



Gastropod grazing of epiphytic lichen-dominated communities depends on tree species

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Abstract

Tree species differ in longevity, canopy structure, and bark texture, chemistry and water storage. Tree species-specific traits play a role in shaping epiphytic vegetation and likely influence the community assembly of organisms feeding on epiphytes. Lichenivorous gastropods, species with calcium-rich shells in particular, need calcium and likely occur more abundantly in and around tree species with high available calcium. We quantified gastropod grazing on the epiphytic lichens *Lobaria pulmonaria* and *Lobaria scrobiculata* transplanted to blocks of adjacent trunks of *Acer platanoides*, *Quercus robur* and *Tilia cordata*. We tested the hypothesis that tree species known to have more available Ca, exhibit more grazing damage on transplanted lichens than trees with lower Ca-availability. The grazing pressure was 1.6–1.8 times higher for lichen transplants on *Acer* and *Tilia* known to produce litter with easily soluble Ca than on *Quercus*, which binds Ca as oxalate. Trees with a high grazing pressure on transplants had greater natural abundance of *Lobaria virens* than of *L. pulmonaria*. Gastropods preferred *L. scrobiculata* to *L. pulmonaria*, evidenced by more observed grazing marks and greater measured biomass loss. We attribute this difference to the lower concentration of carbon-based secondary compounds in *L. scrobiculata*. However, the strength of the preference varied between the three tree species receiving lichen transplants and was strongest on *A. platanoides*, while gastropods on *T. cordata* grazed equal amounts of each transplanted lichen. In conclusion, tree species influenced grazing patterns of gastropods on epiphytic lichens. In addition to bark pH and other factors, we have shown that tree species-specific differences in grazing pressure play a role in shaping the epiphytic macrolichen community.

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Keywords: Community assembly; Herbivory; Lichenized fungi; *Lobaria*; Secondary compounds

Introduction

Gastropod preference for epiphytic lichen species depends on various lichen traits, for instance secondary compounds, growth form and nutrient quality (Lawrey 1983; Gauslaa 2005; Asplund, Johansson, Nybakken, Palmqvist, & Gauslaa

2010; Asplund & Wardle 2013). The presence of lichenivorous gastropods has the potential to modify lichen species composition (Asplund, Larsson, Vatne, & Gauslaa 2010; Frøberg, Stoll, Baur, & Baur 2011; Boch, Prati, & Fischer 2016). Asplund, Larsson et al. (2010) found that the most palatable *Lobaria* species (*Lobaria scrobiculata* and *Lobaria amplissima*) are restricted to higher portions of the tree trunks, where they experience lower grazing pressure by gastropods, while less palatable species (*Lobaria virens* in

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particular) often thrive under higher grazing pressure at the base of trunks.

Trees as habitats for epiphytes differ with respect to e.g. bark texture, bark chemistry, longevity, microclimate and hydrology, which play important roles in shaping epiphytic communities (Kuusinen 1996; Uliczka & Angelstam 1999; Thor, Johansson, & Jönsson 2010). Differences between tree species may also influence the community assembly of organisms feeding on epiphytes. For instance, there are many gastropod individuals beneath tree canopies producing litter rich in available forms of Ca (alkaline salts) such as *Acer* and *Tilia* (Wäreborn 1969; Nation 2007), whereas *Quercus* litter with Ca bound as poorly soluble calcium oxalate supports fewer gastropods. Some terrestrial gastropods climb trees to feed on epiphytic lichens and algae (Kerney & Cameron 1979). When soil-dwelling gastropod communities differ on the ground around the trunks of individual trees, tree-specific climbing gastropod communities are also likely to occur. We thus expect that tree-specific grazing pressure is an additional driver shaping tree species-specific variation in epiphytic vegetation.

In this study, we quantified gastropod grazing on the epiphytic lichens *Lobaria pulmonaria* and *L. scrobiculata* transplanted to trunks of *Acer platanoides*, *Quercus robur* and *Tilia cordata*. We used this set-up to test the following hypotheses: (i) grazing is higher on lichens transplanted to *A. platanoides* and *T. cordata* than to *Q. robur*. (ii) The strength of gastropod grazing preference varies between tree species. (iii) Trees with a high grazing pressure on transplants have different composition of epiphytic lichen vegetation than trees with less grazing.

Materials and methods

This study was conducted in a deciduous broadleaved forest, on a monzonite bedrock, dominated by *A. platanoides*, *Q. robur* and *T. cordata* (collectively composing 78% of the basal area) at Langangen, Telemark, S Norway (59°11'40"N, 9°83'45"E, 100–180 m a.s.l.). These forests supported spatially very rich occurrences of *L. pulmonaria* and *L. virens*; fewer trees supported *L. amplissima*, whereas *L. scrobiculata* did not occur in the studied stands, but was scarcely present in an extended area at few kilometres distances. Common understorey plants were *Hepatica nobilis*, *Anemone nemorosa*, *Convallaria majalis*, *Cardamine bulbifera*, *Ranunculus ficaria*, *Galium odoratum*, *Lathyrus vernus*, *Polygonatum multiflorum*, *Lysimachia europaea*, *Viola riviniana*, *Festuca altissima*, *Melica nutans*, *Ranunculus auricomus*, *Scrophularia nodosa* and *Silene dioica*.

We identified 23 blocks that each included similar-sized neighbouring trunks of one *A. platanoides*, one *Q. robur* and one *T. cordata*. Each block was inside a locally homogeneous stand with respect to its vegetation. The minimum distance between blocks was 100 m. For each tree, we measured DBH and bark pH. Bark pH was measured at three

spots on the trunk at breast-height with a flat-headed probe (ExStik PH100, Exttech Instrument Corporation, U.S.A) after spraying with 0.1 M KCl as described by Farmer, Bates, and Bell (1990). We collected soil in the root zone of each tree to a depth of 5 cm and estimated the basal area of tree trunks ($\text{m}^2 \text{ha}^{-1}$) with a relascope. We visually estimated cover of each foliose and fruticose lichen species as well as the total cover of crustose lichens and bryophytes on the two basal metres for each trunk. Due to time constraints, we were not able to identify bryophytes or crustose lichens to species. We collected one thallus of each macrolichen species per trunk for analysis of epiphytic lichen carbon to nitrogen ratio (C:N).

Dried soil samples (72 h at 50 °C) were sieved through a 2 mm mesh and ground to powder in a ball mill. 10 ml of the powder was shaken in 25 ml deionized water, left over night, and then shaken again before pH was measured with an inoLab pH 720 (WTW, Germany). Collected lichen samples were cleaned from tree bark and debris and ground to powder in a ball mill before C and N were analysed on 5 mg subsamples with an Elementar Vario MICRO cube (Elementar Analysensysteme GmbH, Hanau, Germany).

On 16 December 2015, *L. pulmonaria* and *L. scrobiculata* were collected from mixed populations of both species on oak trunks in a homogenous oak forest in Tysnes, Norway (59°98'85"N, 5°46'68"E, 25 m a.s.l.). The thalli were stored air-dry at –18 °C until the start of the experiment. We randomly selected 76 thalli of each species and weighed them air-dry. We calculated the air-dry to oven-dry ratio from 5 additional thalli weighed air-dry at the same time as the transplants, then dried them at 70 °C for 48 h before dry mass (DM) was recorded. On 19–22 July 2016, we transplanted one thallus each of *L. pulmonaria* and *L. scrobiculata* to each selected trunk in every block. The thalli were sewn onto nylon nets that were stapled onto the trunks at breast height using plastic staples (Takkurat® Dr. Gold & Co. KG, Nürnberg, Germany) following Asplund, Larsson et al. (2010). The average DM of the thalli was 0.28 ± 0.01 g with no significant difference in DM at start between the two species ($t=0.32$, $P=0.376$, t -test). We harvested the transplants on 1–2 October 2016, dried and weighed them as described above. The loss of biomass was ascribed to gastropod grazing due to the characteristic grazing marks (Baur, Fröberg, Baur, Guggenheim, & Haase 2000). Grazing preference was calculated as the amount (DM) consumed of the lichen transplant of interest divided by the total amount (DM) consumed of both lichen transplants following Lockwood (1998).

In order to quantify carbon-based secondary compounds (CBSCs), the transplants were ground to powder with a ball mill. Approximately 20 mg lichen powder was extracted in 1.5 ml acetone two times for 30 min and then 30 min in 1.5 ml methanol. The combined supernatants were evaporated and re-dissolved in 1000 μl methanol. The extracted compounds were quantified by HPLC with an ODS Hyper-sil column, 50×4.6 mm using 0.25% orthophosphoric acid and 1.5% tetrahydrofuran in Millipore water (A) and 100% methanol (B) as mobile phases at 2 ml min^{-1} , and UV-

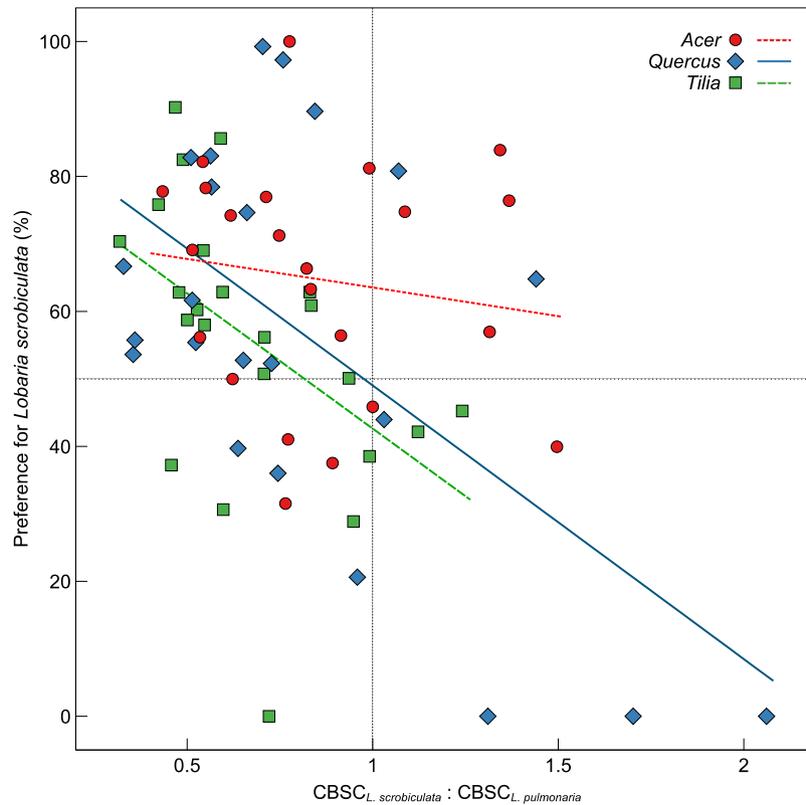


Fig. 1. Preference of *Lobaria scrobiculata* over *L. pulmonaria* – transplanted to *A. platanoides*, *Q. robur* and *T. cordata* – in relation to the ratio of carbon-based secondary compound concentration in *L. scrobiculata* and in *L. pulmonaria*.

detection at 245 nm, following Nybakken, Asplund, Solhaug, and Gauslaa (2007). Compound identification was based on retention times, online UV spectra and co-chromatography of commercial standards of usnic acid and stictic acid.

Statistical analysis

We used linear mixed effects models, using block as a random factor, to test for the effect of (i) lichen transplant species and tree species on percent grazing, (ii) tree species on soil pH and community-weighted means of N and C:N, (iii) tree species and DBH on bark pH. We calculated community-weighted average values of N and C:N for each tree following Garnier et al. (2007) and Fortunel et al. (2009):

$$\text{trait}_{\text{weighted}} = \sum_{i=1}^n p_i \times \text{trait}_i$$

where p_i is the cover of species i as a proportion of the total cover of all lichen species, and trait_i is the trait value (N or C:N) of species i .

The community composition of epiphytic lichens was visualized using non-metric multidimensional scaling (NMDS) on the basis of a Bray–Curtis distance matrix using the metaMDS function in the R package vegan (Oksanen et al. 2016). Total grazing, soil pH and bark pH were fitted as vectors onto the NMDS ordination using the function envfit

Table 1. Linear mixed effects model testing for the effect of tree species and for the ratio between the concentration of carbon-based secondary compounds (CBSCs) of *Lobaria scrobiculata* and of *L. pulmonaria* on the preference for *L. scrobiculata*. Numbers in bold represent significant effects at $P < 0.05$.

	X^2 (P)
Tree species	6.0 (0.049)
CBSC _{LS} :CBSC _{LP}	18.5 (<0.001)
Interaction	3.6 (0.168)

(Oksanen et al. 2016) and 999 permutations. We used the ordiellipse function (Oksanen et al. 2016) to plot the 95% confidence intervals (CI), based on standard error, of group scores for each of the three tree species onto the NMDS ordination. All analyses were performed in R 3.2.5 (R Core Team 2018).

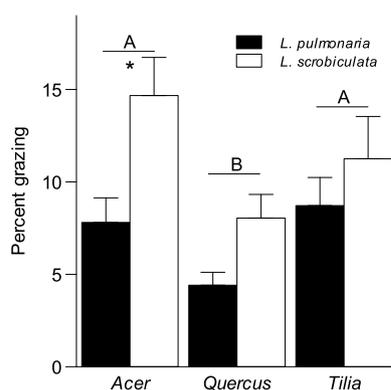
Results

Gastropods showed a higher preference for *L. scrobiculata* than for *L. pulmonaria* (Fig. 1, Table 1). In most trees (see Fig. 1), *L. scrobiculata* had lower concentration of CBSCs than *L. pulmonaria* (Table 2). However, when the CBSC concentration in *L. scrobiculata* increased relative to the con-

Table 2. Mean concentrations \pm ISE (mg g^{-1}) of carbon-based secondary compounds in transplanted *Lobaria pulmonaria* and *L. scrobiculata*.^a

	<i>L. pulmonaria</i>	<i>L. scrobiculata</i>	$F_{1,110}$ (P)
Constictic acid	19.93 \pm 0.88	9.88 \pm 0.65	99.32 (<0.001)
Cryptostictic acid	1.32 \pm 0.09	0.64 \pm 0.05	64.95 (<0.001)
Stictic acid	28.48 \pm 1.07	19.86 \pm 0.06	39.70 (<0.001)
Norstictic acid	7.37 \pm 0.24	3.96 \pm 0.19	134.47 (<0.001)
Methyl norstictic acid	0.68 \pm 0.03	0.25 \pm 0.02	240.14 (<0.001)
Total stictic acid complex	57.74 \pm 1.94	34.59 \pm 1.68	85.65 (<0.001)
<i>m</i> -Scrobiculin	–	7.30 \pm 0.42	–
Usnic acid	–	8.09 \pm 0.38	–
Total CBSCs	57.74 \pm 1.94	49.97 \pm 1.78	9.09 (0.003)

^aCBSC concentrations were not affected by host tree species during the transplantation period.

**Fig. 2.** Percent grazing on *Lobaria pulmonaria* and *L. scrobiculata* transplanted to *A. platanoides*, *Q. robur* and *T. cordata*. Groups topped with the same capital letter are not significantly different ($P > 0.05$) according to a Tukey's test. Asterisks denote significant ($P < 0.05$) difference between lichen species transplanted to the same tree species.**Table 3.** Linear mixed effects model testing for the effect of lichen species and tree species on percent grazing using concentration of the stictic acid complex as covariate. The response is log-transformed.

	X^2 (P)
Lichen (L)	4.9 (0.027)
Tree species (T)	29.0 (<0.001)
Stictic acid complex (S)	3.2 (0.074)
L \times T	8.4 (0.015)
L \times S	1.7 (0.191)
T \times S	3.9 (0.144)
L \times T \times S	13.4 (0.001)

centration in the *L. pulmonaria* present on the same trunk, the preference for *L. scrobiculata* decreased (Fig. 1, Table 1).

We found a significant tree species effect on lichen grazing (Fig. 2, Table 3). Total grazing was 1.8 times higher on lichens transplanted on *A. platanoides* than those on *Q. robur*, whereas lichens on *T. cordata* experienced 1.6 times more

grazing than lichens on *Q. robur*. There was a significant lichen species \times tree species interaction effect on grazing (Table 3), suggesting that the preference for *L. scrobiculata* differed between tree species. As such, *L. scrobiculata* transplanted to *A. platanoides* experienced 1.9 times more grazing than *L. pulmonaria*, while there was no significant difference between the two lichen species when transplanted to the other tree species. There was no significant effect of stictic acid complex ($P = 0.074$) in this model but including this covariate improved the fit of the model and thus did explain some of the variation (Table 3).

Soil pH was significantly higher beneath *A. platanoides* canopies than beneath those of *Q. robur* and *T. cordata* (Table 4). Likewise, *Acer* had higher bark pH than the other two tree species (Table 4), but only when DBH was used as a covariate.

The species composition of the epiphytic macrolichen vegetation on *Tilia* significantly differed from that on the other two tree species (Fig. 3). *T. cordata* supported a community with more Parmeliaceae-species, whereas the other two trees, *Acer* in particular, had higher frequency and cover of bryophytes, cephalo- and cyanolichens. Only one single *T. cordata* trunk hosted a natural occurrence of cephalo- or cyanolichens (*L. pulmonaria*). The community composition of macrolichens correlated with total grazing, bryophyte cover as well as bark and soil pH (Fig. 3). Host tree DBH or basal area did not correlate with lichen species composition. Trees with higher total grazing on transplants had a higher ratio between naturally occurring *L. virens* and *L. pulmonaria* ($F_{1,15} = 11.43$, $P = 0.004$). The Lobariaceae species and cyanolichens in other families were separated from the Parmeliaceae-species along the first NMDS axis, which correlated with pH. The higher dominance of N-fixing species on *A. platanoides* and *Q. robur* resulted in significantly higher community-weighted average thallus N concentration and lower C:N in macrolichens on these tree species (Table 4). With increasing bark pH the community-weighted thallus N increased ($F_{1,45} = 12.59$, $P < 0.001$) and C:N decreased ($F_{1,45} = 12.46$, $P < 0.001$).

Table 4. Mean (\pm SE) of soil pH, bark pH and the community weighted means of thallus N and C:N in the lichen community on *A. platanoides*, *Q. robur* and *T. cordata*. Mean values followed by different letters are significantly different ($P < 0.05$) according to a Tukey's test. Bold letters denote significant effects.

	<i>Acer</i>	<i>Quercus</i>	<i>Tilia</i>	$F_{2,44}$ (P)
Soil pH	5.23 \pm 0.11a	4.90 \pm 0.08b	4.77 \pm 0.10b	8.00 (0.001)
Bark pH*	5.01 \pm 0.12a	4.75 \pm 0.11b	4.66 \pm 0.10b	5.41 (0.008)
Community weighted thallus N (%)	2.15 \pm 0.25a	1.47 \pm 0.13b	0.91 \pm 0.04b	12.27 (<0.001)
Community weighted thallus C:N	24.76 \pm 4.45b	31.32 \pm 3.16b	46.21 \pm 1.94a	9.43 (<0.001)

* DBH included as covariate ($F = 9.55$, $P = 0.003$).

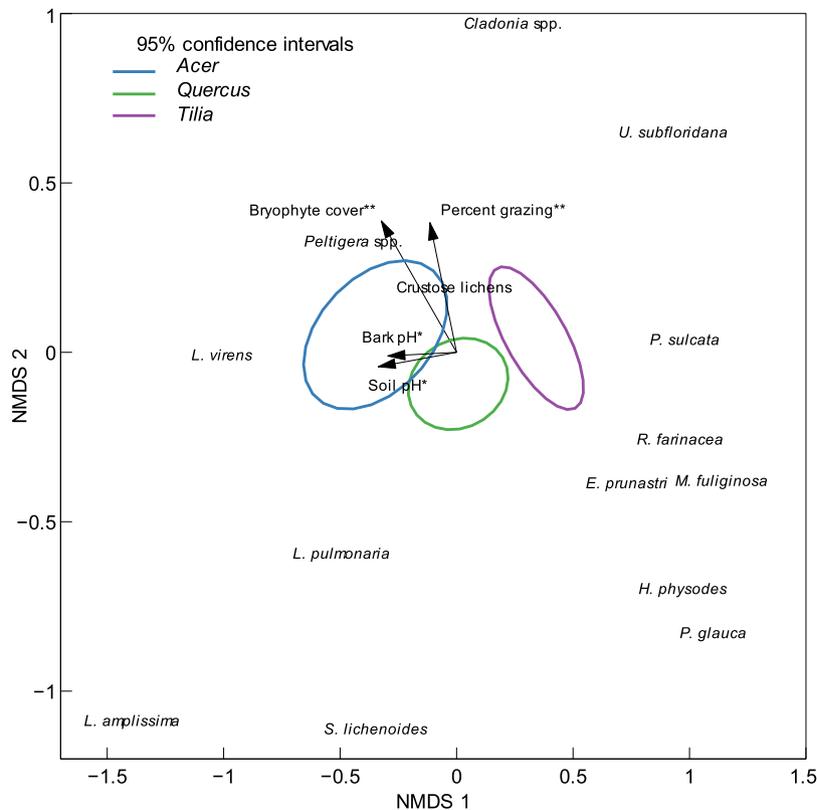


Fig. 3. Non-metric multidimensional scaling (NMDS) ordination plot of the epiphytic lichen community on *A. platanoides*, *Q. robur* and *T. cordata*. The ellipses are 95% confidence intervals of the tree species centroids (based on SE-values). The arrows show the direction of increasing bark pH, soil pH, bryophyte cover and percent grazing on transplanted lichens to the specific trees. The length of the arrows is proportional to the correlation between the variable and the ordination. * and ** denote significant correlations at $P < 0.05$ and $P < 0.01$, respectively. Genus names: *E* = *Evernia*, *H* = *Hypogymnia*, *L* = *Lobaria*, *M* = *Melanelixia*, *P. glauca* = *Platismatia glauca*, *P. sulcata* = *Parmelia sulcata*, *R* = *Ramalina*, *S* = *Scytinium*, *U* = *Usnea*.

Discussion

We found higher grazing of lichen transplants on *A. platanoides* and *T. cordata* than on *Q. robur*, consistent with our first hypothesis. The observed lower grazing of lichens on *Q. robur* mirrors previous observations of lower abundance of snails in the litter of *Q. robur* than in litter of other more Ca-rich broadleaved trees (Wäreborn 1969). Tree species influenced the elemental composition of lichens that had been transplanted to paired, neighboring tree species in an earlier study (Asplund, Ohlson, & Gauslaa 2015), with possible consequences also for the consumer level. Yet,

tree species-specific differences in climbing gastropods are poorly documented because of inefficient sampling protocols for such night-active grazers (Vatne, Solhøy, Asplund, & Gauslaa 2010). Boch et al. (2016) found higher grazing pressure on lichens in broadleaved *Fagus sylvatica*-forests than in *Picea abies*-forests, but their approach comparing grazing in two separate forest types does not allow conclusions on the importance of tree species *per se*.

In our field experiment, gastropods preferred *L. scrobiculata* to *L. pulmonaria*, as found in a previous field grazing experiment (Asplund, Larsson et al. 2010). The preference for *L. scrobiculata* may contribute to its rareness in stud-

ied gastropod-rich forests. This pattern likely occurs because most *L. scrobiculata* thalli have lower concentrations of CBSCs, and the preference for *L. scrobiculata* decreased when the difference in CBSCs between the two species decreased. Reducing the concentration of CBSCs in these species by acetone rinsing, greatly increased lichen palatability both in field and lab experiments (Gauslaa 2005; Asplund & Gauslaa 2008; Asplund 2011; Asplund & Wardle 2013). Meanwhile, Asplund, Gauslaa, and Merinero (2016) showed that the cyanolichen *L. scrobiculata* has much lower carbon-to-nitrogen ratio than does the cephalolichen *L. pulmonaria*, which may contribute to the higher palatability of *L. scrobiculata*.

Not only the total grazing pressure, but also the strength of the gastropods' feeding preferences varied among tree species, consistent with our second hypothesis. On *A. platanoides*, gastropods grazed twice as much on *L. scrobiculata* compared with *L. pulmonaria*, while the two lichens were similarly grazed on the two other tree species. A possible explanation for this pattern is that there are tree species-specific communities of lichenivorous gastropods, and that various gastropod species differ in their feeding preferences (Baur, Baur, & Fröberg 1994), and that there are tree species-specific communities of lichenivorous gastropods. However, here is a need to develop efficient protocols for assessing climbing gastropods to characterize gastropod communities on trees. Furthermore, stemflow base cation concentrations vary between paired tree species (Asplund et al. 2015), which may contribute to tree species-specific effects on gastropods. For instance, trees with lower pH and less Ca may have more slugs relative to snails than trees with higher concentrations of Ca (Kerney & Cameron 1979).

The shift from cyano-/cephalolichen-dominated communities to communities dominated by Parmeliaceae-species was likely affected by a reduction in bark pH, although other bark characteristics may also contribute. *T. cordata*, with significantly lower bark pH than *A. platanoides*, often hosted acidophytic lichens like *Evernia prunastri*, *Melanelixia fuliginosa*, *Parmelia sulcata* and *Cladonia* spp. while trees supporting cephalo- and cyanolichens require higher bark pH (Gauslaa 1985). Tree species-specific lichen community assembly is well described in the literature and is suggested to be driven by bark pH, various physical bark parameters, and microclimate influenced by the canopy structure (Gauslaa 1995; Ellis 2012). In the studied forests, epiphytic lichen communities were not only affected by abiotic factors; the shift in epiphyte vegetation on trunks with high grazing pressure is consistent with our third hypothesis. For instance, trees with high grazing pressure on lichen transplants had higher abundance of *L. virens* than of *L. pulmonaria*, consistent with earlier reported low palatability of *L. virens* to gastropods (Asplund, Larsson et al. 2010). Thus, *L. virens* has a competitive advantage under high grazing pressure.

Whereas the effect of herbivory on vascular plant community assembly is well studied (e.g. Crawley 1996; Olf & Ritchie 1998), lichen–lichenivore interactions are less known

as a community-shaping factor. Boch et al. (2016) found that gastropod grazing reduces growth of green algae and non-lichenized fungi and thus promotes a higher lichen diversity on *F. sylvatica*, while, snail grazing decreases lichen diversity on top of limestone pavements, but increases the diversity of endolithic lichens that live inside the rock and thus escape lichenivorous snails (Fröberg et al. 2011).

In conclusion, gastropod grazing varies among species of broadleaved deciduous trees, and thus plays a role in shaping their epiphytic communities. These findings complement the established notion that host-tree specific epiphyte communities are mainly driven by direct abiotic factors by suggesting indirect biotic effects through lichenivorous gastropods. However, we need a better knowledge of tree species-specific gastropod communities to improve our understanding of how these animals impact on epiphyte community assembly.

Author contributions

JA, OVS and YG conceived and designed the experiments. OVS performed the experiments. JA analysed the data. JA and YG wrote the manuscript; OVS provided advice.

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