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RESEARCH PAPER

The importance of foundation species identity: A field experiment with lichens and their associated micro-arthropod communities

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Abstract

Foundation species provide habitat and modify the availability of resources to other species. In nature, multiple foundation species may occur in mixture, but little is known on how their interactions shape the community assembly of associated species. Lichens provide both structural habitat and resources to a variety of associated organisms and thereby serve as foundation species. In this study, we use mat-forming lichens and their associated micro-arthropods as a miniature ecosystem to study potential synergies between foundation species diversity and the abundance and functional diversity of higher trophic levels. We created lichen patches with monocultures and mixtures of up to four species, and extracted Collembola (identified to species level), Oribatida, Mesostigmata, Pseudoscorpiones, and Araneae with Tullgren apparatuses after 106 days of incubation within a natural lichen mat. We found that different lichen species supported different arthropod abundances. For 19 out of a total of 55 lichen mixtures and arthropod groups, we found non-additive, synergistic effects on arthropod abundance, although the specific lichen mixture causing synergistic effects differed with arthropod group. In addition, synergistic effects on arthropod abundance were more common for arthropod groups at lower trophic levels. The functional diversity of lichen mixtures explained patterns in Collembola abundance, but in the opposite direction than hypothesized because synergistic responses were more frequent in functionally similar lichen mixtures. Finally, we found few effects of lichen mixture identity or diversity on the functional diversity of Collembola communities. When applied to large-scale ecosystems, our results suggest that understanding interactions between coexisting foundation species and identifying those species that drive synergistic effects of foundation species on consumer biota, is likely to be of importance to biodiversity conservation and restoration efforts.

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Keywords: Collembola; Community assembly; Habitat heterogeneity; Oribatida; Functional traits; Functional diversity

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Introduction

Foundation species provide physical habitat and modulate the availability of resources to other species. Therefore, they are important drivers of biodiversity (Ellison, 2019; Tews et al., 2004; Thomsen et al., 2018), ecosystem functioning (Bulleri et al., 2016) and stability (Narwani et al., 2019), and are of particular relevance to biological conservation (Ellison et al., 2005). Examples of foundation species include veteran trees such as hollow oaks that support diverse arthropod communities (Siitonen & Ranius, 2015), the roots of coastal mangrove forests that provide effective nurseries to many marine species (Robertson & Duke, 1987), and Arctic plants that support distinct invertebrate communities (Coulson et al., 2003). While many studies illustrate the importance of single foundation species, multiple foundation species co-occur and interact in natural ecosystems (Angelini et al., 2011; Dijkstra et al., 2012; Vozzo & Bishop, 2019), and together they can facilitate a plethora of associated species (Thomsen et al., 2018). To date, however, relatively few studies have experimentally tested how multiple, co-occurring, terrestrial foundation species drive the assembly of their associated communities.

Mixing foundation species could have either additive or non-additive effects on associated communities. In case of additivity, a mixture of foundation species would support levels of abundance or diversity that are intermediate to each species in isolation. In contrast, synergistic or antagonistic interactions would support higher or lower levels, respectively, than expected from the species in isolation. The literature features ample examples of such non-additive effects of mixtures of producer species on community assembly of other trophic levels (Eisenhauer et al., 2019). For instance, Wardle & Nicholson (1996) found both greater and smaller microbial biomass in two-species grass mixtures than expected from monospecific stands, and De Deyn et al. (2008) found more diverse nematode communities in mixed-plant communities than in monocultures. Further, contrasting effects of mixed-forests stands and their leaf litter (which provides habitat as well as nutrients) on soil fauna have been found across studies (Korboulewsky et al., 2016). These studies conclude that species identity of producers can be a more important driver of community assembly of consumers than is species richness *per se* (De Deyn et al., 2004; Korboulewsky et al., 2016; St John et al., 2006; Wardle et al., 2006), and stress the importance of a functional approach to understanding mixture effects.

The functional traits of foundation species provide a useful framework for understanding how they interact and shape their associated communities. As such, the structural properties of a species may determine to what extent it creates suitable habitat. For example, more complex macrophytes (in terms of their fractal dimensions) support greater numbers and biomass of small animals (McAbendroth et al., 2005), and the structural complexity of Douglas fir is a strong driver of associated arthropod abundances (Halaj et al., 2000). On a smaller scale, the fractal dimensions of foliose lichens predict the distribution of associated arthropod body sizes (Shorrocks et al., 1991). These effects may manifest across trophic levels, as for example invertebrate parasitoids are known to increase with increasing habitat complexity (Langellotto & Denno, 2004). Moreover, species traits of foundation species can create the required microclimatic conditions that associated species need. For example, desert shrubs provide shade and nutrients to other plant species (Angelini et al., 2011), and some lichens provide both food and shelter to Gastropods (Baur & Baur, 1997) and smaller invertebrates (Bates et al., 2012). Similarly, mosses exert strong effects on water and heat fluxes in underlying soil (Soudzilovskaia et al., 2013) and thereby influence the taxonomic and functional composition of invertebrate communities (Bokhorst et al., 2014; Salmane & Brumelis, 2008, 2013). While mosses often occur in conditions that can guarantee relatively stable moisture conditions to associated arthropods, lichens often dry out intermittently, which causes the two groups of producers to support contrasting invertebrate communities (Bokhorst et al., 2019). However, few, if any, studies have compared how lichen species with contrasting traits affect invertebrate communities when they are grown in mixtures.

In this study, we used terricolous, mat-forming lichens as model to test how the composition and diversity of foundation species affects associated species at higher trophic levels. As such, we compare the abundance, community composition, and functional diversity of arthropod communities in lichens grown in monocultures and mixtures of up to four species. We consider these lichens to be an appropriate model for exploring questions about foundation species at small spatial scales as they meet many of the criteria outlined by Ellison et al. (2005). As such, lichens provide structural habitat and resources to a variety of invertebrates (Asplund & Wardle, 2017). Lichen traits such as structural complexity, capacity to retain moisture, growth form, and nutrient status determine their suitability to arthropods, and these traits all vary among lichen species (Bokhorst et al., 2015). Further, a complex of interlinked lichen traits determines the moisture regime in lichen mats (Ellis et al., 2021), which is of great importance to soil microarthropods (Bokhorst et al., 2015) because their distribution and life-history is driven directly and indirectly by moisture availability (Tsiafouli et al., 2005). For example, microarthropods living on lichen species with poor water holding capacity would need to be either adapted to desiccation or be able to move when faced with dry conditions between rainfalls. Lastly, mat-forming lichens cover extensive areas in boreal forest and tundra ecosystems (Asplund et al., 2017; Crittenden, 2000) and any interactions with arthropods thus manifest across significant spatial scales. Lichens are an ideal model system from a practical perspective as they lack specialized structures to maintain homeostasis such as roots, and can therefore be harvested, moved and manipulated without being harmed (e.g. Asplund et al. 2015;

Bidussi et al. 2016). In our experiment, we used the lichen species *Cladonia arbuscula, C. stellaris, C. uncialis*, and *Cetraria islandica* which we expect to differ in their three-dimensional structure, water holding capacity and thermal regulation. They were collected from and placed back into the field in monocultures and mixed-species patches, from which arthropods (Collembola, Oribatida, Mesostigmata, Pseudoscorpiones, and Araneae) were extracted after an incubation period of 106 days. Collembola were determined to species level.

We used this set-up to test the hypothesis that mixing lichen species (as model foundation species) has synergistic rather than additive effects on associated arthropod communities. We predict that synergistic effects will be stronger when more lichen species are mixed and when the mixed lichen species are more functionally diverse. This is because we expect arthropod abundance and diversity to respond positively to the increased habitat heterogeneity created within mixed-species lichen mats (see Tews et al., 2004). To further understand the drivers of any synergistic responses of arthropods to mixing, we also test whether the functional diversity (based on structural, nutritional and moisture traits) of lichen mixtures predicts arthropod abundance. Finally, we compare the functional traits and functional diversity of Collembola (based on their position in the soil profile, body size, mobility, and moisture preference) in different lichen mixtures, and test whether functional diversity of Collembola displays synergistic (versus additive) responses to lichen mixing. Through this work, we aim to offer insights about the ecological role of foundation species identity, traits and mixtures in altering communities of the animals for which they provide habitat.

Materials and methods

Study site

This study was performed at the Kollåsen nature reserve (59° 45′ N, 10° 56′ E), in Nordre Follo, Southeast Norway at approximately 190 m a.s.l. The site is located on pre-Cambrian gneiss bedrock and lies above the post-glacial loess deposits. It therefore has shallow, nutrient-poor, organic soils that are limited to depressions in the landscape. *Pinus sylvestris* and *Picea abies* dominate the site with undergrowth of *Vaccinium myrtillus* and *Calluna vulgaris* while dense lichen mats dominated by *Cladonia* species and *Cetraria islandica* cover the abundant rocky outcrops. The site has a humid continental/hemiboreal climate (Köppen classification *Dfb*). The nearest weather station, Ås NMBU (station ID 17,850) at 14 km from the field site and at 92 m a.s.l., recorded an average air temperature of 14.2 °C over the four month period from June to September 2017 (by month: 14.5, 16.1, 14.6 and 11.6 °C) with 390.6 mm of precipitation (Seklima.no, Norwegian Meteorological Institute, 2017).

Experimental setup

We collected *Cladonia arbuscula, Cladonia stellaris, Cladonia uncialis*, and *Cetraria islandica* subsp. *islandica* approximately one kilometer east-southeast of the experimental site, just outside the Kollåsen nature reserve (59°44′ N, 10°57 E) in May 2017. These species are all typical mat-forming lichens and are common in our study area and throughout the northern biome in general. The species differ in their morphological complexity. All four species have upright, fruticose thalli. While *Cetraria islandica* has flattened lobes, the *Cladonia* species have structurally more complex shrub-like podetia and branch in twos (dichotomic; *C. uncialis*), threes (trichotomic; *C. arbuscula*), or fours (tetrachotomic; *C. stellaris*) (Table 1). In addition, *Cladonia* thalli are hollow (Hammer, 1995, 2000) and these cavities should be readily accessible to micro-arthropods and provide additional habitat. All lichens used in this study have relatively low nutrient status, ranging from 0.34 to 0.59% N and 0.020 to 0.046% P (Table 1, data from Asplund & Wardle, 2013).

Table 1. Overview of lichen species used in the experiment and their traits.

Lichen species	Abbreviation	Branching complexity*	% Nitrogen†	Water holding capacity (% water at saturation) ± sd
Cladonia arbuscula	a	Predominantly trichotomic, some tetrachotomic branching, anisotomic	0.36	335 ± 31.2
Cladonia uncialis biuncialis	u	Predominantly dichotomic branching, anisotomic	0.34	287 ± 20.6
Cladonia stellaris	s	Predominantly tetrachotomic, some trichotomic or pentachotomic branching, isotomic	0.51	341 ± 26.0
Cetraria islandica	i	Dichotomic branching, flattened lobes	0.59	210 ± 27.7

*Ahti et al. (2013); Thell et al. (2011).
† Asplund et al. (2013), collected from the same locality as this study.

The collected lichens were identified to species, divided into mono-specific clumps of multiple (3–10) thalli, and cleaned from litter and necromass (dead or senescent thallus parts) in the lab. At this stage, lichens were dried at room temperature, but they were moistened whenever they needed to be handled due to the brittle nature of dried lichen thalli. We then created monospecific patches (see Appendix A: Fig. S1) of each of the four lichen species, and mixed species patches of all the 11 possible two- three- and four-species combinations. Each patch was placed in a cylinder of 15 cm diameter (176 cm^2) of 10 cm high nylon insect netting (mesh size 2.5 mm). The cylinders had open bottoms and tops, to allow free movement of arthropods in and out of the lichen patches. Each patch was 100% covered by lichen and mixed-species patches were made up equally of all component lichen species in the patch (by cover). Because lichen species differ in biomass per unit area, total biomass differed among (but not within) different lichen mixtures. The lichen patches were incubated within homogenous lichen mats in the field from June 21 to October 4, 2017. The experiment consisted of 10 blocks (i.e., lichen mats) spaced on average 83 m apart. All of the selected lichen mats were located on a gneiss bedrock outcrop of at least 5 × 5 m, with very little soil. Within each block, the 15 patches (each with a different species composition) were randomly placed in a 3 × 5 pattern with between 30 cm and one meter between neighboring patches (Fig. 1). Each block contained one replicate of each of the lichen treatments (i.e., 4 monospecific and 11 mixture patches), adding up to a total of 10 × 15 = 150 lichen patches used in the experiment.

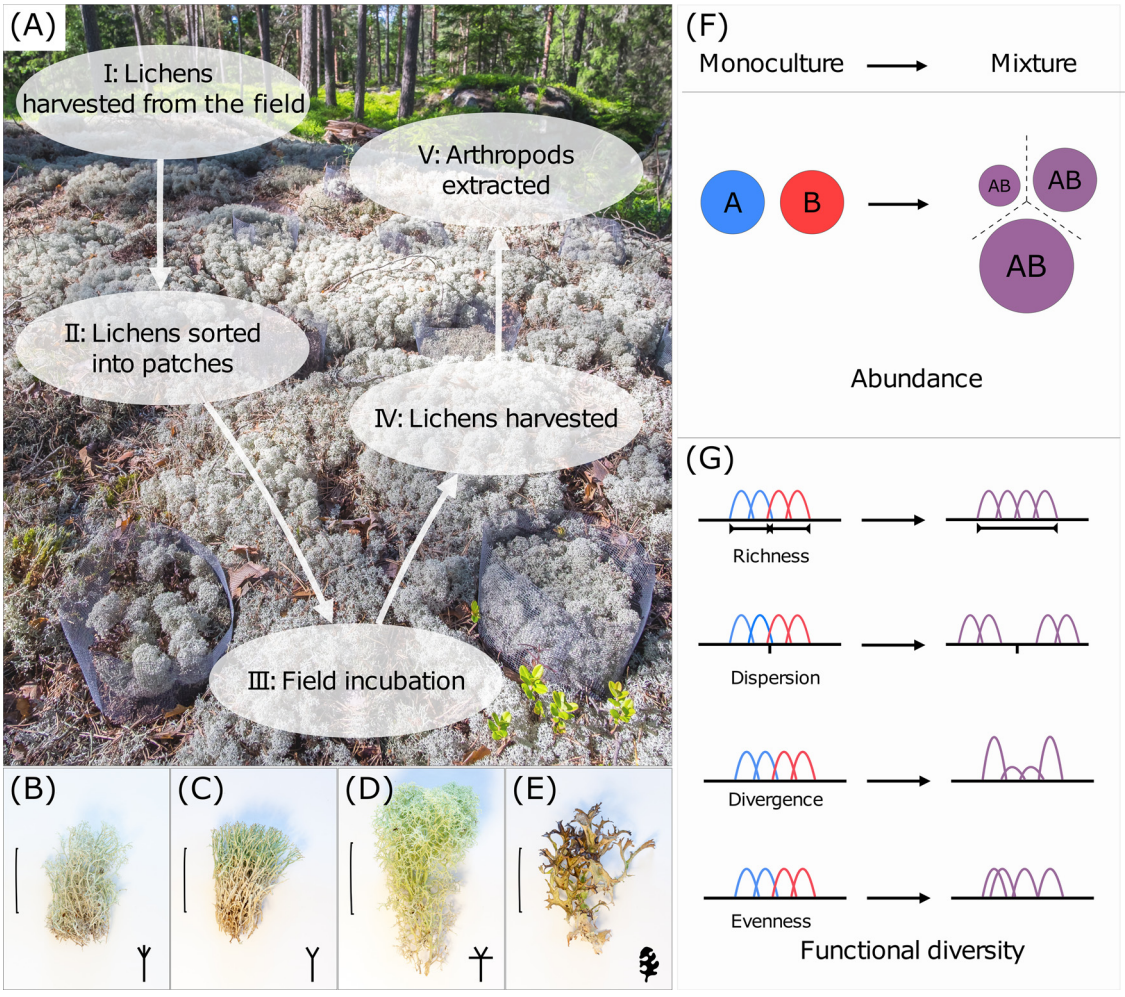

Fig. 1. Graphical summary of the field experiment (A). The lichen species used were (B) *Cladonia arbuscula* (branching in threes; trichotomic), (C) *C. uncialis* (branching in twos; dichotomic), (D) *C. stellaris* (branching in fours; tetrachotomic), and (E) *Cetraria islandica* (flattened lobes). The scale bars indicate 5 cm. In panels F and G, the potential effects of lichen diversity on associated arthropod communities are illustrated. First, the abundance of arthropods ((F); depicted by the size of the circles) in lichen mixtures (AB) can either be the average, larger, or smaller than the abundance in monocultures (A and B) Further, we expect mixing lichens will affect several functional diversity indices (G). Functional richness, the width of occupied trait space (here depicted for one trait dimension only) is expected to increase in a mixed lichen community. This will be matched by an increase in functional dispersion (the mean distance in trait space of individual species to the centroid of all species) and functional divergence (traits more dispersed towards the edges of trait space). Lastly, mixing may lead to a less regular distribution of traits in trait space, and therefore a reduction in functional evenness.

Arthropod identifications

The lichen patches were collected from the field on October 4, 2017, 106 days after placement in the field, and transported to the lab in plastic bags to avoid desiccation. We consider the >100 day duration of this experiment sufficient for arthropods to recolonize the lichen patches and this is supported by results from Åström & Bengtsson (2011), who found ample recolonization of moss patches in a similar ecosystem after 70 days. After harvest, the lichen patches were transferred and compressed into 10 cm diameter rings (which is easily done and not problematic when lichens are wet), within an extraction apparatus modified after Macfadyen (1961) and used by Roos et al. (2020). The temperature was gradually increased from 30 °C to 65 °C over the course of four days of extraction and samples remained in the extractor at 65 °C until completely dry (after 13−14 days). Arthropods were extracted into saline water and extractions were performed in two batches. Samples that were not immediately extracted were stored at 6 °C in the dark and subsequently extracted in a second batch (these batches were accounted for in the statistical analyses). Collembola were identified to species following Hopkin (2007) and Fjellberg (1998, 2007). Acari were grouped into Oribatida (including Astigmatina) and Mesostigmata. In addition, Pseudoscorpiones and Araneae were also counted.

Lichen functional traits and functional diversity indices

After field incubation and after arthropods had been extracted, we measured the water holding capacity (WHC) of each lichen patch. Several methodologies exist to measure WHC of individual lichen thalli (e.g. Gauslaa, 2014; Roos et al., 2019), but we measured WHC on the entire lichen patch *sensu* Van Zuijlen et al. (2020). To do so, we first cleaned the lichen patches of plant litter (e.g. pine needles) and water saturated them at room temperature for 15 min. Subsequently, the lichen patches were placed in between two soil sieves (bottom one with 2 mm mesh size, top one with 5 mm mesh size) and forcefully shaken 10 times to remove excess water. Lichen patches were then weighed (Mettler PE160, max 160 g, $d = 0.001$ g, Mettler Instruments AG, Zürich, Swiss) and subsequently dried for 96 h in ventilated drying ovens at 70 °C. After drying, lichen patches were weighed again for dry weight (Sartorius ENTRIS323I - 1S, 320 g x 0.001 g, Sartorius AG, Göttingen, Germany). Water holding capacity was expressed as dry weight / wet weight x 100. To test whether monoculture lichen patches have different water holding capacities, we performed Kruskal-Wallis tests and *post-hoc* Mann-Whitney U-tests in R (R Core Team, 2020).

In addition to water holding capacity, we quantified structural complexity on an ordinal scale (1−4, see Table 1) and lichen nutrient status (% Nitrogen, derived from Asplund & Wardle, 2013) for each lichen species to compute the functional dispersion of these traits for each of the lichen mixtures using the dbFD function of the R- package FD (Laliberté et al., 2014). Here, the relative abundance of each lichen in a specific mixture was determined on the basis of its cover. Functional dispersion is a diversity index that is independent of species richness (Laliberté et al., 2014), which is necessary as our lichen mixtures inherently differ in species richness (2—4 species). Because too few lichen species were included in some of the mixtures, other indices such as functional evenness could not be computed.

Arthropod abundance and additivity of mixing lichens

The abundances of Collembola, Oribatida, Mesostigmata, Pseudoscorpiones and Araneae were calculated as the number of animals per gram lichen dry weight. Then, to determine differences in abundance between the different lichen mixtures, ANOVA or Kruskal-Wallis tests were used, with Tukey HSD or Dunn tests for post-hoc comparison. To assess the additivity of the effect of mixing lichen species on the abundance of Collembola, Oribatida, Mesostigmata, Pseudoscorpiones, and Araneae, we calculated a standardized difference between the observed abundance in a mixture (O) and the expected (additive) abundance (E) for that mixture. Specifically, we calculated the expected arthropod abundance for a specific lichen mixture based on the mean arthropod abundance in each of the components in monoculture (within the same experimental block). We then calculated the standardized difference between observed and expected abundance as (O-E)/E (Wardle et al., 1997). A resulting value of zero would indicate no difference (i.e. an additive effect), a negative value would indicate a lower abundance than expected (non-additive, antagonistic effect) and a positive value would indicate a higher abundance than expected (non-additive, synergistic effect). To test whether standardized differences in abundance differed from zero, we ran mixed-effects models with lichen mixture as fixed effect and experimental block as random effect, and with the intercept set to zero; lmer(abundance ~ 0 + lichen mixture + (0 + 1|block), data = df) using the lme4-package (Bates et al., 2014) in R. In this case, removing the intercept is justified, as our interest was to specifically test whether the model estimates differ from zero. For both Pseudoscorpiones and Araneae, two strong outliers, in mixtures of *C. stellaris* and *C. islandica* with and without *C. arbuscula* of block 3, respectively, were removed, as its inclusion compromised model integrity. In addition, we ran similar models for arthropod abundance averaged for mixtures that combined all six two-species mixtures together, all four three-species mixtures together, and the four species mixtures. Differences between groups were tested with the emmeans-

package using the comparisons="TRUE" argument (Lenth et al., 2017) in R (Tukey method with alpha = 0.05). Finally, to assess how the functional dispersion of lichen mixtures (as described above) impacts the effect mixing lichens has on arthropod abundance, we ran mixed-effects models in R, using the standardized difference of the abundance of each arthropod group as a response variable and lichen functional dispersion as a fixed factor with experimental block as random factor.

Because we consider lichen water holding capacity to be an important trait determining habitat suitability for arthropods, we explored how water holding capacity drives the abundance of each group of arthropods (Collembola, Oribatida, Mesostigmata, Pseudoscorpiones, and Araneae) in lichen patches. To do this, we performed model selection on linear mixed-effects models with the lme4-package in R (Bates et al., 2014). In these models, lichen water holding capacity, lichen mixture identity, and prey abundance (= Collembola + Oribatida) was included as fixed effect for the predatory Mesostigmata, Pseudoscorpiones, and Araneae. We used Akaike information criterion (AIC) to evaluate models (see: Johnson & Omland, 2004) and if δAIC < 2, the simplest model was preferred. First, we selected for a random effects structure with restricted maximum likelihood (REML) in a full model that included lichen mixture, water holding capacity and (for predatory Mesostigmata, Pseudoscorpiones and Araneae) prey abundance, as well as the two-way interactions among these factors. Experimental block was selected as a random effect for all arthropod groups, while extraction batch was unimportant and not included in further analyses. However, as our data did not support complex random structures with both random slopes and intercepts (because this resulted in singular fits), we defined random intercepts only. Then, as fixed effects, we considered lichen mixture and lichen water holding capacity, and (for predatory animals) the total abundance of prey using maximum likelihood (ML). Because of limited interpretability, the three-way interaction between all potential fixed effects was not considered in these models, although the most complex model did include three two-way interactions. To avoid issues with heteroscedasticity of the residuals and violation of normality, data for Collembola, Oribatida was log transformed and data for Mesostigmata, Pseudoscorpiones and Aranea was square root transformed. Due to scaling issues, water holding capacity was included in the models as a fraction with one integral part, not as a percentage (e.g., 2.5 instead of 250%).

Collembola functional diversity and additivity of mixing lichens

We selected functional traits of Collembola (Appendix A: Table S1) that relate to the major axes of trait variation and potential use of different niches, using data for identified species from Ellers et al. (2018), Salmon et al. (2014) and Fjellberg (1998, 2007), and personal databases of S. Salmon and A. Fjellberg. First, Collembola were assigned an edaphic group, which reflects their vertical position within the soil profile, and this provides a useful classification in terms of species' dispersal ability and tolerance to abiotic variability (Van Dooremalen et al., 2013). As such, Collembola living on top of the soil (epi-edaphic) have the highest dispersal ability and tolerance, while sub-surface living species (hemi-edaphic) and true soil-dwelling species (eu-edaphic) are less mobile and rely more on stable environments. In addition, we included relative furca length compared to abdomen length as a proxy for the development of locomotory organs (Brackenbury & Hunt, 1993; Salmon et al., 2014). Further, we included body length, as well as moisture preference defined as (1) xerophilic: living in dry environments, (2) xero−mesophilic, (3) mesophilic: no preference for dry or wet environments, (4) hygro-mesophilic, and (5) hydrophilic: living in wet environments (Ellers et al., 2018).

Together with species abundances, these traits were then used to compute four functional diversity indices (based on multiple traits) of the Collembola communities of each lichen monoculture and mixture patch: functional richness, functional divergence, functional dispersion, and functional evenness using the dbFD function of the R- package FD (Laliberté et al., 2014). Functional richness refers to the total volume of the functional space occupied by the Collembola community, while functional divergence and evenness describes the regularity and divergence in trait abundance within this volume (Villéger et al., 2008). Functional dispersion constitutes the mean distance (in trait space) of each individual species to the centroid of all species (Laliberté & Legendre, 2010). For each lichen patch, these functional indices were weighted by the relative abundance of all the Collembola species present, and the "Caillez" method was used to correct for negative eigenvalues that cannot be represented in a Euclidian space. We then used separate ANOVA (with Tukey HSD post-hoc) or non-parametric Kruskal-Wallis (Funn test post-hoc) analyses to test for differences between functional indices for single species lichen patches and those with two, three, or four lichen species. In addition, for the mixed-species lichen patches, we calculated the standardized differences between observed and expected functional diversity (analogous to the standardized differences for abundance described above). We then tested whether these differences differed from zero using similar linear mixed-effects models (with block as random effect) in R to those used for arthropod abundance described above.

Results

Lichen mixture effects on arthropod abundance

The water holding capacity of mat-forming lichens differed between lichen monocultures at harvest (Kruskal-Wallis chi-squared = 30.587, df = 3, $P < 0.001$). *Cetraria*

islandica had the lowest water holding capacity while the more complex *Cladonia* species, notably *C. arbuscula* and *C. stellaris*, had higher water holding capacities (Table 1, Appendix A: Fig. S2). The lichen species grown in monocultures also supported different arthropod abundances at harvest. Specifically, *C. stellaris* supported relatively high abundances of Collembola, Oribatida, and Mesostigmata, but no significant differences between lichen species were found for Pseudoscorpiones and Araneae (Appendix A: Fig. S3, Appendix A: Table S2). Mixtures with *C. stellaris* typically had the highest Collembola, Oribatida and Mesostigmata abundance, but no differences were found among mixtures for the other arthropod groups. No significant differences at $P = 0.05$ in Collembola species richness, diversity (Shannon's diversity index) or evenness (Pilou's evenness) were found between lichen monocultures or mixtures (data not shown).

Mixing lichen species had either additive or synergistic effects on the abundance of associated arthropods (Figs. 2 and 3). Specifically, for Collembola, we found synergistic effects for four (out of 11 total) mixtures where the standardized difference was significantly above zero; all these mixtures included the functionally similar *C. arbuscula* and *C. uncialis*. As such, the synergistic effects on Collembola abundance decreased with increasing functional dispersion of the lichen mat (Table 2). However, lichen functional dispersion did not significantly affect the mixing effects on the other arthropod groups (Table 2). For Oribatida, five different lichen mixtures produced synergistic effects, four of which were mixtures that included *C. islandica* (Fig. 3). Further, Mesostigmata showed synergistic responses in four mixtures, which all included either *C. islandica* together with *C. arbuscula*, or *C. islandica* together with *C. uncialis*. Pseudoscorpiones and Araneae both showed synergistic responses for three lichen mixtures, all of which included *C. stellaris* (Fig. 3). Overall, mixtures of two, three, and four lichen species had synergistic effects on the abundance of Collembola and Mesostigmata (Figs. 2 and 3). For Oribatida and Pseudoscorpiones, synergistic effects were found for two- and three-species mixtures, while for Araneae synergistic effects were found in the mixtures of three and four lichen species. However,

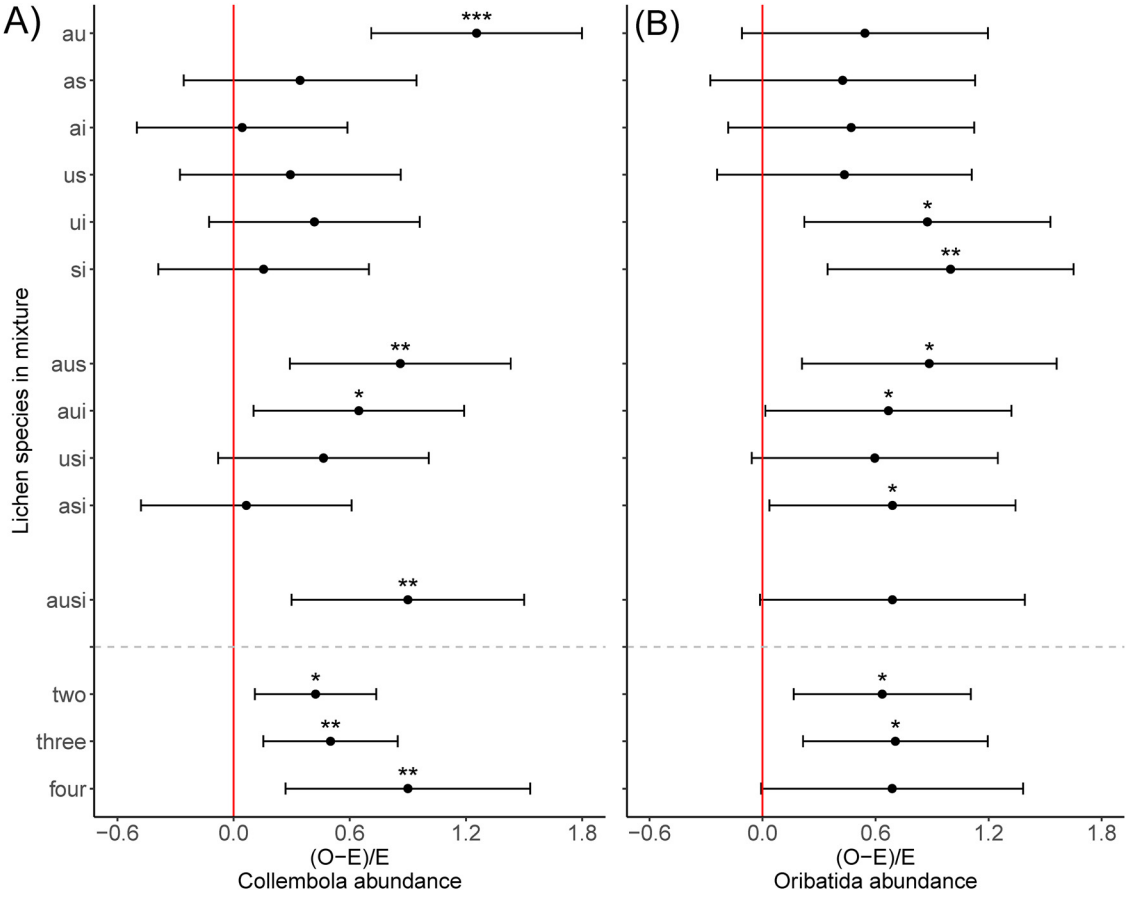

Fig. 2. Model estimates +/- 95% CIs for standardized (observed (O) versus expected (E)) abundance per gram dry weight lichen for (A) Collembola and (B) Oribatida. A positive value indicates that abundances in a mixture are higher than expected by the mean of the components (i.e. a synergistic non-additive effect). The emmeans package (Lenth et al., 2017) was used to compare effect size of treatments for each micro-arthropod group, but none of these differences were significant (Tukey's method with alpha = 0.05). Asterisks denote significant differences of the model fit from zero (*$p = 0.05$, ** $p = 0.001$, *** $p < 0.001$). a = Cladonia arbuscula, i = Cetraria islandica, s = Cladonia stellaris, u = Cladonia uncialis.

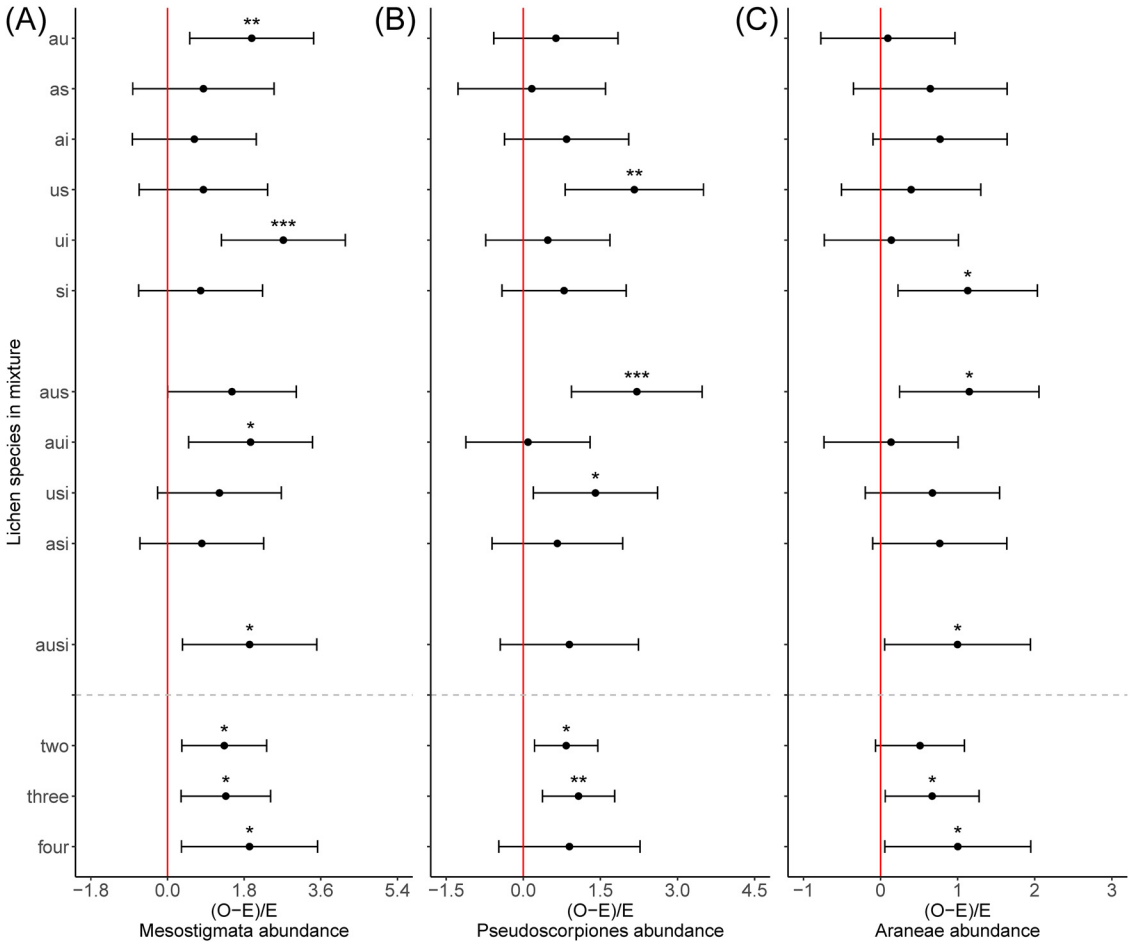

Fig. 3. Model estimates +/- 95% CIs for standardized (observed (O) versus expected (E)) abundance per gram dry weight lichen for (A) Mesostigmata, (B) Pseudoscorpiones, and (C) Araneae. A positive value indicates that abundances in a mixture are higher than expected by the mean of the components (i.e. a non-additive effect). Asterisks denote significant differences of the model fit from zero (*p = 0.05, ** p = 0.001, *** p < 0.001). a = Cladonia arbuscula, i = Cetraria islandica, s = Cladonia stellaris, u = Cladonia uncialis. The emmeans package in R (Lenth et al., 2017) was used to compare effect size of treatments within in each micro-arthropod group among each other, but none of these differences were significant (Tukey's method with alpha = 0.05).

Table 2. Linear mixed-effects model testing for the effect of functional dispersion of lichen mixtures on standardized (i.e., (observed-expected)/expected) abundances of arthropods and the functional dispersion of Collembola. The marginal R^2 describes the variance explained by the fixed effect only (functional dispersion), while the conditional R^2 also incorporates variation explained by the random effect (experimental block). Denominator degrees of freedom are 93.5.

	Estimate	SE	t (P)	Marginal R^2	Conditional R^2
Abundance					
Collembola	−2.76	0.84	−3.28 (<0.001)	0.081	0.231
Oribatida	0.24	0.82	0.29 (0.769)	<0.001	0.432
Mesostigmata	−2.47	1.98	−1.25 (0.215)	0.010	0.361
Pseudoscorpiones	2.01	3.53	0.57 (0.570)	0.003	0.036
Araneae	0.21	2.27	0.09 (0.925)	<0.001	0.315
Functional dispersion					
Collembola	−0.08	0.29	−0.28 (0.782)	<0.001	0.326

the strength of these synergistic effects did not increase with increasing number of lichen species from 2 to 4 in the mixture.

In the model selection process, the abundance of Collembola and Oribatida was best predicted by lichen mixture identity (Table 3), while for the abundance of Mesostigmata a complex model that included lichen mixture identity, lichen water holding capacity, prey abundance as well as their two-way interactions was selected. Pseudoscorpiones

Table 3. Results of mixed-effects model selection based on AIC for arthropod abundances. All models included experimental block as random effect. Data was transformed to improve normality of residuals and avoid heteroscedasticity. To calculate p-values of fixed effects, type III Analysis of Variance was performed using Kenward-Roger's method. The marginal R^2 describes the variance explained by the fixed effects only, while the conditional R^2 also incorporates variation explained by the random effect. WHC refers to lichen water holding capacity. The number of observations = 144.

Arthropod group	Fixed effects selected in model	Estimate	*F*-value	*P*-value	Marginal R^2	Conditional R^2
Collembola [a]	Model intercept	1.17		<0.001	0.233	0.497
	Lichen mixture		4.221	<0.001		
Oribatida [a]	Model intercept	2.40		<0.001	0.273	0.545
	Lichen mixture		5.491	<0.001		
Mesostigmata [b]	Model intercept	−0.46		0.542	0.700	0.746
	Lichen mixture		3.048	<0.001		
	WHC	0.17	2.897	0.092		
	Prey abundance	-0.03	1.508	0.222		
	LM:WHC		2.614	0.003		
	LM:PA		2.283	0.010		
	WHC:PA	0.02	2.655	0.107		
Pseudoscorpiones [b]	Model intercept	0.45		<0.001	0.122	0.125
	WHC	-0.10	8.112	0.005		
	Prey abundance	0.00	12.386	<0.001		
Araneae [b]	Model intercept	0.33		<0.001	0.121	0.232
	Prey abundance	0.01	18.118	<0.001		

[a]Data were log transformed.
[b]Data were square root transformed.

abundance decreased with increasing water holding capacity but increased with prey abundance. Araneae abundance was positively correlated to and best modelled by total prey abundance alone.

Collembola functional traits and diversity

The individual functional traits of Collembola communities differed between lichen monocultures (Appendix A: Fig. S4A-D). The largest community-weighted body size was found in *Cladonia stellaris* and the smallest in *Cetraria islandica*. Xero-mesophilous Collembola were most abundant in *Cetraria islandica*, and least abundant in *Cladonia uncialis*. Epi-edaphic species were better represented in *Cetraria islandica* than in *Cladonia arbuscula*. Furca class showed no variation across the different lichens. In general, dominant trait values (i.e. the most frequently occurring ordinal trait class) varied little among Collembola communities harvested from different lichen mixtures (Appendix A: Table S3). The functional richness of the Collembola communities was overall low, and highest in *Cladonia stellaris* and lowest in *Cetraria islandica* (Appendix A: Fig. S5A). Further, we found no differences in functional richness when averaged for all lichen mixtures of two, three, or four species (Appendix A: Fig. S5A). In addition, we found no differences among lichen monocultures or among species mixtures in functional divergence, dispersion, or evenness for Collembola communities (Appendix A: Fig. S5B−D). Similarly, we found few non-additive effects of lichen mixtures on the standardized measures (i.e., (observed − expected)/expected) of functional diversity for the Collembola community (Fig. 4A). However, there was a significant synergistic effect on functional richness when mixing *C. uncialis* with *C. islandica,* and when these two species were combined with *C. arbuscula* (Fig. 4A). For functional dispersion and divergence, we found synergistic effects when mixing *C. arbuscula* with *C. stellaris* (Fig. 4B, C), but no effects on functional evenness (Fig. 4D). Lichen species richness or functional dispersion did not influence the lichen-mixing effect (Table 2).

Discussion

We used mat-forming lichens and their associated microarthropods (Collembola, Oribatida, Mesostigmata, Pseudoscorpiones, and Araneae) as model ecosystem to study how foundation species in monocultures and mixtures shape the assembly of associated communities. We found that different lichen species support contrasting arthropod abundances and that mixing them sometimes has non-additive, synergistic effects on arthropod abundances, but never antagonistic effects. The occurrence of non-additive effects depended on which species were combined, while the number of lichens beyond two in the mixture was unimportant. Further, we found that lichen identity was most important for the abundance of consumers and that synergistic responses were less common at higher trophic levels. These findings are in agreement with the general pattern that the impact of

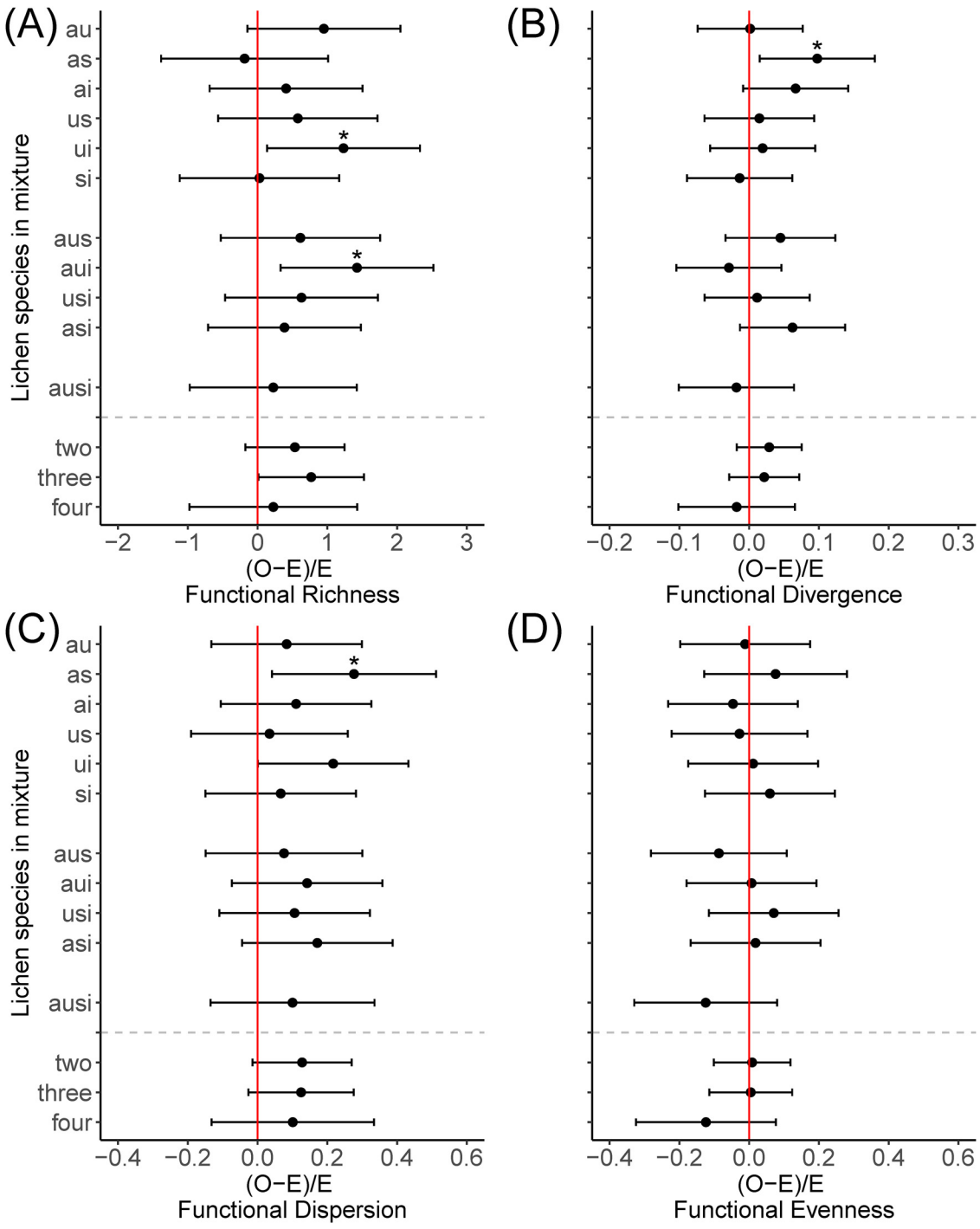

Fig. 4. Model estimates +/- 95% CIs for standardized ((observed − expected)/expected) functional richness (A), functional divergence (B), functional dispersion (C), and functional evenness (D). A positive estimate indicates that functional indices in a mixture are higher than expected by the mean of the components (i.e. a synergistic non-additive effect). Asterisks denote significant differences of the model fit from zero (*p = 0.05, ** p = 0.001, *** $p < 0.001$). a = Cladonia arbuscula, i = Cetraria islandica, s = Cladonia stellaris, u = Cladonia uncialis. The emmeans package in R (Lenth et al., 2017) was used to compare effect size of treatments within in each micro-arthropod group among each other, but none of these differences were significant (Tukey's method with alpha = 0.05).

biodiversity at one trophic level (e.g. primary producers) on other trophic levels (e.g. secondary consumers) decreases with trophic distance (Scherber et al., 2010). In our ecosystem, the functional diversity of lichen mixtures explained patterns in Collembola abundance, but in the opposite direction than we expected: synergistic responses in Collembola abundances to lichen mixing were found more frequently in functionally similar than in functionally diverse lichen

mixtures. Further, we found few effects of lichen mixing or diversity on the functional diversity of Collembola communities.

We found that the identity of the lichen species in the mixture is a more important driver of non-additive effects than is the number of species in mixture *per se*. This is in line with some earlier studies on mixing effects in different systems, for example for litter and soil arthropods in mixed forest stands (Korboulewsky et al., 2016), arthropod abundance in grasslands (Koricheva et al., 2000), and invertebrate species associated with decomposing wood (Andringa et al., 2019). However, an important challenge remains in identifying the drivers of synergistic responses for specific lichen mixtures and across arthropod groups, especially because the effects of functional diversity of lichen mixtures on arthropod communities were not always consistent with our expectations. Specifically, mixing lichen species that were the most functionally similar and thus generated the mixtures with the lowest functional diversity (i.e. *Cladonia arbuscula* and *C. uncialis*) often had non-additive effects on Collembola abundance. However, it is possible that the lichen traits included in this study did not capture all traits relevant to Collembola and thus the suitability of lichens as their habitat. Specifically, our model selection procedure chose a model that also included lichen (mixture) identity as opposed to just water holding capacity (WHC) alone, indicating that other lichen traits that varied among the lichen species may also be important. As such, Bokhorst et al. (2015) found that lichen N content was more important than lichen WHC in predicting Collembola richness and abundance. However, the abundance of Oribatida often responded to the inclusion of the morphologically dissimilar *Cetraria islandica* to the *Cladonia* species in the mixtures. Here, the responses of Oribatida are in line with our predictions and indicate that lichens supporting high abundance (such as *C. stellaris* and to lesser extent *C. uncialis*) overcompensate for lichen species that support low abundance such as *C. islandica.* We suggest that *C. stellaris* supports high abundances due to its structural complexity and relatively high water holding capacity, which creates a more stable microclimate. In contrast to Collembola, Bokhorst et al. (2015) found that WHC was important for Oribatida, which corresponds to our finding that the inclusion of *C. islandica* (which has a low WHC) reduced the abundance of Oribatida and had synergistic effects when in mixture with other species.

The interactions within (competition) and between trophic levels (including intra-guild predation) can affect the abundance of primary consumers such as Collembola and Oribatida (Aupic-Samain et al., 2019). We found that the abundance of predators at higher trophic levels, such as Pseudoscorpiones and Araneae, depended more on prey availability than on the lichen species present in the mixtures or lichen water holding capacity. Importantly, predatory arthropods could regulate micro-arthropod abundance and community composition top-down, although such effects are likely species-specific (Schneider & Maraun, 2009). From other studies, there is some evidence that predators exert stronger top-down regulation in mixed producer communities compared to monocultures, if basal resources (i.e. prey and their resources) are more abundant (Thakur & Eisenhauer, 2015). Because the larger predators included in this study (i.e. Araneae) are more mobile than small predators (e.g. Pseudoscorpiones) or primary consumers, their associations with the lichen mats likely manifest on a larger spatial scale than captured by our experimental lichen patches. Larger mobile predators (e.g., Araneae, Myriapoda) may punctually prey on lichen-dwelling micro-arthropods and may have moved outside the lichen patches before sampling. It seems unlikely that these larger predators would not only actively select different experimental lichen patches within the larger lichen mat but also reside there long enough to affect prey abundance between treatments. Considering that predator abundance was positively related to prey abundance, any influence by passing predators was clearly negligible or not strong enough to affect this association found in the experimental patches. Studying how such mobile predators affect micro-arthropods would require larger scale experiments. Finally, it is important to note that even species-poor soil-arthropod food webs can display complex and species-specific interactions (Crotty & Adl, 2019) and the current study lacks the taxonomic resolution needed to explicitly address the effects of such interactions and whether predators effectively control micro-arthropod abundances. In future experiments, predatory arthropod groups could be excluded from the lichen patches to tease apart the effects that trophic interactions have on community assembly in lichen patches of contrasting diversity.

Diversity of one trophic level (e.g. producers) can support and promote the taxonomic diversity of higher (consumer) trophic levels (e.g. Basset et al. 2012) and their functional diversity (Ebeling et al., 2018), with consequences for ecosystem functioning (Schuldt et al., 2018). We found that the diversity of producers (lichens) increased abundance at the next trophic levels (micro-arthropods) but the functional diversity of the Collembola communities was generally not affected. We suggest that this may be due to the high degree of generalism and functional redundancy that is characteristic of soil faunal groups (Potapov et al., 2020; Setälä et al., 2005). Further, the Collembola species in our dataset contained species that are common in Fennoscandia, whereas it is often the case that rare species contribute disproportionally to functional differences across species communities (Leitão et al., 2016). Although the functional composition of Collembola communities in lichen mixtures differed to a minor degree from those in lichen monocultures, the increased abundance of micro-arthropods could still impact ecosystem processes such as decomposition, given the role that Collembola have as litter fragmenters and fungal hyphal grazers and thus drivers of the composition of the microbial decomposer community (Coulibaly et al., 2019).

Our study organisms, i.e. mat-forming lichens, can be viewed as foundation species as they are numerically abundant and account for substantial biomass in several types of ecosystems such as mountains, polar regions and boreal forest floors (Asplund et al., 2017). In addition to the trophic interactions lichens may have with other organisms, our results suggest that they engage in non-trophic facilitative interactions with many invertebrate species across different trophic levels and that lichen diversity may have important implications for invertebrate abundance. Further, lichens may control microclimatic conditions (Mallen-Cooper et al., 2021; Van Zuijlen et al., 2020) experienced by their associated invertebrates and microorganisms. Although the foundation species concept originates from aquatic ecology (Angelini et al., 2011), we believe the concept has merit for terrestrial systems as well. As such, the potential importance of lichens as foundation species extends beyond mat-forming lichens on boreal forest floors to epiphytic and terricolous lichens growing on plants and rocks in other ecosystems. In old-growth forest canopies for example, lichens and other non-vascular producers cover virtually all surfaces (Sillett & Antoine, 2004), potentially housing a significant invertebrate diversity and biomass. While it is established that epiphytic vascular plants contribute greatly to invertebrate biomass and diversity in tropical forest canopies (Ellwood & Foster, 2004), we lack similar estimates to quantify the contribution of epiphytic lichens and other non-vascular producers to invertebrate biomass and diversity across different ecosystems.

The generality of results from ecological experiments on small-scale ecosystems such as the mat-forming lichen communities used in this study stems from the identification of ecological mechanisms that explain how nature *can* work, but not necessarily how nature *must* work (Drake & Kramer, 2012; Srivastava et al., 2004). As such, previous studies using mosses and soil micro-arthropods as miniature ecosystems have contributed to our understanding of general ecological processes and dynamics such as habitat destruction and isolation (Gonzalez & Chaneton, 2002; Starzomski & Srivastava, 2007), landscape connectivity (Åström et al., 2011; Shackelford et al., 2018), recolonization (Starzomski et al., 2008), and the role of nutrients (Bokhorst et al., 2019) and defense compounds (Asplund et al., 2015). Using mat-forming lichens, we establish that mixed assemblages of primary producers have non-additive or synergistic effects on the abundance of associated species. These results are relevant for underpinning discussion on how to manage production forests for biodiversity; as single-species versus mixed forest stands (Wang et al., 2019), and whether species mixing increases ecosystem services (Felton et al., 2016; Gamfeldt et al., 2013). In theory, it is possible that mixing foundation species would have negative effects if habitat heterogeneity were to increase to the extent that it results in habitat fragmentation (Tews et al., 2004) but this "threshold" was not passed in the current study. Regardless of the scale of the ecosystem, we believe it is important to identify and understand interactions between foundation species to support biodiversity conservation and restoration efforts.

Author statements

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Permissions

Fylkesmannen Oslo and Akershus provided permission to work in Kollåsen nature reserve (permit ref. no. 2017/17,688–3 M-NA).

Data

Data associated with this study is deposited in the NMBU Open Research Database (http://dataverse.no/) at (https://doi.org/10.18710/5F3QGT).

CRediT authorship contribution statement

Ruben E. Roos: Conceptualization, Investigation, Formal analyses, Data curation, Visualization, Writing – original draft, Writing – review & editing. **Tone Birkemoe:** Conceptualization, Investigation, Writing – review & editing. **Stef Bokhorst:** Conceptualization, Investigation, Writing – review & editing. **David A. Wardle:** Conceptualization, Supervision, Writing – review & editing. **Johan Asplund:** Conceptualization, Funding acquisition, Investigation, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors of this paper have no conflicts of interest to report.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.04.004.

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