Effects of forest management on bryophyte species richness in Central European forests

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Abstract

We studied the effect of three major forest management types (unmanaged beech, selection beech, and age class forests) and stand variables (SMI_d , soil pH, proportion of conifers, litter cover, deadwood cover, rock cover and cumulative cover of woody trees and shrubs) on bryophyte species richness in 1050 forest plots in three regions in Germany. In addition, we analysed the species richness of four ecological guilds of bryophytes according to their colonized substrates (deadwood, rock, soil, bark) and the number of woodland indicator bryophyte species. Beech selection forests turned out to be the most species rich management type, whereas unmanaged beech forests revealed even lower numbers than age-class forests. Increasing conifer proportion increased bryophyte species richness but not the number of woodland indicator bryophyte species. The richness of the four ecological guilds mainly responded to the abundance of their respective substrate. We conclude that the permanent availability of suitable substrates is most important for bryophyte species richness in forests, which is not stringently linked to management type. Therefore, managed age-class forests and selection forests may even exceed unmanaged forests in bryophyte species richness due to higher substrate supply and therefore represent important habitats for bryophytes. Typical woodland indicator bryophytes and their species richness were negatively affected by SMI_d (management intensity) and therefore better indicate forest integrity than the species richness of all bryophytes. Nature conservation efforts should focus on the reduction of management intensity. Moreover, maintaining and increasing a variability of substrates and habitats, such as coarse woody debris, increasing structural heterogeneity by retaining patches with groups of old, mature to over-mature trees in managed forests, maintaining forest climate conditions by silvicultural methods that assure stand continuity, e.g. by selection cutting rather than clear cutting and shelterwood logging might promote bryophyte diversity.

1. Introduction

One of the most significant landscape elements in Central Europe are forests. In Germany, approximately 31% of the surface is covered by mainly managed forests. Natural or unmanaged forests exist only in fragments, comprising less than 3% of total forest area (BMELV, 2014). Ongoing efforts to increase the proportion of green energy focus on additional harvest of wood as well-meant strategy to counteract climate change (Schulze et al., 2012) act as additional threat for forest ecosystems because often these short-rotation plantations are mainly composed of fast-growing tree species which are often untypical for the sites where they are cultivated. Therefore, ecologically sustainable and conservation-compatible practices in managed forests, such as integrative multifunctional forest management programs (e.g. Borrass et al., 2017), as well as the abandonment of formerly managed forests gain importance for the conservation of biodiversity in the European landscape. Moreover, Ammer et al. (in press) highlighted the importance of understanding the relationships between different components of management, forest structure and biodiversity. This demands the solid investigation of environmental, structural and forest management variables to test their effects on biodiversity. Usually, studies investigating management effects on biodiversity comprise species groups such as mammals, birds, beetles or higher plants whereas equally important forest organisms such as cryptogam plants are strongly underrepresented (but see Paillet et al., 2010; Boch et al., 2013a, b). Among cryptogams, bryophytes constitute an important and permanent component of the forest flora and diversity. They colonize various substrates, which are unsuitable for vascular plants, because of low light intensity or low nutrient level, such as deadwood, bark, rocks, and open soil (Smith, 1982; Bates, 1992). They provide shelter habitats, food, and nest material for many animals (Gerson, 1982; Boch et al., 2013c). Due to their high abundance in forests they are considerable primary producers of biomass, conduct photosynthesis around the year, and are therefore influencing the carbon and nutrient cycles (e.g. Turetsky, 2003).

In forests, different ecological guilds of bryophytes can be distinguished by the substrate on which they are growing, including terricolous, lignicolous, corticolous and saxicolous species that occur on soil, deadwood, bark of living trees and shrubs, or rocks, respectively. As diversity and quality of these substrates is affected by forest management, bryophytes are suitable indicators for the effect of management on forest conditions (Rose, 1992). Especially typical woodland bryophytes, which are strictly depending on forest conditions (Rose, 1999; Nordén et al., 2007; Preussing et al., 2011; Schmidt et al., 2011; Kriebitzsch et al., 2013, Mölder et al., 2015), are valuable indicator organisms to estimate the naturalness and integrity of forest stands (Frego, 2007).

Some studies dealt with forest management effects on bryophytes and demonstrated their sensitivity to management practices. However, comparative studies on bryophyte diversity in forest ecosystems were mostly restricted to boreal regions and only compared unmanaged with managed forests (e.g. Andersson and Hytteborn, 1991; Frisvoll and Prestø, 1997; Ross-Davis and Frego, 2002; Nelson and Halpern, 2005; Vellak and Ingerpuu, 2005; reviewed in Paillet et al., 2010). The studies from temperate European forests were restricted to only one study region and one ecological guild such as epiphytes (Friedel et al., 2006; Mežaka and Znotiņa, 2006; Bardat and Aubert, 2007; Fritz et al., 2008, 2009a, 2009b; Kiraly and Ódor, 2010) or epixylic species (Andersson and Hytteborn, 1991; Ódor et al., 2006) or incorporated only one forest type (Márialigeti et al., 2009; Horvat et al., 2017; Schall et al., 2018). Thus, a comprehensive assessment how different groups of bryophytes respond to a range of management regimes across different regions is still lacking.

In addition, the relationship between the diversities of bryophytes and vascular plants has only rarely been studied in forests (but see Ingerpuu et al., 2003), and it is unclear whether management affects both groups similarly. In grasslands, bryophyte diversity is a very good indicator not only for the total vascular plant diversity but also for the diversities of many individual plant and animal taxa. In fact, bryophyte diversity showed the strongest relation

with of the overall diversity of grasslands (Manning et al., 2015 referring to multidiversity *sensu* Allan et al., 2014). In forests, the richness of terricolous bryophyte and herb species seems to be positively related as well (Márialigeti et al., 2009). However, it remained open whether particular forest conditions affect the presence of typical woodland indicator species of both bryophytes and vascular plants in the same way.

We therefore conducted a large-scale investigation on the relationship between forest management and bryophyte species richness across a broad range of management types in three regions in Germany, allowing to generalize our findings for temperate, lowland to montane forests in Central Europe. We included bryophytes of all ecological guilds and analysed management responses of each ecological guild, of the group of woodland indicator bryophyte species and of all bryophyte species together. Furthermore, to test the accordance of management responses on the vegetation, we studied the relationship between species richness of bryophytes and herbaceous vascular plants on the forest floor.

Our main questions are:

- 1) How does the species richness of all bryophytes and of woodland indicator bryophyte species respond to forest management?
- 2) How does bryophyte species richness respond to variation in environmental variables?
- 3) How is the richness of bryophytes and herbaceous vascular plants related?

2. Methods:

2.1 Study system

The investigations were carried out within the large-scale and long-term ‘Biodiversity Exploratories’ project, which provides an advantageous framework to analyse land-use effects on different species groups including bryophytes. We studied bryophytes in 1050 forest plots in three regions of Germany (Fig. A.1) which differ in geological and climatic conditions (Fischer et al., 2010). Moreover, the historic forest management likely differed between the

regions and still might affect the current forest attributes on the landscape level (cf. Wäldchen et al., 2011).

The most northern region is the UNESCO-Biosphere reserve Schorfheide-Chorin, located in the northeast of Germany. It is a post glacial moraine composed landscape, on mainly sandy, acidic soils with variable proportions of loam. The climate has a slightly sub-continental character and has the lowest mean annual precipitation of the three study regions with 520 to 600 mm.

The second region in the middle of Germany, the Hainich-Dün, comprises the National Park Hainich and its surrounding areas in a mid-elevation mountain range, with a mean annual precipitation of 750–800 mm. This region is characterized by shell limestone and Loess soils bearing one of the largest unfragmented European Beech forests of Germany.

The third region is situated in the southwest of Germany in the Biosphere area Schwäbische Alb. This area is part of the Swabian Jura, a middle mountain range formed by calcareous bedrock. Its climate has a montane character with relatively high mean annual precipitation of 935–965 mm. The forests in this region are more fragmented than the ones in the other study regions.

For the Biodiversity Exploratories project approx. 500 plots were established in each region.

The plots were selected from the intersection points of a 100 m × 100 m grid distributed across forested area, after discarding forest edges, i.e. plots fully or partially overlapping with settlements, grasslands, agricultural fields, water bodies, and rare azonal forest types such as floodplain forests, as well as plots intersected by roads, with the aim to represent the most common forest and management types in the particular region (see Fischer et al., 2010). They represent the whole regional range of forest management types, comprising (i) unmanaged and uneven-aged forests dominated by European beech (*Fagus sylvatica*); (ii) selection forests which were also mainly dominated by European beech and which is a type of continuous-cover forest where individual trees or small groups of trees are harvested; and (iii) age-class

forests which are dominated by European beech in all three regions, or Norway spruce (*Picea abies*) in Hainich-Dün and Schwäbische Alb or Scots pine (*Pinus sylvestris*) in Schorfheide-Chorin. The age-class forests comprised different developmental stages of even-aged structure due to harvests at 80 to 120 year intervals, either by conventional clear cuts or shelterwood logging. For this study, we randomly selected a representative subset of 1050 out of 1535 plots: 441 in Schorfheide-Chorin, 271 in Hainich-Dün, and 338 in the Schwäbische Alb. The plots had a size of 20 m × 20 m and were restricted to forest interiors.

2.2 Management and environmental variables

In addition to the three main management types of unmanaged, selection, and age-class forests, we recorded height and diameter at breast height (DBH) of each tree in a circular forest inventory area of 500 m², which was concentric with our plots and calculated the basal area (BA) of each plot. We then quantified forest management intensity (SMI_d sensu Schall and Ammer, 2013) by relating the basal area to their carrying capacity (BA_{cc}). Forest management intensity thus measures the deviation of the actual stocking from a fully stocked mature forest ($= 1 - BA \times BA_{cc}^{-1}$), due to young stand age, harvests and thinnings. Basal area carrying capacity was quantified species specifically using the 95% quantile of observed values for beech dominated forests as reference (45 m² ha⁻¹). Subsequently the carrying capacity of other tree species were estimated relative to beech based on yield tables (oak and other broadleaves: 36 m² ha⁻¹; pine and larch: 51 m² ha⁻¹; spruce and fir: 63 m² ha⁻¹; Douglas-fir: 69 m² ha⁻¹). In mixed stands, forest management intensity was quantified relative to the current tree species composition ($= 1 - \sum BA_i \times BA_{cc,i}^{-1}$, with *i* representing tree species). As this measure does not account for different tree species, it was not possible to use it independently from our management categories.

For age-class forests, we used the proportion of conifers based on canopy cover estimations as a continuous measure (see below) instead of using coniferous, deciduous and mixed forests as

categories. Furthermore, we estimated the cover of litter, bare ground, deadwood, and rocks for a measure of substrate availability for different guilds of bryophytes.

Close to the center of each plot, a soil sample was taken from the uppermost soil horizon (A, H or E horizon), which comprised approximately the uppermost 10 cm of the soil core. The samples were air dried and sieved to <2 mm. The soil pH was determined with a glass electrode in the supernatant of a soil suspension using a 1:2.5 mixture of soil and 0.01 M CaCl_2 .

2.3 Vegetation data

Between April 2007 and September 2008, we sampled bryophyte species in all plots and estimated their percentage cover in each of four ecological guilds, according to their colonized substrates on the plot. The four guilds comprised terricolous bryophytes on the forest floor, lignicolous bryophytes on deadwood, saxicolous bryophytes on rocks or stones, and corticolous bryophytes (epiphytes) on the bark of living trees and shrubs including species growing up to a height of 2 m. This method probably underestimates the overall bryophyte species richness because we could not assess species restricted to tree crowns. However, it has been shown that sampling many tree individuals in a stand, i.e. the level of a plot, keeps the number of overlooked bryophyte species relatively low (Boch et al., 2013d; Kiebach et al., 2016).

To investigate the relationship of bryophytes to forest vegetation, we recorded all vascular plant species of the forest floor and their percentage cover, separately for herbaceous species (including ferns and seedlings of woody species), shrubs (woody species from >0 to 5 m height), first tree layer (tree height between 5 and 10 m), and second tree layer (trees higher than 10 m) in spring and summer. We then calculated the cumulative cover of the two tree layers and the shrub layer (called ‘cumulative cover of woody species’ henceforth) as a proxy

for light availability in the stands (cf. Ewald et al., 2011). Nomenclature of vascular plants followed Wisskirchen and Häupler (1998). Afterwards, we classified all recorded bryophyte and herb species into categories according to their typical habitat requirements with regard to forest affinity and forest dependency, i.e. typical woodland species, according to Preussing et al. (2011) for bryophytes and Schmidt et al. (2011) for vascular plants. For each plot, we counted the numbers and calculated the proportions of typical woodland indicator species of bryophytes and herbs, defined as those which mainly occur in closed forests (= forest specialist species; category 1.1 *sensu* Preussing et al., 2011; Schmidt et al., 2011). The numbers of typical woodland indicator bryophyte species were used to test whether these species are better indicators for forest integrity (Preussing et al., 2011).

2.4 Data analyses

To examine the relationship between forest management and bryophyte species richness we conducted three separate analyses of co-variance, because of the non-orthogonality of management types and dominant tree species. In the first model, we analysed differences between managed and unmanaged forests and included all plots. In the second model, we tested different management types (unmanaged vs. selection vs. age-class) but considered only deciduous stands. As selection forests were restricted to deciduous forests of the Schwäbische Alb and Hainich-Dün, we excluded the Schorfheide-Chorin region from this analysis. In the third model, we tested the effect of the proportion of coniferous trees within the subset of age-class forests. As we were analysing count data, we chose GLM models with Poisson errors. Sequential *Chi-square* tests were used to analyse the significance of deviance changes among our predictors associated with factors added to the model in the sequence shown in Tabs. 1–3. In all three models, region and the co-variates region, soil pH, rock cover, deadwood cover, litter cover and cumulative cover of woody species (trees and shrubs)

were fitted first. This way, we corrected the effect of forest management for regional differences and differences in habitat variables and substrate availability. No model selection was performed, but substrate availability was included only for corresponding groups of bryophytes. In addition, we included interactions between co-variables and region. Furthermore, we included the SMI_d as a proxy for management intensity and its interaction with management and region, as well as the region-by-management interaction into the model. We analysed species richness of all bryophytes, as well as woodland indicator bryophyte species and the four ecological guilds, separately. In addition, we calculated linear regressions to test the relationship between species richness of herbaceous plants and terricolous bryophytes as well as between woodland indicating bryophytes and herbs. Data were analysed using R, Version 3.3.3 (R CORE TEAM, 2017) and the nlme package (Pinheiro et al., 2017).

3. Results

3.1 Overall and regional species richness

Overall, we found 186 different bryophyte species (167 mosses, 19 liverworts). Most species occurred in Schwäbische Alb (131 mosses, 14 liverworts), followed by Hainich-Dün (105 mosses, 10 liverworts), and Schorfheide-Chorin (72 mosses, 12 liverworts). The bryophyte species numbers per plot ranged from 2 to 45 species (overall mean 12.7 ± 0.2 SE species per 400 m²). Mean values differed significantly among the regions, whereas Schwäbische Alb had highest species richness and Schorfheide-Chorin the lowest (Tabs. 1–3, A.1, Fig. A.2). This pattern was mainly caused by an evident higher number of corticolous and saxicolous species in Schwäbische Alb compared with the other two regions (Tab. A.1). Regarding mean terricolous and lignicolous species numbers, we found less pronounced differences among the

regions and in case of lignicolous species even no regional differences within age-class forests (Tabs. 1–3, A.1).

3.2 Management induced differences in species richness

In general, bryophyte species richness was higher in managed than in unmanaged forests (Tabs. 1, A.1, Fig. 1a). This difference was mainly because of higher numbers of lignicolous and terricolous species in managed than in unmanaged forests (Tab. A.1, Fig. 1a). However, within the regions we observed this pattern only in Hainich-Dün and Schorfheide-Chorin. In the Schwäbische Alb we found the opposite result due to high numbers of saxicolous and corticolous species, which compensated the low numbers of lignicolous and terricolous bryophyte species in unmanaged European beech forests (Tab. A.1). Increasing management intensity (SMI_d) decreased the total species richness, mainly because of decreasing numbers of corticolous and saxicolous species. This pattern was consistent among management type, as indicated by the non-significant $SMI_d \times$ management interaction (Tab. 1). Among deciduous forests, the selection forests harboured the highest number of total, corticolous and saxicolous species (Tabs. 2, A.1, Fig. 1b). Within age-class forests we observed a positive relation between the proportion of conifer trees in the canopy and the total species richness, mainly due to strongly increasing numbers of lignicolous and terricolous bryophytes, while saxicolous and corticolous species numbers decreased (Fig. 2).

3.3 Environmental variables and bryophyte species richness

The richness of terricolous bryophyte species was decreasing with increasing soil pH values (Tab. 1). Increasing substrate availability of rocks or deadwood had strong benefiting effects on the number of saxicolous or lignicolous species, which also resulted in increasing total species numbers (Tab. 1). Increasing cover of litter decreased terricolous species richness and therefore also total species richness, which was also indicated by the significant interaction

between conifer proportion and litter cover (Tab. 3). Overall, increasing cumulative cover of woody species (shrubs and trees) had positive effects on corticolous and negative effects on lignicolous and terricolous species. Within deciduous and age-class forests it additionally negatively affected the richness of saxicolous species (Tabs. 2, 3). Similarly to the direct management effects, the patterns between management-related variables and bryophytes were not consistent among regions and management types as indicated by significant interactions (Tabs. 1–3).

3.4 Woodland indicator bryophyte species

On average the number of woodland indicator bryophyte species was 2.9 (± 0.1 SE) per plot. This corresponds to a mean proportion of 22.8% of the total species richness. Generally, woodland indicator bryophyte species were positively correlated to total bryophyte species richness (Fig. A.3). Therefore, numbers of woodland indicator bryophyte species revealed similar patterns of region and management effects compared to total species richness (Figs. 3a, 3b), with the exception of conifer proportion in the canopy that had no benefiting effects on the richness of woodland indicator bryophyte species within age-class stands, although it increased the total species richness significantly (Fig. 2). Corresponding to patterns of total species richness, we observed also benefiting effects of increasing rock cover, as well as negative effects of management intensity on the richness of woodland indicator bryophyte species across and within the studied forest types of deciduous and age-class stands. However, again these patterns and their significance differed among regions and management types as indicated by significant interactions (Tabs. 1–3).

3.5 Relation of herb and bryophyte species richness

Generally, the richness of terricolous bryophyte and herbaceous vascular plant species was positively related both across and within regions. In Schwäbische Alb we observed the

closest, in Hainich-Dün the weakest correlation between the richness of these plant taxa (Fig. 3a). Overall, the number of woodland indicator bryophyte species was positively related to the number of woodland indicator herb species (Fig. 3b). However, the correlation was weak and no longer significant when analysed separately for the three regions.

4. Discussion

4.1 Regional effects

Overall, bryophytes proved to be important parts of forest vegetation in all study regions. Regional differences in species richness are probably caused by considerable climatic (most importantly precipitation) and geological differences (e.g. landscape texture, soil types) leading to differing substrate availability and suitability of forest habitats for bryophytes (Vanderpoorten and Engels, 2002; Bates et al., 2004). Furthermore, the regions vary in air quality with regard to former and current atmospheric pollution (see Boch et al., 2013a) and eutrophication which are considered to have strong impacts on bryophytes (e.g. Friedel and Müller, 2004; Mitchell et al., 2005; Davies et al., 2007). Finally, the historic forest use over the last centuries differed among the regions and continued to affect the current forest attributes on the landscape level (Wäldchen et al., 2011). Given all these fundamental differences among the study regions, this highlights the importance to investigate more than one region to detect general patterns between forest management and bryophyte vegetation.

4.2 Effects of forest management and environmental variables on bryophytes

Generally, the studied managed forests had more species than the unmanaged ones. Especially age-class forests with high proportions of conifers revealed high species densities due to high numbers of lignicolous and terricolous species. Lignicolous species generally benefited from the abundance of suitable deadwood substrates (e.g. Humphrey et al., 2002), which was larger in the studied coniferous forests probably due to retention of logging debris and stumps

therein (see also Müller et al., 2015). Furthermore, special attributes of spruce or pine deadwood such as their resin content, high acidity, low nutrient, high moisture availability and slow decomposition (e.g. Fengel and Wegener, 1984; McAlister, 1995; Kahl et al., 2017) are responsible for the colonization of specialist bryophyte species adapted to acidic and nutrient poor conditions of deadwood, resulting in highly diverse bryophyte communities on coniferous stumps and logs. In contrast, beech deadwood has a moderate pH and lacks resin (Fengel and Wegener, 1984) which results often in high abundances of only few, highly competitive and opportunistic moss species.

Interestingly, the richness of terricolous bryophyte species was decreasing with increasing soil pH values, which is in contrast to many other studies reporting a positive bryophyte diversity-soil pH relationship (e.g. Tyler, T. 2005; Tyler et al., 2018) and contradicts the general opinion that soil acidification might be responsible for the decline of bryophyte species richness (e.g. Delgado and Ederra, 2013). However, this finding might be masked by a tree species effect, as mean soil pH is on average lower in our coniferous forests plots, than to one of the deciduous forest plots (3.9 ± 0.06 SE in coniferous vs. 4.8 ± 0.05 in deciduous forest plots): the richness of terricolous bryophyte species in conifer forests likely profited from higher light availability on the ground due to a less closed canopy (Tinya et al., 2009) and reduced litterfall compared with deciduous forests. These conditions facilitate the occurrence of thick mats of terricolous bryophyte species composed of feather mosses in conifer forests, which are rather typical for montane or boreal forests (Ross-Davis and Frego, 2002; Nelson and Halpern, 2005; Vellak and Ingerpuu, 2005). In contrast, in beech forests the conditions are rather unfavorable for terricolous bryophytes (Márialigeti et al., 2009). Their presence relies on bare soil patches (e.g. at slopes) or occasional soil disturbances, which remove at least temporarily the thick litter layers that hinders bryophyte growth (Dzwonko and Gawroński, 2002). Such soil disturbances can be created by animals (wild boar), wind throw, or forest management practices such as logging trails. The latter ones lead to additional

positive effects of management on microhabitat availability for bryophytes in managed forests, and this may explain the high bryophyte diversity found in selection forests because this type of forest management is characterized by repeated disturbances. However, we should keep in mind that other taxa might depend on structures and processes of old growth forests and low levels of anthropogenic disturbance and might be negatively affected by these frequent disturbances (Bauhus et al., 2009). In contrast, bryophytes are potentially prone to destruction by clear cuttings (e.g. Fenton et al., 2003; Nelson and Halpern, 2005), and consequently, age-class forests may fail to provide any reliable long-term refuge for forest species.

Low numbers of corticolous species observed in conifer dominated forests can be mainly attributed to ‘epiphyte-repellent’ conditions of the stems of coniferous trees (Barkman, 1958; Fengel and Wegener, 1984; Mežaka and Znotiņa, 2006; Kiraly and Ódor ,2010). However, species-rich epiphyte communities on broad-leafed shrubs or little trees of European rowan (*Sorbus aucuparia*) and elder (*Sambucus nigra* and *S. racemosa*) that grow in the understorey of coniferous forests, can compensate for the lack of epiphytes on pine and spruce to a certain amount and can provide suitable epiphyte habitats despite low density of broad-leafed trees (Hazell et al., 1998).

Selection forest was the most bryophyte species-rich management type among all deciduous forests. This forest type is characterized by uneven-aged structure of trees due to long-term, continuous forest utilization by single tree harvest and continuous self-regeneration of beech. These near-natural forest structures accompanied with forest-typical microclimate conditions favor species-rich corticolous communities in contrast to homogenous structures in age-class forests (Bardat and Aubert, 2007; Kiraly and Ódor, 2010; Boch et al., 2013a). In addition, bryophytes in selection and age-class forests might profit from land-use induced habitat availability, including retention of medium sized deadwood and stumps, and soil disturbances on logging trails, benefiting lignicolous and terricolous species.

The number of bryophytes in unmanaged forests was surprisingly low in our study, contradicting the findings of a generally negative effect of forest management on bryophyte diversity reported by Horvat et al. (2017), who studied bryophyte diversity among differently managed silver fir-beech forests in the western Pyrenees including stands which were abandoned since >40 years, Kaufmann et al. (2017) who compared the bryophyte diversity of primeval and production beech forests in the western Carpathian Mountains, and the ones reviewed in Paillet et al. (2010). On the one hand, our results can be attributed to negative long-term effects of land-use history and the slow regeneration of old-growth forests with their typical attributes comprising a multilayered forest structure with a wide range of tree ages, site-adapted mixed tree species compositions and large amounts of deadwood of different type and decay stage (Standovar et al., 2006). Whereas some forest sites in Schwäbische Alb and Hainich-Dün have been abandoned for more than 70 years, most unmanaged forests have been abandoned only since two decades (Huss and Butler-Manning, 2006). Therefore, in some of the recently abandoned forests typical attributes of real natural forests still lack. Additionally, due to decelerated re-colonization of slow dispersing bryophytes to sites of enhanced forest attributes the bryophyte vegetation of unmanaged forests might still suffer from legacy effects of former management impacts (Aude and Lawesson, 1998; Snäll et al., 2004; Fritz et al., 2008). On the other hand, the negative management effects on bryophytes reported by Paillet et al. (2010) stem mostly from boreal regions (twelve out of fourteen studies analysed), and there is an urgent need to include more temperate forest before we can draw general conclusions on management effects on bryophytes.

Forest management intensity (SMI_d), which is negatively related to stand volume (in our case $R^2 = 0.7239$; $p < 0.0001$), was decreasing total bryophyte species richness, mainly because of a general decrease in the richness of corticolous and saxicolous species. This reflects the preference of these species for old stands and trees, providing more suitable microhabitats

than young ones (Gustafsson et al., 1992; Fritz et al., 2009a, 2009b; Boch et al., 2013a, d). Furthermore, due to high tree age, more species had the opportunity to colonize their bark. Stand-age is related to canopy density and multi-layered forest structures which probably result in more forest-typical conditions of microclimate, comprising less variation in temperature and generally higher air humidity, conditions considered to be favorable for epiphytic species in general (Frahm, 2003; Bardat and Aubert, 2007), and forest specialists in particular (McGee and Kimmerer, 2002). In addition to forest management and site attributes, further factors likely determine bryophyte species richness on the plot level, which we might have excluded from our study because of the sampling design. For example the presence of suitable microhabitats and substrate diversity on very small scale (Mills and MacDonald, 2005), which is not *per se* related to forest management types and age-structure, also can provide important micro-hotspots such as large stumps, steep ridges, or creeks even in unnatural tree plantations. Furthermore, local species assemblages, representing only a proportion of the forests' species pool, fluctuate both in space and time (Zobel, 1997), which results in the deviation between the potential and the actually observed bryophyte vegetation on particular sites. Finally, management affects the bryophyte vegetation not only by altering species richness but also by changing bryophyte species composition, whereas management-compatible species replace the incompatible ones (Vellak and Ingerpuu, 2005).

4.3 Woodland indicator bryophyte species

Although coniferous plantations provide higher bryophyte species richness than deciduous ones in our research areas, an increasing proportion of conifers had no benefiting effects on woodland indicator bryophyte species. On the one hand, this might be biased by the categorization of these species, as woodland indicator bryophyte species are largely linked to ancient deciduous stands, whereas coniferous stands on ancient forest sites were less regarded

in studies on woodland indicator species (Preussing et al., 2011; Schmidt et al., 2011; Mölder et al., 2015). On the other hand, our findings at least indicate the general preference of these woodland species for deciduous forests, which are typical in our research areas, and implies the failure of conifer plantations to provide suitable adequate refuges or alternative habitats for them (Gustafsson et al., 1992). Confirming this, we found positive relations between litter cover and negative relations to management intensity, both attributes of rather old, closed deciduous forests, with woodland specialist bryophytes. However, conifer forests provide at least habitat for some woodland indicator bryophyte species, especially deadwood specialists (see also Coote et al., 2012).

4.4 Relation of herb and bryophyte species richness

The overall positive correlation between the richness of terricolous bryophyte and vascular plant species reflects similar demands on light, moisture and nutrient conditions on the forest floor (Tinya et al., 2009). Patterns of bryophyte species richness mainly resembled the ones of vascular plants with respect to management impacts as observed in Boch et al. (2013b), as well as Ingerpuu et al. (2003). However, the strength of correlation was lower than in earlier studies (Pharo et al., 1999; McMullan-Fisher et al., 2010), and surprisingly even lower when numbers of woodland specialists of bryophytes and vascular plants were compared. This might be attributed to differing demands on soil properties as stated by Lalanne et al. (2008), and adaptations of typical woodland vascular plant species (especially spring geophytes), enabling their growth on the forest floor despite of large litter amounts contrary to specialized woodland bryophytes (Cavard et al., 2011; Bartels and Chen, 2012), whose occurrence relies mostly on availability of other substrates than bare soil (deadwood, bark, rocks) in dense deciduous forests. Therefore, beech age-class forests might be suitable for typical woodland vascular plants but not necessarily for bryophytes. This corresponds to the findings of Tullus et al. (2018) who found destructive effects of shelterwood logging, resulting in age-class

forests, on bryophytes of conservation concern. Overall, our findings might imply that woodland specialist bryophytes are better indicators for forest integrity than woodland specialist vascular plants because bryophyte occurrence integrates substrate availability in forests in addition to prevailing light, nutrient and humidity conditions.

5. Conclusions

Long-term effects of past management still affect current forest structure and bryophyte communities in unmanaged forests, which highlight the importance of long-term improvement of forest conditions ensuring the re-colonization of slow dispersing woodland bryophyte species from refuges. Most important for bryophyte species richness is the permanent availability of suitable substrates, which is not stringently linked to the management type. Therefore managed age-class forests and selection forests can provide important microhabitats for many bryophytes, including woodland indicator species, and exceed species numbers of unmanaged forests. Due to the reliability of typical woodland bryophytes as indicators of forest integrity, nature conservation efforts should focus on the number and promotion on the total richness of this group. This includes the reduction of management intensity, as well as maintaining and increasing habitat diversity and a variability of substrates, such as coarse woody debris, the improvement of complex forest structures and habitat heterogeneity by retaining patches with groups of old, mature to over-mature trees in managed forests, maintaining forest climate conditions by silvicultural methods that assure stand continuity, e.g. by selection cutting rather than clear cutting and shelterwood logging (Humphrey et al., 2002; Gustafsson et al., 2004; Frego, 2007; Schulze et al., 2016).

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Tab. 1: GLM summary for differences in bryophyte species richness between managed and unmanaged forests (n = 1050). Deviance changes (GLM with Poisson errors) are shown along with the significance level (* significant at 5%, ** significant at 1%, *** significant at 0.1%). Significant differences are indicated by bold values. Cells with ‘---’ indicate unsuitable factor for the particular ecological guild.

All plots (n = 1050)		All bryophytes	Corticolous bryophytes	Saxicolous bryophytes	Lignicolous bryophytes	Terricolous bryophytes	Woodland bryophytes
Source of variation	<i>df</i>	<i>Deviance</i>	<i>Deviance</i>	<i>Deviance</i>	<i>Deviance</i>	<i>Deviance</i>	<i>Deviance</i>
Region	2	641.43***	590.25***	1356.28***	21.56***	58.49***	389.41***
Soil pH	1	3.32	---	---	---	118.45***	13.7***
Cover of rocks	1	56.11***	---	108.14***	---	---	25.51***
Cover of deadwood	1	25.09***	---	---	18.18***	---	0.71
Cover of litter	1	43.03***	---	---	---	415.36***	5.32*
Cumulative cover of woody species	1	3.57	80.61***	3.13	8.79**	40.13***	4.7*
Management (managed vs. unmanaged)	1	37.61***	0.24	41.21***	61.04***	65.98***	2.76
SMI _d	1	62.77***	140.65***	22.63***	0.25	2.22	37.89***
Management x SMI _d	1	1.3	3.58	0.44	0.01	0.02	0.69
Region x soil pH	2	0.95	---	---	---	20.99***	4.22
Region x cover of rocks	2	9.05*	---	245.68***	---	---	8.03*
Region x cover of deadwood	2	13.69**	---	---	64.76***	---	3.55
Region x cover of litter	2	69.74***	---	---	---	83.55***	36.09***
Region x cumulative cover of woody sp.	2	0.74	42.82***	22.43***	3.15	6.75*	8.05*
Region x management	2	15.93***	9.37**	33.13***	9.44**	5.45	0.25
Region x SMI _d	2	55.21***	54.52***	32.88***	9.56**	10.6***	19.96***
Residual Deviance	>985	2650.7	2807.2	4864.8	1765.2	2752.2	1559.6

Tab. 2: GLM summary for differences in bryophyte species richness among deciduous forests (unmanaged vs. selection vs. age class, n = 467). Deviance changes (GLM with Poisson errors) are shown along with the significance level (* significant at 5%, ** significant at 1%, *** significant at 0.1%). Significant differences are indicated by bold values. Cells with ‘---’ indicate unsuitable factor for the particular ecological guild.

Deciduous forest plots of Schwäbische Alb and Hainich-Dün (n = 467)		All bryophytes	Corticolous bryophytes	Saxicolous bryophytes	Lignicolous bryophytes	Terricolous bryophytes	Woodland bryophytes
Source of variation	df	Deviance	Deviance	Deviance	Deviance	Deviance	Deviance
Region	1	376.3***	159.30***	710.57***	13.27***	1.72	115.77***
Soil pH	1	19.63***	---	---	---	15.33***	18.59***
Cover of rocks	1	56.86***	---	72.41***	---	---	19.47***
Cover of deadwood	1	9.82**	---	---	1.97	---	0.07
Cover of litter	1	5.17*	---	---	---	94.10***	12.83***
Cumulative cover of woody species	1	7.58**	20.38***	10.39**	0.60	1.82	0.08
Management (managed vs. unmanaged)	1	2.74	2.92	5.40*	7.10**	12.67***	0.45
Management type (age class vs. selection)	1	63.66***	37.11***	238.75***	0.01	2.58	31.56***
SMI _d	1	38.07***	122.90***	26.74***	2.97	6.43*	15.46***
Management x SMI _d	1	4.74*	11.02***	1.18	0.16	0.09	1.72
Management type x SMI _d	1	36.02***	37.98***	9.83**	9.98**	1.21	21.04***
Region x soil pH	1	10.75**	---	---	---	0.13	7.64**
Region x cover of rocks	1	22.83***	---	135.91***	---	---	11.30***
Region x cover of deadwood	1	0.04	---	---	8.40**	---	0.44
Region x cover of litter	1	1.17	---	---	---	0.33	0.30
Region x cumulative cover of woody sp.	1	1.73	13.73***	26.28***	0.37	0.01	1.90
Region x management	1	4.08*	3.99*	20.26***	8.67**	2.20	0.36
Region x management type	1	0.08	10.13**	21.96***	13.66***	14.56***	2.02
Region x SMI _d	1	19.68***	34.62***	4.91*	4.39*	0.42	11.79***
Residual Deviance	>449	1491.5	1298.0	2835.8	680.0	1008.8	805.7

Tab. 3: GLM summary for differences in bryophyte species richness among age class forests (n = 826) with regard to the proportion of conifers on the canopy cover of the tree layer. Deviance changes (GLM with Poisson errors) are shown along with the significance level (* significant at 5%, ** significant at 1%, *** significant at 0.1%). Significant differences are indicated by bold values. Cells with ‘---’ indicate unsuitable factor for the particular ecological guild.

Managed age-class forest plots (n = 826)		All bryophytes	Corticolous bryophytes	Saxicolous bryophytes	Lignicolous bryophytes	Terricolous bryophytes	Woodland bryophytes
Source of variation	df	Deviance	Deviance	Deviance	Deviance	Deviance	Deviance
Region	2	314.30***	398.28***	581.89***	9.67**	11.95**	253.17***
Soil pH	1	7.23**	---	---	---	73.29***	0.25
Cover of rocks	1	43.39***	---	281.24***	---	---	23.13***
Cover of deadwood	1	16.11***	---	---	10.36**	---	0.16
Cover of litter	1	44.79***	---	---	---	342.31***	3.03
Cumulative cover of woody species	1	0.01	98.81***	15.37***	5.65*	39.88***	10.61***
Proportion of conifers	1	50.67***	48.82***	74.03***	91.30***	103.34***	3.56
SMI _d	1	38.05***	156.09***	4.17*	0.251	8.22**	39.00***
Proportion of conifers x SMI _d	1	0.04	0.84	7.07**	15.61***	0.19	0.11
Region x soil pH	2	5.85	---	---	---	30.79***	12.87**
Region x cover of rocks	2	4.27	---	145.17***	---	---	0.01
Region x cover of deadwood	2	8.76*	---	---	40.96***	---	4.51
Region x cover of litter	2	88.70***	---	---	---	121.08***	45.19***
Region x cumulative cover of woody sp.	2	5.2	22.13***	2.53	12.75**	0.25	6.07*
Region x proportion of conifers	2	30.08***	35.20***	4.76	29.01***	21.86***	12.89**
Region x SMI _d	2	56.93***	64.37***	31.88***	5.70	2.28	21.61***
Residual Deviance	>776	1825.0	2155.3	2772.2	1322.4	2136.9	1105.4

Figures

Fig. 1: The effect of management across a) all 1050 forest plots from the three regions in Germany and b) within 476 deciduous forest plots of the Schwäbische Alb and the Hainich-Dün region (note that selection forests did not occur in the Schorfheide-Chorin region) on bryophyte species richness of all, corticolous (Cort), saxicolous (Sax), lignicolous (Lig), terricolous (Terr) and woodland indicator bryophyte species (WL sp). Significant differences among groups are indicated by asterisks (significance levels: *** $p < 0.001$; ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$, n.s. > 0.05). In Fig. 1b vertical lines indicate significant or non-significant differences based on the contrasts from the model (Tab. 2). The upper line indicates the contrast between managed and unmanaged, the lower line the ones between age-class and selection forests.

Fig. 2: The relationships between the proportion of conifers in the canopy and bryophyte species richness of all, corticolous (Cort), saxicolous (Sax), lignicolous (Lig), terricolous (Terr) and woodland indicator bryophyte species (WL sp) in 826 age-class forest plots from three regions in Germany. (significance levels: *** $p < 0.001$; ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$, n.s. $p > 0.05$).

Fig. 3: Relationships between a) terricolous bryophyte and herb species numbers in the Schwäbische Alb (A): $y = 0.7x - 0.7$, $R^2 = 0.23$, Hainich-Dün (H): $y = 0.41x - 0.04$, $R^2 = 0.06$, Schorfheide-Chorin (S) region: $y = 0.31x + 0.9$, $R^2 = 0.14$, all $p < 0.001$; and b) numbers of woodland indicator bryophyte species and woodland indicator herb species in 1050 forest plots ($y = 0.17x + 0.83$, $R^2 = 0.06$, $p < 0.001$).

Appendix A. Supplementary material

Supplementary material

Tab. A.1: Mean bryophyte species richness $\pm$ SE per 400 m² plot and number of replicates (N) among the forest management types in the three regions and the overall means.

Region Management	N	Total species number	Corticolous species	Saxicolous species	Lignicolous species	Terricolous species	Woodland bryophytes
<i>Schwäbische Alb</i>							
Unmanaged	20	21.7 $\pm$ 2.1	9.3 $\pm$ 1.2	8.3 $\pm$ 1.7	5.7 $\pm$ 1.0	4.7 $\pm$ 0.9	5.3 $\pm$ 0.8
Managed	318	16.8 $\pm$ 0.4	6.8 $\pm$ 0.2	3.4 $\pm$ 0.3	6.1 $\pm$ 0.2	4.9 $\pm$ 0.2	4.3 $\pm$ 0.1
Age-class	264	15.8 $\pm$ 0.4	6.5 $\pm$ 0.3	2.3 $\pm$ 0.2	6.3 $\pm$ 0.2	5.1 $\pm$ 0.3	3.9 $\pm$ 0.1
Selection	54	21.7 $\pm$ 1.0	8.3 $\pm$ 0.6	8.9 $\pm$ 0.7	5.1 $\pm$ 0.3	4.0 $\pm$ 0.4	6.0 $\pm$ 0.4
Total	338	17.1 $\pm$ 0.4	6.9 $\pm$ 0.2	3.7 $\pm$ 0.3	6.1 $\pm$ 0.2	4.9 $\pm$ 0.2	4.3 $\pm$ 0.1
<i>Hainich-Dün</i>							
Unmanaged	56	8.6 $\pm$ 0.5	4.8 $\pm$ 0.3	0.4 $\pm$ 0.3	3.7 $\pm$ 0.3	2.0 $\pm$ 0.3	2.4 $\pm$ 0.2
Managed	215	11.7 $\pm$ 0.4	5.1 $\pm$ 0.2	0.9 $\pm$ 0.2	5.6 $\pm$ 0.2	4.1 $\pm$ 0.2	2.9 $\pm$ 0.1
Age-class	163	11.5 $\pm$ 0.5	4.8 $\pm$ 0.2	0.9 $\pm$ 0.2	5.6 $\pm$ 0.2	4.4 $\pm$ 0.3	2.7 $\pm$ 0.2
Selection	52	12.0 $\pm$ 0.6	6.2 $\pm$ 0.5	0.9 $\pm$ 0.4	5.7 $\pm$ 0.4	3.1 $\pm$ 0.3	3.5 $\pm$ 0.3
Total	271	11.0 $\pm$ 0.3	5.0 $\pm$ 0.2	0.8 $\pm$ 0.1	5.2 $\pm$ 0.2	3.7 $\pm$ 0.2	2.8 $\pm$ 0.1
<i>Schorfheide-Chorin</i>							
Unmanaged	42	7.5 $\pm$ 0.4	3.0 $\pm$ 0.3	1.5 $\pm$ 0.3	3.5 $\pm$ 0.3	2.4 $\pm$ 0.3	1.8 $\pm$ 0.2
Managed age-class	399	10.7 $\pm$ 0.2	3.1 $\pm$ 0.1	0.3 $\pm$ 0.1	6.1 $\pm$ 0.1	5.2 $\pm$ 0.2	1.8 $\pm$ 0.1
Total	441	10.4 $\pm$ 0.2	3.1 $\pm$ 0.1	0.4 $\pm$ 0.1	5.9 $\pm$ 0.1	4.9 $\pm$ 0.1	1.8 $\pm$ 0.1
<i>All regions</i>							
Unmanaged	118	10.4 $\pm$ 0.7	4.9 $\pm$ 0.3	2.1 $\pm$ 0.4	4.0 $\pm$ 0.3	2.6 $\pm$ 0.2	2.7 $\pm$ 0.2
Managed	932	13.0 $\pm$ 0.2	4.8 $\pm$ 0.1	1.5 $\pm$ 0.1	6.0 $\pm$ 0.1	4.8 $\pm$ 0.1	2.9 $\pm$ 0.1
Age-class	826	12.5 $\pm$ 0.2	4.5 $\pm$ 0.1	1.1 $\pm$ 0.1	6.1 $\pm$ 0.1	5.0 $\pm$ 0.1	2.7 $\pm$ 0.1
Selection	106	16.9 $\pm$ 0.8	7.3 $\pm$ 0.4	5.0 $\pm$ 0.6	5.3 $\pm$ 0.3	3.5 $\pm$ 0.3	4.8 $\pm$ 0.3
Total	1050	12.7 $\pm$ 0.2	4.8 $\pm$ 0.1	1.6 $\pm$ 0.1	5.8 $\pm$ 0.1	4.6 $\pm$ 0.1	2.9 $\pm$ 0.1

Fig. A.1: Location of the three study regions Schorfheide-Chorin (A; northeast), Hainich-Dün (B; centre) and Schwäbische Alb (C; southwest) in Germany and detailed maps indicating the distribution of the plots among the study regions. Plots are symbolized by dots, with forests marked by grey areas.

Fig. A.2: Total species richness (Schwäbische Alb (ALB): 338 plots, Hainich-Dün (HAI): 271 plots, Schorfheide-Chorin (SCH): 441 plots) and species richness within the three forest management types age-class (264, 163, 399), selection (54, 52, 0) and unmanaged (20, 56, 42) among the three regions. Note that selection forests did not occur in the Schorfheide-Chorin region.

Fig. A.3: Positive correlation between numbers of woodland indicator bryophyte species and total bryophyte species among the study regions Schwäbische Alb (Alb) – solid line: $y = 0.33x - 1.1$, $R^2 = 0.72$; Hainich-Dün (Hai) – long dashed line: $y = 0.31x - 0.55$, $R^2 = 0.65$; Schorfheide-Chorin (Sch) – short dashed line: $y = 0.16x + 0.18$, $R^2 = 0.23$.