Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe – reflecting substrate quality or shaped by climate and forest conditions?

Jacob Heilmann-Clausen[1][*], Erik Aude[2], Klaas van Dort[3], Morten Christensen[4], Andrej Piltaver[5], Mirjam Veerkamp[6], Ruben Walleyn[†], Irén Siller[7], Tibor Standovár[8], Péter Òdor[9]

[1]Center for Macroecology, Evolution and Climate, Biological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark, [2]HabitatVision A/S, Solsortevej 7, DK-8410 Rønde, Denmark, [3]Forestfun, Leeuweriksweide 186, NL-6708 LN Wageningen, The Netherlands, [4] Hvidtjørnevej 1, 4180 Sorø, Denmark, [5]Institute for systematic of higher fungi, Zofke Kvedrove 24, SI-1000 Ljubljana, Slovenia, [6]Pelikaanweg 54, NL-3985RZ Werkhoven, The Netherlands, [7]Institute for Biology, Faculty of Veterinary Science, Szent István University, H-1400 Budapest, Pf. 2., Hungary (Turcsanyine.Siller.Iren@aotk.szie.hu), [8]Department of Plant Systematics, Ecology and Theoretical Biology, Eötvös University, Pázmány P. stny. 1/C, H-1117 Budapest, Hungary (standy@ludens.elte.hu), [9]MTA Centre for Ecological Research, Institute of Ecology and Botany, H-2163 Vácrátót, Alkotmány u. 2-4., Hungary (odor.peter@okologia.mta.hu).

Running title

Bryophytes and fungi on dead beech logs in Europe

Keywords

Biodiversity, community gradients, dead wood, decomposers, *Fagus sylvatica*, forest reserves, guilds, landscape history, variation partitioning, wood-decay

Abstract

Aim Fungi are drivers of wood-decay in forested ecosystem, while bryophytes use dead wood as a platform for their autotrophic lifestyle. We tested the hypothesis that fungal communities on beech logs are mainly structured by substrate quality, while bryophyte communities are structured by climatic gradients. In addition we tested if community structure in both organism groups is altered along a gradient from nearly pristine forest to forests heavily affected by management and human disturbance in the past.

Location Europe

Methods We surveyed 1207 fallen beech logs in 26 of the best preserved forest stands across six European countries, representing a gradient in overall naturalness of the forest landscape. Recorded species were classified in ecological guilds. Indirect ordination and variation partitioning was used to analyse the relation between species composition and environmental variables, recorded at log or site level.

Results In total, 10,367 bryophyte and 15,575 fungal records were made, representing 157 and 272 species, respectively. Fungal communities were most clearly structured by substrate quality compared to bryophyte ones. In both groups a distinct turnover in species composition was evident along a longitudinal gradient from Central to Western Europe. Fungi specialised in trunk rot and specialised epixylic bryophytes were scarcely represented in Atlantic regions, and partly replaced by species belonging to less specialised guilds. Variables related to climate and forest conditions were confounded along this main geographical gradient in community composition

Main conclusions We found bryophyte and fungal communities co-occurring on fallen beech logs in European beech forest reserves to differ in their response to biogeographical drivers and local scale habitat filters. Both groups responded to major gradients in climate and forest conditions, but the loss of specialist guilds in degraded forest landscapes points to a functionally important effect of forest landscape degradation at the European continental scale.

INTRODUCTION

It is well known that diversity patterns may differ among organism groups, along elevational, latitudinal and human disturbance gradients (e.g. Fukami & Wardle, 2005; Rahbek, 2005; Sundquist *et al.*, 2013), but in many cases it is poorly understood why these differences occur. Comparisons across taxonomical or functional groups are one way to increase understanding of these patterns (Fukami & Wardle, 2005). In this respect, decaying wood offers an interesting study system, because it hosts several different organism groups playing different functional roles within well-delimited habitat patches. Fungi are the principal drivers of wood-decay (Boddy & Heilmann-Clausen, 2008) and hence crucial for most other organism groups associated with dead wood. In contrast, wood-living bryophytes are not directly involved in wood decay, but use dead wood as a platform for their autotrophic lifestyle. Some bryophytes are obligate epixylic, but a major part of the species utilising dead wood are able to grow and may even be more common on other substrates, including soil, rocks and the bark of living trees (Stokland *et al.,* 2012).

Beech species (*Fagus* spp.) are widespread and typical trees of temperate deciduous forests throughout the Northern Hemisphere (Fang & Lechowicz, 2006; Bradshaw *et al.,* 2010). European beech (*Fagus sylvatica* L.) is the most widespread species in the genus. It is an important and often dominant tree species throughout temperate lowland forests of Northwest-Europe and in low mountain ranges in Central Europe, following the Appenines down to southern Italy (Bradshaw *et al.,* 2010). European beech forests are among the most degraded and fragmented ecosystems in the world, with less than 0.1 % remaining in near pristine condition (Schmitt *et al.,* 2009; Brunet *et al.,* 2010). Many associated organisms are hence threatened with extinction, nationally or even at the global scale. This is especially the case for specialists associated with habitats – e.g. old trees and decaying wood – lacking in managed forests (Brunet *et al.,* 2010;). The biogeography of the flora of European beech forests is relatively well known (e.g. Willner *et al.,* 2009) and several recent papers have provided a first European scale assessment of saproxylic beetle diversity (Lachat *et al.,* 2012; Gossner *et al.* 2013; Müller *et al.,* 2013). In comparison little is known on large scale biodiversity patterns of fungi and bryophytes (Qian *et al.,* 1999; Ódor *et al.*, 2006; Heilmann-Clausen & Boddy, 2008).

More broadly, the importance of local habitat filters for determining community structure has been studied quite extensively for both wood-inhabiting fungi and bryophytes, in different forest types. Wood decay stage, tree species and microclimatic factors have been shown to be

important filters influencing species composition at individual fallen trees in both groups (Ódor & van Hees, 2004; Heilmann-Clausen *et al.* 2004; Boddy & Heilmann-Clausen, 2008). Several studies have found a clear link between lowered dead wood amounts and decreasing species richness in managed forests (for reviews see ; Müller & Bütler 2010; Laussauce *et al.,* 2011), while others have indicated that forest fragmentation and temporal habitat discontinuity influence species composition at the landscape scale, even in the presence of ample and adequate habitats in local hot spots (e.g. Heilmann-Clausen & Christensen, 2005; Löbel *et al.,* 2006; Ódor *et al.,* 2006; Paltto *et al.,* 2006). Unfortunately none of these studies accounted for the potential importance of climate in a comprehensive way, and hence it is difficult to evaluate to what degree forest conditions, habitat quality and climate interacts in shaping bryophyte and fungal communities.

In this study we explored community composition of wood-inhabiting bryophytes and fungi based on a comprehensive dataset collected in a standardised way in beech forest reserves across six countries in Europe, from Sweden in the north, Belgium in the west to Slovenia in the south and Hungary in the east. The dataset represents an extension of the dataset analysed by Ódor *et al.* (2006) that focussed on species richness patterns. For both organism groups the analysed dataset is the geographically most extensive so far using a standardised sampling protocol.

It was our overall expectation that substrate quality, climate and forest conditions all contribute to explain community composition of fungi and bryophytes on fallen logs across study sites. Because fungi have a direct role in wood decay while bryophytes use dead wood only as a substrate we hypothesised that: (1) the relative contribution of substrate quality was stronger for fungi compared to bryophytes; and (2) regional climatic factors were more important for explaining differences in bryophyte community composition. Finally, (3) we hypothesised that variables related to forest conditions (including history) were equally important in explaining community structure in both organism groups, with ecologically degraded communities prevailing in forest landscapes characterized by lack of naturalness and habitat loss.

MATERIAL AND METHODS

Study objects

The study was conducted in 26 beech stands, in 16 forest reserves, in Belgium, Denmark, Hungary, The Netherlands, Slovenia and Sweden. The stands represent some of the most natural beech forests within each country. They are all protected as non-intervention forest reserves, but their historical management is very different. Due to an intensive history of forest management and fragmentation, stands in The Netherlands and Sweden were generally small, which is the reason for the study design in these countries, where several small stands aggregated within larger nature reserves were studied (Table 1; Fig. 1). In Belgium only one forest reserve was included, but divided in a core area and a buffer zone with different management history.

In each stand between five (minimum 25 at reserve level) and 125 fallen beech logs were selected following a stratified random approach, with the aim to secure a balanced representation of six log decay stages (see Ódor & van Hees, 2004) and three diameter classes (diameter at breast height 20-50 cm; 50-80 cm; >80 cm). Due to an unbalanced representation of decay stages and size classes, it was not possible to fulfil this goal in some stands, especially in Belgium and The Netherlands. Several variables were recorded for each log in the field, or at stand or reserve level based on various sources. We divided the recorded variables in three variable sets: (i) Substrate variables included all variables recorded in the field to characterize the individual studied log, i.e. size, decay stage, bark and moss cover and soil contact; (ii) Climate and soil variables were recorded at reserve level, and included a number of key variables describing soil type, elevation and temperature, rainfall, snow cover and continentality based on actual measurements from meteorological stations near the study sites; (iii) Forest condition variables were recorded at stand or reserve level and included naturalness, dominant tree age, reserve size and dead wood volume based on actual measurements or recorded data for each stand, as well as several variables describing the current and past (18-19th century) forest cover in a 5 km radius around the centre point of each stand. A radius of 5 km has been found to be relevant in earlier landscape studies of wood-inhabiting fungi (Paltto *et al.,* 2006). We also analysed a 10 km radius in the early phase of analysis, but as this radius always resulted in slightly poorer fit with relevant response variables, we did not include this scale in the final analyses. Details, names and abbreviations of all variables and their classification as substrate, climate and soil or forest condition variables are shown in Table 2. All variables were standardised by range (i.e. obtaining values ranging from 0 to 1) before further analyses.

Fungi and bryophyte surveys

All included logs were surveyed thrice for fungal fruit bodies and once for wood-inhabiting bryophytes recording all species growing directly on wood or bark. The fungal surveys were conducted at three occasions over the fungal season in order to obtain a robust recording of species producing fruit bodies on the studied logs. Among the macrofungi (fungi with fruit bodies visible to the naked eye) all groups were sampled, except fully resupinate corticoid fungi, non-stromatic pyrenomycetes and inoperculate discomycetes with fruit bodies regularly smaller than 10 mm. At each survey fruit bodies were recorded in the field or collected for identification in the laboratory. For both fungi and bryophytes recordings from the log, including the root plate (if present) and major branches of the crown (diameter > 10 cm, if present) and the snag up to 2 m (if present) were merged for each log. Surveys were carried out in 2001-2002 except for Sweden where field work was conducted in 2004.

For fungi the taxonomic treatment follows Hansen & Knudsen (1992-2000), but nomenclature has been updated to match with indexfungorum.org (accessed 18. June 2014). For bryophytes nomenclature follows Hill *et al.* (2006) for mosses, and Grolle & Long (2000) for liverworts. *Plagiochila porelloides* and *P. asplenioides* as well as *Plagiothecium nemorale* and *P. succulentum* were not separated. Among the fungi *Antrodiella semisupina* was treated in a collective sense including *A. faginea* and *A. pallescens*, *Physisporinus sanguinolentus* was not distinguished from *P. vitreus* and *Pluteus plautus* was treated in a collective sense.

Classification of species

Compared to earlier reports based on part of the present dataset (e.g. Ódor *et al.,* 2006), we excluded some species groups to secure standardized sampling across study sites. Thus litter-inhabiting and ectomycorrhizal fungi, which only occasionally occur on dead wood, were omitted. Similarly, in the bryophyte dataset, species associated to the soil of the uprooted part of the logs were omitted. The remaining taxa were classified in ecological guilds. Bryophytes were classified based on their normal substrate preference as epilithic, epiphytic, epixylic, opportunistic or terricolous according to textbooks (Frahm & Frey, 1992; Smith, 2004; Schumacker & Vana, 2005) and field experience of the authors (see Odor *et al.*, 2006). Fungi were classified as early ruderals, combative invaders, cord-formers, late stage specialists, trunk rotters or with unknown/other ecology, based primarily on Boddy & Heilmann-Clausen (2008), but with input from other sources, especially Heilmann-Clausen (2001), Hansen & Knudsen (1992-2000), and field experience of the authors. For further details see Appendix S1 and S2 in Supporting Information.

Data analysis

The overall structure of the fungi and the bryophyte dataset was explored by Detrended Correspondence Analysis (DCA, Hill & Gauch, 1980) in PCord vers. 4.25. (McCune & Mefford, 1999). Down-weighting of rare species was not applied, but species poor logs (less than five species) and infrequent species (less than three records) were omitted from the dataset to increase the robustness of results (cf. Økland, 1999). DCA is an unconstrained ordination technique and hence extracted sample scores in the ordination space are based solely on the species recorded on each log. The relationships between DCA axes and environmental variables were studied by simple mixed-effect models (Zuur *et al.*, 2009) using environmental variables as independent, DCA axes as dependent variables and site as a random factor. Owing to confounded variation among some variables and limited degrees of freedom for stand-level variables, we did not attempt to construct more complex multivariate models. In all models the significance of the relationships were tested by F-statistics, and with p-values Bonferroni-Holm adjusted, due to the multiple comparisons. The regression modelling was done in R 2.15.2 environment (The R Development Core Team, 2012), using the "nlme" package (Pinheiro *et al.*, 2011).

The ecological nature of the gradients extracted in DCA, was analysed further by testing for non-random patterns in the distribution of ecological guilds along each DCA axis using one way ANOVAs, based on the DCA axis scores for each species. Tukey's HSD were used for post-hoc comparisons of means.

The relative importance of the three groups of explanatory variables (substrate, climate and soil and forest condition, Table 2) on species composition in both organism groups were analysed by variation partitioning (Legendre & Legendre, 1998) using partial Canonical Correspondence Analysis (Leps & Smilauer, 2003). The pool of explanatory variables in each variable set was selected by forward selection via Monte Carlo simulation under the full model using 499 permutations. During the selection process the automatic selection procedure of Canoco 4.5 was used (ter Braak & Smilauer, 2002).

RESULTS

In total we recorded 157 species of bryophytes and 272 species of fungi on the 1207 investigated logs. A large proportion of the recorded species occurred on less than three logs,

and similarly many logs had less than five species present in either group. After pruning out these species poor logs and low frequent species, the bryophyte dataset was reduced to 9689 records of 114 species on 893 study objects, while the fungal dataset contained 12967 records of 210 species on 965 study objects.

In both datasets three ordination axes were extracted in the DCA. In the fungal dataset the ordination axes 1 to 3 had gradient lengths of 3.98, 3.64 and 3.30 SD units respectively, with eigenvalues of 0.40, 0.30 and 0.19. The DCA of the bryophyte dataset similarly produced ordination axes with lengths of 3.71, 3.52 and 3.58 SD units and corresponding eigenvalues of 0.53, 0.32 and 0.19.

Relationships between DCA axes and environmental variables

All extracted ordination axes were significantly related to environmental variables (Table 3), and in both organism groups a clear geographical clustering was evident in the ordination space defined by axis 1 and 2 (Fig. 2).

For bryophytes, the first axis was best explained by snow cover, temperature range, elevation, naturalness and longitude, implying that this axis separated Atlantic lowland sites in northern Europe from highland sites in central Europe with a continental montane climate, long snow cover and high naturalness. The second axis in the bryophyte ordination was, best explained by decay stage and related substrate variables nested within site (Table 3). The third bryophyte ordination axis was significantly related only to substrate variables with decay stage having the highest F-value.

In the fungal ordination axis 1 was best explained by decay stage, while axis 2 expressed a geographical gradient (Fig. 2), best explained by longitude and temperature range (Table 3), implying that the axis represented a gradient in continentality. The third and weakest fungal ordination axis was only related to substrate variables with log size (DBH) having the highest F-value. It is important to note that correlation among some environmental variables was very pronounced (Appendix S3) and hence the relations between closely related environmental variables and ordination axes are not independent.

Optima of guilds

The distribution of bryophyte and fungal guilds was significantly non-random along the analysed DCA ordination axes (ANOVA, $p < 0.0001$ except for axis 3 in the fungal ordination

with p=0.0058; F-values were 6.3, 6.9 and 28.7 for axes 1-3 in the bryophyte ordination, and 25.7, 5.3 and 3.4 for the corresponding fungal axes). Among the bryophytes, epilithic and epixylic species had significantly lower optima along axis 1 compared to terricolous and opportunistic species, while epiphytes and epixylic species were separated along axis 2 (Fig. 3). Along axis 3 epiphytes and epilithic species were significantly separated from epixylic, terricolous and opportunistic species. The axis 1 optima of epilithic and epixylic species were lower than the general distribution of samples in the same ordination space, indicating these guilds to have a disproportional strong influence on the community gradient, due to a high prevalence in Slovenia and Hungary.

In the fungal ordination a significant turnover in guilds was evident along ordination axis 1. Early ruderals had significantly higher optima than all other groups, but also combative invaders had a high optima indicating prevalence on weakly decayed logs. In contrast, late stage specialists had the lowest optima. Along axis 2 species classified as trunk rotters had significantly higher optima than late stage specialists, cord-formers and species with different or unknown strategies. The distribution of cord-formers was narrow and particularly low, indicating this guild to be very sparsely represented towards the continental end of this gradient. Finally late stage specialists were significantly separated from species with unknown or different ecology along axis 3.

Variation partitioning

The CCA based variation partitioning of the fungal and bryophyte datasets showed marked differences between the two datasets (Fig. 4): Substrate variables independently explained 8 % of the explained variance in the bryophyte dataset, versus 23 % in the fungal dataset. Climate and soil and forest condition variables in combination accounted for 77 % of the explained variance in the bryophyte dataset, compared to 63 % in the fungal dataset. The individual contribution of climate and soil variables was similar in both datasets (21 %), while variables describing forest conditions were slightly more important in explaining variation in the fungal dataset (20 % versus 15 %). Further, the shared contribution of forest condition and climate and soil variables was almost double as high in bryophytes (40 %) compared to fungi (22 %). In total, the selected explanatory variables explained 22.7% of the total inertia in the bryophyte CCA and 10.3% of the total inertia in the fungal CCA. As shown by Økland (1999) total inertia is not comparable between datasets, and in our case the difference probably reflect inherent differences in data-structure, especially the larger species pool and higher

frequency of infrequent species in the fungal dataset compared to the bryophyte dataset (cf. Ódor et al. 2006)).

DISCUSSION

Local filters

In this study we found clearly different patterns in community structure of wood-inhabiting fungi and bryophytes on fallen beech logs, distributed in 26 protected beech stands in six European countries. Fungal community composition was strongly structured by local filters, particularly wood decay stage at log level, while bryophyte communities were most strongly shaped by site and landscape level filters relating to climate and forest conditions (especially naturalness).

A distinct turnover in fruiting patterns of fungal species composition during wood decay is well established from previous studies (Stokland *et al.,* 2012), but our study is the first to demonstrate the generality of a strong, common decay gradient shaping fungal communities on decaying beech logs at the European continental scale. The optima of fungal guilds along the gradient show a transition from early ruderals in initial decay stages, over combative invaders and trunk rotters in intermediate decay stages and with cord-formers and late stage specialists having the latest optima. This turnover corresponds roughly to a shift from ruderal to combative species, combined with the effect of substrate modification favouring species specialised in utilising residual compounds from previous decay (Heilmann-Clausen, 2001; Boddy & Heilmann-Clausen, 2008).

For the bryophytes the effect of decay stage was smaller than for fungi and subordinate to the effect of variables related to climate and forest conditions. This may partly reflect that decay stage was estimated based on the physical decay stage of logs, reflecting the activity of decomposer fungi, while time since tree death would be the most relevant variable to address for bryophytes. However, our analyses show a strong geographical differentiation of bryophyte communities within our dataset, with the clear expression of a successional gradient only after accounting for differences in species pools among sites. Several previous studies have reported a clear successional turnover in bryophyte species composition as wood decays, with epiphytes dominating in early decay stages and epixylic species restricted to strongly decayed logs (e.g. Söderström, 1988; Rambo & Muir, 1998; Ódor & van Hees 2004; Kushnevskaya *et al.,* 2007). This corresponds very well with the turnover in guilds found

along ordination axis 2 and 3 in this study, with the interesting addition, that epilithic species, when present, seem to co-occur with epiphytes, while terricolous species grouped with the epixylics.

Geographical gradients in bryophyte communities

Variables related to climate and forest conditions were confounded along the principal bryophyte community gradient, and the variation partitioning approach suggested that most of the explained variation is shared between both set of variables. Previous studies have found that obligate epixylic bryophytes are sensitive to lack of naturalness at the local scale, due to discontinuity in the presence of suitable substrates, especially large diameter dead logs in managed forests (Andersson & Hytteborn, 1991; Rambo and Muir, 1998; Saboljevic *et al.,* 2010), but also due to the lack of stability in forest climate caused by forestry operations, facilitating more robust, weft-forming bryophytes that are less sensitive to desiccation (Clausen, 1964; Ódor & van Hees, 2004). As shown by Ódor *et al.* (2006) the average alpha diversity (species richness per log) is very variable within our dataset, being very high in Slovenia, and lowest in Belgium, The Netherlands and Denmark, reflecting the principal gradient in bryophyte species composition found in this study. The optima of bryophyte guilds along the first ordination axis showed that bryophyte assemblages in countries with low alpha diversity were dominated by opportunistic and terricolous species, while obligate epixylic, and to a lesser extent epiphytic species were very scarce. Thus, low alpha diversity was related to a depletion of functional types in the community, and in particular to a poor representation of specialised epixylic species on decayed logs. However, a direct or indirect effect of climatic drivers cannot be ruled out, and the strong relation between the first ordination axis and snow cover and elevation is intriguing. In a study from the Czech Republic, Jansová (2006) found that growth and local extinction dynamics of bryophyte communities on beech logs were more intensive in wintertime than in the summer. This suggest that the length of the snow free period in winter may be an important factor structuring epixylic communities, just as it has been shown for groundliving bryophytes in alpine snow-beds (e.g. Hohenwallner *et al.,* 2011). In our dataset, the winterperiod without snow cover was longest for sites in Belgium and The Netherlands, and hence negatively correlated with stand naturalness. Whether a shorter snow cover may benefit opportunistic species, which often have higher growth rates than true epixylic specialists, remains untested.

Geographical gradients in fungal communities

Even though the dominant gradient in fungal communities was related to log decay stage, regional filters also play an important role. Thus, axis 2 in the fungal ordination represents a distinct geographical gradient, strongly related to longitude and temperature range, and with weaker relations to several forest condition variables. Overall, this suggests a distinct turnover in fungal community structure with increasing continentality. Wood-inhabiting fungi are known to differ considerably in their microclimatic tolerances and preferences (Boddy & Heilmann-Clausen, 2008; Stokland *et al.,* 2012) but only a limited number of studies have explored the importance of macroclimate for community composition in wood-inhabiting fungi, and mainly in relation to distinct elevational gradients (Lindblad, 2001; Gómez-Hernández *et al.*, 2012). In a previous paper (Ódor *et al.*, 2006) we suggested that trunk rotters (heart rot agents in Ódor *et al.* (2006)), which are normally considered stress-tolerant (Boddy & Heilmann-Clausen, 2008), could be favoured under continental climates. The current guild based analysis lends support to this hypothesis, but due to the confounding of climate and forest condition variables, direct effects of forest history or naturalness cannot be ruled out.

Studies from Fennoscandia have reported a clear relation between forest fragmentation and lack of naturalness on one side and the depletion of fungal communities for habitat specialists on the other (Paltto *et al.,* 2006; Penttilä *et al.,* 2006; Berglund *et al.,* 2011; Nordén *et al.,* 2013). Unfortunately, these studies have not accounted for the potential effect of climate in a comprehensive way, but in a regional scale study in Germany, Bässler *et al.* (2010) reported that resource availability was more important than climate for wood-inhabiting fungi on large diameter dead wood. In our dataset, trunk rotters constitute an important group of habitat specialists that only produce fruit bodies on large decaying logs or living trunks with internal rot (Boddy & Heilmann-Clausen, 2008). Hence, their optima in Slovenia and Hungary, hosting the most natural beech stands, could reflect higher continuity in the presence in coarse dead wood habitats and less fragmented forests in this part of Europe. The significant disassociation of trunk rotters with cord-formers and late stage specialists along DCA axis 2 support this interpretation. The two latter guilds all have traits that make them relatively competitive in managed forests with low input of large diameter dead wood: Cord-formers are typically able to grow on various types of woody material, and are very competitive in invading already colonized resources, e.g. dead branches falling from the canopy to the forest floor (Boddy, 1999; Boddy & Heilmann-Clausen, 2008). Late state specialists include mainly

basidiomycetes, not least agarics belonging to the genera *Mycena, Pluteus* and *Psathyrella*. Except for the preference for well-decayed wood, little is known on the precise habitat requirements in this guild, but they are rarely restricted to large diameter dead wood and several species occur even on cut stumps, sawdust and other man-made substrates (e.g. Runge, 1975; Babos, 1991). In a parallel analysis of the fungal dataset used here, but with a strict focus on forest naturalness we found that beta-diversity was significantly lower in late stages of decay in less natural forest reserves compared to more natural sites (Halme *et al.,* 2013). This could reflect a depletion of trunk-rotters to the benefit of more ruderal cord-formers and late stage agarics, resulting in more uniform fungal communities on strongly decayed logs in degraded forests, but further studies are needed to confirm the validity of this hypothesis.

CONCLUSIONS

In this study we found that bryophyte and fungal communities co-occurring on fallen beech logs in European beech forest reserves differed considerably in their responses to biogeographical drivers and substrate quality. In accordance with our hypothesis 1, fungal communities were structured by a common and strong successional gradient over the European continental scale, while bryophyte communities on the same logs were more strongly structured by regional filters, with effects of substrate quality nested at regional level. In other words, considerable species pool differences were evident for bryophytes, but not for fungi. Species in both groups often have wide distribution ranges, which would assume low effects of species pools. However, several specialised bryophyte species (mainly epixylics) are predominantly dispersed by large asexual diaspores, and hence dispersal limited at the landscape scale (Löbel & Rydin 2009), which suggest that communities of wood-inhabiting bryophytes might be more sensitive to habitat fragmentation and breaks in continuity than fungal communities.

The tests of hypothesis 2 (regional climatic factors are more important for bryophytes than for fungi) and hypothesis 3 (forest conditions are equally important in both groups) proved difficult due to the confounding of important climatic and forest condition variables along the identified community gradients. However, our results pointed to a pronounced effect of climatic variables on fungal communities at the European scale, and our data do not support wood-inhabiting fungi to be less affected by regional climate compared to bryophytes, although drivers and mechanisms seem to differ among the two organism groups.

With some variation a distinct community turnover was observed in both wood-inhabiting bryophytes and fungi, along a longitudinal gradient from Central (Slovenia and Hungary) to Western Europe (Belgium & the Netherlands), with substrate specialists depending on large fallen logs being scarcely represented in the latter countries. Based on this, but also considering the overall landscape history of Europe (Kaplan *et al.,* 2009), we interpret this depletion to reflect mainly a response to the severe forest loss and broken habitat continuity in Western Europe, but with a probable interaction with climatic factors. It seems plausible that both epixylic bryophytes and fungi causing trunk rot might be more competitive in continental climates: Epixylic bryophytes due to the longer period with snow cover, which may decrease competition from more opportunistic species, and trunk rotting fungi due to the higher level of microclimatic stress, reducing competition from cord-formers and late stage specialists. We hope that future studies addressing geographical gradients in biodiversity connected to dead wood can be optimized to focus more on the independent effects of climate and forest history on biodiversity on dead wood. At least in Europe the confounding relation between climate and anthropocentric forest loss and degradation is deeply embedded in history (Kaplan *et al.,* 2009), which makes the design of relevant studies difficult. Carefully designed studies over the naturalness gradient in the core areas of beech at Balkan and in the Carpathians could probably overcome this problem, but we also encourage studies on other tree species, from other continents or using experimental set-ups to increase the knowledge on the generality of climate and habitat loss effects on wood-inhabiting biodiversity.

ACKNOWLEDGEMENTS

References

Andersson L.I. & Hytteborn H. (1991) Bryophytes and decaying wood: a comparison between managed and natural forests. *Holarctic Ecology,* **14**, 121–130.

Arcanum (2006) *Digitized maps of the Habsburg Empire. The second military survey 1806–1869*. DVD-Rom. Arcanum Kft., Budapest.

Babos, M. (1981) Mycological examination of sawdust depots in Hungary. *Studia botanica Hungarica*, **15**, 31–44.

Bässler, C., Müller, J., Dziock, F. & Brandl, R. (2010) Effects of resource availability and climate on the diversity of wood-decaying fungi. *Journal of Ecology,* **98**, 822–832.

Berglund, H., Hottola, J., Penttilä, R. & Siitonen, J. (2011) Linking substrate and habitat requirements of wood-inhabiting fungi to their regional extinction vulnerability. *Ecography*, **34**, 864–875.

Boddy, L. (1999) Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. *Mycologia,* **91**, 13–32.

Boddy, L. & Heilmann-Clausen, J. (2008) Basidiomycete community development in temperate angiosperm wood. *Ecology of Saprotrophic Basidiomycetes* (eds. L. Boddy, J.C. Frankland & P. van West), pp. 211–237. Elsevier.

Bradshaw, R.H.W., Kito, N., Giesecke, T. (2010) Factors influencing the Holocene history of Fagus. *Forest Ecology and Management*, **259**, 2204–2212.

Brunet, J., Fritz, Ö. & Richnau, G. (2010) Biodiversity in European beech forests – a review with recommendations for sustainable forest management. *Ecological Bulletins,* **53**, 77–94.

Christensen, M., Hahn, K., Mountford, E., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S. & Vrska, T. (2005) Dead wood in European beech forest reserves. *Forest Ecology and Management*, **210**, 267–282.

Clausen, E. (1964) The tolerance of hepatics to desiccation and temperature. *Bryologist*, **67**, 411–417.

Fang, J. & Lechowicz, M.J. (2006) Climatic limits for the present distribution of beech (*Fagus* L.) species in the world. *Journal of Biogeography*, **33**, 1804–1819.

Frahm, J. P. & Frey, W. (1992) *Mossflora*. Ulmer Verlag, Stuttgart.

Fukami, T., & Wardle, D.A. (2005) Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B*, **272**, 2105–2115

Gignac, L.D. & Dale, M.R.T. (2005) Effects of fragment size and habitat heterogeneity on cryptogam diversity in the low-boreal forests of Western Canada. *The Bryologist*, **108**, 50–66.

Gómez-Hernández, M., Williams-Linera, G., Guevara, R. & Lodge, D.J. (2012) Patterns of macromycete community assemblage along an elevation gradient: options for fungal gradient and metacommunity analyses. *Biodiversity and Conservation*, **21**, 2247–2268.

Gossner, M.M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W. & Müller, J. (2013) Current ''near-to-nature'' forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conservation Biology* **27**, 605–614.

Grolle, R. & Long, D.G. (2000) An annotated check-list of the Hepaticae and Anthocerotae of Europe and Macaronesia. *Journal of Bryology* **22**, 103–140.

Halme, P., Ódor, P., Christensen, M., Piltaver, A., Veerkamp, M., Walleyn, R., Siller, I. & Heilmann-Clausen, J. 2013. The effects of habitat degradation on metacommunity structure of wood-inhabiting fungi in European beech forests. *Biological Conservation* **168**, 24-30.

Hansen, L. & Knudsen, H. (eds.), (1992–2000) *Nordic Macromycetes, vol I–III*. Nordsvamp, Copenhagen.

Heilmann-Clausen, J. (2001) A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. *Mycological Research*, **105**, 575–596.

Heilmann-Clausen, J. & Boddy, L. (2008) Distribution patterns of wood decay basidiomycetes at the landscape to global scale. *Ecology of Saprotrophic Basidiomycetes* (eds. L. Boddy, J.C. Frankland & P. van West), pp. 263–275. Elsevier.

Heilmann-Clausen, J. & Christensen, M. (2005) Wood-inhabiting macrofungi in Danish beech-forests – conflicting diversity patterns and their implications in a conservation perspective. *Biological Conservation*, **122**, 633–642.

Heilmann-Clausen, J, Aude, E. & Christensen, M. (2004) Cryptogam communities on decaying deciduous wood – does tree species diversity matter? *Biodiversity and Conservation*, **14**, 2061-2078.

Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis, an improved ordination technique. *Vegetatio*, **42,** 47–58.

Hill, M.O., Bell, N., Bruggeman-Nannaenga, M.A., Brugues, M., Cano, M. J., Enroth, J., Flatberg, K.I., Frahm, J. P., Gallego, M.T., Gariletti, R., Guerra, J., Hedenas, L., Holyoak, D.T., Hyvönen, J., Ignatov, M.S., Lara, F., Mazimpaka, V., Munoz, J. & Söderström, L.

(2006) An annotated checklist of the mosses of Europe and Macaronesia. *Journal of Bryology,* **28**, 198–267.

Hohenwallner, D., Zechmeister H.G., Moser D., Pauli H., Gottfried M., Reiter K. & Grabherr, G. (2011) Alpine bryophytes as indicators for climate change: a case study from the Austrian Alps. *Bryophyte ecology and climate change* (eds. Z. Tuba, N.G. Slack & L.R. Stark), pp. 237–250. Cambridge University Press, Cambridge.

Jansová, I. (2006) Seasonal growth and dynamics of epixylic bryophytes in Bohemian old-growth forest. *Journal of Bryology*, **28**, 123–132.

Jonsson, B. G., Kruys, N. & Ranius, T. (2005) Ecology of species living on dead wood. Lessons for dead wood management. *Silva Fennica,* **39**, 289–309.

Kaplan, J.O., Krumhardt, K.M. & Zimmermann, N. (2009) The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews*, **28**, 3016–3034.

Kushnevskaya, H., Denis, M., Shorohova, E. (2007) Patterns of epixylic vegetation on spruce logs in late-successional boreal forests. *Forest Ecology and Management,* **250**, 25-33.

Lachat, T., Wermelinger, B., Gossner, M.M., Bussler, H., Isacsson, G. & Muller, J. (2012) Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. *Ecological Indicators* **23**, 323–331.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011) Deadwood as a surrogate for forest biodiversity: metaanalysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators* **11**, 1027–1039.

Lepš, J. & Šmilauer, P. (2003) *Multivariate Analysis of Ecological Data using Canoco*. Cambridge University Press, Cambridge, UK.

Lindblad, I. (2001). Diversity of poroid and some corticoid wood inhabiting fungi along the rainfall gradient in tropical forests, Costa Rica. *Journal of Tropical Ecology*, **17**, 353-369.

Löbel, S. & Rydin, H. (2009) Dispersal and life-history strategies in epiphyte metacommunities: alternative solutions to survival in patchy, dynamic landscapes. *Oecologia*, **161**, 569–579.

Löbel, S., Snäll, T. & Rydin, H. (2006) Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. *Journal of Ecology*, **94**, 856–868.

Logue, J. B. Mouquet, N., Peter, H., Hillebrand, H. & Metacommunity Working Group. (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology and Evolution*, **26**, 482–491.

McAlister, S. (1997) Cryptogam communities on fallen logs in the Duke Forest, North Carolina. *Journal of Vegetation Science*, **8**, 115–124.

McCune, B. & Mefford, M.J. (1999) *Multivariate Analysis of Ecological Data, Version 4.25.*

MjM Software, Gleneden Beach, Oregon.

Müller, J. & Bütler, R. (2010). A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research* **129**, 981–992.

Müller, J., Brunet, J., Brin, A., Bouget, C., Brustel, H., Bussler, H., Förster, B., Isacsson, G., Köhler, F., Lachat, T., Gossner, M.M. (2013) Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. *Insect Conservation and Diversity*, **6**, 162-169.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E. and Ovaskainen, O. (2013) Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *Journal of Ecology,* **101**, 701-712.

Ódor, P., Heilmann-Clausen, J., Christensen, M., Aude, E., van Dort, K. W., Piltaver, A., Siller, I., Veerkamp, M. T., Walleyn, R., Standovár, T., van Hees, A. F. M., Kosec, J., Matočec, N., Kraigher, H. & Grebenc, T. (2006) Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biological Conservation*, **131**, 58–71.

Ódor, P. & Standovár, T. (2002) Substrate specificity and community structure of bryophyte vegetation in a near-natural montane beech forest. *Community Ecology*, **3**, 39–49.

Ódor, P. & van Hees, A.F.M. (2004) Preferences of dead wood inhabiting bryophytes for decay stage, log size and habitat types in Hungarian beech forests. *Journal of Bryology*, **26**, 79–95.

Ódor, P., van Hees, A.F.M, Heilmann-Clausen, J., Christensen, M., Aude, E., van Dort, K.W., Piltaver, A., Siller, I., Veerkamp, M.T., Grebenc, T., Kutnar, L., Standovár, T., Kosec, J., Matočec, N., Kraigher, H. (2004) *Ecological succession of bryophytes, vascular plants and fungi on beech coarse woody debris in Europe.* Nat-Man working report 51. www.flec.kvl.dk/natman

Økland, R. H. (1999) On the variation explained by ordination and constrained ordination axes. *Journal of Vegetation Science*, **10**, 131–136.

Paltto, H., Nordén, B., Götmark, F. & Franc, N. (2006) At which spatial and temporal scales does landscape context affect local density of Red Data Book and Indicator species? *Biological Conservation,* **133**, 442–454.

Penttilä, R., Lindgren, M., Miettinen, O., Rita, H. & Hanski, I. (2006) Consequences of forest fragmentation for polyporous fungi at two spatial scales. *Oikos*, **114**, 225–240.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & The R Development Core Team (2011) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-102.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters,* **8**, 224–39

Qian, H., Klinka, K. & Song, X. (1999) Cryptogams on decaying wood in old-growth forests on southern coastal British Columbia. *Journal of Vegetation Science*, **10**, 883–894.

Raabe, S., Müller, J., Manthey, M., Dürhammer, O., Teuber, U., Göttlein, A., Förster, B., Brandl, R. & Bässler, C. (2010) Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. *Forest Ecology and Management*, **260**, 1956–1964.

Rambo, T.R. & Muir, P.S. (1998) Bryophyte species association with coarse woody debris and stand ages in Oregon. *The Bryologist*, **101**, 366–376.

Runge, A. (1975) Pilzsukzession auf Laubholzstümpfen. *Zeitschrift für Pilzkunde*, **41**, 31–38.

Saboljevic, M., Vujicic, M., Saboljevic, A. (2010) Diversity of saproxylic bryophytes in old-growth and managed beech forests in the central Balkans. *Plant Biosystems*, **144**, 234-240.

Schmitt, C. B., Burgess, N. D., Coad, L., Belokurov, A., Besançon, C.Boisrobert, L. 2009. Global analysis of the protection status of the world's forests. Biological Conservation, 142: 2122–2130.

Schumacker, R. & Vana, J. (2005) *Identification keys to the liverworts and hornworts of Europe and Macaronesia*. Sorus, Poznań, Poland.

Smith, A.J.E. (2004) *The moss flora of Britain and Ireland*. Cambridge University Press, Cambridge.

Söderström, L. (1988) Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. *Nordic Journal of Botany*, **8**, 89–97.

Stokland, J.N., Siitonen, J. & Jonsson, B.G. 2012. *Biodiversity in dead wood*, Cambridge University Press, Cambridge.

Sundqvist, M.K., Sanders, N.J. & Wardle, D.A. (2013) Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 261–280.

ter Braak, C. J. F. & Smilauer, P. (2002) *Canoco 4.5*. Biometris, Wageningen and České Budějovice.

The R Development Core Team (2012). R. 2.15.2. *A language and environment for statistical computing*. www.r-project.org.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentivenga, S. (2011) Advances, challenges, and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B*, **366**, 2403–2413.

Willner, W., Di Pietro, R. & Bergmeier, E. (2009) Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography,* **32**, 1011–1018.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G. (2009). *Mixed effects models and extension in ecology with R*. Springer, New York.

BIOSKETCH

This study was initiated as part of a collaborative EU project on Nature Based Management of Beech in Europe (Nat-Man) with the aim to highlight the importance of dead wood for biodiversity across Europe. The fungal dataset was collected by J.H.-C., M.C., A.P., M.V., R.W. and I.S., the bryophyte dataset by P.Ó., E.A. and K.D. J.H.-C. had the lead role in writing the manuscript; analyses were made by J.H.-C. and P.Ó. with considerable contributions from T.S. and E.A. P.Ó. was the coordinator of the field work making the study possible.

Editor: Peter Linder

Table 1. List of the 26 protected beech stands in Europe, in which fungi and bryophyte communities on fallen beech logs were inventoried for this study. The column 'Abbrev.' lists the site abbreviations shown in in Fig 1.

Site name	Abbrev.	Country code*	No. of sampled logs	Stand size (ha)	Dead wood volume (m^3/ha)	Tree age (yrs)**	Natural-ness score*	Latitude	Longitude
Zoniënwoud, core area	ZOK	B	125	18	139	220	2	50.75	4.42
Zoniënwoud, buffer zone	ZON	B	67	80	24	150	1	50.75	4.42
Silkeborg Vesterskov, Knagerne	KNA	DK	25	6	152	230	2	56.13	9.53
Møns Klinteskov, Kalsterbjerg	MON	DK	50	25	100	350	2	54.96	12.54
Strødam	STR	DK	50	25	181	250	2	55.97	12.27
Suserup Skov	SUS	DK	50	19	176	350	3	55.37	11.55
Velling Skov	VEL	DK	25	24	114	275	2	56.04	9.5
Kekes	KEK	H	97	63	99	350	4	47.87	20
Õserdõ	OSE	H	110	25	164	250	2	48.05	20.43
Krokar	KRO	SI	101	73	153	350	4	45.54	14.78
Rajhenavski Rog	RAJ	SI	110	51	299	350	4	45.66	15.02
Äskemossen	ASK	S	25	8	25	200	1	57.09	12.57
Dömestorp	DOM	S	50	18	25	200	1	56.41	12.98
Biskopstorp, Holkåsen	HOL	S	50	6	70	300	2	56.8	12.89
Biskopstorp, Kvinnsåsen	KVI	S	15	2	25	250	2	56.81	12.91
Biskopstorp, N Kroksjön	NKR	S	25	10	25	250	2	56.8	12.89
Biskopstorp, Trälhultet	TRA	S	10	6	25	250	2	56.81	12.91
Valaklitt	VAL	S	25	10	75	250	2	57.1	12.55
Utrecht, Amelisweerd	AMW	NL	5	3	72	150	1	52.1	5.18
Veluwe, Dassenberg	DAB	NL	33	12	63	200	1	52.07	5.88
Veluwe, Drie	DRI	NL	21	5	44	200	1	52.07	5.88
Veluwe, Gortelsebos	GOB	NL	11	15	66	200	1	52.07	5.88
Utrecht, Oostbroek	OOB	NL	10	3	72	150	1	52.1	5.18
Veluwe, Speulderbos	SPB	NL	42	27	44	200	1	52.25	5.72
Veluwe, Weversbergen	WEB	NL	32	12	49	100	1	52.07	5.88
Utrecht, Wulperhorst	WUH	NL	44	3	72	200	1	52.1	5.18

*B: Belgium; DK: Denmark; H: Hungary; NL: The Netherlands; S: Sweden; SI: Slovenia. **For explanation, see Table 2.

Table 2. List of environmental variables recorded in this study on fungi and bryophyte communities on beech logs in Europe, and their affiliation to defined variable sets.

Variable name	Variable set	Description	Data type	Min, mean and max
DECAY STAGE	Substrate	Average decay stage of log[*]	ordinal, six stages	1-**3.1**-6
DBH	Substrate	Diameter at breast height	continuous, cm	10-**56.2**-135
BARK COVER	Substrate	Bark cover of log	continuous, %	0-**38.6**-100
SOIL CONTACT	Substrate	Soil contact of log	continuous, %	0-**71.6**-100
MOSS COVER	Substrate	Moss cover on log[¶]	continuous, %	0-**24.3**-100
SNAG	Substrate	Presence/absence of snag	binary	
ELEVATION	Climate and soil	Elevation	continuous, m	2-**373**-1120
TEMP_MIN	Climate and soil	Mean temperature of the coldest month[†]	continuous, °C	-4.7-**-0.4**-3.4
TEMP_MAX	Climate and soil	Mean temperature of the warmest month[†]	continuous, °C	15.5-**16.6**-18.2
TEMP_RANGE	Climate and soil	Temperature difference between coldest and warmest month[†]	continuous, °C	14.4-**17.0**-20.2
TEMP_AVE	Climate and soil	Mean annual temperate[†]	continuous, °C	5.7-**7.82**-9.4
PRECIPITATION	Climate and soil	Mean annual precipitation[†]	continuous, mm	586-**988**-1579
SNOW COVER	Climate and soil	Mean number of days per year with snow cover[†]	continuous, days	25-**68.3**-140
LANG'S RAINFALL INDEX	Climate and soil	Mean annual precipitation/mean annual temperature	continuous, mm/°C	74.2-**130.4**-205.1
SOIL_RICH	Climate and soil	Soil richness[‡]	ordinal, four stages	1-**2.7**-4
NATURALNESS	Forest conditions	Naturalness of the stand as a forest[¶]	ordinal, four stages	1-**2.3**-4
TREE AGE	Forest conditions	Highest age of the dominant trees	continuous, year	100-**262.7**-300
STAND SIZE	Forest conditions	Area of the strict forest reserve	continuous, hectar	2.2-**31.5**-80
CWD VOLUME	Forest conditions	Volume of dead wood in the reserve[§]	continuous, $m^3.ha^{-1}$	24-**119.5**-299
FOREST COVER	Forest conditions	Present forest cover, 5 km radius[**]	continuous, %	9.4-**61.2**-98.2
DECIDUOS COVER	Forest conditions	Present cover of deciduous forest, 5 km radius[**]	continuous, %	0.9-**32.4**-95.5
CONIFEROUS COVER	Forest conditions	Present cover of coniferous forests, 5km radius[**]	continuous, %	0-**16.2**-66.6
CONIFEROUS SHARE	Forest conditions	Present coniferous forest share[**]	continuous, %	0-**27.6**-83
PAST FOREST COVER	Forest conditions	Past forest cover, 5 km radius[††]	continuous, %	0-**58.1**-90
FOREST COVER CHANGE	Forest conditions	Change in forest cover, 5 km radius[‡‡]	continuous, %	-41.5-**3.1**-43.9

[*]Based on Ódor & van Hees (2004); [†]Based on data from smhi.se, normals 1961-1990 (S), dmi.dk, normals 1961-1990 (DK), knmi.nl, normals 1971-2000 (NL), meteo.be, normal 1971-2000(B), met.hu, normals 1971-2000 (H), meteo.arso.gov.si, normals 1971-2000 (SI); [‡]1: sand (NL, DK), granite (S); 2: loam-sand and clay (NL); 3: sand-clay and loam-sand (DK), andesite (H), loess (B); 4: limestone (SL, H), chalk (DK); [¶]1: Recently managed forests with a homogenous structure and low levels of dead wood, dominant trees generally =< 200 yrs, gaps in tree continuity possible; 2: Recently managed forests with a homogenous structure and moderate levels of dead wood, dominant trees generally > 200 yrs, no gaps in tree continuity; 3: Forests affected by selective cuttings in the past, but with a heterogeneous structure and abundant dead wood; dominant trees generally > 200 yrs, no gaps in tree continuity; 4: More or less virgin forests, with no documented human influence; [§]based on Christensen *et al.* (2005) and Örjan Fritz pers comm.; [**]Based on Corine, 2007 data; [††]Based on Videnskabernes Selskab kort 1762-1820 (DK); Generalstabens karta över Halland 1839-1842 (S); Nieuwe Geographische Reise- en Zak-Atlas, Jan Christiaan Sepp 1773 (NL); Plan Topographique de la Ville de Bruxelles, Joseph de Ferraris, 1777 (B); Second Military Survey of the Habsburg Empire 1806-1869 (Arcanum 2006, H and SI); [‡‡]Present forest cover minus past forest cover.

Table 3. Simple mixed-effects models between environmental variables and DCA ordination axis scores based on bryophytes and fungal communities using site as a random factor. For substrate variables the degree of freedom was 862 for bryophytes and 933 for fungi. For site level variables (Climate and soil, forest conditions) the degree of freedoms was 22 in both groups. For each variable the direction of the effect (+ or - sign) and the F-value is given.

		Bryophytes						Fungi					
		Axis 1		Axis 2		Axis 3		Axis 1		Axis 2		Axis 3	
	Variable set	sign	F	sign	F	sign	F	sign	F	sign	F	sign	F
DECAY STAGE	Substrate	+	31.1****	-	216.1****	+	342.9****	-	1441.2****	-	24.1**	+	10.1**
DBH	Substrate	-	7.2	+	11.6	-	10.3**	+	0	+	0	-	22.5****
BARK COVER	Substrate	-	26.7**	+	169.1****	-	244****	+	873.2****	+	19.5**	-	15.2***
SOIL CONTACT	Substrate	+	16.9****	-	86.6****	+	184.7****	-	370.4****	-	7.7*	+	3.8
MOSS COVER	Substrate	+	1.6	-	7.5	+	93.7****	-	118.9****	-	8.8*	-	3.4
ELEVATION	Climate and soil	-	61.3****	-	0	-	2.1	+	0.1	+	44.2****	-	1.5
TEMP_MIN	Climate and soil	+	19.5**	-	6.5	-	0.5	+	0.6	-	87.3****	+	0
TEMP_MAX	Climate and soil	+	0.8	-	17.4**	-	3.3	+	0.8	-	7	-	0.7
TEMP_RANGE	Climate and soil	-	48.9****	+	1.6	+	0	-	0.3	+	151.9****	-	0.39
TEMP_AVE	Climate and soil	+	6	-	11.5*	-	3.7	+	1.6	-	22**	+	0
PRECIPITATION	Climate and soil	-	5.7	+	3.1	+	1.2	+	5	+	2.6	-	3.2
SNOW COVER	Climate and soil	-	52.1****	+	1.8	+	0	+	0	+	41.1****	-	2.3
LANG'S RAINFALL INDEX	Climate and soil	-	8.6	+	10	+	3.7	+	0.9	+	11	-	2
SOIL_RICH	Climate and soil	-	22.5**	-	6.1	-	1.2	-	4.1	+	7.7	-	0.7
NATURALNESS	Forest conditions	-	53.2****	+	0.2	-	0.5	-	0.8	+	25.9***	-	2
TREE AGE	Forest conditions	-	24.4**	+	2.9	-	0.1	-	2.5	+	20.4**	+	0
STAND SIZE	Forest conditions	-	10.3	-	3.9	-	0.8	-	0	+	3.7	-	0.5
CWD VOLUME	Forest conditions	-	17.5**	-	1.1	-	1	-	1.7	+	4.6	-	2.8
FOREST COVER	Forest conditions	-	8.4	+	4	+	0.2	+	0.8	+	16.7**	-	1.2
DECIDUOS COVER	Forest conditions	-	13.2*	-	0.8	-	0.8	-	2	+	27.8***	-	1.1
CONIFEROUS COVER	Forest conditions	+	2.4	+	24.3**	+	4.1	+	4.3	-	0.3	+	0
CONIFEROUS SHARE	Forest conditions	+	10.35	+	10.93	+	1.42	+	9.91	-	2.68	+	0.49
PAST FOREST COVER	Forest conditions	-	11.9*	-	0.9	-	0	-	1.4	+	8.1	-	5.6
FOREST COVER CHANGE	Forest conditions	+	0.3	+	15.7*	+	0.4	+	7.1	+	0.2	+	1.8
LATITUDE	Not included	+	7.8*	+	9.2	+	8.4	-	0.6	-	3.3	+	1.8
LONGITUDE	Not included	-	33.3***	+	3.5	+	0.1	-	1.7	+	183.2****	-	0

****$P < 0.0001$, ***$P = 0.0001 - < 0.001$, ** $P = 0.001 - < 0.01$, * $P = 0.01 - < 0.05$
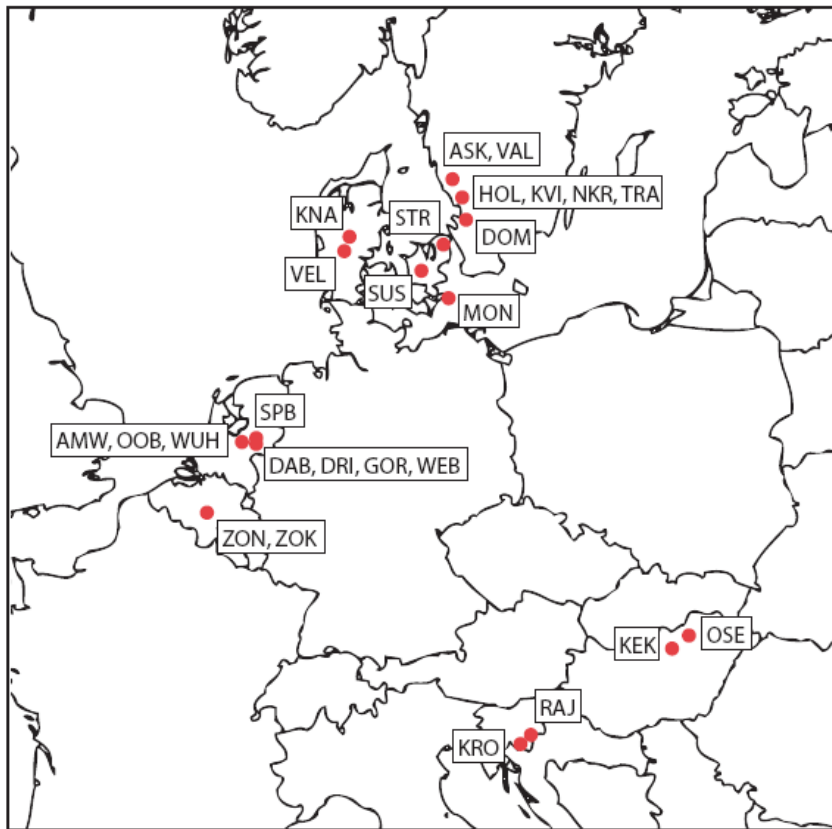
Fig. 1. Map showing the location of 26 protected beech stands in which fungi and bryophyte communities on fallen beech logs were inventoried for this study. For full names of stands, see Table 1.
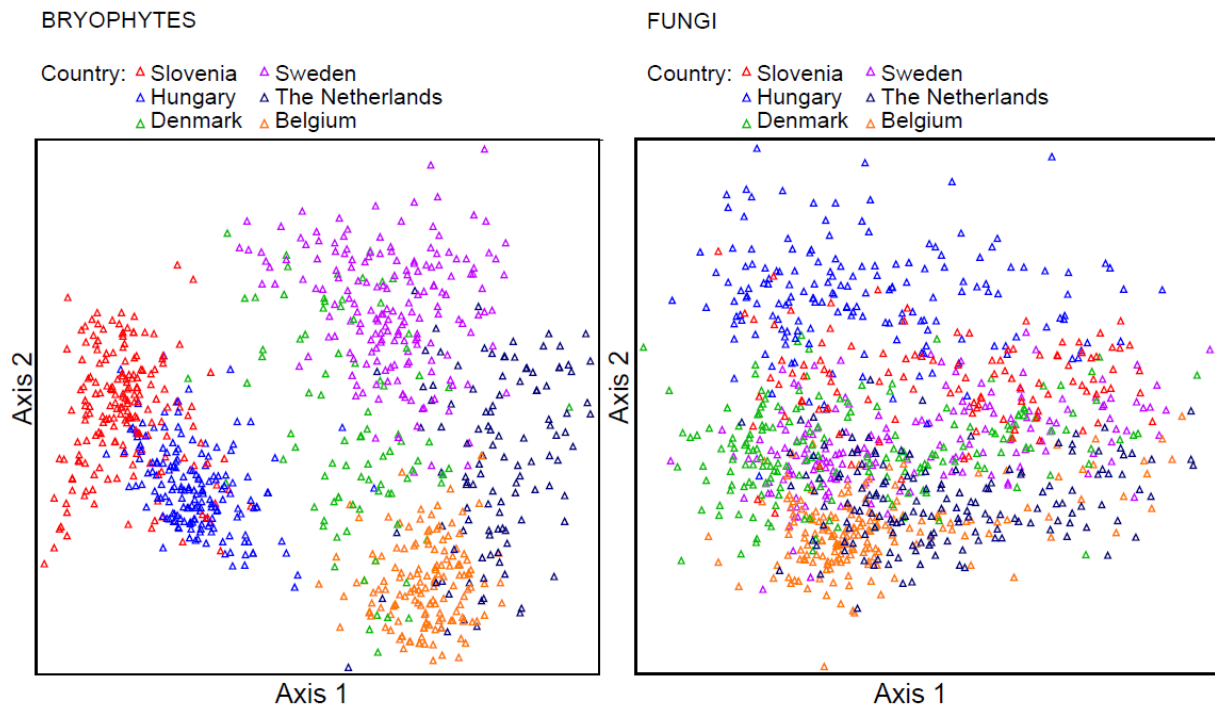
Fig. 2. Diagrams showing the position of sampling units (beech logs) in the ordination space defined by axis 1 and 2 of the DCA based on the bryophyte dataset (left column; 893 logs) and fungal dataset (right column; 965 logs) collected from 26 sites in Europe. The samples (logs) are colour coded according to country.
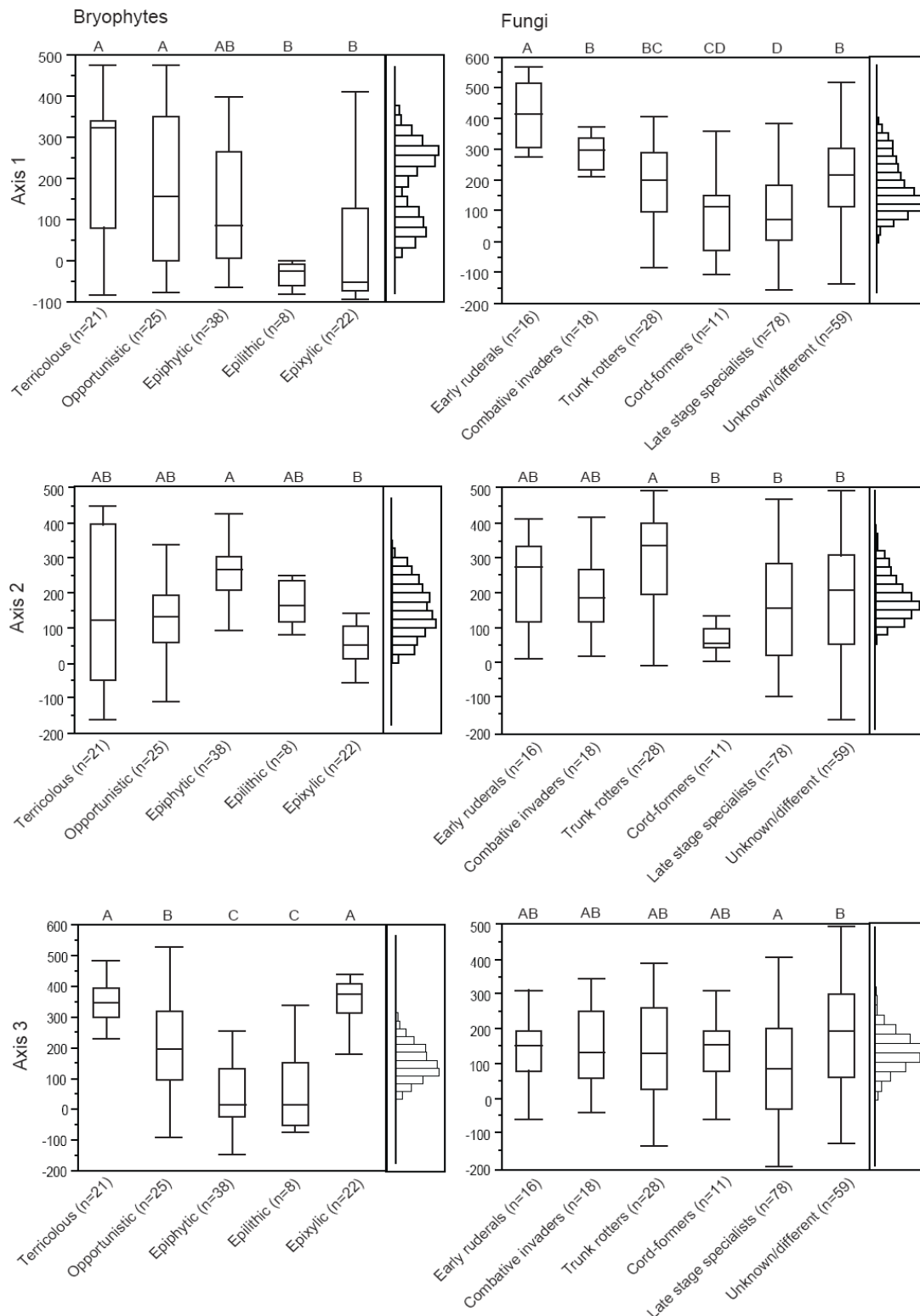
Fig. 3. Boxplots showing the distribution of defined ecological guilds along ordination axes extracted in the DCA based on the bryophyte dataset (left panel) and fungal dataset (right panel) collected from 26 sites in Europe. Different letters indicate significantly different means (p<0.05) based on Tukey's HSD tests comparing all means. Side-bars show the distribution of samples (logs) along the same ordination axes.
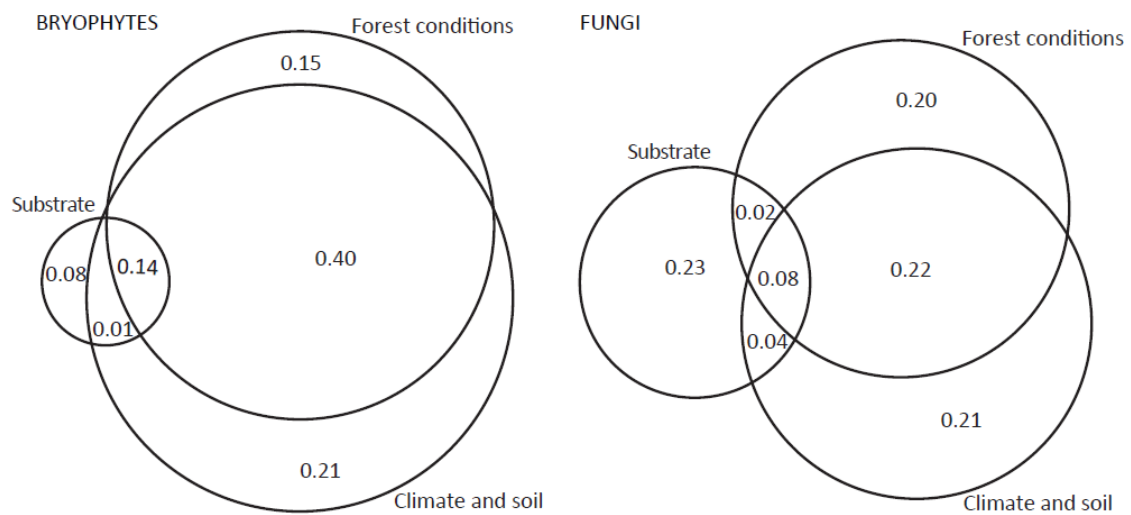
Fig. 4. Venn diagrams, showing the relative contribution of substrate, forest condition and climate variables in explaining variance in the CCAs for bryophytes (left; 893 logs) and fungi (right; 965 logs) on fallen beech logs across 26 sites in Europe. The circles are scaled to show their overall contribution to the explained variance in each dataset, with overlapping areas scaled to show the approximate level of shared contribution for each combination of variable sets.

Appendix S1: Descriptions of fungal guilds in dead wood, as classified for this study on fungal communities on beech logs in European forest reserves.

Guild	Strategy	Classification in Boddy & Heilmann-Clausen (2008)
Early ruderals	Ruderal fungi with weak combative abilities, causing white rot in wood and bark in early decay stages, often more common on branches, than on logs; establishment via latent invasion in living wood, or via spores on freshly exposed dead wood; fruit bodies very tolerant to desiccation; mainly corticoids and heterobasidiomycetes.	Ruderal primary colonizers and natural pruners + desiccation and heat and desiccation tolerant secondary invaders
Combative invaders	Combative fungi causing rapid white rot in early to intermediate decay stages; equally common on logs and branches; establishing via latent invasion in living wood, or from establishment via spores in recently dead wood; fruit bodies tolerant to desiccation; mainly polypores.	Secondary, combative invaders
Cord formers	Very combative fungi causing white rot in intermediate to late decay stages; found on many types of dead wood, sometimes on other litter; establishing via mycelial cords; fruit bodies tolerant to desiccation or not; mainly agarics and gastromycetes.	Cord formers
Trunk rotters	Combative or stress tolerant fungi causing white or brown rot in wood in early to late decay stages; fruit bodies more or less restricted to logs; establishment via latent invasion or heart rot in living trees or via infection in standing dead trees; fruit bodies relatively tolerant to desiccation; mainly polypores and agarics.	Heart rot agents
Late stage specialists	Fungi causing white rot or utilizing residual compounds from previous decay, and restricted to wood in advanced stages of decay; fruit bodies found on several types of dead wood; establishing by airborne spores in already decayed wood; fruit bodies mainly sensitive to desiccation; mainly agarics.	Late stage polypores and agarics
Unknown/different	Species with unknown or different strategies in dead wood, including mycoparasites	

Boddy, L. & Heilmann-Clausen, J. (2008) Basidiomycete community development in temperate angiosperm wood. *Ecology of Saprotrophic Basidiomycetes* (eds. L. Boddy, J.C. Frankland & P. van West), pp. 211–237. Elsevier.

Appendix S2: Species included in the final dataset, their classification in ecological guilds and scores in the ordinations.

Fungi

Species	Guild	dca1	dca2	dca3
Annulohypoxylon cohaerens (Pers.) Y.M. Ju, J.D. Rogers & H.M. Hsieh	Unknown/different	353.69	53.67	191.17
Annulohypoxylon multiforme (Fr.) Y.M. Ju, J.D. Rogers & H.M. Hsieh	Unknown/different	311.54	309.83	110.04
Antrodiella hoehnelii (Bres.) Niemelä	Unknown/different	255.92	330.16	284.76
Antrodiella semisupina (Berk. & M.A. Curtis) Ryvarden	Unknown/different	184.97	133.28	335.96
Armillaria gallica Marxm. & Romagn.	Cord	111.57	23.60	-30.27
Armillaria mellea (Vahl: Fr.) P.Kumm.	Trunk rotters	193.12	331.58	-63.26
Armillaria ostoyae (Romagn.) Herink	Cord	353.62	-27.38	282.56
Arrhenia epichysium (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys	Late stage specialist	19.95	328.37	186.25
Ascocoryne cylichnium (Tul.) Korf	Late stage specialist	152.01	40.46	153.38
Ascocoryne sarcoides (Jacq.: Fr.) Groves & Wilson	Unknown/different	428.63	118.75	174.45
Ascocoryne sp.	Unknown/different	173.64	85.12	300.02
Ascotremella faginea (Peck) Seaver	Unknown/different	297.11	-15.70	196.36
Auricularia auricula-judae (Bull.: Fr.) Wettst.	Early ruderals	348.81	325.14	267.50
Auricularia mesenterica (Dicks.) Pers.	Unknown/different	220.74	481.34	52.35
Biscogniauxia nummularia (Bull.: Fr.) O.K.	Unknown/different	299.36	277.36	315.83
Bjerkandera adusta (Willd.: Fr.) P.Karst.	Combative invader	346.47	220.04	77.31
Bjerkandera fumosa (Pers.: Fr.) P.Karst.	Combative invader	331.70	95.15	101.40
Bolbitius reticulatus (Pers.: Fr.) Rick.	Late stage specialist	30.79	198.68	66.41
Bulgaria inquinans (Pers.: Fr.) Fr.	Unknown/different	513.89	201.33	202.08
Byssomerulius corium (Persoon) Parmasto	Early ruderals	405.68	399.84	260.64
Calocera cornea (Batsch: Fr.) Fr.	Unknown/different	310.04	238.01	78.53
Camarops lutea (Alb. & Schw.) Nannf.	Unknown/different	61.03	-115.04	492.09
Camarops polysperma (Mont.) Miller	Trunk rotters	-83.76	243.85	347.03
Camarops tubulina (Alb. & Schw.) Shear	Trunk rotters	46.84	170.04	361.59
Ceriporia excelsa (Lund.) Parm.	Late stage specialist	201.79	206.87	154.72
Ceriporia purpurea (Fr.) Donk	Late stage specialist	222.64	399.09	39.78
Ceriporia reticulata (Hoffm.: Fr.) Dom.	Late stage specialist	41.12	336.80	357.59
Ceriporiopsis gilvescens (Bres.) Dom.	Late stage specialist	170.71	233.59	-38.31
Cerrena unicolor (Bull.: Fr.) Murr.	Combative invader	274.98	408.08	331.20
Chlorociboria aeruginascens (Nyl.) Kanouse	Unknown/different	-187.26	83.45	393.98
Chondrostereum purpureum (Pers.: Fr.) Pouz.	Early ruderals	542.86	64.92	145.32
Clitopilus hobsonii (Berk.) P.D.Orton	Unknown/different	231.36	23.80	297.44
Clitopilus scyphoides (Fr.: Fr.) Singer	Unknown/different	-9.52	-110.90	-165.21
Conocybe subpubescens P.D.Orton	Late stage specialist	39.83	34.04	-72.05
Coprinellus disseminatus (Pers.) J.E. Lange	Late stage specialist	254.90	72.95	41.74
Coprinellus micaceus (Bull.) Vilgalys, Hopple & Jacq. Johnson	Cord	184.61	69.37	1.49
Coprinellus radians (Desmazières) Vilgalys, Hopple & Jacq. Johnson	Unknown/different	222.64	359.22	60.57
Coprinellus tardus (P. Karsten) P. Karsten	Unknown/different	206.06	462.09	209.96
Coprinopsis laanii (Kits van Wav.) Redhead, Vilgalys & Moncalvo	Late stage specialist	100.61	-46.78	-240.45
Coprinopsis lagopides (P. Karst.) Redhead, Vilgalys & Moncalvo	Late stage specialist	32.36	150.29	-164.64

Coprinopsis lagopus (Fr.) Redhead, Vilgalys & Moncalvo	Late stage specialist	190.76	457.72	228.59
Crepidotus applanatus (Pers.) P.Kumm.	Late stage specialist	152.97	342.66	-20.74
Crepidotus lundellii Pilat	Unknown/different	259.89	485.74	173.42
Crepidotus mollis (Schaeff.: Fr.) Staude	Unknown/different	264.34	189.24	-20.47
Crepidotus versutus (Peck) Sacc.	Late stage specialist	297.16	61.45	-46.77
Datronia mollis (Sommerf.: Fr.) Donk	Combative invader	349.75	260.58	62.73
Delicatula integrella (Pers.: Fr.) Pat.	Late stage specialist	54.09	-74.79	-148.80
Dentipellis fragilis (Pers.: Fr.) Donk	Trunk rotters	46.72	337.21	249.83
Discina parma J.Breitenb. & Maas Geest.	Late stage specialist	-39.30	392.69	-171.05
Eutypa spinosa (Pers.: Fr.) Tul. & C.Tul.	Unknown/different	173.68	204.27	144.69
Exidia nucleata (Schwein.) Burt.	Early ruderals	291.95	12.40	145.94
Exidia nigricans (With.) P. Roberts	Early ruderals	430.01	298.08	44.60
Flammulaster limulatus (Fr.) Watling	Late stage specialist	-10.22	403.30	89.14
Flammulina velutipes (Curt.: Fr.) P.Karst.	Unknown/different	399.12	306.18	-56.75
Fomes fomentarius (L.: Fr.) Fr.	Trunk rotters	257.66	243.92	187.75
Fomitopsis pinicola (Swartz: Fr.) P.Karst.	Trunk rotters	286.47	215.68	112.46
Fuscoporia ferrea (Pers.) G. Cunn.	Unknown/different	-44.74	139.21	373.17
Fuscoporia ferruginosa (Schrad.) Murrill	Unknown/different	3.12	348.32	243.53
Galerina marginata (Batsch) Kuhner	Late stage specialist	46.26	192.85	102.65
Galerina triscopa (Fr.) Kuhner	Late stage specialist	-140.31	88.47	-140.67
Ganoderma lipsiensis (Batsch) Atk.	Trunk rotters	194.71	135.02	68.56
Ganoderma pfeifferi Bres.	Trunk rotters	243.07	259.08	359.24
Gelatoporia pannocincta (Romell) Niemelä	Trunk rotters	-5.78	394.33	168.20
Gymnopilus sapineus (Fr.: Fr.) Maire	Late stage specialist	142.35	-66.19	140.23
Henningsomyces candidus (Pers.: Fr.) O.K.	Late stage specialist	-74.95	-0.69	136.23
Hericium coralloides (Scop.: Fr.) Pers.	Trunk rotters	57.99	356.37	259.76
Hohenbuehelia auriscalpium (Maire) Singer	Late stage specialist	-79.76	-6.17	47.82
Hohenbuehelia fluxilis (Fr.: Fr.) P.D. Orton	Early ruderals	281.63	266.55	-94.88
Hyphodontia radula (Pers.: Fr.) E.Langer & Vesterh.	Unknown/different	237.35	5.01	320.13
Hypholoma capnoides (Fr.: Fr.) P.Kumm.	Late stage specialist	105.43	323.28	-172.02
Hypholoma fasciculare (Huds.: Fr.) P.Kumm.	Cord	144.78	25.52	99.59
Hypholoma lateritium (Schaeff.: Fr.) P.Kumm.	Late stage specialist	85.53	113.50	270.84
Hypocrea citrina (Pers.: Fr.) Fr.	Unknown/different	218.18	-73.89	385.36
Hypocrea gelatinosa (Tode: Fr.) Fr.	Unknown/different	114.11	279.63	13.64
Hypoxylon fragiforme (Pers.: Fr.) Kickx	Early ruderals	422.74	134.69	173.23
Hypoxylon macrocarpum Pouz.	Unknown/different	-16.32	195.65	401.02
Hypoxylon rubiginosum (Pers.: Fr.) Fr.	Unknown/different	212.49	0.66	364.90
Inonotus cuticularis (Bull.: Fr.) P.Karst.	Trunk rotters	287.77	438.33	225.04
Inonotus obliquus (Pers.: Fr.) Pilat	Trunk rotters	114.34	493.78	100.92
Ischnoderma resinosum (Schrad.: Fr.) P.Karst.	Trunk rotters	217.33	392.01	122.43
Kretzschmaria deusta (Hoffm.) P.M.D. Martin	Trunk rotters	86.73	212.31	112.14
Kuehneromyces mutabilis (Schaeffer) Singer & A.H. Smith	Late stage specialist	166.28	-21.88	-47.19
Laxitextum bicolor (Pers.: Fr.) Lentz	Combative invader	278.84	76.26	240.64
Lentaria epichnoa (Fr.) Corner	Late stage specialist	-45.99	204.83	-58.71
Lentinellus cochleatus (Pers.: Fr.) P.Karst.	Late stage specialist	383.17	438.19	139.62
Lenzites betulinus (L.: Fr.) Fr.	Combative invader	227.36	350.49	8.77

Lycoperdon perlatum Pers.: Pers.	Cord	57.14	13.12	14.41
Lycoperdon pyriforme Schaeff.: Pers.	Cord	-29.46	299.02	82.07
Marasmius rotula (Scop.: Fr.) Fr.	Unknown/different	53.93	429.85	246.89
Megacollybia platyphylla (Pers.: Fr.) Kotl. & Pouz.	Cord	59.27	25.22	295.61
Meripilus giganteus (Pers.: Fr.) P.Karst.	Trunk rotters	193.05	40.71	234.14
Multiclavula mucida (Pers.) R.H. Petersen	Unknown/different	210.36	243.32	-86.16
Mutinus caninus (Huds.: Pers.) Fr.	Cord	118.91	6.10	222.28
Mycena abramsii (Murr.) Murr.	Late stage specialist	99.07	-43.79	71.61
Mycena acicula (Schaeff.: Fr.) P.Kumm.	Late stage specialist	236.97	209.19	0.92
Mycena adscendens (Lasch) Maas Geest.	Late stage specialist	277.19	-86.29	8.80
Mycena arcangeliana Bres.	Late stage specialist	9.43	380.66	182.41
Mycena crocata (Schrad.: Fr.) P.Kumm.	Late stage specialist	20.67	320.52	191.40
Mycena erubescens Höhn.	Unknown/different	201.17	139.05	266.11
Mycena galericulata (Scop.: Fr.) Quél.	Late stage specialist	2.43	150.06	179.60
Mycena haematopus (Pers.: Fr.) P.Kumm.	Late stage specialist	79.84	118.40	228.18
Mycena hiemalis (Osb.: Fr.) Qu□l.	Unknown/different	107.69	148.66	102.08
Mycena olida Bres.	Unknown/different	-134.95	283.67	362.96
Mycena picta (Fr.: Fr.) Harm.	Late stage specialist	-110.86	-61.87	-17.90
Mycena polygramma (Bull.: Fr.) Gray	Late stage specialist	84.13	167.53	201.66
Mycena pseudocorticola Kuhn.	Unknown/different	304.37	268.93	253.41
Mycena renati Quél.	Late stage specialist	63.70	407.34	192.54
Mycena speirea (Fr.: Fr.) Gillet	Unknown/different	123.86	21.44	2.14
Mycena tintinabulum (Fr.) Quél.	Late stage specialist	198.97	255.64	-92.38
Mycena vitilis (Fr.) Quél.	Unknown/different	-27.16	-68.69	138.33
Mycoacia aurea (Fr.) J. Erikss. & Ryvarden	Late stage specialist	197.23	-4.25	-89.01
Mycoacia uda (Fr.) Donk	Late stage specialist	243.72	-96.91	146.37
Mycetinis alliaceus (Jacquin) Earle	Late stage specialist	68.61	288.15	191.47
Nemania atropurpurea (Fr.: Fr.) Pouzar	Late stage specialist	-37.21	151.37	89.38
Nemania chestersii (Rogers & Whalley)	Late stage specialist	194.98	32.06	362.06
Nemania serpens (Pers.: Fr.) Gray	Late stage specialist	219.10	19.18	313.40
Neobulgaria pura (Fr.) Petrak	Unknown/different	383.75	72.71	90.41
Oligoporus alni (Niemelä & Vampola) Piątek	Unknown/different	206.26	160.55	329.13
Ossicaulis lignatilis (Pers.: Fr.) Redhead & Ginns	Trunk rotters	181.63	495.46	108.64
Oudemansiella mucida (Schrad.: Fr.) Höhn.	Unknown/different	305.90	244.10	109.88
Panellus serotinus (Pers.: Fr.) Kuhn.	Combative invader	286.46	116.98	-5.69
Panellus stipticus (Bull.: Fr.) P.Karst.	Early ruderals	291.59	339.83	21.47
Peniophora cinerea (Pers.: Fr.) Cooke	Early ruderals	535.10	120.55	172.10
Peniophora incarnata (Pers.: Fr.) P.Karst.	Early ruderals	516.66	370.34	132.61
Peziza micropus Pers.: Fr.	Late stage specialist	181.55	258.78	125.21
Phallus impudicus L.: Pers.	Cord	135.39	109.05	299.33
Phlebia livida (Pers.: Fr.) Bres.	Late stage specialist	107.14	228.96	308.50
Phlebia radiata Fr.: Fr.	Combative invader	367.63	144.79	67.95
Phlebia rufa (Pers.: Fr.) M.P.Christ.	Combative invader	327.39	-9.71	219.76
Phlebia tremellosa (Schrad.: Fr.) Burds. & Nakas.	Unknown/different	163.56	35.18	120.42
Phleogena faginea (Fr.: Fr.) Link	Unknown/different	207.80	49.83	112.24
Pholiota adiposa (Batsch) P. Kumm.	Trunk rotters	358.33	137.18	-4.02

Pholiota lenta (Pers.: Fr.) Singer	Late stage specialist	293.30	102.24	-89.16
Pholiota squarrosa (Weigel: Fr.) P.Kumm.	Trunk rotters	11.21	319.97	-170.90
Pholiota squarrosoides (Peck) Sacc.	Trunk rotters	170.98	360.99	-20.37
Pholiotina brunnea (J.E. Lange & Kühner ex Watling) Singer	Late stage specialist	-61.02	-59.93	-77.47
Phyllotopsis nidulans (Pers.: Fr.) Singer	Unknown/different	317.85	337.24	-63.95
Physisporinus vitreus (Pers.) P. Karst.	Unknown/different	43.99	-37.24	21.23
Pleurotus dryinus (Pers.: Fr.) P.Kumm.	Trunk rotters	277.74	-36.38	382.53
Pleurotus ostreatus (Jacq.: Fr.) P.Kumm.	Trunk rotters	406.43	57.22	73.70
Pleurotus pulmonarius (Fr.) Quél.	Trunk rotters	374.33	329.94	42.00
Plicaturopsis crispa (Pers.: Fr.) Reid	Early ruderals	517.57	249.45	113.84
Pluteus cervinus (Batsch) Singer	Late stage specialist	52.24	110.02	173.37
Pluteus chrysophaeus (Schaeff.) Quél.	Late stage specialist	107.05	319.51	-111.04
Pluteus cyanopus Quél.	Late stage specialist	71.83	445.06	135.67
Pluteus hispidulus (Fr.: Fr.) Gillet	Late stage specialist	30.19	-32.30	-170.01
Pluteus insidiosus Vellinga & Schreurs	Late stage specialist	-11.89	-62.33	-155.57
Pluteus leoninus (Schaeff.: Fr.) P.Kumm.	Late stage specialist	-38.56	-113.71	-168.82
Pluteus luctuosus Boud.	Late stage specialist	-111.13	181.26	-33.80
Pluteus nanus (Pers.: Fr.) P.Kumm.	Late stage specialist	4.80	298.29	-49.31
Pluteus phlebophorus (Dittm.: Fr.) P.Kumm.	Late stage specialist	-22.74	149.19	-62.20
Pluteus plautus (Weinm.) Gillet	Late stage specialist	114.53	41.87	-30.41
Pluteus podospileus Sacc. & Cub.	Late stage specialist	0.05	17.47	-90.51
Pluteus romellii (Britz.) Sacc.	Late stage specialist	42.17	318.21	265.78
Pluteus salicinus (Pers.: Fr.) P.Kumm.	Late stage specialist	-27.81	164.40	318.99
Pluteus thomsonii (Berk. & Br.) Dennis	Late stage specialist	-10.47	241.93	58.78
Pluteus umbrosus (Fr.) P.Kumm.	Late stage specialist	-22.41	136.83	79.11
Polyporus badius (Pers.) Schw.	Late stage specialist	153.53	-0.69	97.14
Polyporus brumalis (Pers.) Fr.: Fr.	Combative invader	332.71	181.48	6.13
Polyporus ciliatus Fr.: Fr.	Combative invader	338.82	225.97	-81.05
Polyporus squamosus (Huds.: Fr.) Fr.	Trunk rotters	219.22	373.18	-31.73
Polyporus tuberaster (Pers.: Fr.) Fr.	Unknown/different	261.90	237.95	37.06
Polyporus varius (Pers.) Fr.: Fr.	Combative invader	207.34	223.08	110.92
Postia stiptica (Pers.: Fr.) Jülich	Late stage specialist	210.91	-131.52	26.78
Postia tephroleuca (Fr.: Fr.) Jülich	Late stage specialist	230.58	37.18	321.77
Psathyrella candolleana (Fr.: Fr.) Maire	Unknown/different	176.36	471.12	-31.91
Psathyrella cernua (Vahl.: Fr.) Hirsch	Trunk rotters	345.16	140.83	-25.31
Psathyrella cotonea (Quél.) Konr. & Maubl.	Unknown/different	209.98	-62.41	-29.78
Psathyrella multicystidiata Kits van Wav	Unknown/different	55.94	-202.14	225.04
Psathyrella obtusata (Pers.: Fr.) A.H.Smith	Late stage specialist	31.34	246.58	394.39
Psathyrella piluliformis (Bull.: Fr.) P.D.Orton	Late stage specialist	70.70	-8.09	59.10
Psathyrella rostellata Örstadius	Late stage specialist	-159.09	10.29	56.83
Psathyrella scobinacea (Fr.) Sing.	Late stage specialist	40.05	-108.71	-217.34
Pseudoclitocybe cyathiformis (Bull.: Fr.) Singer	Late stage specialist	156.08	206.31	44.85
Psilocybe horizontalis (Bul) Vellinga & Noordel.	Early ruderals	567.42	-21.61	70.29
Pycnoporus cinnabarinus (Jacq.: Fr.) P.Karst.	Early ruderals	407.74	81.33	128.43
Ramaria stricta (Pers.: Fr.) Quél.	Cord	-54.79	46.39	323.70
Resupinatus applicatus (Batsch: Fr.) Gray	Unknown/different	267.00	290.65	-0.63

Schizophyllum commune Fr.: Fr.	Early ruderals	497.80	302.69	89.19
Schizopora flavipora (Berk. & M.A. Curtis ex Cooke) Ryvarden	Unknown/different	301.42	-61.97	229.59
Schizopora paradoxa (Schrad.) Donk	Early ruderals	274.32	203.56	297.12
Sidera vulgaris (Fr.) Miettinen	Late stage specialist	28.09	-9.76	354.78
Simocybe centunculus (Fr.: Fr.) P.Karst.	Late stage specialist	152.21	328.62	-19.72
Simocybe rubi (Berk.) Singer	Late stage specialist	54.61	-75.24	-142.27
Simocybe sumptuosa (P.D.Orton) Singer	Late stage specialist	233.17	-67.34	193.13
Skeletocutis nivea (Jungh.) Keller	Unknown/different	268.17	-28.47	314.18
Spongipellis delectans (Peck) Murrill	Trunk rotters	165.73	451.46	248.43
Spongipellis pachyodon (Pers.) Kotlaba & Pouzar	Trunk rotters	311.61	392.02	75.49
Steccherinum fimbriatum (Pers.: Fr.) J.Erikss.	Cord	-108.13	62.35	420.31
Steccherinum nitidum (Pers.: Fr.) Vesterh.	Late stage specialist	-77.75	313.60	174.26
Steccherinum ochraceum (Pers.: Fr..) Gray	Combative invader	230.31	287.71	229.33
Stereum hirsutum (Willd.) Pers.	Combative invader	302.20	247.40	134.92
Stereum rugosum (Pers.: Fr.) Fr.	Combative invader	218.45	52.10	229.47
Stereum subtomentosum Pouz.	Combative invader	232.20	-10.54	287.00
Trametes gibbosa (Pers.: Fr.) Fr.	Combative invader	300.76	117.76	106.45
Trametes hirsuta (Wulfen: Fr.) Pilat	Early ruderals	371.59	294.62	31.15
Trametes versicolor (L.: Fr.) Quel.	Combative invader	280.41	102.36	34.55
Trametopsis cervina (Schweinitz) Tomsovský	Trunk rotters	275.89	483.10	-33.06
Tremella foliacea Pers.	Unknown/different	357.66	51.98	-28.00
Tremella mesenterica Retz: Fr.	Unknown/different	428.65	229.23	31.25
Trichaptum abietinum (Pers.: Fr.) Ryvarden	Unknown/different	477.13	-64.25	263.15
Trichaptum pergamenum (Fr.) G. Cunn.	Unknown/different	390.12	301.83	-110.20
Trichoderma viride Pers (*Hypocrea rufa* (Pers.) Fr.) s.lato	Unknown/different	289.21	261.65	219.33
Tubaria conspersa (Pers.: Fr.) Fayod	Late stage specialist	227.43	-110.84	-88.47
Tyromyces chioneus (Fr.: Fr.) P.Karst.	Late stage specialist	274.63	130.98	291.36
Xanthoporia nodulosa (Fr.) Ţura, Zmitr., Wasser, Raats & Nevo	Unknown/different	421.25	296.54	154.63
Xerula radicata (Relhan: Fr.) Dörfelt	Unknown/different	72.43	327.60	131.71
Xylaria hypoxylon (L.: Fr.) Grev.	Unknown/different	203.36	116.80	170.67
Xylaria longipes Nitschke	Unknown/different	-72.72	280.77	-89.70
Xylaria polymorpha (Pers.: Fr.) Grev.	Trunk rotters	114.16	188.06	7.04

Bryophytes

Species	Guild	DCA 1	DCA 2	DCA 3
Amblystegium serpens (Hedw.) Br. Eur.	Opportunistic	39.22	98.53	71.21
Amblystegium varium (Hedw.) Lindb.	Opportunistic	212.81	336.15	-87.39
Anomodon attenuatus (Hedw.) Hüb.	Epiphytic	6.68	91.74	-21.01
Anomodon viticulosus (Hedw.) Hook. & Tayl.	Epiphytic	44.48	273.50	-13.14
Antitrichia curtipendula (Hedw.) Brid.	Epiphytic	237.66	421.00	169.47
Aulacomnium androgynum (Hedw.) Schwaegr.	Epixylic	409.18	-54.33	-7.89
Blepharostoma trichophyllum (L.) Dum.	Epixylic	-84.13	72.74	374.06
Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	Opportunistic	14.39	134.16	101.64
Brachythecium rutabulum (Hedw.) B., S. & G.	Opportunistic	232.31	115.20	182.15
Brachythecium salebrosum (Web. & Mohr.) B., S. & G.	Opportunistic	176.86	-8.77	126.94
Bryum moravicum Podp.	Opportunistic	121.46	106.50	91.84
Calliergonella cuspidata (Hedw.) Loeske	Terricolous	339.46	-58.11	389.05
Calypogeia azurea Stotler et Crotz	Opportunistic	-74.56	56.68	524.74
Calypogeia suecica (H. Am et J. Press.) K. Müll.	Epixylic	-72.15	52.36	435.84
Campylopus flexuosus (Hedw.) Brid.	Opportunistic	474.84	257.25	274.12
Campylopus introflexus (Hedw.) Brid.	Opportunistic	439.91	56.80	170.84
Campylopus pyriformis (K. F. Schultz) Brid.	Opportunistic	463.65	59.13	-86.52
Cephalozia bicuspidata (L.) Dum.	Opportunistic	187.15	-109.78	364.83
Cephalozia catenulata (Hüb.) Lindb.	Epixylic	-96.52	39.85	416.70
Cephaloziella rubella (Nees) Warnst.	Epixylic	-76.53	95.11	380.70
Ceratodon purpureus (Hedw.) Brid.	Opportunistic	235.36	88.10	-58.17
Chiloscyphus polyanthos (L.) Corda	Epixylic	-77.46	3.84	409.64
Ctenidium molluscum (Hedw.) Mitt.	Epilithic	-61.61	162.42	286.26
Dicranella heteromalla (Hedw.) Schimp.	Epiphytic	326.14	425.28	360.24
Dicranoweisia cirriata (Hedw.) Lindb. Ex Milde	Terricolous	391.87	174.19	-30.40
Dicranum montanum Hedw.	Epiphytic	364.78	223.08	65.76
Dicranum scoparium Hedw.	Opportunistic	292.73	278.87	241.71
Dicranum tauricum Sap.	Epiphytic	384.96	-88.68	-25.90
Dicranum viride (Sull. and Lesq.) Lindb.	Epiphytic	-48.08	224.32	157.67
Encalypta streptocarpa Hedw.	Epilithic	-11.61	224.61	40.24
Eurhynchium angustirete (Broth.) T. Kop.	Terricolous	-79.21	129.94	305.42
Eurhynhium striatum (Hedw.) Schimp.	Terricolous	323.30	-48.11	296.84
Fissidens dubius P. Beauv	Epilithic	-71.29	142.49	320.82
Frullania dilatata (L.) Dum.	Epiphytic	-0.78	286.57	5.97
Frullania tamarisci (L.) Dum.	Epiphytic	252.46	414.24	194.19
Grimmia hartmanii Schimp.	Epilithic	-12.61	244.23	-62.75
Herzogiella seligeri (Brid.) Iwats.	Epixylic	161.12	-22.47	250.96
Homalothecium philippeanum (Spruce.) B., S. & G.	Epilithic	-41.14	166.22	12.93
Homalothecium sericeum (Hedw.) B., S. & G.	Epiphytic	82.11	298.94	125.08
Hylocomium splendens (Hedw.) Br. Eu.	Terricolous	328.53	417.36	428.70
Hypnum cupressiforme Hedw.	Opportunistic	209.00	173.19	157.40
Hypnum jutlandicum Holmen & Warncke	Opportunistic	476.38	266.90	155.42
Isothecium alopecuroides (Dubois) Isov.	Epiphytic	35.44	259.70	192.41
Isothecium myosuroides Brid.	Epiphytic	303.58	336.57	248.43
Jungermannia leiantha Grolle	Epixylic	-76.28	36.86	407.49
Lejeunea cavifolia (Ehrh.) Lindb.	Epiphytic	-65.16	240.02	5.11

Lepidozia reptans (L.) Dum.	Epixylic	-45.24	77.03	391.79
Leucobryum glaucum (Hedw.) Angstr.	Epixylic	473.53	254.10	278.58
Leucodon sciuroides (Hedw.) Schwaegr.	Epiphytic	-39.24	265.57	-18.12
Lophocolea bidentata (L.) Dum.	Terricolous	321.05	-161.22	320.18
Lophocolea heterophylla (Schrad.) Dum.	Epixylic	180.86	22.92	181.19
Lophocolea minor Nees	Epixylic	29.28	107.66	357.59
Metzgeria conjugata Lindb.	Epiphytic	-68.74	248.02	6.40
Metzgeria furcata (L.) Dum.	Epiphytic	89.19	266.45	81.72
Mnium hornum Hedw.	Terricolous	342.22	73.40	313.47
Mnium marginatum (Dicks) P. Beauv.	Epixylic	-60.56	146.36	222.30
Mnium stellare Hedw.	Epixylic	21.33	32.76	360.01
Neckera besseri (Lobarz.) Jur.	Epiphytic	-17.52	119.60	-46.34
Neckera complanata (Hedw.) Hüb.	Epiphytic	121.26	285.39	177.72
Neckera crispa Hedw.	Epiphytic	-59.40	228.51	152.67
Neckera pumila Hedw.	Epiphytic	75.44	298.94	48.72
Nowellia curvifolia (Dicks.) Mitt. in Godman	Epixylic	-32.82	125.35	343.65
Orthotrichum affine Brid.	Epiphytic	363.63	369.85	-59.83
Orthotrichum diaphanum Brid.	Epiphytic	373.27	275.94	-149.72
Orthotrichum lyellii Hook. & Tayl.	Epiphytic	107.47	323.66	-42.97
Orthotrichum stramineum Hornsch. ex Brid.	Epiphytic	89.27	281.50	5.30
Ortotrichum speciosum Nees	Epiphytic	272.66	262.03	-67.15
Oxyrrhynchium hians (Hedw.) Loeske	Terricolous	36.48	-151.51	391.93
Paraleucobryum longifolium (Hedw.) Loeske	Epiphytic	-27.51	193.70	149.84
Plagiochila porelloides (Torrey ex Nees) Lindenb.	Opportunistic	-15.66	225.41	277.69
Plagiomnium affine (Bland.) T. Kop.	Terricolous	116.84	292.65	408.62
Plagiomnium cuspidatum (Hedw.) Kop.	Opportunistic	-1.82	111.95	136.20
Plagiomnium ellipticum (Brid.) Kop.	Opportunistic	-76.93	163.78	220.50
Plagiomnium undulatum (Hedw.) Kop.	Terricolous	-18.35	115.99	304.44
Plagiothecium cavifolium (Brid.) Iwats.	Terricolous	93.64	47.39	315.60
Plagiothecium denticulatum (Hedw.) Br. Eur.	Epixylic	133.65	148.98	321.25
Plagiothecium laetum Br. Eur.	Epiphytic	377.88	25.76	361.92
Plagiothecium nemorale (Mitt.) Jaeg.	Epixylic	74.34	166.60	334.73
Plagiothecium undulatum (Hedw.) Br. Eur.	Terricolous	370.98	440.56	486.80
Plasteurhynchium striatulum (Spruce) M. Fleish.	Opportunistic	364.88	-54.36	188.69
Platygyrium repens (Brid.) B., S. & G.	Epiphytic	25.30	125.11	13.65
Pleurozium schreberi (Brid.) Mitt.	Terricolous	315.93	402.94	456.76
Pohlia nutans (Hedw.) Lindb.	Terricolous	312.22	-57.03	-13.39
Polytrichastrum formosum (Hedw.) G.L.Sm.	Terricolous	366.39	121.03	264.53
Polytrichastrum longisetum (Sw. ex Brid.) G.L.Sm.	Opportunistic	461.54	-37.91	2.02
Porella platyphylla (L.) Pfeiff.	Epiphytic	103.06	300.05	133.64
Pseudoleskeella nervosa (Brid.) Nyh.	Epiphytic	28.51	103.01	20.93
Pseudoscleropodium purum (Hedw.) Fleisch.	Terricolous	406.35	-129.56	356.82
Pterigynandrum filiforme Hedw.	Epiphytic	-0.44	186.27	45.47
Ptilidium pulcherrimum (G. Web.) Vainio	Opportunistic	386.98	133.36	-77.35
Ptilium crista-castrensis (Hedw.) De Not.	Terricolous	334.44	389.34	544.22
Pylaisia polyantha (Hedw.) Schimp.	Epiphytic	36.68	169.04	-18.78
Radula complanata (L.) Dum.	Epiphytic	-29.06	251.68	67.91
Rhizomnium punctatum (Hedw.) Kop.	Epixylic	-5.12	92.26	309.13
Rhynchostegium confertum (Dicks.) B., S. & G.	Epiphytic	381.57	-135.62	23.60

Rhynchostegium murale (Hedw.) B., S. & G.	Epilithic	-43.45	236.44	12.77
Rhytidiadelphus loreus (Hedw.) Warnst.	Terricolous	284.75	392.12	379.76
Rhytidiadelphus squarrosus (Hedw.) Warnst.	Terricolous	333.86	255.00	360.61
Rhytidiadelphus triquetrus (Hedw.) Warnst.	Terricolous	-83.99	161.79	235.56
Riccardia latifrons (Lindb.) Lindb.	Epixylic	-23.79	12.69	373.35
Riccardia multifida (L.) S. Gray	Epixylic	-94.64	45.25	384.41
Riccardia palmata (Hedw.) Carruth.	Epixylic	-71.94	139.11	314.67
Sanionia uncinata (Hedw.) Loeske	Opportunistic	7.72	174.77	269.48
Sciuro-hypnum populeum (Hedw.) Ignatov & Huttunen	Opportunistic	21.05	198.12	23.47
Sciuro-hypnum reflexum (Starke) Ignatov & Huttunen	Opportunistic	305.54	467.87	322.94
Syntrichia ruralis (Hedw.) F.Weber & D.Mohr	Epilithic	-7.81	144.16	-57.15
Tetraphis pellucida Hedw.	Epixylic	241.71	143.94	379.60
Thamnobryum alopecurum (Hedw.) Gang.	Epiphytic	-84.82	114.93	331.82
Thuidium tamariscinum (Hedw.) B., S. & G.	Terricolous	27.17	99.93	341.71
Tortella tortuosa (Hedw.) Limpr.	Opportunistic	-60.53	202.74	204.02
Tortula subulata Hedw.	Epilithic	-21.51	81.50	-74.73
Ulota crispa (Hedw.) Brid.	Epiphytic	105.85	268.56	-45.14
Zygodon conoideus (Dicks.) Hook. & Tayl.	Epiphytic	399.61	363.99	-30.36
Zygodon rupestris Schimp. Ex Lor.	Epiphytic	69.71	307.26	74.70

1   Appendix S3: Kendall rank correlation matrix for all included variables. Correlations with Kendall's tau exceeding +0.5/-0.5 are highlighted in
2   bold.

3

	DECAY STAGE	DBH	BARK COVER	SOIL CONTACT	MOSS COVER	ELEVATION	TEMP_MIN	TEMP_MAX	TEMP_RANGE	TEMP_AVE	PRECIPITATION	SNOW COVER	LANG'S RAINFALL INDEX	SOIL_RICH	NATURALNESS	FOREST AGE	FOREST SIZE	CWD VOLUME	FOREST COVER	DECIDUOS COVER	CONIFEROUS COVER	CONIFEROUS SHARE	PAST FOREST COVER	FOREST COVER CHANGE	LATITUDE	LONGITUDE
DECAY STAGE	1																									
DBH	-0.08	1																								
BARK COVER	**-0.67**	0.10	1																							
SOIL CONTACT	0.46	-0.01	-0.39	1																						
MOSS COVER	0.10	0.05	0.01	0.05	1																					
ELEVATION	0.11	-0.16	-0.04	-0.13	-0.02	1																				
TEMP_MIN	-0.11	0.09	0.08	-0.01	0.06	-0.46	1																			
TEMP_MAX	-0.03	-0.01	0.01	-0.14	-0.12	-0.06	**0.58**	1																		
TEMP_RANGE	0.13	-0.11	-0.09	-0.01	-0.07	**0.53**	**-0.92**	-0.49	1																	
TEMP_AVE	-0.10	0.02	0.04	-0.08	-0.09	-0.31	**0.73**	**0.79**	**-0.68**	1																
PRECIPITATION	0.03	-0.21	0.04	-0.10	0.10	**0.57**	-0.37	-0.09	0.39	-0.13	1															
SNOW COVER	0.12	-0.14	-0.08	-0.05	-0.03	**0.61**	**-0.80**	-0.36	**0.79**	**-0.54**	**0.55**	1														
LANG'S RAINFALL INDEX	0.05	-0.19	0.02	-0.09	0.13	**0.58**	**-0.54**	-0.25	**0.52**	-0.31	**0.83**	**0.70**	1													
SOIL_RICH	0.16	-0.05	-0.15	-0.11	-0.23	**0.50**	-0.28	0.11	0.34	-0.13	0.10	0.34	0.11	1												
NATURALNESS	0.17	-0.04	-0.13	-0.12	-0.08	**0.56**	**-0.51**	-0.08	**0.55**	-0.32	0.25	**0.63**	0.40	0.49	1											
TREE AGE	0.17	-0.07	-0.12	-0.08	-0.09	0.46	**-0.51**	-0.19	**0.54**	-0.35	0.22	**0.59**	0.39	0.43	**0.86**	1										
FOREST SIZE	0.12	-0.15	-0.13	-0.13	-0.19	0.42	-0.27	0.18	0.34	-0.08	0.08	0.34	0.16	**0.54**	0.45	0.37	1									
CWD VOLUME	0.15	0.11	-0.15	-0.04	-0.10	0.25	-0.27	0.01	0.25	-0.15	0.01	0.33	0.12	**0.54**	**0.57**	**0.51**	0.23	1								
FOREST COVER	0.07	-0.10	-0.05	-0.03	-0.01	**0.59**	**-0.66**	-0.29	**0.65**	-0.44	**0.64**	**0.63**	**0.65**	0.22	0.37	0.31	0.14	0.23	1							
DECIDUOS COVER	0.15	-0.05	-0.11	-0.04	-0.11	0.49	-0.41	-0.05	0.49	-0.29	0.19	0.29	0.16	0.49	0.41	0.26	0.39	0.21	0.42	1						
CONIFEROUS COVER	-0.07	-0.08	0.11	0.02	0.24	0.03	-0.14	-0.31	0.06	-0.21	0.37	0.28	0.42	-0.40	-0.03	0.01	-0.30	-0.11	0.16	-0.36	1					
CONIFEROUS SHARE	-0.09	-0.03	0.11	0.05	0.20	-0.07	-0.03	-0.32	-0.05	-0.17	0.28	0.16	0.32	-0.47	-0.14	-0.08	-0.37	-0.16	0.03	-0.48	**0.87**	1				
PAST FOREST COVER	0.12	0.03	-0.11	-0.07	-0.03	0.48	-0.38	0.00	0.38	-0.27	0.20	0.38	0.24	0.45	0.50	0.32	0.38	0.38	0.49	**0.60**	-0.24	-0.34	1			
FOREST COVER CHANGE	-0.04	-0.14	0.06	0.05	0.05	0.06	-0.17	-0.25	0.16	-0.16	0.42	0.23	0.35	-0.27	-0.12	-0.03	-0.19	-0.25	0.20	-0.18	**0.59**	**0.53**	-0.34	1		
LATITUDE	-0.09	0.06	0.13	0.13	0.26	**-0.56**	0.08	-0.35	-0.16	-0.10	-0.25	-0.27	-0.24	**-0.63**	-0.47	-0.32	**-0.57**	-0.34	-0.29	-0.36	0.27	0.30	-0.47	0.18	1	
LONGITUDE	0.11	-0.09	-0.09	0.01	-0.08	0.47	**-0.93**	**-0.56**	**0.88**	**-0.67**	0.37	**0.74**	0.47	0.35	0.47	0.48	0.23	0.29	**0.65**	0.43	0.09	-0.02	0.36	0.18	-0.09	1

4