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Collembola Communities, 20 Years After the Establishment of Distinct Revegetation Treatments in a Severely Eroded Area in South Iceland

Zespoły skoczogonków Collembola po 20 latach od wprowadzenia różnych metod rekultywacji na silnie zerodowanym obszarze w południowej Islandii

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Abstract: Several restoration methods have been developed to aid ecosystem development from highly degraded Icelandic deserts into fully vegetated functional ecosystems. Despite the critical role of soil biota in many key ecosystem processes, the effect of restoration efforts on soil biota has rarely been explored. We took advantage of a large-scale restoration field experiment, to study the effect of distinct revegetation treatments on the taxonomic and functional composition of Collembola communities. Soil samples were taken from plots (one ha. each) that had received functionally distinct revegetation treatments; i: grass + fertilizer, ii: birch seedlings, iii: willow cuttings, iv: lupine and v: control. We show that different revegetation treatments led to the establishment of distinct collembola communities in terms of density and taxonomic and functional composition, 20 years after the revegetation process had started. Life-forms were responsive to revegetation treatment, which suggests that the treatments had induced successional trajectories that lead to distinct habitat conditions, especially with respect to abiotic stress. In contrast to literature, eu-edaphic species were dominating in plots exposed to high levels of disturbance and fluctuations in abiotic conditions. Further research is needed to unravel to which extent resource supply and abiotic habitat conditions steer Collembola community development across successional trajectories.

Keywords: ecosystem restoration, Collembola, soil biota, functional traits, Iceland, revegetation

Streaszczenie: Szereg metod rekultywacji zostało opracowanych w celu przyspieszenia procesu przekształcania mocno zdegradowanych pustyń islandzkich w porośnięte roślinnością ekosystemy lądowe. Wpływ rekultywacji na organizmy glebowe jest rzadko badany, mimo że odgrywają one decydującą rolę w wielu kluczowych procesach zachodzących w ekosystemach. Celem przeprowadzonego na dużą skalę eksperymentu było zbadanie wpływu różnych zabiegów rekultywacyjnych na skład taksonomiczny i funkcjonalny zespołów skoczogonków Collembola. Próbki gleby pobrano z poletek (każde o powierzchni 1 ha), na których zastosowano różne zabiegi; i: trawa + nawóz, ii: sadzonki brzozy, iii: sadzonki wierzby, iv: łubin i v: kontrola. Uzyskane wyniki wykazały, że po 20 latach od rozpoczęcia rekultywacji, poszczególne zabiegi przyczyniły się do powstania zróżnicowanych pod względem zagęszczenia, składu taksonomicznego i funkcjonalnego zespołów skoczogonków. Stwierdzono wyraźną zależność udziału form życiowych skoczogonków od metody rekultywacji, co daję podstawę sądzić, że zastosowane zabiegi zainicjowały różne trajektorie sukcesji, prowadzące do powstania odmiennych zwłaszcza pod względem czynników abiotycznych warunków siedliskowych. Inaczej niż we wcześniejszych badaniach, wykazano, że gatunki euedaficzne dominowały na poletkach narażonych na wysoki poziom zakłóceń i wahania czynników abiotycznych. Zwrócono uwagę, że konieczne są dalsze badania, które pozwolą określić w jakim stopniu zasoby i warunki abiotyczne siedliska wpływają na kształtowanie się zespołów Collembola w różnych przebiegach sukcesji.

Słowa kluczowe: odbudowa ekosystemów, Collembola, organizmy glebowe, cechy funkcjonalne, Islandia

Introduction

Iceland, an active volcanic island just south of the Arctic Circle, has experienced severe land degradation during the last centuries (Dugmore et al. 2009; Arnalds 2015). Clear-cutting of woodlands and livestock grazing, in combination with harsh climatic conditions and natural disturbance events such as volcanic eruptions, has resulted in extensive barren or poorly vegetated areas (Gísladóttir et al. 2010; Eddudóttir, Erlendsson, and Gísladóttir 2020) with low soil organic carbon pools (Óskarsson et al. 2004). At present, about 42% of Iceland's terrestrial surface area is estimated to be barren or poorly vegetated (Arnalds, Dagsson-Waldhauserova, and Olafsson 2016). Ongoing erosion, frequent freeze-thaw cycles, low water holding capacity and nutrient deficiency commonly prevent these areas from recovering by themselves (Arnalds 2015).

Various restoration methods have been developed to aid ecosystem development from sandy deserts into fully vegetated functional ecosystems, such as grasslands, heathlands, or birch forests. Sowing of native grasses or exotic nitrogen fixing lupine (*Lupinus nootkatensis*) and planting of downy birch (*Betula pubescens*) or willow shrubs (*Salix* spp.) are among revegetation treatments commonly used in Iceland to overcome biotic and abiotic thresholds that prevent ecosystem succession by itself (Aradóttir 1998). Evaluation of these restoration efforts has generally focused either on aboveground biotic properties such as plant community structure (Grétarsdóttir et al. 2004), or abiotic properties such as carbon sequestration (Arnalds, Orradóttir, and Aradóttir 2013).

During the last decades, awareness of above- and belowground linkages, and their significance for ecosystem functioning and community development, has increased considerably (Bardgett et al. 2005; Bardgett 2018). Plants, for instance, as integrating organisms across those compartments, affect soil community assemblies through their input of litter and root exudates, mutualistic relationships, and habitat formation (Kardol and De Long 2018). Indeed, a number of studies have shown that plant community composition is a strong driver of soil fauna community structures (Salamon et al. 2004; Viketoft et al. 2009; Bezemer et al. 2010; Eisenhauer et al. 2011; Krab et al. 2019; Lu et al. 2021). At the same time, soil biota play a critical role in plant community development through mutualism and their control on pest dynamics, and carbon and nutrient cycling (Van der Putten et al. 2013; Bardgett and van der Putten 2014) and thus may steer or influence aboveground successional trajectories (De Deyn et al. 2003; Kardol, Martijn Bezemer, and van der Putten 2006). Despite increased recognition of the importance of soil organisms for ecosystem functioning, they are rarely included in monitoring or evaluation of ecosystem restoration success.

Given the crucial role of soil biota in driving key ecosystem functions and development (Van der Putten et al. 2016), it is essential to ensure facilitation of soil communities when selecting and applying restoration treatments. A limited, but growing number of papers, emphasize the importance of above- and belowground linkages for restoration ecology (Eviner and Hawkes 2008; Heneghan et al. 2008; Kardol and

Wardle 2010; Van der Putten et al. 2013). Distinct plant functional groups, for instance, are likely to promote different soil food-webs (Holtkamp et al. 2008; Bezemer et al. 2010; Perez et al. 2013; Cortois et al. 2016; Beugnon et al. 2019), which may have important implications for various ecosystem processes (van Dijk et al. 2009; de Vries et al. 2013), including successional rate and direction (Kardol, Martijn Bezemer, and van der Putten 2006; Van der Bij et al. 2018). Hence, different successional trajectories, induced by distinct revegetation, are likely to shape distinct soil communities and may leave soil legacies long after treatment (Wubs et al. 2019).

An accumulating body of literature shows that trait-based approaches may complement taxonomic indices by improving our understanding and predictive capabilities of ecosystem responses relevant in community ecology (de Bello et al. 2010). Collembola communities, for instance, may serve as an interesting indicator tool to be evaluated from a trait perspective. They are among the most diverse and abundant invertebrate groups in the top-soil layer at northern latitudes (Petersen 2002) and are responsive to changes in (micro-)climate (Wolters 1998; Holmstrup et al. 2018), litter quality and soil properties (Chagnon, Hébert, and Paré 2000; Hasegawa 2002), as well as land-use type or disturbance (Malmström 2012). As they exhibit a wide range of morphological and life history traits that reflect their adaptation to the environment, functional indices have been successfully used to describe Collembola community responses to changes in environmental conditions or land-use management (Vandewalle et al. 2010; Makkonen et al. 2011; Martins da Silva et al. 2016; Joimel et al. 2021).

Collembola can be classified by life-form according to their vertical stratification as epigeic (surface), eu-edaphic (soil) and hemi-edaphic (top-soil, litter) species. As life-form commonly reflects morphological adaptations to environmental conditions, Collembola life-form is now frequently included as "functional trait" when exploring drivers of functional composition of Collembola communities. Generally, eu-edaphic species are assumed to be less tolerant to abiotic stress (Bokhorst et al. 2012; Martins da Silva et al. 2016; Holmstrup et al. 2018) and are characterized by reduced appendages, pigmentation and number of ocelli compared to epigeic species.

In this study, we took advantage of a long-term restoration experiment in a severely eroded desert area in Iceland, where soil biological legacy effects were presumed to be minimal. It provided unique conditions to study the effect of different plant successional trajectories, induced by different revegetation efforts, on Collembola communities. We tested whether different revegetation treatments have led to distinct taxonomic and functional compositions of Collembola communities, 20 years after revegetation.

1. Methods

1.1. Site description and experimental set-up

The study was conducted at Geitasandur, a sandy desert in South Iceland (63°29` N, 20°13` W). The area is sparsely vegetated due to severe erosion and is characterised by unsteady surfaces and frost heaving. The soils are classified as Andosols with a gravelly surface, about 0.2% organic carbon content and relatively low water retention (Arnalds, Orradóttir, and Aradóttir 2013). The region received about 68 mm of precipitation monthly during May-September 2000-2019, with an average temperature of 9.7°C during the same period (Icelandic Meteorological Office, personal communication).

In 1999, the Landbót restoration experiment was established at Geitasandur, in which 40 plots (one ha each) received 10 different revegetation treatments (see Aradóttir and Halldórsson (2018) and Arnalds, Orradóttir and Aradóttir (2013) for details about Landbót). In this study, four treatments of distinct plant functional types were sampled, as well as control plots (Table 1).

Table 1. Description of initial revegetation treatments applied in 1999 and surface descriptions of plots at the time of sampling

	Treatment (1999)*	Plot description (2019)**
C	Control, no treatment.	Sand, gravel pebbles and rocks. Vegetation cover scattered, below <10%.
G	Seeding of grasses *Poa pratensis* and *Festuca rubra*, 17.3 and 9.7 kg ha^{-1} respectively + 50 kg ha^{-1} N and 27 kg ha^{-1} P_2O_5. Fertilization was repeated 2001, 2003, 2005 and 2012.	Discontinuous vegetation cover, characterised by patches of mosses, lichens, biocrust, bare sand, sedges, rushes and forbs. Total vegetation cover ~ 60%, vascular plant cover ~ 30%.
L	Seeding of lupine *Lupinus nootkatensis.*	Dense lupine cover (monoculture).
B*** W***	Planting of eighty downy birch *Betula pubescens* (B) clusters (6 x 30 m) in three contour strips, and planting of 80 woolly willow cuttings *Salix lanata* (W) in clusters (8 x 25 m) in four contour strips. Birch and willow clusters shared plots, each plot contained four and two separated clusters of birch and willow, respectively. The area between clusters received treatment as in G.	Downy birch has reached about 1.5-3 m height, the understory is mostly bare sand with patches of mosses. Willow clusters are characterized by a short but continuous cover of willow shrubs, mosses, lichens, biocrust, and some forbs, rushes and sedges. Total vegetation cover surrounding the clusters was ~ 70%, with a ~11 % of vascular plant cover.

*Based on Aradóttir and Halldórsson (2018) and Aradóttir et al. (2008). ** Based on K. Svavarsdóttir and A.L Aradóttir (unpublished data) in combination with rough visual estimations at the time of sampling. *** Sampling took place within birch clusters or willow clusters, which were treated as independent treatments.

1.2. Sampling of Collembola

Collembola were sampled four times from July until October 2019, using a cylindrical soil corer (ø 5 cm) to a depth of five cm. Eight soil cores were taken randomly per treatment every sampling time, resulting in a total of 32 samples of 15.9 cm^3 per treatment. We combined two samples into a composite sample (n=16) for analysis every sampling time but extracted Collembola from separate samples in a MacFadyen high gradient extraction apparatus (Macfadyen 1961) by a gradual increase of temperature from 25-60 °C during nine days. Collembola were collected in benzoic acid and stored in 75% ethanol until identification and identified to species level according to (Fjellberg 1998; 2007; Hopkin 2007).

1.3. Community indices

To explore the effect of restoration treatments on taxonomic community composition we computed Collembola density, species richness (S), Shannon-Weaver species diversity (H'; Eq.1) and Pilou's species evenness (J; Eq.2) per composite sample as:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \qquad (1)$$

$$J = \frac{H'}{\ln (S)} \qquad (2)$$

in which p_i is the relative abundance of the *i*th species, and *S* is the total number of species in a sample.

Three morphological traits, which reflect vertical stratification and sensitivity to environmental change, were selected based on literature (Moretti et al. 2017; Yin et al. 2020): ocelli, furca, and pigmentation. Each trait was scored from zero to four (Table 2) and a final life-form score of a species was obtained through the sum of the scores, divided by the maximum possible, according to Martins da Silva et al. (2016). Hence, higher life-form values indicate surface dwelling species with higher tolerance to abiotic stress factors. In addition, reproductive mode was included as a categorical trait and body size as a qualitative trait. Body size values (maximum length) and reproduction were based on literature (Fjellberg 1998; 2007; Hopkin 2007).

Table 2. Description of functional traits used in the analysis

Trait	Type	Attribute	Score
Number of ocelli*	Ordinal	0	0
		1-4	2
		5-8	4
Furca*	Ordinal	Absent	0
		Reduced/short	2
		Well developed	4
Pigmentation*	Ordinal	None	0
		Moderate	2
		Strong	4
Reproduction	Ordinal	Parthenogenetic	0
		Sexual	4
Body size	Quantitative	Length	(mm)

* Traits used to compute life-form.

To analyse the response of individual traits to restoration treatments, a community weighted mean (CWM; Eq.3) was calculated as:

$$CWM = \sum_{n=1}^{n} p_i * x_i \qquad (3)$$

where is the relative abundance of the *i*th species, is the trait value of the *i*th species and *n* is the number of species in the community.

To explore the effect of restoration treatments on the functional composition of Collembola communities we calculated three components of functional diversity: richness, evenness, divergence, along with Rao's quadratic entropy index of diversity (RaoQ), for each sample in accordance with Villéger, Mason, and Mouillot (2008) and Götzenberger et al. (2021). As Collembola abundances and richness varied greatly between samples within treatments, we chose to compute functional diversity based on total species abundances per treatment as well. Functional richness (FRic) describes the amount of functional space filled by a community, and functional evenness (FEve) represents the evenness of abundance distribution in this space. Functional divergence (FDiv) indicates the degree to which the abundance of community is distributed toward the extremities of occupied functional trait space (Villéger, Mason, and Mouillot 2008; Mason and Mouillot 2013). RaoQ describes the sum of dissimilarities in the functional space among all possible pairs of species weighted by the product of relative abundances (de Bello et al. 2011).

Shannon diversity was computed using the vegan-package (Oksanen et al. 2020) and all trait-based indices through the FD-package (Laliberté, Legendre, and Shipley 2014).

1.4. Statistical analyses

All statistical analyses were performed using R statistical software (R Core Team 2020) and conducted irrespective of sampling time as we could not detect any temporal pattern in Collembola density throughout the season. Species abundances were ln transformed prior to analyses to meet assumptions of normality and homoscedasticity, after which the effect of revegetation treatment on both Collembola density and species richness was tested with a one-way ANOVA. A Tukey HSD post-hoc test was used to obtain differences between treatments. Graphic presentations of model outputs were performed with back transformed values.

To overcome non-normal data distributions for taxonomic and functional diversity indices, we made use of Kruskal-Wallis tests to assess whether diversity indices differed between treatments. When rejected, a Dunn's test was used as post-hoc test to obtain multiple comparisons between treatments.

2. Results

Collembola density differed significantly between revegetation treatments (ANOVA, $P < 0.001$). A Tukey HSD post-hoc test revealed that lupine (L) plots hosted significantly higher densities than all other treatments. Birch (B) plots also held significantly higher densities than grass (G) and control (C) plots, but grass sowing and planting of willow (W) had not led to significantly higher densities over C plots (Fig.1A).

Species richness similarly was significantly affected by revegetation treatment (ANOVA, $P < 0.001$). B and L treatments had both led to the establishment of Collembola communities with significantly higher number of species per sample than no revegetation treatment (Fig. 1B). In total, 14 out of 15 species were present in L plots, whereas only three species were recorded in G plots (Table 3). *Mesaphorura macrochaeta* was the only shared species for all treatments, whereas *Xenylla humicola* and *Desoria* sp. were only recorded from L plots.

Kruskal-Wallis tests revealed that Collembola communities differed significantly in Shannon diversity ($P < 0.001$) and species evenness ($P = 0.001$) between treatments. Shannon diversity was significantly higher in L than all other treatments (Fig. 2A), but species evenness in L only differed significantly from G and C plots (Fig. 2B).

A Kruskal-Wallis test revealed a significant difference in CWM-life-form between treatments ($P < 0.001$), with significantly higher values in L plots than all other treatments (Fig.3A). CWM-reproduction and CWM-body-size were only significantly lower in B than L ($P = 0.001$; $P = 0.01$; results not shown). Of all functional diversity indices (results not shown), only functional evenness (FEve) differed significantly between treatments ($P < 0.001$). FEve was found to be lowest in L plots, but B, W and L showed wider ranges of FEve than G and C (Fig. 3B).

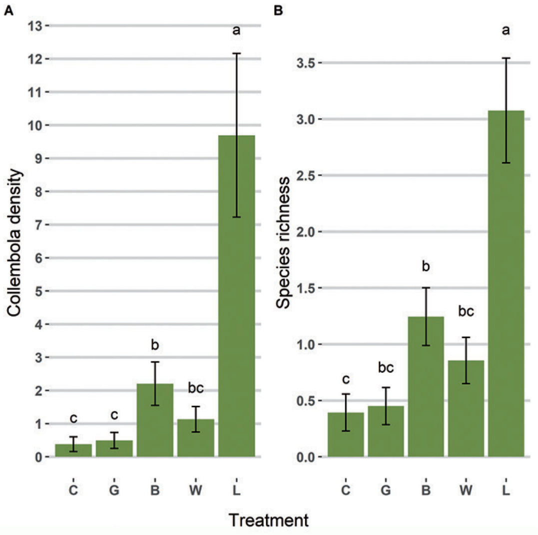

Figure 1. Mean number of Collembola (A) and mean species richness (B) per sample by revegetation treatment (n=16). C: control, G: grass + fertilizer, B: birch, W: willow, L: lupine. Error bars represent SE

Table 3. List of all species found by treatment (mean abundance m^{-2}), and species richness and functional diversity based on total abundances per treatment. C: control, G: grass, B: birch, W: willow, L: Lupine. EU: Eu-edaphic, H: hemi-edaphic, EP: epigeic

Species	Treatment				
	C	G	B	W	L
Desoria sp. EP	–	–	–	–	39.3
Folsomia sp. EU*	–	–	19.7	–	59.0
Folsomia quadrioculata H	21.0		118.0	92.5	98.3
Isotoma anglicana EP	–	–	–	–	256.0
Isotoma caerulea EP	–	19.7	39.3	55.5	1002.0
Isotoma viridis EP	–	–	–	37.0	511
Isotoma spp. EP**	–	–	19.7	37.0	98.3
Isotomiella minor EU	–	–	78.6	18.5	197
Isotomodes bisetoses EU	–	78.6	39.3	37.0	–
Isotomodes productus EU	62.9	–	–	–	39.3
Mesaphorura macrochaeta EU	126	157	511	277	275
Micranurida pygmaea H	–	–	19.7	–	118
Proisotoma minuta H	–	–	–	55.5	59.0
Parisotoma notabilis H	–	–	452	37.0	3184
Willemia scandinavica EU	21	–	–	55.5	157
Xenylla humicola H	–	–	–	–	39.3
Species richness	4	3	8	9	14
FRic	0.41	0.39	3.42	3.15	3.47
FEve	0.23	0.10	0.64	0.61	0.48
FDiv	0.68	0.63	0.67	0.79	0.62
RaoQ	0.60	1.22	1.61	2.83	2.51

**F. spinosa* or *F. fimetaria*, ***I. viridis, I. anglicana* or *I. caerulea*.

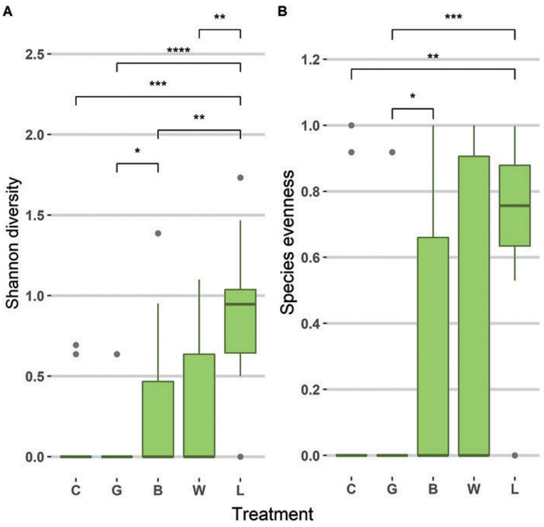

Figure 2. Boxplot of species diversity (A) and species evenness (B) by treatment (n=16). Significant differences are marked (*P<0.05; **P<0.01; ***P<0.001), based on Dunn's post-hoc test for multiple comparisons. C: control, G: grass, B: birch, W: willow, L: lupine

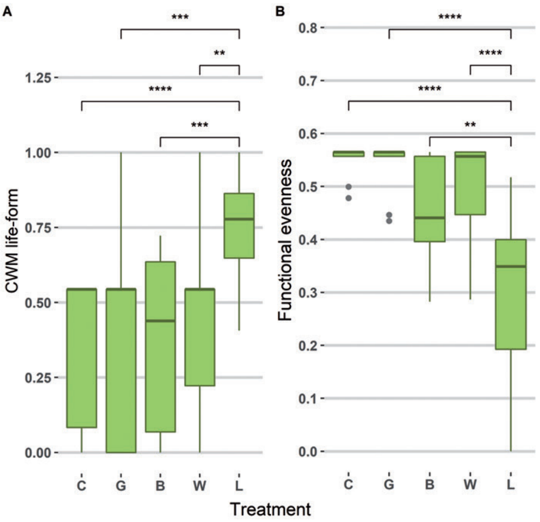

Figure 3. Boxplot of CWM-life-form (A) and functional evenness (B) by treatment (n=16). Significant differences are marked (P*<0.05; ***P*<0.01; ****P*<0.001), based upon Dunn's test for multiple comparisons. C: control, G: grass, B: birch, W: willow, L: lupine**

3. Discussion

3.1. Taxonomic composition

Our results clearly show that different revegetation treatments lead to the establishment of distinct Collembola communities in terms of abundances and taxonomic community composition. Apparently, lupine has created conditions that supports denser and more diverse collembola communities than other revegetation treatments.

At plot level, Collembola community composition is mainly driven by resource supply, abiotic (micro-)habitat conditions and pathways of dispersal (Ettema and Wardle 2002; Ingimarsdóttir et al. 2012; Nielsen 2019). As dispersal limitations were assumed to be equal among treatments, abiotic habitat conditions have likely been a strong driver of Collembola communities. The revegetation treatments had induced very distinct aboveground successional trajectories, resulting in large differences in vegetation cover, plant species composition (K. Svavarsdóttir and A.L. Aradóttir, unpublished data) and patchiness. L plots were characterised by a much denser and homogeneous vegetation cover than any other treatment, which may have supported greater Collembola densities through the provision of higher resource supplies. However, the higher species richness and diversity, rather than density alone, suggest habitat conditions suitable for a greater range of species in L.

As we did not include reference sites, we cannot conclude to what extent Collembola communities resemble target systems. However, none of the treatments had reached Collembola densities similar to heath- or grasslands at comparable latitudes (Petersen and Luxton 1982; Bokhorst et al. 2018), tundra ecosystems (Sørensen et al. 2006) or Icelandic grasslands (Holmstrup et al. 2018).

3.2. Life form

The observed differences in CWM-life-form further indicate dissimilar habitat conditions, with more epigeic species thriving in habitats shaped by L. A dense lupine cover is likely to reduce fluctuations in temperature and moisture, as well as wind or water erosion and cryoturbation, thereby facilitating the establishment of hemi-edaphic/epigeic species. The upward shift in vertical stratification of Collembola communities was the result of a relatively greater increase in hemi-edaphic/epigeic species, not a reduction of eu-edaphic species abundance. Although eu-edaphic species are generally reported as less stress-tolerant with lower dispersal rates, known to colonise at later successional stages (Hodkinson, Coulson, and Webb 2004; Hågvar 2010), our results show a contrasting pattern. C and G plots were characterised by sparse patches of vegetation, resembling a primary successional stage, frequently exposed to erosional processes. Yet, these plots were predominantly inhabited by eu-edaphic species (*M. macrochaeta* and *Isotomodes* spp.). We hypothesize that surface conditions of Iceland's sandy deserts may be too harsh and unstable to support hemi-edaphic/epigeic species, whereas eu-edaphic species may find shelter within the soil environment.

We found life-form to be a promising parameter to be responsive to environmental conditions, which provides potential for Collembola as bio-indicators when monitoring or evaluating restoration efforts. However, in order to gain insight in less extreme differences in habitat conditions across treatments (e.g., food-web related, soil properties, etc.), it may be necessary to include a broader trait spectrum. Ecophysiological traits or feeding guilds, for instance, could complement life-form to achieve a more comprehensive insight in Collembola community responses to revegetation treatments, as well as the underlying mechanisms driving them (Potapov et al. 2020).

3.3. Functional diversity

Functional evenness (FEve) differed significantly between several treatments (Fig. 3B). As all selected traits were related to life-form, FEve reflects to a large extent the regularity of life-form distribution in a community. The higher FEve values for C and G can be explained by low species richness and the high dominance of two eu-edaphic species with similar traits. Lower values, but wider ranges, of FEve for B and L reflect the dominance of eu-edaphic/hemi-edaphic and hemi-edaphic/epigeic species, respectively, but with a greater spectrum of trait scores present in their communities than C and G.

No significant difference was detected in functional richness, divergence and RaoQ between treatments. Apparently, Collembola communities of all treatments were predominantly occupied with a narrow set of trait values. However, Collembola abundance and species richness data were skewed for all treatments and showed heteroscedasticity of residuals. The high variation in Collembola density within treatments reflects the patchy nature of Collembola spatial distribution (Berg 2012), which further prevented us from detecting additional patterns of functional diversity.

Conclusion

We showed that different revegetation treatments have led to the establishment of distinct Collembola communities in terms of density, taxonomic diversity, vertical stratification and functional evenness. Although these differences are likely, to a large extent, to be the result of distinct abiotic conditions, we encourage future research to disentangle direct effects of vegetation (resource input) and indirect by altering abiotic habitat conditions. Furthermore, we showed that Collembola communities have potential as a bio-indicator when monitoring or evaluating restoration of severely degraded ecosystems.

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