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RESEARCH ARTICLE

Contrasting drivers of community-level trait variation for vascular plants, lichens and bryophytes across an elevational gradient

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Abstract

1. Across environmental gradients, community-level functional traits of plants can change due to species turnover, intraspecific variation and their covariation. Studies on vascular plants suggest that species turnover is the main driver of trait variation across gradients, although intraspecific variation can also be important. However, there is limited knowledge about whether this holds for non-vascular primary producers such as lichens and bryophytes. We hypothesized that intraspecific variation is more important for non-vascular than for vascular primary producers because they lack specialized structures to maintain homeostasis and should therefore be more responsive to extrinsic factors.
2. To assess the relative importance of species turnover versus intraspecific variation for vascular plants, lichens and bryophytes, we estimated species abundance and measured chemical (tissue nitrogen (N) and phosphorous (P) content, N:P ratio and pH) and non-chemical (specific leaf or thallus area, dry matter content and water holding capacity) functional traits along an elevational gradient in alpine southern Norway. We calculated community-weighted mean traits and quantified the relative contribution of species turnover, intraspecific variation and their covariation to total trait variation across the gradient.
3. We found mixed support for our hypothesis: the contribution of intraspecific variation to total trait variation for N and N:P was higher in lichens than in vascular plants and bryophytes, but in general the contribution of intraspecific variation differed among functional traits and producer groups. Nutrient variables (N, P and N:P) were significantly impacted by intraspecific variation for vascular plants and lichens but not for bryophytes. Non-chemical traits and pH were mainly driven by species turnover effects in all primary producer groups.
4. Our results highlight that while nearly all studies on primary producer trait variation across environments have focused on vascular plants, trait variation of other

Roos and van Zuijlen contributed equally to this work.

largely neglected but ecologically important producer groups, such as lichens and bryophytes, may show very different responses to the same environmental factors. In order to fully understand how future environmental changes impact on community- and ecosystem-level processes, traits of primary producers other than vascular plants—and their within-species variation—need to be considered in systems where these groups are abundant.

KEYWORDS

alpine ecology, climate gradient, community-weighted mean, functional traits, intraspecific variation, non-vascular plants, species turnover, tundra

1 | INTRODUCTION

Over the last decades, trait-based approaches have taken centre stage in ecological research. In contrast to methods based on species identifications, trait-based approaches allow for generalizations across multiple species, communities, and entire ecosystems necessary to answer a variety of ecological questions (Enquist et al., 2015; Funk et al., 2017; Levine, 2016; McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007). Recent examples of such trait-based studies include those that attempt to understand how traits relate to community assembly (Bagousse-Pinguet, Bello, Vandewalle, Leps, & Sykes, 2014; Kumordzi et al., 2015), competitive interactions (Kunstler et al., 2016) and coexistence (Adler, Fajardo, Kleinhesselink, & Kraft, 2013); how communities respond to disturbance (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013) and climate change (Bjorkman et al., 2018); and how traits underpin ecosystem services (Faucon, Houben, & Lambers, 2017; Kohler et al., 2017; Lavorel, 2013; Lavorel et al., 2011), agricultural production (Wood et al., 2015) and ecosystem restoration (Zirbel, Bassett, Grman, & Brudvig, 2017). Although the trait-based approach finds its roots within plant ecology, there is also a growing use of it beyond the plant kingdom (Moretti et al., 2017).

Functional traits of common species contribute more to the ecological functioning of a community than those of rare species in the majority of cases, in line with Grime's mass ratio hypothesis (Grime, 1998). Thus, in order to capture a community by one mean trait value, this value is often weighted by the relative abundance of each species within that community to yield a 'community weighted' trait value (Garnier et al., 2004). To understand how these community-weighted trait values respond to environmental change, gradients provide powerful tools (Malhi et al., 2010). For example, lower temperatures with increasing elevation (Körner, 2007), and subsequent declining availability of nutrients (notably nitrogen (N) and phosphorus (P), see Huber et al., 2007), lead to a shift in community-weighted trait values from those associated with rapid resource acquisition to resource conservation in vascular plants (Read, Moorhead, Swenson, Bailey, & Sanders, 2014; Sundqvist, Sanders, & Wardle, 2013). As such, plants at higher elevations generally have leaves with lower tissue nutrient concentrations and low specific leaf area (SLA), although there are many exceptions (Read et al., 2014; Reich & Oleksyn, 2004; Sundqvist, Giesler, & Wardle, 2011; van de Weg, Meir, Grace, & Atkin, 2009).

An increasing number of studies over the past decade have contributed to the realization that traits can vary considerably within as well as between species (Adler et al., 2013; Enquist et al., 2015; Kraft, Valencia, & Ackerly, 2008; Kuebbing, Maynard, & Bradford, 2018; Messier, McGill, & Lechowicz, 2010; Violle et al., 2012). This poses questions about whether variation in community-level trait values along gradients is driven primarily by species turnover (which incorporates both the presence/absence of species in the community and the abundance structure of species that are present) or intraspecific trait variation. In most studies on vascular plants, species turnover is the main driver of community-weighted mean trait values, but intraspecific variation often plays an important role (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Kichenin, Wardle, Peltzer, Morse, & Freschet, 2013; Lepš, Bello, Šmilauer, & Doležal, 2011; Mayor et al., 2017; Messier et al., 2010; Siefert et al., 2015), depending on the trait considered (Derroire, Powers, Hulshof, Varela, & Healey, 2018). In contrast to vascular plants, a limited number of studies suggest that intraspecific variation in other primary producers such as lichens may be more important than changes in species composition. For example, Asplund and Wardle (2014) showed that intraspecific variation was the main driver of changes in community-level trait values of epiphytic lichens across a strong successional gradient, and Coyle (2017) found that phenotypic plasticity allowed lichen species to persist along gradients within forest canopies. In Figure 1, we present a conceptual framework of the drivers of community-level trait changes across environmental gradients such as elevation. It shows that species turnover and intraspecific variation can each result in the same community-level trait response and that when they occur together, they can also increase each other's effects and thus result in an even stronger response. This is potentially applicable to any trait of any group of organism across any environmental gradient.

The apparent lack of trait studies on the non-vascular component of vegetation, in particular lichens and bryophytes (Deane-Coe & Stanton, 2017; Martin & Mallik, 2017), persists despite their ubiquitous presence and importance in many ecosystems around the

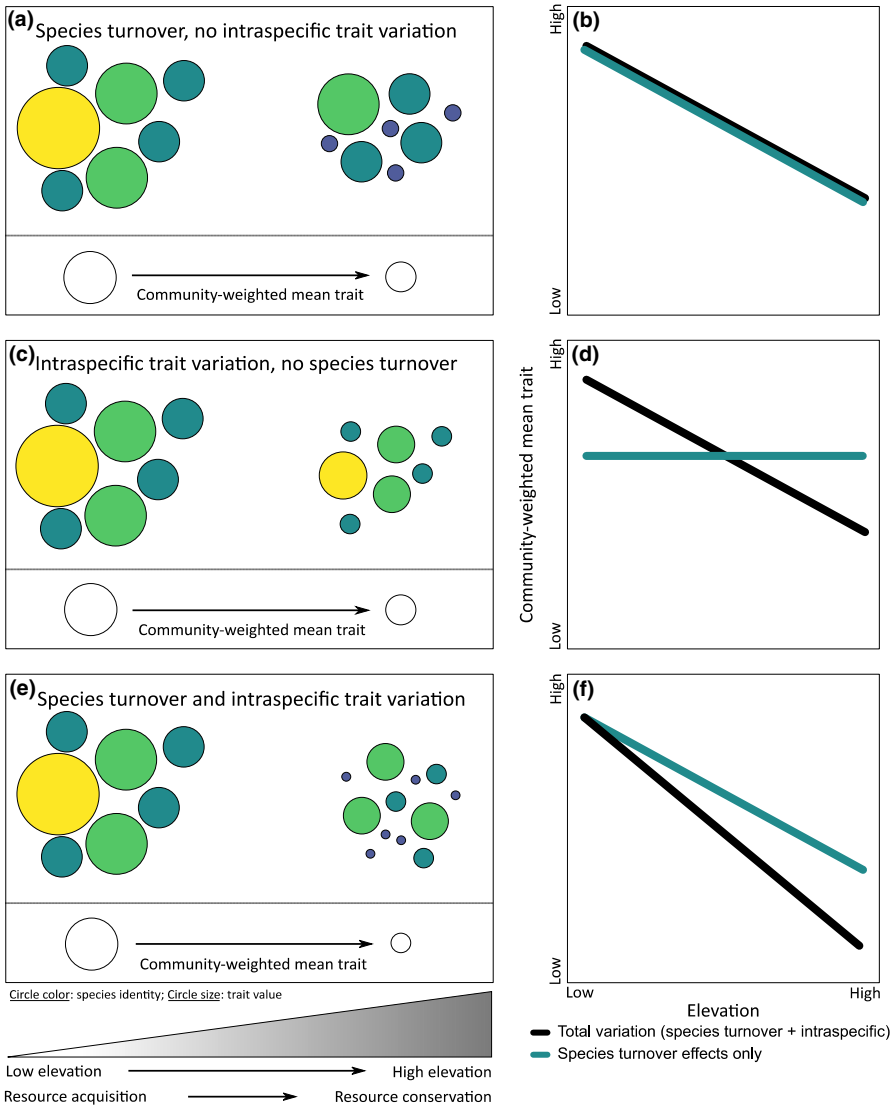

FIGURE 1 A conceptual figure of the drivers of community-level trait changes across environmental gradients such as elevation. As elevation increases, primary producer traits will change from those associated with resource acquisition towards those associated with resource conservation. The panels to the left illustrate communities, where symbol colour indicates species identity and symbol size depicts the trait value (e.g. tissue nitrogen content). The size of open circles indicate the community-weighted mean trait value as calculated from the sum of each species' trait value multiplied by its relative abundance. The right-hand-side panels show the change in community-weighted mean, depicted in *x*–*y* plots, that corresponds to the examples in the left-hand-side panels. In (a) and (b), the community-weighted mean trait value changes through alterations in species abundance and identity (i.e. species turnover), while trait values within species are fixed (no intraspecific trait variation). In contrast, in (c) and (d), the change in community-weighted mean trait value is driven only by intraspecific trait variation (no species turnover). In (e) and (f), both species turnover and intraspecific trait variation drive changes in the community-weighted mean trait value, which together result in an even stronger response. Note that in this case, species turnover and intraspecific variation act in a similar direction and have a positive covariation (both mechanisms reduce the community-level trait value), but they can also act in opposing directions, in which case their covariation is negative. In this study, we test our hypothesis that, although both species turnover and intraspecific trait variation will likely contribute simultaneously across an elevational gradient, species turnover will be the dominant driver of changes in community-weighted traits for vascular plants, while intraspecific trait variation will be the dominant driver for lichens and bryophytes

world, and notably those at high elevations and latitudes. Lichens and bryophytes contribute to global nutrient and carbon (C) cycling and hydrology and are involved in many trophic interactions (Asplund & Wardle, 2017; Cornelissen, Lang, Soudzilovskaia, & During, 2007; Elbert et al., 2012; Lindo & Gonzalez, 2010; Porada, Weber, Elbert, Pöschl, & Kleidon, 2014; Turetsky, 2003; Turetsky et al., 2012). In addition, both lichens and bryophytes respond strongly to experimental climate change (Elmendorf et al., 2012; Matos et al., 2017; Tuba, Slack, & Stark, 2011). They differ from vascular plants in their lack of specialized structures to regulate rates of water loss from their tissues (i.e. poikilohydry) and poor ability to take up nutrients from soil—although many are well adapted in absorbing N from

atmospheric sources or in association with N_2-fixing cyanobacteria. As expected from organisms that reflect their immediate environment, large intraspecific variation has been found in lichen traits such as nutrient concentrations (Asplund & Wardle, 2014; Palmqvist et al., 2002) and specific thallus area (STA; analogous to plant's specific leaf area, see: Asplund, Sandling, & Wardle, 2012; Gauslaa et al., 2009; Snelgar & Green, 1981; Solhaug, Lind, Nybakken, & Gauslaa, 2009). Similarly, large intraspecific responses have been found in bryophyte traits, such as photosynthetic and N_2-fixation rates (Gavazov, Soudzilovskaia, Logtestijn, Braster, & Cornelissen, 2010; Skre & Oechel, 1981; Turetsky et al., 2012). Yet, the relative importance of species turnover versus intraspecific variation as drivers of community-level traits across gradients has not directly (i.e. in the same study system) been compared among vascular and non-vascular components of vegetation.

In this study, we aim to assess the relative importance of species turnover versus intraspecific variation as drivers of community-level trait variability across an elevational gradient, separately for each of three groups of primary producers: vascular plants, lichens and bryophytes. To do this, we sampled species for all three groups along a gradient with a range of approximately 500 m in alpine Finse, southern Norway. We test the hypothesis that community-level trait variation across the gradient is driven mainly by changes in species turnover for vascular plants and mainly by intraspecific variation for lichens and bryophytes (Figure 1). We expect this because lichens and bryophytes reflect their immediate surroundings more than vascular plants, since they are less capable of regulating their moisture and nutrient status. The results of this study will contribute to our understanding of drivers of trait variation of previously understudied but ecologically important non-vascular primary producers, and how this compares to drivers of trait variation for vascular plants. Further, because elevational gradients can be used as space-for-time substitutions for predicting the effects of future climate warming (Elmendorf et al., 2015; Sundqvist et al., 2013), our study aims to better understand the mechanisms by which community-level trait variation of vascular plants, lichens and bryophytes will respond to future increases of temperature in alpine ecosystems.

2 | MATERIALS AND METHODS

2.1 | Study site and plot selection

This study was performed at Finse, southern Norway (60°33'N–60°38'N, 7°34'E–7°42'E), in July and August 2016. The Finse meteorological station is located at 1,210 m a.s.l. and has an average yearly temperature of −2.1°C and 1,030 mm yearly precipitation (Norwegian Meteorological Institute, 2018a). The average summer (June–August) temperature in 2016 was 7.3°C, and total summer precipitation was 303.9 mm (Norwegian Meteorological Institute, 2018b).

We selected five sites along an elevational gradient spanning 480 m, at approximately 1,120, 1,240, 1,360, 1,480 and 1,600 m a.s.l., all on south-facing slopes on acidic granite and gneiss bedrock. The lowest site is situated approximately 150 m above the nearest tree line (*Betula pubescens* ssp. *czerepanovii*). Because many lichens respond negatively to snow cover (Bidussi, Solhaug, & Gauslaa, 2016; Niittynen & Luoto, 2018) and are therefore absent from depressions in the landscape where snow accumulates, we selected sites on exposed ridges that support communities with a mixed cover of vascular plants, lichens and bryophytes. The vascular plant communities are relatively species poor, with *Empetrum nigrum*, *Vaccinium uliginosum* and *Betula nana* as most common at the lowest elevations and *Carex bigelowii* and *Salix herbacea* at the higher elevations. Common lichen species are *Cladonia arbuscula s. lat.*, *C. rangiferina* and *Flavocetraria nivalis*. The bryophyte species *Pleurozium schreberi* and *Dicranum acutifolium* are common at lower elevations, while *Polytrichum hyperboreum*, *P. alpinum* and *Racomitrium lanuginosum* are common at higher elevations. At each site, we selected five 1-m^2 plots within a 100 m radius by haphazardly throwing an object, on the condition that all three groups (i.e. vascular plants, lichens and bryophytes) were present. Within elevations, the median distance between replicate plots was ca. 43 m. Because of the high small-scale spatial heterogeneity (e.g. in topography, microclimate, soil fertility and biodiversity) in these communities, which occurs over the meter scale (Björk et al., 2007; Opedal, Armbruster, & Graae, 2015), this distance is sufficient to ensure adequate independence among plots and is in line with previous studies along elevational gradients in these types of environments (e.g. Veen et al., 2017).

2.2 | Temperature gradient

Air temperature was measured 20 cm above ground in each plot at 20-min intervals between 5 September 2016 and 22 August 2017, using shaded Tinytag loggers (Plus 2 TGP-4017; Gemini Co., UK). For each elevation, we calculated mean annual temperature, average temperature at the coldest and the warmest day, number of diurnal freeze–thaw cycles, monthly mean temperature in January and July and the number of growing degree days (defined as number of days with average temperature above 5°C; see Table S1). Mean July temperature decreased on average by 0.9°C with each level (120 m) of increasing elevation (ANOVA, $F = 240.7$, $p < .001$; Figure 2), which corresponds well with the mathematical dry adiabatic lapse rate with elevation of 9.8°C/1,000 m. The growing season was 54 days shorter at the highest site compared to the lowest site in our gradient (GLM with Poisson's distribution; analysis of deviance, Resid. Dev = 0.716, $p < .001$; Figure 2). These data show that our selected sites were placed along a distinct and strong growing season temperature gradient.

2.3 | Vegetation survey and harvesting

To quantify species composition along the gradient, vascular plant, lichen and bryophyte cover were estimated in each plot between 11 and 24 July 2016 (see Table S2 for a species list). This cover was estimated visually with a 1 × 1 m metal frame, divided with plastic wire into four quadrats of 50 × 50 cm. Each quadrat was divided into 25

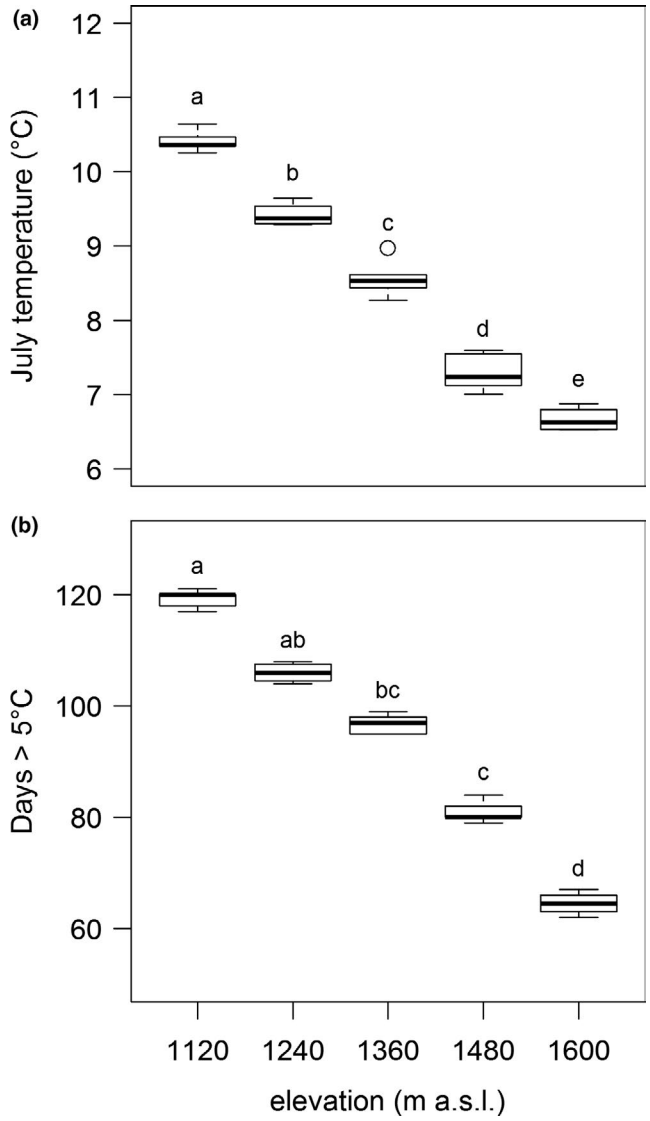

FIGURE 2 Box-and-whisker plot of mean July temperature (a) and number of days when average temperature exceeded 5°C (b) for each elevation. Significant differences between elevation levels are denoted with different letters (at α = .05, Tukey's post hoc tests)

10 × 10 cm squares to allow for more accurate cover estimates. We estimated the cover for each species per quadrat and subsequently calculated the whole-plot cover from the average cover across all four quadrats. Between 28 July 2016 and 18 August 2016, one quadrat per plot was destructively harvested and all aboveground materials were collected and sorted to species for functional trait measurements. For some rare species, it was not possible to collect sufficient material, and we therefore restricted our analysis to the most abundant vascular plant, lichen and bryophyte species that collectively composed at least 80% of the cover per group per plot, in line with other studies (Pakeman & Quested, 2007). For bryophytes, we were not able to attain data on 80% of the cover for one plot at 1,480 m a.s.l and one at 1,600 m a.s.l., and these two plots were therefore excluded from further analyses. In case insufficient material was available for a given species within the harvested quadrat, we sampled additionally from the other quadrats in the same plot or within the immediate surroundings of the plot, making sure that equal numbers of individuals were sampled from both infrequent and abundant species. After harvest, vascular plant samples were stored in moist, sealed plastic bags at 4°C until trait measurements. Lichens and bryophytes were kept in paper bags and air-dried at room temperature. Except for the common species *Ptilidium ciliare*, liverworts were excluded from bryophyte community trait analysis due to their minor contribution to vegetation cover.

2.4 | Selection of functional traits

In this study, we use a selection of 'soft' (i.e. easy to measure, sensu Hodgson, Wilson, Hunt, Grime, & Thompson, 1999) eco-physiological traits that are known to exert a strong impact on ecosystem C and N cycling rates (Perez-Harguindeguy et al., 2013) and are related to the fast–slow continuum of plant strategies (e.g. Reich & Flores-Moreno, 2017; Wright et al., 2004). Specifically, we measured N and P concentrations and their ratio, specific leaf area (SLA) for vascular plants and bryophytes, specific thallus area (STA) for lichens and leaf dry matter content (LDMC) in vascular plants. Further, we measured water-holding capacity (WHC) for lichens and bryophytes. Such hydration traits are particularly relevant in poikilohydric organisms such as lichens and bryophytes, as their ability to retain moisture ultimately determines their photosynthetic activity (Gauslaa, Solhaug, & Longinotti, 2017). In addition, we measured tissue pH, identified by Cornelissen et al. (2006) as a proxy for 'hard' traits such as decomposability and acidification potential. To allow comparisons between groups, we used only leaves from vascular plants, excluding stems and belowground parts. For lichens and bryophytes, we used complete thalli and shoots, respectively (cleaned from decaying necromass if present), with the exception of bryophyte SLA for which we used only the leaves to enable a better comparison with SLA of vascular plants.

2.5 | Specific leaf area and leaf dry matter content in vascular plants

To determine SLA and LDMC for each vascular plant species in each plot, we used 30 young but fully developed (i.e. current growing season) and undamaged leaves sampled from 15 shoots, except for small leaved species (leaf length < 0.5 cm) for which we used 150 leaves. For LDMC, the partial rehydration method (Vaieretti, Díaz, Vile, & Garnier, 2007; Vendramini et al., 2002) was used, and for SLA, we followed the standard protocols described in Perez-Harguindeguy et al. (2013) and Cornelissen et al. (2003). Leaves were scanned with a CanoScan LiDE220 at 400 dpi, and leaf surface area was calculated in the image processing software ImageJ (version 1.51p). After scanning, leaves were dried at 60°C for 72 hr and weighed (Sartorius ED224S, 0.1 mg readability). Measures of LDMC were determined as the oven-dry mass divided by the fresh mass (expressed in mg/g), while SLA was calculated as leaf area divided by dry mass (expressed in mm^2/mg).

2.6 | Specific thallus area and water-holding capacity in lichens

To determine STA and WHC in lichens, an adaptation of the protocol described by Gauslaa and Coxson (2011) was used. For each species in each plot, 10 intact thalli of each species were selected and cleaned. The thalli were saturated by spraying with demineralized water and incubated for 30 min in a sealed container lined with moistened (demineralized water) tissue paper. The lichen thalli were then placed on a light table and flattened under a glass plate. Highly branched thalli were cut into several pieces to minimize overlap. Images of these thalli were taken with a Nikon D5500 in combination with a Sigma 105mm f2.8 DG macro HSM lens with a resolution of 6,000 × 4,000 pixels (jpeg-format). Thallus surface area was measured using the image processing software Image J (version 1.51p). After taking the images, lichens were again saturated (see above), blotted dry and weighed (using a Sartorius ED224S scale). Finally, thalli were dried at room temperature and stored in desiccators with silica gel 48 hr prior to weighing dry mass. We calculated STA as thallus area divided by dry mass (expressed in mm^2/mg), and WHC was calculated as '(wet mass − dry mass)/ area' (expressed in mg/mm^2; water per thallus area).

2.7 | Specific leaf area and water-holding capacity in bryophytes

SLA of bryophytes was measured using an adapted version of the protocol of Lang, Huey, Ahrens, and Bechberger (2018) which provides more accurate measurements than previous bryophyte SLA protocols that measure shoot area rather than leaf area (Bond-Lamberty & Gower, 2007). Leaves were picked carefully from the bryophytes by using extremely fine antimagnetic tweezers (Dumont Swissmade type 5, Electron Microscopy Sciences, USA) and a dissecting microscope. For larger-leaved mosses (such as *Polytrichum* spp. and *Dicranum* spp.), we selected 20 leaves from three shoots, while for small-leaved species (such as *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilidium ciliare*), we selected 45 leaves from three shoots. We selected young but fully developed leaves from the upper one-third of the shoots. For branched species, leaves were selected from both the main stem and side branches. These leaves were then prepared on microscope slides and flattened with a cover glass. Pictures were taken using a Leica DFC320 digital camera mounted on a Leica MS5 stereo microscope (Leica Microsystems GmbH, Germany), using a 0.63× objective together with a 1.0× 0.63× camera objective and a light table. Photoshop Elements 14 and ImageJ v1.51k were used to select and measure leaf area (mm^2). Since bryophyte leaves were often curled and folded under the cover glass, the area of all double parts was measured twice. To allow comparisons of bryophyte SLA with vascular plant SLA, we oven-dried the leaves at 50°C for 24 hr and weighed using a Mettler Toledo UMX2 ultra-microbalance (1 µg readability, Mettler Toledo, Switzerland). We calculated SLA as leaf area divided by dry mass (expressed in mm^2/mg).

For each bryophyte species for each plot, WHC was measured using an adaptation of the protocols of Pypker, Unsworth, and Bond (2006); Elumeeva, Soudzilovskaia, During, and Cornelissen (2011); and Michel, Payton, Lee, and During (2013). For each sample, 10 living shoots were collected (i.e. the top part of the shoot with green leaves) and submersed in demineralized water for 30 min. Shoots were then placed on moistened filter paper in sealed Petri dishes for approximately 24 hr. Subsequently, shoots were blotted dry and water-saturated mass was weighed (Sartorius EDS224S), after which the samples were air-dried and weighed again. For each batch of samples, one sample was oven-dried at 40°C for 6 hr and weighed to provide a conversion factor for that batch from air-dry to oven-dry mass. WHC was calculated as '(wet mass − dry mass)/dry mass' (expressed in g/g).

2.8 | Nitrogen and phosphorous content and tissue pH

Vascular plant, lichen and bryophyte samples were ground to powder using a Retsch MM400 ball mill (5 ml tubes, 30 Hz, 5–10 min) for analysis of N and P (in %), by using Kjehldahl analysis, from which the N:P ratio was calculated. For pH measurement, powder from each sample was suspended in demineralized water in a 1:8 ratio (Cornelissen et al., 2006) using a KS 501 digital shaker (1 hr at 325 rpm; IKA-Werke GmbH & Co. KG, Germany) and subsequently centrifuged for 10 min at (2,115 *g*, Hettich Universal 16). We then measured pH with a WTW InoLab pH 720 instrument equipped with a WTW pH SenTix 81 electrode (pH 0–14, temp. 0–100°C; Xylem Analytics, USA) after calibration to pH 4 and 7 calibration fluid.

2.9 | Data analysis

2.9.1 | Community composition across elevation

We performed two-dimensional non-metric dimensional scaling analyses using Bray–Curtis dissimilarity coefficients to depict differences with elevation in vascular plant, lichen and bryophyte communities using the R package vegan (Oksanen et al., 2015). For these analyses, we used two dimensions (k = 2). Although adding a third dimension would decrease stress (Figure S1), stress levels at two dimensions were acceptable and below the stress >0.2 criterion sensu Clarke, 1993 (vascular plants: 0.147, lichens: 0.128, bryophytes: 0.161). We therefore reported ordinations for two dimensions, bearing in mind that depiction of ordination plots in more than two dimensions creates significant difficulties in interpretation. Data were subjected to Wisconsin double standardization, but were not transformed. We used the ordiellipse function (Oksanen et al., 2015) to plot the 95% confidence intervals (CI) of group scores of the five elevations onto the NMDS ordination.

2.9.2 | Community-level trait calculations

To assess how traits vary across elevation, we calculated community-weighted mean values for all traits for each group (vascular plants,

lichens and bryophytes) per plot. The community-weighted mean is the sum of the relative trait values of all species, in which the trait value of each species is weighted by its relative abundance within the community (e.g. Garnier et al., 2004; Kichenin et al., 2013). To quantify the contribution of species turnover and intraspecific variation to changes in community-weighted mean traits, we calculated community-weighted means in two different ways: as so-called specific averages and fixed averages (see Lepš et al., 2011). First, 'specific' averages were calculated from the plot-specific trait values per species as follows:

$$\text{Specific average} = \sum_{i=1}^{s} p_i x_{i\_\text{plot}}$$

where p_i is the relative abundance of the i^{th} species based on cover in the plot, S is the number of species, and x_{i_plot} is the specific trait value of the ith species for the specific plot in which it was sampled. Second, 'fixed' averages were calculated in similar fashion but with trait values averaged over all plots within the gradient for each species. Fixed average traits are therefore plot-independent, meaning that they reflect the 'mean trait approach': one species has one mean trait value regardless of the specific plot where it is found. Then, we calculated the contribution of intraspecific trait variation based on the following principle: if there are differences in 'fixed' averages between plots, this can only be the result of species turnover. However, if there are differences in 'specific' averages between plots, this can be the result of both species turnover and intraspecific trait variation. Hence, we can define:

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

For the analyses, we treated the specific average (which includes the effect of both species turnover and intraspecific variation), fixed average (effect of species turnover) and the difference between them (effect of intraspecific variation) in each group for each functional trait as response variables in parallel one-way ANOVAs, with elevation treated 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 5,000 iterations (sensu Anscombe, 1953). Whenever the specific average (= total trait variation) was impacted by elevation at a significance level $p = .05$, pairwise comparisons using permutation tests were performed to check for differences between elevation levels. In addition, we quantified how much variability can be accounted for by the individual components (species turnover effects or intraspecific variability effects) by following the Sum of Squares (SS) decomposition method described by Lepš et al., 2011. When species turnover effects and intraspecific effects vary independently, then $SS_{\text{specific}} = SS_{\text{fixed}} + SS_{\text{intraspecific}}$; however, if they are correlated, then SS_{specific} will be higher (positive correlation) or lower (negative correlation). As such, we calculated the SS_{cov} component, which is the covariation between species turnover and intraspecific variability effects, by subtracting SS_{fixed} and $SS_{\text{intraspecific}}$ from SS_{specific}. The analyses were performed using the R packages lmPerm (Wheeler, 2010) and rcompanion (Mangiafico, 2016) in R, version 3.4.0 (R Core Team, 2017).

2.9.3 | Contribution of intraspecific variability between groups

To test whether the proportional contribution of intraspecific variation (in comparison with species turnover) to community-level trait changes across the elevational gradient differed between vascular plants, lichens and bryophytes, we calculated the absolute difference between specific averages and fixed averages for each group, divided by the specific average. We performed this analysis on chemical traits (N, P, N:P and pH) only, because non-chemical traits (SLA, STA, WHC and LDMC) were measured differently between primary producer groups and their values cannot be compared directly. The calculated proportions were arcsine transformed to meet the assumptions for ANOVA using linear mixed effects models with elevation and primary producer group as fixed factors and plot as a random effect. Whenever ANOVA results were significant, Tukey's post hoc tests at $p = .05$ were used to test differences between means for elevations. These analyses were performed in R, version 3.4.0 (R Core Team, 2017), using the packages nlme (Pinheiro et al., 2017) and emmeans (Lenth, 2018).

3 | RESULTS

The NMDS show that for all three primary producer groups, the communities at the lowest three elevations (1,120, 1,240 and 1,360 m a.s.l.) group together along the first ordination axis, and separately from the two highest elevations (1,480 and 1,600 m a.s.l.) (Figure 3). In the ordination space, the lichen community compositions appear more similar across elevations than do the vascular plant and the bryophyte communities (Figure 3).

3.1 | Functional traits across elevations

3.1.1 | Chemical traits

For the vascular plant community, foliar N increased by 24%, foliar N:P increased by 42%, and pH increased by 16% from the lowest to the highest elevation; foliar P showed a marginally non-significant decline (total trait variation values in Figure 4). Species turnover contributed most to the total variation in N and pH, whereas intraspecific variation contributed most to total variation in P and N:P across the elevational gradient (Figure 5; and indicated by the positioning of the different lines in Figure 4, see also the explanation in Figure 1). The covariation of species turnover and intraspecific variation was negative for N and P, but positive for N:P.

All lichen chemical traits changed significantly with elevation (total trait variation values in Figure 4). Lichen N increased by 78% and N:P increased by 136% with increasing elevation, while P

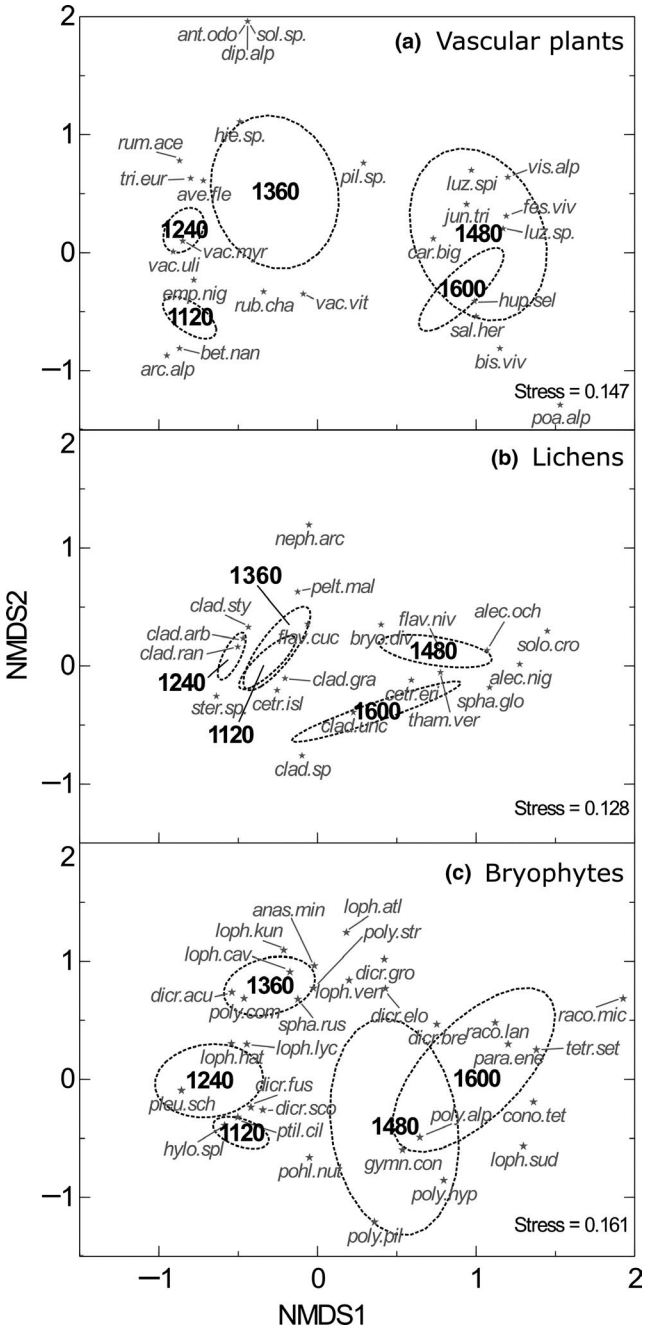

FIGURE 3 Results of non-metric multidimensional scaling (NMDS) analysis showing differences with elevation for (a) vascular plant, (b) lichen and (c) bryophyte community composition. The elevation label (in m a.s.l.) denotes the positions of the centroid for community composition for each elevation; dashed ellipses denote 95% confidence intervals around these positions. Species abbreviations place species in ordination space, but were moved in some cases to increase readability (indicated with an arrow); abbreviations correspond to species names in Table S2

generally decreased. Acidity (pH) varied significantly with elevation but not in a clear overall direction. Intraspecific variability effects contributed to most of the trait variation explained by elevation for N, P and N:P, although species turnover effects were also significant for N and N:P (Figure 5). In contrast, species turnover effects were the main driver of pH variation. There was a strong positive covariation of species turnover and intraspecific variation for all traits.

Bryophyte P decreased by 43% and N:P ratio increased by 120% with increasing elevation, while N showed a marginally non-significant increase and pH was unresponsive (total trait variation values in Figure 4). Species turnover was the main driver for total trait variation across the elevational gradient for the chemical traits in the bryophytes, and this effect was statistically significant for all traits except pH (Figure 5). There was no significant change of intraspecific variation across elevation, but there was a strong positive covariation between species turnover effects and intraspecific variation for P and N:P.

3.1.2 | Non-chemical traits

Vascular plant SLA showed a marginally non-significant increase across the gradient, while LDMC decreased by 16% with increasing elevation (total trait variation values in Figure 6). Species turnover explained most of the total trait variation across the elevational gradient for both SLA and LDMC (Figure 5). Although the relative contribution of species turnover to total variation in SLA across the elevational gradient was large and significant, a strong negative covariation with intraspecific variability effects led to a marginally non-significant response of total variation. The covariation of species turnover and intraspecific variation was also negative for LDMC.

For the lichen community, STA increased by 37%, while WHC decreased by 24% with increasing elevation (total trait variation values in Figure 6). Species turnover had a significant role in determining the total response of both traits to elevation, while there was no effect of intraspecific variation (Figure 5). There was a strong positive covariation between species turnover and intraspecific variation for both traits.

For the bryophyte community, SLA decreased by 68%, and WHC decreased by 25%, from the lowest to highest elevation (total trait variation values in Figure 6). For both SLA and WHC, total variation explained by elevation was mainly driven by species turnover effects, which was significant for both traits (Figure 5). For WHC, intraspecific variation also contributed significantly to total trait variation. The covariation of species turnover and intraspecific variation was slightly negative for SLA, while for WHC, it was strongly positive.

3.1.3 | Intraspecific variability effects between groups

The contribution of intraspecific variation to the community-level trait values showed a significant interaction between elevation and group identity (vascular plants, bryophytes or lichens) for N, P and N:P but not for pH, which means that the contribution of intraspecific variation changes differently across elevation for the three groups (Table 1). Furthermore, lichens overall showed greater intraspecific variation when compared to vascular plants and bryophytes for *N* (15% in lichens vs. 7% in vascular plants and 8% in

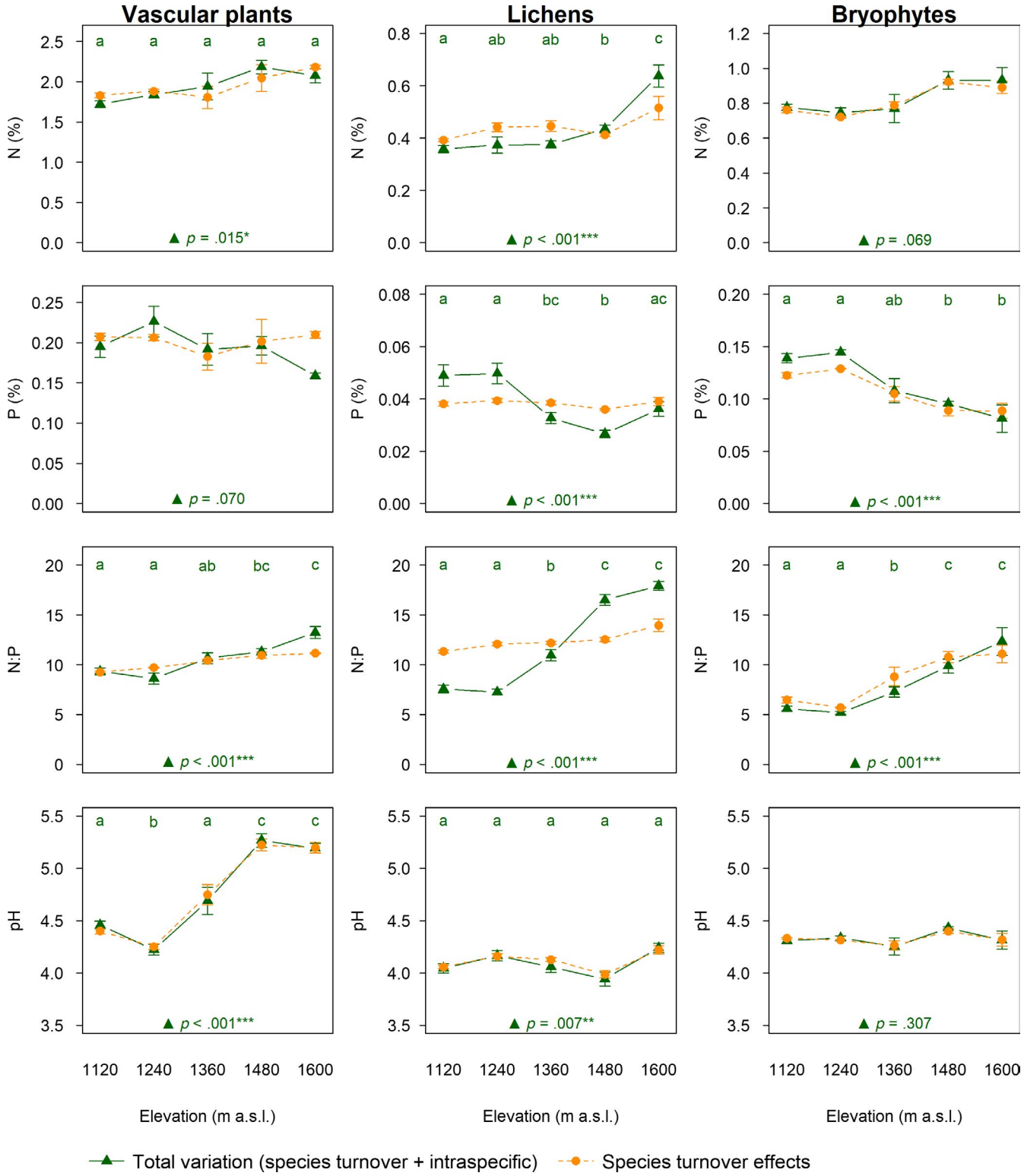

FIGURE 4 Community-weighted means (±*SE*) of nitrogen concentration (% N), phosphorus concentration (% P), N:P ratio and pH for vascular plants (left column), lichens (middle column) and bryophytes (right column) across elevation. The green lines with triangles denote the total variation (specific average values), and orange dotted lines with circles denote species turnover effects only (fixed average values). Therefore, the larger the difference between green and orange lines, the larger the contribution of intraspecific variation (see Figure 1 for a more detailed explanation). In the bottom of each panel, the *p*-values from the permutational ANOVAs are presented for the response of total trait variation to elevation and denoted with *(<.05), **(<.01) or ***(<.001). Significant differences between elevation levels are denoted with different letters (at α = .05, permutational pairwise comparisons). Note that the scales for N and P are different for the three groups

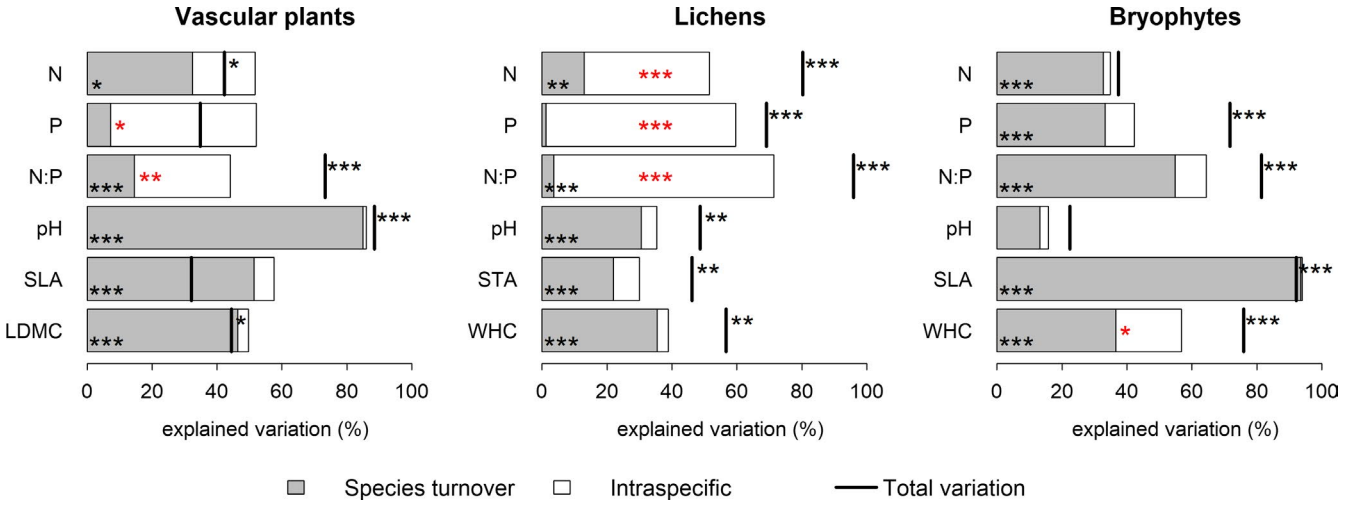

FIGURE 5 The contributions of species turnover and intraspecific variation to trait variation explained by elevation (as percentage of total variation in traits, including variation not explained by elevation) for vascular plant, lichen and bryophyte functional traits. The measured traits include nitrogen concentration (N), phosphorous concentration (P), N:P ratio, pH, specific leaf area (SLA), specific thallus area (STA), leaf dry matter content (LDMC) and water holding capacity (WHC). Grey bars indicate effects of species turnover, while white bars show intraspecific variability effects. The black lines denote total variation (i.e. the sum of species turnover and intraspecific variability effects and their covariation) explained by elevation. If the total variation is greater than the sum of species turnover and intraspecific variability effects (black bar above the columns), covariation is positive. In contrast, if total variation is smaller than the sum of its components, the covariation is negative (black bar crossing the column). For example, intraspecific variability effects explain most of the variation for lichen tissue N and the covariation between intraspecific and species turnover effects is strongly positive. The significance of the response of the different components to elevation is denoted with *($p < .05$), **($p < .01$) or ***($p < .001$); subscript refers to species turnover, superscript to total variation, and symbols at the baseline to intraspecific variation (in red)

bryophytes; $p < .001$) and N:P (36% for lichens vs. 10% for vascular plants and 17% for bryophytes; $p < .001$).

4 | DISCUSSION

We hypothesized that across elevation, intraspecific variation is the most important driver of community-level trait variation in lichens and bryophytes, while species turnover is most important in vascular plants. In line with our hypothesis, we found that species turnover is the most important contributor to total variation across the gradient for most of the vascular plant traits that we considered (Figure 1a and b). Further and in support of our hypothesis, some of the lichen traits are mainly driven by intraspecific variation (Figure 1c and d), although others are driven by species turnover (Figure 1a and b). Against our predictions, species turnover effects mainly drive variation for all bryophyte functional traits across the gradient (Figure 1a and b). However, even when intraspecific variation is small, we found that it greatly enhances the total variation explained by elevation for lichen traits and some bryophyte traits, through positive covariation with species turnover effects (Figure 1e and f). A summary of the different trait responses to elevation is given in Figure 7. We now explore these findings and discuss their broader implications.

Our finding that species turnover is the main contributor to variation in most vascular plant traits across elevation is consistent with previous studies (e.g. Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Mayor et al., 2017). However, we also found that intraspecific variation is the most important contributor to vascular plant P and N:P, which confirms earlier findings that the relative contributions of inter- and intraspecific variation can differ greatly among both traits and study systems (Derroire et al., 2018). For lichens, we found that intraspecific variation is the main contributor to variation in nutrient concentrations across the gradient, which is consistent with the fact that lichens lack specialized organs for nutrient and water uptake and are therefore less well adapted than vascular plants in regulating their physiology across changing environmental conditions. Although intraspecific variation does not contribute to changes in lichen STA and WHC across elevation, the residual variation in these traits shows a relatively large intraspecific component (Figure S2), indicating that intraspecific changes occur independent of elevation, for example as a response to local variation in light exposure through shading by vascular plants (Gauslaa, Lie, Solhaug, & Ohlson, 2006; Hilmo, 2002).

Our results for the bryophytes are in direct contrast to our hypothesis, since species turnover is the main driver of total variation for all traits across the gradient, which is likely driven by the high rate of species turnover across the gradient. However, bryophyte WHC also showed significant intraspecific variation, suggesting that the overlap of bryophyte species among elevations was still large enough to enable within-species variation to be detected. Further, intraspecific variation may still be important at some spatial scales even when it is very weak at others. As such, the residual variation in bryophyte traits that cannot be explained by elevation has a large intraspecific

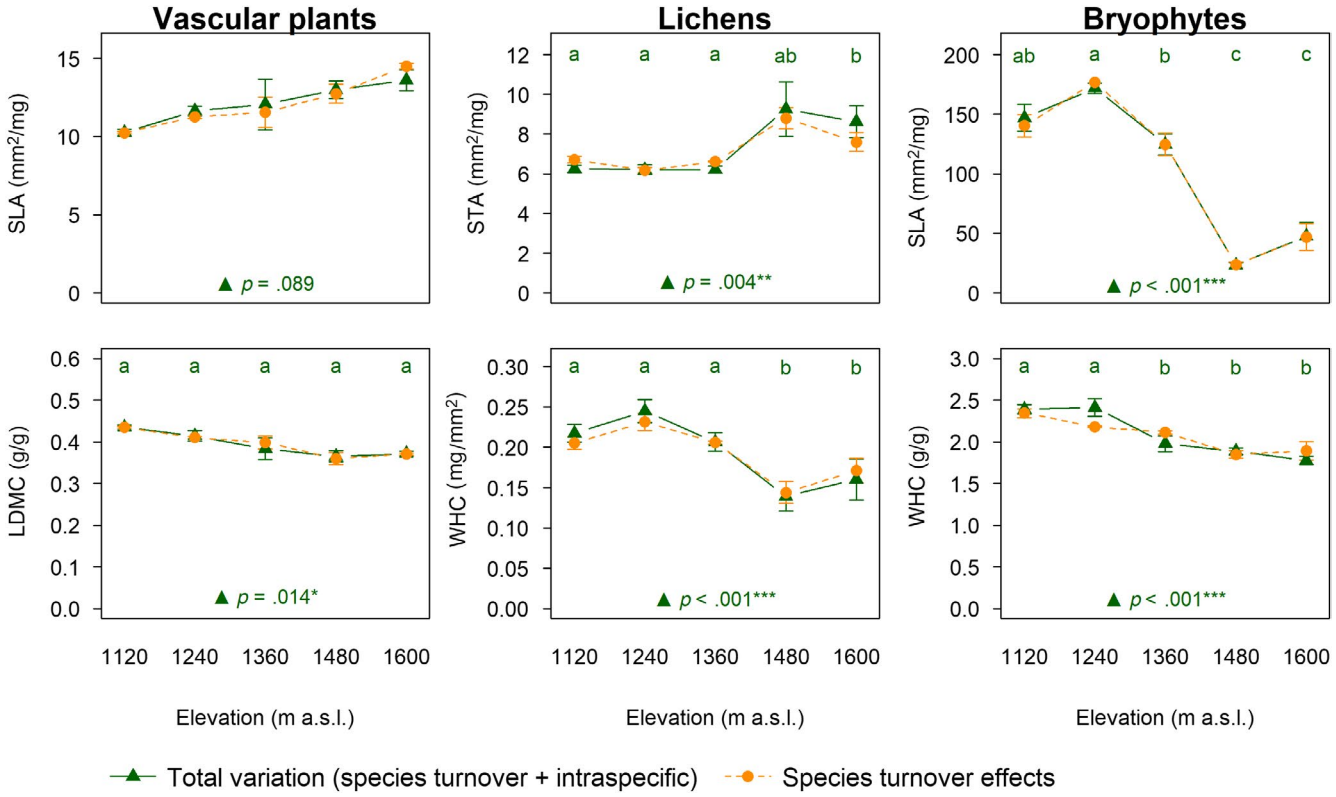

FIGURE 6 Community-weighted means (±*SE*) of specific leaf area (SLA), specific thallus area (STA), leaf dry matter content (LDMC) and water-holding capacity (WHC) for vascular plants, lichens and bryophytes across elevation. Green lines with triangles denote the total variation (specific average values); orange dotted lines with circles denote species turnover effects only (fixed average values). The green lines with triangles denote the total variation (specific average values), and orange dotted lines with circles denote species turnover effects only (fixed average values). Therefore, the larger the difference between green and orange lines, the larger the contribution of intraspecific variation (see Figure 1 for a more detailed explanation). In the bottom of each panel, the *p*-values from the permutational ANOVAs are presented for the response of total trait variation to elevation, and denoted with *(<.05), **(<.01), or ***(<.001). Significant differences between elevation levels are denoted with different letters (at α = .05, permutational pairwise comparisons). Note that the scales and units may differ among the three groups. [Correction added after online publication on 29 November 2019: units for Lichen WHC values were corrected from mm^2/mg to mg/mm^2]

TABLE 1 Results of ANOVA combined with mixed-effects models testing the effect of elevation, group (vascular plants, lichens and bryophytes) and their interaction on intraspecific variation (proportion of total trait value) for chemical traits

	Nitrogen	Phosphorous	N:P	pH
	F (*p*)	*F* (*p*)	*F* (*p*)	*F* (*p*)
Elevation	2.24 (.102)	0.81 (.537)	2.71 (.059)	0.89 (.489)
Group	**9.51 (<.001)**	2.05 (.143)	**42.53 (<.001)**	0.14 (.867)
Elevation × Group	**3.09 (.009)**	**3.53 (.004)**	**7.63 (<.001)**	1.96 (.080)

Note: The response variable, that is intraspecific variation (proportion of total trait value), was arcsine-transformed before analysis. Significant *p*-values (at α = .05) are in bold. *df*: Elevation = 4, 20; Group = 2, 38; Elevation × Group =8, 38.

variability component (Figure S2), suggesting that within-species variation may be important at more local spatial scales in response to factors that vary within elevation, such as light availability, snow depth (Niittynen & Luoto, 2018) and soil moisture (Tobias & Niinemets, 2010).

The relative importance of intraspecific variation across the gradient does not only differ between the three producer groups in our study, but also between traits within groups, which is in line with what has been shown in the vascular plant literature (see Siefert et al., 2015). In our study, tissue nutrient concentrations of vascular plants and lichens show more intraspecific variation across the gradient than the other, non-chemical traits. Although we found similar responses for nutrient concentrations within bryophyte species that are present at more than one elevation, this effect is unimportant in influencing the community-weighted means across the gradient because of very high species turnover. Meanwhile, variation across the gradient in tissue pH is driven almost exclusively by species turnover for all three groups. This is in line with the results from Cornelissen, Sibma, Logtestijn, Broekman, and Thompson

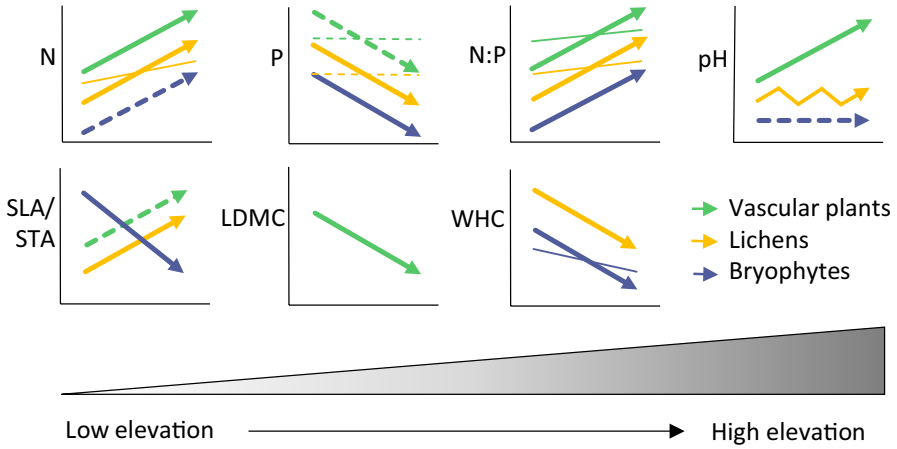

FIGURE 7 Summary of community-level vascular plant (green), lichen (yellow) and bryophyte (blue) functional trait responses to increasing elevation: nitrogen (N) and phosphorous (P) concentration, N:P ratio, tissue pH, specific leaf area (SLA) and specific thallus area (STA), leaf dry matter content (LDMC) and water-holding capacity (WHC). Thick lines with arrow tips denote the total variation (species turnover effects and intraspecific variation), while thin lines denote species turnover effects only. Thin lines are only shown when the species turnover effects differ from the total trait variation and thus when there is a strong effect of intraspecific variation on the total trait response. Solid lines denote significant trait responses to elevation at $p < .05$, while dashed lines denote non-significant trait responses at $p \geq .05$. Increasing or decreasing dashed lines indicate trends ($0.05 \leq p < .1$), while flat dashed lines indicate traits that are unresponsive to elevation ($p > .1$). Note that the figure only indicates general patterns across elevation, *y*-axes do not represent the same scales across primary producer groups, and measurements of SLA/STA and of WHC differ between primary producer groups

(2011) for vascular plants, which show that tissue pH is highly species-specific and therefore unlikely to be strongly responsive to environmental factors such as substrate pH at the within-species level. Similarly, SLA in bryophytes seems also species-specific; within-species variation could be unresponsive to changes across the gradient because bryophyte leaves are often consistently one cell-layer thick, meaning that leaf thickness cannot be varied by changing the numbers of cell layers, leading to leaf thickness being relatively inflexible.

While theory predicts that as elevation increases and environmental conditions become harsher, plant traits should shift from those associated with rapid resource acquisition towards resource conservation, some field studies reveal contrasting patterns (Mayor et al., 2017; Read et al., 2014; Sundqvist et al., 2013). In our study, we found that some traits change towards being more resource conservative with increasing elevation, as shown by a decrease in P and WHC for lichens and bryophytes, a decrease in SLA for bryophytes and an increase in N:P in all groups (Figure 7), in accordance with previous work (Güsewell, 2004; Koerselman & Meuleman, 1996). However, other traits show opposing responses. For instance, vascular plant and lichen tissue N, vascular plant SLA and lichen STA increase, while vascular plant LDMC decreases with elevation, indicating a shift towards a more nutrient acquisitive strategy (Figure 7). However, for vascular plant SLA and N, the strong negative covariation between species turnover and intraspecific effects indicates that within some individual plant species, values of these traits may decrease with elevation (see also Anderegg et al., 2018; Kichenin et al., 2013). A likely mechanism for more acquisitive community-level traits at higher elevations is a shift in the dominant functional types. For example, for vascular plants, as elevation increases, shrubs are replaced by species with lower stature or tussock-like growth forms (such as graminoids) which characteristically have more acquisitive leaf traits (Freschet, Cornelissen, Logtestijn, & Aerts, 2010).

The mechanisms behind the responses of STA and SLA to elevation for lichens and bryophytes are likely to be different to those for vascular plants, because their poikilohydric nature means that their traits are likely to be less related to resource strategy. We found that lichen STA increases with elevation in a similar manner to vascular plant SLA, but suggest that this is driven by a different mechanism. As such, lichen STA is strongly linked to WHC and is therefore mainly associated with water economy (Gauslaa, 2014; Phinney, Solhaug, & Gauslaa, 2018), meaning that decreasing water loss by evapotranspiration with increasing elevation due to lower temperatures would cause a shift towards a lichen community with a higher STA and thus lower WHC. This is likely to also be the mechanism underpinning the decreasing WHC in bryophytes with elevation and is in line with findings from Henriques, Rigal, Borges, Ah-Peng, & Gabriel, 2017, who showed that bryophyte leaf traits associated with protection against water loss decreased with elevation. In contrast to lichens and vascular plants, SLA in the bryophyte community decreased strongly with increasing elevation, and this was driven by a shift from species with one cell-layer thin leaves (such as *Pleurozium schreberi*) towards those with thicker leaves containing lamellae (such as *Polytrichum* spp). Since bryophyte SLA was measured at the leaf-level, while WHC was measured on shoots, our measurements for bryophyte SLA and WHC are likely to be at least partly decoupled. However, we still lack a complete understanding of the mechanisms behind the strong response of bryophyte SLA to elevation.

5 | CONCLUSIONS

Our findings highlight that the contribution of intraspecific versus species turnover to community-level shifts in plant traits differs greatly among primary producer groups. Across our gradient, lichens exhibited a great deal of intraspecific plasticity in traits that respond strongly to elevation, notably N concentration and N:P ratio. This suggests that under future climate warming, lichen species may be more capable than vascular plant and bryophyte species in acclimating to new environmental conditions, at least if these parallel the environmental changes along our elevational study gradient. Because intraspecific variability can help maintain community stability and functioning under changing environmental conditions (Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Malyshev et al., 2016), the lichen communities would be more likely to resist environmental change than the bryophyte and vascular plant communities which lack the intraspecific plasticity needed to cope with environmental change. This line of thought is contrasted by studies showing that lichen (and bryophyte) communities respond negatively in terms of diversity and abundance to global change phenomena such as increased temperatures and changes in precipitation and snow cover (Alatalo, Jägerbrand, Chen, & Molau, 2017; Bidussi et al., 2016; Elmendorf et al., 2012; Jägerbrand, Kudo, Alatalo, & Molau, 2012; Lang et al., 2012). In most of these studies, the decline of non-vascular vegetation observed under climate warming is likely due to increased competition from vascular plants. Thus, lichen communities would only benefit from their intraspecific plasticity in areas where conditions are too harsh for vascular plants to establish, even under climate warming, such as higher elevations and exposed ridges.

While nearly all studies on primary producer trait variation across environments have focused on vascular plants, our study shows that trait variation of other largely neglected producer groups such as lichens and bryophytes may show very different responses to the same environmental factors. Non-vascular groups such as lichens and bryophytes are severely underrepresented in the trait literature (but some trait databases now exist, e.g. Bernhardt-Römermann, Poschlod, & Hentschel, 2018; Henriques, Ah-Peng, & Gabriel, 2017; Rambold et al., 2014), even though lichens and bryophytes are important components of many ecosystems, notably at high elevation and latitude. In order to fully understand and predict how future environmental changes will translate into shifts in community structure and ecological functioning, traits of primary producers other than vascular plants need to be considered in systems where these groups are important components of the overall community of primary producers. Further, our study highlights the importance of including intraspecific variation in functional trait studies, as we showed that some traits were almost completely driven by intraspecific variation, while for other traits, intraspecific variation greatly enhanced or mediated the community-level response to elevation.

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AUTHORS' CONTRIBUTIONS

K.v.Z. and R.E.R. contributed equally to this work. J.A. designed the study in consultation with D.A.W., K.K., S.B., S.I.L. and T.B. Field and laboratory work was conducted by K.v.Z. and R.E.R. with support of J.A., K.K., S.I.L. and T.B. Writing and data analysis were led by K.v.Z. and R.R. All authors contributed to revisions and discussions and approved the final version.

DATA AVAILABILITY STATEMENT

Data associated with this manuscript are deposited in the NMBU Open Research Data database (https://doi.org/10.18710/FR0QNN). Species occurrences are registered in the GBIF database, for vascular plants (https://doi.org/10.15468/fsoskq), lichens (https://doi.org/10.15468/asarqe) and for bryophytes (https://doi.org/10.15468/g28uix).

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