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ORIGINAL ARTICLE

What factors influence colonization of lichens, liverworts, mosses and vascular plants on snags?

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Abstract

The dead standing trees i.e. snags are known as habitat for epiphytic and epixylic species including first of all lichens and bryophytes. The vascular plants are much rarer on this type of coarse woody debris (CWD). The eighty snags (CWD elements higher than 1.5 m) of Norway spruce *Picea abies* and beech *Fagus sylvatica* in the Karkonosze Mts. were examined for the presence of lichens, liverworts, mosses and vascular plants. The height of snags, their decomposition stage, cover of bark, diameter at breast height (DBH) as well as site conditions (elevation, slope and aspect, presence in forest community) were measured and noted. The percent cover of plants and lichens were estimated on each snag. Totally 99 taxa were recorded. There lichen species were dominant (44), followed by mosses (34), liverworts (13) and there were only 8 vascular plants. The total species richness varied from 1 to 22 taxa. The species composition growing on snags was subjected to canonical correspondence analysis and statistical analyses. They revealed that the species identity of snag is one of the most important factors influencing species composition. The number of species is positively correlated with DBH whereas decomposition stage, presence of bark, snag height are not significant factors. The species richness increases also with altitude what is connected with higher abundance of spruce snags. The occurrence of snags in this area is mainly associated with forest management practices in the past. Despite of some observed patterns in colonization of snags they are important habitat especially for lichens.

Keywords Biodiversity · Epixylic bryophytes · Forest condition · Standing deadwood

Introduction

Snags i.e. standing dead trees are along fallen trees (logs) and stumps component of so called coarse woody debris (CWD). In contradiction to the remaining CWD elements they are not so frequent and do not catch such high interest of researchers (Angers et al. 2012). The snags are known as important habitat for nesting birds (Zarnowitz and Manuwal 1985; Drapeau et al. 2009). Some of birds e.g. woodpecker *Picoides arcticus* prefer almost only standing deadwood (Bull 1983; Nappi et al. 2003; Bütler et al. 2004). They are important source of tree hollows and many hollow-nesting species have preference for cavities in standing dead trees (McElhinny et al. 2005). Snags also affect phytoclimate. Under canopy of snags forest floor is more insolated due to higher amplitudes of daily temperatures (Harmon et al. 1986). Snags sometimes are treated as a transitory state between living tree and fallen bole (Angers et al. 2012). They decompose slower than logs which are in close adherence to the forest floor and soil (Boulanger and Sirois 2006). Their decay is important process in forest ecosystem dynamics. During the decomposition many other organisms become to inhabit standing deadwood. These are invertebrates (e.g. beetles), and epiphytic and/or epixylic plant species. The vascular plants are much rarer on this type of CWD. The supply of snags in forest ecosystem depends on mortality rate of trees. Snags occur at all stages of forest growth, but the factors that lead to mortality usually change as the forest ages (Neitro et al. 1985; Greif and Archibold 2000). The causes of snag formation may include suppression and competition in

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the early age of forest, whereas in the elderly stadium insect damage, fungal diseases. The other possible anthropogenic factors are air pollution, fire and improper forest management (Greif and Archibold 2000). The snag survival i.e. a time since death of living tree till fall of snag, also depends on many factors. The time can be result of species identity, size of tree, exposure to wind, climate, soil type, stand history and disturbance regime (Harmon et al. 1986; Garber et al. 2005). Additionally exposure and slope are also significant factors that increase exposure to wind (Sefidi and Mohadjer 2010).

The situation of snags i.e. altitude, slope, inclination and surrounding vegetation, their abundance may have impact on the colonization of other organisms. In this study we observed two frequent tree species namely Norway spruce *Picea abies* and European beech *Fagus sylvatica* in montane forest in southern Poland. They were examined for the presence of lichens and plants including liverworts, mosses and vascular plants. We hypothesize that species identity of snag and its trait (e.g. decomposition, cover of bark, size) as well as extrinsic factors (light conditions, altitude) have important influence on species pool inhabiting it and distinct spatio-temporal patterns of colonization can be distinguished.

Material and methods

The study was performed in Karkonosze Mts. both in protected part (Karkonosze National Park) and in its buffer zone. In both parts forest management practices were aimed to improve forest health after dieback of spruce in 80s of twentieth century but they differ in intensity. At present, the average age of treestand in national park is estimated at 90 years, whereas in buffer zone - 68 years (Danielewicz et al. 2013). It has severe cold climate typical for montane area. The mean annual temperature ranges from 0.1 °C (at the top of Śnieżka Mt) to 6.9 °C in lower parts (Fig. 1). The vegetation is distributed along an altitude gradient: foothills (up to 500 m a.s.l.); a lower forest montane zone (500–1000 m), which includes patches of a fir-spruce mixed coniferous forest, the *Abieti-Piceetum* community; mixture of acidophilus beech forest i.e. the *Luzulo luzuloidis-Fagetum* community, and a fertile beech forest, the *Dentario enneaphylli-Fagetum* association (order *Fagetalia*) and planted *Picea abies* forest; an upper forest montane zone (1000–1250 m), where a subalpine reedgrass spruce forest – *Calamagrostio villosae-Piceetum* occurs (Staniaszek-Kik et al. 2016; Chmura et al. 2016). In total 180 study plots (10 m × 10 m) were randomly established within occurring types of forests. The cutting areas or places of massive dieback of trees were omitted. The plots were placed only in well-developed and healthy sites (Chmura et al. 2016) belonging to four aforementioned forest communities (Table 1). The snags that were studied occurred from 522 m a.s.l up to 1261 m (Table 1). There were 80 snags: 68 of spruce and 12 of beech. The height of snags, their decomposition stage (1–4 degrees in 8-degree class scale after Holeksa (2001), modified by Zielonka and Piątek (2004), percent cover of bark, diameter at breast height (DBH) in cm as well as site conditions: altitude (m a.s.l.), slope and shade (1–5 degree scale based on percent cover of tree canopy; Chmura et al. 2016), were measured and noted. The percent cover of plants and lichens were estimated visually (using 0,1,2,5 and 10% intervals). Number of species (S), Shannon-Wiener diversity index (H), and Pielou's evenness index (J) were calculated per each snag. Nomenclature of taxa follows Fałtynowicz and Kossowska (2016) for lichens, Klama (2006) for liverworts, Ochyra et al. (2003) for mosses and vascular plants after Tutin et al. (1993). The particular species was treated as generalist when was commonly occurred in many types of substratum available in a forest e.g.: mineral soil, base of trees, bark and wood of snags, whereas specialist it is species confined to deadwood and/or trunks of living trees. Specialists are rather epixylic and/or epiphyte species. The classification of species was based primary on our observation of the organisms and the knowledge from the literature.

All statistical analyses were conducted using R software (R Core Team 2018). To explore diversity of species composition of lichens, bryophytes and vascular plants growing on snags Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) was applied. This analysis was chosen due to long ecological gradients (more than 6.0 SD along first axis) using the algorithm implemented in R package *vegan* using (*decorana*) function (Oksanen et al. 2016). To assess the differences in species composition between two species of phorophytes a passive projection of vector representing species of snag was adopted according to (*vegan::envfit*) function. To examine influence of environmental factors on species composition constrained correspondence analysis (CCA) was performed by means of *vegan::cca()* function. In order to avoid intercorrelated factors variance inflation factor (VIF) was checked using function (*vegan::vif.cca*). Variance partitioning among altitude, snag traits (cover of bark, DBH, decay and height) and site conditions (slope, shade) were calculated and shown on Venn diagrams. For calculation of significance permutation test with 999 iterations was employed. The Wilcoxon sum rank test was performed to examine differences between spruce and beech snags. The Spearman rank correlation test was used to examine relationships between chosen variables.

Results

In total 663 floristic records and 99 taxa were recorded. There, lichen species were most numerous (44), followed by mosses (34), liverworts (13) and there were only 8 vascular plants (Table 2). Amongst lichens 18 species (40.9%) were specialist

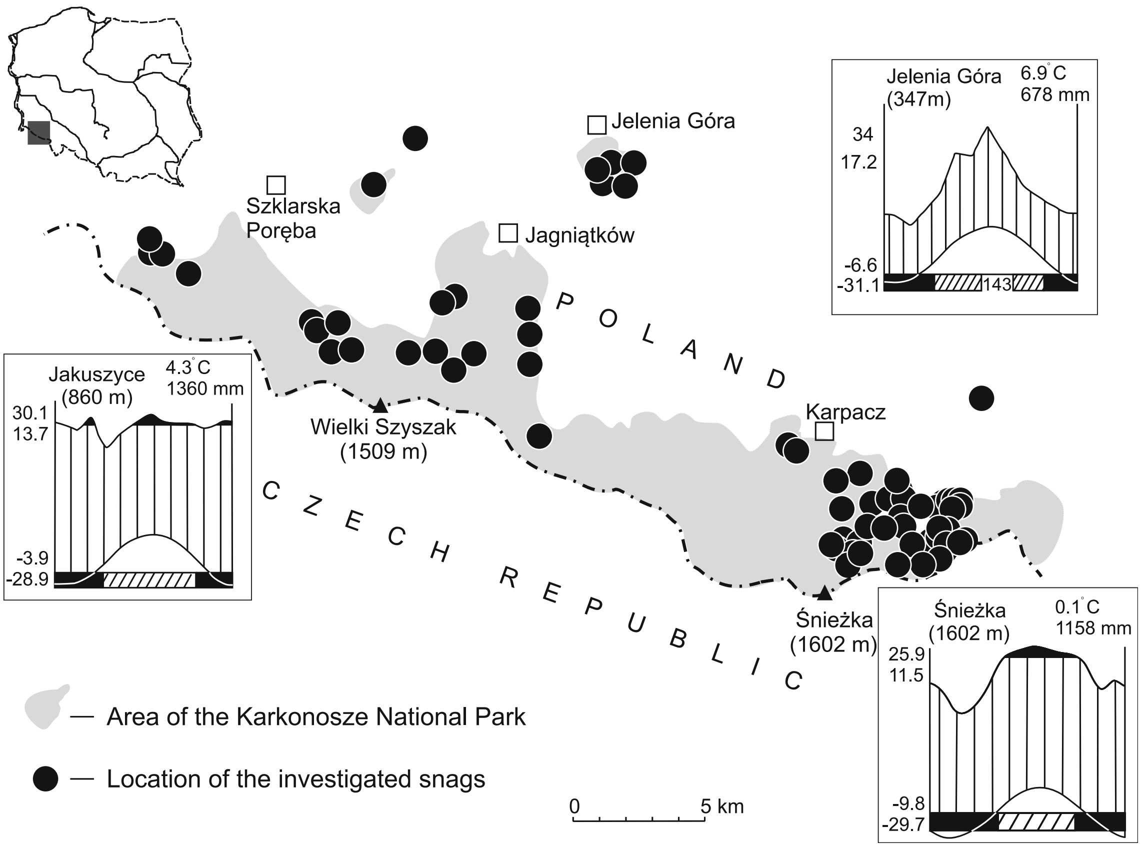

Fig. 1 The distribution of the investigated snags and climactic conditions of the area

and 26 generalists (59.1%), whereas in vascular plants 100% of species are generalists (Table 2). In liveworts 15.4% species are specialist and 84.6% are generalist, whereas in a group of bryophytes 11.8% are specialists and 88.2% are generalists. On snags the total species richness varied from 1 to 22 taxa. The majority of floristic records were collected from spruce snags (553) and from beech snags – 110. According to DCA the species identity of snag (*Picea abies* or *Fagus sylvatica*) is significant factor in terms of species composition ($r^2 = 0.31$, $p = 0.001$, DCA vector fitting). Detailed analysis that took into account cumulative cover of species of particular groups showed that on spruce snags significantly higher number of lichens cover was recorded, in turn on beech snags higher cover of mosses was reported (Table 3). There is no significant difference in species richness but value of Shannon-Wiener index and evenness index was higher on beech snags (Table 3). The canonical correspondence analysis (CCA, Fig. 2) demonstrated that one of the most significant factors

Table 1 The characteristics of site condition and traits of spruce and beech snags as well as number of particular plots in distinguished categories of forest (Wilcoxon sum rank test, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

	Beech				Spruce			
	Mean	SD	MIN	MAX	Mean	SD	MIN	MAX
Altitude [m a.s.l]	614.8	99.6	522	783	1023.7***	133.4	688	1261
Height [cm]	475.5	367.7	160.0	1350	528.3	353.9	150.0	1350
DBH [cm]	44.6***	15.8	23.0	70.	22.8	10.9	11.0	69
Decay [1–8 classes]	1*	0.7	1	3	2	0.8	1	4
bark cover [%]	65.4	30.0	20.0	95	56.1	30.7	0	100
	Managed		Protected		Managed		Protected	
CVP	–		–		27		23	
AP	–		–		8		3	
F	3		8		–		–	
PA_F	1		–		2		5	

CVP, *Calamagrostio villosae-Piceetum*; *AP*, *Abieti-Piceetum*; *F*, *Fagetalia*; *PA_F*, planted *Picea abies* forest

Table 2 The list of species recorded on snags

Name of species	Base of trees	Trunks of trees	Bark	Decaying wood	Specialist	Generalist
Liverworts:						
Barbilophozia attenuata	+		+	+		+
Blepharostoma trichophyllum	+		+			+
Calypogeia integristipula	+		+	+		+
C. neesiana	+		+			+
Cephalozia bicuspidata	+		+	+		+
C. lunulifololia	+		+	+		+
Lepidozia reptans	+			+		+
Lophocolea heterophylla	+	+	+	+		+
Lophozia ventricosa	+		+	+		+
Metzgeria furcata	+	+	+		+	
Plagiochila porelloides	+		+			+
Ptilidium pulcherrimum	+	+	+		+	
Scapania umbrosa	+		+			+
Mosses:						
Amblystegium juratzkanum	+		+			+
A. serpens	+	+	+	+		+
Brachytheciastrum velutinum	+	+	+	+		+
Brachythecium rutabulum	+	+	+			+
B. salebrosum	+	+	+	+		+
Campylidium calcareum	+		+			+
Ceratodon purpureus	+			+		+
Dicranella heteromalla	+			+		+
Dicranodontium denudatum	+		+	+		+
Dicranum scoparium	+	+	+			+
Herzogiella seligeri	+		+	+		+
Hypnum andoi	+		+	+		+
H. cupressiforme	+	+	+	+		+
H. cupressiforme var. *filiforme*		+	+		+	
H. pallescens	+		+			+
Mnium hornum	+		+	+		+
Orthodicranum montanum	+	+	+	+		+
Orthotrichum pumilum		+	+	+	+	
Paraleucobryum longifolium	+		+	+		+
Plagiomnium cuspidatum	+			+		+
Plagiothecium curvifolium	+		+	+		+
P. laetum	+	+	+	+		+
P. nemorale	+			+		+
P. platyphyllum	+			+		+
P. succulentum	+		+			+
Pohlia nutans	+	+	+	+		+
Polytrichastrum formosum	+		+	+		+
Pterigynandrum filiforme		+	+	+	+	
Rosulabryum moravicum	+		+			+
Sanionia uncinata	+		+	+		+
Sciuro-hypnum reflexum	+		+			+
S. starkei	+		+	+		+
Tayloria serrata	+		+		+	
Tetraphis pellucida	+	+	+	+		+
Lichens:						
Bacidina arnoldiana	+		+	+	+	
Biatora amaurospoda	+	+	+	+	+	
Candelariella reflexa		+	+		+	
C. vitellina	+		+		+	
Chaenotheca ferruginea		+		+	+	
C. trichialis		+	+		+	
Cladonia deformis	+		+			+
C. digitata	+		+	+		+
C. fimbriata	+		+			+
C. ochrochlora	+		+	+		+
C. polydactyla	+		+			+
Cladonia sp.	+		+	+		+
Dimerella pineti	+		+		+	

Table 2 (continued)

Name of species	Base of trees	Trunks of trees	Bark	Decaying wood	Specialist	Generalist
Graphis scripta		+	+		+	
Hypocenomyce caradocensis	+	+	+	+	+	
H. scalaris	+	+	+	+		+
Hypogymnia physodes	+	+	+	+		+
Lecania cyrtella		+		+	+	
Lecanora conizaeoides	+	+	+	+	+	
L. glabrata		+	+		+	
L. pulicaris		+	+		+	
Lecidella elaeochroma		+	+		+	
Lepraria elobata	+	+	+	+		+
Lepraria incana	+		+			+
L. jackii	+	+	+	+		+
L. lobificans	+		+	+		+
Lepraria sp.	+	+	+	+		+
L. toensbergiana	+		+			+
Melanelia subaurifera		+	+			+
Micarea botryoides	+	+	+			+
M. peliocarpa	+		+			+
M. prasina	+	+	+	+		+
Omphalina umbellifera	+			+	+	
Opegrapha varia		+	+		+	
Parmeliopsis ambigua		+	+	+		+
Pertusaria amara		+	+			+
P. leioplaca		+	+		+	
Placynthiella dasaea	+		+	+		+
P. icmalea	+		+	+		+
Platismatia glauca		+	+			+
Pseudevernia furfuracea		+	+	+		+
Scoliciosporum chlorococcum		+		+		+
Strangospora pinicola		+		+	+	
Trapeliopsis flexuosa	+	+	+	+		+
Vascular plants:						
Calamagrostis arundinacea	+			+		+
C. villosa	+			+		+
Deschampsia flexuosa	+		+			+
Dryopteris carthusiana	+		+			+
Fagus sylvatica	+			+		+
Oxalis acetosella	+		+	+		+
Senecio nemorensis ssp. *fuchsii*	+			+		+
Trientalis europaea	+		+	+		+
Vaccinium myrtillus	+		+	+		+

in terms of impact on species composition is altitude (pseudo-F = 4.77, $p = 0.001$), bark cover (pseudo-F = 1.72, $p = 0.008$), DBH (pseudo-F = 3.24, p = 0.001) and height of snags (Pseudo-F = 1.78, $p = 0.004$). The analyzed variables explain only 22.1% of variance in species composition (Fig. 3). Taking into account combined snags the number of species is positively correlated with DBH (rs = 0.39, $p < 0.001$), whereas decomposition stage, presence of bark, height of snag are not significant factors. The total species richness increases also with altitude (rs = 0.24, $p = 0.02$) (Fig. 4). Taking into account particular groups of species lichens were negatively correlated with altitude but in turn mosses were positively correlated. The cover of liverworts and mosses were negatively correlated with height of snags, whereas lichens were positively correlated with DBH. The bark cover was significant for lichens which were positively correlated with it (Table 4).

Discussion

Conditions of snags presence

In this study within study plots we found 80 snags and all of them were colonized by lichens and in some cases by plants as well. It is relatively small number when compared to all available snags. Per 100 m^2 plot from 0 to 5 snags were recorded. In temperate European forests the density of snags per hectare ranges from 4.0 (Perry and Thill 2013) to ca 100 (Marage and Lemperiere 2005). The low number of studied snags can affect results of found snag flora. For instance overall species richness of bryophytes depends on CWD abundance and diversity (Müller et al. 2015). The total species pool of plant and lichens inhabiting snags depend on observed number of snags in the area. Another factor that can have an impact on

Table 3 The descriptive statistics of combined percent cover of particular groups of plants and lichens on snags (Wilcoxon sum rank test, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

	Beech				Spruce			
	Mean	SD	MIN	MAX	Mean	SD	MIN	MAX
Lichens	10.9	15.7	1	50	32.3***	21.17	0	85
Liverworts	1.8	1.9	0	5	1.3	1.4	0	5
Mosses	12.5***	11.0	3	50	2.7	2.9	0	20
Vascular plants	0.5	0.9	1	3	0.4	0.9	0.2	5
Total cover	25.5	18.41	4.00	58.00	35.74	23.13	1.00	100.00
S	9.7	5.7	4	22	8.2	3.9	1	19
H	1.9**	0.5	0.8	2.6	1.4	0.6	0	2.5
J	0.9***	0.1	0.6	1	0.7	0.3	0	1

observation of species colonizing snags is species identity of tree. In the present study spruce snags prevailed. In the years of 1960–1980 massive decline of *Picea abies* stands were observed due to i.e. air pollution and fungal diseases. At present the main drivers of dying out of spruce is climate change and emissions of SO_2 and NOx (Jadczyk 2009; Modrzyński 2003; Korzybski et al. 2013). Aforementioned processes contributed to snag recruitment, however, the dominance of spruce in snags is first of all a result of the overall dominance of this tree in Karkonosze Mts. The percentage of spruce *Picea abies* in the treestand is estimated at 90% in this area including the lower montane belt where it occupies 85% of treestand despite it is natural habitat for beech forests (Danielewicz et al. 2013). The physicochemical properties of the bark and wood vary among tree species (Petrillo et al. 2015) therefore it can be expected that it can affect colonizing lichens and plants. Bark of beech is less acid (5.0–5.4) than spruce (3.6–3.9) (Fengel and Wegener 1983; Marmor and Randlane 2007).

Characterization of epixylic flora

Many of found species in this study are generally regarded as epixylic thus their presence is not surprising (Heilmann-Clausen et al. 2014). In total 24 species were classified as

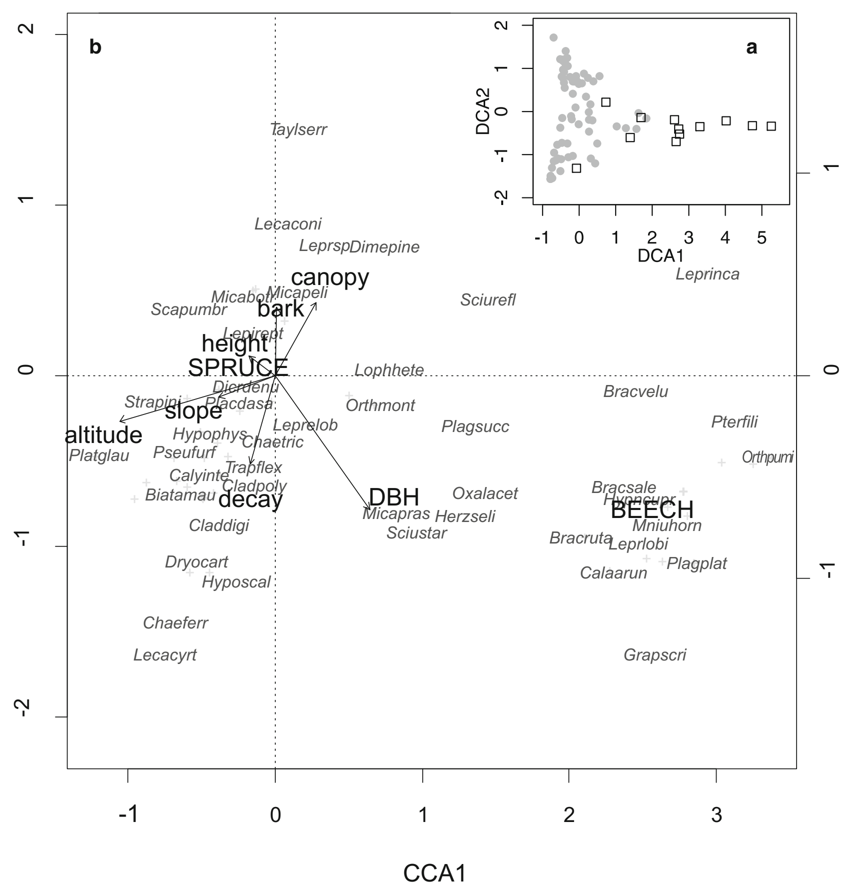

Fig. 2 The ordination of snags along the first two axes of Detrended Correspondence Analysis (DCA; $\lambda_1 = 0.74$ $\lambda_2 = 0.67$; grey circles - spruce snags, empty squares - beech snags). DCA explain 7.8% and 14.8% of species variance (**a**). Biplot of Canonical Correspondence Analysis (CCA, $\lambda_1 = 0.61$ $\lambda_2 = 0.43$) showing species and environmental factors on 80 snags. The first four letters indicate genus name the next four letters indicate species name. The most frequent species are shown (**b**)

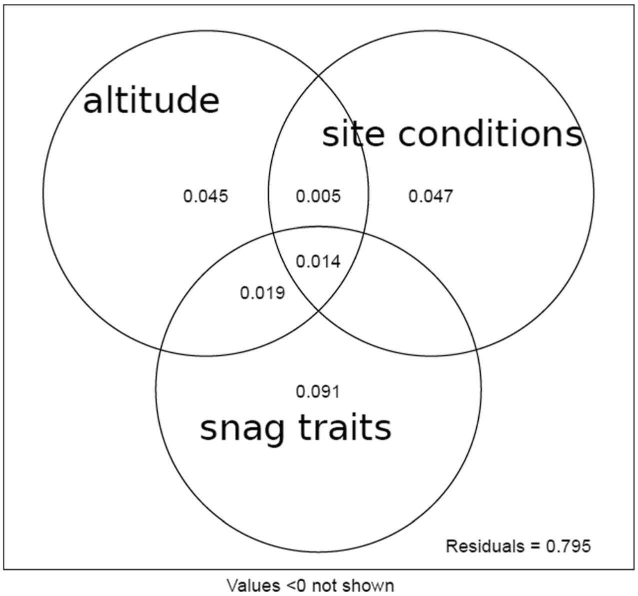

Fig. 3 The explained variance partitioning in three groups of factors. Abbreviations: Altitude (elevation a.s.l. m), site conditions: slope, shade, snag trails: height, DBH, bark cover, decomposition class

specialists. Amongst specialist lichens species as eg. *Chaenotheca ferruginea, Dimerella pineti, Graphis scripta, Hypocenomyce caradocensis, Lecanora conizaeoides, L. glabrata and L. pulicaris* are considered as epiphyte species but also occasionally found on deadwood. Majority of epixylic species are former epiphyte that survived after death of tree. A lot species encountered on permanent plots situated in healthy sites in Karkonosze National Park (Kossowska et al. 2007) were not found in this study. The lichen community is dominated rather by common and wide niche species. Liverworts are also usually quite common. These are *Metzgeria furcata* and *Ptilidium pulcherrimum* epiphytic liverworts, known to occur on bark of trees (Górski 2006). As regards mosses *Orthotrichum pumilum* and *H. cupressiforme* var. *filiforme* are known as obligate epiphyte species thus their preference to microhabitats associated with trunks, bark make them specialist species (Kürschner et al. 2012; Vanderpoorten et al. 2004). In turn, vascular plants are hardly to be regarded as specialists. Only few species are present on snags and in general on deadwood they most frequently are to be found on logs. For them deadwood an additional substratum (Harmon et al. 1986). The differences in species composition of colonizing species observed between two tree species are caused by several factors. One of them is altitude and environmental factors associated with it: temperature, moisture, epigeic vegetation. Total species richness of colonizing flora and DBH of snags increase with increasing altitude what is caused by shift of distribution of beech and spruce (Grytnes et al. 2006; Spitale 2016). In our study higher cover of bryophytes was observed on beech snags which generally are at lower elevation than spruce (Table 1). It contradicts the results by Goia and Gafta (2018) who claimed there was no consistent relationship between bryophyte preference to beech deadwood vs spruce deadwood and altitude. As lichens are concerned they were more frequent on spruce logs which mostly occurred at higher altitude. It is congruent with study by Vondrák et al. (2018) who observed the highest alpha diversity of lichens at the highest study plot in Carpathians. In turn, Ardelean et al. (2015) claimed that for lichen species on deadwood, the vegetation type had more significant effect on species richness than altitude, management, slope and aspect. In our case they were more abundant on spruce snags which were more frequent in coniferous forests what partially confirm it. We found that lichens in general had higher cover than mosses. In spruce snags mean cover was more than 32% whereas on beech snags about 10% - a little lower than cover of mosses. Apart from the dominance of lichens in terms of species richness (they consitute 40% of total snag flora) their higher abundance also

Fig. 4 The Spearman rank correlation analysis between DBH, altitude and number of species found on snags

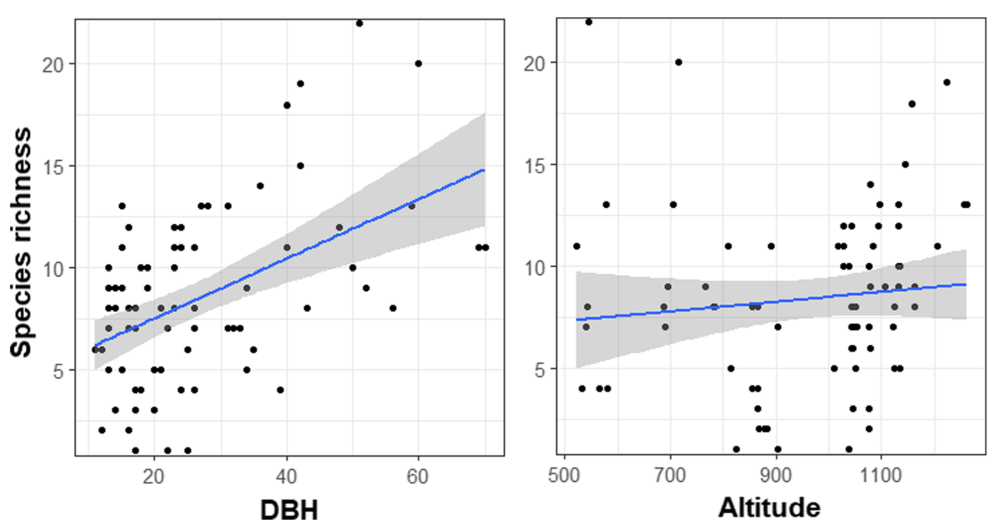

Table 4 The Spearman rank intercorrelations of particular groups and snag traits and altitude $*p < 0.05$, $**p < 0.01$, $***p < 0.001$, NS – non-significant)

	Altitude	Height	DBH	Decay	Bark cover	Lichens	Liverworts	Mosses	Vascular plants
Lichens	0.43***	NS	−0.14	NS	0.23*	–	NS	−0.36***	NS
Liverworts		−0.24*	NS	NS	NS	NS		0.30**	NS
Mosses	−0.36***	−0.34	0.47	NS	NS	−0.36***	0.30**	–	NS
Vascular plants	NS	NS	0.38***	NS	NS	NS	NS	NS	NS

confirm the fact that snags are preferred by lichens. In other work Machowska (2015) found 28 lichen species that 17 were found on spruce snags in Karkonosze National Park. Seven species were also reported in the present study e.g. *Cladonia digitata*, *Hypocenomyce caradocensis*, *H. scalaris*, *Lecanora conizaeoides*, *Lepraria jackii* whereas 32 were new e.g. *Cladonia fimbriata*, *Frutidella pullata*, *Pseudevernia furfuracea*.

Influence of snag properties on epixylic flora

Amongst CWD types lichens most frequently occur on snags (Humphrey et al. 2002 and literature cited therein). However, our results are not in concordance with their finding that lichens are more frequent on decorticate snags. In our case we took into account cover instead of species richness but despite this our result is the opposite because cover of lichens was positively correlated with bark cover (Samuelsson et al. 1994). For bryophytes, which combined number of liverworts and mosses amounted to 47, snags are not preferable type of substratum among CWD. Stumps harbour a greater species pool of bryophytes than logs and snags. The probable reasons are bigger moisture, higher surface area of contact with soil and higher avilaibility of microsites on hardwood and softwood with diversified decay (Müller et al. 2015). It is believed that epixylic mosses and liverworts are weak competitors and thus they have highest cover of debarked trunks because they avoid competiton with lichens on bark. One of the most frequent moss species is *Tetraphis pellucida* typical epixylic species which also frequentely occur on logs (Machowska 2015). We observed negative correlation between covers of mosses and lichens what is congruent with known pattern of colonization of lichens and bryophytes.

Other factors are important e.g. size of snag and decay. The mosses were positively correlated with DBH of snags but negatively with height of snags. In the case of living trees this would be impossible because usually height of tree increases with DBH but snags during decomposition can be broken. The higher preference of mosses for large diameter was observed in work by Humphrey et al. (2002) but for logs and stumps. Bearing in mind that many species occur both on snags and logs this pattern is also true for snags. Our results confirm that some liverworts species that are considered as late epixylics are associated with more advanced phases of decay. These are: *Blepharostoma trichophyllum*, *Cephalozia lunulifololia*, *Lepidozia reptans* (Söderström 1988). According to Machowska (2015) low fraction of liverworts can be encounterd on snags. She found only 3 species, whereas in this study there were 13.

The vascular plants was the most species-poor group comprising only 8 species. As many studies showed there are no mandatory epixylic vascular plants. For this group CWD is not important substratum. Much more number of species occur on logs but they have contact with soil and it is easier to colonize. Moreover, logs are more moist and can accumulate humus during decomposition enabling penetration by vascular plants (Harmon et al. 1986). Snags due to dry wood, large distance to ground, vertical position are unfavourable substratum for vascular plants to be colonized. Nevertheless, species that occur e.g. *Oxalis acetosella*, *Vaccinium myrtillus*, *Calamagrostis villosa* are frequntely observed on many types of CWD elements were also reported in other studies (Zielonka and Piątek 2004; Nowińska et al. 2009; Kirchner et al. 2011). The vascular plants showed preference for snags with larger DBH what is in with line with the same pattern for logs (Staniaszek-Kik et al. 2014; Chećko et al. 2015; Chmura et al. 2018). It is probably a result of higher diversity of niches (cavities, crevices, humus) and more stable conditions. Larger snags can decompose slower than smaller ones (Harmon et al. 1986).

Almost 20% of species variation is explained by studied factors and among them snag traits seem to play the most crucial role. The other important variables that can have an impact on shaping snag communities are associated with species pool of vascular plants growing on mineral soil, epigeic bryophytes and lichens inhabiting living trees. From these groups of organisms snag-inhabiting taxa recruit. Previous works (Staniaszek-Kik et al. 2014, 2016; Chmura et al. 2016) revealed importance of plant communities in colonization of logs by vascular plants. It can be expected that the same mechanisms take place.

Conclusions

The communities occurring on snags are rather species-poor what is reflected by impact of snag attributes on species composition. The neighborhood, especially factors related to altitude and vegetational gradient are important. Despite of some observed patterns in colonization of snags they are significant habitat only for lichens what can be confirmed by number of found species on snags and comparison of data from literature.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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