure allowed testing for significant differences in species composition among treatments. The p-values for multiple testing were adjusted using the Bonferroni correction (Table IV-1). In addition, pairwise dissimilarities for q ={0, 1, 2} were subjected to a multivariate homogeneity of group dispersions analysis (Anderson et al., 2006), calculated using the function '*betadisper*' in the 'vegan' package (Oksanen et al., 2018). This analysis tests whether the average within-treatment β-diversity (β-dispersion), measured by the average distance to the group centroid, differs between treatments. High β-dispersion indicates heterogeneous communities, and low β-dispersion homogenous communities. Since β-dispersion was measured within treatments in one year, the results represent community homogenization, not biotic homogenization over time, *sensu* Olden and Rooney (2006).

Differences in within-treatment β-diversity between the three treatments were assessed in an ANOVA, followed by a Tukey's Honest Significant Difference test using the function '*TukeyHSD.betadisper*'. The results for all taxonomic groups and Hill numbers are presented in Table IV-S2 and Fig. IV-S1 and IV-S2.

IV.4 Results

Among the 1660 species recorded in our study, non-saproxylic beetles (n = 335) were the most species-rich group, followed by epigeic beetles (n = 313), saproxylic beetles (n = 221), epigeic spiders (n = 138), bees and wasps (n = 90), epigeic bryophytes (n = 71), wood-inhabiting fungi (n = 70), vascular plants (n = 61), epigeic lichens (n = 49), epixylic bryophytes (n = 44), and birds (n = 43), while the lowest number of species occurred in two groups, epigeic lichens (n = 14) and ants (n = 13) (Fig. IV-2).

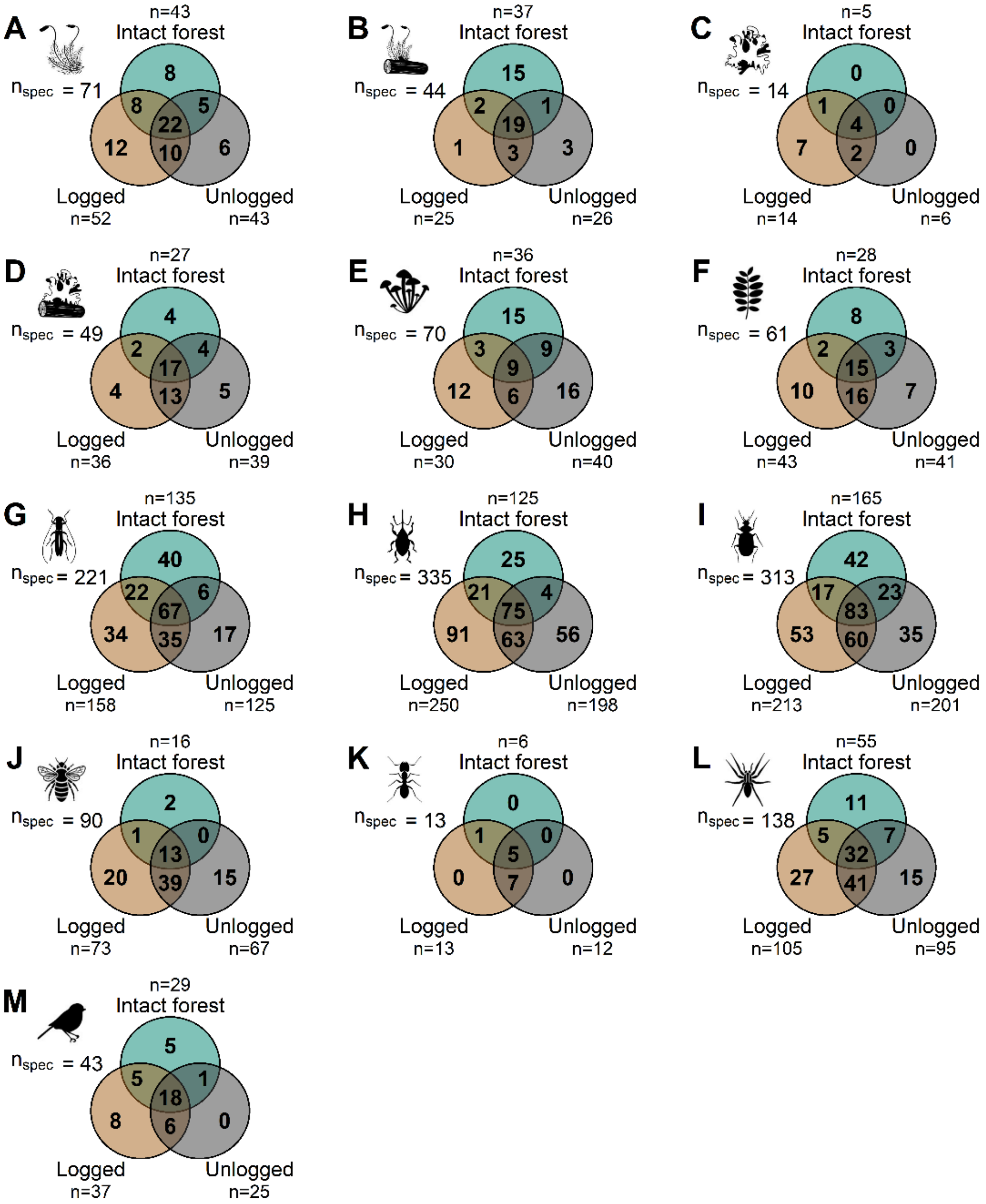

Figure IV-2: Venn diagrams depicting the number of unique and shared species on logged, unlogged, and intact forest plots for 13 taxonomic groups. n_{spec} indicates the total number of sampled species in the respective species group. A) epigeic bryophytes, B) epixylic bryophytes, C) epigeic lichens, D) epixylic lichens, E) wood-inhabiting fungi, F) vascular plants, G) saproxylic beetles, H) non-saproxylic beetles, I) epigeic beetles, J) bees and wasps, K) ants, L) epigeic spiders, and M) birds.

IV.3.1 Between-treatment β-diversity

The PERMANOVA revealed that the between-treatment β-diversity of saproxylic taxa (i.e., epixylic bryophytes and lichens, wood-inhabiting fungi, and saproxylic beetles) differed significantly between logged, unlogged, and intact forest plots for rare (q = 0), common (q = 1), and dominant species (q = 2) (Table IV-1).

Table IV-1: Pairwise permutational multivariate analysis of variance (PERMANOVA) comparing between-treatment β-diversity for logged, unlogged, and intact forest plots with respect to Hill numbers q = {0,1,2} and 13 taxonomic groups. The p-values were adjusted for multiple testing using the Bonferroni correction.

Taxonomic group	**Treatment**	**F-statistic**			**R-squared**			**Adj. p-value**		
		q=0	**q=1**	**q=2**	**q=0**	**q=1**	**q=2**	**q=0**	**q=1**	**q=2**
Epigeic bryophytes	logged-unlogged	2.552	2.837	**3.222**	0.053	0.058	**0.065**	0.081	0.084	**0.042**
	logged-forest	**4.993**	**4.236**	2.887	**0.106**	**0.092**	0.064	**0.003**	**0.009**	0.081
	unlogged-forest	**3.490**	**3.959**	**4.174**	**0.077**	**0.086**	**0.090**	**0.018**	**0.018**	**0.021**
Epixylic bryophytes	logged-unlogged	2.226	3.110	2.912	0.058	0.080	0.075	0.225	0.075	0.102
	logged-forest	**5.949**	**9.998**	**11.526**	**0.139**	**0.213**	**0.238**	**0.003**	**0.003**	**0.003**
	unlogged-forest	**7.443**	**9.978**	**9.703**	**0.167**	**0.212**	**0.208**	**0.003**	**0.003**	**0.003**
Epigeic lichens	logged-unlogged	**4.862**			**0.132**			**0.018**		
	logged-forest	**7.657**			**0.180**			**0.003**		
	unlogged-forest	**5.476**			**0.180**			**0.018**		
Epixylic lichens	logged-unlogged	**20.542**	**20.486**	**21.181**	**0.363**	**0.363**	**0.370**	**0.003**	**0.003**	**0.003**
	logged-forest	**29.433**	**39.016**	**40.470**	**0.443**	**0.513**	**0.522**	**0.003**	**0.003**	**0.003**
	unlogged-forest	**59.388**	**58.821**	**60.834**	**0.616**	**0.614**	**0.622**	**0.003**	**0.003**	**0.003**
Wood-inhabiting fungi	logged-unlogged	**19.903**	**20.111**	**19.205**	**0.369**	**0.372**	**0.361**	**0.003**	**0.001**	**0.001**
	logged-forest	**13.450**			**0.278**			**0.003**		
	unlogged-forest	**26.444**			**0.417**			**0.003**		
Vascular plants	logged-unlogged	2.572	0.456		0.058	0.011		0.129	1.000	
	logged-forest	**14.175**	**64.318**		**0.272**	**0.629**		**0.003**	**0.003**	
	unlogged-forest	**21.331**	**56.590**		**0.337**	**0.574**		**0.003**	**0.003**	
Saproxylic beetles	logged-unlogged	**11.450**	**13.587**	**17.717**	**0.120**	**0.139**	**0.174**	**0.003**	**0.003**	**0.003**
	logged-forest	**173.278**	**222.252**	**130.305**	**0.681**	**0.733**	**0.617**	**0.003**	**0.003**	**0.003**
	unlogged-forest	**214.339**	**304.260**	**241.156**	**0.726**	**0.790**	**0.749**	**0.003**	**0.003**	**0.003**

Taxonomic group	**Treatment**	**F-statistic**			**R-squared**			**Adj. p-value**		
		q=0	**q=1**	**q=2**	**q=0**	**q=1**	**q=2**	**q=0**	**q=1**	**q=2**
Non-saproxylic beetles	logged-unlogged	1.238	0.474	1.023	0.029	0.011	0.024	0.651	1.000	1.000
	logged-forest	**64.946**	**112.487**	**33.043**	**0.619**	**0.738**	**0.452**	**0.003**	**0.003**	**0.003**
	unlogged-forest	**58.621**	**117.882**	**33.786**	**0.594**	**0.747**	**0.458**	**0.003**	**0.003**	**0.003**
Epigeic beetles	logged-unlogged	3.234	1.250	0.644	0.071	0.029	0.015	0.108	0.804	1.000
	logged-forest	**62.087**	**34.761**	**20.707**	**0.608**	**0.465**	**0.341**	**0.003**	**0.003**	**0.003**
	unlogged-forest	**40.490**	**36.964**	**27.241**	**0.503**	**0.480**	**0.405**	**0.003**	**0.003**	**0.003**
Bees and wasps	logged-unlogged	1.426	**3.785**	**5.727**	0.033	**0.083**	**0.120**	0.570	**0.014**	**0.001**
	logged-forest	**83.359**			**0.698**			**0.003**		
	unlogged-forest	**93.917**			**0.723**			**0.003**		
Ants	logged-unlogged	**5.805**	0.595	0.538	**0.121**	0.014	0.013	**0.006**	0.617	0.633
	logged-forest	**60.108**			**0.619**			**0.003**		
	unlogged-forest	**52.212**			**0.585**			**0.003**		
Epigeic spiders	logged-unlogged	1.867	0.341	0.263	0.043	0.008	0.006	0.297	1.000	1.000
	logged-forest	**166.049**	**343.348**	**294.145**	**0.806**	**0.896**	**0.880**	**0.003**	**0.003**	**0.003**
	unlogged-forest	**162.773**	**255.889**	**195.149**	**0.803**	**0.865**	**0.830**	**0.003**	**0.003**	**0.003**
Birds	logged-unlogged	**6.538**	**4.750**	3.529	**0.116**	**0.087**	0.066	**0.003**	**0.003**	0.057
	logged-forest	**54.034**	**47.098**	**32.153**	**0.500**	**0.466**	**0.373**	**0.003**	**0.003**	**0.003**
	unlogged-forest	**96.980**	**96.433**	**71.294**	**0.698**	**0.697**	**0.629**	**0.003**	**0.003**	**0.003**

The only exception was epixylic bryophytes, in which between-treatment β-diversity did not differ between logged and unlogged plots for all Hill numbers. In contrast to saproxylic taxa, the differences in the between-treatment β-diversity of non-saproxylic taxa between treatments decreased when moving from rare (q = 0) to common (q = 1) to dominant (q = 2) species. For all nine non-saproxylic taxa, their between-treatment β-diversity in intact forest plots differed significantly from that in either logged or unlogged plots. Differences in between-treatment β-diversity between logged and unlogged plots were determined for only three of the nine non-saproxylic taxa: epigeic bryophytes, ants, and birds (Table IV-1). Epixylic bryophytes, vascular plants, non-saproxylic beetles, and epigeic spiders were the only groups, in which between-treatment β-diversity between logged and unlogged forests did not differ significantly (Table IV-1).

IV.3.2 Within-treatment β-diversity

Among rare species (q = 0), within-treatment β-diversity differed significantly for seven taxonomic groups in all three treatments (Fig. IV-3, Table IV-S2). A lower within-treatment β-diversity of communities on unlogged plots than in intact forest was determined for five taxonomic groups: epixylic lichens, wood-inhabiting fungi, saproxylic beetles, bees and wasps, and ants (Fig. IV-3, Table IV- S2). This finding indicated that disturbance led to more homogeneous communities. Compared to intact forest, disturbances on the logged and unlogged plots increased the within-treatment β-diversity of epigeic beetles only (Fig. IV-3I).

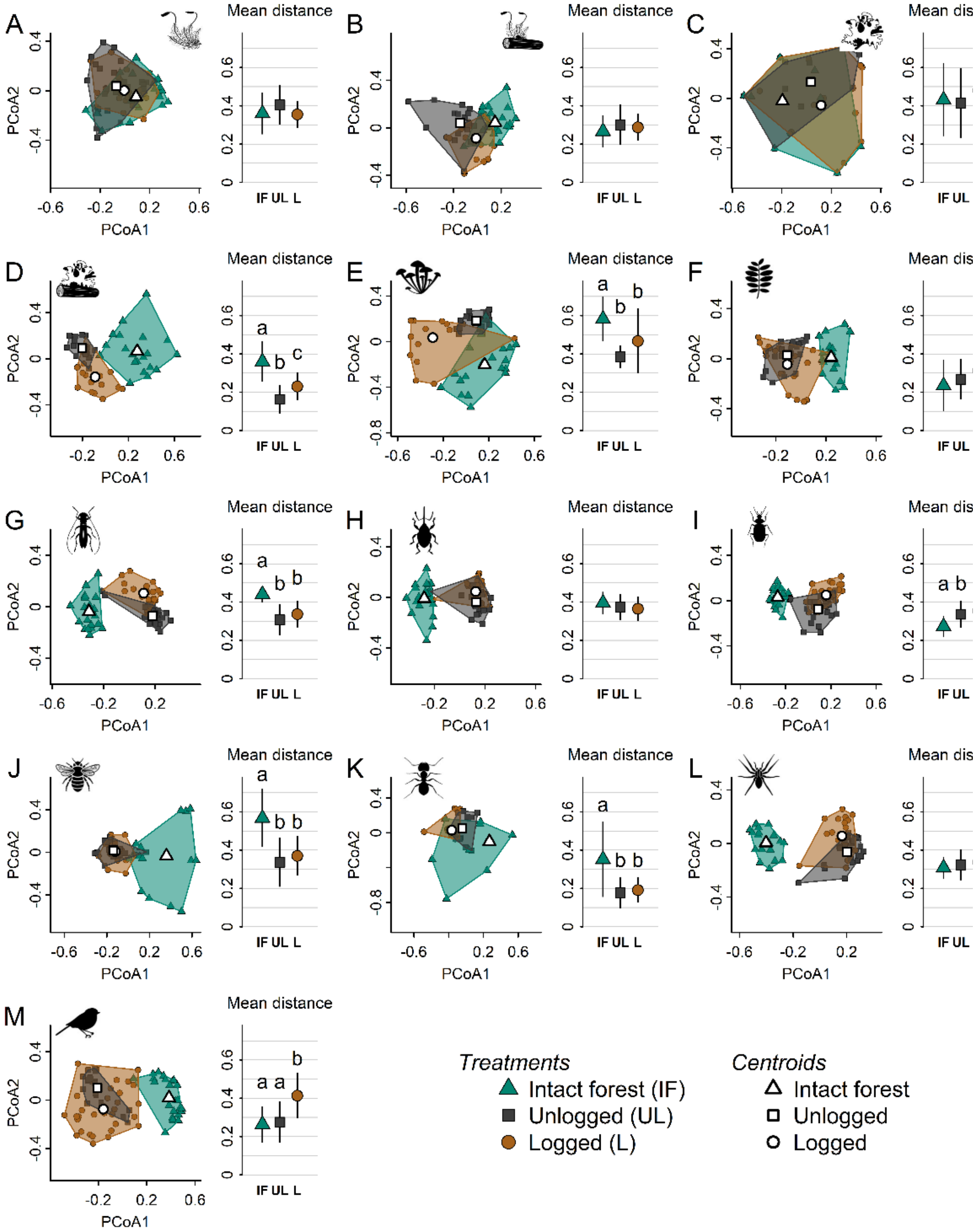

Figure IV-3: Multivariate dispersion of community dissimilarity (within-treatment β-diversity) along with the respective centroid for rare species (q = 0) of: A) epigeic bryophytes, B) epixylic bryophytes, C) epigeic lichens, D) epixylic lichens, E) wood-inhabiting fungi, F) vascular plants, G) saproxylic beetles, H) non-saproxylic beetles, I) epigeic beetles, J) bees and wasps, K) ants, L) epigeic spiders, and M) birds in logged, unlogged, and intact forest plots. The right-hand plots show the mean (±SD) distance from the centroid within every treatment; the lower-case letters indicate significantly different ($p < 0.05$) dispersions between treatments. The smaller the mean distance from the centroid, the less the within-treatment β-diversity.

Salvage logging did not decrease the within-treatment β-diversity of any of the investigated taxonomic groups. For wood-inhabiting fungi (Fig. IV-3E), saproxylic beetles (Fig. IV-3G), bees and wasps (Fig. IV-3J), and ants (Fig. IV-3K), within-treatment β-diversity of the communities in the logged and unlogged plots was similar, and less than that of the communities in intact forest. Epixylic lichens (Fig. IV-3D) and birds (Fig. IV-3M) were the only groups in which their communities had a higher within-treatment β-diversity on logged than on unlogged disturbed plots, indicating that salvage logging led to more heterogeneous communities.

Common ($q = 1$) and dominant species ($q = 2$), differed significantly in their within-treatment β-diversity only for epixylic lichens, saproxylic beetles, and birds (Fig. IV-S1 and IV-S2, Table IV-S2). For epixylic lichens, within-treatment β-diversity on logged and unlogged plots was similar and significantly lower than on intact forest plots, for both common and dominant species (Fig. IV-S1D, IV-S2D). For saproxylic beetles, the least within-treatment β-diversity, and thus the strongest community homogenization, occurred on unlogged plots for common species (Fig. IV-S1G) and on unlogged and intact forest plots for dominant species (Fig. IV-S2G). Bird communities were the most homogeneous on unlogged and intact forest plots (Fig. IV-S1M, IV-S2M).

IV.5 Discussion

Over a decade after a windthrow disturbance, both windthrow and salvage logging had led to significant changes in the between-treatment β-diversity of 13 taxonomic groups. This finding was most pronounced for saproxylic taxa and for rare species ($q = 0$). Among rare species, windthrow disturbance led to more homogeneous communities (i.e., less within-treatment β-diversity) for five groups and to more heterogeneous communities for two groups. However, salvage logging did not lead to community homogenization in any species group; rather, it created more heterogeneous communities for epixylic lichens, saproxylic beetles, and birds.

An important contribution of our study is that it was conducted 11 years after a windthrow, which is twice as long as ~70% of currently available salvage logging studies (reviewed in Thorn et al. 2018). Indeed, alterations in between- and within-treatment β-diversity were still present 11 years after the windthrow disturbance. Disturbance effects on biodiversity change with the amount of time after a disturbance (Royo et al., 2016), such that differences in β-diversity are more likely to decrease over the course of forest succession. Our study revealed that, for all taxonomic groups, their between-treatment β-diversity differed between intact forest and disturbed sites (Table IV-1), which indicates that differences in community composition induced by the windthrow disturbance can persist for over a decade thereafter. Only half of the studied groups showed differences within-treatment β-diversity, mainly between communities on intact forest plots vs. unlogged and logged plots (Fig. IV-3). Because the effects of salvage logging diminish over time (Leverkus, Polo, et al., 2020), this finding suggests that over the course of succession the differences between logged and unlogged forests disappear faster than the differences between intact forest and unlogged plots.

IV.5.1 Between-treatment β-diversity

The observed changes in between-treatment β-diversity for all 13 taxonomic groups across the three treatments (Table IV-1) were not surprising, because natural disturbances and salvage logging alter both habitat structure and resource availability, resulting in large differences compared to intact forest (Lindenmayer et al., 2008). Unlike unlogged and logged disturbed forests, intact forests provide greater vertical heterogeneity, which may promote the species richness of taxa that use resources in the forest canopy, such as birds, fungi, and saproxylic beetles (Heidrich et al., 2020). For example, vertical heterogeneity was shown to impact the community composition of saproxylic beetles, with differences between the communities found near the ground vs. those in the forest canopy (Seibold et al., 2018). Thus, in intact forests, vertical heterogeneity may be an important determinant of community composition. Moreover, while intact forests are characterized by shady, moist conditions, a windthrow creates a sudden shift towards higher insolation and increased desiccation (Swanson et al., 2011; Wohlgemuth et al., 2019), leading to a turnover from species adapted to closed forests to species adapted to open habitats. This was observed in our study, as the between-treatment β-diversity of all non-saproxylic groups differed significantly between intact forest and both logged and unlogged plots whereas there were few differences between logged and unlogged plots (Table IV-1).

Among non-saproxylic groups adapted to thrive in open habitats, such as vascular plants, epigeic beetles, and spiders, the between-treatment β-diversity differed between intact forest and both logged and unlogged plots but not between logged and unlogged plots (Table IV-1). Among saproxylic groups, the between-treatment β-diversity of epixylic lichens, wood-inhabiting fungi, and saproxylic beetles differed between unlogged and logged forests, irrespective of the Hill number (Table IV-1). The most likely reason for these differences is that wind-disturbed forests contain large amounts of deadwood, which are removed by salvage logging operations (Waldron et al., 2014). Although 11 years after the windthrow large amounts of deadwood on both unlogged and logged plots have decomposed, the persistence of logs on the unlogged plots may explain the differences in β-diversity between logged and unlogged sites. Epixylic bryophytes were the only saproxylic group that did not respond to deadwood removal by salvage logging (Table IV-1). However, because epixylic bryophytes use deadwood only as a growth substrate, it was unlikely that the larger amount of deadwood on unlogged plots would have affected their community composition.

Similarly, the between-treatment β-diversity of half of the non-saproxylic groups (vascular plants, non-saproxylic beetles, epigeic beetles, and epigeic spiders) did not significantly differ between logged and unlogged forests (Table IV-1). This finding is not surprising, since those species groups do not directly depend on deadwood.

IV.5.2 Within-treatment β-diversity

Stand-replacing natural disturbances lead to drastic changes in forest structure (Turner, 2010). Because salvage logging takes place within the first few months after a natural disturbance, it is generally considered to be an additional disturbance that interacts with the previous natural disturbance (Leverkus, Lindenmayer, et al., 2018). Accordingly, we hypothesized that a first wave of community homogenization (reduction in within-treatment β-diversity) would occur in response to the windthrow disturbance, followed by a second wave caused by salvage logging. For rare species ($q = 0$) in five of the studied groups, within-treatment β-diversity on the unlogged and logged plots was lower than in intact forests (Fig. IV-3). However, a direct comparison between unlogged and logged plots showed either a lack of differences between them or higher within-treatment β-diversity on the logged plots for wood-inhabiting fungi (Fig. IV-3). These results demonstrate that a windthrow disturbance can lead to communities that are more homogeneous than those in intact forest. However, in contrast to our expectation, salvage logging did not further homogenize the communities of wind-disturbed forests, irrespective of species relative abundance, i.e., different levels of q. For pollinators (bees and wasps) and saproxylic beetles, our findings of community homogenization are in line with those of Wermelinger et al. (2017), who studied wind-felled spruce forests. The absence of an increasing degree of homogenization with increasing disturbance can be understood as follows. The response of species to a disturbance depends on the biological legacies left behind by the disturbance (Lindenmayer et al., 2008). In a wind-felled forest, these legacies include the amounts of lying and standing deadwood, structural heterogeneity, and a pit-and-mound microtopography (Waldron et al., 2014). Salvage logging after a windthrow reduces the amount of deadwood, thus mostly affecting saproxylic groups (Thorn et al., 2018). On the logged plots of our study, ~50 m^3/ha of deadwood was left on the ground after salvage logging that sustained both saproxylic and non-saproxylic species. This would account for similar community homogenization of saproxylic groups on logged plots. However, compared to unlogged disturbed forests, salvage logging led to community heterogenization, and thus a higher within-treatment β-diversity, for rare species of epixylic lichens and birds (Fig. IV-3), as well as for common (Fig. IV-S1) and dominant (Fig. IV-S2) species of saproxylic beetles and birds. For epixylic lichens and saproxylic beetles, this can be explained by the fact that salvage logging can change the diameter and decay classes of deadwood (Priewasser et al., 2013; Waldron et al., 2013). The windthrow resulted in large amounts of deadwood of similar size and decay stages on the unlogged plots. During salvage logging operations only the tree trunks were removed and the use of chainsaws on wind-felled trees facilitated colonization by wood-inhabiting fungi, accelerating deadwood decomposition (Thorn et al., 2014). Hence, on some plots salvage logging resulted in a shift from a large surplus of similar-sized deadwood to a smaller amount of deadwood varying widely in size and decay stage. On the logged plots, this may have led to more heterogeneous communities of saproxylic beetles and epixylic lichens.

IV.5.3 Importance of species relative abundance

Using a Hill number approach, we showed that the weighting of species as rare, common, or dominant reveals differences in patterns of between- and within-treatment β-diversity, not only among taxonomic groups with different habitat requirements but also within groups. For non-saproxylic organisms, the differences in between-treatment β-diversity across the three treatments decreased when moving from rare ($q = 0$) to common ($q = 1$) to dominant (q = 2) species (Table IV-1). These findings suggest that a windthrow disturbance and subsequent salvage logging will have the strongest effect on the β-diversity of species with small relative abundances. The majority of species in a community are of low abundance (McGill et al., 2007) and likely to be habitat specialists, found in either logged or unlogged plots. Indeed, disturbed forests host many specialized and rare species whose presence depends on the availability of relatively large areas of disturbed forest (Thorn, Chao, Georgiev, et al., 2020).

For epigeic beetles, we found lack of differences in between-treatment β-diversity between logged and unlogged plots for all different levels of *q* (Table IV-1), but communities of rare (q = 0) epigeic beetles were more homogeneous, having lower within-treatment β-diversity, on intact forest plots (Fig. IV-3). Post-fire salvage logging decreases the abundance of forest-dwelling ground beetles (Carabidae) and increases the abundance of open-habitat specialists (Koivula et al., 2006). Thus, our finding for β-diversity suggests that ground beetles respond more to habitat openness than to post-disturbance management.

The between-treatment β-diversity of rare species of ants differed between treatments (Table IV-1). Since ants are positively affected by higher ground temperatures (Grevé et al., 2018), a higher within-treatment β-diversity in open-land habitats would be expected. However, for rare species, our results showed a lower within-treatment β-diversity in logged and unlogged forests than in intact forest (Fig. IV-3K). According to this finding, windthrow, not salvage logging, leads to the homogenization of ant communities. In addition, neither between- and within-treatment β-diversity differed across treatments (Table IV-1) for common (Fig. IV-S1) and dominants (Fig. IV-S2) species, indicating that rare species were mostly responsible for the community response of ants to the windthrow disturbance.

The absence of a difference in within-treatment β-diversity between logged and unlogged sites for bees and wasps (Fig IV-3) was consistent with the findings of Wermelinger et al. (2017), who investigated pollinators 5 years after a windthrow that struck spruce forests in Switzerland.

For birds, a trend in which within-treatment β-diversity in intact forests decreased from rare to dominant species was determined (Fig. IV-3M, Fig. IV-S1M, Fig. IV-S2M). For all three Hill numbers, the within-treatment β-diversity was higher on the logged plots than in intact forest. Thus, the results for common and dominant species (those with higher relative abundances) indicate that bird communities in unlogged and intact forests are dominated by communities consisting of the same highly abundant generalist species.

IV.6 Conclusion

This study showed that, over a decade after a disturbance, salvage logging had led to significant changes in the between-treatment β-diversity of the 13 studied taxonomic groups, depending on their preferences for deadwood and open-habitats and on species relative abundance. However, within-treatment β-diversity was determined by the natural disturbance rather than by salvage logging, as homogenization of the communities of most saproxylic and half of the non-saproxylic groups occurred in response to the windthrow but not to salvage logging. Eleven years after a windthrow, the effect of this disturbance on between-treatment β-diversity were still apparent whereas the effect of subsequent salvage logging was no longer discernible. In terms of within-treatment β-diversity, both types of disturbance had the strongest effect on species with small relative abundances (i.e., rare species). Our results demonstrate that the benefits of salvage logging must be carefully weighed against the long-lasting impact on communities of rare species. Long-term studies are needed to determine whether the effects of disturbance and salvage logging on β-diversity persist over even longer periods of time.

IV.7 Acknowledgements

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IV.8 Supporting Information

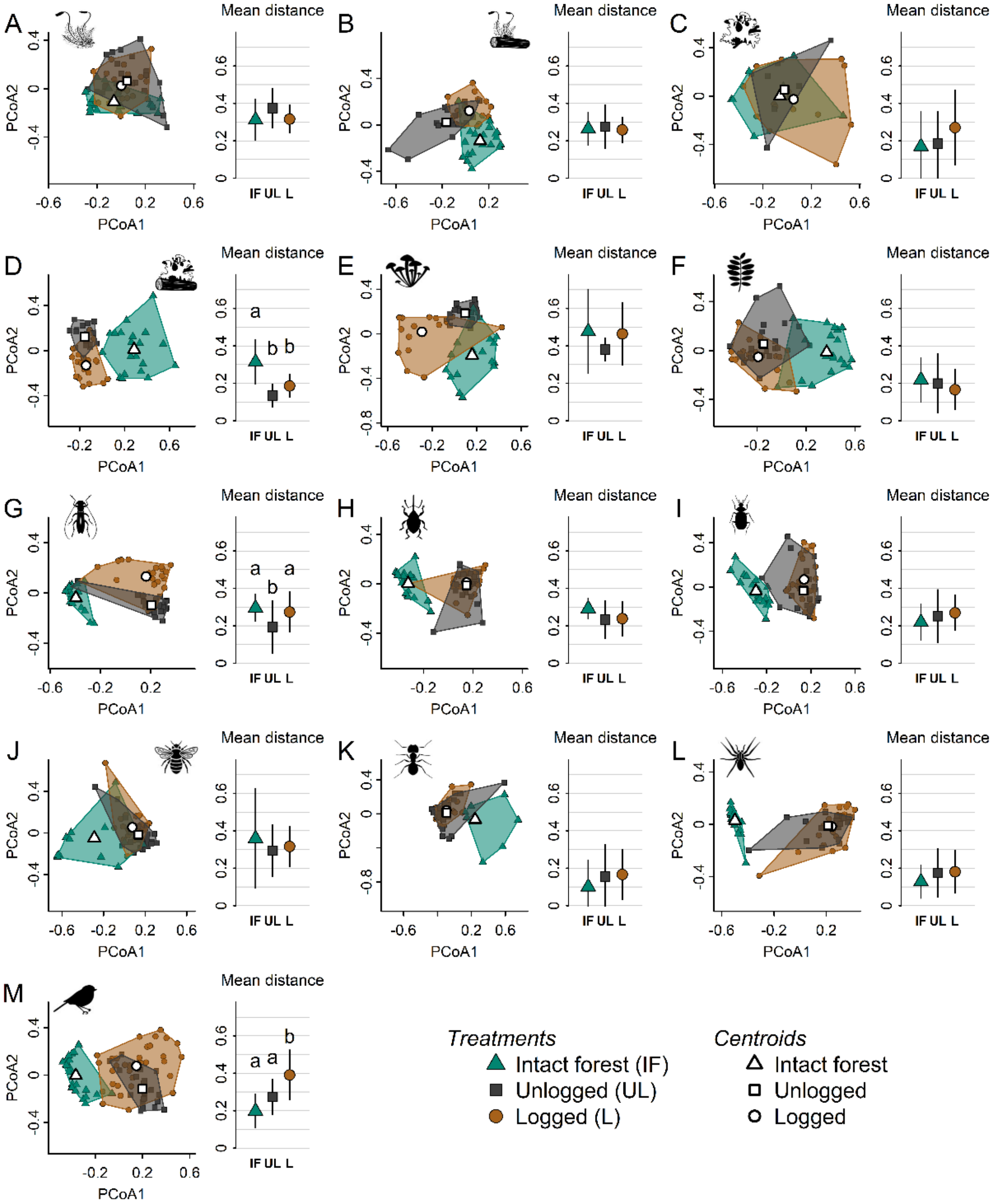

Figure IV-S1: Multivariate dispersion of community dissimilarity (within-treatment β-diversity) along with the respective centroid for common species (q = 1) of: A) epigeic bryophytes, B) epixylic bryophytes, C) epigeic lichens, D) epixylic lichens, E) wood-inhabiting fungi, F) vascular plants, G) saproxylic beetles, H) non-saproxylic beetles, I) epigeic beetles, J) bees and wasps, K) ants, L) epigeic spiders, and M) birds in logged, unlogged, and intact forest plots. The right-hand plots show the mean (±SD) distance from the centroid within every treatment; the lower-case letters indicate significantly different ($p < 0.05$) dispersions between treatments. The smaller the mean distance from the centroid, the less the within-treatment β-diversity.

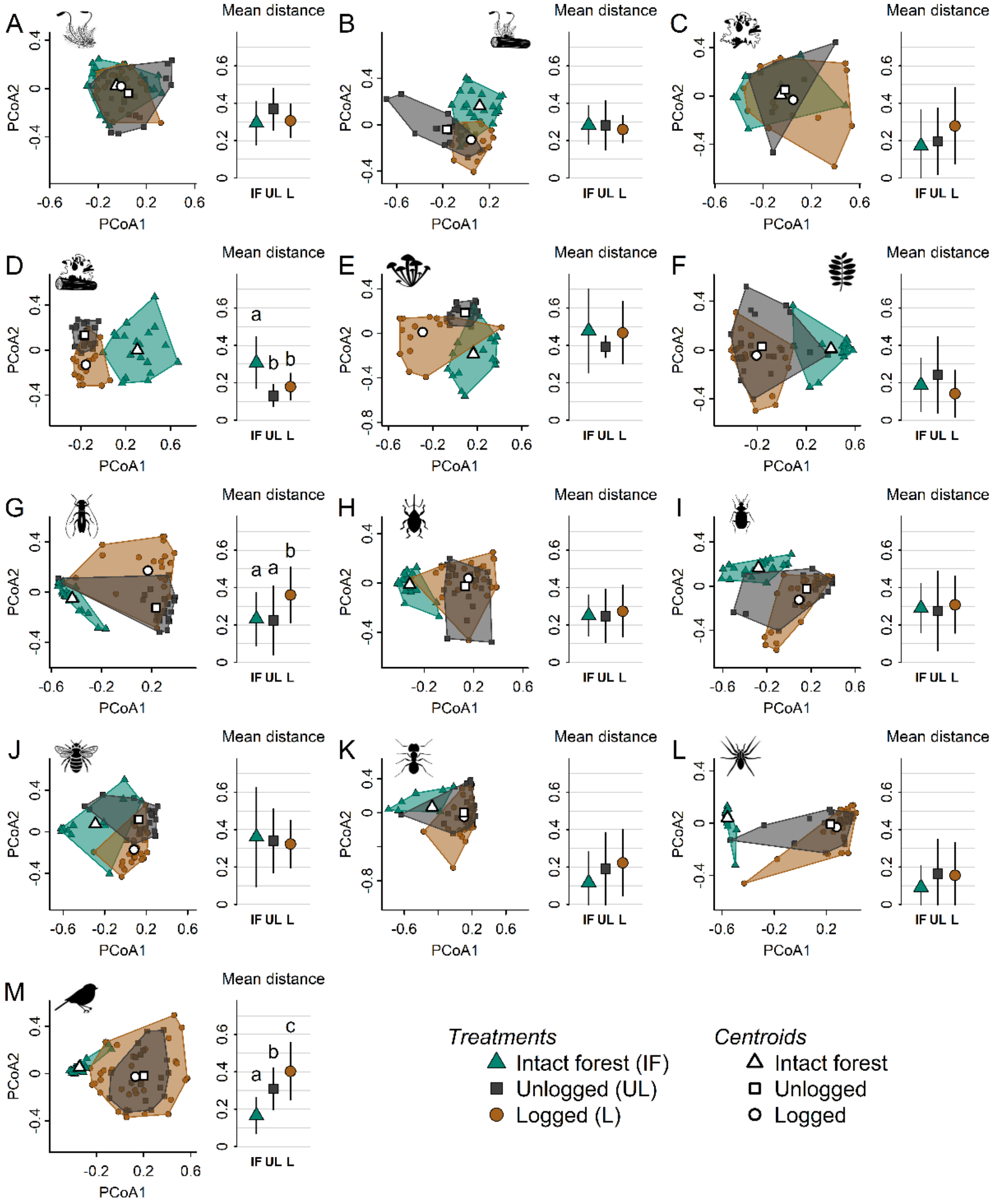

Figure IV-S2: Multivariate dispersion of community dissimilarity (within-treatment β-diversity) along with the respective centroid for dominant species ($q = 2$) of: A) epigeic bryophytes, B) epixylic bryophytes, C) epigeic lichens, D) epixylic lichens, E) wood-inhabiting fungi, F) vascular plants, G) saproxylic beetles, H) non-saproxylic beetles, I) epigeic beetles, J) bees and wasps, K) ants, L) epigeic spiders, and M) birds in logged, unlogged, and intact forest plots. The right-hand plots show the mean (±SD) distance from the centroid within every treatment; the lower-case letters indicate significantly different ($p < 0.05$) dispersions between treatments. The smaller the mean distance from the centroid, the less the within-treatment β-diversity.

Table IV-S1: Number of plots and survey methods for thirteen study species groups used to study the effects of natural disturbance and salvage logging on biodiversity, 11 years following a major windstorm.

Taxonomic group	**Plots**			**Method**	**Reference**
	Logged	**Unlogged**	**Intact forest**		
Bees and wasps	22	22	20	Flight interception traps	(Achterberg et al., 2010)
Saproxylic beetles	22	22	20	Flight interception traps	(Achterberg et al., 2010)
Non-saproxylic beetles	22	22	20	Flight interception traps	(Achterberg et al., 2010)
Epigeic beetles	20	20	20	Pitfall traps	(Abraham, 2013)
Epigeic Spiders	20	20	20	Pitfall traps	(Abraham, 2013)
Ants	20	20	20	Pitfall traps	Abraham, 2013)
Wood-inhabiting fungi	17	19	20	Survey of deadwood objects	(Bässler et al., 2012)
Epigeic bryophytes	24	24	20	Survey in 200 m^2 relevees	(Bässler et al., 2012)
Epigeic lichens	23	16	20	Survey in 200 m^2 relevees	(Bässler et al., 2012)
Epixylic bryophytes	19	19	20	Survey of deadwood objects	(Bässler et al., 2012)
Epixylic lichens	19	19	20	Survey of deadwood objects	(Bässler et al., 2012)
Vascular plants	24	20	20	Survey in 200 m^2 relevees	(Bässler et al., 2012)
Birds	32	24	20	Point-count sampling	(Bibby et al., 2000)

Table IV-S2: Results of multivariate homogeneity of group dispersion (PERMDISP) followed by a Tukey's HSD test for comparison of the within-treatment β-diversity between logged, unlogged and intact forest plots, for Hill numbers q = {0,1,2} and 13 taxonomic groups.

Hill number	Taxonomic group	Treatment comparison	Estimate	LCL	UCL	p-Value
q=0	Epigeic bryophytes	logged-forest	-0.006	-0.072	0.061	0.978
		unlogged-forest	0.045	-0.021	0.111	0.240
		unlogged-logged	0.051	-0.013	0.114	0.141
	Epixylic bryophytes	logged-forest	0.020	-0.042	0.081	0.722
		unlogged-forest	0.029	-0.032	0.090	0.486
		unlogged-logged	0.010	-0.052	0.072	0.925
	Epigeic lichens	logged-forest	0.038	-0.104	0.179	0.797
		unlogged-forest	0.125	-0.039	0.289	0.165
		unlogged-logged	0.087	-0.064	0.239	0.351
	Epixylic lichens	logged-forest	**-0.112**	**-0.174**	**-0.050**	**0.000**
		unlogged-forest	**-0.186**	**-0.248**	**-0.124**	**0.000**
		unlogged-logged	**-0.074**	**-0.137**	**-0.011**	**0.017**
	Wood-inhabiting fungi	logged-forest	**-0.115**	**-0.209**	**-0.022**	**0.012**
		unlogged-forest	**-0.197**	**-0.288**	**-0.106**	**0.000**
		unlogged-logged	-0.081	-0.176	0.013	0.105
	Vascular plants	logged-forest	0.078	-0.002	0.159	0.058
		unlogged-forest	0.033	-0.044	0.110	0.562
		unlogged-logged	-0.045	-0.123	0.032	0.339
	Saproxylic beetles	logged-forest	**-0.103**	**-0.136**	**-0.071**	**0.000**
		unlogged-forest	**-0.133**	**-0.166**	**-0.101**	**0.000**
		unlogged-logged	-0.030	-0.062	0.002	0.072
	Non-saproxylic beetles	logged-forest	-0.030	-0.074	0.015	0.253
		unlogged-forest	-0.022	-0.067	0.023	0.465
		unlogged-logged	0.008	-0.036	0.051	0.906
	Epigeic beetles	logged-forest	**0.081**	**0.043**	**0.120**	**0.000**
		unlogged-forest	**0.063**	**0.025**	**0.102**	**0.001**
		unlogged-logged	-0.018	-0.056	0.019	0.478
	Bees and wasps	logged-forest	**-0.197**	**-0.294**	**-0.100**	**0.000**
		unlogged-forest	**-0.231**	**-0.329**	**-0.134**	**0.000**
		unlogged-logged	-0.034	-0.123	0.055	0.631
	Ants	logged-forest	**-0.161**	**-0.252**	**-0.069**	**0.000**
		unlogged-forest	**-0.175**	**-0.266**	**-0.083**	**0.000**
		unlogged-logged	-0.014	-0.100	0.071	0.915

Hill number	Taxonomic group	Treatment comparison	Estimate	LCL	UCL	p-Value
	Epigeic spiders	logged-forest	0.029	-0.015	0.074	0.258
		unlogged-forest	0.015	-0.029	0.059	0.687
		unlogged-logged	-0.014	-0.057	0.029	0.716
	Birds	logged-forest	**0.150**	**0.082**	**0.218**	**0.000**
		unlogged-forest	0.011	-0.065	0.087	0.934
		unlogged-logged	**-0.139**	**-0.210**	**-0.068**	**0.000**
q=1	Epigeic bryophytes	logged-forest	0.014	-0.092	0.120	0.945
		unlogged-forest	**0.107**	**0.001**	**0.213**	**0.048**
		unlogged-logged	0.093	-0.008	0.194	0.079
	Epixylic bryophytes	logged-forest	-0.107	-0.217	0.002	0.056
		unlogged-forest	-0.070	-0.179	0.040	0.284
		unlogged-logged	0.038	-0.073	0.149	0.692
	Epigeic lichens	logged-forest	**0.193**	**0.037**	**0.349**	**0.012**
		unlogged-forest	0.001	-0.179	0.182	1.000
		unlogged-logged	**-0.192**	**-0.359**	**-0.024**	**0.021**
	Epixylic lichens	logged-forest	**-0.096**	**-0.186**	**-0.006**	**0.035**
		unlogged-forest	**-0.123**	**-0.213**	**-0.033**	**0.005**
		unlogged-logged	-0.027	-0.118	0.064	0.759
	Wood-inhabiting fungi	logged-forest	-0.013	-0.144	0.119	0.971
		unlogged-forest	-0.096	-0.224	0.031	0.173
		unlogged-logged	-0.084	-0.217	0.049	0.292
	Vascular plants	logged-forest	-0.052	-0.152	0.047	0.421
		unlogged-forest	-0.020	-0.115	0.075	0.872
		unlogged-logged	0.032	-0.063	0.128	0.692
	Saproxylic beetles	logged-forest	-0.022	-0.079	0.036	0.642
		unlogged-forest	**-0.101**	**-0.159**	**-0.044**	**0.000**
		unlogged-logged	**-0.080**	**-0.136**	**-0.024**	**0.003**
	Non-saproxylic beetles	logged-forest	-0.054	-0.117	0.009	0.110
		unlogged-forest	-0.060	-0.123	0.003	0.067
		unlogged-logged	-0.006	-0.067	0.055	0.970
	Epigeic beetles	logged-forest	0.051	-0.032	0.133	0.313
		unlogged-forest	0.033	-0.050	0.116	0.605
		unlogged-logged	-0.018	-0.098	0.063	0.861
	Bees and wasps	logged-forest	-0.043	-0.179	0.093	0.725
		unlogged-forest	-0.065	-0.201	0.070	0.482
		unlogged-logged	-0.022	-0.147	0.102	0.904
	Ants	logged-forest	0.066	-0.050	0.183	0.365
		unlogged-forest	0.054	-0.063	0.170	0.510

Hill number	Taxonomic group	Treatment comparison	Estimate	LCL	UCL	p-Value
		unlogged-logged	-0.012	-0.121	0.097	0.961
	Epigeic spiders	logged-forest	0.053	-0.030	0.137	0.277
		unlogged-forest	0.048	-0.036	0.131	0.361
		unlogged-logged	-0.006	-0.087	0.075	0.983
	Birds	logged-forest	**0.193**	**0.121**	**0.264**	**0.000**
		unlogged-forest	0.075	-0.005	0.155	0.071
		unlogged-logged	**-0.118**	**-0.193**	**-0.043**	**0.001**
q=2	Epigeic bryophytes	logged-forest	0.054	-0.067	0.174	0.536
		unlogged-forest	**0.153**	**0.033**	**0.274**	**0.009**
		unlogged-logged	0.100	-0.015	0.214	0.100
	Epixylic bryophytes	logged-forest	-0.119	-0.247	0.008	0.070
		unlogged-forest	-0.086	-0.213	0.041	0.244
		unlogged-logged	0.034	-0.095	0.163	0.806
	Epigeic lichens	logged-forest	**0.218**	**0.047**	**0.390**	**0.009**
		unlogged-forest	-0.007	-0.205	0.191	0.996
		unlogged-logged	**-0.226**	**-0.409**	**-0.042**	**0.013**
	Epixylic lichens	logged-forest	**-0.120**	**-0.237**	**-0.002**	**0.046**
		unlogged-forest	-0.099	-0.217	0.019	0.116
		unlogged-logged	0.021	-0.099	0.140	0.908
	Wood-inhabiting fungi	logged-forest	-0.012	-0.143	0.119	0.974
		unlogged-forest	-0.087	-0.214	0.041	0.238
		unlogged-logged	-0.075	-0.207	0.058	0.372
	Vascular plants	logged-forest	-0.046	-0.170	0.077	0.641
		unlogged-forest	0.054	-0.064	0.173	0.517
		unlogged-logged	0.101	-0.018	0.219	0.110
	Saproxylic beetles	logged-forest	**0.129**	**0.046**	**0.211**	**0.001**
		unlogged-forest	-0.007	-0.090	0.076	0.976
		unlogged-logged	**-0.136**	**-0.217**	**-0.055**	**0.000**
	Non-saproxylic beetles	logged-forest	0.023	-0.074	0.120	0.835
		unlogged-forest	-0.003	-0.100	0.094	0.997
		unlogged-logged	-0.026	-0.120	0.069	0.787
	Epigeic beetles	logged-forest	0.018	-0.108	0.143	0.938
		unlogged-forest	-0.015	-0.140	0.110	0.956
		unlogged-logged	-0.033	-0.155	0.090	0.797
	Bees and wasps	logged-forest	-0.038	-0.186	0.110	0.809
		unlogged-forest	-0.021	-0.169	0.127	0.939
		unlogged-logged	0.017	-0.118	0.153	0.948
	Ants	logged-forest	0.106	-0.034	0.245	0.173

Hill number	Taxonomic group	Treatment comparison	Estimate	LCL	UCL	p-Value
		unlogged-forest	0.073	-0.066	0.213	0.423
		unlogged-logged	-0.032	-0.163	0.098	0.823
	Epigeic spiders	logged-forest	0.064	-0.055	0.184	0.407
		unlogged-forest	0.073	-0.046	0.193	0.311
		unlogged-logged	0.009	-0.108	0.126	0.981
	Birds	logged-forest	**0.237**	**0.156**	**0.319**	**0.000**
		unlogged-forest	**0.144**	**0.052**	**0.236**	**0.001**
		unlogged-logged	**-0.093**	**-0.179**	**-0.007**	**0.031**

Chapter V: General discussion

The main aim of this thesis was to increase our understanding about the mid- to long-term effects of natural disturbances and salvage logging on different facets of biodiversity and additionally on water quality.

Firstly, I was interested in understanding how natural disturbances, such as windstorms and bark beetles infestations, followed by salvage logging would affect concentrations of nitrates and dissolved organic carbon (DOC) in streams situated in disturbed, forested watersheds (chapter II). The natural disturbances led to time-lagged peaks of nitrates in streamwater. However, the nitrate concentrations did not exceed the international health limits and returned to their pre-disturbance level within 10 years after the disturbance. Natural disturbances did not lead to peaks of DOC. Overall, salvage logging had no impact on nitrate and DOC concentrations.

Secondly, I investigated how both disturbances impacted the α-diversity (chapter II) and β-diversity (chapter IV) of multiple taxonomic groups. Even though not completely consistent over all studied years and groups, I found a decrease of α-diversity for saproxylic taxonomic groups on salvage-logged plots and an increase of α-diversity for taxa associated with logged plots, respectively open-land habitats (chapter II). Even 11 years after the disturbances, community composition (between-treatment β-diversity) of 13 taxonomic groups differed significantly between wind-felled, salvage-logged and intact forest sites (chapter IV). Windthrow was the main driver of community homogenization as within-treatment β-diversity on wind-felled plots was lower than the β-diversity of communities found in intact forests. Salvage logging did not lead to further community homogenization in any taxonomic group, as within-treatment-β-diversity effects of salvage logging did not superimpose on the effects of windthrow (chapter IV).

Thirdly, I aimed at finding how the effects of both disturbances on taxonomic, functional and phylogenetic diversity as well as β-diversity would differ if species relative abundance was taken into account during the calculations of different biodiversity indices. I found that rare non-shared species, rare functional groups and rare evolutionary lineages of birds were more strongly impacted by salvage logging than the common and dominant ones (chapter III). In addition, among all 13 studied taxonomic groups, most often significant differences in between- and within-treatment β-diversity were found for rare species were analyzed (chapter IV).

V.1 Effect on water quality

In a previous study in the Bavarian Forest National Park, Beudert et al. (2015) investigated the effect of large-scale bark beetle infestation on biodiversity and leaching of nitrates into streamwater. In chapter II, I extended the study of Beudert et al. (2015) and next to the leaching of nitrates, I investigated additionally the leaching of dissolved organic carbon (DOC) into streamwater. The lack of both significant peaks of DOC concentrations after the natural disturbances and any significant effects of salvage logging on DOC concentrations, suggest that in my case DOC concentrations were not affected by the natural disturbance or salvage logging.

For nitrates, however, I found significant temporal leaching into streamwater that was associated with the non-intervention management. This finding is in line with other studies, which also showed an increase in nitrate concentration after windthrow (Hellsten et al., 2015) and after bark beetle infestation (Beudert et al., 2015). Even though, the nitrate concentrations increased after the disturbances, similarly to results of Beudert et al. (2015), I found that nitrate leaching did not exceeded World Health Organization's threshold of 50 mg L^{-1}. This is important as it shows that leaving deadwood in disturbed forests would not significantly affect water quality and would not pose a risk to human health.

As salvage logging removes part of the deadwood, one could expect that salvage logging might reduce leaching of nitrates caused by the natural disturbance. However, during salvage logging operations, especially post-wildfire, the surface soil layer could be damaged by the heavy machinery, which often results in increased erosion, turbidity, export of solutes and nutrients to streamwater (Silins et al., 2014; Smith et al., 2012). Based on that, one could also expect that salvage logging may contribute to worsening of the water quality. However, in contrast to these expectations, I found that conducting salvage logging in wind-felled or bark-beetle-killed forests did not significantly change the nitrate concentrations, hence did not affect water quality. In line with my findings, leaving wind-felled forests unlogged or performing salvage logging seems to have little effect on nitrate concentration in surface water (BAFU, 2008). Therefore, from a forest management perspective the results of chapter II suggest that performing salvage logging in wind-felled and bark-beetle-infested forests would not affect water quality. In addition, the results also suggest that a non-intervention strategy in watersheds disturbed by windthrow or bark-beetles is congruent with the provision of clean drinking water, which is a crucial ecosystem service that mountainous forests provide.

V.2 Effects on biodiversity

V.2.1 Effects on α-diversity

In chapter II, I found an increase in α-diversity of mostly deadwood-dependent and species groups related to open habitats on unlogged plots. Salvage logging additionally increased the α-diversity of species groups related to open habitats, but decreased the α-diversity of deadwood-dependent species groups. These findings correspond quite well to the findings of Thorn et al. (2018), who also showed that salvage logging can increase α-diversity of taxa associated with open habitats but can decrease α-diversity of taxa depending on deadwood. The decrease of α-diversity in deadwood-dependent taxa and species most probably reflects the reduction of deadwood and biological legacies that salvage logging causes (Lindenmayer et al., 2006; Thorn et al., 2018).

V.2.2 Effects on biodiversity facets and β-diversity

The majority of the studies about salvage logging focus on measures of species taxonomic diversity, rather than on other facets such as phylogenetic and functional diversity (Leverkus et al., 2015). In this regard, this thesis increases our understanding about the effects of salvage logging on different biodiversity facets by investigating non-shared bird species (taxonomic dissimilarity), functional groups (functional dissimilarity) and evolutionary lineages (phylogenetic dissimilarity) (chapter III). Based on a global dataset of bird communities (chapter III), I showed that communities found in salvage-logged sites differed from disturbed, unlogged sites not only for taxonomic, but also for functional and phylogenetic diversity. Moreover, bird compositional dissimilarity between logged and unlogged plots was lowest for functional diversity and also phylogenetic dissimilarity mirrored the taxonomic one. These findings mean that salvage logging possibly acts as an environmental filter, which selects for diverse bird species that are evolutionary distant but at the same time have similar functional traits between the bird communities in salvage-logged and disturbed, unlogged forests.

In addition to comparing the dissimilarities between unlogged and logged plots, I also explored the temporal dissimilarities that occur in the bird communities of unlogged sites by chance. For this purpose, I applied null models that are often used to quantify the difference between observed patterns of co-occurrence against the expected levels of co-occurrence when species are randomly drawn from a given set of species (Gotelli, 2000). With the help of this approach possible stochasticity effects were taken into account. The results of the null models revealed that the differences in bird communities of naturally disturbed and salvage-logged plots are higher than the differences that occur by chance in the unlogged plots during the natural forest succession. Therefore, salvage logging is a major factor that leads to significant alternations in bird communities. As birds are one cosmopolitan group that plays important role in providing different ecosystem services, alternations in bird communities induced by salvage logging, may potentially have an impact on bird-mediated services such as seed dispersal (Rost et al., 2009) or provision of nesting cavities for secondary hole-nesters (Hutto et al., 2006).

Disturbance effects on biodiversity change with the amount of time after a disturbance (Royo et al., 2016). An important contribution of the thesis is the finding that differences in bird community dissimilarities caused by salvage logging were present not only during the first few years after the natural disturbance, but they persisted up to 17 years (chapter III). Previous long-term studies on the effects of salvage logging on birds have shown that differences in bird communities gradually diminish over time (Hobson et al., 1999). However, in my case bird dissimilarities between unlogged and salvage-logged plots showed no sign of decrease, suggesting that the effect of salvage logging are potentially long lasting and may persist even longer than two decades. Nonetheless, future studies should focus on extending the time series after disturbance to more than two decades. Eleven years after the windthrow and salvage logging, I found more significant differences in community composition (between-treatment β-diversity) between intact forests and either logged or unlogged plots, then between logged and unlogged plots (chapter IV). The effects of salvage logging can also diminish over time (Leverkus, Polo, et al., 2020). Thus, my findings suggest that over the course of succession the compositional differences between logged and unlogged forests disappear faster than the differences between intact forest and unlogged or logged plots. Disturbed, unlogged and logged forests differ mainly in terms of amount of deadwood and biological legacies (Lindenmayer et al., 2008). From management perspective this implies that one could reduce β-diversity differences between logged and unlogged sites by setting aside unlogged patches in salvage-logged forests.

Many salvage logging studies lack undisturbed forests as a control in their study design. This may limit the ability of the studies to evaluate the strength of the salvage logging effects, relative to processes that occur in undisturbed forests. In chapters II and IV, I tried to overcome this problem by investigating α- and β-diversity in naturally disturbed, salvage-logged and intact forests for 13 taxonomic groups. The number of species between intact forests and the other treatments differed mainly depending on their requirements to open habitats or deadwood resources. Similarly, contrasting results among the different taxa were also found for within-treatment β-diversity. For instance, windthrow led to more homogeneous communities for five taxonomic groups and to more heterogeneous communities for two groups compared to intact forests. In contrast to my expectations, I found that salvage logging does not act as an additional environmental filter that can further homogenize the communities found in unlogged plots. The results for within-treatment β-diversity show that salvage logging leads to compositionally very similar communities within the salvaged plots. Within-treatment β-diversity in salvage-logged plots was either similar to the β-diversity in unlogged plots or was higher for only two taxonomic groups. These results lead to the conclusion that salvage logging does not further homogenize the biological communities of taxonomic groups, which have been already homogenized by the windthrow disturbance.

V.2.3 Hill numbers and species relative abundance

In chapters III and IV, I used the Hill numbers approach in order to investigate how the effects of natural disturbances and salvage logging on different biodiversity facets and β-diversity would differ when species relative abundance is taken into account during the calculation of different diversity indices. In chapter III, I showed that the compositional differences in dissimilarities of shared species (taxonomic diversity), functional groups (functional diversity) and evolutionary lineages (phylogenetic diversity) were highest for rare species ($q = 0$), which are species registered with single or very few observations on the study plots. This means that salvage logging exerts the strongest impact on rare bird species, bird species with rare functional traits and bird species that are evolutionary distant. Similarly, for most studied groups significant difference in between- and within-treatment β-diversity were found for rare species ($q = 0$), hence windthrow and salvage logging have the strongest β-diversity effects on species with low relative abundances (chapter IV). Species with low relative abundances experience the highest temporal turnover in communities (Magurran et al., 2003). Possible explanation is that species with low relative abundances are probably habitat specialists that due to their special requirements are best adapted to exploit either unlogged or logged plots. In chapter II, there were cases when certain rare specialist species were found only on unlogged or salvage-logged plots. This could explain the differences in birds' compositional dissimilarity for rare species ($q = 0$)

for taxonomic, functional and phylogenetic diversity between unlogged and salvaged-logged plots.

Rare species can influence ecosystem services directly or indirectly through interactions with other species (Dee et al., 2019). Therefore, widespread management practice, like salvage logging, which affects rare species may have unexpected implications for forest ecosystem services. To ensure the success of sustainable management in the time of ongoing global climate change and increase of forest disturbances, future studies need to deepen our understanding on how rare species affect ecosystem functioning through interaction with more common ones.

V.3 Limitations

A possible limitation of the study design in chapter II is that the studied watersheds did not cover the entire gradient of salvage-logged area. In all five watersheds the amount of salvage-logged area varied only between 0% and 21%. Therefore, the conclusions I draw in this chapter about effects of salvage logging on nitrate and DOC concentrations are valid for disturbed watersheds, in which maximum 21% of the area is salvage-logged. Salvage logging, especially intensive logging with heavy machinery, increases soil disturbance (Malvar et al., 2017). Thus, it can be expected that more intensive logging operations covering 21% to 100% of the disturbed watershed’s area may increase soil erosion, resulting in an increase of nitrate and DOC concentrations in streamwater. However, this should be addressed in further studies.

V.4 Conclusions

Global climate change has increased the occurrence of extreme weather events, which together with management-induced changes in forest structure (i.e. planting of fast-growing conifers and fire suppression) have increased the susceptibility of European forests to natural disturbances (Seidl et al., 2011). Simultaneously, due to socio-economic factors the increase in natural disturbances has resulted in an unprecedented expansion of salvage logging, which are expected to increase in the near future worldwide (Leverkus, Lindenmayer, et al., 2018; Lindenmayer et al., 2017). Therefore, in order to manage disturbed forests in a sustainable fashion, forestry authorities, decision-makers and landscape managers need to consider the potential long-term effects of post-disturbance salvage logging on biological diversity. Based on the findings in chapters II, III and IV, the most important conclusions for the effects of salvage logging are:

- Salvage logging is a major driver of compositional differences not only for taxonomic diversity, but also for other biodiversity facets such as functional and phylogenetic diversity.
- The effects of salvage logging are long-lived, as the compositional changes in bird communities between salvaged and unsalvaged forest sites lasted for 17 years. Differences in species compositions did not decrease over the years, but even increased at the end of the studied time span. This implies that the compositional differences of bird communities could persist even longer than two decades.
- Compared to undisturbed forests, windthrows are the main factor leading to community homogenization of saproxylic and open-land taxonomic groups. Salvage logging does not further increase the community homogenization of saproxylic and open-land taxonomic groups. Moreover, salvage logging can even increase community heterogenization of rare wood-inhabiting fungi, as well as common and dominant saproxylic beetles, provided that the logging operations increase deadwood heterogenization.
- Compositional differences between logged and unlogged plots disappear faster than the differences between intact forest and unlogged plots.
- Salvage logging exerts the strongest impact on rare bird species ($q = 0$), bird species with rare functional traits and bird species that are evolutionary distant.

- Windthrows and salvage logging have the strongest β-diversity effects on species with low relative abundances ($q = 0$).
- A non-intervention strategy in disturbed watersheds is congruent with the provision of clean drinking water and setting aside disturbed forests would not lead to increased human health risk.
- Conducting salvage logging in up to 20% of a disturbed forest has no effect nitrate and DOC concentrations. Therefore, salvage logging should not be justified based on the assumption that it prevents leaching of nitrates or DOC into streams in disturbed, forested watersheds. Future studies should focus on more intensive logging operations covering >20% of the disturbed area.
- A mosaic of disturbed, unlogged and salvage-logged forests would be a valuable management strategy for maximizing α- and β-diversity.

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Appendix A

A.1 Affidavit

Affidavit

I hereby declare that my thesis entitled: **„Sustainable management of naturally disturbed forests “** is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore I verify that the thesis has not been submitted as part of another examination process neither in identical nor in similar form.

Besides I declare that if I do not hold the copyright for figures and paragraphs, I obtained it from the rights holder and that paragraphs and figures have been marked according to law or for figures taken from the internet the hyperlink has been added accordingly.

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, die Dissertation: **„Nachhaltiges Management von natürlichen Störungen in Wäldern“**, eigenständig, d. h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen, als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat.

Weiterhin erkläre ich, dass bei allen Abbildungen und Texten bei denen die Verwertungsrechte (Copyright) nicht bei mir liegen, diese von den Rechtsinhabern eingeholt wurden und die Textstellen bzw. Abbildungen entsprechend den rechtlichen Vorgaben gekennzeichnet sind sowie bei Abbbildungen, die dem Internet entnommen wurden, der entsprechende Hypertextlink angegeben wurde.

Würzburg,__________________

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Signature/Unterschrift

A.2 Author contributions

Statement of individual author contributions

Chapter II

Georgiev, K.B., Beudert, B., Bässler, C., Feldhaar, H., Heibl, C., Karasch, P., Müller, J., Perlik, M., Weiss, I., Thorn, S. (accepted). Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity. *Forest Ecology and Management*	
Participated in	**Author initials, responsibility decreasing from left to right**
Study design	JM, ST, KBG
Data collection	KBG*, BB*, ST*, HF*, CH*, PK*, MP*,IW*
Data analysis and interpretation	KBG, ST, CB
Writing of first draft	KBG†, BB†
Manuscript editing and revisions	KBG, ST, BB, JM, HF

* contributed equally

† contributed equally to the water part

Chapter III

Georgiev, K.B., Chao, A., Castro, J., Chen, Y., Choi, C., Fontaine, J.B., Hutto, R.L., Lee, E., Müller, J., Rost, J., Żmihorski, M., Thorn, S., (2020). Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities. *Journal of Applied Ecology* 57:6, 1103-1112. doi:10.1111/1365-2664.13599	
Participated in	**Author initials, responsibility decreasing from left to right**
Study design	ST, JM
Method development	AC, YC

Data collection	KBG*, ST*, RLH*, JC*, CC*, JBF*, EL*, JR*, MZ*
Data analysis and interpretation	KBG, ST
Writing of first draft	KBG
Later drafts and revisions	KBG, ST, RLH, JC, JBF, JR, MZ, CC, EL

* contributed equally

Chapter IV

<table>
<tr><td colspan="2">Georgiev, K.B., Bässler, C., Feldhaar, H., Heibl, C., Karasch, P., Müller, J., Perlik, M., Weiss, I., Thorn, S. (submitted). Windthrow and salvage logging cause long-lasting changes in the β-diversity of multiple species groups. *Journal of Applied Ecology*</td></tr>
<tr><th>Participated in</th><th>Author initials, responsibility decreasing from left to right</th></tr>
<tr><td>Study design</td><td>JM, ST, KBG</td></tr>
<tr><td>Data collection</td><td>KBG*, ST*, HF*, CH*, PK*, MP*, IW*</td></tr>
<tr><td>Data analysis and interpretation</td><td>KBG, ST, CB</td></tr>
<tr><td>Writing of first draft</td><td>KBG</td></tr>
<tr><td>Manuscript editing and revisions</td><td>KBG, ST, JM, CB, HF</td></tr>
</table>

* contributed equally

A.3 Publication list

Publications as part of the doctoral thesis

Georgiev, K.B., Chao, A., Castro, J., Chen, Y., Choi, C., Fontaine, J.B., Hutto, R.L., Lee, E., Müller, J., Rost, J., Żmihorski, M., Thorn, S. (2020). Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities. *Journal of Applied Ecology* 57(6), 1103–1112

Georgiev, K.B., Beudert, B., Bässler, C., Feldhaar, H., Heibl, C., Karasch, P., Müller, J., Perlik, M., Weiss, I., Thorn, S. (accepted). Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity. *Forest Ecology and Management*

Georgiev, K.B., Bässler, C., Feldhaar, H., Heibl, C., Karasch, P., Müller, J., Perlik, P., Weiss, I., Thorn, S. (submitted). Windthrow and salvage logging cause long-lasting changes in the β-diversity of multiple species groups. *Journal of Applied Ecology*

Additional publications

Kortmann, M., Müller, J.C., Baier, R., Bässler, C., Buse, J., Cholewińska, O., Förschler, M.I., Georgiev, K.B., Hilszczański, J., Jaroszewicz, B., Jaworski, T., Kaufmann, S., Kuijper, D., Lorz, J., Lotz, A., Łubek, A., Mayer, M., Mayerhofer, S., Meyer, S., Morinière, J., Popa, F., Reith, H., Roth, N., Seibold, S., Seidl, R., Stengel, E., Wolski, G.J., Thorn, S. (2021). Ecology versus society: Impacts of bark beetle infestations on biodiversity and restorativeness in protected areas of Central Europe. *Biological Conservation* 254(10)

Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T.P., Donato, D.C., Durska, E., Macdonald, E., Feldhaar, H., Fontaine, J.B., Fornwalt, P.J., Hernández, R.M.H., Hutto, R.L., Koivula, M., Lee, E.-J., Lindenmayer, D., Mikusiński, G., Obrist, M.K., Perlík, M., Rost, J., Waldron, K., Wermelinger, B., Weiß, I., Żmihorski, M., Leverkus, A.B. (2020). Estimating retention benchmarks for salvage logging to protect biodiversity. *Nature Communications* 11(4762)

Thorn, S., Chao, A., Bernhardt-Römermann, M., Chen, Y.H., Georgiev, K.B., Heibl, C., Müller, J., Schäfer, H., Bässler, C., 2020. Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests. *Ecology* 101(3).

Friess, N., Müller, J.C., Aramendi, P.,Bässler, C., Brändle, M., Bouget, C., Brin, A.,Bussler, H., Georgiev, K.B., Gil, R., Gossner, M.M., Heilmann-Clausen, J., Isacsson, G., Krištín, A., Lachat, T., Larrieu, L., Magnanou, E., Maringer, A., Mergner, U., Mikolávs, M., Opgenoorth, L., Schmidl, J., Svoboda, M., Thorn, S., Vandekerkhove, K., Vrezec, A., Wagner, T., Winter, M.-B., Zapponi, L., Brandl, R., Seibold, S. (2019). Arthropod communities in fungal fruitbodies are weakly structured by climate and biogeography across European beech forests. *Diversity and Distributions* 25(5), 783–796

A.4 Curriculum Vitae

Personal data

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2017 – 2021: PhD candidate, University of Würzburg in collaboration with the Bavarian Forest National Park

2008 – 2009: Master of Science, Ecology and Environmental Protection, University of Sofia “St. Kliment Ohridski”, Bulgaria

2003 – 2007: Bachelor of Science, University of Sofia “St. Kliment Ohridski”, Bulgaria

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