



RESEARCH PAPER

Open Access



Altitude is a better predictor of the habitat requirements of epixylic bryophytes and lichens than the presence of coarse woody debris in mountain forests: a study in Poland

Damian Chmura^{1*} , Jan Żarnowiec¹  and Monika Staniaszek-Kik² 

Abstract

Key message: In order to preserve the continuity of epiphytic and epixylic cryptogamic flora, two things are essential: maintaining the near-natural character of a forest community in relation to the montane zonation and more sustainable forest management in relation to deadwood.

Context: Lichens and bryophytes are common species that inhabit dead wood. The relationship between their habitat requirements, which can be expressed by their Ellenberg indicator values and the characteristics of dead logs, are not yet known.

Aims: We formulated the hypothesis that altitude is positively correlated with the demands of species for higher light and lower temperature, while the decomposition stage of deadwood is positively correlated with species' requirements for nutrients and moisture. Moreover, we assumed that there would be differences in the habitat requirements among specific groups of species, i.e., lichens, liverworts, and mosses.

Methods: A total of 629 logs that were colonized by bryophytes and lichens were analyzed in terms of their mean Ellenberg indicator values in order to determine whether there is a link between the location, decomposition of logs and the species' environmental requirements.

Results: Altitude correlated with the moisture and nutrients in the habitats of liverworts and mosses and light and soil acidification only in mosses.

Conclusions: The obtained results demonstrate that the altitudinal distribution of epixylic species in a montane region is of greater importance than the deadwood properties like decomposition stage and moisture content.

Keywords: Ellenberg indicator value system, Hepatics, mosses, Lichens, Elevation, Montane region

1 Introduction

The generation of deadwood into the environment is a result of natural processes and human disturbance (Harmon et al. 1986). The latter includes thinning tree stands, cutting trees, the dieback of trees due to pollution as well as forest restoration and afforestation etc. Both natural processes and forest management practices

Handling Editor: Laurent Bergès

* Correspondence: dchmura@ath.bielsko.pl

¹Institute of Environmental Protection and Engineering, University of Bielsko-Biala, Willowa Str 2, 43-309 Bielsko-Biala, Poland

Full list of author information is available at the end of the article



© The Author(s). 2022 **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

are accompanied by deadwood being left on the forest floor (Rondeux and Sanchez 2009). Deadwood includes stumps—i.e., remnants of cut and broken trees, snags—dead standing trees, and logs that are slowly decomposing, cut fallen trunks, and windthrows or windsnaps, i.e., uprooted trees or trees that have been broken by the wind, respectively (Stathers et al. 1994; Merganičová et al. 2012). The so-called coarse woody debris (CWD) forms an important or at least an additional substratum and niche for many living organisms (Lassauce et al. 2011). For bryophytes (mosses and liverworts) and lichens, CWD is a more important habitat than for vascular plants (Harmon et al. 1986; Goia and Gafta 2019; Hämäläinen et al. 2020). The deadwood-inhabiting, i.e., the epixylic flora of bryophytes is usually richer than the vascular plant flora that colonizes deadwood, especially in mountain and boreal regions (Ódor et al. 2004; Ditrlich et al. 2014). Only in lowlands are there a few exceptions, e.g., Białowieża Primeval Forest where vascular epixylic flora is more species rich (Chlebicki et al. 1996). The frequency, abundance, and species composition of plants on CWD depend on many environmental factors at a very small scale, including the properties of the deadwood, e.g., decomposition stage and rate, and those at a higher spatial scale. The latter includes the type of surrounding vegetation, altitude etc. (Müller et al. 2015; Vrška et al. 2015; Petrillo et al. 2016; Chmura et al. 2016; Staniaszek-Kik et al. 2019). The colonization processes of plants and lichens on deadwood have been described in many studies since Hackiewicz-Dubowska (1936) and McCullough (1948) who were the first to identify the decomposition classes of logs and snags. All proposal scales are based on decomposition advancement such as a change in shape (from round to flat), in hardness (from hard to soft wood), in wood structure (falling of branches and bark), in wood chemistry (chemical changes in decaying wood and release of some substances), in wood moisture (the increasing water content). Other researchers, including Dynesius and Jonsson (1991); Holeksa (2001); Zielonka and Piątek (2004) and Ódor and van Hees (2004) have presented their own or have modified the existing scale of deadwood decay. Their decay scale was based on the physical features of the fallen logs and did not depend on the coverage of vascular plants and mosses. The decay classes are a useful tool for predicting the succession of plants and lichens as well as the time that the decomposed wood remains on the forest floor. It is a proxy of moisture and the release of nutrients into the substratum (Petrillo et al. 2015). Many studies have shown that as dead trees decompose, CWD becomes moist, soft, flat, and therefore favorable for seedling recruitment and the occurrence of lichens.

The relationships between the habitat requirements of epixylic species and their presence on deadwood are not fully known. For instance, the known habitat associations of species have not yet been fully analyzed. There have been a few papers that have emphasized the life-history traits of deadwood colonizers and the properties of deadwood and its surroundings, e.g., for bryophytes (Bardat and Aubert 2007; Barbé et al. 2017; Żarnowiec et al. 2021) and vascular plants (Chečko et al. 2015; Chmura et al. 2016). However, we do not know which factors are more important in determining species presence, the characteristics of the deadwood itself, or the characteristics of the surrounding forest habitat.

The habitat requirements of epixylic lichens, liverworts, and mosses have not been studied at an elementary level, i.e., in terms of the tolerance of a species to light, temperature, moisture, nutrients etc. The studies by Bardat and Aubert (2007) are exceptions. They used the Ellenberg indicator values (EIV) for light, humidity, temperature, and pH (Ellenberg et al. 1991) for the bryophyte communities on three sites in France that were under three different silvicultural management practices. Strong correlations between the EIV and actual measurements were found (Diekmann 2003). Thus, EIV can be (phyto)indicators of environmental conditions. This is the reason the EIV are regarded as a valuable tool that is widely used in applied ecology (Simmel et al. 2021 and see literature cited therein). If the indicative applicability of the EIV for bryophytes was found to be useful, we wanted to test the validity of the Ellenberg indicator values (EIV) of bryophytes and lichens in order to determine any possible associations with the properties of the deadwood and climatic/vegetational factors in a montane region.

We selected the forest belts of the Karkonosze Mts (Sudeten Mts, southern Poland) in which there are forests that are protected within a national park and managed forests in the buffer zone, respectively. In addition, in the 1980s, an ecological disaster (mostly air pollution) occurred that led to a massive dieback of the dominant tree—the spruce *Picea abies* L. H. Karst. At present, in both the Karkonosze National Park and its buffer zone, the restoration of the forests in which dead trees are felled and left on the forest floor is continuing (Staniaszek-Kik et al. 2019). This situation enhances colonization by many epixylic lichens and bryophytes.

We formulated the general hypothesis that altitude-driven climatic factors are more important than the properties of deadwood. In particular, species' responses (e.g., their habitat requirements as reflected in the EIV) are more dependent on altitude than the species composition for which local factors (properties of deadwood and close environment) can be more significant.

Our first hypothesis was that altitude is positively correlated with the EIV for light due to the higher light availability in the upper montane zone spruce forests than in the lower montane zone beech forests, and negatively with the temperature requirements of a species (i), whereas the decomposition stage of deadwood is positively correlated with the EIV for nutrients and moisture (ii). In addition, we assumed that the responses of specific groups of organisms (lichens, liverworts, and mosses) to environmental factors would differ. For instance, we expected that in the case of lichens, the relationships between their EIV and altitude might be weaker because this group was previously more confined to host trees than to a vertical distribution. We believed that lichens were more light- and temperature-demanding species, while mosses would prefer more moisture and that overall bryophytes would be more confined to sites with a higher acidity and nutrient content (iii).

2 Material and methods

2.1 Study area

The study was conducted in the forests of the Karkonosze Mts including the area that belongs to the Karkonosze National Park (KNP) and its buffer zone (Sudeten Mts, southern Poland). The Karkonosze Mts are under the influence of a suboceanic climate with a significant effect from the continental air masses. The mean annual temperature ranges from 7.9 °C in the foothills to 0.4 °C on Mt Śnieżka and the mean annual precipitation increases from approx. 700–750 mm in the foothills to about 1500 mm in the upper parts (Sobik et al. 2013). The vegetation is zonal from the foothills (up to 500 m a.s.l.); the lower forest montane belt (500–1000 m a.s.l.), which includes a fir-spruce mixed coniferous forest of the *Abieti-Piceetum* association (AP) and natural beech forests (F) *Luzulo luzuloidis-Fagetum* and small areas of *Hordelymo-Fagetum*; an upper forest montane belt (1000–1250 m a.s.l.), which has a subalpine reed grass spruce forest *Calamagrostio villosae-Piceetum* (CVP); a subalpine zone (1250–1450 m a.s.l.) and an alpine zone (1450–1602 m a.s.l.). There is also a part of the forest where the spruce *P. abies* was planted. Spruce is the most dominant tree followed by the beech *Fagus sylvatica* L., Scots pine *Pinus sylvestris* L., and others (Danielewicz et al. 2013). From 1960 to 1980, extensive atmospheric pollution, i.e., sulfur dioxide, nitrogen, and dust, which were contained in the atmospheric air as well as acid rain caused an ecological disaster that reached its maximum in the 1980s during which there was a massive dieback in the spruce stands, especially in the upper-mountainous spruce forests. The pollution damaged the leaves, which made them vulnerable to attack by insect pests and parasitic fungi. One

consequence of this phenomenon was a massive dieback of spruce trees (Fabiszewski and Wojtuń 1994; Stachurski et al. 1994). The contemporary threat to spruce is climate change, including increasing temperatures, strong winds and drought (Korzybski et al. 2013). In recent decades, foresters and conservationists decided to undertake revitalization programs of the forest ecosystems. Dead trees are felled and snags as well as uprooted trees are left in the forests in order to facilitate the natural regeneration of forests (Danielewicz et al. 2013; Staniaszek-Kik et al. 2016, 2019).

2.2 Data collection and ecological indices

The study area was examined for the presence/absence of coarse woody debris (CWD) including logs and 180 permanent plots (10 m × 10 m) were established using a random-stratified sampling, which covered all types of forests as well as the protected and managed parts of the area. Finally, the following classes were obtained CVP [206 logs], AP [102], F [205], PA_PF [117], protected areas [423], and managed areas [206] (Chmura et al. 2016). Logs, which were defined as pieces of CWD that were longer than 0.5 m and with a lower diameter that was greater than 10 cm, were included in the present study (Staniaszek-Kik et al. 2016). The number of logs per a plot ranged from 1 to 10. The logs belonged to spruce (447 logs), beech (155), birch *Betula pendula* Roth (20), rowan *Sorbus aucuparia* L. (3), larch *Larix decidua* Mill. (2), and two were unidentifiable. A total of 629 logs that were colonized by bryophyte species (29 liverworts, 68 mosses) and/or 56 lichen species were analyzed to determine the species composition and cover abundance of a species. The percentage cover of each species on each log was estimated visually using the following scale: 1, 2, 4, 8, 10 and then at 10% intervals (10, 20...90). The nomenclature follows Klama (2006) for liverworts, Ochyra et al. (2003) for mosses and Fałtynowicz and Kossowska (2016) for lichens.

Two groups of environmental factors were included—the variables that are associated with the properties of a log and its location in a forest (Species identity of log, TreeCover—Tree canopy over a log, Adherence—degree of the adherence of a log to the forest floor, Decomposition—scale of decomposition, Area, BarkCover—cover of bark on a log, Length – length of a log, Moisture—moisture of a log). The second group were the climatic factors, i.e., the variables that are associated with altitude (m a.s.l.), slope, and exposure (ELEVINDEX) whereas the potential annual direct incident radiation, i.e., PADI R and approximate heat load, i.e., AHL, use a formula that incorporates the latitude (it applies only to 0–60°N), slope and slope aspect. The Ellenberg indicator values (EIV) for light (L), temperature (T), moisture (F), nitrogen (N), and soil reaction (R) were used as the habitat

associations of lichens, liverworts, and mosses (Ellenberg and Leuschner 2010). The EIV were computed as the cover-weighted means of all of the species (CWM) that were present on a log using the R package *FD* (Laliberté and Legendre 2010) and the presence/absence data, i.e., as arithmetic means. These were computed separately for lichens, liverworts, and mosses. Only species that were assigned to a specific value were included in the calculations. The species that were assigned x were excluded from the calculations. A detailed description of all of the variables is presented in Table 1.

2.3 Analysis of data

All of the statistical analyses and visualizations were performed using the R language and environment (R Core Team 2019). The relationship between the environmental factors and the EIV as well as the intercorrelations was examined visually using a principal components analysis (PCA). Prior to this, the analysis data were scaled, and function implemented in the *ade4* package; *dudi.pca* was used to run the PCA. The PCA graphs

were created using the *factoextra* package, which helps to show the contribution of a specific variable separately for each of the taxonomic groups. In order to select the most important factors among the studied environmental variables, we performed a random forest analysis (RF) based on Breiman's random forest algorithm (Breiman 2001) using the *randomForest* package (Liaw and Wiener 2002), which is a machine learning method that helps in the classification and regression models when there are a large number of predictors. It is a robust technique that can handle the non-normal distribution and collinearity of variables. We performed 500 regression trees for each of the EIV and selected the models that explained more than 30% of the variances (Dyderski et al. 2017). Prior to the RF analyses, the predictor variables were transformed using the Yeo-Johnson power transformations (Yeo and Johnson 2000) and then centered and scaled in order to reduce any skewness and to avoid the biases that might be associated with the uneven ranges among the variables using the *caret* package (Kuhn 2008). The results of the RF are presented for

Table 1 List and description of the environmental variables and Ellenberg indicator values

Code of variable	Description and source	Type
Characteristics of a log		
TreeCover	This was estimated visually based on the following scale: (1—30% of canopy cover; 2—30–40%; 3—40–60%; 4—60–80%; 5—> 80%)	Ordinal (1–5)
Adherence	Degree of adherence of a log to the forest floor (%)	Interval
Decomposition	Decomposition class of a log based on an eight-degree scale (Holeksa 2001)	Ordinal (1–8)
Area	Area of a log surface (m ²), which was calculated using the formula for a truncated cone	Interval
BarkCover	Cover of bark on a log (%)	Interval
Length	Length of a log (m)	Interval
Moisture	1—dry, completely dry to the touch; 2—intermediate, slightly perceptible moisture to the touch; 3—moist, water flows when pressure is applied	Ordinal (1–3)
SPRUCE	Species identity of a log (1—spruce, 0—not a spruce)	Binary (0,1)
Climatic factors		
ELEVINDEX	Value combined elevation (m a.s.l.), slope aspect and slope inclination (Ewald 2009)	Interval
PADIR	Potential annual direct incident radiation (McCune and Keon 2002)	Interval
AHL	Approximated heat load: $\ln(\text{RAD}, \text{MJ} \times \text{cm}^{-2} \times \text{year}^{-1})$ rescaled and folded about the NE = SW line (McCune, Keon 2002)	Interval
Ellenberg indicator values (Ellenberg and Leuschner 2010)		
L	Light	Ordinal (1–9)
T	Temperature	Ordinal (1–9)
F	Moisture	Ordinal (1–12)
R	Substrate reaction; acidity	Ordinal (1–9)
N	Nitrogen; nutrition	Ordinal (1–9)

‘importance plots’ and ‘partial dependence plots’. The former shows the hierarchy of the relative importance among the predictors (where the highest importance is scaled as 100%) and the percentage of the explained variances and the latter depicts the dependence for the most important predictors. The significance of the differences in the EIV among the taxonomic groups was analyzed using linear mixed-effect models (LLM), which were implemented in the *lmer4* package. In these LLM, a plot was regarded as a random effect due to the spatial dependence of the logs that were located within the same study plot. The significance of the models was determined using the *LmerTest* and *car* packages. For multiple comparisons among the taxonomic groups, the Tukey post hoc test was used via a procedure that was implemented in the *multcomp* package and the marginal means, i.e., the means with the excluded random effect were calculated using the *lsmeans* package. In order to examine the species diversity of the lichen, liverwort, and moss communities independent of the environmental factors, ordination analyses were performed using the *vegan* package (Oksanen et al 2019). The EIV were excluded from the ordination analyses because their values were derived from the species composition and therefore were not independent. The species identity of a tree was

included as the binary variable SPRUCE (1—spruce tree, 0—not a spruce). Prior direct ordination Detrended Correspondence Analysis (DCA) was run to determine the length of a gradient in order to select the redundancy analysis RDA or canonical correspondence analysis CCA. For the lichens and mosses, RDA was selected (canonical variant of PCA) because the gradients of the first axis were shorter than 2.0 SD units while for the liverworts, the SD values exceeded 3.0 and therefore CCA was run. For all of the direct ordination analyses, 999 iterations of the permutation test were performed. The pseudo-F (equivalent of the *F* statistic in permutational tests) and *p* value were computed. The variance inflation factor (VIF) was computed in order to exclude any redundant data that correlated with the other variable factors. Venn diagrams are also presented to show the variance partitioning among the log properties, climatic factors, and the EIV to explain the drivers of the species composition.

3 Results

3.1 Relationships between the EIV and environmental factors

The PCA showed some common patterns for each of the taxonomic groups: lichens, liverworts and mosses

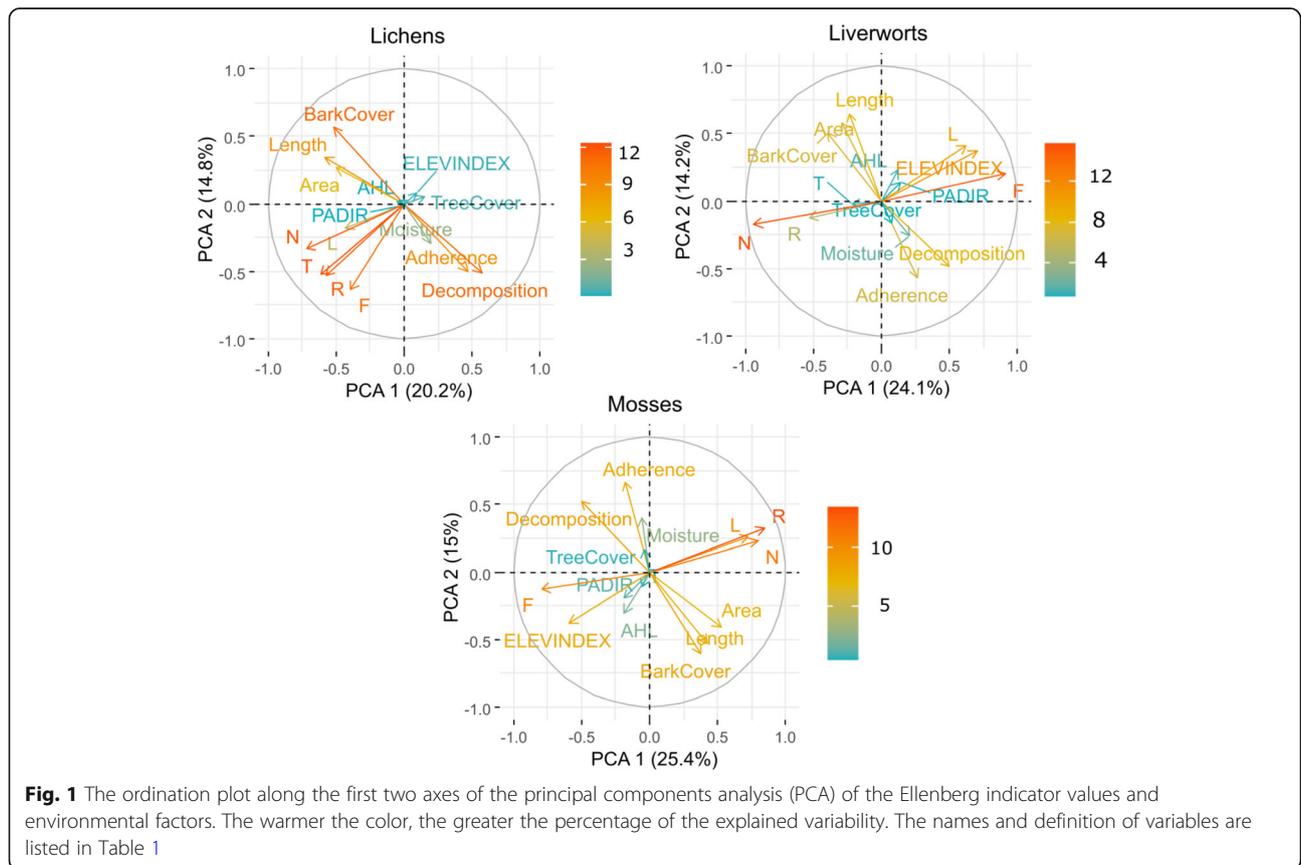


Fig. 1 The ordination plot along the first two axes of the principal components analysis (PCA) of the Ellenberg indicator values and environmental factors. The warmer the color, the greater the percentage of the explained variability. The names and definition of variables are listed in Table 1

(Fig. 1). The climatic factors ELEVINDEX, AHL, and PADIR were usually grouped together, and the log properties that indicated the intensity of decay, i.e., decomposition, moisture, and adherence tended to group together as well. The log features that are indicators of slow decay, i.e., BarkCover, area, and length were also closely associated. As far as the EIV are concerned, the PCA revealed strong positive intercorrelations in the lichens, which were positively but weakly correlated with AHL and PADIR and negatively with ELEVINDEX and TreeCover. In the liverworts, EIV-F and EIV-L were positively correlated with ELEVINDEX whereas the EIV for nitrogen (EIV-N) and soil reaction (EIV-R) were correlated negatively with this variable. The EIV-L, EIV-R, and EIV-N in the mosses were negatively correlated with ELEVINDEX while EIV-F correlated positively.

According to the random forests, only moisture in the liverworts (EIV-F), nitrogen in the liverworts and mosses (EIV-N) and the substratum reaction (EIV-R) explained more than 50% of the variance. Around 30 to 40% of the explained variance in EIV-F and EIV-L, were reported for mosses. In the lichens, none of the EIV reached at least 30% (Table 2). Among the independent factors, in each case, the ELEVINDEX had the greatest importance

(Fig. 2) followed by the AHL and PADIR. In the liverworts and mosses, along with an increasing ELEVINDEX, the values of EIV-F increased while EIV-N decreased whereas the values of EIV-R and EIV-L decreased in the case of the mosses (Fig. 3). In the liverworts, along decomposition, EIV-F increased while EIV-N decreased (Fig. 3).

3.2 Comparison of the EIV among the taxa

There were significant differences in all EIV among taxa (Fig. 4). The type of calculation (cover-weighted vs arithmetic means) did not matter. The lichens were characterized by the highest values of EIV-L and EIV-T. The mosses had the highest EIV-F and EIV-R values whereas the lichens had the lowest. The liverworts had the highest value of EIV-N and the lowest was recorded for the lichens (Fig. 4).

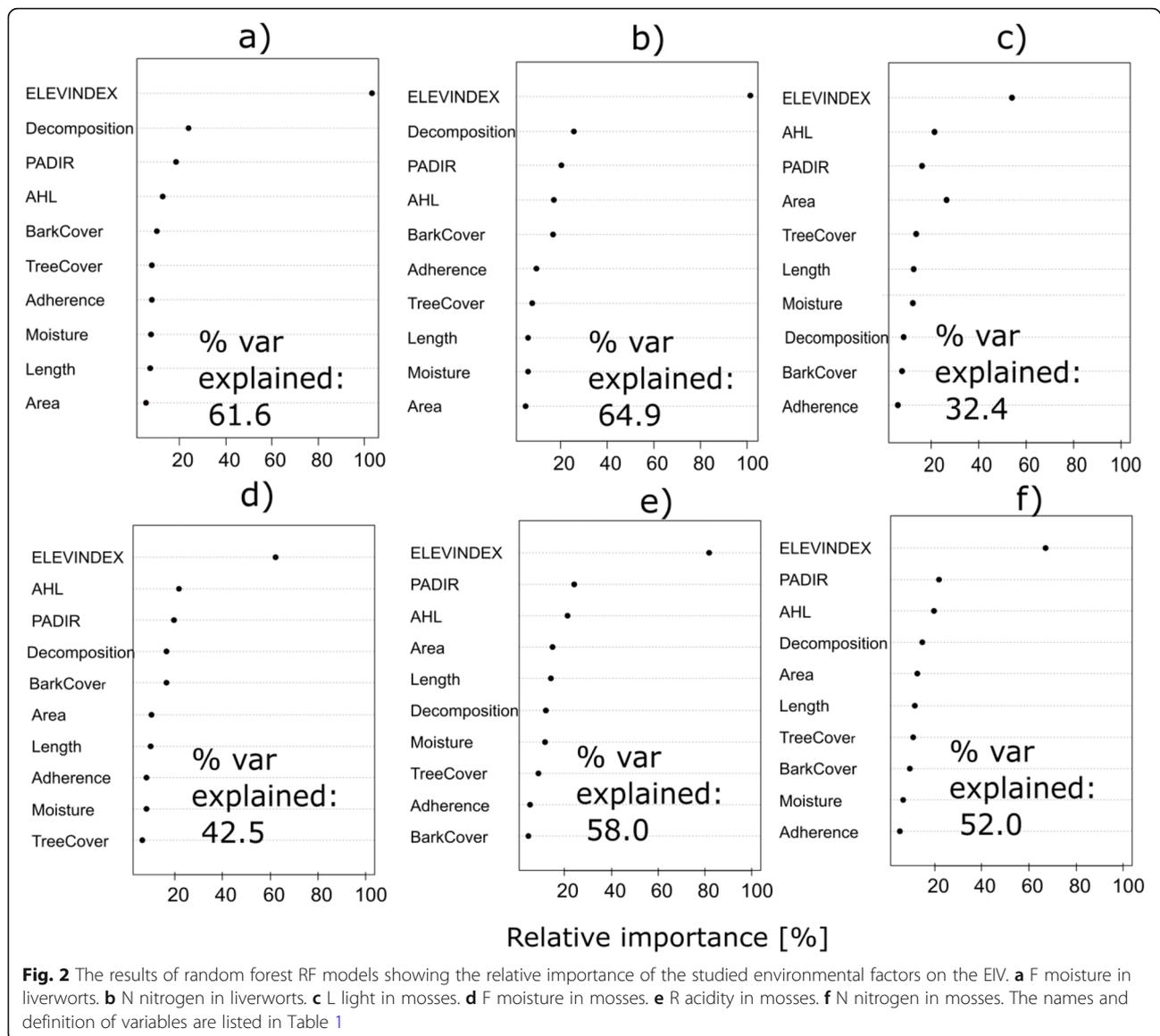
3.3 Ordination analyses

In all of the ordination analyses except the species identity of the liverworts, SPRUCE was located close to ELEVINDEX. According to the RDA, all of the variables except AHL explained the species composition for the lichens (Table 3). Species such as *Lecanora conizaeoides*

Table 2 The results of the random forest models

EIV	Statistic	Lichens	Liverworts	Mosses
Cover-weighted mean:				
Light	Mean of squared residuals	2.65594	0.2522	0.23332
	% Var explained	6.61	24.87	32.44
Temperature	Mean of squared residuals	4.55343	0.3585	0.5550
	% Var explained	1.63	1.15	8.04
Moisture	Mean of squared residuals	3.8875	0.1657	0.2657
	% Var explained	6.07	61.62	42.54
Soil reaction	Mean of squared residuals	1.23351	0.0894	0.4216
	% Var explained	3.28	13.26	57.39
Nitrogen	Mean of squared residuals	3.4508	0.6622	0.2561
	% Var explained	11.86	65.3	51.61
Arithmetic:				
Light	Mean of squared residuals	2.5082	0.2492	0.1788
	% Var explained	7.32	20.99	26.34
Temperature	Mean of squared residuals	4.58016	0.3622	0.2843
	% Var explained	2.26	1.17	1.74
Moisture	Mean of squared residuals	3.87035	0.1671	0.1947
	% Var explained	5.34	62.31	29.94
Soil reaction	Mean of squared residuals	1.1727	0.0824	0.3569
	% Var explained	1.22	15.64	57.55
Nitrogen	Mean of squared residuals	3.4551	0.6735	0.2133
	% Var explained	10.45	63.69	44.72

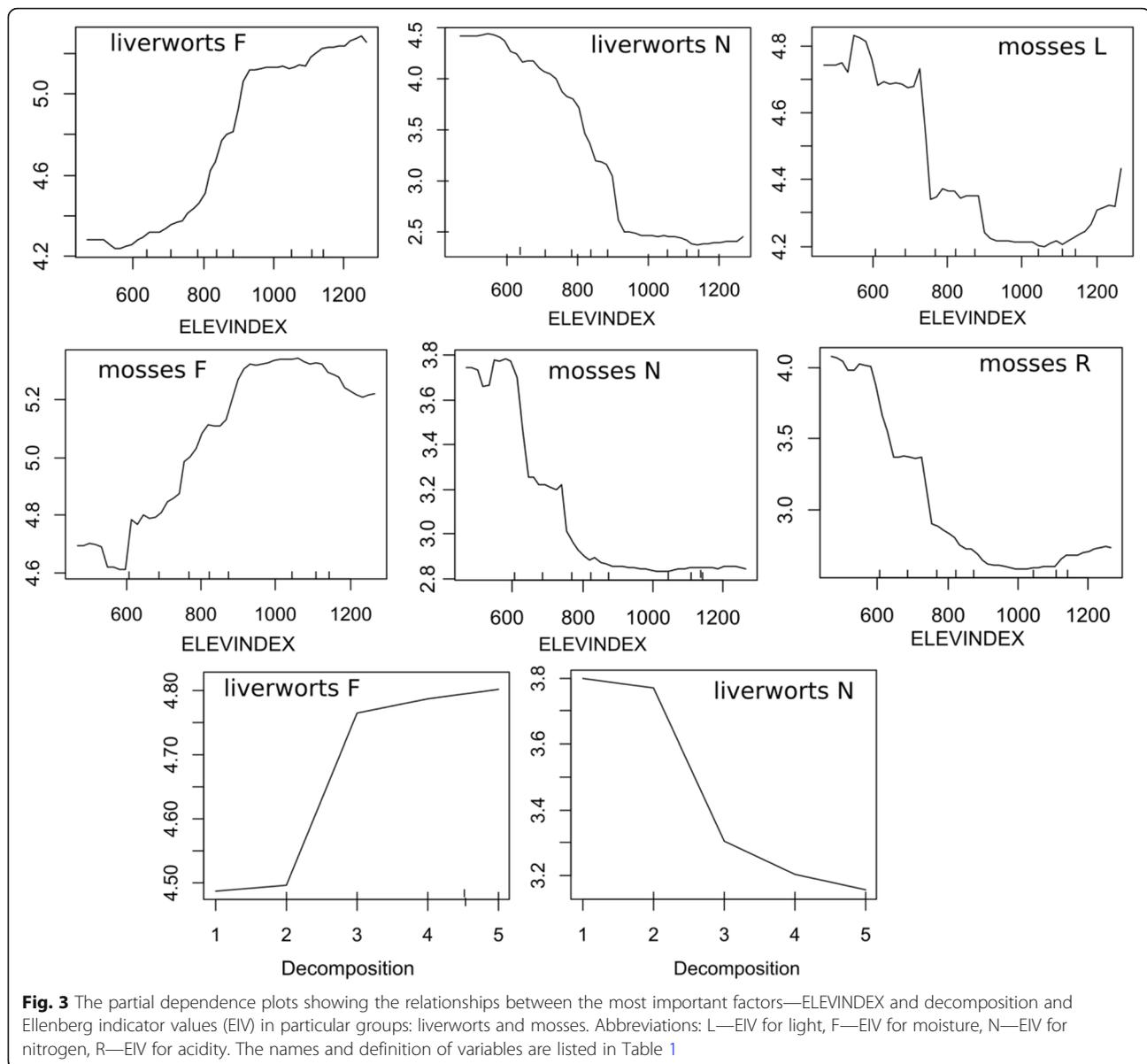
Explanations: EIV Ellenberg indicator value, L light, T temperature, F moisture, R acidity, N nitrogen, cwm cover-weighted mean, binary arithmetic mean



Nyl. ex Cromb were associated with high values of BarkCover and Length, while representatives of *Cladonia* genus were confined to higher values of Moisture. The majority of species, e.g., *Micarea prasina* Fr. and *Trapeziopsis flexuosa* (Fr.) Coppins and P. James preferred shade under higher values of TreeCover. *Cladonia digitata* (L.) Hoffm. and *Lepraria jackii* Tønsberg appeared to be dependent on ELEVINDEXX (Fig. 5). The permutation test in the CCA in the liverwort community indicated that the variables that were associated with the size of a log, area, and length did not explain the species diversity (Table 3). *Barbilophozia floerkei* (Web. and Mohr) Loeske, and *Calyptogea neesiana* (C. Massal. and Carestia) Müll.Frib. were located at higher values of ELEVINDEXX while *Cephaloziella rubella* (Nees) Warnst. was located close to Decomposition and *Ptilidium*

pulcherrimum (Weber) Vain. was located close to BarkCover all of which are driven by local factors (Fig. 5). The RDA, which was based on the moss species data, demonstrated that only AHL and Length were not significant factors (Table 3). *Dicranum scoparium* (L.) Hedw. and *Orthodicranum montanum* (Hedw.) Loeske were the most confined to Decomposition while *Brachytheciastrum velutinum* (Hedw.) Ignatov et Huttunen preferred logs with a higher surface area as did *Hypnum cupressiforme* Hedw. and *Herzogia seligeri* (Brid.) Z. Iwats (Fig. 5).

According to the variance partitioning, EIV contributed most to explaining the species diversity in the liverworts (35.6%) followed by the mosses (20.8%) while the lowest EIV was for the lichens (18.7%). The interaction of all three groups of



explanatory factors was weak—the highest in the liverworts (1.4%) while there was no interaction in the lichens (Fig. 6). In the lichens, the log traits explained more variance than the climatic factors in contrast to the liverworts and mosses for which the climatic factors explained more of the species variation than log traits (Fig. 6).

4 Discussion

4.1 Altitudinal factors vs local factors explaining the habitat requirements of species

The PCAs revealed that there were differences among the taxonomic groups in the relationships between the EIV and environmental factors. In the lichens, the EIV were strongly internally correlated while in the

liverworts and mosses, the EIV for nitrogen and acidity were especially intercorrelated. Such intercorrelations between the EIV might bias the results of the bioindication and could mean that the EIV do not perform well (Pakeman et al. 2008), which has been shown in other studies (Cornwell and Grubb 2003, Wagner et al. 2007). In the liverworts and mosses, the EIV for nitrogen and the substratum reaction were positively correlated with ELEVINDEX whereas the EIV for moisture was negatively correlated. The climatic factors ELEVINDEX, AHL and PADIR correlated with each other except for the lichens. The Moisture, Adherence and Decomposition were also intercorrelated, which is in line with the fact that they were factors that enhanced the rate of decomposition,

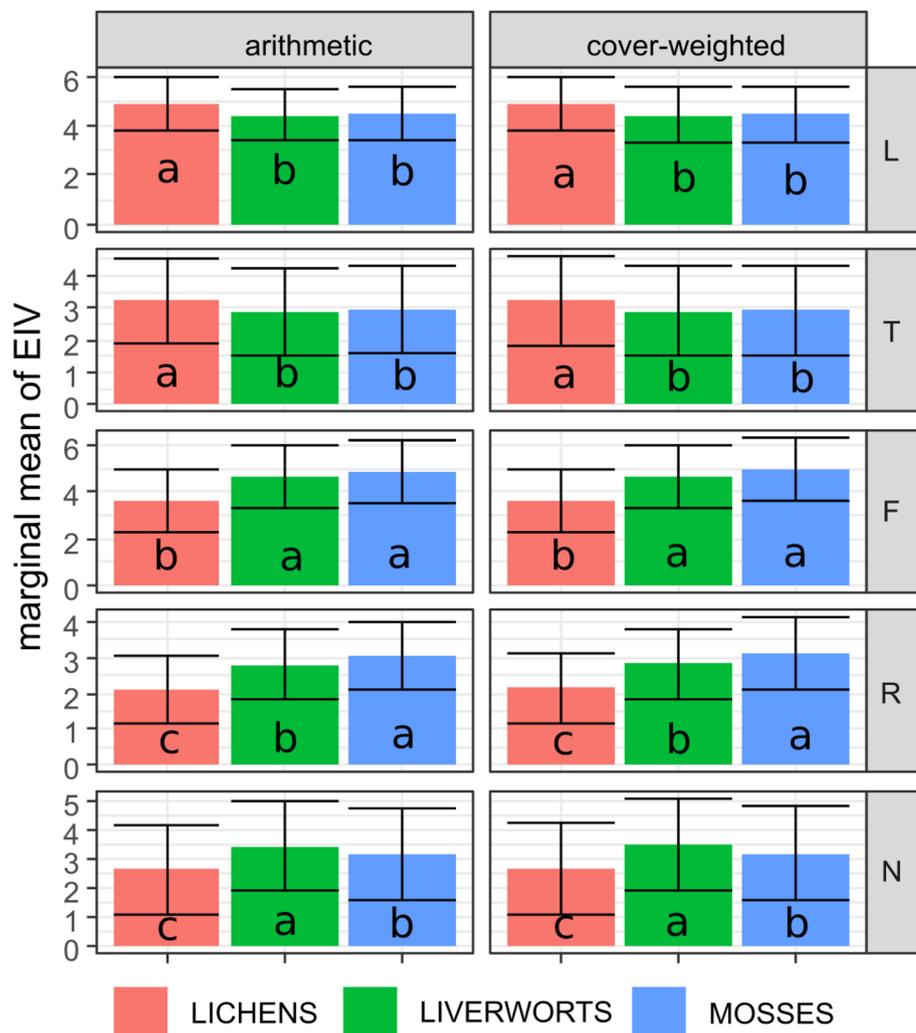
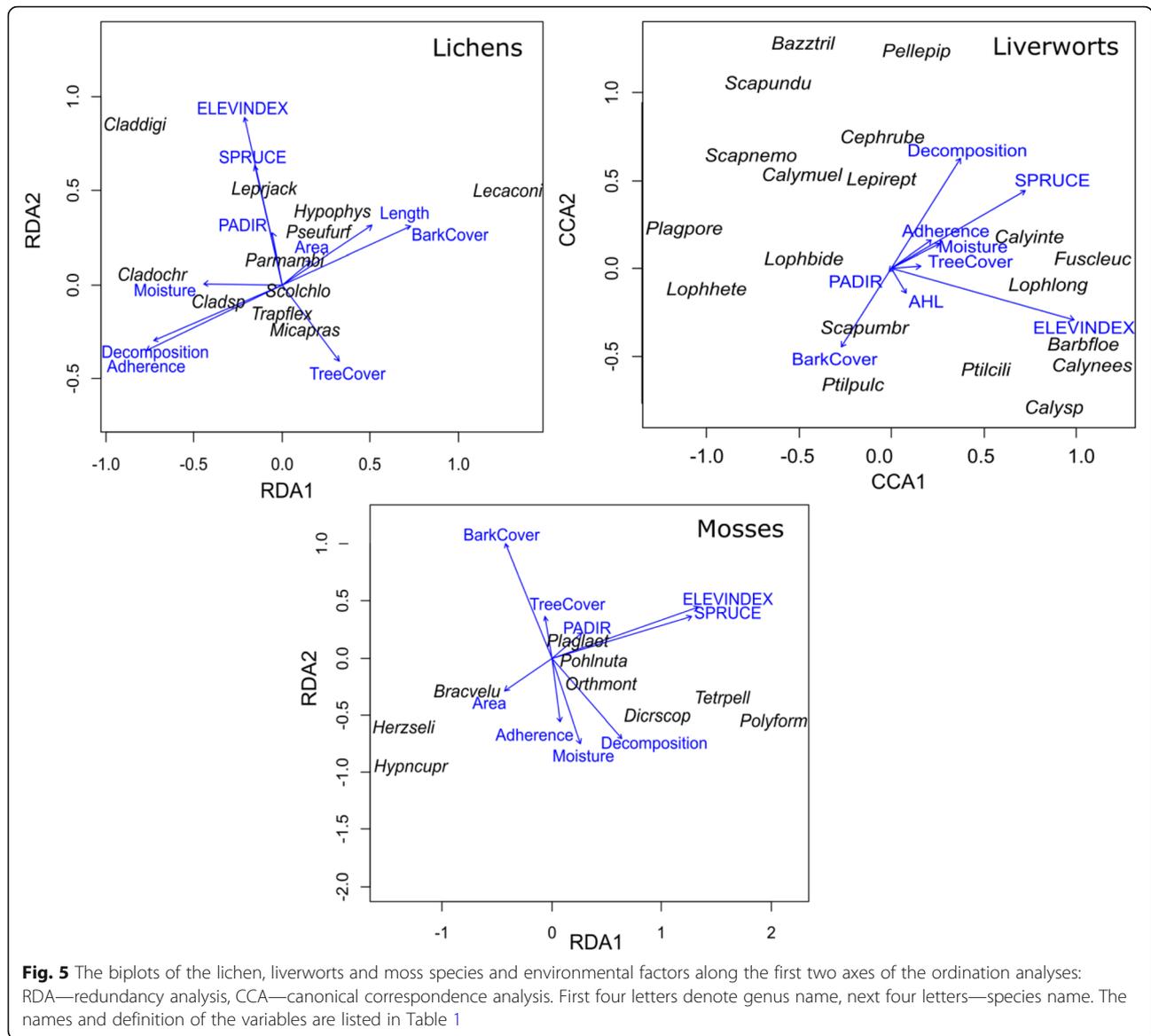


Fig. 4 Comparison of the marginal means of the Ellenberg indicator values (EIV) among the lichens, liverworts and mosses growing on coarse woody debris (based on the LMM models). The same letters mean no significant difference at $p < 0.05$. Abbreviations: L—EIV for light, T—EIV for temperature, F—EIV for moisture, N—EIV for nitrogen, R—EIV for acidity

Table 3 The significance of the environmental variables in the ordination space (RDA, CCA) in explaining the species communities based on 999 iterations of the permutation tests

Variable	Lichens (RDA)		Liverworts (CCA)		Mosses (RDA)	
	variance	pseudo-F	Chi-square	pseudo-F	Variance	pseudo-F
Decomposition	0.2525	13.8765***	0.1136	9.0847***	0.9376	23.7119***
BarkCover	0.1071	5.8858***	0.0297	2.3762**	0.2070	5.2354***
Length	0.0517	2.8431**	0.0169	1.3513 ns	0.0730	1.8461 ns
Adherence	0.0829	4.5554***	0.0341	2.7237***	0.2178	5.5082 ***
Moisture	0.0435	2.3921*	0.0300	2.3967***	0.1647	4.1655***
Area	0.0733	4.0299***	0.0175	1.4024 ns	0.3734	9.4431***
TreeCover	0.1309	7.1949***	0.0285	2.2794**	0.2219	5.6120***
PADIR	0.0302	1.6591 ns	0.0426	3.4079***	0.1280	3.2364**
ELEVINDEX	0.2231	12.2582***	0.4346	34.7517***	2.7474	69.4780***
AHL	0.0249	1.3673 ns	0.0298	2.3841**	0.0727	1.8379 ns
SPRUCE	0.0707	3.8840***	0.0666	5.3222***	0.4896	12.3812***

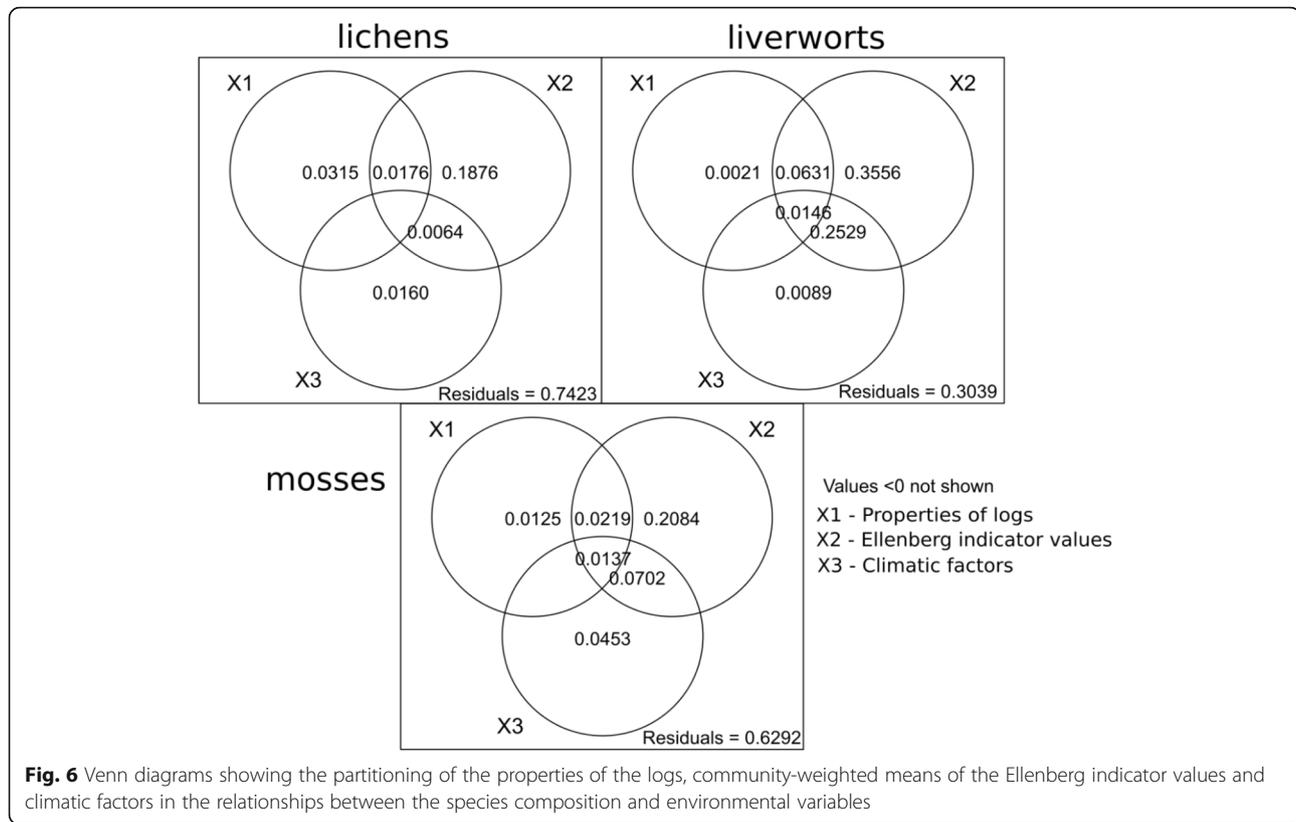
* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns non-significant



while Area, Length and BarkCover, which are proxies of the size and durability of CWD that were also internally correlated, were factors that slowed the decomposition rate (Harmon et al. 1986, Kushnevskaia and Shorohova, 2018).

The study indicated that altitude was the most important factor in the habitat requirements of the studied species. Other climatic factors such as AHL and PADIR were the next important variables (Fig. 2). Thus, the first hypothesis was supported by the obtained data. The analysis of the RF models enabled us to rank the magnitude of the relationship between the specific environmental variables and the EIV. According to Wolf (1993), altitude is a complex ecological factor that can explain most of the variations in bryophyte species data. Another important factor is the local topography (Bruun et al.

2006). In our study, the characteristics of CWD were topographic factors (substratum and neighborhood), which provided microclimate conditions (log moisture and a higher amount of light over fallen trees) and edaphic conditions (release of nutrients during CWD decay). The predominance of ELEVINDEX (combined altitude and slope) over the other analyzed variables was huge. These results also supported hypothesis 1 because ELEVINDEX is one of the climatic factors. Elevation was more important than the forest structure in driving the taxonomic and functional diversity in the lichens (Bässler et al. 2016). In a majority of models, other climatic factors such as AHL and PADIR were the next significant factors. Only in the liverworts was decomposition the second important environmental factor. Together with increasing decay, moisture also increased, which is



a pattern that is already known (Harmon et al. 1986; Edmonds 1991; Petrillo et al. 2015; Chmura et al. 2017), although nitrogen decreased. According to Přívětivý et al. (2017), during decay in both beech and spruce, the wet mass moisture increased from 47% to 69% and 36% to 62%, respectively. A similar pattern was revealed for nitrogen in epixylic vascular plants (Chmura et al. 2017). Despite the documented evidence of the release of nitrogen compounds during decay, it does not lead to appearance of more nitrogen-demanding species. According to Laiho and Prescott (2004), CWD does not contribute much to the N and P cycling in forests because these elements are in forms that are weakly available for plants. In addition, as the substratum becomes more unstable, many other factors can play roles. We expected that altitude would be positively correlated with light due to more thinned tree stand of spruce at a higher altitude compared to the beech forest while it would be negatively correlated with temperature (hypothesis 2). Although the PCA suggested such a pattern in the liverworts, in the mosses, it was the reverse and was also a stronger trend, which was shown by the RM model. This difference between the liverworts and mosses was probably the result of competition or a shift in the altitudinal distribution patterns between the two groups. Bruun et al. (2006) showed that the mean liverwort richness and their relative contribution to the total richness

appeared to increase with altitude, whereas for mosses this trend was very weak. Because spruce is the dominant tree at higher altitudes, and beech occurs in the lower regions, Goia and Gafta (2019) showed that there might be differences in the bryophyte preference for spruce vs beech. According to the Venn diagram, the EIV best explained the species composition, which is obvious because this is an example of circular reasoning and therefore is not important. The contribution of the log properties and climatic factors is much more noteworthy. Only in the mosses did the latter explain more than the properties of the logs while in the remaining groups, it was the reverse. In turn, in the liverworts, the percentage of the explained variance by the independent variables was very small. Although the highest percentage was shown by the EIV, in this case, it was rather an artifact and should be treated with caution. What is interesting is that the values of the unexplained variance varied between 74% in the lichens and 30% in the liverworts, which indicates that not all of the possible factors that control species composition were considered.

4.2 Comparison of the habitat requirements of epixylic lichens and bryophytes and the usefulness of the EIV for deadwood

The obtained data and their analyses showed that the EIV relative to a limited species pool of epixylic lichens

and bryophytes can be applicable. There were significant differences among the taxonomic groups for each of the EIV; however, there were no differences between the cover-weighted and arithmetic means, which proved that the method of computation did not matter. The lichens turned out to be the most light-demanding and thermophilus species (support for hypothesis 3). Moreover, species such as *Lecanora conizaeoides* and *Cladonia coniocrea*, which were present in the study, were also reported to be sensitive to light availability by Jüriado et al. (2009), which was also expressed using the Ellenberg indicator values. The mosses followed by the liverworts were characterized by the highest value of moisture compared to the other taxonomic groups (support for hypothesis 3). Other studies have shown that because bryophytes are sensitive to fluctuations in the air humidity and cannot cope with water loss, they have evolved physiological and anatomical mechanisms to absorb water (During and van Tooren 1990; Vanderpoorten and Engels 2002; Ingerpuu et al. 2019; Spitale 2016). The EIV for the soil reaction can be linked to the pH of the tree bark. Bark acidity is believed to have the greatest impact on the composition of lichen species (Löbel et al. 2006; Jüriado et al. 2009). The lichens were more frequent and abundant in the upper forest montane zone and their percent cover increased along with altitude, especially on spruce logs compared to beech logs (Staniaszek-Kik, Stefańska 2012). Spruce is an acid bark tree, i.e., pH 3.4–4.0 (Marmor and Randlane 2007), and the litter on the forest floor in spruce forests is characterized by a higher acidity, which might explain the lowest values of the EIV for soil reaction in the lichens. Lichens can be sensitive to bark pH; however, although it varies among trees, their total cover generally decreases with an increase in the pH of the bark (Jüriado et al. 2009). Jüriado et al. (2009) also stated that bark pH is higher in the case of trees with a more extensive cover of bryophytes. Since Barkman (1958), it has been known that bryophytes generally favor a high bark pH and can even alter it, which might explain higher values of EIV for R in the case of the mosses and liverworts. The only EIV for which the liverworts had the highest mean value was nitrogen. In addition to high humidity, liverworts prefer high nutrient levels (especially nitrogen and phosphorus) as well as high soil moisture (Söderström 1988).

The applicability of the EIV has been confirmed in many types of habitats not only those of a natural origin, including forests (Szymura et al. 2014), grasslands (Wagner et al. 2007), bogs (Jagodziński et al. 2017), fens (Navrátilová et al. 2017) and colliery waste tips (Kompala-Bąba et al. 2020). A previous paper (Chmura and et al. 2017) provided evidence that the EIV of epixylic vascular plants also yielded reliable results. The specific EIV corresponded to the local or altitudinal environmental

factors. The present study demonstrated that epixylic bryophytes and lichens performed similarly to vascular plants. Despite the uncommon and untypical substratum that deadwood is, their EIV were linked with the environmental factors at various scales that ranged from the local scale, i.e., the properties of CWD to the larger scale, i.e., altitudinal gradient. Although the EIV of the epixylic flora of both plants and lichens might not improve bioindication using epigeic species, they are not useless because they do deliver predictable results (Ewald 2009).

5 Conclusions

The obtained results demonstrate that the altitude has a strong effect on the distribution of epixylic species in a montane region is of extreme importance, which has been shown in previous works for vascular plants (Staniaszek-Kik et al. 2014, 2016; Chmura et al. 2016). Undoubtedly, previous ecological disasters and reconstructions of forest stands have an impact on epixylic flora, especially liverworts and mosses, the majority of which are former epiphytes or early epixylics. The release of deadwood due to felling trees causes an additional substratum for bryophytes to form. On deadwood, bryophytes do not have to compete with vascular plants, which usually appear later at a more advanced decomposition stage. Future climate scenarios can pose a threat to mosses and liverworts. Some sources assume that the scenarios for climate change in Northern Europe suggest an increase in precipitation, which usually leads to an increase in air humidity (Ingerpuu et al. 2019). On the other hand, there are also hypotheses that in the future, droughts and warmer winters will occur. It could be hypothesized that, under a regime of increased droughts or warmer winters, some xerophytic bryophytes and lichens would increase in abundance at the expense of the more mesophytic species in forest communities (Bates et al. 2005). Bryophytes are very sensitive to environmental changes including climate change and they can be treated as indicators of future climate scenarios (Gignac 2001, 2011). Nevertheless, if bryophytes increase in species richness due to climate change including rising temperatures and drought or, conversely, to humidity, some bryophyte species will be endangered. Thus, the presence of a substratum, e.g., deadwood, which usually holds more moisture and provides different microclimatic conditions than those on the forest floor will be essential for the persistence of mosses and liverworts as well as for lichens in the future.

Acknowledgements

The authors thank two anonymous reviewers for helpful remarks on earlier version of the paper and Michele Simmons (Manassas, VA, USA) for language correction.

Code availability

Not applicable.

Authors' contributions

JZ and MSK conceived the ideas and designed methodology. MSK collected the data. DC developed the model, analyzed the data, and wrote the original version of manuscript. JZ and MSK reviewed and edited manuscript. MSK acquired the funding. All authors contributed to the final draft and gave final approval for publication.

Funding

Part of this work was supported by the Statutory Funds of the Institute of Environmental Protection and Engineering of the University of Bielsko-Biala and the Department of Geobotany and Plant Ecology, the University of Łódź, Łódź, Poland.

Availability of data and materials

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations**Ethics approval and consent to participate**

The authors declare that they obtained the approval of Karkonosze National Park for conducting the study—license number: 5/2003 (366).

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no competing interests.

Author details

¹Institute of Environmental Protection and Engineering, University of Bielsko-Biala, Willowa Str 2, 43-309 Bielsko-Biala, Poland. ²Department of Geobotany and Plant Ecology, University of Lodz, 90-136 Łódź, Poland.

Received: 11 September 2020 Accepted: 21 January 2022

Published online: 17 March 2022

References

- Barbé M, Fenton NJ, Bergeron Y (2017) Boreal bryophyte response to natural fire edge creation. *J Veg Sci* 28(5):915–927. <https://doi.org/10.1111/jvs.12552>
- Bardat J, Aubert M (2007) Impact of forest management on the diversity of corticolous bryophyte assemblages in temperate forests. *Biol Conserv* 139(1–2):47–66. <https://doi.org/10.1016/j.biocon.2007.06.004>
- Barkman JJ (1958) Phytosociology and Ecology of Cryptogamic Epiphytes. Van Gorcum, Assen, The Netherlands, p 628
- Bässler C, Cadotte MW, Beudert B, Heibl C, Blaschke M, Bradtka JH, Langbehn T, Werth S, Müller J (2016) Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. *Ecography* 39(7):689–698. <https://doi.org/10.1111/ecog.01789>
- Bates JW, Thompson K, Grime JP (2005) Effects of simulated long-term climatic change on the bryophytes of a limestone grassland community. *Global Change Biol* 11(5):757–769. <https://doi.org/10.1111/j.1365-2486.2005.00953.x>
- Breiman L (2001) Random Forests. *Mach Learn* 45(1):5–32. <https://doi.org/10.1023/A:1010933404324>
- Bruun HH, Moen J, Virtanen R, Grytnes JA, Oksanen L, Angerbjörn A (2006) Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *J Veg Sci* 17(1):37–46. <https://doi.org/10.2307/4096776>
- Chečko E, Jaroszewicz B, Olejniczak K, Kwiatkowska-Falińska AJ (2015) The importance of coarse woody debris for vascular plants in temperate mixed deciduous forests. *Can J Forest Res* 45(9):1154–1163. <https://doi.org/10.1139/cjfr-2014-0473>
- Chlebicki A, Żarnowiec J, Cieślirski S, Klama H, Bujakiewicz A, Zaluski T (1996) Epixylites, lignicolous fungi and their links with different kinds of wood. In: Faliński J.B., Muleńko W., Majewski T. (Eds.). Cryptogamous plants in the forest communities of Białowieża National Park. Functional groups analysis and general synthesis (Project CRYPTO 3). *Phytocoenosis* 8 (N.S.). *Archiv Geobot* 6:75–110
- Chmura D, Żarnowiec J, Staniaszek-Kik M (2016) Interactions between plant traits and environmental factors within and among montane forest belts: a study of vascular species colonising decaying logs. *Forest Ecol Manag* 379:216–225. <https://doi.org/10.1016/j.foreco.2016.08.024>
- Chmura D, Żarnowiec J, Staniaszek-Kik M (2017) Do Ellenberg's indicator values apply to the vascular plants colonizing decaying logs in mountain forests? *Flora Morphol Distrib Funct Ecol Plants* 234:15–23. <https://doi.org/10.1016/j.flora.2017.06.008>
- Cornwell WK, Grubb PJ (2003) Regional and local patterns in plant species richness with respect to resource availability. *Oikos* 100(3):417–428. <https://doi.org/10.1034/j.1600-0706.2003.11697.x>
- Danielewicz W, Raj A, Zientarski J (2013) Ekosystemy leśne [Forest ecosystems]. In: Knapik R, Raj A (eds) *Przyroda Karkonoskiego Parku Narodowego* [The nature of Karkonosze National Park]. Karkonoski Park Narodowy, pp 279–301 (in Polish)
- Diekmann M (2003) Species indicator values as an important tool in applied plant ecology – a review. *B Appl Ecol* 4(6):493–506. <https://doi.org/10.1078/1439-1791-00185>
- Dittrich S, Jacob M, Bade C, Leuschner C, Hauck M (2014) The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. *Plant Ecol* 215(10):1123–1137. <https://doi.org/10.1007/s11258-014-0371-6>
- During HJ, van Tooren BF (1990) Bryophyte interactions with other plants. *Bot J Linn Soc* 104(1–3):79–98. <https://doi.org/10.1111/j.1095-8339.1990.tb02212.x>
- Dyderski MK, Tyborski J, Jagodziński AM (2017) The utility of ancient forest indicator species in urban environments: a case study from Poznań, Poland. *Urban For Urban Green* 27:76–83. <https://doi.org/10.1016/j.ufug.2017.06.016>
- Dynesius M, Jonsson BG (1991) Dating uprooted trees: comparison and application of eight methods in a boreal forest. *Can J For Res* 21(5):655–665. <https://doi.org/10.1139/x91-089>
- Edmonds RL (1991) Organic matter decomposition in western United States forests. US Forest Service General Technical Report No. INT-280, 118–128
- Ellenberg H, Leuschner C (2010) *Vegetation Mitteleuropas mit den Alpen*. Ulmer, Stuttgart
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1991) *Zeigerwerte von Pflanzen in Mitteleuropa*. – Scr. Geobot. 18:1–248.
- Ewald J (2009) Epigeic bryophytes do not improve bioindication by Ellenberg values in mountain forests. *Basic Appl Ecol* 10(5):420–426. <https://doi.org/10.1016/j.baae.2008.09.003>
- Fabiszewski J, Wojtuń B (1994) Die begleitenden ökologischen Erscheinungen des Waldsterbenprozesses im Sudetengebirge. *Prace Inst Bad Leśnych B* 21: 195–210
- Fałtynowicz W, Kossowska M (2016) The lichens of Poland. A fourth checklist. *Acta Bot Siles Monogr* 8:3–122
- Gignac LD (2001) Bryophytes as indicators of climate change. *The Bryologist* 104(3):410–420. <https://www.jstor.org/stable/3244774>. [https://doi.org/10.1639/0007-2745\(2001\)104\[0410:BAIOCC\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2001)104[0410:BAIOCC]2.0.CO;2)
- Gignac LD (2011) Bryophytes as predictors of climate change. In: Tuba Z, Slack NG, LIR S (eds) *Bryophyte Ecology and Climate Change*. Cambridge University Press, Cambridge, pp 461–482
- Goia I, Gafta D (2019) Beech versus spruce deadwood as forest microhabitat: does it make any difference to bryophytes? *Plant Biosys* 153(2):187–194. <https://doi.org/10.1080/11263504.2018.1448011>
- Hackiewicz-Dubowska M (1936) La végétation des troncs putrescents dans la forêt vierge de Białowieża. *Comptes Rendus des séances de la Société des Sciences et de Lettres de Varsovie* 29:1–31 (in Polish with French summary)
- Hämäläinen A, Strengbom J, Ranius T (2020) Low-productivity boreal forests have high conservation value for lichens. *J Appl Ecol* 57(1):43–54. <https://doi.org/10.1111/1365-2664.13509>
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Lienkaemper GW (1986) Ecology of coarse woody debris in temperate ecosystems. In: *Advances in Ecological Research*, vol 15. Academic Press, pp 133–302
- Holeksa J (2001) Coarse woody debris in a Carpathian subalpine spruce forest. *Forstw. Cbl* 120(1–6):256–270. <https://doi.org/10.1007/BF02796097>
- Ingerpuu N, Kupper T, Vellak K, Kupper P, Söber J, Tullus A, Zobel M, Liira J (2019) Response of bryophytes to afforestation, increase of air humidity, and enrichment of soil diaspore bank. *Forest Ecol Manag* 432:64–72. <https://doi.org/10.1016/j.foreco.2018.09.004>
- Jagodziński AM, Horodecki P, Rawlik K, Dyderski MK (2017) Do understorey or overstorey traits drive tree encroachment on a drained raised bog? *Plant Biology* 19(4):571–583. <https://doi.org/10.1111/plb.12569>

- Jüriado I, Liira J, Paal J, Suija A (2009) Tree and stand level variables influencing diversity of lichens on temperate broad-leaved trees in boreo-nemoral floodplain forests. *Biodivers Conserv* 18(1):105–125. <https://doi.org/10.1007/s10531-008-9460-y>
- Klama H (2006) Systematic catalogue of Polish liverwort and hornwort taxa. In: Szwejkowski J (ed) An annotated checklist of Polish liverworts and hornworts. Szafer Institute of Botany. Polish Academy of Sciences, Kraków, pp 83–100
- Kompala-Bąba Agnieszka, Sierka Edyta, Dyderski Marcin K., Bierza Wojciech, Magurno Franco, Besenyei Lynn, Błorńska Agnieszka, Rys Karolina, Jagodziński Andrzej M., Woźniak Gabriela (2020) Do the dominant plant species impact the substrate and vegetation composition of post-coal mining spoil heaps? *Ecological Engineering* 143:105685. <https://doi.org/10.1016/j.ecoleng.2019.105685>
- Korzybski D, Mionskowski M, Dmyterko E, Bruchwald A (2013) Stopień uszkodzenia świerka jodły i modrzewia w Sudetach Zachodnich. *Sylwan* 157(2):104–112
- Kuhn M (2008) Building predictive models in R using the caret package. *J Stat Soft* 28(5):1–26. <https://doi.org/10.18637/jss.v028.i05>
- Kushnevskaia H, Shorohova E (2018) Presence of bark influences the succession of cryptogamic wood-inhabiting communities on conifer fallen logs. *Folia Geobot* 53(2):175–190. <https://doi.org/10.1007/s12224-018-9310-y>
- Laiho R, Prescott CE (2004) Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Can J Forest Res* 34(4):763–777. <https://doi.org/10.1139/x03-241>
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91(1):299–305. <https://doi.org/10.1890/08-2244.1>
- Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol Indic* 11(5):1027–1039. <https://doi.org/10.1016/j.ecolind.2011.02.004>
- Liaw A, Wiener M (2002) Classification and Regression by randomForest. *R News* 2(3):18–22
- Löbel S, Snäll T, Rydin H (2006) Species richness patterns and metapopulation processes – evidence from epiphyte communities in boreo-nemoral forests. *Ecography* 29(2):169–182. <https://doi.org/10.1111/j.2006.0906-7590.04348.x>
- Marmor L, Randle T (2007) Effects of road traffic on bark pH and epiphytic lichens in Tallinn. *Folia Cryptogam Estonica Fasc* 43:23–37
- McCullough HA (1948) Plant succession on fallen logs in a virgin spruce-fir forest. *Ecology* 29(4):508–513. <https://doi.org/10.2307/1932645>
- McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. *J Veg Sci* 13(4):603–606. <https://doi.org/10.1111/j.1654-1103.2002.tb02087.x>
- Merganičová K, Merganič J, Svoboda M, Bače R, Šebeň V (2012) Deadwood in forest ecosystems. *Forest Ecosystems—More than Just Trees*, In Tech Book, pp 81–108. <https://doi.org/10.5772/31003> Available from: <https://www.intechopen.com/books/forest-ecosystems-more-than-just-trees-deadwood>
- Müller J, Boch S, Blaser S, Fischer M, Prati D (2015) Effects of forest management on bryophyte communities on deadwood. *Nova Hedwigia* 100(3-4):423–438. https://doi.org/10.1127/nova_hedwigia/2015/0242
- Navrátilová J, Hájek M, Navrátil J, Hájková P, Frazier RJ (2017) Convergence and impoverishment of fen communities in a eutrophicated agricultural landscape of the Czech Republic. *App Veg Sci* 20(2):225–235. <https://doi.org/10.1111/avsc.12298>
- Ochyra R, Żarnowiec J, Bednarek-Ochyra H (2003) Census catalog of Polish mosses. Polish Academy of Sciences, Kraków, Poland
- Ódor P, van Hees AF (2004) Preferences of dead wood inhabiting bryophytes for decay stage, log size and habitat types in Hungarian beech forests. *J Bryol* 26(2):79–95. <https://doi.org/10.11179/037366804225021038>
- Ódor P, van Hees AFM, Heilmann-Clausen J, Christensen M, Aude E, van Dort KW, Piltaver A, Siller I, Veerkamp MT, 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 Rep* 51
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Michin PR, O'Hara RB, Simpson GL, Solyoms P, Henry M, Stevens H, Szoecs E, Wagner H (2019) Community Ecology Package. R package version 2.5–6 <https://CRAN.R-project.org/package=vegan>
- Pakeman RJ, Reid CL, Lennon JJ, Kent M (2008) Possible interactions between environmental factors in determining species optima. *J Veg Sci* 19(2):201–208. <https://doi.org/10.3170/2007-8-18353>
- Petrillo M, Cherubini P, Fravolini G, Marchetti M, Ascher-Jenull J, Schärer M, Synal HA, Bertoldi D, Camin F, Larcher R, Egli M (2016) Time since death and decay rate constants of Norway spruce and European larch deadwood in subalpine forests determined using dendrochronology and radiocarbon dating. *Biogeosciences* 13(5):1537–1552. <https://doi.org/10.5194/bg-13-1537-2016>
- Petrillo M, Cherubini P, Sartori G, Abiven S, Ascher J, Bertoldi D, Egli M (2015) Decomposition of Norway spruce and European larch coarse woody debris (CWD) in relation to different elevation and exposure in an Alpine setting. *iForest* 9(1):154–164. <https://doi.org/10.3832/IFOR1591-008>
- Přívětivý T, Baldrian P, Šamonil P, Vrška T (2017) Deadwood density and moisture variation in a natural temperate spruce-fir-beech forest. <https://doi.org/10.20944/preprints201705.0215.v1>
- Rondeux J, Sanchez C (2009) Review of indicators and field methods for monitoring biodiversity within national forest inventories. Core variable: Deadwood. *Environ Monit Assess* 164(1-4):617–630. <https://doi.org/10.1007/s10661-009-0917-6>
- Simmel J, Ahrens M, Poschlod P (2021) Ellenberg N values of bryophytes in Central Europe. *J Veg Sci* 32(1):e12957. <https://doi.org/10.1111/jvs.12957>
- Sobik M, Błaś M, Migala K (2013) Climate. In: Knapik R, Raj A (eds) The nature of the Karkonosze National Park. Karkonoski Park Narodowy, Jelenia Góra, pp 147–186 (In Polish)
- Söderström L (1988) Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in northern Sweden. *Nord J Bot* 8(1): 89–97. <https://doi.org/10.1111/j.1756-1051.1988.tb01709.x>
- Spitale D (2016) The interaction between elevational gradient and substratum reveals how bryophytes respond to the climate. *J Veg Sci* 27(4):844–853. <https://doi.org/10.1111/jvs.12403>
- Stachurski A, Zimka JR, Kwicień M (1994) Forest decline in Karkonosze Poland. I. Chlorophyll, phenols, defoliation index and nutrient status of the Norway spruce (*Picea abies* L.). *Ekol Pol* 42(3-4):286–316
- Staniaszek-Kik M, Szczepanska K (2012) Epixylic lichen biota in the Polish part of the Karkonosze Mts (West Sudety Mts). *Fragm Flor Geobot Polon* 19(1):137–151 (in Polish with English summary)
- Staniaszek-Kik M, Żarnowiec J, Chmura D (2014) Colonisation patterns of vascular plant species on decaying logs of *Fagus sylvatica* L. in a lower mountain forest belt: a case study of the Sudeten Mountains, (Southern Poland). *App Ecol. Environ Res* 12(3):601–613. https://doi.org/10.15666/aeer/1203_601613
- Staniaszek-Kik M, Żarnowiec J, Chmura D (2016) The vascular plant colonization on decaying logs of *Picea abies* in mountain forest belts: the effects of forest community type, cryptogam cover, log decomposition and forest management. *Eur J For Res* 135(6):1145–1157. <https://doi.org/10.1007/s10342-016-1001-8>
- Staniaszek-Kik M, Żarnowiec J, Chmura D (2019) The effect of forest management practices on the deadwood resources and structure in protected and manager forests during tree-stand reconstruction after dieback of Norway spruce. *Baltic For* 25(2):249–256. <https://doi.org/10.46490/vol25iss2pp249>
- Stathers RJ, Rollerson TP, Mitchell SJ (1994) Windthrow handbook for British Columbia forests. Research program working paper No. 9401 (No. MIC-94-07589/XAB).
- Szymura TH, Szymura M, Maciól A (2014) Bioindication with Ellenberg's indicator values: A comparison with measured parameters in Central European oak forests. *Ecol Indicators* 46:495–503. <https://doi.org/10.1016/j.ecolind.2014.07.013>
- Team RC (2019) R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna <https://www.R-project.org/>
- Vanderpoorten A, Engels P (2002) The effects of environmental variation on bryophytes at a regional scale. *Ecography* 25(5):513–522. <https://doi.org/10.2307/3683656>
- Vrška T, Přívětivý T, Janík D, Unar P, Šamonil P, Král K (2015) Deadwood residence time in alluvial hardwood temperate forests—A key aspect of biodiversity conservation. *For Ecol Manag* 357:33–41. <https://doi.org/10.1016/j.foreco.2015.08.006>
- Wagner M, Kahmen A, Schlumprecht H, Audorff V, Perner J, Buchmann N, Weisser WW (2007) Prediction of herbage yield in grassland: How well do Ellenberg N-values perform? *Appl Veg Sci* 10(1):15–24. <https://doi.org/10.1111/j.1654-109X.2007.tb00499.x>
- Wolf JH (1993) Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Ann Missouri Bot Gard* 80(4):928–960. <https://doi.org/10.2307/2399938>
- Yeo I-K, Johnson R (2000) A new family of power transformations to improve normality or symmetry. *Biometrika* 87(4):954–959. <https://doi.org/10.2307/2673623>

Żarnowiec J, Staniaszek-Kik M, Chmura D (2021) Trait-based responses of bryophytes to the decaying logs in Central European mountain forests. *Ecological Indicators* 126:107671. <https://doi.org/10.1016/j.ecolind.2021.107671>

Zielonka T, Piątek G (2004) The herb layer and dwarf shrubs colonisation of decaying logs in subalpine forest in the Polish Tatra Mountains. *Plant Ecol* 172(1):63–72. <https://doi.org/10.1023/B:VEGE.0000026037.03716.fc>

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

