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# Decomposability of lichens and bryophytes from across an elevational gradient under standardized conditions

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Lichens and bryophytes are abundant primary producers in high latitude and high elevation ecosystems, and they play an important role in ecosystem processes such as decomposition and nutrient cycling. Despite their importance, little is known about the decomposability of lichens and bryophytes either among or within species, at the whole community level, or how this decomposability is affected by their functional traits. Here, we studied decomposability of lichens and bryophytes at the community-level and individual species-level (using 21 species and genera) collected from an elevational gradient in alpine Norway. In order to isolate the elevation effect on litter quality, we used a standardized laboratory bioassay to measure decomposability. In contrast to our expectations, we found that community-level decomposability of lichens and bryophytes increased with elevation and thus decreasing temperature. In contrast, phosphorus release from the litter decreased with elevation while nitrogen release was unresponsive. Decomposability was explained by nutrient concentrations, litter pH and primary producer group identity (lichens versus bryophytes) at both the individual species and community levels. Species turnover (changes in species composition and abundance) was the main driver of decomposability across elevation at the community level, despite some of the traits explaining decomposability showing high intraspecific variability. Our study highlights the importance of among-species variation in determining lichen and bryophyte decomposability. Further, the higher decomposability that we found for higher elevations suggests that global warming might result in a shift towards slower decomposable lichen and bryophyte species.

Keywords: alpine ecology, cryptogams, decomposition, elevational gradient, functional traits, tundra

## Introduction

Decomposition, the decay of organic matter, is an important ecosystem process that drives carbon and nutrient cycling (Chapin et al. 2011). The decomposition of

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plant litter is determined by three main factors: litter quality (determined by the functional traits of the plant), the physico-chemical environment (e.g. climate and soil abiotic properties) and the decomposer community (i.e. fungi, bacteria and soil fauna), as well as the interactions between them (Swift et al. 1979). Traditionally, climatic factors (notably temperature and moisture) have been regarded as the predominant controls of decomposition rates, with litter quality being of subordinate importance, and with the decomposer community exerting a regulatory role only at local scales (Swift et al. 1979, Lavelle et al. 1993, Aerts 1997). However, more recent studies have shown that species-driven litter quality differences have a much larger effect than climate-driven variation on local-scale variation in plant litter decomposition both within biomes (Cornwell et al. 2008) and across biomes (Djukic et al. 2018). Therefore, the indirect effects of expected future climate change, as manifested through vegetation shifts, will likely have a larger impact on decomposition, by altering litter quality, than will the direct effects of increasing temperature on decomposer activity (Cornelissen et al. 2007a, DeMarco et al. 2014). In this light, it is important to isolate indirect climatic effects, i.e. how changes in community composition caused by climate alter litter quality, from more direct climatic effects on litter decomposition.

Litter quality is determined in a large part by the functional traits of the species that provide the litter. Traits associated with the leaf economics spectrum, i.e. plant strategies ranging from slow to fast returns on investments of nutrients and carbon (Wright et al. 2004), have been linked to decomposition at different scales, i.e. leaf, whole-plant and community-level, within and across biomes (Quested et al. 2007, Santiago 2007, Cornwell et al. 2008, Freschet et al. 2012, Makkonen et al. 2012). In general, litter decomposability increases with increasing nutrient concentrations, specific leaf area (SLA) and associated traits, while it decreases with increasing secondary compounds and structure-related traits such as lignin (Cornelissen and Thompson 1997, Kazakou et al. 2006, Lang et al. 2009). An increasing number of studies have highlighted that key functional traits can also vary substantially within species (Albert et al. 2010, Messier et al. 2010, Violle et al. 2012), which poses the question how intraspecific trait variation contributes to litter decomposability. Although several studies have considered within-species variation in decomposability (Sariyildiz and Anderson 2003, Wardle et al. 2009, Sundqvist et al. 2011a), only one study to date has considered the role of intraspecific variability in functional traits in driving decomposition processes at the whole community level, using an abundance-weighted mean approach (Jackson et al. 2013).

The vast majority of litter decomposition studies has been on vascular plants, and decomposability of other primary producers such as lichens and bryophytes have been studied only sparingly. Further, lichens and bryophytes are underrepresented in trait-based studies on ecosystem functioning (St. Martin and Mallik 2017), despite their major contribution to aboveground biomass and species richness at higher latitudes and elevations (Matveyeva and Chernov 2000) and their impacts on biogeochemistry and ecosystem processes (Cornelissen et al. 2007b, Asplund and Wardle 2017). Lang et al. (2009) explored the decomposability of several subarctic bryophyte, lichen and vascular plant species, and found high variation both across these three groups and among species within each group, which were related to the initial chemical composition of the species. Further, Asplund and Wardle (2013) found that variation in decomposability among lichen species was strongly related to N and phosphorous (P) concentrations, as well as litter pH and secondary compounds. Further, Campbell et al. (2010) found decomposition rates of epiphytic lichen species to be related to N concentration and morphological characteristics, and Hagemann and Moroni (2015) found decomposition of lichen and bryophyte species in a boreal forest to be mainly controlled by interactions between litter type and litter carbon, N and hemicellulose content. In order to scale up from individual species to understanding the role of lichens and bryophytes at the ecosystem-scale, it is important to quantify functional traits and decomposability at the community level. However, no studies to date have considered community-level decomposability of lichens and bryophytes in relation to their traits.

Elevational gradients act as powerful natural experiments for testing the effects of variation of climatic factors, notably temperature (Körner 2007, Sundqvist et al. 2013), and can therefore be used for providing insights about the ecological impacts of future climate change. For vascular plants, recent studies have shown that declining temperature with increasing elevation often causes a shift in vascular plant functional traits from those associated with rapid resource acquisition to those linked to resource conservation (Sundqvist et al. 2013, Read et al. 2014, Mayor et al. 2017). This in turn often leads to a decrease in plant litter quality characteristics with increasing elevation, such as reduced nutrient concentrations and greater levels of secondary compounds (Sundqvist et al. 2011b, De Long et al. 2016), although these types of changes in functional traits with elevation do not always drive decomposition per se (Sundqvist et al. 2013). To date, only one study has explored the response of community-level functional traits of non-vascular primary producers to elevation (Roos et al. 2019), and while they found strong responses of several lichen and bryophyte traits to elevation both across- and within-species, it remains unclear as to how this in turn affects the decomposability of their litter.

In this study, we investigated how the decomposability of non-vascular vegetation (i.e. lichens and bryophytes) at the individual and whole community levels change along an alpine elevational gradient in southern Norway, by using a standardized laboratory bioassay. We also explored the contributions of species turnover and intraspecific variability to variation in community-level measures of decomposability across the gradient, and the role of lichen and bryophyte functional traits in driving this variability. Specifically, we tested the following three hypotheses: 1) decomposability of lichens and bryophytes decreases with increasing elevation, 2) species turnover effects are more important in driving decomposability across elevation than is intraspecific variation and 3) variation in the decomposability of lichens and bryophytes can be explained by variation in their functional traits, both at the individual and whole community levels. By addressing these hypotheses, we aim to improve our understanding of what drives lichen and bryophyte decomposability across elevation, which will help to inform how lichen and bryophyte communities drive ecosystem processes under increasing temperatures in the future.

## Material and methods

### Field site and experimental set-up

The field sites are located near Finse, in southern central Norway. Finse is situated at 1220 m a.s.l. north of the Hardangervidda mountain plateau, approximately 250 m above the treeline. It has an average yearly temperature of 2.1°C and 1030 mm yearly precipitation. The average temperature from 1 June to 31 August 2016 was 7.3°C and precipitation was 303.9 mm (Norwegian Meteorological Institute 2018). The elevational gradient used in this study was established in the summer of 2016, to study functional traits of vascular plants, lichens and bryophytes (Roos et al. 2019). In this study we used one site at each of five elevations as described by Roos et al. (2019), i.e. 1120, 1240, 1360, 1480 and 1600 m a.s.l., spanning approximately 500 m in elevation. All sites were on acidic granite–gneiss bedrock on wind-exposed ridges on south-facing slopes, and were dominated by lichen–heath vegetation. The growing season was 54 days shorter at the highest compared to the lowest elevation and air temperature in July decreased on average by 0.9°C with each level (120 m) of increasing elevation (Roos et al. 2019; Supplementary material Appendix 1 Table A1). At each site (i.e. elevation), five 1-$m^2$ plots were randomly selected within a 100 m radius, consisting of a mixed vegetation of vascular plants, lichens and bryophytes. After plot selection, the resulting median distance between plots within elevations was ca 43 m, which is sufficient to ensure adequate independence among plots, given the high spatial heterogeneity in tundra communities (Björk et al. 2007, Opedal et al. 2015) and is in line with previous studies along elevational gradients in similar environments (Sundqvist et al. 2011a, Veen et al. 2017, Roos et al. 2019).

For each $1 \times 1$ m plot, all lichen and bryophyte species present were recorded, and their cover was visually estimated in July 2016 (see Roos et al. 2019 for further details). From these data, we calculated the abundance of each lichen and bryophyte species as a proportion of the total cryptogam cover in that plot. One quadrat of $50 \times 50$ cm within each plot was destructively harvested in August 2016, and extra material was collected from outside each plot to gather enough biomass for each of the most abundant lichen and bryophyte species for performing decomposability analysis. For each plot, the selected species of lichens and bryophytes composed at least 80% of the total cover of cryptogams in that plot, which is in line with what is recommended for studies that involve determining community-level measures of plant traits and processes (Garnier et al. 2004, Pakeman and Quested 2007). For the community-level decomposability calculations, we chose to combine the bryophyte and lichen communities into one cryptogam community because of limited material available for decomposability analysis, and because of the low cover of bryophytes in some of the plots. All collected material was air-dried and stored at −18°C.

For decomposability analysis (as a proxy for litter quality), we used fresh (i.e. living) lichen and bryophyte material, because unlike vascular plants, ground-covering lichens and bryophytes do not produce senesced litter that falls off, but instead start decomposing at the bottom layer while still being photosynthetically active at the top layer. Therefore, most previous studies on lichen and bryophyte decomposition have used living material (Campbell et al. 2010, Asplund and Wardle 2013, Asplund et al. 2013, Hagemann and Moroni 2015), although some studies have used only the senesced parts of bryophyte shoots (Lang et al. 2009, Jonsson et al. 2014). In addition, Lang et al. (2009) tried to induce senescence of lichen material by incubating wet lichens in darkness and subsequently freezing them in liquid $N_2$, but reported that even this treatment could not guarantee complete tissue death and may have produced artefacts.

Functional traits measured for each species per plot were taken from the study of Roos et al. (2019), and we chose only traits that were measured in the same way for both lichens and bryophytes. As such, the traits that we selected were N and P concentration, N:P ratio, pH and water holding capacity (WHC), which have been found to be related to decomposition (Cornelissen et al. 2006, Cornwell et al. 2008, Lang et al. 2009, Makkonen et al. 2012). All traits were measured at the thallus- or shoot-level; WHC (in $g\,g^{-1}$) was measured as (water-saturated weight − dry-weight)/dry-weight on intact shoots and thalli, while N and P (% of mass) and pH were measured on ground material. For further details on trait measurements see Roos et al. (2019).

### Decomposability bioassay

To determine decomposability of lichens and bryophytes as a proxy for litter quality, we used a standardized laboratory bioassay as described by Wardle et al. (1998) and Asplund and Wardle (2013). For each cryptogam sample, a petri dish of 9 cm diameter was two-thirds filled with standardized peat soil (530% water content at dry mass basis), freshly collected from a spruce forest in Ås, Norway (59°40′N, 10°46′E), which was homogenized (e.g. mixed and sieved) before use. A disc of nylon mesh with 1-mm holes was placed on top of the soil, above which was placed 1 g (± 0.1) of cryptogam material (air-dry). The exact weights were recorded at 0.0001 g readability, and corrected with an air-dry to oven-dry ratio calculated from spare material for each species that was dried at 60°C for 48 h. We closed and sealed the petri-dishes with isolation tape to minimise water loss and incubated them for 90 days at 22°C, in darkness to prevent regrowth of bryophytes and lichens. We emphasize that our use of this method is not meant to inform in any way on what the decomposition rates of litter would actually be in the field. Instead, we are using it as a standardized bioassay method to provide a relative measure of decomposability as influenced by litter quality, in line with several other studies which have used this approach for similar types of high latitude ecosystems (Wardle et al. 1998, 2009, Silfver et al. 2007, Sundqvist et al. 2011b, Asplund and Wardle 2013, Lagerström et al. 2013, Broadbent et al. 2017).

After incubation, the remaining litter was cleaned from soil particles, air-dried and weighed. Weights were corrected with the air-dry to oven-dry ratio calculated for each species (60°C for 48 h). Decomposability was expressed by decay rate k, which was calculated as log(post-incubation weight/pre-incubation weight) (Olson 1963). After weighing, samples were ground to powder using a ball mill, and nitrogen (N) and phosphorous (P) concentrations were determined following Kjeldahl digestion. Pre-incubation N and P concentrations of all the litters used in this study were measured in exactly the same way, and these data are presented in Roos et al. (2019). For each species and each plot, N and P release during decomposition was calculated as the difference between the absolute nutrient content (concentration × biomass) before incubation and after incubation, divided by the absolute initial nutrient content, and expressed as a percentage.

## Data analysis

To determine how community level decomposability and N and P release changes across elevation, we calculated abundance-weighted means for the cryptogam (lichens and bryophytes) community at the whole plot level. For each plot, we weighted each species' decomposability by its relative cover. The community-weighted mean was then calculated by taking the sum of the abundance-weighted decomposability of all measured lichen and bryophyte species per plot (Garnier et al. 2004). This was calculated in two ways: 'specific' averages used plot-specific decomposability per species (or taxon-level when we were unable to sort material down to species-level), while 'fixed' averages used a fixed decomposability per species, averaged over all plots across the gradient. Within-species (intraspecific) variation in decomposability was then calculated as the difference between 'specific' averages (total variation) and 'fixed' averages (variation caused by community changes, i.e. species turnover effects), following Lepš et al. (2011). The three components (specific, fixed and intraspecific) of community-level decomposability were used as response variables in parallel one-way ANOVAs, with elevation specified as a factor with five levels. Because the distributional assumptions for the regular F-test were not fulfilled, we used permutation tests instead. Iterations terminated when the estimated standard deviation fell below 0.1 of the estimated p-value, with a minimum of 50 iterations, or continued until a maximum of 5000 iterations (Anscombe 1953). Whenever the specific mean of decomposability (total variation) was affected by elevation at significance level $\alpha = 0.05$, pairwise comparisons were performed using permutation tests (Benjamini–Hochberg correction) to check for differences between elevation levels. In addition, we quantified how much variability can be accounted for by the individual components by breaking down the sum of squares (SS) across the three ANOVA models as follows: $SS_{specific} = SS_{fixed} + SS_{intraspecific} + SS_{cov}$, where $SS_{cov}$ is the covariation between species turnover effects (fixed) and intraspecific variability effects (intraspecific) (Lepš et al. 2011). We used the same calculations for community-level N and P release and functional traits.

To assess the relationship between decomposability and functional traits at the community level, we carried out multiple linear regression using linear models, with community-weighted mean decay rate k as the response variable and community-weighted mean functional traits as fixed factors. We expected primary producer group (lichen or bryophyte) to affect the outcome of the multiple regression, so we included the ratio of bryophyte cover to total cryptogam (bryophyte + lichen) cover determined for each plot as an additional fixed effect. We calculated abundance-weighted functional trait means for the cryptogam (lichens and bryophytes) community at the whole plot level using the trait data presented by (Roos et al. 2019). For the multiple regression analysis, we removed N:P ratio before model selection because it was collinear with P (Spearman's rho = −0.74, $p < 0.001$), and we then followed a stepwise model selection using Akaike information criterion (AIC).

To assess the relationship between decomposability and traits across the entire data set (with each species in each plot as a separate data point), we carried out an ANCOVA using linear mixed effects models. We included decay rate per sample as the response variable, primary producer group (lichen, bryophyte) as a categorical fixed effect, functional traits (N, P, N:P, pH and WHC) as continuous fixed effects, and plot nested in elevation as random effects. To take into account the heterogeneous variance of the observations, we specified a fixed variance structure, which allows for larger residual spread if decay rate increases. Phosphorous was collinear with N:P ratio (Spearman's rho = −0.74, $p < 0.001$) and WHC (Spearman's rho = 0.72, $p < 0.001$) and was therefore excluded before analysis. We followed a stepwise model selection using Akaike information criterion (AIC). The conditional coefficient of determination ($R^2$) was calculated to provide a measure of the variance explained by the entire model, including both fixed and random effects (Nakagawa and Schielzeth 2013).

Finally, we assessed intraspecific decomposability by analysing the effect of elevation on decay rate of each individual species for which we had decomposability measures of at least three out of five plots per elevation, using separate one-way

ANOVAs for each species. If effects of elevation were significant at α = 0.05, post hoc tests were performed using Tukey's HSD to explore differences between means. The analyses were performed using the R-packages cati (Taudiere and Violle 2015), lmPerm (Wheeler and Torchiano 2016), rcompanion (Mangiafico 2019), nlme (Pinheiro et al. 2018), MASS (Venables and Ripley 2002) and MuMIn (Barton 2018) in R ver. 3.5.2 (<www.r-project.org>).

## Results

### Community level decomposability

Decomposability of lichens and bryophytes at the whole community level increased with increasing elevation (total variation; permutational ANOVA, iterations = 5000, p = 0.026), with higher decomposability at the higher two elevations compared to the lower three elevations, although differences between elevational means were not identified by Tukey's post hoc test at α = 0.05 (Fig. 1a). The variation in decomposability across elevation was mostly driven by species composition, while intraspecific variability effects were very small (Fig. 1a). Nitrogen release at the community level was unresponsive to elevation (total variation; permutational ANOVA, iterations = 211, p = 0.886; Fig. 1b). For N release, species turnover effects and intraspecific variation both changed with elevation, but in opposite directions, resulting in a strong negative covariation between the two, leading to no detectable response in the total variation (Fig. 1b). Community-level P release decreased with increasing elevation (total variation; permutational anova, iterations = 5000, p < 0.001; Fig. 1c). The variation in P release was mostly driven by species turnover effects, but intraspecific variation greatly improved the total variation explained by elevation because of its positive covariation with species turnover effects (Fig. 1c).

Cryptogam community-weighted functional traits N and N:P increased while P decreased with increasing elevation, with these changes being explained to a large extent by intraspecific variability effects (Supplementary material Appendix 1 Fig. A1). Community-weighted pH varied across elevation and WHC tended to decrease with increasing elevation, and these changes were mainly driven by species turnover effects (Supplementary material Appendix 1 Fig. A1). Multiple regression of community-weighted mean decomposability against community-weighted functional traits resulted in a final model that included N, P, pH, the square of pH, relative bryophyte cover and the interaction of pH and relative bryophyte cover as predictors (Table 1). Model predictions showed that in general, increasing N and P enhanced decomposability, while pH and bryophyte cover decreased decomposability (Fig. 2). Further, low values of relative bryophyte cover resulted in a decrease in decomposability with increasing pH, but with the reverse occurring when the relative bryophyte cover was high (Supplementary material Appendix 1 Fig. A2).

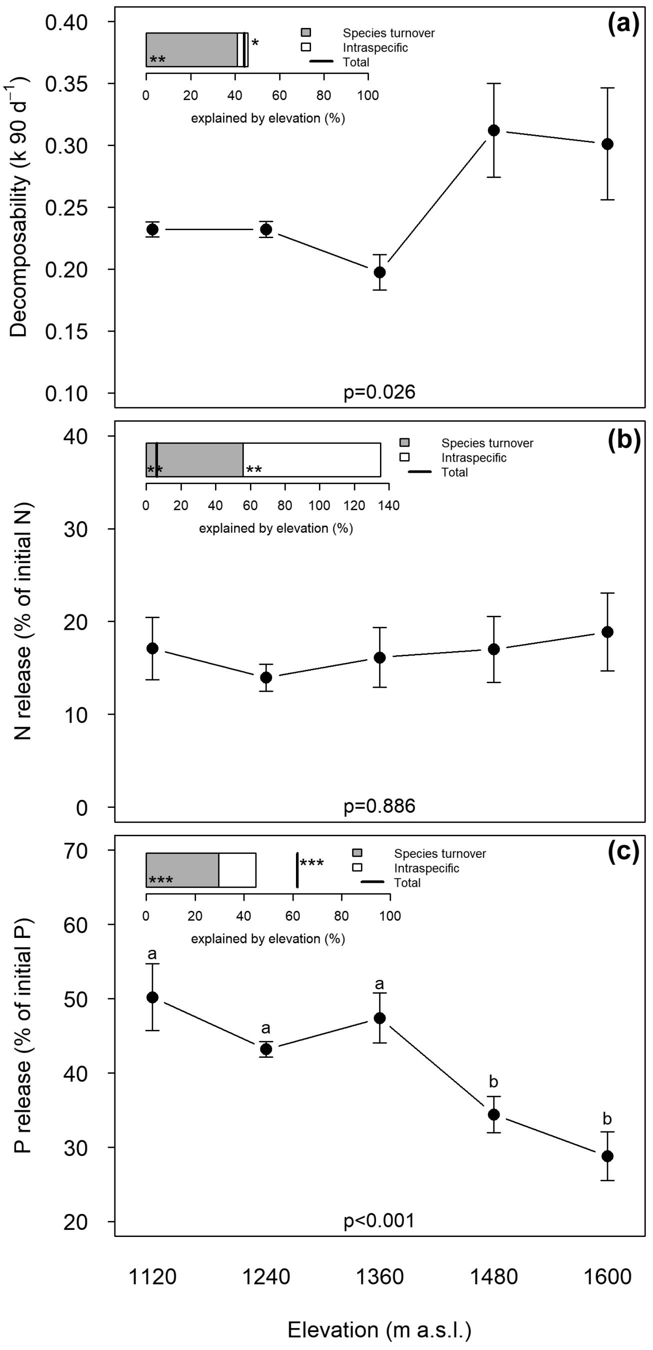

Figure 1. Community-weighted mean decomposability (a), nitrogen (N) release (b) and phosphorus (P) release (c) of lichens and bryophytes across elevation (decomposability expressed as decay rate k (90 days$^{-1}$), N and P release expressed as percentage of the initial concentration). p-values are denoted at the bottom of each panel. Variation explained by elevation is shown in the top left corner of each panel: the grey part of the column corresponds to species turnover effects, the white part corresponds to intraspecific variability effects and the black bar denotes the total variation, i.e. the sum of species turnover and intraspecific variability and their covariation. Significant differences are denoted with * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

Table 1. Results of the final model selected following multiple regression of community-weighted decomposability (decay rate k (90 days$^{-1}$)) of cryptogams (parameter estimates and standard errors, t statistic and p-value), explained by community-weighted functional traits (N, P, pH) and cover of bryophytes relative to total cryptogam cover. Linear models were used with functional traits and relative bryophyte cover as fixed effects.

| | Estimate | SE | t | p |
|---|---|---|---|---|
| (Intercept) | 21.39 | 7.44 | 2.82 | 0.012 |
| Nitrogen | 0.48 | 0.07 | 6.54 | <0.001 |
| Phosphorus | 1.05 | 0.45 | 2.31 | 0.034 |
| pH | −9.88 | 3.71 | −2.66 | 0.016 |
| Relative bryophyte cover (BRYO) | −4.92 | 2.20 | −2.24 | 0.039 |
| pH$^2$ | 1.14 | 0.45 | 2.51 | 0.023 |
| pH × –BRYO | 1.12 | 0.53 | 2.11 | 0.050 |

Number of observations (n) = 24, degrees of freedom (df) = 17, R$^2$ = 0.82.
Parameters excluded during model selection: water holding capacity (WHC).

### Individual level decomposability

Decomposability at the individual level (i.e. where each species in each plot represented a separate data point) was best explained by a model that included primary producer group (bryophytes versus lichens), pH and the square of pH as predictors (Table 2). Lichens overall had a higher decomposability than bryophytes (Fig. 3). Model predictions showed that both primary producer groups had the lowest decomposability at approximately pH = 4, while above this value, decomposability increased with increasing pH (Fig. 3). At the within-taxon level, decomposability of *Cladonia rangiferina/stygia* decreased while that of *Polytrichum* spp. increased with increasing elevation (Fig. 4). The decomposability of no other species responded to elevation at p = 0.05, but decomposability of *Cladonia arbuscula* and *Cetraria* spp. showed a marginally non-significant response (p<0.1) (Fig. 4).

## Discussion

Contrary to our first hypothesis, we found that decomposability of lichens and bryophytes at the community level overall increased with increasing elevation. Meanwhile,

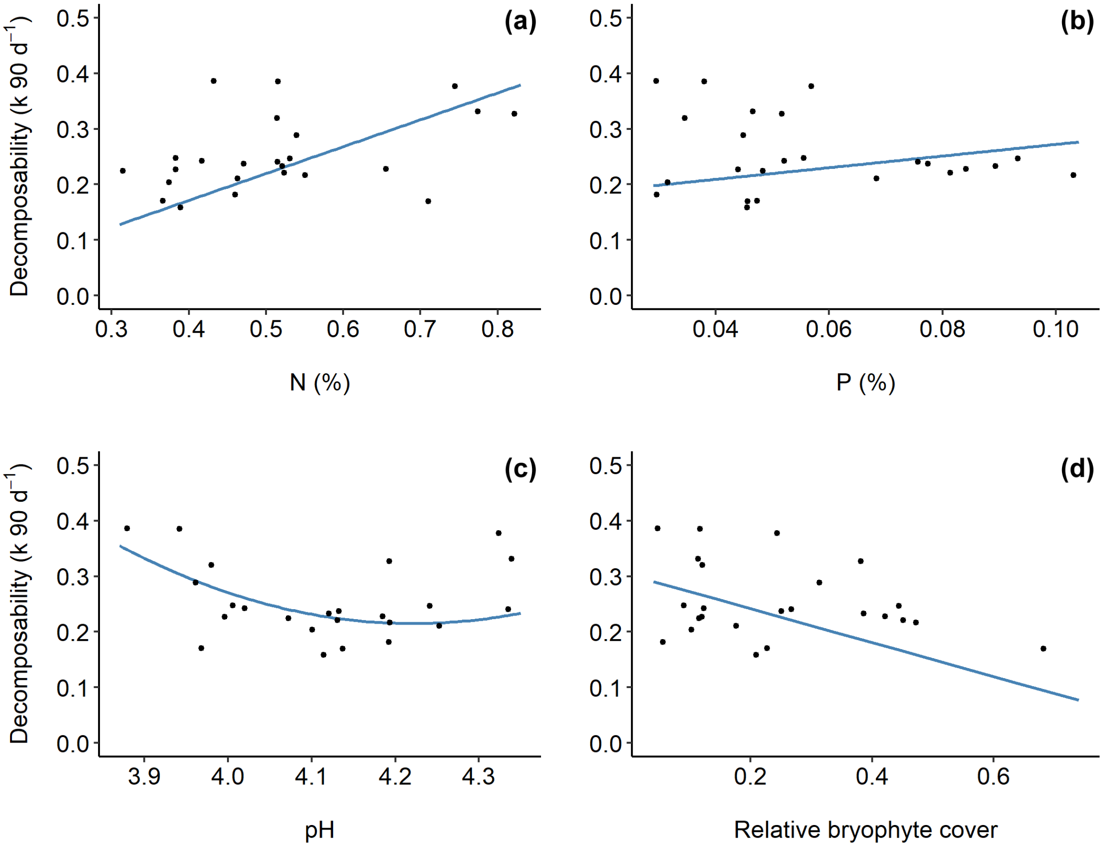

Figure 2. Community-weighted mean decomposability (decay rate k (90 days$^{-1}$)) of cryptogams (lichens and bryophytes) explained by community-weighted (a) nitrogen (N), (b) phosphorous (P), (c) litter pH and (d) cover of bryophytes as a proportion of total cryptogam cover. Dots denote the actual measurements at plot-level, while lines denote model predictions of the regression model presented in Table 1. For each panel figure, the model predictors not shown in the graph were set to mean values.

Table 2. Results of ANCOVA after model selection of decomposability (decay rate k (90 days$^{-1}$)) of cryptogams at the individual level (numerator and denominator degrees of freedom, F statistic and p-value), explained by primary producer group (lichens versus bryophytes) and functional traits (pH). Mixed effects models were used with primary producer group and traits as fixed factors, and plot nested within elevation as random effects.

| | df | F | p |
|---|---|---|---|
| (Intercept) | 1, 114 | 317.99 | <0.001 |
| Primary producer group | 1, 114 | 29.95 | <0.001 |
| pH | 1, 114 | 22.96 | <0.001 |
| $pH^2$ | 1, 114 | 17.38 | <0.001 |

Conditional $R^2 = 0.69$. Parameters excluded during model selection: nitrogen (N), nitrogen to phosphorous ratio (N:P) and water holding capacity (WHC).

community-level P release decreased with increasing elevation, while N release did not change with elevation. In line with our second hypothesis, we found that community-level decomposability was driven by species turnover across elevation, while intraspecific variation was mostly unimportant, despite several species being present across the whole gradient. Further, we found that variation in all functional traits except WHC explained decomposability, in line with our third hypothesis. At the community level N and P concentrations, pH and the relative cover of bryophytes explained decomposability, while at the individual level only primary producer group and pH explained decomposability.

The increase in litter decomposability with elevation at the community level was driven by a combination of functional traits, including N and N:P which also increased with elevation (Supplementary material Appendix 1 Fig. A2). This is in line with previous studies for which decomposition rates of lichens and bryophytes were positively related to nutrient concentrations (Lang et al. 2009, Asplund and Wardle 2013). However, the increase in N and decomposability with elevation contrasts earlier work on vascular plants that frequently shows a shift from a nutrient acquisitive to a nutrient conservative strategy with increasing elevation and associated declining temperature (Sundqvist et al. 2013, Read et al. 2014, Mayor et al. 2017). As such, previous studies in various ecosystems have found vascular plant litter decomposability to show either a negative or neutral response to increasing elevation (Salinas et al. 2010, Sundqvist et al. 2011a, Fujii et al. 2017). However, some work has shown greater vascular plant N concentrations at higher elevations (Körner 1989, Morecroft et al. 1992), which could be the result of a surplus in N availability due to reduced growth caused by colder temperatures (Körner 2003).

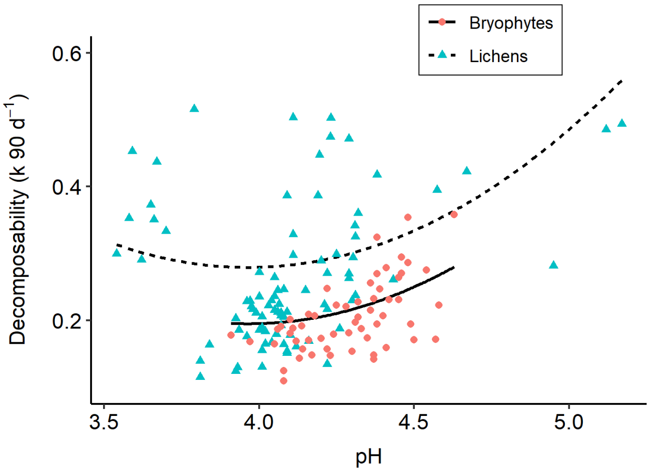

Figure 3. Decomposability (decay rate k (90 days$^{-1}$)) of individual lichen and bryophyte samples explained by their pH. Dots and triangles denote the actual plot-level measurements for each bryophyte and each lichen species, respectively, while lines denote model predictions based on the ANCOVA model presented in Table 2.

The increasing cryptogam N:P ratios that we found with increasing elevation indicate a shift from mainly N-limited decomposition towards more P-limited decomposition (Güsewell and Verhoeven 2006). In line with this, the amount of P released during decomposition also decreased with elevation, which aligns with previous work on decomposition of vascular plants across an elevational gradient in subarctic tundra (Sundqvist et al. 2011a). This could be the result of the decrease that we observed for P concentration in cryptogam material with elevation prior to decomposition, given that lichens with low initial nutrient concentrations have been found to lose nutrients more slowly during decomposition (Campbell et al. 2010). In contrast, N release was not related to initial N concentration, and was poorly explained by elevation due to the opposing effects of species turnover and intraspecific variation.

Irrespective of elevation, decomposability was related to both the relative abundance of the two primary producer groups (i.e. bryophytes versus lichens) and pH, both at the community level and at the individual level (community-level pH and relative abundance of bryophytes were not correlated with elevation (Supplementary material Appendix 1 Table A2)). The importance of growth forms in driving decomposability is well recognized (Quested et al. 2003, Dorrepaal et al. 2005), and bryophytes have previously been shown to decompose particularly slowly (Hobbie 1996, Cornwell et al. 2008, Lang et al. 2009, Hagemann and Moroni 2015), meaning that higher proportions of bryophytes should result in lower decomposability. Previous studies have found that decomposability increases with increasing pH in lichens (Asplund and Wardle 2013) and vascular plants (Cornelissen et al. 2006). In our study, the link between litter pH and decomposability at the community-level was less straight-forward, because we found a non-linear relationship where decomposability was relatively high at low pH. At the individual species level, our results show that decomposability changes little with increasing pH until the pH gets beyond a certain threshold (roughly 4.2), after which it increases rapidly. We also found that the relationship between pH and decomposability was more apparent for bryophytes than for lichens, which is in contrast to Lang et al. (2009) who found that decomposability was related to pH for lichen but not for bryophyte material. However, for our study, the overall relationship between lichen decomposability and pH

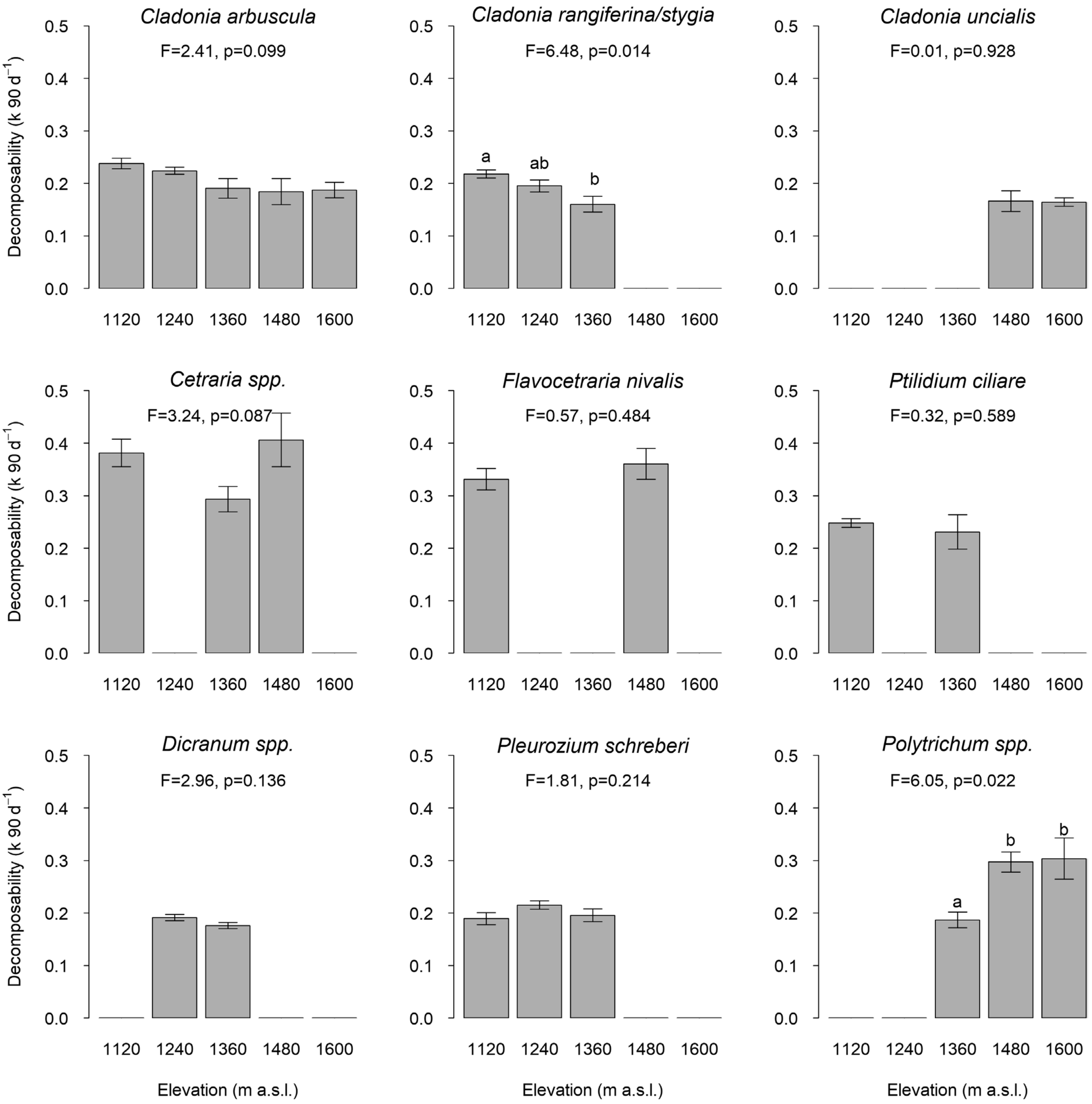

Figure 4. Mean (± SE) decomposability (decay rate k (days$^{-1}$)) of each abundant lichen and bryophyte species across elevation. Different letters denote significant differences between elevation levels using Tukey HSD at $\alpha = 0.05$.

was weakened by *Flavocetraria nivalis*, which has a low pH but relatively high decomposability (Supplementary material Appendix 1 Fig. A3).

Species turnover was the main driver of community decomposability across elevation, which is consistent with findings from previous studies across strong environmental gradients (Wardle et al. 2009, Sundqvist et al. 2011a), and suggests that community decomposability is more responsive to environmental gradients across which there is a greater shift in community composition, i.e. high species turnover. Thus, the increase in decomposability at higher elevations in our study must be the result of increasing dominance by faster-decomposing lichen and bryophyte species at higher elevations. Consistent with this, slow-decomposing lichens such as *Cladonia arbuscula* and *C. rangiferina/stygia*, dominated the lower elevations, while faster-decomposing *Cladonia* spp. and *Cetraria* spp. were abundant at the higher elevations. Similarly, slow-decomposing *Pleurozium schreberi* dominated the bryophyte community at the lower elevations while faster-decomposing *Polytrichum hyperboreum* was the most abundant bryophyte at higher elevations. Overall, the shift in species composition with increasing elevation involves a general decrease of species known to be associated with boreal habitats and an increase in species associated with alpine and arctic habitats. The smaller stature and more compact growth form of those arctic–alpine species that dominate at higher elevations might result in less dilution of N (Körner 2003), which could have resulted in the observed higher litter quality and decomposability of these species.

Within-species variability contributed little to variation in decomposability at the community level across the elevational gradient, even though some of the traits that explained community-level decomposability were in a large part determined by intraspecific variation, notably P and N:P ratio. Similarly, Jackson et al. (2013) found that while intraspecific variability was important in explaining overall community-level trait variability it was a poor predictor of litter decomposability, meaning that within-species trait variation may not necessarily be an important driver of ecosystem processes. However, in the present study, intraspecific variation was an important driver of nutrient release across elevation and made an important contribution to the total variation in P release at the community level explained by elevation, while it greatly reduced the total variation in community level N release explained by elevation. At the within-taxon level, we only found significant effects of elevation on decomposability of *C. rangiferina/stygia* and *Polytrichum* spp. In our study, *Polytrichum* spp. was not separated to species and the increase in decomposability of *Polytrichum* with elevation may therefore not be a within-species response, but rather due to species turnover within the genus. As such, the middle elevation contained only *P. strictum*, while the highest two elevations mainly contained *P. hyperboreum* (Supplementary material Appendix 1 Table A3). This species shift could have resulted in the observed increase in decomposability within the *Polytrichum* genus, consistent with Lang et al. (2009), who found that *P. strictum* had the lowest decomposability among all the non-*Sphagnum* mosses, while *P. commune* had the highest. This highlights the importance of between-species variation in decomposability, even among closely related species.

To conclude, we showed that community-level decomposability of lichens and bryophytes increased with increasing elevation, and that variation in both community and individual level decomposability was driven by nutrient concentrations, pH and the identity of the primary producer group. In line with previous work on vascular plants (Jackson et al. 2013), our study highlights the importance of among species differences in driving decomposability of cryptogam material, even along our relatively short (500 m) elevational gradient with considerable species overlap. It suggests that while within-species variation of primary producer traits can help explain community-level trait variation (Albert et al. 2010, Violle et al. 2012, Roos et al. 2019), it may not necessarily explain community-level variation in ecosystem processes, although intraspecific variation was important for N release in our study. Our findings lead us to expect that among species differences may be even more important in driving decomposability along very large environmental gradients because of more profound species shifts, while intraspecific variation may be more significant at shorter environmental gradients (Siefert et al. 2014). Our findings also indicate that future climate warming (as reflected by lower elevations) may not necessarily result in better litter quality and thus faster decomposition at least when cryptogams are considered. In a scenario where lichen and bryophyte species from lower elevations move upwards as a result of global warming, their lower decomposability might offset the expected increase in decomposition rates caused by higher decomposer activity, potentially leading to a negative feedback on carbon cycling (Cornelissen et al. 2007a). Given that lichens and bryophytes often respond negatively to climate warming due to increased competition from vascular plants (Pajunen et al. 2011, Maliniemi et al. 2018), this scenario is likely to occur most strongly for lichen and bryophyte-dominated ecosystems where vascular plants struggle to establish or persist, such as wind-exposed ridges. Further, our study shows that effects of future climate warming on decomposability of lichens and bryophytes will be greatest when it causes a high turnover of species.

## Data availability statement

Data is available through NMBU Open Research Data – Dataverse Network Norway (<https://dataverse.no/>) doi: 10.18710/LQCNY9, <https://doi.org/10.18710/LQCNY9>.

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*Author contributions* – JA designed the study in consultation with KvZ, RR, KK, SL and DW. KvZ and RR conducted field and lab work. KvZ analysed the data and led the writing in collaboration with RR, KK, SL, DW and JA.

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Supplementary material (available online as Appendix oik-07257 at <www.oikosjournal.org/appendix/oik-07257>). Appendix 1.