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Effects of elevation on the lichen community palatability in an alpine ecosystem

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Master of Science in Ecology

Preface

This thesis is the final part of my master's degree in general Ecology at the department of Ecology and Natural Resource Management, Norwegian University of Life Sciences. I want to thank Johan Asplund and Tone Birkemoe for their guidance and feedback. Further I want to thank my family for their support.

Gaspard Levavasseur

Abstract

Lichens are present in almost all terrestrial ecosystems, and in some of them, they are the main primary producers. Most studies focus on vascular plant communities, even studies on ecosystems where lichens represent an important part of the primary production, such as alpine ecosystems. For example, the effect of elevation on primary producer community palatability has been studied numerous times for vascular plants, but not once for the lichen communities. In my study, I assess the effect of elevation on palatability, I determine if the community response is due to intraspecies mechanisms or to species turnover, and I identify which other functional traits could explain the change observed in palatability.

I collected samples of 14 lichen species, on five sites along an elevation gradient, from 1120 m a.s.l. to 1600 m a.s.l. The samples were used to perform a feeding bioassay using snails, *Cepaea hortensis*. I had access to data previously collected at the same sites on other functional traits, and I used these data to determine which functional traits could explain the change observed in palatability.

I found that as elevation increased, so did palatability, and the intraspecies variation was strongly connected to the increase in palatability. Four of the five functional traits (nitrogen concentration, phosphorous concentration, water holding capacity and specific thallus areal) explained the effect of elevation on palatability. However, the study revealed no relationship between palatability and decomposability.

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1 Introduction

Lichen are primary producers found in most terrestrial ecosystems; between 8-10 % of the terrestrial ecosystems are dominated by lichen (Nash 2008). The importance of lichen varies greatly from one ecosystem to another, from representing under a percent of the total biomass to being the main primary producer. Lichens get more important in ecosystems considered stressful for vascular plants: boreal coniferous forest, dune systems, high altitude, maritime rocks (Nash 2008). In alpine ecosystems, as elevation increases, conditions become harsher for vascular plants, and lichen communities become a more important part of the primary production.

Nutrients captured by the lichen community are released by decomposition and lichenivory. An important range of living organisms feed on lichens: microorganisms, gasteropods, arthropods and mammals (Nybakken et al. 2010; Asplund et al. 2010). The way organisms feed on lichen varies greatly, for example some herbivores show clear preferences for some lichen species, or feed principally on some parts of the lichen (Asplund et al. 2010; Baur et al. 1994). Several factors have been identified as playing a role in the level of lichenivory experienced by different species: the form of the thallus, the quality and quantity of Carbon Based Secondary Compounds (CBSCs), and the nutrient concentration (Asplund 2011, Asplund et al. 2010; Nybakken et al. 2010; Nash 2008). These characteristics determine how useful as a food source the lichen is for its consumers.

For primary producers in terrestrial ecosystems, several studies have focused on palatability and its relation to other functional traits, such as N:P ratio, N, P and C concentration, water holding capacity (WHC), specific leaf/thallus area (SLA/STA) and decomposability (Asplund et al. 2010; Dostálek et al. 2020; Kagata et al. 2011; Descombes et al. 2017). For vascular plants, a relation was found between nutrient concentration and palatability, and palatability was also explained by decomposability, where species decomposing at the faster rate had a higher palatability (Grime et al. 1996, Wardle et al. 1998). Similar explanation of palatability by functional traits was not necessarily observed for lichens, for example no relation was found between palatability and decomposition (Asplund et al. 2013). Further, an increase in N concentration, due to fertilization of the lichens, has been found to result in a decrease in palatability (Asplund et al. 2017). The quality and quantity of CBSCs present in a lichen play an important part in the palatability of a lichen species (Asplund et al. 2013; Asplund et al. 2010).

The study of the response of functional traits at the community level is a field that strongly developed in the last decade, and is now well furnished for vascular plants. However, it is less developed for the lichen community, and for lichen palatability at the community level I did not find any studies. In the present study, I examine the response of the lichen palatability at the community level, using community weighted means of the functional trait.

The alpine environment provides us with a temperature gradient in a relatively small geographical area, and so gives us the opportunity to study the effect of the temperature variation on the lichen community. The better we understand the adaptation the community undergoes along this gradient, the better we will be able to predict and understand the consequences that global warming will have on these communities. Effects of the elevation gradient on plant communities in alpine landscapes have been studied before, and are well documented for vascular

plants. Effects of the elevation change on different functional traits of plant communities have been studied for an important range of functional traits: nitrogen, carbon and phosphorous concentration, pH, SLA/STA, WHC, palatability, dry matter concentration and height (Matteodo et al. 2013; Roos et al. 2019; van Zuiljen et al. 2020; Choler et al. 2005). Primarily, these studies were concentrating mainly on vascular plant communities, but in the late years, some research have also been focusing on cryptogam communities or comparing the response of vascular plant communities to cryptogam communities. It appears that the responses to altitude change of the different communities of primary producers were not as similar as we could expect, as the results from Roos et al. (2019) show: N and P concentration react in a similar way to elevation change, but for pH, SLA/STA, the response vary in function of the type of primary producer. SLA/STA increase with elevation both for vascular plants and lichen, but SLA decreases for bryophytes. Tissue PH shows an increase only for vascular plants, while it is irresponsive for bryophytes. Regarding lichens, the trend is not clear, but elevation has an effect on the pH of the community. Generally, the reaction of primary producer communities to an elevation gradient in alpine ecosystems has been shown for vascular plants to be a tendance of the functional traits to change toward a strategy of resource economy as altitude increases. However, the same trend was not found so clearly for cryptogam (Roos et al. 2019; Freschet et al. 2010; Henriques et al. 2017).

The variation of a functional trait of a community in response to a change, is coming from two sources: intraspecies variation and species turnover (Lepš et al. 2011; Bolnick et al. 2011). The source of variation of functional traits is function of the type of primary producer (Roos et al. 2019). Understanding these sources of variation will be of prime importance to understand the way these communities will respond to climate change (Bolnick et al. 2011). For vascular plant communities, the response of functional traits is mainly driven by species turnover, with some disparity in the origin of the variation (Ross et al. 2019; Siefert et al. 2015). For bryophytes communities, the species turnover is clearly the main driver of functional traits variation. For lichen communities, for nutrients and chemical functional traits, intraspecies variation is more important, but species turnover is determinant for morphological functional traits, as SLA and WHC.

In my study, I focus on the palatability of the alpine lichen community along an elevation gradient starting at 1120 m and with the highest site at 1600 m. From the data collected by Roos et al. (2019) and van Zuiljen et al. (2020), I already know how some functional traits of the lichen community react along the elevation gradient. While WHC and P concentration decrease, N concentration, N:P ratio, STA increase. For the pH no clear trend could be detected. I want to establish whether there is a connection between these traits and palatability, a connection that has not been found in precedent studies (Asplund and wardle 2013). Most studies on palatability of primary producers in alpine ecosystems have focused foremost on vascular plants. For the type of ecosystem that I study, it is important to acquire a more wholefull picture, because of the important part represented by cryptogam community in the primary production. It is also important to note the particularity of palatability of the lichen community: lichens are equipped with diverse CBSC. As several studies (Roos et al. 2019; van Zuilen et al. 2020;) have shown, some of them at the same sites as the ones I used for my sampling, different types of primary producers

will not react to the elevation gradient in the same way, so the understanding of the plant community pass by an understanding of the lichen community.

In the present study, palatability is determined by doing a feeding test using *Cepae hortensis*, a generalist snail species, that have been used before on feeding test of lichen (Asplund and Wardle 2013). The biomass eaten during a day long feeding test give me a way to determine the palatability of the five lichen communities, each elevation level corresponding to a community. With these data, I am also able to determine the source of variation of the palatability, separating the variation due to species turnover from the one due to intraspecific variation. I will use this setup to assess the following three hypotheses, that

- (1) community-level lichen palatability will decrease with elevation. Palatability in other groups has been showed to decrease as condition become harsher. In my study, I suppose that the highest elevation will represent a more stressful environment than the lowest.
- (2) community-level lichen palatability is driven by intraspecies variation. Nutrient concentration is an important factor influencing palatability in several groups, and I know that the variation of P and N concentration are, in the lichen communities that I study, driven by intraspecies variation.
- (3) community-level lichen palatability is positively correlated to the N and P concentration. Lichen community nutrient concentration has been mentioned to be related to palatability in vascular plants before, but also in lichens. Several of the traits influencing palatability and decomposability are common, and I expect to see a positive correlation between the two.

2 Material and methods

2.1 Study sites, plots selection and elevation gradient

The sampling sites are situated near Finse, Norway, and were established during summer 2016. The average temperature was then 7.3°C from June 1 to August 31, and the precipitation was 303,9 mm (Roos et al. 2019). In 2020, the average temperature during the same period was 6,8°C, and the precipitation was 258,1 mm. At the lowest site, the growing season was 54 days longer than at the highest. In July, the temperature dropped by 0,9 °C with each level (120 m) of increased elevation (Roos et al. 2019). The five sites are situated at the following altitudes: 1120 m, 1230 m, 1340 m, 1480 m and 1600 m, all on acidic granite-gneiss bedrock, with south-facing ridges exposed to wind (Roos et al. 2019). At each elevation level, five 1 m² plots were randomly established, and the cover of each lichen species at the sites were recorded in 2016 (Roos et al. 2019). For this study, I used a list (annex 2) of the dominating lichen species for each site, and sampled enough of each species (at least five g) on the list to conduct the feeding experiment. Decomposability was estimated by van Zuijlen (2020) based on material harvested in 2016. The decomposability data that I used are from this study. The other functional traits, N:P ratio, N concentration, P concentration, Water Holding Capacity (WHC) and Specific Thallus Area (STA) are from the study of Roos et al. (2019).

2.2 Palatability

To assess the palatability of the lichen community, I used a feeding experiment similar to the one done by Asplund et al. (2013). For this feeding test, I used the species *Cepaea hortensis*, a generalist snail that has been used before in similar feeding tests (Asplund and Wardle 2013; Gauslaa 2005). *C. hortensis* feeds on a broad specter of vegetal, and is a common species with a broad distribution area in Europe. Adults' shells are typically around 2 cm in diameter. The animals used in this study were collected during the two weeks before the experiment. About ¼ was collected in Oslo, and the rest in Ås. Only adult snails were collected. The mean weight was 1,33 g ± 0,34 SE. As far as I know, none of the snails had been used in a feeding experiment before. The snails were starved for 48 hours before the test. For each species at each plot, one thallus portion was placed in a plastic box of a base radius 26 mm and 40 mm high. To better preserve humidity in the box, a 2-3 mm thick layer of plaster was deposited on their bases (pictures of the boxes in annex 3). The thalli were air dried and weighted before being put in boxes. The lichen was rehydrated as we put the individuals of the species *C. hortensis* in the boxes, and the boxes were locked for 24 hours. After the experiment, thalli were air dried before being weighted again. The biomass consumed in gram during the feeding experiment, was determined by doing the difference between the weight before and after the experiment. This is the value that I use as an estimate of the palatability.

2.3 *Specific thallus areal (STA), water-holding capacity (WHC), Nitrogen (N), Phosphorous (P) concentration and N:P ratio*

The values of these functional traits were collected in 2016, and an in-depth description of the method of collection and measurement is available in Roos et al. (2019). Briefly, pictures of 10 individuals per plot per species was taken, and the pictures of the thallus was used to measure the STA. Water holding capacity was calculated by measuring the difference between the hydrated mass and the dry mass, and then divided by the area. The method used by Roos et al. (2019) was established and described by Gauslaa and Coxson (2011).

For N and P concentration, thallus was grounded to powder and analyzed by using Kjeldahl's analysis. Results are expressed as a percentage of the element in the dry mass of the thalli. The decomposability values used in the study are also from samples collected in 2016, and the description of the method is to find in van Zuijlen (2020). The values that I used are the decaying rate corresponding to the log of the difference between the mass before and after a 90 day long assays of decomposability.

2.4 *Data analysis*

To separate the source of the variation of the functional traits due to species-turnover from the one due to intraspecies variation, I used the method described by Lepš et al. (2011). Following this method, I use three different community parameters: The specific average, the fixed average and the intraspecific variability effect.

Specific average:

$$\text{Specific average} = \sum_{i=1}^S p_i x_{i-habitat}$$

p_i is the proportion of the i -th species in my study this correspond to the relative cover, in one plot. S is the number of species on the plot. $x_{i-habitat}$ is the specific mean trait value of the i -th species in one plot.

Fixed average:

$$\text{Fixed average} = \sum_{i=1}^S p_i x_i$$

x_i is the weighted mean value of the i -th species for all plots where the species is found.

The intraspecific variability effect is calculated by subtraction of the fixed mean to the specific mean.

Intraspecific variability effect:

$$\text{Intraspecific variability effect} = \text{Specific average} - \text{Fixed average}$$

The variation observed in the fixed average reflects the species turnover, and the specific average reflect both the changes due to intraspecies variation and the species turnover. The intraspecific variability effect reflects the intraspecies variation. This method was used for palatability, but also with the data collected in 2016 for the following traits: N concentration, P concentration, N:P ratio, decomposability, WHC and STA. For each trait, I used intra-species variation, species turnover and their covariation as response variables, and the five levels of elevation as a factor in three one-way permutational ANOVAs. I used permutation ANOVAs because the condition of a regular f-test could not be fulfilled. I 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: $SS_{\text{specific}} = SS_{\text{fixed}} + SS_{\text{intraspecific}} + SS_{\text{cov}}$, where SS_{cov} is the covariation between species turnover effects (SS_{fixed}) and intraspecific variability effects ($SS_{\text{intraspecific}}$) (Lepš et al. 2011).

For all the functional traits, I performed pairwise permutations tests to determine the existence of difference between the levels of elevation for the community weighed specific traits. The p-value was corrected using the false discovery rate (FDR) correction.

A multiple linear regression analysis was done to determine which of the other functional traits could be used to explain the palatability at the community level. I used the palatability weighted mean of each plot as the response variable, and the N, P, STA, WHC and decomposability as predictor variables. N:P ratio was not included in the model, because it is directly dependent of N and P.

One-way ANOVAs were performed for the species present on at least three sites. For the species where a significant effect of the elevation was detected, I performed a pair-wise permutation test as a post hoc test. These tests were performed by using the weighted specific mean of the species.

3 Results

3.1 Variation of biomass consumed across five sites

Palatability vary significantly with elevation. Tested with a PermANOVA test ($p < 0.001$), palatability increase by **61 %** from the lowest site to the highest. There is an increase in palatability between the first and second site, and palatability is at the lowest for the third and fourth site, before increasing to the highest value for the last site. The increase between the site with the lowest palatability, site 4, and the one with the highest, site 5, is by **91 %**.

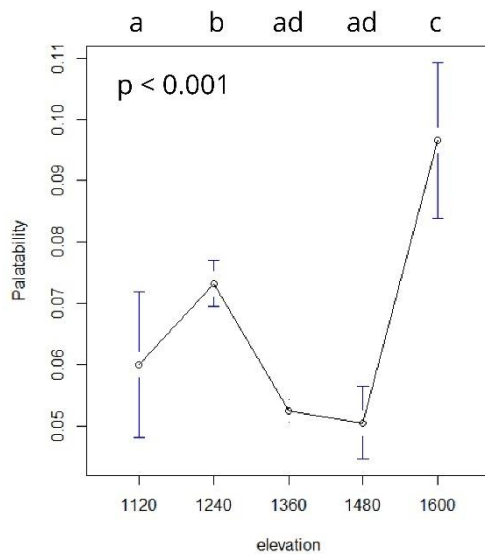


Figure 1. Mean weighted palatability with standard error. Significant differences between elevation are denoted with different letters ($\alpha=0,5$, pairwise permutation test).

3.2 Origin of the variation of palatability

The decomposition of the total variation of palatability due to elevation is driven mainly by intraspecific variation ($p < 0.001$), but species turnover plays a significant role ($p = 0.032$). The covariance of the intraspecies variation and species turnover is negative (- 48 %). See table 1 (below).

3.3 Turnover and intraspecies variation

The same method used on palatability for decomposing the total variation due to elevation is used with the other following functional traits: N concentration, P concentration, N:P ratio, STA and decomposability. N concentration shows the same response as palatability; most of the variation is due to intraspecies variation, and the covariation of species turnover and intraspecies variation is negative. Decomposability, WHC and STA, are mainly driven by species turnover and the covariation is positive. P concentration and N:P ratio are, as N concentration and palatability, driven by intraspecies variation, but the covariation is positive. The variation of N concentration, palatability, WHC, and N:P ratio are explained only partially by just one of the sources of variation.

For the decomposability and the STA, the intraspecies variation are small, representing respectively 3.7 % and 8 % of the variation. For P concentration, the part of the total variation explained by the intraspecies variation is superior to the species turnover part, 57 % and 4 % of the variation.

Table 1. Relative contribution of species turnover and intraspecific variation in explaining differences in functional traits. The p-value is within brackets, highlighted values correspond to a p value inferior to 0.05.

	relative contribution of			
	Species turnover	intraspecific variation	Covariation	total
N	1.03(0.481)	1.59 (0.277)	-1.82	0.79 (p<0.001)
Decomposability	0.27 (0.099)	0.03 (p<0.001)	0.072	0.38 (0.039)
WHC	0.28 (0.052)	0.008 (0.13)	0.06	0.35 (0.055)
STA	0.42 (0.001)	0.08 (p<0.001)	0.10	0.61 (0.001)
NP	0.11 (<0.001)	0.50 (p<0.001)	0.35	0.96 (p<0.001)
P	0.04 (0.27)	0.57 (p<0.001)	0.21	0.83 (p<0.001)
Palatability	0.21 (0.032)	1.15 (p<0.001)	-0.48	0.88 (p<0.001)

3.4 Effect of elevation on functional traits

The result of the Permanova we performed for the other functional traits show a significant difference between the sites at $p < 0.01$ for all the functional traits except for WHC ($p = 0.055$).

A pairwise two-sample permutation test is conducted as a post hoc test for each of the functional traits, with a fdp method of p adjustment and significant level of difference at $p < 0.5$. Results are reported in table 3 for palatability and in annexe 1 for the other functional traits. Regarding palatability, at a level of significance of $p < 0.05$, three of the sites show no significant differences between them: site 1 (0.06), site 3 (0.052), and site 4 (0.051). Site 2 (0.073) and 5 (0.097) was clearly different of the 3 others. Palatability is the sole functional trait for which the test shows a significant difference between site 1 and site 2 ($p = 0.044$), an increase of 22 % of the palatability between these two sites. STA and WHC seem to vary relatively little across the gradient. For both, the only significant differences are found between the sites 2 and 3, and between 2 and 4. For decomposability, no pair of sites show any significant level of difference. For N concentration, P concentration, N:P ratio the picture is more similar to the one I find on palatability, where most pair of sites show a significant difference. A table with the totality of the pairwise permutation test results is disponible in annex.

3.5 Predicting palatability with functional traits

The multiregression analysis result in the model presented in table 2. Of the five explanatory factors I choose to test, four is found to explain palatability: N concentration, P concentration, WHC and STA. Palatability increases with N and P, but decreases with STA and WHC. No relation is found between decomposability and palatability.

Table 2. Results of the model selected by multi linear regression of community-weighted palatability, explained by functional traits N concentration, P concentration, STA and WHC.

multiple linear regression				
coefficients	estimate	SE	t value	Pr(> t)
intercept	0.049182	0.020375	2.414	0.0255
N	0.169579	0.022353	7.586	<0.001
STA	-0.006673	0.002273	-2.936	0.008
P	0.771361	0.268507	2.873	0.009
WHC	-0.174369	0.07367	-2.367	0.028
multiple R ²	0.7952			
p-value	<0.001			

3.6 The effect of elevation on individual species

Of the eight species presents at three or more sites, four show significant variation in palatability across the elevation gradient, tested with ANOVA. The palatability of *Flavocetraria nivealis* ($f = 5.334$, $p = 0.0302$) and *Cladonia gracilis* ($f = 12.41$; $p = 0.001$) increase with elevation (Fig 2 a,d). The palatability of *Cladonia arbuscula* ($f = 14.11$; $p = 0.001$) and *Cladonia rangiferina* ($f = 18.77$; $p < 0.001$) decrease with elevation (Fig 2 b,c). The results of the pairwise permutation test are summarized in figure 2. For four species: *C. uncialis*, *C. islandica*, *Stereocaulon sp.* and *F. cucullate*, no significant change is observed. The range of increase or decrease varies importantly from one species to another. The most important variation in palatability is observed for *C. uncialis*, the palatability increases 60 times between the lowest mean, site 2 (1240m), and site 4 (1480m). The second most important variation is an increase in palatability for *C. gracilis*, increasing seven times between site 4 (1480m) and site 5 (1600m).

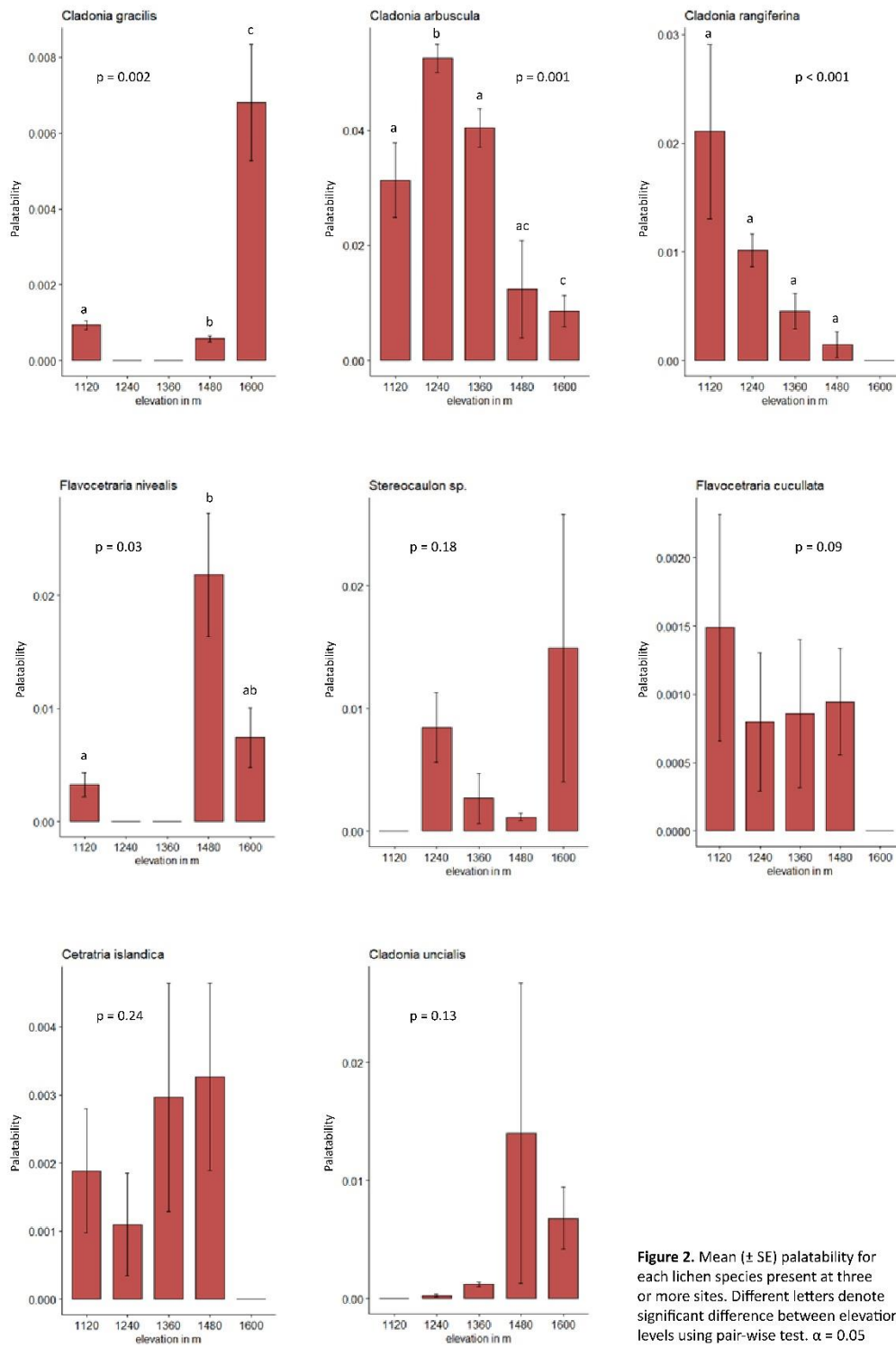


Figure 2. Mean (\pm SE) palatability for each lichen species present at three or more sites. Different letters denote significant difference between elevation levels using pair-wise test. $\alpha = 0.05$

4 Discussion

My first hypothesis was not confirmed by my results: I found a significant decrease in the palatability of the lichen community as the elevation increased.

My second hypothesis was confirmed by my results. I found a significant increase in the palatability of the lichen community as the elevation increase.

My third hypothesis was partly sustained by my results: N and P concentration were positively correlated to the palatability, but the decomposability was not correlated to the palatability. I also found that the palatability was negatively correlated to two other functional traits: WHC and STA.

4.1 Increase of palatability of the lichen community in function of the elevation

As the elevation increases, the conditions will be harsher for the lichen community, with less days without snow and a higher number of days with a temperature below zero degrees. My hypothesis based on these facts was that the elevation increase will induce a strategy of resource economy for the lichen community. Thus, the response corresponding to a resource economy strategy for the functional trait I am studying, palatability, should be a decreased palatability. I found, at the contrary, that the general pattern was an increase of the palatability at the community level as the elevation increased. From the lowest site to the highest site, the palatability increased by 61%.

Studies on vascular plant communities tend to show a decrease of palatability as the elevation increases. In alpine ecosystems, the highest palatability has been found on the warmest sites (Dostálek et al. 2020; Lemoine et al. 2014). However, an increase of palatability has been mentioned by Descombe et al. (2017), and Buckley et al. (2019), that second study focusing not on the palatability at a community level but just on one species. Several studies found that functional traits may react differently to a gradient. It has also been found that the same functional traits can react differently from one group of primary producers to another (Roos et al. 2019, Albert et al. 2010, Kichenin et al. 2013).

A possible explanation to the observed increase of palatability at the community level in my study, is that the herbivory activity decreases as the elevation increases. Dostálek et al. (2020) linked an increase of palatability of vascular plants to a decrease of insect's herbivory at higher elevation in alpine ecosystems. Another explanation might be that lichens grow slower as the elevation increases, and that slow growth relates to higher N concentration (Wardle et al. 2018). As I will discuss later, the N concentration has a positive effect on palatability (Kurokawa et al. 2010; Craine et al. 2002).

Yet another explanation might be that higher elevations are associated to a decrease in water stress, due to less evapotranspiration. Roos et al., 2019 reported a decrease in WHC for the exact same lichen community that I studied. As WHC is one of the factors negatively correlated to palatability, its decrease will lead to an increase of the lichen community palatability.

4.2 Explanation of the palatability of the lichen community by functional traits

The multi linear regression analysis determined four significant explanatory factors: N concentration, P concentration, WHC and STA. The positive correlation between palatability and

N concentration is contradictory with the findings of Asplund (2010), showing that N fertilized lichen was less preferred by gasteropods. In van Zuiljen's et al. study (2020) of the decomposability of cryptogam communities, she shows a positive correlation between decomposability and both N concentration and P concentration. However, she also found that WHC was not selected as an explanatory factor in the final model.

My results show that palatability is driven mainly by intraspecies variation, as two of the functional traits positively correlate to palatability: P and N concentration. The variation of the two other traits selected as explanatory factors, WHC and STA, is driven by species turnover. Van Zuiljen et al. (2020) shows that decomposability variation is driven mainly by species turnover, and that two of the explanatory factors N concentration and P concentration vary due to intraspecies mechanisms. In my study, the model resulting from multilinear regression excludes decomposability as an explanatory factor; at the community level, decomposability seems not to be correlated to palatability, which is consistent with the results found by Asplund and Wardle (2013) and van Zuiljen et al. (2020).

To explain the absence of direct connection between palatability and decomposability of the lichen community, it is important to precise that the method used to determine palatability and decomposability are not meant to represent the actual observations in the field. The used measure of palatability does not represent the actual observable level of herbivory activity. The same applies to the decomposability rate that does not represent the actual rate of litter decomposition in the field. However, the used method to assess palatability and decomposability gives the possibility to directly relate them without interference of factors like herbivore density.

From other studies and from my results, I know that nutrient concentration and CBSCs are determinant for both decomposability and palatability (Asplund 2010, Asplund and Wardle 2013; Gauslaa et al. 2005). Nutrient concentration seems to affect palatability and decomposability in similar ways. N and P concentration relate positively to palatability and decomposability. We know that CSBCs are detrimental to herbivory and microbial activity. But not all functional traits affects the decomposability rate and palatability. For example decomposability correlates to the litter pH (van Zuiljen et al. 2020) and the palatability correlates to WHC and STA.

Asplund and Wardle (2013) found no link neither between decomposability and palatability, nor between palatability and nutrient concentration. In the study of van Zuiljen et al. (2020), WHC was excluded during the model selection and STA was not tested as an explanatory factor for decomposability. I assume that STA is not playing a significant role in the decomposability of the lichen community. From the results of these two studies and mine, I have a strong assumption that palatability and decomposability are not correlated at a community level, in opposition to the link found in vascular plants communities between these two traits. This absence of relations between palatability and decomposability at a community level might be due to the following: Morphological functional traits play a role for the palatability of the lichen community, but are less important for the decomposability. Some other factors, like litter quality, influence on the decomposability, but not on the palatability. Another explanation could be that in the feeding essay, I used an herbivore from another ecosystem, while in the decomposability bioassay the lichens used might still have had parts of the original microbial community on them. A third explanation could be that, in the field, the microbial community and the herbivore

community react differently to the elevation gradient, and thus induce different changes in respectively the palatability and decomposability of the lichen community.

As I mentioned before, Dostálek et al. (2020) detected a decreased level of insect herbivory on vascular plants, related to increased elevation. Further, this decrease corresponded to an increase in palatability. Our results show the importance of the relation between nutrient concentration and palatability of the lichen community, similar to the results of prior studies on lichen that define N as a good predictor of palatability (Asplund 2010).

Sustaining that theory, the results of the pairwise tests of the functional traits weighted-means show clearly that some of the functional traits have a greater variation along the gradient. Precisely, from the results of the pair-wise tests, I can separate the functional traits in two groups. For the first group, including N:P ratio, N concentration, P concentration and palatability, most of the sites are significantly different from one another. In the second group, which includes decomposability, WHC and STA, just a few sites differ significantly. This confirms the trend observed with several of our results, that palatability seems to relate more in its response to elevation to the chemical traits and nutrient concentration, and less to morphological traits of the lichen community. It also shows that morphological traits have less plasticity than chemical traits. This is a clear difference to the relation observed in the vascular plant communities, where no effects of the elevation were detected regarding the palatability at the species level (Descombe et al. 2020), or where palatability clearly connects to leaves' morphological traits (Dostálek et al. 2017, Descombe et al. 2020).

4.3 Intraspecies variation is driver of variability of the lichen community palatability

As I discussed before, the lichen palatability at the community level is driven by several factors: CBCS, thallus form, thickness and nutrient concentrations. Some of these factors – nutrient concentration and CBSC – are of chemical origin, and I suppose that they are the main origin of palatability plasticity for lichen species. In a precedent study, the chemical functional traits linked to the nutrient concentration of the lichen community were mainly driven by intraspecies variation (Roos et al. 2019). Morphological traits, such as thallus toughness and type of thallus, have surely an impact. For example, a study showed higher consumption rate by snails on fruticose than on foliose thallus (Asplund and Wardle 2013). Those morphological traits show less variation in my study. I suppose that the palatability follows a similar pattern to the one expressed by the chemical traits and nutrient concentrations. The intraspecies variation is also clearly the most important source of variation for these traits in precedent studies (Roos et al. 2019). When it comes to my results, they show an intraspecies variation superior to the species turnover. The covariation for the palatability is negative. This might be, as suggested by Leps et al. (2011), the results of one source of variation compensating over the other one. Thus, the increase of palatability is due to intraspecies effect, and the species turnover is in fact decreasing the palatability. I assume that some of the species that are only present at the higher sites contribute negatively to the palatability.

4.4 Increase of the palatability of different species

Eight of the species was collected at three or more sites. For four of these, the elevation have a significant impact on the palatability. The range of variation observed for individual species is maximal for *Cetreraria islandica*; its palatability increase by a factor of 20.9. The minimal variation is for the species *Flavocetraria cucullata*, where the palatability increases by a factor of 1.9. These numbers show the important palatability plasticity of some of the lichen species, and this plasticity is reflected at the community level by the relative importance of the intraspecies variation.

Not all the species show a trend similar to the one exhibited by the community; in fact, two of the species show a reduction of palatability: *Cladonia arbuscula* and *Cladonia rangiferina*. *C. rangiferina* is the only species reported as having a significant decrease in decomposability in van Zuijlen et al. (2020), and this study finds that the decomposability of the cryptogam community increases with elevation. This different response of individual species is present also for several functional traits of vascular plants, leaf N and P concentration, SLA (Kichenin et al. 2013).

As I discussed earlier, the different types of primary producers respond differently to the same gradient. In lichen communities, a similar difference of response between species has been observed before, along an elevation gradient, or with an artificially created temperature gradient, but also in vascular and bryophytes communities (Roos et al. 2019; Sancho et al. 2017; Knutsen 2018).

5 Conclusion

The study shows that palatability of lichen communities increases with elevation, and this increase is driven by intraspecies mechanisms. Climate change impacts the primary producer communities of alpine ecosystems. My results indicate that the predicted increase in temperature will induce a decrease of the palatability, thus a slower recycling of the nutrient via herbivory.

The impact of climate change might not be the same on the different types of primary producers; the results I obtained on the effect of elevation for the lichen community present some similarities and dissimilarities with vascular plants and bryophytes communities. An important dissimilarity that I observed, is the absence of correlation of decomposability and palatability for the lichen community, a link which is present in vascular plant communities. Another important difference is the role of intraspecies mechanisms in the variation of palatability in the lichen community. This is in accord with other studies that find that intraspecies mechanisms seem to generally play a more important role in the plasticity of the lichen's communities than for vascular plants and bryophytes.

These differences show that we cannot assume that trends found for vascular communities will be similar for lichen communities. Thus, it is important to not just focus on one kind of plants, to understand the impact that the climate change will have on primary producers. This is especially important for ecosystems like the one I studied, where the lichen community do an important part of the primary production.

6 References

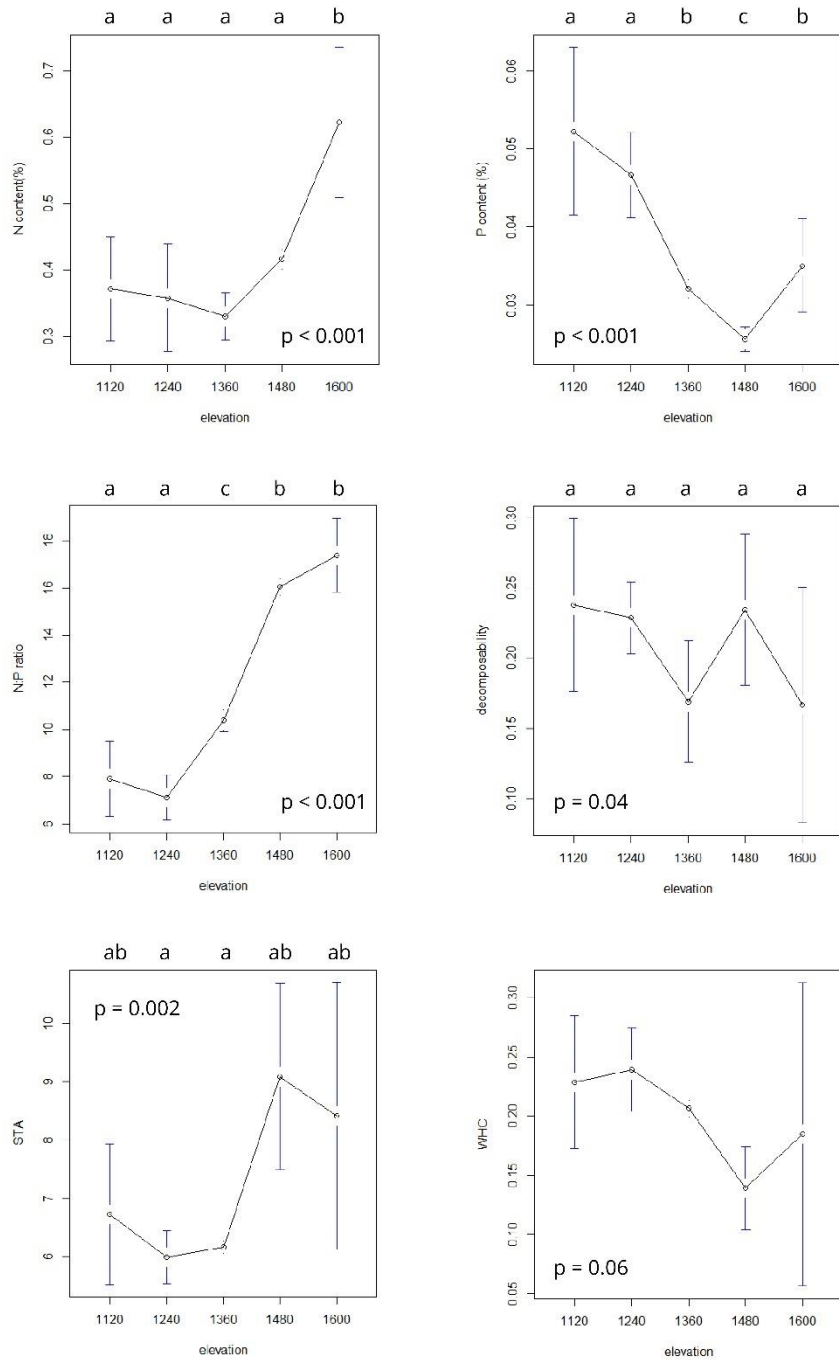
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7 Appendix



ANNEX 1 Community-weighted means (\pm SE) of N content, P content, N:P ratio, decomposability, STA, WHC for lichens across elevation. In the frame of each graph, the P values for permutational ANOVAs are presented. Significant differences between elevation levels are denoted with different letters (at $\alpha = 0.5$, post hoc pairwise test).

species	site 1120 m	site 1240 m	site 1360 m	site 1480 m	site 1600 m
	cover	species	cover	species	cover
<i>Cetraria islandica</i>	0.059	<i>Cetraria islandica</i>	0.036	<i>Cetraria islandica</i>	0.029
<i>Cladonia arbuscula</i>	0.505	<i>Cladonia arbuscula</i>	0.713	<i>Alectoria ochroleuca</i>	0.141
<i>Cladonia gracilis</i>	0.019	<i>Cladonia rangiferina</i>	0.139	<i>Cetraria ericetorum</i>	0.087
<i>Cladonia rangiferina</i>	0.392	<i>Cladonia uncialis</i>	0.002	<i>Cetraria islandica</i>	0.201
<i>Flavocetraria cucullata</i>	0.024	<i>Flavocetraria cucullata</i>	0.012	<i>Cladonia arbuscula</i>	0.012
<i>Flavocetraria nivalis</i>	0.076	<i>Stereocaulon sp.</i>	0.096	<i>Cladonia gracilis</i>	0.025
				<i>Cladonia uncialis</i>	0.024
				<i>Cladonia rangiferina</i>	0.021
				<i>Cladonia uncialis</i>	0.429
				<i>Flavocetraria cucullata</i>	0.018
				<i>Flavocetraria nivalis</i>	0.018
				<i>Solorina crocea</i>	0.018
				<i>Stereocaulon sp.</i>	0.009
				<i>Stereocaulon sp.</i>	0.038
				<i>Sphaerophorus globosus</i>	0.129
				<i>Thamnolia vermicularis</i>	0.158
					0.138
					0.030
					0.129
					0.038

Annex 2: list of the species collected at each site. Cover corresponds to the average relative cover.



Annex 3: one of the boxes used during the feeding experiment.



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