Journal of Biogeography

Journal of Biogeography (*J. Biogeogr.*) (2014) **41**, 2269–2282

ORIGINAL ARTICLE

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] and 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, DK-8410 Rønde, Denmark, [3]Forestfun, NL-6708 LN Wageningen, The Netherlands, [4]Morten Christensen Consult, 4180 Sorø, Denmark, [5]Institute for Systematic of Higher Fungi, SI-1000 Ljubljana, Slovenia, [6]NL-3985RZ Werkhoven, The Netherlands, [7]Institute for Biology, Faculty of Veterinary Science, Szent István University, H-1400 Budapest, Hungary, [8]Department of Plant Systematics, Ecology and Theoretical Biology, Eötvös University, H-1117 Budapest, Hungary, [9]MTA Centre for Ecological Research, Institute of Ecology and Botany, H-2163 Vácrátót, Hungary

*Correspondence: Jacob Heilmann-Clausen, Center for Macroecology, Evolution and Climate, Biological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark.
E-mail: jheilmann-clausen@bio.ku.dk
†Deceased September 2008.

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 whether 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 into ecological guilds. Indirect ordination and variation partitioning was used to analyse the relationship 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 more clearly structured by substrate quality than were bryophyte communities. In both groups a distinct turnover in species composition was evident along a longitudinal gradient from Central to Western Europe. Fungi specialized in trunk rot and specialized epixylic bryophytes were scarcely represented in Atlantic regions, and partly replaced by species belonging to less specialized guilds. Variables related to climate and forest conditions were confounded along this main geographical gradient in community composition.

Main conclusions We found that bryophyte and fungal communities co-occurring on fallen beech logs in European beech forest reserves differed in their responses 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.

Keywords

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

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/jbi.12388

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; Sundqvist *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 utilizing 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 north-western 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 about 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; Raabe *et al.*, 2010). 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; Lassauce *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 hotspots (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 interact 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 standardized way in beech forest reserves across six countries in Europe, from Sweden in the north, Belgium in the west, Slovenia in the south, and Hungary in the east. The dataset represents an extension of the dataset analysed by Ódor *et al.* (2006) that focused on species richness patterns. For both organism groups the analysed dataset is the geographically most extensive so far using a standardized 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 hypothesized that: (1) the relative contribution of substrate quality was stronger for fungi than for bryophytes; and (2) regional climatic factors were more important for explaining differences in bryophyte community composition. Finally, (3) we hypothesized 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 a lack of naturalness and habitat loss.

MATERIALS 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. Owing 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 into a core area and a buffer zone with different management history.

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 Fig. 1.

Site name	Abbrev.	Country code*	No. of sampled logs	Stand size (ha)	Dead wood volume (m^3/ha)	Tree age (years)	Naturalness score†	Latitude (decimal degrees)	Longitude (decimal degrees)
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, Gortelse Bos	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.

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). Owing 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 into three variable sets: (1) 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; (2) 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; and (3) forest condition variables were recorded at stand or reserve level and included

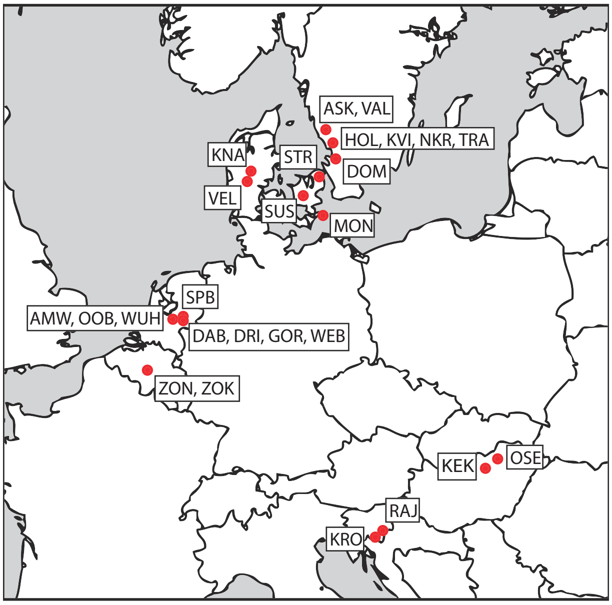

Figure 1 Map of Europe showing the location of 26 protected beech stands in which fungi and bryophyte communities on fallen beech logs were inventoried for this study. For full names of stands, see Table 1.

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 (18th–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 standardized by range (i.e. obtaining values ranging from 0 to 1) before further analyses.

Fungi and bryophyte surveys

All included logs were surveyed three times for fungal fruit bodies and once for wood-inhabiting bryophytes recording all species growing directly on wood or bark. The fungal surveys were conducted on 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 in Sweden, where fieldwork was conducted in 2004.

For fungi, the taxonomic treatment follows Hansen & Knudsen (1992–2000), but nomenclature has been updated to match with Index Fungorum (http://www.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 *Plagiochila asplenioides*, as well as *Plagiothecium nemorale* and *Plagiothecium succulentum*, were not separated. Among the fungi, *Antrodiella semisupina* was treated in a collective sense including *Antrodiella faginea* and *Antrodiella pallescens*; *Physisporinus sanguinolentus* was not distinguished from *Physisporinus vitreus*; and *Pluteus plautus* was treated in a collective sense.

Classification of species

Compared with 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 with the soil of the uprooted part of the logs were omitted. The remaining taxa were classified into 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 Ódor *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 Appendices 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 4.25 (McCune & Mefford, 1999). Down-weighting of rare species was not applied, but species-poor logs (fewer than five species) and infrequent species (fewer 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.

Table 2 List of environmental variables recorded in this study on fungi and bryophyte communities on fallen 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, 1**6.6**, 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, 5-km 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: http://www.smhi.se/, normals 1961–1990 (Sweden); http://www.dmi.dk/, normals 1961–1990 (Denmark); http://www.knmi.nl/, normals 1971–2000 (The Netherlands); http://www.meteo.be/, normals 1971–2000 (Belgium); http://www.met.hu/, normals 1971–2000 (Hungary); http://www.meteo.arso.gov.si/met/en/, normals 1971–2000 (Slovenia).

‡1: sand (The Netherlands, Denmark), granite (Sweden); 2: loam-sand and clay (The Netherlands); 3: sand-clay and loam-sand (Denmark), andesite (Hungary), loess (Belgium); 4: limestone (Slovenia, Hungary), chalk (Denmark).

§1: Recently managed forests with a homogenous structure and low levels of dead wood, dominant trees generally ≤ 200 years, gaps in tree continuity possible; 2: recently managed forests with a homogenous structure and moderate levels of dead wood, dominant trees generally > 200 years, 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 years, 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, Naturcentrum AB, pers. comm.

**Based on CORINE2007 land cover data (available from the European Environment Agency, http://www.eea.europa.eu/publications/COR0-landcover).

††Det Kongelige Danske Videnskabernes Selskab (1762–1820) (Denmark); Generalstabens karta över Halland 1839–1842, here derived from Malmström (1939) (Sweden); Sepp (1773) (The Netherlands); de Ferraris (1777) (Belgium); Arcanum, (2006) (Hungary and Slovenia).

‡‡Present forest cover minus past forest cover.

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, owing to the multiple comparisons. The regression modelling was conducted in R 2.15.2 (R 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 honestly significant difference (HSD) tests 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 canonical correspondence analysis (CCA; Lepš & Šmilauer, 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 & Šmilauer, 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 fewer than three logs, and similarly many logs had fewer than five species present in either group. After pruning out these species-poor logs and infrequent 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, respectively, 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 groups of organism a clear geographical clustering was evident in the ordination space defined by axes 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 (diameter at breast height) having the highest *F*-value. It is important to note that correlation among some environmental variables was very pronounced (see Appendix S3) and hence the relationships 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, respectively, 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 than 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 that these guilds have a disproportional strong influence on the community gradient, owing 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 compared with 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 with 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% vs. 15%). Further, the shared contribution of forest condition and climate and soil variables was almost twice as high in bryophytes (40%) as in fungi (22%). In total, the selected explanatory variables

Table 3 Simple mixed-effects models between environmental variables and detrended correspondence analysis (DCA) ordination axis scores based on bryophytes and fungal communities on fallen beech logs in Europe using site as a random factor. For substrate variables the degrees of freedom were 862 for bryophytes and 933 for fungi. For site-level variables (climate and soil, forest conditions) the degrees of freedom were 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

****$P < 0.0001$, ***$P = 0.0001$ to < 0.001, **$P = 0.001$ to < 0.01, *$P = 0.01$ to < 0.05.

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 reflects inherent differences in data structure, especially the larger species pool and higher frequency of infrequent species in the fungal compared with the bryophyte dataset (cf. Ódor *et al.*, 2006).

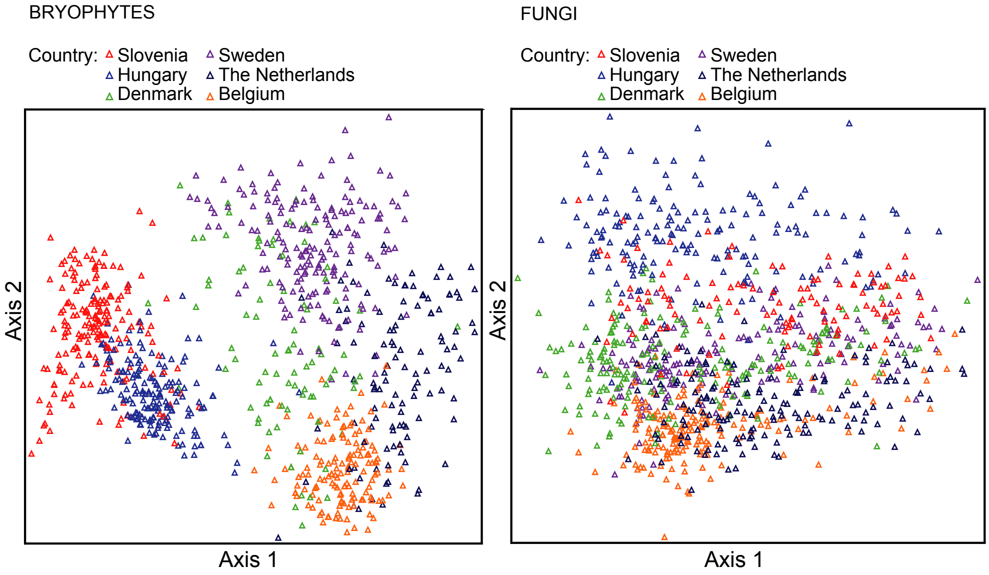

Figure 2 Diagrams showing the position of sampling units (fallen beech logs) in the ordination space defined by axis 1 and 2 of the detrended correspondence analysis (DCA) based on the bryophyte dataset (left; 893 logs) and fungal dataset (right; 965 logs) collected from 26 sites in Europe. The samples (logs) are colour coded according to country.

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 specialized in utilizing 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 the fact that the 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 to the turnover in guilds found along ordination axes 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 a lack of naturalness at the local scale, owing to discontinuity in the presence of suitable substrates, especially large-diameter dead logs in managed forests (Andersson & Hytteborn, 1991; Rambo & Muir, 1998; Saboljevic *et al.*, 2010), but also owing 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,

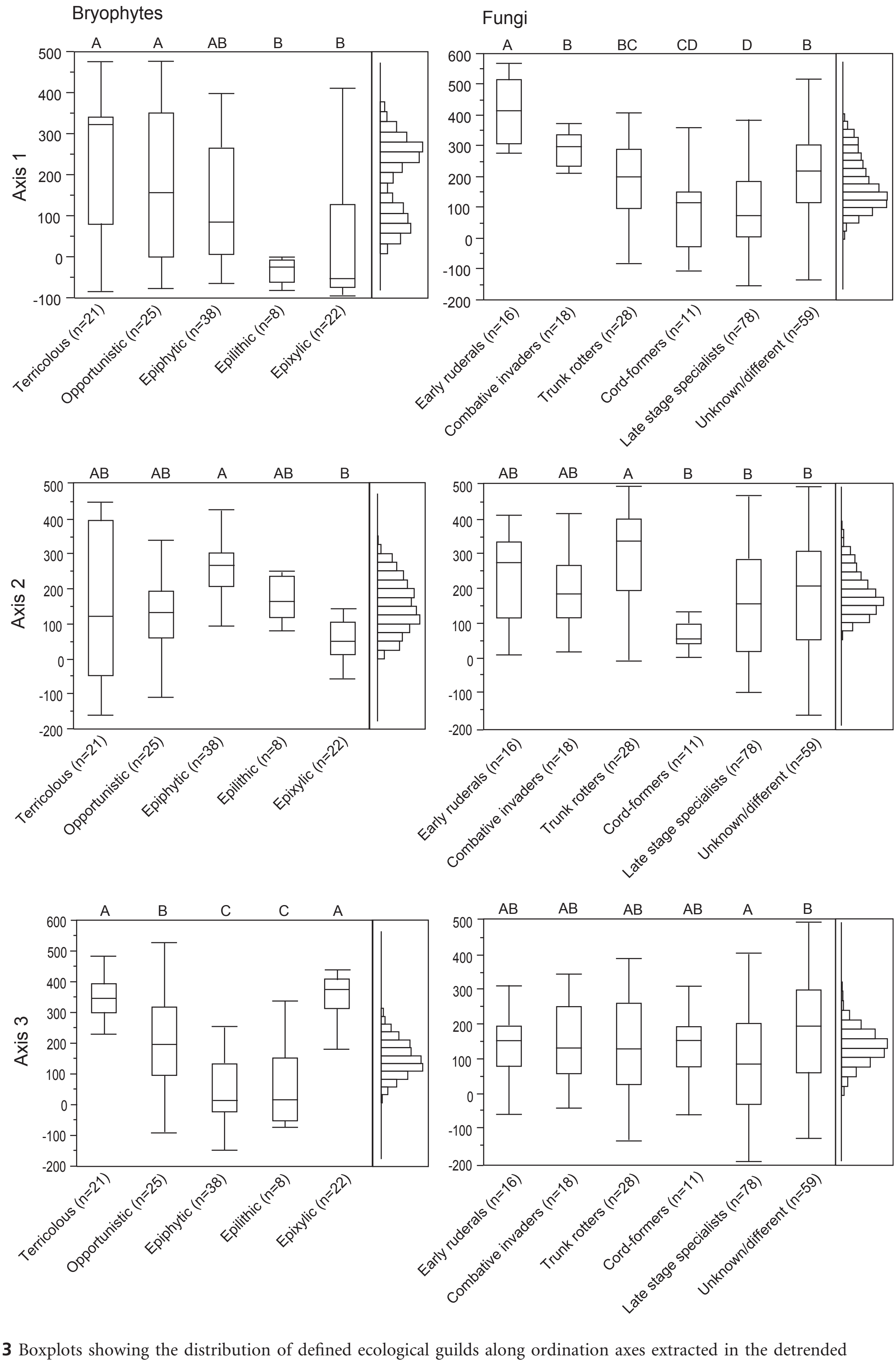

Figure 3 Boxplots showing the distribution of defined ecological guilds along ordination axes extracted in the detrended correspondence analysis (DCA) based on the bryophyte dataset (left panel) and fungal dataset (right panel) collected from fallen beech logs at 26 sites in Europe. Different letters 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.

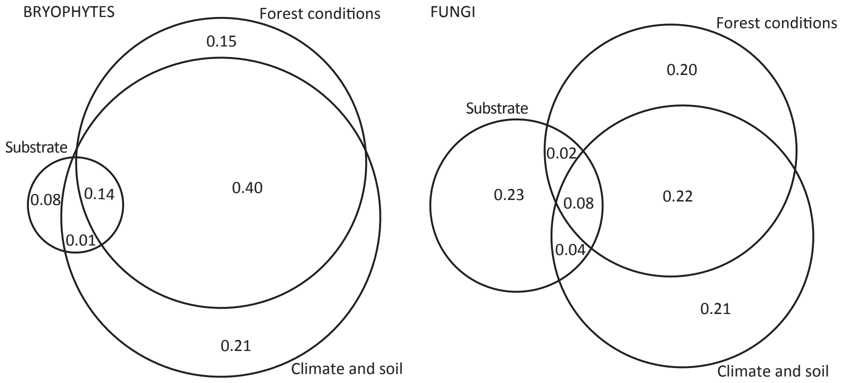

Figure 4 Venn diagrams, showing the relative contribution of substrate, forest condition and climate variables in explaining variance in the full canonical correspondence analysis (CCA) for bryophytes (left; 893 logs) and fungi (right; 965 logs) on fallen beech logs across 26 sites in Europe. The circles 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.

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 specialized epixylic species on decayed logs. However, a direct or indirect effect of climatic drivers cannot be ruled out, and the strong relationship 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 the winter than in the summer. This suggests 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 ground-living bryophytes in alpine snow-beds (e.g. Hohenwallner *et al.*, 2011). In our dataset, the winter period 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 relationships 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 few studies have explored the importance of macroclimate for community composition and mainly in relation to elevational gradients (Lindblad, 2001; Gómez-Hernández *et al.*, 2012). Previously, we suggested that trunk rotters, which are normally considered stress tolerant (Boddy & Heilmann-Clausen, 2008), could be favoured under continental climates (Ódor *et al.*, 2006; as heart rot agents). The current guild-based analysis supports this hypothesis, but because of the confounding relationship between climate and forest condition variables, direct effects of forest history or naturalness cannot be ruled out.

Studies from Fennoscandia have reported a clear relationship between forest fragmentation and lack of naturalness and the depletion of fungal communities for habitat specialists (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) found 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 depending on large decaying logs or living trunks with internal rot (Boddy & Heilmann-Clausen, 2008). Hence, their optima in Slovenia and Hungary could reflect the fact that beech forests in general are more natural 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 supports this interpretation. The two latter guilds all have traits that make them 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 may even utilize other types of plant litter (Boddy, 1999). 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 their exact habitat requirements, but they are rarely restricted to large-diameter dead wood and several species occur even on cut stumps, sawdust and other man-made substrates (Runge, 1975; Babos, 1981). 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 than in 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 first hypothesis, 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 the 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 specialized bryophyte species (mainly epixylics) are predominantly dispersed by large asexual diaspores, and hence dispersal-limited at the landscape scale (Löbel & Rydin, 2009), which suggests that communities of wood-inhabiting bryophytes might be more sensitive to habitat fragmentation and breaks in continuity than fungal communities.

The tests of our second hypothesis (regional climatic factors are more important for bryophytes than for fungi) and third hypothesis (forest conditions are equally important in both groups) proved difficult because of the confounding relationship between 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 being less affected by regional climate than bryophytes, although drivers and mechanisms seem to differ among the two groups of organism.

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 and 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 because of the longer period with snow cover, which may decrease competition from more opportunistic species, and trunk rotting fungi because of 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 relationship 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 in the Balkans 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

The study was supported by the EU 5th Framework Programme Nat-Man (QLRT1-CT99-1349). During the preparation of the manuscript the Aage V. Jensen Foundation supported J.H.-C., while P.Ó. was supported by the Hungarian Science Foundation (OTKA 68218, 79158) and the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. Slovenian partners were financed through Ministry of Education (Project No. 404-501), Ministry of Agriculture (Project No. 2552/8), Ministry of Environment and Spatial Planning (Project No. 2523-02-100324). Fieldwork in Belgium was supported by the Forestry Department of the Flemish Government (NKB-2001-KUT-5) and in Sweden by the County Administrative Board of Halland. The authors are grateful for fieldwork assistance provided by E. Szurdoki, K. Kenderes, G. Turcsányi, J. Siller (Hungary); H. Kraigher, L. Kutnar, T. Grebenc, D. Jurc, I. Smolej, T. Levanič, M. Rupel (Slovenia); and B. van Os (The Netherlands). In Sweden Örjan Fritz provided much help with the selection of study sites and by supplying information on the management history. Hans Henrik Bruun is thanked for advice on gradient analysis, while Helle Sørensen provided statistical advice. Finally, Ariel Bergamini and two anonymous referees provided constructive comments on the manuscript.

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* (ed. by L. Boddy, J.C. Frankland and P. van West), pp. 211–237. Elsevier, London.

ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO 4.5*. Biometrics, Wageningen and Ceské Budejovice.

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.

Det Kongelige Danske Videnskabernes Selskab (1762–1820) *Historical topographical maps of Denmark*. Det Kongelige Danske Videnskabernes Selskab, Copenhagen, Denmark.

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.

deFerraris, J. J. F. (1777) *Plan topographique de la ville de Bruxelles*. L. A. Dupuis, Mechelen, Belgium.

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: Biological Sciences*, **272**, 2105–2115.

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*, Vols 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* (ed. by L. Boddy, J.C. Frankland and P. van West), pp. 263–275. Elsevier, London, UK.

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., Muñoz, 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* (ed. by Z. Tuba, N.G. Slack and L.R. Stark), pp. 237–250. Cambridge University Press, Cambridge, UK.

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

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.

Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd edn. Elsevier, Amsterdam.

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.

Malmström, C. (1939) Hallands skogar under de senaste 300 åren. *Meddelanden från Statens Skogsförsöksanstalt*, **31**, 171–300.

McCune, B. & Mefford, M.J. (1999) *Multivariate analysis of ecological data, version 4.25*. MjM Software, Gleneden Beach, OR.

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. & 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. & 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., 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 seminatural beech forests in Europe. *Biological Conservation*, **131**, 58–71.

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. & R Core Team (2011) *nlme: linear and nonlinear mixed effects models*. R package version 3.1-102. Available at: http://cran.r-project.org/web/packages/nlme/index.html.

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.

R Core Team (2012) *R: a language and environment for statistical computing*. Version 2.15.2. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org/.

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.

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

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.

Sepp, J. C. (1773) *Nieuwe Geographische Reise- en Zak-Atlas*. Jan Christiaan Sepp, Amsterdam.

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

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, UK.

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.

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.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

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

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

Appendix S3 Kendall rank correlation matrix for all included variables.

BIOSKETCH

This study was initiated as part of the project 'Nature Based Management of Beech in Europe' (Nat-Man) under the EU 5th Framework Programme with the aim to highlight the importance of dead wood for biodiversity across Europe.

Author contributions: The fungal dataset was collected by J.H.-C., M.C., A.P., M.V., R.W. and I.S. and 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 fieldwork making the study possible.

Editor: Peter Linder