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Lichen Chemical Traits Influence Palatability and can Mediate the Impact of Lichenivores on Nutrient Cycling

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Abstract

Lichen functional traits are known to regulate trophic interactions and biogeochemical processes. Consumption of lichens by lichenivorous macrofauna is thought to contribute significantly to the disappearance of lichen litter, and as such lichenivores convert a large amount of lichen biomass into faeces. However, precisely how this conversion influences decomposition rates and nutrient release from lichens remains unknown.

In this thesis, I tested the effect of lichen litter conversion into faeces on decomposition, and investigated the relationship between lichen functional traits, palatability and decomposition. I conducted a no-choice feeding bioassay with the generalist snail *Cepaea hortensis* on 12 lichen species with natural (control) and reduced (acetone rinsed) concentrations of secondary compounds. I performed a standardized decomposition experiment on both control and acetone rinsed groups of intact lichen thalli as well as faeces produced during grazing by *C. hortensis.* I measured morphological traits of lichen thalli and chemical traits of lichen thalli and snail faeces to test their effects on palatability and decomposition. Of the measured traits, palatability was significantly correlated only with concentrations of secondary compounds while decomposition rate was predominantly associated with C:N ratio. Given these results, I here show that palatability and decomposition of lichen are driven by different chemical traits and that the effect of lichenivore conversion of lichen litter into faeces on nutrient cycling depends on initial litter quality.

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1 Introduction

Much attention has been given to the influence of vascular plants on ecosystem processes and nutrient fluxes. In contrast, lichens have been largely ignored in this regard despite making up large parts of the photoautotrophic biomass in various important ecosystems. Lichens can become highly abundant and dominate the ground cover in sites that are too nutrient-poor, dry or cold to sustain vascular plant communities (Asplund & Wardle, 2017; Nash, 2008). In such environments, lichens can be important contributors to the carbon and nutrient cycles. Additionally, epiphytic lichen litter is commonly more nutrient rich than leaf litter, meaning that the contribution to nutrient cycling is large relative to the biomass of litter produced (Asplund & Wardle, 2017; Knops et al., 1997). Understanding which factors influence lichen decomposition is therefore of great interest.

Lichens are a highly morphologically diverse group, varying greatly in growth form and size, resulting in a high functional diversity both within and between species (Asplund & Wardle, 2017). This high functional diversity further results in varying decomposition rates. Uncovering the relationships between functional traits and decomposition allows insights into the intrinsic mechanisms controlling decomposition of lichens.

Functional ecology has traditionally considered traits that influence the fitness of organisms. According to Violle et al. (2007), functional traits can be defined as "morpho-physio-phenological" traits that indirectly impact fitness through their effects on growth, reproduction and survival, so-called "response traits". However, organisms also possess "effect traits" that mediate their effects on the environments they inhabit (Lavorel & Garnier, 2002). Such traits have been thoroughly explored for vascular plants in recent years and the link between functional traits and diverging effects on important ecosystem services is well established for these (Cadotte, 2017; de Bello et al., 2010; Diaz et al., 2004). However, for other autotrophic organisms such as lichens, little research has been conducted on this matter (Cornelissen et al., 2007) although recent efforts have been made to establish a framework for functional traits, including effect traits in lichen ecology (Ellis et al., 2021). In a 2-year decomposition experiment on bryophytes, lichens and vascular plants, Lang et al. (2009) found lichen decomposition rates to be positively correlated with initial thallus pH, N and K levels and showed a great variation in lichen species' decomposability. For instance, mass loss was

significantly lower for species in the family *Cladoniaceae* than for other lichens. On the other hand, the lichen *Alectoria ochroleuca* (Hoffm.) Massal. was found to be highly decomposable with a mass loss of about 90%, surpassing even the most decomposable vascular plant species included in the study.

To determine the role of traits in lichen palatability and decomposability, Asplund and Wardle (2013) included 28 lichen species, representing different functional categories and differing in N-fixing capability, growth form and substrate preference, as well as differing concentrations of carbon-based secondary compounds (CBSCs). They found that N-fixing lichens and foliose species had higher decomposition rates whereas non-N-fixing and fruticose species had lower decomposition rates, but higher palatability (Asplund & Wardle, 2013). Furthermore, high N and P concentrations and thallus pH were reliable predictors of high decomposition rates (Asplund & Wardle, 2013).

The secondary compound profile is a highly relevant functional trait in lichens. Lichens contain varying amounts of CBSCs produced by the fungal symbiont, some of which play an important role in deterring lichenivores (Gauslaa, 2005). Lichens show large qualitative and quantitative variation of such compounds (Huneck, 1999; Shukla et al., 2016). These can be safely extracted from lichen thalli with acetone without harming the organism. As described by Solhaug and Gauslaa (2001), this acetone-rinsing method has provided substantial insights into the ecological role of lichen secondary compounds. Asplund and Wardle (2013) found that non-destructive removal of CBSCs with acetone had significant effects for species containing CBSCs, positively affecting both consumption and decomposition rates, as well as the release of nitrogen during decomposition. In addition, several studies have shown some lichen secondary compounds, including the prevalent usnic acid to be antimicrobial *in vitro* (Cocchietto et al., 2002; Huneck, 1999; Mitrović et al., 2011; Nekhoroshev et al., 2022), which might explain their observed negative effect on decomposability.

Macrodetritivores have been shown to contribute significantly to the disappearance of lichen litter (McCune & Daly, 1994), underlining the importance of macrodetritivore-driven transformation of lichen litter in ecosystems. Lichen grazing by gastropods has also been shown to alter the distribution of lichens and contribute to the shaping of lichen communities (Asplund et al., 2010; Fröberg et al., 2011; Gauslaa et al., 2018), which suggests that lichenivory is common in nature and that a large amount of lichen biomass is converted to gastropod faeces

even before senescence has taken place. Furthermore, it is known that the palatability of lichens changes as they become litter (Asplund & Wardle, 2012).

Considering their potentially large contributions to biogeochemical cycles, there is a disproportionate lack of data on the effect of macrodetritivores on the decomposition of vascular plants and other phototrophic organisms. Joly et al. (2020) showed that detritivores accelerated carbon cycling of a diverse group of plant litters by increasing the lability of litter when converting it to faeces, with a 38.1% average increase in C loss for faeces compared to intact litter over 180 days. This positive trend was also consistent across litter and detritivore species (Joly et al., 2020). Furthermore, they found that this effect was stronger for more recalcitrant litter than for more readily decomposable litters. This inverse relationship between the effect of conversion and original litter quality was even stronger for the release of N during decomposition. When converted to faeces, N loss was greatly increased for litters with a slow release of N whereas it was greatly decreased for litters that readily release N during decomposition (Joly et al., 2020). Thus, macrodetritivores seem to ultimately even out the differences in N-loss during decomposition driven by litter physicochemical traits. A possible explanation for this, presented by Joly et al. (2020) could be that the physical protection of N-rich structures is ruptured when litter is converted to faeces, resulting in increased N-leaching. These results provide strong evidence of increased lability of faeces compared to intact litter in an ongoing controversy regarding the role of macro-detritivores in litter decomposition (David, 2014; Frouz, 2018; Joly et al., 2020). Despite the frequent interactions between snails and lichens, and the importance of lichens in nutrient and carbon cycling, we currently lack knowledge of how lichenivory affects lichen decomposability.

1.1 Research objectives and hypotheses

I aim to assess the effect of lichen litter conversion into faeces by the White-lipped snail (*Cepaea hortensis* O.F. Müller, 1774) on the decomposition of varying lichen species, as well as explore the relationships between lichen functional traits, lichen palatability and decomposition rate of intact and converted litter. I will do this by measuring traits and chemical profiles of different lichens and experimentally determining consumption rates of lichen as well as decomposition rates of intact (uningested) and converted (faeces) lichen litter. I hypothesize that (i) the decomposition rates of lichens will depend on their functional traits, notably C:N ratio, CBSC concentrations, STM and WHC (ii) decomposition rates will be higher for faeces

as opposed to intact lichens and this effect will depend on C:N ratio, and (iii) consumption rates of lichens by *C. hortensis* will be inversely correlated with CBSC concentration.

No previous studies have evaluated the combined effects of lichen traits and lichenivore conversion of lichen litter into faeces on the decomposition of differing lichen species. By testing these hypotheses, I seek to advance the understanding of how lichenivores mediate the role of lichens in carbon and nutrient cycling.

2 Materials and methods

2.1 Collection of materials

Lichen specimens were collected in Ås, Norway and Ski, Norway between June and August 2023. White lipped snails (*C. hortensis*) were collected in Ås, Norway and kept in a cool, dark environment for 3 days to ensure dormancy until the start of the palatability experiment. Organic soil for the decomposition experiment was collected in a spruce dominated forest at Åsmåsan, Ås, Akershus SE Norway (59° 40′ 11.7″ N 10° 46′ 52.1″ E). The soil was homogenized with a 2 mm sieve and kept refrigerated for up to 10 days until the decomposition experiment.

2.2 Acetone rinsing

Lichen material for half of the samples was rinsed with acetone to extract secondary compounds according to Solhaug and Gauslaa (2001). Dry lichen thalli were fully submerged in 100% acetone for approximately 30 minutes and left to dry on filter paper immediately after removal. This submersion time has been shown not to negatively affect the viability of the lichen species included in this study (Asplund & Wardle, 2013). As extraction efficiency varies for the different species, the concentration of secondary compounds was reduced by between 49.2% (*Lobaria pulmonaria* (L.) Hoffm.) and 92% (*Hypogymnia physodes* (L.) Nyl.).

2.3 WHC and STM

Water holding capacity (WHC) and Specific thallus mass (STM) was determined according to Gauslaa and Coxon (2011) for five thalli of each lichen species used in this study. Before measuring their hydrated mass, lichens were thoroughly sprayed with water and kept moist for about 30 minutes to allow the water to disperse in the thallus. Excess water was removed by lightly pat drying the lichens with a paper towel. To measure the thallus area, hydrated lichens were scanned with an EPSON Perfection V550 (Seiko Epson Corporation, Suwa, Japan) at a resolution of 360 dpi. The lichens were pressed down with a glass plate while scanning to level the thallus surface. The area was measured using colour thresholding in ImageJ ver. 1.53t (Rasband, 2022). STM was determined by dividing dry mass (g) by area (cm^2). WHC was calculated using the following formula: $\frac{\text{Hydrated mass(g)} - \text{Dry mass(g)}}{\text{Area } (cm^2)}$

2.4 Palatability experiment

A no-choice feeding bioassay following Asplund and Wardle (2013) was conducted to determine the palatability of the lichen species. Five thalli were used for each lichen species and treatment for a total of 120 samples. Dry mass was measured to the nearest 0.1 mg using a Sartorius extend ED224S digital scale. Sample mass was kept similar within the species but varied between species based on available material (see appendix 1). Sample mass was reduced for *H. physodes* and *Xanthoria parietina* (L.) Th. Fr. due to limited materials. Each thallus was placed in a box with one adult and one juvenile snail for approximately 21 hours. The remaining lichen material was then dried and weighed, and biomass consumed was expressed as a percentage of initial mass.

2.5 Decomposition experiment

Snail faeces were produced by letting snails feed on designated lichen treatments. Faeces were continuously collected and dried at 30°C immediately after collection to avoid fungal growth. Decomposition of both intact lichen and faeces was assessed using a standardized laboratory bioassay following Wardle et al (1998) and Asplund and Wardle (2013). Petri dishes (ø: 9 cm) were filled with 17 g soil with a gravimetric water content of ~ 75%. The lichen and faeces samples were separated from the soil with a 50 µm mesh and the petri dishes were sealed with insulation tape to minimize loss of moisture. The sealed petri dishes were placed in a dark environment to prevent lichen growth. The average temperature during decomposition was 22.4°C. Eight samples were made for each lichen treatment whereas the sample number for faeces varied between 2 and 8 for the different species and treatments because the rate of grazing and faeces production varied greatly, resulting in limited access to faeces for some treatments. Initial mass of the different treatments varied depending on available material and was significantly different for lichen litter and faeces with means of 0.47 g and 0.20 g, respectively (see appendix 2). Each sample was dried and weighed before the experiment and again after 96 days of decomposition.

2.6 Chemical analysis

Lichen thalli were ground to a fine powder with a steel ball mill in preparation for chemical analysis. Acetone extraction of secondary compounds and High-Performance Liquid Chromatography (HPLC) was performed on all treatments of lichen and faeces according to the protocol found in Nybakken et al. (2007). Approximately 50 mg of material was used for acetone rinsed lichen powder and faeces, and 25 mg for control lichens and faeces. For extraction of secondary compounds, 2 ml tubes containing the material were filled with approximately 1.5 ml acetone, vortexed and then shaken for 30 min. The tubes were then centrifuged for 5 min and the supernatant was transferred to new tubes. This extraction was repeated twice and tubes with supernatant were put in a Concentrator Plus centrifuge concentrator (Eppendorf Company, Hamburg, Germany) until all the acetone had evaporated. Extracts of acetone rinsed lichen powder were dissolved in 1 ml MeOH and control lichen extracts in 2 ml MeOH. Faeces extracts were dissolved in 0.5 ml MeOH irrespective of treatment.

The HPLC analysis was conducted using a 1100 Series HPLC (Agilent Technologies, Waldbronn, Germany). Separation was achieved on an ODS Hypersil 60×4.6 mm column and flow rate was 2 ml min^{-1}. Injection volume was 10 µl for lichens and 20 µl for faeces, with the exception of *X. parietina*, which had an injection volume of 40 µl for lichens and 20 µl for faeces. Temperatures were set at 25 °C for the oven and 22 °C for the injector. The mobile phases consisted of two solvents: Solvent A, composed of 0.25% orthophosphoric acid and 1.5% tetrahydrofuran in Millipore water, and solvent B, which was 100% methanol, following the gradient specified in Nybakken et al. (2007). The detection wavelength was 245 nm, and the identification of compounds was based on retention times, online UV spectra and cochromatography with commercial standards.

The carbon and nitrogen content of all 48 treatments was analysed using a Vario MICRO cube elemental analyzer (Elementar Company, Germany). Approximately 5 mg of material was weighed on a XP6 Microbalance (Mettler-Toledo International Inc.) and packed in tin foil in preparation for combustion analysis.

2.7 Statistical analysis

All statistical analyses were performed using R version 4.3.3 (R Core Team, 2023) and R-studio. Linear mixed effects models were constructed to explain the impact of explanatory variables on each of these response variables: 1. overall mass and nutrient loss of lichens and faeces, 2. mass loss of lichens, and 3. palatability of lichens. Species identity was included as a random effect to account for variability among the 12 species in the study. The models of best fit were determined with the dredge function in the MuMIn package, using AIC as selection criterion. All the initial models used for selection included the numerical variables C:N ratio and CBSCs. The models for lichen decomposition and palatability also included STM and WHC. The categorical variables treatment and material type, the interaction between them and their interaction with all numerical variables were used for the model selection for overall decomposition whereas the other two models did not include material type. For model 1, the response variables mass loss and C loss were log-transformed whereas N-loss was not as it included negative values. Simple linear regressions were performed to test the isolated effects of medullary and cortical CBSCs on palatability as well as the relationship between palatability and decomposition. Differing CBSC concentrations and C:N ratio between material types and treatments along with the effect of acetone rinsing on decomposition and palatability of individual species was tested with Welch's Two Sample t-tests.

3 Results

The total concentrations of CBSCs were significantly lower in faeces than in lichens with a mean of 17.36 mg g^{-1} in lichens vs. 2.24 mg g^{-1} in faeces ($p < 0.001$, Welch's t-test). Acetone rinsing significantly reduced the total concentration of CBSCs in both lichens (Table 1) and the resulting faeces. Control lichens had an average CBSC concentration of 27.53 mg g^{-1} compared to 7.19 mg g^{-1} in rinsed lichens ($p < 0.001$, Welch's t-test). Faeces based on control lichens had an average concentration of 3.75 mg g^{-1} compared to 0.726 mg g^{-1} in faeces based on rinsed lichens ($p < 0.001$, Welch's t-test). C:N ratio before decomposition was significantly lower for faeces (mean = 38.10) than unconsumed lichens (mean = 47.64; $p = 0.001$, Welch's t-test) (see appendix 2).

Table 1. Initial carbon %, nitrogen % of control lichens, CBSC concentrations (mg g^{-1}) in control and acetone rinsed lichens and the extraction efficiency of cortical (C) and medullary (M) compounds.

Species	C%	N%		CBSC concentrations mg g^{-1}				Extraction efficiency %	
				Controls		Acetone			
				M	C	M	C	M	C
Anaptychia ciliaris	41.24	1.26	-	-	-	-	-	-	-
Cladonia arbuscula	42.06	0.44	M: Fumarprotocetraric acid C: Usnic acid	8.28	6.90	4.90	1.23	40.82	82.17
Cladonia stellaris	42.56	0.45	M: Perlatolic acid, C: Usnic acid	2.22	9.35	0.24	2.00	89.1	78.61
Evernia prunastri	43.56	1.05	M: Evernic acid C: Atranorin, Chloroatranorin, Usnic acid	29.80	15.37	0.92	5.93	96.91	61.42
Hypogymnia physodes	42.85	0.94	M: Physodic, 3-hydroxyphysodic, Protocetraric and Physodalic acid C: Atranorin, Chloroatranorin	63.93	8.35	2.40	3.34	96.25	60
Lasallia pustulata	42.76	1.29	M: Gyrophoric acid C: -	19.84	-	8.48	-	57.26	-
Lobaria pulmonaria	44.6	2.14	M: Stictic, Constictic, Peristictic, Norstictic and Methyl norstictic acid C: -	29.93	-	15.20	-	49.21	-
Platismatia glauca	43.43	0.72	M: Caperatic acid, C: Atranorin, Chloratranorin	0.96	6.86	0.05	2.06	94.80	69.97
Pseudovernia furfuracea	44.95	1.01	M:Physodic, 2-O-methylphysodic and 3-hydroxyphysodic acid C: Atranorin, Chloratranorin	20.70	13.18	1.87	2.03	90.97	84.60
Ramalina farinacea	41.85	1.01	M: Protocetraric acid C: Usnic acid	44.91	4.89	20.18	4.21	55.07	13.91
Usnea dasopoga	42.89	1.30	M: Salazinic acid C: Usnic acid	16.11	24.40	2.84	7.35	82.37	69.88
Xanthoria parietina	40.91	1.17	M: - C: Parietin	-	5.28	-	0.10	-	98.11

3.1 Overall decomposition

There was a clear inverse relationship between C:N ratio and decomposition (Table 2). Lower C:N ratios were associated with higher decomposability of both lichens and faeces (fig. 2) and there was a significant difference in this effect between lichens and faeces on C loss and N loss, but not mass loss (fig. 4). C loss during decomposition was more strongly correlated with C:N ratio for intact lichen litter than for faeces. N loss was consistently lower for faeces, with a mean of 23.07% than for lichens with a mean of 40.26% and the interaction effect between C:N ratio and material type (Table 2) suggests that N loss in intact lichen litter may be more dependent on initial C:N ratio than faeces N loss. The negative effect of C:N ratio was stronger for the control treatment than for acetone rinsed material (fig. 2).

Decomposition rates were generally higher for acetone rinsed material than non-rinsed material with a mean mass loss of 51.93% in the control group compared to 55.03% in the acetone rinsed group. However, decomposition increased with increasing CBSC concentration. Welch's Two Sample t-test showed that acetone rinsing had a significant positive effect on mass loss only for the two lichen species *Cladonia arbuscula* (Wallr.) Flot. ($p<0.001$) and *L. pulmonaria* ($p=0.014$) while mass loss was significantly lower for acetone rinsed *Ramalina farinacea* (L.) Ach. compared to controls ($p=0.017$). Mass loss was also higher for faeces based on acetone rinsed *L. pulmonaria* compared to the control faeces of this species ($p=0.017$) (fig. 1). Furthermore, the significant three-way-interaction between CBSCs, treatment and material type suggests a dynamic relationship where the effect of CBSC concentrations on decomposition depends on both acetone rinsing and conversion to faeces (Table 2). The relationship of treatment and CBSC effect on decomposition differed significantly between the two material types. Decomposition increased drastically with increasing CBSC content for faeces based on acetone rinsed lichens (fig. 3).

Table 2. ANOVA table from linear mixed effects model of overall decomposition of lichens and faeces showing obtained F values and associated p-values for fixed effects on mass, C and N loss. Significant values are highlighted in boldface. The intercept is predicted mass loss when predictors are at reference level/zero. Main effects are the effects of single predictors whereas interaction effects show how one or more variables influence the effect of another predictor on the response variable.

	Mass loss%	**C loss %**	**N loss %**
(Intercept)	**16936.99 (<.0001)**	**11583.61 (<0.001)**	**108.98 (<0.001)**
Main effects:			
C/N ratio	**100.55 (<0.001)**	**100.82 (<0.001)**	**250.06 (<0.001)**
CBSCs	**22.61 (<0.001)**	**12.90 (<0.001)**	**120.26 (<0.001)**
Treatment	**17.90 (<0.001)**	**9.44 (0.002)**	0.10 (0.756)
Material type	0.14 (0.703)	1.72 (0.191)	**121.56 (<0.001)**
Interaction effects:			
C/N ratio : Material type	1.00 (0.317)	**83.14 (<0.001)**	**120.34 (<0.001)**
CBSCs : Material type	0.12 (0.725)	**6.46 (0.012)**	2.34 (0.127)
Treatment : Material type	**10.72 (0.001)**	**5.77 (<0.001)**	**11.04 (0.001)**
C/N ratio : Treatment	29.42 **(<0.001)**	0.64 (0.426)	**322.72 (<0.001)**
CBSCs : Treatment	0.67 (0.415)	2.39 (0.123)	2.69 (0.101)
CBSCs : Treatment : Material type	**22.06 (<0.001)**	**6.89 (0.009)**	**15.65 (<0.001)**

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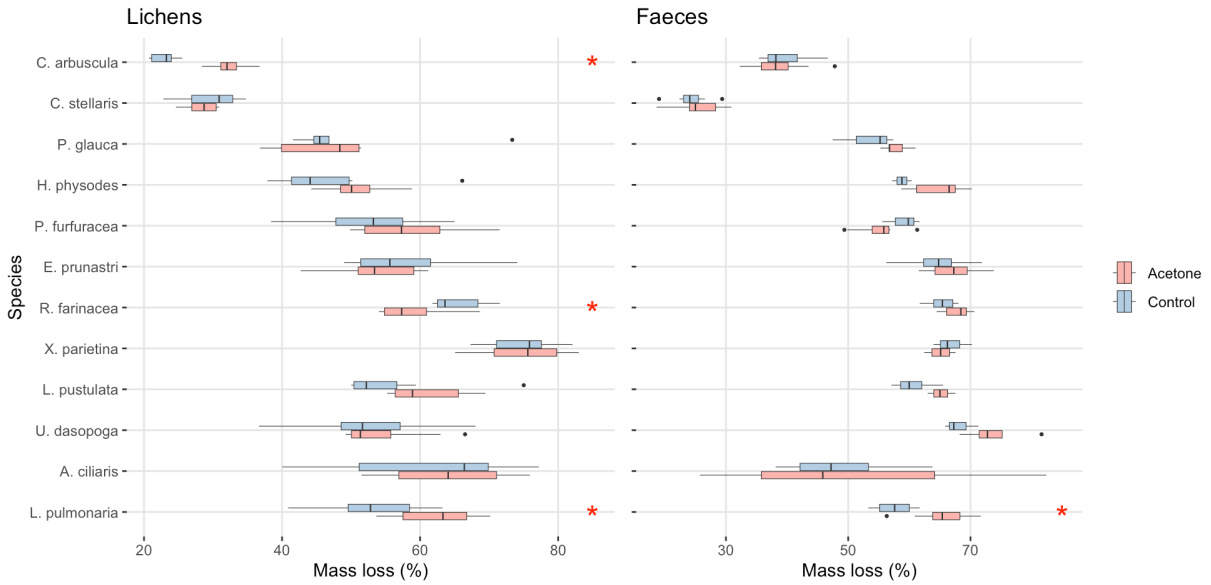

Figure 1: Decomposition in percentage mass loss by species and treatment of lichens and faeces. Species are sorted in ascending order by initial C:N ratio of control lichens. Species with significantly different mass loss between treatments are annotated with red stars.

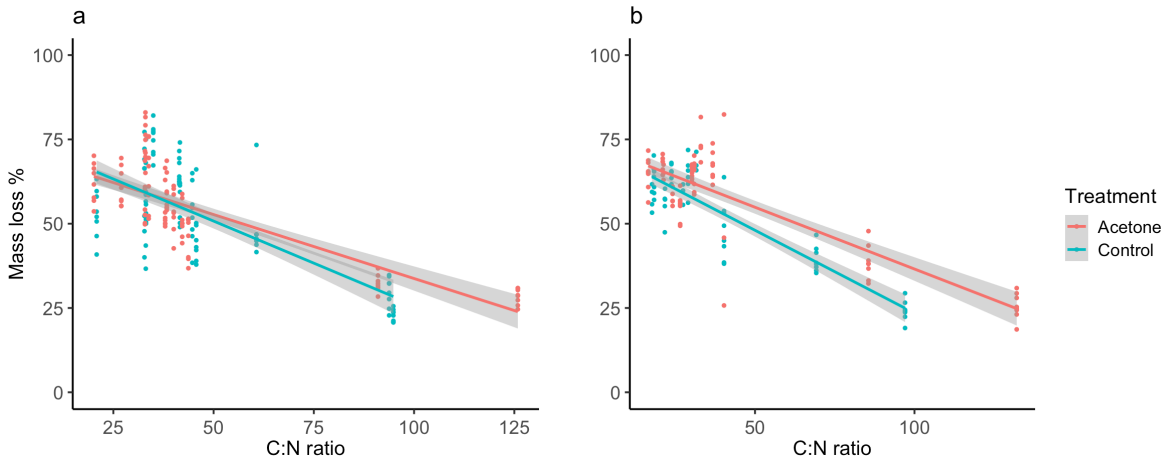

Figure 2: Decomposition in percentage mass loss by C:N ratio of a) lichens and b) faeces.

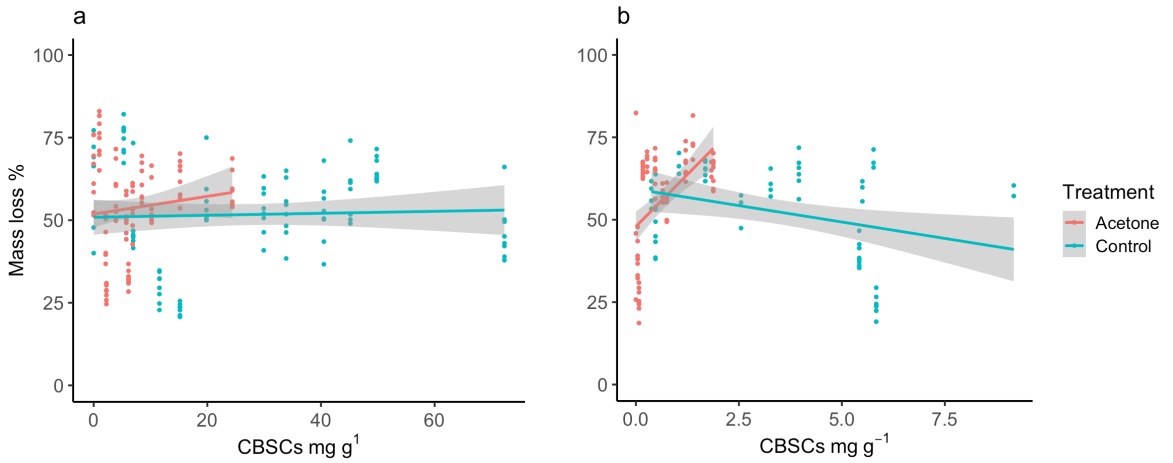

Figure 3: Decomposition in percentage mass loss by CBSC content of a) lichens and b) faeces. Note the different values on x-axes.

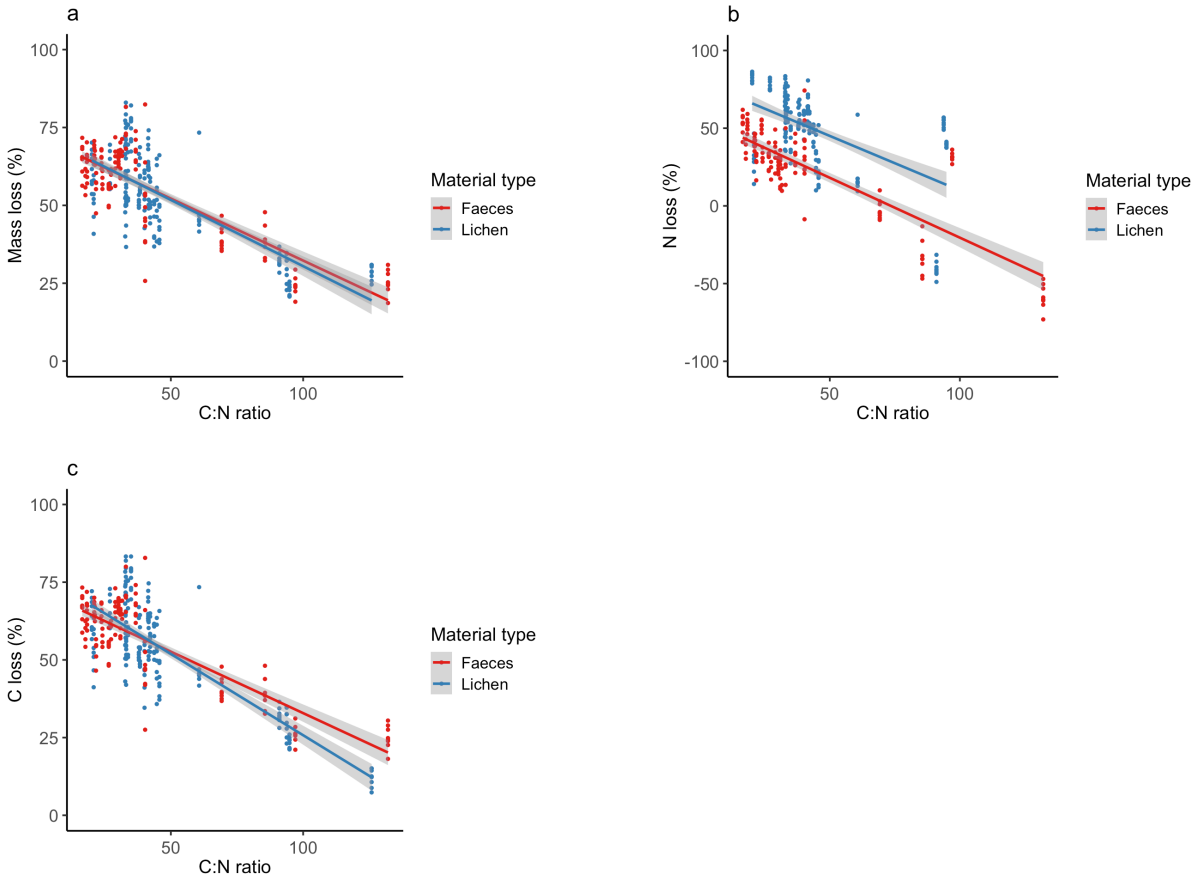

Figure 4: The relationship between C:N ratio and a) mass loss, b) N loss, and c) C loss for faeces and lichens in decomposition

3.2 Lichen decomposition

Effects on mass loss were also analyzed for intact lichen litter, excluding faeces. The optimal model determined by the AIC criterion differed from the model for overall decomposition and included only C:N ratio, WHC and the interaction term between WHC and treatment as predictor variables (Table 3). C:N ratio was the strongest predictor of decomposability also for lichen decomposition in isolation. Water holding capacity (WHC) was also found to be significant, but its importance differed between treatments (fig. 5). There was no effect of acetone rinsing on lichen decomposition rate.

Table 3. ANOVA table from linear mixed effects model of lichen decomposition showing obtained F-values with associated degrees of freedom and p-values. Significant values are highlighted in boldface.

	numDF, denDF	**F-value**	**p-value**
(Intercept)	1, 178	**13362.09**	**<0.001**
Main effects:			
WHC	1, 10	**17.15**	**0.002**
C/N ratio	1, 178	**30.94**	**<0.001**
Interaction effects:			
WHC : Treatment	1, 178	**23.69**	**<0.001**

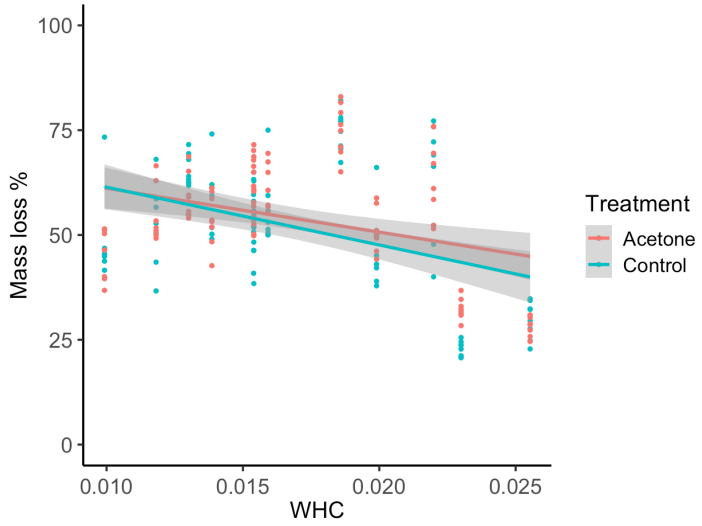

Figure 5: Relationship between mass loss and WHC in the decomposition of acetone rinsed and control lichens.

3.3 Palatability

Palatability was significantly reduced with increasing CBSC concentrations (fig. 7), however there was no significant effect of treatment in the LME model (Table 4). Welch Two Sample t-test showed that acetone rinsing had a significant positive effect on palatability ($p<0.05$) for 5 of the 12 species included (fig.6). The ratio of mean concentration of secondary compounds in faeces to lichens was 6.46 times higher for cortical compounds than for medullary compounds. Simple linear regression further showed that the concentration of medullary CBSCs was inversely correlated with palatability ($p = 0.007$) whereas the concentration of cortical CBSCs was not ($p = 0.244$) (fig. 8). Extraction efficiency of medullary compounds was on average higher for the species for which acetone rinsing had a significant effect (84.82% compared to 64.45% in the unaffected group). Regression models showed no significant relationships between lichen consumption and mass loss in either lichen or faeces decomposition.

Table 4. ANOVA table from linear mixed effects model of palatability showing obtained F-values with associated degrees of freedom and p-values. Significant values are highlighted in boldface.

	numDF, denDF	**F-value**	**p-value**
(Intercept)	1, 105	**398.07**	**<.0001**
Main effects:			
STM	1, 10	1.21	0.2963
CBSCs	1, 105	**30.94**	**<0.001**
Treatment	1, 105	0.74	0.3927
Interaction effects:			
CBSCs : Treatment	1, 105	3.3531	0.0699

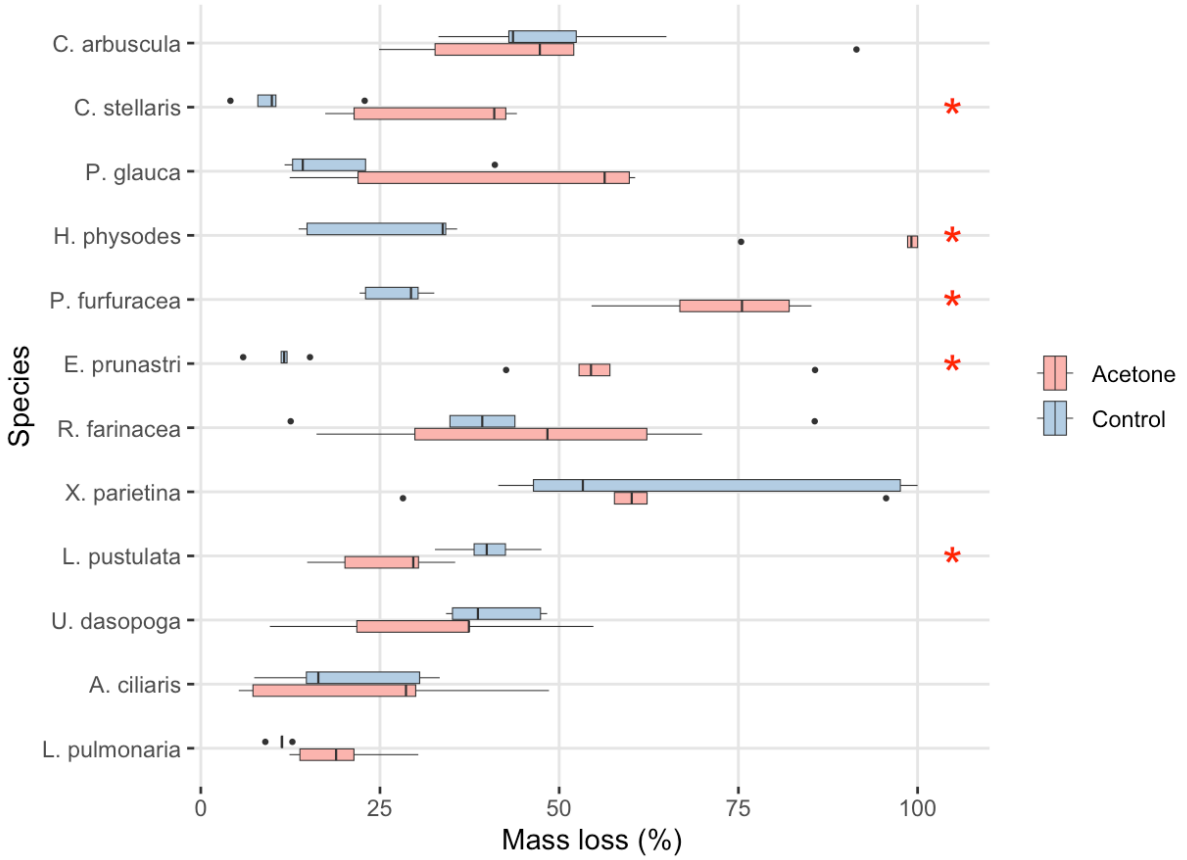

Figure 6: Palatability in percentage mass loss of acetone rinsed and non-rinsed lichens. Species with significantly different mass loss between treatments are annotated with red stars.

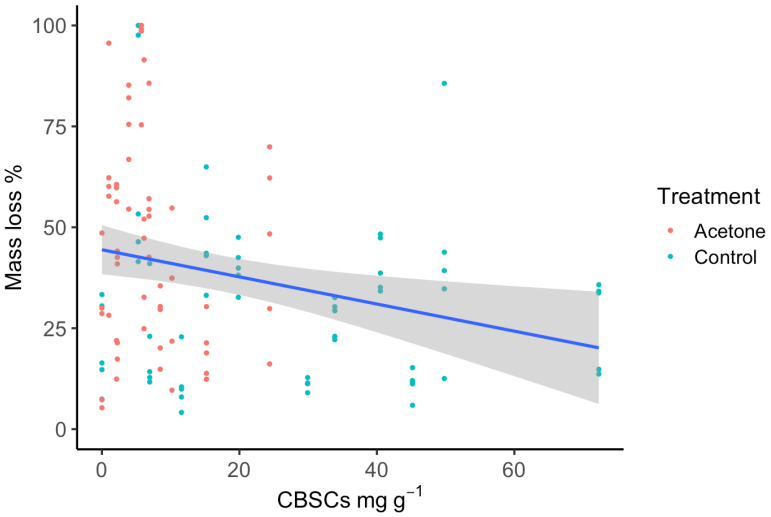

Figure 7: Palatability in percentage mass loss could be predicted by the total concentration of secondary metabolites found in lichen species.

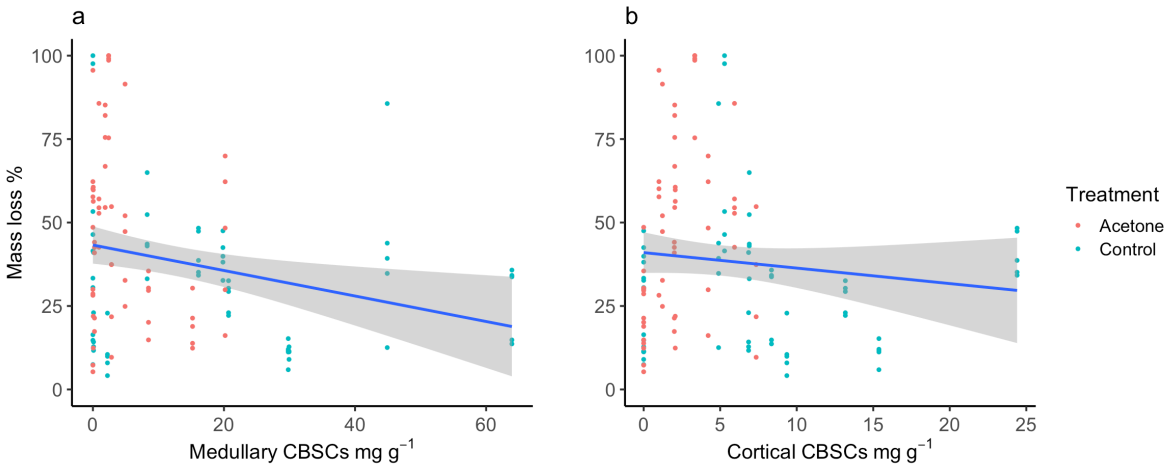

Figure 8: Regression of the effects of a) medullary and b) cortical CBSCs on palatability

4 Discussion

My first hypothesis that lichen decomposition would depend on functional traits was partly supported by my results. C:N-ratio was the most important variable in regulating decomposition of both intact lichens and faeces. The data available on lichen decomposition, especially comparing lichen litter to faeces is sparse, although some studies have found macro- and mesofauna to contribute to lichen decomposition through feeding activities (Asplund et al., 2013; McCune & Daly, 1994). More comprehensive data is available for leaf litter and conversion into faeces by macroarthropods (for review, see David (2014)). In a similar study using various vascular plant litter and detritivores, (Joly et al., 2020) found that conversion of leaf litter into faeces accelerated C loss and had an equalizing effect on C and N loss dependence on litter quality in decomposition. I found evidence for the latter in lichens, as the relationship between C:N ratio and C and N loss was stronger for intact lichens than for faeces. However, I did not find conversion into faeces to accelerate either mass loss, C loss or N loss. In fact, intact lichens had a considerably higher N loss than faeces. This reduction in N-loss after conversion is partially in line with Joly et al. (2020), who found that N-loss was greatly reduced for *Acer pseudoplatanus* (L.) and *Quercus robur* (L.) litter when converted into faeces by the snail *Cepaea nemoralis* (L.), which is closely related to *C. hortensis.* These findings refute the first part of my second hypothesis that faeces are more readily decomposable than intact lichens. The second part of this hypothesis, stating that the effect of conversion on decomposition would depend on initial C:N ratio was supported for C loss and N loss, but not for mass loss. In some cases where initial C:N ratio was high the measured nitrogen content was higher after decomposition than before. This observation may be ascribed to the microorganisms present on the samples post-decomposition and their N-immobilization (Janssen, 1996).

Surprisingly, the significantly reduced C:N ratio in faeces compared to intact lichens did not increase the decomposition of faeces. Considering the otherwise strong relationship between C:N ratio and decomposition rates this could indicate that some other compensatory factor is simultaneously reducing the lability of faeces. Higher decomposition and mineralization rates in faeces are commonly attributed to increased microbial colonization due to increased available surface area caused by litter fragmentation during digestion (Frouz, 2018). Inversely, the compaction of particles in faecal pellets may reduce the available surface area and grinding

such pellets into smaller particles has been shown to increase respiration (Suzuki et al., 2013). Such compaction may have compensated for decreased C:N ratio in faeces.

Previous research has found that respiration in faeces is high in the early stages of decomposition but rapidly decreases over time to the same level or even lower than intact leaf litter (Frouz & Šimek, 2009; Maraun & Scheu, 1995). The opposite has also been observed and this effect may vary with litter type (Rawlins et al., 2007; Suzuki et al., 2013). For further studies on the effect of lichenivores on lichen decomposition it could be illuminating to measure respiration at different temporal stages of decomposition to uncover potential different dynamics between microorganisms and faeces vs. intact lichen litter.

My results corroborate previous findings that N content and C:N ratio are important variables for lichen decomposition (Asplund & Wardle, 2013; Hagemann & Moroni, 2015; van Zuijlen et al., 2020). Furthermore, Lang et al. (2009) noted than lichens in the *Cladoniaceae* family are particularly slow-decomposing, which was true also in the current study, where *C. arbuscula, C. stellaris* (Opiz) Pouzar & Vezda and faeces based on these had both the lowest mass loss during decomposition and the highest C:N ratio.

In line with my first hypothesis, WHC was found to be a significant predictor for lichen decomposition rates, but this result may have been confounded by other factors such as the high C:N ratios of *C. arbuscula* and *C. stellaris* which also had the highest measured WHC. The humidity was kept constant during the decomposition experiment and the impact of WHC on decomposition across species may have been more apparent in a field study with naturally fluctuating moisture levels.

The ambiguous results regarding the effect of CBSC concentration on decomposition indicate that such compounds had little to no impact on the decomposition process in the current study. A larger number of samples, particularly of faeces, and possibly the inclusion of more species would probably be needed to produce a meaningful result in this regard. Further, as shown by Asplund et al. (2013), the effect of phenolic compounds on decomposition may be more pronounced in the presence of fungal-feeding mesofauna, which in the current study was denied access to the decomposing material. The effect of CBSC removal by acetone rinsing was found to be significant for mass loss and C loss in overall decomposition of both lichens and faeces, but not significant for mass loss in lichens alone, although the effect of rinsing on total CBSC

concentration was more apparent for lichens and all treatments of faeces had relatively low concentrations. Faeces of *L. pulmonaria* had differing mass loss between treatments, but this result should be interpreted with caution as HPLC analysis of secondary compounds in faeces revealed at least some contamination from other species of both treatments of *L. pulmonaria* as well as controls of *Anaptychia ciliaris* (L.) Körber and *C. stellaris* (see appendix 3). This contamination may have been limited to only some of the faeces material as HPLC was only conducted on a very small amount and the material was not homogenized.

The role of secondary metabolites, including phenolics in suppressing litter decomposition and nutrient cycling is well established for vascular plants (Chomel et al., 2016; Hättenschwiler & Vitousek, 2000) and extracts of lichen CBSCs from eg. *C. arbuscula, Evernia prunastri* (L.) Ach*., Lasallia pustulata* (L.) Mérat and *Pseudevernia furfuracea* (L.) Zopf are known to have antimicrobial properties (Cosar et al., 1988; Huneck, 1999; Ingólfsdóttir et al., 1998; Ranković et al., 2007). In the current study, acetone rinsing significantly corresponded to higher decomposition rates for only 2 of 12 lichen species. In contrast, Asplund and Wardle (2013) found acetone rinsing to significantly increase decomposition rates for 10 of 28 lichen species, including *L. pulmonaria*. The variable effect of acetone rinsing on palatability among species may partially have been a function of varying extraction efficiency of medullary secondary compounds (Table 1). *A. ciliaris* and *X. parietina* do not contain any medullary CBSCs and rinsing should therefore not be expected to affect the palatability of these species.

CBSC concentration was the sole significant predictor for palatability of lichens, highlighting the importance of these compounds in deterring grazers. This finding supports my third hypothesis that consumption rate is inversely related to CBSC concentration and is in line with previous literature, consistently showing reduced lichen palatability in response to increasing CBSC concentrations (Asplund & Wardle, 2013; Gauslaa, 2005; Wieners et al., 2018).

My results show that cortical substances were present in faeces in higher concentrations than medullary substances, indicating a higher consumption of cortical substances by *C. hortensis*. Moreover, decreased palatability was significantly related to medullary, but not cortical CBSC concentrations. Previous research has shown that secondary compounds located in the cortex, such as atranorin, parietin and usnic acid act mainly as sunscreens, protecting the photobiont from UV radiation, whereas herbivore defense is commonly attributed to medullary secondary compounds (Solhaug & Gauslaa, 2012). Studies have shown that gastropods and other

macrofauna prefer the upper cortex and the photobiont layer located directly beneath it, while avoiding the medulla and that this can be attributed to medullary CBSCs (Asplund, 2011; Gauslaa et al., 2010). However, recent research has proposed a deterrent effect of the cortical compound usnic acid against lichenivores, but that this effect is compensated for by the nutritious primary metabolite D-arabitol present in *Usnea taylorii* (Hooker f. & Taylor) (Gadea et al., 2019). Whether this trade-off between deterring compounds and nutrition can be generalized for lichens is yet to be determined.

5 Conclusions

My findings suggest that microbes involved in breakdown of lichens and faeces are more sensitive to macronutrient composition, i.e. the composition of carbon and nitrogen, while the presence and concentration of secondary metabolites are more important for lichenivorous macrofauna. These results partially concur with previous research by Asplund and Wardle (2013) which showed N and P concentrations to be strongly correlated with lichen decomposition, but not consumption by *C. hortensis*. I found no evidence for a relationship between palatability and decomposition rates, further supporting the notion that these two processes are driven by different functional traits.

Lichen conversion into faeces by *C.hortensis* had no effect on mass loss or C loss but did significantly reduce N loss during decomposition. Conversion also attenuated the relationship between litter quality, i.e. C:N ratio on C and N loss, which has previously been found for plant litter. Contrary to previous literature, CBSC concentration had no apparent antimicrobial effect in decomposition.

These findings provide new insights into the role of macrofauna in lichen decomposition. Previous results on the effect of litter conversion into faeces have been variable, depending on both litter species and detritivore species and the subject is still a matter of controversy. Future investigations into their role in lichen decomposition should include lichenivores from various taxa such as *Lepidoptera* and *Coleoptera* to uncover potential differential effects among these on lichen decomposition.

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APPENDIX 1: Number of samples, initial mass (g) ±SD and mass loss (g) ±SD for acetone rinsed and control lichens in palatability bioassay.

Species	**Treatment**	**No. Samples**	**Mean Initial Mass (g) (±SD)**	**Mean mass loss (g) (±SD)**
Anaptychia ciliaris	Control	5	0,19928 (0,0079)	0,0411 (0,0224)
Anaptychia ciliaris	Acetone rinsed	5	0,20172 (0,0040)	0,04884 (0,0373)
Cladonia arbuscula	Control	5	0,1704(0,0054)	0,08044 (0,0183)
Cladonia arbuscula	Acetone rinsed	5	0,17232 (0,0031)	0,08602 (0,0457)
Cladonia stellaris	Control	5	0,2561(0,0020)	0,02828 (0,0179)
Cladonia stellaris	Acetone rinsed	5	0,25144 (0,0035)	0,08372 (0,0324)
Evernia prunastri	Control	5	0,2451 (0,0041)	0,02746 (0,0082)
Evernia prunastri	Acetone rinsed	5	0,24658 (0,0025)	0,14414 (0,0391)
Hypogymnia physodes	Control	5	0,06848 (0,0023)	0,01814 (0,0078)
Hypogymnia physodes	Acetone rinsed	5	0,06882 (0,0032)	0,06526 (0,0092)
Lasallia pustulata	Control	5	0,20476 (0,0077)	0,0823 (0,0122)
Lasallia pustulata	Acetone rinsed	5	0,19988 (0,0081)	0,05236 (0,0176)
Lobaria pulmonaria	Control	5	0,2107 (0,0060)	0,02346 (0,0025)
Lobaria pulmonaria	Acetone rinsed	5	0,2112 (0,0044)	0,04098 (0,0155)
Platismatia glauca	Control	5	0,15368 (0,0033)	0,03134 (0,0182)
Platismatia glauca	Acetone rinsed	5	0,15016 (0,0027)	0,06304 (0,0342)
Pseudevernia furfuracea	Control	5	0,2031 (0,0051)	0,05582 (0,0097)
Pseudevernia furfuracea	Acetone rinsed	5	0,20156 (0,0026)	0,14686 (0,0256)
Ramalina farinacea	Control	5	0,2093 (0,0055)	0,09072 (0,0573)
Ramalina farinacea	Acetone rinsed	5	0,2099 (0,0032)	0,095 (0,0463)
Usnea dasopoga	Control	5	0,24598 (0,0023)	0,10022 (0,0167)
Usnea dasopoga	Acetone rinsed	5	0,24524 (0,0028)	0,07912 (0,0424)
Xanthoria parietina	Control	5	0,08164 (0,0041)	0,05458 (0,0209)
Xanthoria parietina	Acetone rinsed	5	0,0825 (0,0016)	0,04994 (0,0188)

APPENDIX 2: Number of samples, initial mass (g) ±SD, mass loss (g) ±SD and initial C:N ratio for acetone rinsed and control lichens/faeces in decomposition bioassay.

Species	Material type	Treatment	No. Samples	Mean Initial Mass (g) (±SD)	Mean mass loss (g) (±SD)	C:N ratio
Anaptychia ciliaris	Lichen	Control	8	0,48814 (0,0063)	0,29989 (0,0642)	32,7597
Anaptychia ciliaris	Lichen	Acetone rinsed	8	0,48700 (0,0032)	0,31138 (0,0467)	33,8073
Cladonia arbuscula	Lichen	Control	8	0,46946 (0,0051)	0,10746 (0,0091)	94,8341
Cladonia arbuscula	Lichen	Acetone rinsed	8	0,46953 (0,0037)	0,15193 (0,0114)	90,9967
Cladonia stellaris	Lichen	Control	8	0,49365 (0,0030)	0,14709 (0,0214)	93,7794
Cladonia stellaris	Lichen	Acetone rinsed	8	0,49026 (0,0043)	0,13923 (0,0116)	125,872
Evernia prunastri	Lichen	Control	8	0,49333 (0,0054)	0,28348 (0,0422)	41,604
Evernia prunastri	Lichen	Acetone rinsed	8	0,49545 (0,0029)	0,26628 (0,0309)	40,0538
Hypogymnia physodes	Lichen	Control	8	0,41131 (0,0054)	0,19211 (0,0395)	45,6717
Hypogymnia physodes	Lichen	Acetone rinsed	8	0,40381 (0,0025)	0,20558 (0,0205)	42,1712
Lasallia pustulata	Lichen	Control	8	0,50023 (0,0024)	0,27838 (0,0426)	33,1311
Lasallia pustulata	Lichen	Acetone rinsed	8	0,49643 (0,0047)	0,30208 (0,0277)	26,9792
Lobaria pulmonaria	Lichen	Control	8	0,49879 (0,0048)	0,26456 (0,0360)	20,8389
Lobaria pulmonaria	Lichen	Acetone rinsed	8	0,49778 (0,0029)	0,31065 (0,0295)	20,1501
Platismatia glauca	Lichen	Control	8	0,49631 (0,0043)	0,24040 (0,0476)	60,6863
Platismatia glauca	Lichen	Acetone rinsed	8	0,49500 (0,0029)	0,22716 (0,0314)	43,7013
Pseudevernia furfuracea	Lichen	Control	8	0,46851 (0,0020)	0,24778 (0,0411)	44,6885
Pseudevernia furfuracea	Lichen	Acetone rinsed	8	0,46868 (0,0047)	0,27450 (0,0400)	32,8813
Ramalina farinacea	Lichen	Control	8	0,49170 (0,0052)	0,32143 (0,0190)	41,4392
Ramalina farinacea	Lichen	Acetone rinsed	8	0,49580 (0,0024)	0,29234 (0,0275)	38,3217
Usnea dasopoga	Lichen	Control	8	0,49991 (0,0016)	0,26061 (0,0480)	33,0858
Usnea dasopoga	Lichen	Acetone rinsed	8	0,49526 (0,0026)	0,26925 (0,0336)	37,9186
Xanthoria parietina	Lichen	Control	8	0,29989 (0,0037)	0,22423 (0,0140)	34,9584
Xanthoria parietina	Lichen	Acetone rinsed	8	0,29960 (0,0019)	0,22510 (0,0193)	32,9959
Anaptychia ciliaris	Faeces	Control	8	0,20056 (0,0005)	0,09651 (0,0173)	40,2798
Anaptychia ciliaris	Faeces	Acetone rinsed	3	0,20030 (0,0007)	0,10293 (0,0579)	40,6746
Cladonia arbuscula	Faeces	Control	8	0,20039 (0,0006)	0,07905 (0,0077)	69,2031
Cladonia arbuscula	Faeces	Acetone rinsed	8	0,20024 (0,0004)	0,07726 (0,0102)	85,5642
Cladonia stellaris	Faeces	Control	7	0,20031 (0,0004)	0,04856 (0,0065)	97,0421
Cladonia stellaris	Faeces	Acetone rinsed	8	0,20069 (0,0006)	0,05126 (0,0077)	132,0434
Evernia prunastri	Faeces	Control	6	0,20007 (0,0007)	0,12893 (0,0103)	29,006
Evernia prunastri	Faeces	Acetone rinsed	7	0,20054 (0,0002)	0,13463 (0,0086)	36,7246
Hypogymnia physodes	Faeces	Control	2	0,15115 (0,0001)	0,08885 (0,0035)	21,7788
Hypogymnia physodes	Faeces	Acetone rinsed	8	0,15039 (0,0005)	0,09741 (0,0065)	30,9367
Lasallia pustulata	Faeces	Control	4	0,20020 (0,0005)	0,12138 (0,0071)	18,352
Lasallia pustulata	Faeces	Acetone rinsed	3	0,19987 (0,0007)	0,13027 (0,0049)	21,3078
Lobaria pulmonaria	Faeces	Control	4	0,20038 (0,0002)	0,11530 (0,0076)	17,7104
Lobaria pulmonaria	Faeces	Acetone rinsed	8	0,20028 (0,0004)	0,13050 (0,0096)	16,5176
Platismatia glauca	Faeces	Control	3	0,20030 (0,0003)	0,10687 (0,0106)	21,7153
Platismatia glauca	Faeces	Acetone rinsed	5	0,20018 (0,0002)	0,11554 (0,0044)	24,1446
Pseudevernia furfuracea	Faeces	Control	3	0,20010 (0,0004)	0,11810 (0,0063)	27,4158

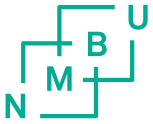
Pseudevernia furfuracea	Faeces	Acetone rinsed	8	0,20036 (0,0007)	0,11044 (0,0079)	26,527
Ramalina farinacea	Faeces	Control	6	0,20050 (0,0005)	0,13090 (0,0048)	23,7818
Ramalina farinacea	Faeces	Acetone rinsed	5	0,20042 (0,0003)	0,13586 (0,0050)	21,057
Usnea dasopoga	Faeces	Control	3	0,20060 (0,0007)	0,13670 (0,0061)	31,5876
Usnea dasopoga	Faeces	Acetone rinsed	4	0,20050 (0,0006)	0,14805 (0,0112)	33,0023
Xanthoria parietina	Faeces	Control	3	0,14950 (0)	0,09987 (0,0048)	18,2642
Xanthoria parietina	Faeces	Acetone rinsed	7	0,20014 (0,0005)	0,13027 (0,0039)	30,2293

APPENDIX 3: Phenolic profiles of rinsed and non-rinsed (control) lichens and faeces. Concentrations are given in mg g^{-1}. Faeces treatments with contamination are marked in red.

Species	Material type	Treatment	3.1 - constictic acid	5 - salazinic acid	5.6 - peristictic acid	6.2 -stictic acid	6.6- caperatic acid	8.4 - norstictic acid	8.8 - protocetraric acid	8.9 - physodalic acid
A. ciliaris	Lichen	Acetone								
A. ciliaris	Faeces	Acetone								
A. ciliaris	Lichen	Control								
A. ciliaris	Faeces	Control								
C. arbuscula	Lichen	Acetone								
C. arbuscula	Faeces	Acetone								
C. arbuscula	Lichen	Control								
C. arbuscula	Faeces	Control								
C. stellaris	Lichen	Acetone								
C. stellaris	Faeces	Acetone								
C. stellaris	Lichen	Control								
C. stellaris	Faeces	Control								
E. prunastri	Lichen	Acetone								
E. prunastri	Faeces	Acetone								
E. prunastri	Lichen	Control								
E. prunastri	Faeces	Control								
H. physodes	Lichen	Acetone								
H. physodes	Faeces	Acetone								
H. physodes	Lichen	Control								
H. physodes	Faeces	Control								0,857022097
L. pustulata	Lichen	Acetone								
L. pustulata	Faeces	Acetone								
L. pustulata	Lichen	Control								
L. pustulata	Faeces	Control								0,096990524
L. pulmonaria	Lichen	Acetone	3,74810501		0,201659073	10,14416974		0,961718173		
L. pulmonaria	Faeces	Acetone								
L. pulmonaria	Lichen	Control	7,970005206		1,315492171	17,64202305		2,553061433		
L. pulmonaria	Faeces	Control								
P. glauca	Lichen	Acetone					0,054986284			
P. glauca	Faeces	Acetone					0,006236488			
P. glauca	Lichen	Control					0,096216			
P. glauca	Faeces	Control					0,022726802			
P. furfuracea	Lichen	Acetone								
P. furfuracea	Faeces	Acetone								
P. furfuracea	Lichen	Control								
P. furfuracea	Faeces	Control								
R. farinacea	Lichen	Acetone								20,18018473
R. farinacea	Faeces	Acetone								
R. farinacea	Lichen	Control								44,91236889
R. farinacea	Faeces	Control								
U. Dasopoga	Lichen	Acetone		2,837037931						
U. dasopoga	Faeces	Acetone								
U. dasopoga	Lichen	Control		16,10732772						
U. dasopoga	Faeces	Control								
X. parietina	Lichen	Acetone								
X. parietina	Faeces	Acetone								
X. parietina	Lichen	Control								
X. parietina	Faeces	Control								

Species	Material type	Treatment	10.8 fumarprotocetraric acid der.	11.1 - protocetraric acid	11.4 - methyl norstictic acid	11.7 - fumarprotocetraric acid	13.5 - cf. 3-hydroxyphysodic acid	13.7 - Evernic acid	Gyrophoric acid
A. ciliaris	Lichen	Acetone							
A. ciliaris	Faeces	Acetone							
A. ciliaris	Lichen	Control							
A. ciliaris	Faeces	Control							
C. arbuscula	Lichen	Acetone	0,359816099			4,545120135			
C. arbuscula	Faeces	Acetone							
C. arbuscula	Lichen	Control				8,280772633			
C. arbuscula	Faeces	Control							
C. stellaris	Lichen	Acetone							
C. stellaris	Faeces	Acetone							
C. stellaris	Lichen	Control							
C. stellaris	Faeces	Control							
E. prunastri	Lichen	Acetone						0,920153677	
E. prunastri	Faeces	Acetone							
E. prunastri	Lichen	Control						29,80483268	
E. prunastri	Faeces	Control						0,065747582	
H. physodes	Lichen	Acetone		0,119809417			0,92380415		
H. physodes	Faeces	Acetone							
H. physodes	Lichen	Control		41,01528199			10,28663259		
H. physodes	Faeces	Control		0,50856023			0,112049907		
L. pustulata	Lichen	Acetone							8,481184057
L. pustulata	Faeces	Acetone							1,833239547
L. pustulata	Lichen	Control							19,84131557
L. pustulata	Faeces	Control							3,270740155
L. pulmonaria	Lichen	Acetone			0,148954306				
L. pulmonaria	Faeces	Acetone							
L. pulmonaria	Lichen	Control			0,445158939				
L. pulmonaria	Faeces	Control							
P. glauca	Lichen	Acetone							
P. glauca	Faeces	Acetone							
P. glauca	Lichen	Control							
P. glauca	Faeces	Control							
P. furfuracea	Lichen	Acetone					0,180803139		
P. furfuracea	Faeces	Acetone					0,0180405		
P. furfuracea	Lichen	Control					3,087241029		
P. furfuracea	Faeces	Control					0,583381375		
R. farinacea	Lichen	Acetone							
R. farinacea	Faeces	Acetone							
R. farinacea	Lichen	Control							
R. farinacea	Faeces	Control							
U. Dasopoga	Lichen	Acetone							
U. dasopoga	Faeces	Acetone							
U. dasopoga	Lichen	Control							
U. dasopoga	Faeces	Control							
X. parietina	Lichen	Acetone							
X. parietina	Faeces	Acetone							
X. parietina	Lichen	Control							
X. parietina	Faeces	Control							

Species	Material type	Treatment	14.7 cf. 2-O-methylphysodic acid	14.8 Tenuiourin?	15.5 - Physodic acid	15.9 -Usnic acid	16.3 - parietin	Chloroatranorin	18.1 - atranorin	21.4 - perlatolic acid	Total	Medullary	Cortical
A. ciliaris	Lichen	Acetone									0	0	0
A. ciliaris	Faeces	Acetone									0	0	0
A. ciliaris	Lichen	Control									0	0	0
A. ciliaris	Faeces	Control				0,475333447					0,475333	0	0,4753334
C. arbuscula	Lichen	Acetone				1,226687346					6,131624	4,9049362	1,2266873
C. arbuscula	Faeces	Acetone				0,042091363					0,042091	0	0,0420914
C. arbuscula	Lichen	Control				6,900058308					15,18083	8,2807726	6,9000583
C. arbuscula	Faeces	Control				5,421425788					5,421426	0	5,4214258
C. stellaris	Lichen	Acetone				2,002613083				0,239220542	2,241834	0,2392205	2,0026131
C. stellaris	Faeces	Acetone				0,051997096		0,01106455	0,010671629		0,073733	0	0,0737333
C. stellaris	Lichen	Control				9,354031497				2,219963785	11,574	2,2199638	9,3540315
C. stellaris	Faeces	Control				3,616547806		1,330899815	0,550493526	0,33682053	5,834762	0,3368205	5,4979411
E. prunastri	Lichen	Acetone				3,9720204		1,381622875	0,579899332		6,853696	0,9201537	5,9335426
E. prunastri	Faeces	Acetone				0,317273177		0,594968188	0,294751002		1,206992	0	1,2069924
E. prunastri	Lichen	Control				5,412816944		7,198901984	2,75884051		45,17539	29,804833	15,370559
E. prunastri	Faeces	Control				0,603897206		2,379855622	0,906703977		3,956204	0,0657476	3,8904568
H. physodes	Lichen	Acetone		0,111542975	1,150004893			2,259125222	1,078426728		5,739704	2,402152	3,3375519
H. physodes	Faeces	Acetone		0,834125909	0,027669228			0,661523476	0,356211799		1,87953	0,8617951	1,0177353
H. physodes	Lichen	Control			11,7723922			5,562461476	2,788438325		72,28223	63,931329	8,3508998
H. physodes	Faeces	Control		4,85609637	0,858010507			2,057743133	0,780236066		9,172696	6,334717	2,8379792
L. pustulata	Lichen	Acetone									8,481184	8,4811841	0
L. pustulata	Faeces	Acetone									1,83324	1,8332395	0
L. pustulata	Lichen	Control									19,84132	19,841316	0
L. pustulata	Faeces	Control									3,27074	3,2707402	0
L. pulmonaria	Lichen	Acetone									15,20461	15,204606	0
L. pulmonaria	Faeces	Acetone	0,267345871					0,090399078	0,108303704		0,466049	0,2673459	0,1987028
L. pulmonaria	Lichen	Control									29,92574	29,925741	0
L. pulmonaria	Faeces	Control						0,219308239	0,155833776		0,375142	0	0,375142
P. glauca	Lichen	Acetone						0,989426219	1,073458417		2,117871	0,0549863	2,0628846
P. glauca	Faeces	Acetone						0,295467814	0,347895403		0,6496	0,0062365	0,6433632
P. glauca	Lichen	Control						3,196332931	3,658829944		6,951379	0,096216	6,8551629
P. glauca	Faeces	Control						1,399121976	1,13053078		2,55238	0,0227268	2,5296528
P. furfuracea	Lichen	Acetone	0,249796321		1,443859486			1,041032494	0,986505458		3,901997	1,8744589	2,027538
P. furfuracea	Faeces	Acetone	0,030969525		0,02224995			0,332710003	0,34554537		0,749515	0,07126	0,6782554
P. furfuracea	Lichen	Control	3,233607914		14,37668237			7,88506327	5,292413169		33,87501	20,697531	13,177476
P. furfuracea	Faeces	Control	0,265935657		0,499527789			2,447677195	1,70073345		5,497255	1,3488448	4,1484106
R. farinacea	Lichen	Acetone				4,214610083					24,39479	20,180185	4,2146101
R. farinacea	Faeces	Acetone				0,270768399					0,270768	0	0,2707684
R. farinacea	Lichen	Control				4,89433428					49,8067	44,912369	4,8943343
R. farinacea	Faeces	Control				1,683754008					1,683754	0	1,683754
U. Dasopoga	Lichen	Acetone				7,349084144					10,18612	2,8370379	7,3490841
U. dasopoga	Faeces	Acetone				1,383621923					1,383622	0	1,3836219
U. dasopoga	Lichen	Control				24,39795364					40,50528	16,107328	24,397954
U. dasopoga	Faeces	Control				5,769481241					5,769481	0	5,7694812
X. parietina	Lichen	Acetone					0,998039232				0,998039	0	0,9980392
X. parietina	Faeces	Acetone					0,167688762				0,167689	0	0,1676888
X. parietina	Lichen	Control					5,283086346				5,283086	0	5,2830863
X. parietina	Faeces	Control					1,045152129				1,045152	0	1,0451521



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