

RESEARCH PAPER

Proglacial slopes are protected against erosion by trait diverse and dense plant communities associated with specific microbial communities



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Abstract

Soil erosion is a severe threat for ecosystems and anthropogenic infrastructure. Glaciers are retreating rapidly due to global warming and the receding ice leaves unvegetated depositions of sediment, which are prone to mobilisation during precipitation events. Vegetation is known to serve as erosion protection, but how above- and belowground plant traits, vegetation cover and plant diversity on community level are jointly affecting erosion is unclear. Additionally, soil microbial communities may have effects on slope stability by promoting plant growth and function. We measured sediment transport on 30 plots of 2 × 3 m size on proglacial slopes of the Gepatschferner glacier (Kauental, Austria) over three years in a natural pristine high alpine environment. Vegetation cover, species abundances and relevant above- and belowground traits were measured for each occurring plant species on community level. Path model analysis revealed that dense and species-rich plant cover characterized by specific plant growth strategies and trait diversity was best suited to decrease erosion. Vegetation properties were also closely linked to the composition of soil microbial communities characterised by next generation amplicon sequencing, which may facilitate soil formation and further enhance the plants' soil stabilising potential. Our study illustrates that erosion control may benefit from a high vegetation cover, which is facilitated by diverse plant communities with complementary morphological traits. These vegetation properties also affect soil microbiota, but their impact on slope protection in combination with the vegetation remains to be elucidated. Our findings may inform nature-based solutions against erosion such as revegetation of alpine slopes using specific seed mixtures.

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Introduction

Soil erosion is globally one of the largest environmental challenges in managed and natural terrestrial ecosystems, as

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it is hampering ecosystem services such as biological productivity, water holding capacity and carbon storage (Poesen, 2018). Erodibility is defined as the susceptibility to detachment of soil particles and is determined by the soil's aggregate stability, infiltration capacity, bulk density, soil texture and organic content (Gyssels, Poesen, Bochet, & Li, 2005), all of which factors are related to the present vegetation and microbial activities (Schulz et al., 2013; Vannoppen, Vanmaercke, De Baets, & Poesen, 2015). Vegetation modifies geomorphological processes and in turn, geomorphic disturbances can influence plant establishment, which is known as biogeomorphic feedback (Eichel, Corenblit, & Dikau, 2016; Haselberger et al., 2021; Matthews, 1992). Due to the positive effects on slope stability, revegetation is a widely applied long-term solution against erosion. For most revegetation purposes large amounts of inexpensive commercially available non-native plants are used to support a dense plant cover, which can cause long-lasting artificial modifications of the existing local ecosystems with negative consequences for native biodiversity (Scotton & Andreatta, 2021). Accordingly, the utilization of native plants is a favourable alternative for slope stabilisation, especially in already vulnerable ecosystems like high alpine landscapes. For this purpose, it is crucial to define those characteristics of local natural plant communities that are relevant for erosion mitigation. The effect of vegetation on soil erosion processes depends on the morphological characteristics of the resident plant species as above- and belowground plant traits are controlling different erosion processes. For example, plant canopy can intercept rainfall, enhance water infiltration, and surface roughness, thereby controlling splash detachment and interrill erosion rates, whereas plant roots increase soil aggregate stability and enhance soil cohesion against shallow mass movements (Freschet et al., 2021; Gyssels et al., 2005; Vannoppen et al., 2015). Furthermore, leaf and root traits related to different plant growth strategies and resource acquisition have been shown to be relevant for erosion processes (Bochet & García-Fayos, 2015; Burylo, Rey, Bochet, & Dutoit, 2012; Burylo, Rey, Mathys, & Dutoit, 2012). For instance, slow-growing but long-lived plant species that are capable of surviving in highly disturbed environments and are more resistant to limited resource availability (Díaz et al., 2016) can play a crucial role in erosion control. However, most studies focus either on the above- or belowground plant parts without accounting for their collective effects on erosion processes, while approaches integrating both are needed for a full assessment of the different mechanisms in controlling erosion. Additionally, the relationship between plant cover and specific plant traits as well as plant diversity in the context of soil erosion remains not well understood.

At the community level different components of biodiversity, such as taxonomic diversity, community composition and the distribution of traits within the community are known to influence ecosystem processes (Carrick & Forsythe, 2020; Mouillot, Villéger, Scherer-Lorenzen, &

Mason, 2011). Considering plant traits for understanding the links between plant community characteristics and ecosystem functions can be a particularly useful approach, because in many cases they can predict the effects on ecosystem functions better than taxonomic diversity (Cadotte, Carscadden, & Mirotnick, 2011; de Bello et al., 2021; Díaz et al., 2007). According to the mass ratio theory (Grime, 1998), ecosystem processes are mainly controlled by the traits of dominant species in a community, which can be expressed by community weighted mean (CWM) trait values. In contrast, positive effects on ecosystem functions could also be due to non-additive effects, such as complementarity effects amongst coexisting species with heterogeneous trait values, which can be expressed by trait diversity indices such as Rao's Q (Dias et al., 2013; Lavorel, 2013). Thus, different species in a community interactively contribute to slope protection (Hou, Zhu, Fu, Lu, & Zhou, 2020). However, most of the research on the effects of vegetation on erosion has been carried out at the scale of few focus species (Burylo et al., 2012; Zhu et al., 2015) and studies on whole naturally occurring plant communities are rare. Therefore, it is essential to study diverse natural plant communities paired with quantitative measurements of sediment erosion to disentangle which components of plant diversity are involved in controlling sediment erosion.

In alpine ecosystems steep slopes at high elevations above the tree line with large proportions of bare ground are especially prone to erosion, particularly under high precipitation events (Pohl, Alig, Körner, & Rixen, 2009). This is particularly the case in glacier forelands, where bare ground is rapidly increasing due to glacier retreat, enhanced by global warming (Rounce et al., 2023). The high geomorphic activity following glacial retreat in the glacier foreland can represent natural hazards impacting downstream ecosystems and society due to sediment-related problems off-site, such as debris flow and landslides or reduced water availability due to sedimentation of streams and reservoirs (Eichel et al., 2016; Losapio et al., 2021). The latter specifically causes problems related to the local hydroelectric reservoir in our study area, affecting power supply generation and periodically leading to costly maintenance measures. After deglaciation, the emerging bare ground is accessible for new biotic colonisation. Microbes are the first organisms to colonise the deglaciated terrain, showing an increase in biomass and diversity and are followed by a subsequent colonisation of plants with a high species turnover along the progressing succession (Fickert & Grüniger, 2018; Hanusch, He, Ruiz-Hernández, & Junker, 2022; Junker et al., 2020, 2021; Némery et al., 2007).

In addition to different levels of diversity, many ecosystem services rely on interactions between plants and other trophic levels (Cardinale et al., 2012; Eisenhauer et al., 2019; Lavorel et al., 2013). For instance, the increasing activity of soil microbes on freshly colonised sediments play a key role in nutrient cycling and soil formation and facilitate the establishment of plants, which depend on the

availability of nutrients in the soil (Knelman et al., 2018; Wojcik, Donhauser, Frey, & Benning, 2020). Plant diversity is directly related to biomass production, which in turn leads to an increase in soil microbial activity (Thakur et al., 2021; Yuan et al., 2017). Through the addition of organic matter and root exudates to the soil, plants and microorganisms are enhancing soil aggregation processes, which are an important factor regarding the ecosystem function of soil stabilisation (Bardgett, Mommer, & De Vries, 2014; Murugan et al., 2019).

In this study we measured sediment transport on erosion plots in a pristine glacier foreland without major anthropogenic disturbances in the Austrian Alps across three vegetation seasons. We investigated the interrelated effects of community-level plant diversity, leaf and root traits, and plant cover on small-scale sediment transport with detailed vegetation surveys and plant species-specific trait measurements. Furthermore, we examined how those plant community properties are related to bacterial and fungal communities in the soil, which may also have implications for soil stability.

We hypothesize that 1) The amount of transported sediment per time is a function of the severity of precipitation events in the same time; 2) Vegetation cover reduces erosion due to soil stabilising effects; 3) Species richness negatively affects erosion either directly or by facilitating a high plant cover or increasing trait diversity through complementarity effects; 4) High above- and belowground trait diversity is negatively related to erosion, either directly or by facilitating a high plant cover *via* more efficient use of resources; 5) Specific dominant plant traits related to plant growth strategies either have direct effects on erosion or facilitate higher plant cover through better stress resistance; 6) Soil microbiota diversity and composition is shaped by the successional stage of associated plant communities and their composition and respond to plant traits.

Materials and methods

Study site

This study was conducted in the proglacial area of the Gepatschferner glacier in the Central Eastern Austrian Alps (46°87'N, 10°74'E). Since the maximum extent during the Little Ice Age the melting glacier uncovered an area of more than 2.5 km² in the glacier forefield and had a recent retreat rate of 30 m per year in 2018/19 and 51 m per year for 2019/20 during our study (Lieb & Kellerer-Pirklbauer, 2019, 2020). The melting glacier deposits large amounts of loose sediment in the proglacial area, which are subject to high rates of morphodynamic sediment reworking, mainly by rill and gully erosion, as well as debris flows and facilitated by intense precipitation events (Hilger et al., 2019). We selected 20 sites (6 × 3 m) on slopes in the glacier foreland differing in time since deglaciation and geomorphic

activity and thus exhibiting varying levels of plant cover and plant communities of different successional stages. The sites were distributed along a plant cover gradient, which was divided into six classes (0–5%, >5–15%, >15–30%, >30–50%, >50–75%, and >75% vegetation cover). Due to the high geomorphic activity in the study area, time since deglaciation could not be used as a suited gradient parameter for site selection. Field observations showed the past influence of geomorphic activity, such as shallow landslides and rockslide of blocky moraine materials. Each site was divided into three plots (2 × 3 m, *n* = 60), which all belonged to the same plant cover class and on which we measured plant community characteristics and sediment erosion separately. The arrangement of three plots per site was necessary for an experiment that started after data sampling for this study and this setup was accounted for in our statistical models. Site selection was done according to several criteria: mean slope angle of 30–35%, flat surface composed of fine-grained sediment without large boulders or sinks, and evenly distributed aspect and elevation classes across all sites. In 10 sites (i.e. 30 plots) each 2 × 3 m plot was framed by metal fences and equipped with metal funnels to guide surface runoff and transport sediment into two 60-litre polyvinylchloride containers (Fig. 1A; Appendix A Fig. 1). Erosion data collection was carried out once per month for each plot in the snow-free months between June and October in 2018–2020 (Appendix A Table 1). During data collection the eroded sediments were separated from the collected runoff and subsequently dried at 105 °C in the laboratory to determine stable dry weights. Specific sediment yield in g m⁻² month⁻¹ was standardised for the number of days for each measurement and the exact plot area. Due to the difficulty of constructing large structures for erosion measurements in this remote field site and maintaining them over several years, it was not possible for us to make these installations for all the 20 study sites. To nevertheless have a larger number of samples for plant and microbial measurements, we additionally established 10 sites without metal fences in which only plant and microbial sampling took place. For examining the effect of precipitation on sediment erosion, a weather station collecting precipitation data every minute was installed at a maximum distance of 1.6 km from the measurement sites. These measurements were used to calculate the mean precipitation per month corresponding to the time period of each erosion measurement (Appendix A Table 2).

Plant community measurements

All vascular plant species were identified on each of the 60 plots during the vegetation peak between July and August 2018 and the abundance (per cent ground cover) per plant species was recorded for each plot (Appendix A Table 3). Above 10% cover the abundance was estimated by incremental steps of 5%. Below 10% cover of a species its abundance values were assessed in steps of 7.5%, 5%, 2.5%, and

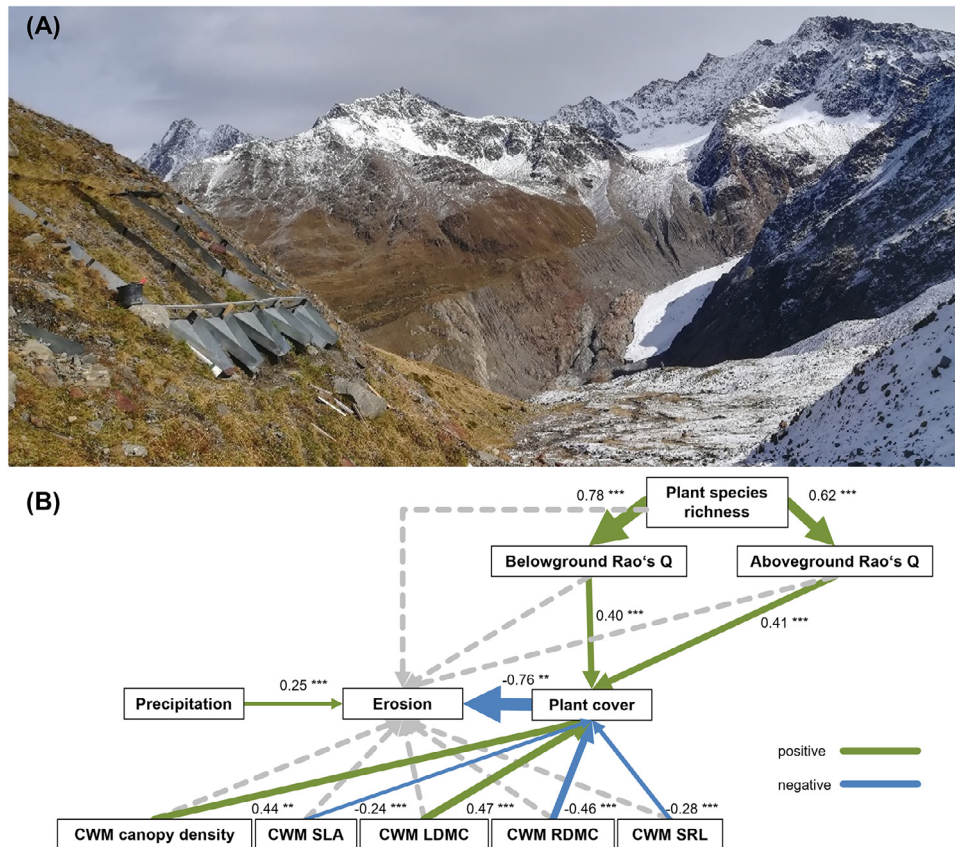


Fig. 1. (A) Study site and erosion plots with metal fences in the proglacial area of the Gepatschferner glacier. (B) Path analysis showing the effect of plant community characteristics on sediment erosion. Significant paths ($p < 0.05$) with a positive relationship are shown as green arrows and negative effects are indicated in blue. Non-significant relationships tested in the model are shown in grey. Standardised path coefficients are denoted next to the arrows and the strength of the relationship is proportional to the arrow width. Asterisks mark the significance of the shown paths (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

1%. Sparsely distributed species with less than one per cent cover were recorded as 0.5% cover and rare species with few single individuals per plot were documented with 0.1%. Total plant cover was defined as per cent ground cover of the total plot area with the remaining area considered as bare ground. We did not remove plants directly from within the erosion plots, in order not to affect natural erosion. Plant individuals including the roots were removed from the soil in the closest possible proximity to the according plot. We aimed at selecting plant individuals with a phenotype matching those observed inside the study plots from communities corresponding to the plot conditions. We measured leaf and root traits of $n = 7$ individuals per plant species in each site where the plant species had at least 5% ground cover in one of the three plots (Appendix A Table 4). For rare plant species we measured $n = 7$ individuals close to one site where they occurred. Traits measured to reflect the different leaf and root phenotypes and growing strategies of the present plant species include canopy density, specific leaf area (SLA), leaf dry matter content (LDMC), root dry matter content (RDMC), specific root area (SRA), and specific root length (SRL). We chose plant traits that were straightforward to measure for large numbers of different plant species

and are known to be related to ecosystem services such as erosion control (de Bello et al., 2021; Hanisch et al., 2020). Canopy density was estimated as the product of leaf area and the number of leaves. Although this does not reflect the real observed canopy density, we think this serves as a good proxy to estimate the varying average canopy density between plant different plant species. Leaf area and number play an important role in sediment retention with larger leaves and canopy density providing larger interception area and thus increasing the plant's ability to retain sediment (Burylo et al., 2012; Kervroëdan, Armand, Saunier, Ouvry, & Faucon, 2018). Leaf and root traits related to different plant growth strategies and resource acquisition were also shown to be relevant for erosion processes (Bochet & García-Fayos, 2015; Burylo et al., 2012, Burylo et al., 2012). SLA is calculated as the leaf area of a fresh leaf divided by its dry mass. High SLA is commonly found in species with fast growth rates and short leaf lifespan, which are more likely to be associated with resource-rich environments. LDMC is calculated as the dry mass of a leaf divided by its fresh mass. LDMC is often negatively correlated to SLA and is also related to leaf growth rates. LDMC is related to tissue density and therefore, leaves with high LDMC tend to

be tough and are often associated with productive, but highly disturbed environments (Cornelissen et al., 2003; Díaz et al., 2016; Wright et al., 2004). SRL is considered the belowground equivalent of SLA and is defined as the root length per given root dry mass. Plants with high SRL are associated with higher root elongation (Bergmann et al., 2020; Kramer-Walter et al., 2016). SRA is reflecting the root surface area per unit mass and is calculated as root area divided by the root dry mass. High SRA is related to a higher number of fine roots and therefore increased nutrient and water absorption (Wasaya, Zhang, Fang, & Yan, 2018). RDMC, calculated as the ratio of root dry mass per unit of root fresh mass and is related to root growth rates and longevity (Birouste, Zamora-Ledezma, Bossard, Pérez-Ramos, & Roumet, 2014). During the peak of the vegetative season in July, mature, well grown plant individuals were removed from the soil and subsequently transported in a cooler to the field station where roots were washed, and measurements took place within 6 h after sampling. Since some of the measured plant traits may vary during the day, sampling took place at least 3 h after sunrise and 3 h before sunset. For some plant species it was difficult to identify real individuals, so the unit on which measurements were taken was the ramet, i.e. the recognisable separate aboveground unit (Cornelissen et al., 2003). One young, fully expanded and hardened leaf without visible damage was measured for each plant individual. Leaves (including petiole) chosen for measurements were removed from the plant immediately before measurements took place to avoid dehydration. Root length was measured to the nearest 1 mm using a calliper. Leaf and root area were obtained by scanning the plant material with a standard scanner device. Numbers of pixels per leaf and root were compared to number of pixels of a 1 cm² reference using the software *imageJ* (see Junker & Larue-Kontić, 2018). The plant material was subsequently frozen and later weighed to determine the fresh mass. For quantifying the dry mass, leaves and roots were placed in a drying oven for 48 h at 80 °C and weighed again.

Microbial sampling and sequence processing

For investigating the composition of bacterial and fungal communities in the soil, we took soil samples from 16 sites from a depth of 3 cm. Each sample was pooled from six locations per site (two in each plot) to obtain a broader coverage of the microbial communities per site. Soil samples were directly transferred to BashingBeads Lysis tubes from the ZymoBIOMICS DNA Miniprep Kit (Zymo Research) containing lysis solution. Lysis tubes were sonicated for 7 min to detach microorganisms from substrate surfaces. Lysis tubes were shaken 5 min at 16 Hz using a ball mill. Extraction and purification of DNA was done following the manufacturer's guidelines (Zymo Research). Amplicon sequencing of isolated DNA samples was performed by Eurofins Genomics (Ebersberg, Germany). The V3-V4

region of the 16S rRNA and the ITS2 region were amplified and sequenced with Illumina MiSeq to identify bacterial and fungal communities respectively.

Demultiplexed, primer trimmed, per sample fastq files were obtained from Eurofins, transferred into Qiita (Gonzalez et al., 2018) and quality controlled using the default settings. Forward reads were trimmed to the first 150 nucleotides. The primary feature tables were generated using Deblur 1.1.0 (Amir et al., 2017) and can be found in Qiita (qiita.ucsd.edu) in study 13,751 as artefacts 118,092 and 118,075 for 16S and ITS, respectively. Sequences can additionally be found in the European Nucleotide Archive (ENA) under the accession number ERP133205. Taxonomy assignment for 16S was done *via* Qiime2's (Bolyen et al., 2019) "feature-classifier" plugin version 2020.11 against Greengenes 13_8 (McDonald et al., 2012). 99% OTUs representative sequences. Taxonomy for ITS reads were assigned by training a feature-classifier with Unite version 04.02.2020 dev97 (Kõljalg et al., 2013). Bacterial, but not fungal features with assigned taxonomy containing the labels c__Chloroplast or f__mitochondria were considered of host or plant origin and removed from the feature table prior to rarefaction. Furthermore, 16S and ITS features with less than 10 reads in all samples combined were removed. Rarefaction depth was manually determined at 20,000 and 12,000 reads per sample by finding a suitable compromise between kept samples and captured alpha diversity by using rarefaction curves for 16S and ITS respectively. This resulted in a table with 4414 bacterial features in 16 samples and another table with 9233 fungal features for the same 16 samples.

Statistical analyses

We used two community-wide measures of plant trait composition, community-weighted means of trait values (CWM) and Rao's Q quadratic entropy. Rao's Q is a multivariate measure of trait diversity, which accounts for the relative abundance of species with more than one trait and allows for clear biological interpretations (Botta-Dukat, 2005; Mammola, Carmona, Guillerme, & Cardoso, 2021). Rao's Q was calculated for the measured above- and belowground plant traits separately. Aboveground Rao's Q included canopy density, SLA and LDMC, whereas belowground Rao's Q contained the measurements for SRL, SRA and RDMC. For CWM calculations the traits of each species were weighted according to the species' relative abundance (percentage cover of a species / total percentage plant cover * 100) to reflect the individual contribution to ecosystem functioning (Villéger, Mason, & Mouillot, 2008). The CWM for each trait and Rao's Q were calculated with the *R* package *FD* (v1.0–12; Laliberté & Legendre, 2010). The obtained diversity measures were then used to investigate the interconnected relationships between sediment erosion and plant community parameters. For this, we carried out a

path analysis with the *R* package *piecewiseSEM* (v2.1.2; Lefcheck, 2016). We included linear mixed effects models with study plots and sites as random factors to account for spatial autocorrelation effects. Mean erosion measurements per month were nested within each plot and each plot was again nested within the according study site (three plots per site). To meet the assumptions for the model, the dependant variable sediment yield was log-transformed. For choosing the best suited model we started with the most complicated model containing all possible variables relevant for our research question (Appendix A, Fig. 2). The plant community parameters included in the original model were plant cover, species richness, belowground Rao's Q , aboveground Rao's Q , and the community-weighted mean values of canopy density, SLA, LDMC, RDMC, SRA, and SRL. We used a backward elimination approach using the Akaike information criterion (AIC) to estimate the robustness of the model compared to other possible models (Shipley, 2013). Additionally, we calculated variance inflation factors (VIF; *R* package *regclass* v1.6; Petrie, 2020) for detecting possible multicollinearities between our parameters, which would result in problems estimating the explained variance. We found multicollinearity issues when including certain plant trait parameters simultaneously in the model, due to their high correlation (Appendix A Fig. 3) and therefore the model including all variables and possible paths could not be calculated. According to this we compared all possible combinations of models and removed any paths that did not

improve the fit of the model. The final model chosen was the one with the lowest AIC score and the most variables retained. Due to multicollinearity with other variables the parameter for CWM SRA had to be removed from the final model. R^2 values as a measure of data variance explained for a particular pathway were calculated for each linear mixed effects model. R^2 values can be differentiated between paths with fixed factors alone (marginal R^2) and paths containing fixed and random factors (conditional R^2). The conditional R^2 includes the effects of inherent conditions of the study plots per site, which are not explained by our other tested parameters.

For testing the relationship between alpha diversity of microbial amplicon sequence variants (ASVs) and plant community parameters, we calculated corresponding regression models. For evaluating the relationship of plant species as well as soil microbial ASV compositions with the measured plant community features and erosion, we used a non-metric multidimensional scaling (NMDS) approach based on Bray-Curtis distances. To reflect the relative abundances of the occurring plant species per plot, the cover of each species was divided by the summed cover of all species present in the community. The microbial dataset was normalised using the cumulative sum scaling (CSS) method, which corrects for differences in sampling depth between samples (*R* package *metagenomeSeq* v1.30.0; Paulson, Stine, Bravo, & Pop, 2013). The NMDS was calculated at plot level for plant community composition ($n = 30$) and at site level for

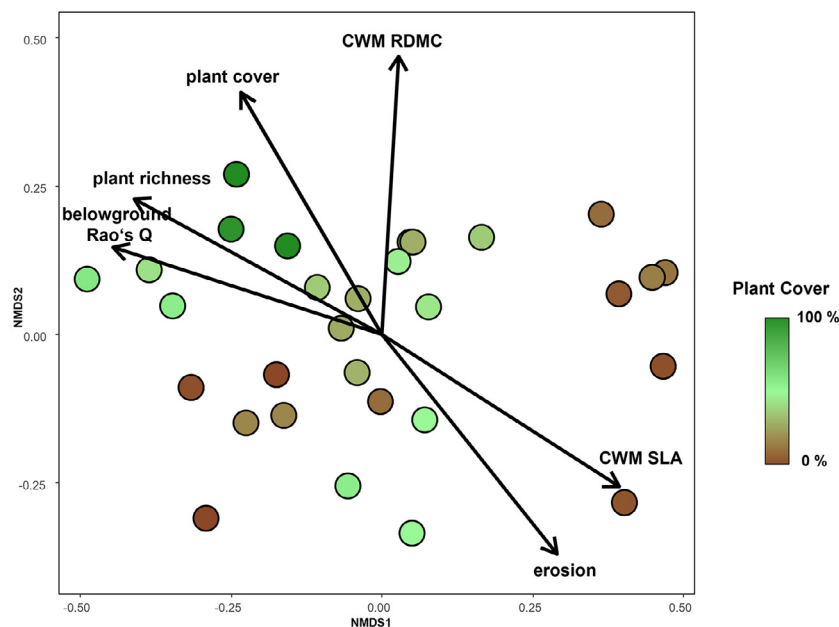


Fig. 2. Ordination (NMDS) of the dissimilarity (Bray–Curtis) in plant community composition of the investigated study plots ($n = 30$). The distance between the points is a measure of dissimilarity in community composition, where higher proximity of points indicates more similar vegetation composition for the respective plots. Plant communities per plot are represented as points with colour reflecting the amount of plant cover in per cent. Arrows indicate parameters that show a significant ($p < 0.05$) relationship with plant community composition. The direction of arrows indicates the most rapid increase for the respective parameter, with the length of arrows being proportional to the strength of its relationship with the community composition.

microbial data ($n = 16$) with the *metaMDS* function of the *R* package *vegan* (v2.5–7; Oksanen et al., 2019) with 9999 permutations. The plant community variables and the erosion measurements were fitted as environmental vectors onto the ordination with the *envfit* function of the *vegan* package using again 9999 permutations. The ordinations were visualised with *ggplot2* (v3.3.2; Wickham, 2016). Further, a Mantel test with 9999 permutations was carried out to assess the correlation between plant and soil microbial community composition. We used random forest analysis (*R* package *rfPermute*, v2.5; Archer, 2020) to determine specific microbial taxa characteristic for different degrees of plant cover. The analysis was conducted using the normalised dataset of microbial read numbers. A repeated k-fold cross validation method was used to train the random forest model (k-fold = 10, repeats = 10; *R* package *caret* v6.0–90; Kuhn, 2020) for finding the best mtry value, in the interval between 1 and $n - 1$, where n is the number of families considered. The random forest analysis was then conducted using the previously calculated mtry, ntree = 999, and nrep = 10. Bacterial and fungal families were ordered by their ability to separate different degrees of plant cover by per cent increase in mean squared error (%IncMSE, variable importance). To illustrate the distribution of the indicator taxa along the plant cover gradient we picked the twelve families with the highest importance and plotted the relative abundance of these taxa for each sampling site. To further assess the relationship between plant cover and the abundance of indicator taxa, we applied Spearman's rank correlations between plant cover per site and standardised read numbers of the twelve most important bacterial and fungal families according to the random forest analysis. All statistical analyses were conducted within *R* v4.0.3 software environment (*R* Core Team, 2020) and statistical significance was assessed at $\alpha = 0.05$.

Results

The overall vegetation cover in our study plots varied between 1% and 85%, with a mean cover of $30\% \pm 3.0\%$ SE. We recorded a total of 66 plant species across all plots. The number of plant species per plot ranged from 2 to 27 with a mean species richness of 11 ± 0.8 . Total measured sediment yield differed greatly amongst plots with values from 1 g m^{-2} to 216 g m^{-2} and a mean amount of $72 \text{ g m}^{-2} \pm 7.8 \text{ g m}^{-2}$. The path analysis revealed relationships between our measured plant community properties and sediment yield (Fig. 1B, Appendix A Table 5). Monthly precipitation significantly increased the measured sediment yield (standardised path coefficient $\beta = 0.25$, $p < 0.001$). Consistent with our hypothesis, soil erosion strongly decreased in sites with higher plant cover ($\beta = -0.76$, $p < 0.01$). We did not detect direct significant effects of plant species richness, trait diversity and CWM trait values on erosion. Plant communities with increased plant cover were dominated by

species with larger canopy density ($\beta = 0.44$, $p < 0.01$), high LDMC ($\beta = 0.47$, $p < 0.001$) and low SLA ($\beta = -0.24$, $p < 0.001$). Both community-weighted mean root traits RDMC and SRL were decreased in communities with high plant cover ($\beta = -0.46$, $p < 0.001$; $\beta = -0.28$, $p < 0.001$; respectively). Communities with increased plant cover were additionally associated with an increased plant trait diversity (Rao's Q), both above- ($\beta = 0.41$, $p < 0.001$) and belowground ($\beta = 0.40$, $p < 0.001$). In turn, both above- and belowground trait diversity were positively related to a higher plant species richness ($\beta = 0.62$, $p < 0.001$ and $\beta = 0.78$, $p < 0.001$; respectively). The overall proportions of explained variance (R^2) of the response variable erosion were $R^2_{\text{marginal}} = 0.73$ for fixed factors alone, and $R^2_{\text{conditional}} = 0.84$ for both fixed and random factors. The difference between marginal and conditional R^2 indicates site specific effects on erosion that could not be explained by the other tested parameters, which can be attributed to the sampling limitations of our study. Due to the limited number of replicates and our sample setup, site-specific effects could not be excluded. In future studies this could be avoided by selecting a higher number of spatially independent replicates as well as by taking into account site-specific variables, such as differences in small-scale topography.

The analysis of the plant community composition based on Bray-Curtis-dissimilarities between plots revealed that plant communities differed regarding some of the measured variables (Appendix A Table 5). Community composition was significantly correlated with sediment erosion (squared correlation coefficient $r^2 = 0.21$, $p < 0.043$; Fig. 2), plant cover ($r^2 = 0.38$, $p < 0.01$), plant species richness ($r^2 = 0.31$, $p < 0.01$), as well as belowground trait diversity ($r^2 = 0.33$, $p < 0.01$). Community-weighted means of SLA ($r^2 = 0.58$, $p < 0.001$) and RDMC ($r^2 = 0.53$, $p < 0.001$) showed a significant relationship with plant community composition. The NMDS resulted in a two-dimensional stress of 0.121.

Regarding the relationship between the soil microbial alpha diversity and measured plant community variables, our regression models did not indicate significant effects for any of the tested parameters. However, we found significant relationships between soil microbial composition and plant community properties (Fig. 3). For soil bacterial composition, we found significant correlations with plant cover ($r^2 = 0.59$, $p < 0.01$), plant species richness ($r^2 = 0.62$, $p < 0.01$), belowground trait diversity ($r^2 = 0.69$, $p < 0.001$), aboveground trait diversity ($r^2 = 0.39$, $p = 0.040$), CWM LDMC ($r^2 = 0.39$, $p = 0.040$), and CWM SRA ($r^2 = 0.38$, $p = 0.047$) and canopy density ($r^2 = 0.56$, $p < 0.01$). Fungal community composition was related to plant species richness ($r^2 = 0.51$, $p < 0.01$), belowground trait diversity ($r^2 = 0.72$, $p < 0.001$), aboveground trait diversity ($r^2 = 0.45$, $p = 0.021$), SLA ($r^2 = 0.57$, $p < 0.01$), LDMC ($r^2 = 0.49$, $p = 0.014$) and RDMC ($r^2 = 0.50$, $p = 0.013$). The NMDS resulted in a two-dimensional stress of 0.146 for the bacterial dataset and 0.128 for fungi.

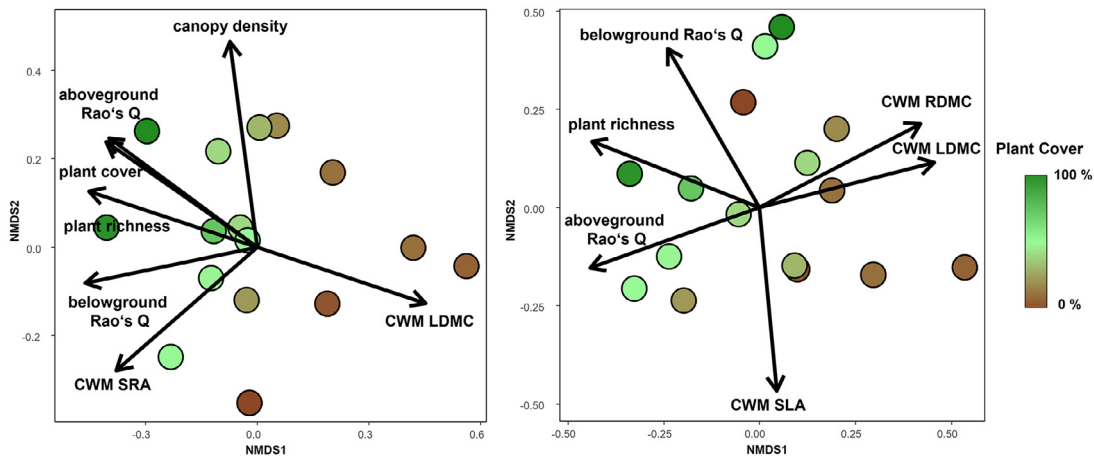


Fig. 3. Ordination (NMDS) of the dissimilarity (Bray–Curtis) in soil bacterial (A) and fungal (B) community composition per study site ($n = 16$). The distance between the points is a measure of dissimilarity in community composition, where higher proximity of points indicates more similar microbial composition for the respective plots. Microbial communities per plot are represented as points with colour reflecting the amount of plant cover in per cent. Arrows indicate plant community parameters that show a significant ($p < 0.05$) relationship with microbial community composition. The direction of arrows indicates the most rapid increase for the respective parameter, with the length of arrows being proportional to the strength of its relationship with the community composition.

Further, we found a significant correlation between plant community composition and both bacterial and fungal community composition in the soil (Mantel $r = 0.7187$, $p < 0.001$; Mantel $r = 0.6295$, $p < 0.001$; respectively).

Random forest models revealed specific microbial families that changed in their abundance with different levels of plant cover (Fig. 4A, F). These differences in microbial taxa abundances regarding plant cover also corresponded to differences in plant species richness and plant trait diversity (Fig. 4B–E). Some of the indicator taxa were associated with a low plant cover and others were more abundant in sites with higher plant cover (Appendix A Table 5). In bacterial samples *Cystobacterineae* (Spearman's rank correlation: $r_s = -0.58$; $p = 0.019$) and *Micrococcaceae* ($r_s = -0.67$; $p < 0.01$) were more abundant in sites with low plant cover. On the other hand, *Hyphomicrobiaceae* ($r_s = 0.59$; $p = 0.015$), *Methylocystaceae* ($r_s = 0.68$; $p < 0.01$), *Mycobacteriaceae* ($r_s = 0.68$; $p < 0.01$), and *Rhodospirillaceae* ($r_s = 0.54$; $p = 0.029$) were more abundant in sites with high plant cover and *Rhizobiaceae* ($r_s = 0.69$; $p < 0.01$) were not detected at all in the six sites with the lowest cover. Similarly, *Xanthobacteraceae* did not occur in sites with low cover except for one ($r_s = 0.58$; $p = 0.018$). *Bradyrhizobiaceae* ($r_s = 0.37$; $p = 0.156$), *Burkholderiaceae* ($r_s = 0.43$; $p = 0.101$), *Caulobacteraceae* ($r_s = 0.30$; $p = 0.266$), and *Acidimicrobiales_EB1017* ($r_s = 0.39$; $p = 0.140$) showed no clear tendencies towards sites with low or high plant cover. One fungal sample (L2a) was consisting only of one family, which was not one of the indicator taxa for the degree of plant cover and is therefore not shown. The fungal families *Alphamycetaceae* ($r_s = -0.51$; $p = 0.041$) and *Filobasidiaceae* ($r_s = -0.55$; $p = 0.028$) were not found in the five sites with the highest plant cover and also *Pleosporaceae* ($r_s = -0.50$; $p < 0.051$) were more abundant in sites with low cover. On

the other hand, *Glomeraceae* ($r_s = 0.64$; $p < 0.01$), *Hydnodontaceae* ($r_s = 0.53$; $p = 0.035$), *Orbiliaceae* ($r_s = 0.68$; $p < 0.01$), *Serendipitaceae* ($r_s = 0.60$; $p = 0.015$), *Thelephoraceae* ($r_s = 0.50$; $p = 0.047$), and *Umbelopsidaceae* ($r_s = 0.67$; $p < 0.01$) were more abundant in sites with high plant cover. *Rickenellaceae* ($r_s = 0.46$; $p = 0.076$) showed a trend of occurring in high plant cover plots, whereas *Pannariaceae* ($r_s = 0.21$; $p = 0.427$) and *Suillaceae* ($r_s = -0.27$; $p = 0.313$) showed no significant correlation with the degree of plant cover.

Discussion

This study highlights relevant plant community characteristics for mitigating erosion in the glacier foreland. A path model integrating different measured plant community variables showed that a high plant cover was the most important parameter related to measured sediment export. A dense vegetation *per se* has long been recognized as an important driver of erosion mitigation (Bautista, Mayor, Bourakhoudar, & Bellot, 2007; Burylo et al., 2012). However, information was lacking on which plant trait characteristics are shaping plant communities within a plant cover gradient in the context of erosion. We found that plant communities with high cover consist of plant species that exhibit larger mean canopy densities. Therefore, a combination of species with denser canopies leads to a more complete and dense overall plant cover. For single plant species it was shown that specific aboveground traits such as higher leaf density and area can enhance surface roughness, which is positively associated with erosion control (Chau & Chu, 2017; Kervroëdan et al., 2018). Further, we were investigating the relationship between plant cover and plant traits related to

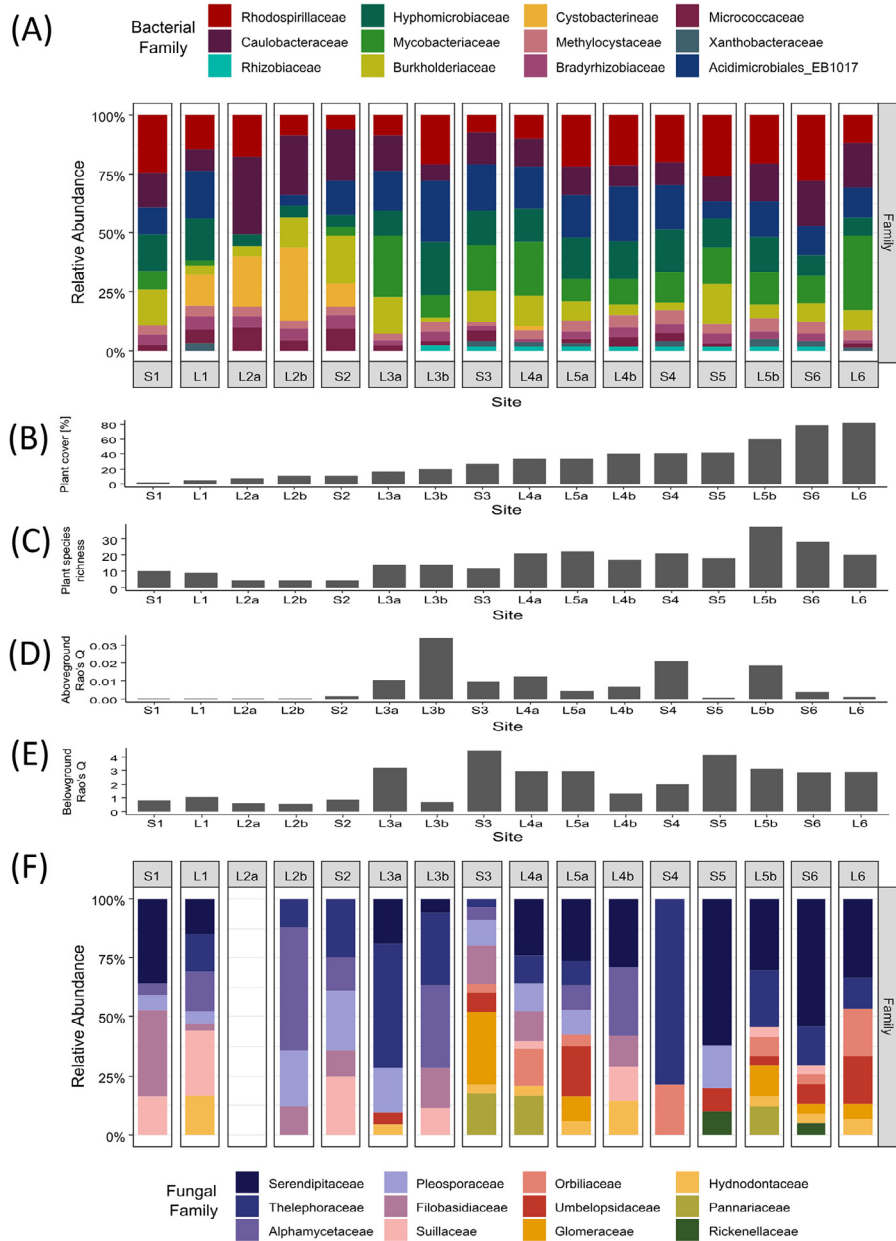


Fig. 4. Relative abundance of bacterial (A) and fungal (F) families in soil samples from 16 study sites with different plant communities, which are indicator taxa for varying degrees of plant cover. The composition represents the relative distribution of normalised 16S rDNA gene and ITS sequence counts for each bacterial and fungal families respectively. Bar graphs in grey (B-E) represent the distribution of different plant community characteristics for the respective study sites.

different growth strategies. Our results indicated that plant communities with high cover are dominated by species with low SLA and high LDMC, two parameters which are indirectly proportional to each other for many plant species. A low SLA and in turn high LDMC are common in slow-growing but long-lived plant species, that are capable of surviving in highly disturbed environments such as glacier forelands, because they are more resistant to limited resource availability and abiotic stress (Hulshof et al., 2013; Midolo, De Frenne, Hölzel, & Wellstein, 2019; Pierce et al., 2017). Additionally, leaves with increased LDMC present a higher

tissue density and are therefore tougher, which can be beneficial for withstanding harsh environmental conditions, such as high precipitation (Cornelissen et al., 2003). Regarding belowground traits, plant communities with high plant cover were more likely to consist of species with both low SRL and RDMC. Plants with low SRL are associated with larger root diameters and increased tissue density, which leads to thicker and denser roots that are shorter per unit mass. Thicker roots with low SRL are more likely to be associated with mycorrhizae, which favours resource uptake in harsh environments (Bergmann et al., 2020; Weemstra, Freschet,

Stokes, & Roumet, 2021). Roots with low RDMC are typically showing faster growth rates (Birouste et al., 2014), which likely facilitates faster successful establishment for plants in unstable soil conditions. All taken together, the plant traits predominantly occurring in plant communities with high plant cover, indicate the presence of stable, long-lived, late succession plant communities, that are able to persist under tough environmental conditions in the glacier foreland. This leads us to the assumption that while tougher plants with a denser canopy and thicker roots may be more beneficial for protecting the ground against soil erosion, they may also be more resilient to erosion processes.

Apart from different dominant sets of mean functional traits, sites with high plant cover and species richness were associated with increased above- and belowground functional trait diversity. This can be attributed to complementarity effects, due to which aboveground biomass and productivity is increasing with plant species richness, because diverse communities can utilise limited resources more efficiently (Cardinale et al., 2011; Michalet, Delerue, Liancourt, & Pugnaire, 2021; Roscher et al., 2012). A plant community with a high number of plant species therefore exhibited a higher variation in trait characteristics than a less diverse vegetation. For roots in particular, this can be explained by vertical segregation of diverse root types of different plant species, which can lead to fewer morphological overlaps amongst plant species and a more exhaustive utilisation of resources through niche differentiation (Díaz et al., 2007; Ravenek et al., 2014). Plant species richness and belowground trait diversity of selected species have been shown to provide beneficial effects for slope stabilisation (Martin, Pohl, Alewell, Körner, & Rixen, 2010; Pohl et al., 2009; Zhu et al., 2015). Although, we did not observe direct effects of taxonomic and trait diversity on erosion in our path model, our results support the previous findings due to the positive association between trait diversity and plant cover and the relationship between high plant cover with low sediment export. The soil-stabilising effects of plant roots are not only depending on species specific root properties but also on the total amount of roots within the soil (Burylo et al., 2012; Vannoppen et al., 2015). This is the case for more diverse plant communities, as plant species richness has been found to positively correlate with overall root biomass and plant trait diversity is a good proxy for root length density in the soil (Helsen, Vannoppen, Honnay, & Poesen, 2016). Therefore, a more diverse root system with a larger number of root functions may be associated with increased root biomass, thus leading to a higher degree of slope stabilisation in association with a denser plant cover.

The abundance of species in a community (i.e. community composition) can be another important driver of ecosystem functions (Carrick & Forsythe, 2020) and thus, exploring the relationships driven by species composition in the context of erosion can provide valuable insights. We found that plant community composition in our study plots showed a significant relationship with soil erosion and was

also correlated with the present number of plant species, plant cover, belowground trait diversity, SLA, and RDMC. Plant community composition may therefore be a relevant aspect for controlling soil erosion processes, possibly due to diversity effects *via* non-additive complementarity amongst species with different belowground trait combinations.

Regarding the relationship between plant communities and soil microbiota, we did not detect any effects of the observed plant community characteristics on microbial alpha diversity. However, community composition of both soil bacteria and fungi in our study sites was influenced by the present number of plant species. Soil microbial community composition was indeed also correlated with the composition of the associated plant community in our study plots, which means similar plant communities are supporting more similar microbial communities. Although, we expected that a higher plant diversity would promote the diversity of soil microbes by increasing the diversity of resources and environmental niches (Prober et al., 2015), we did not find evidence that more diverse plant communities cooccur with more diverse soil microbial communities. Interestingly, the results of previous studies are inconclusive with respect to this expectation. Some studies observed a positive relationship between plant species richness and density and soil microbial richness (Porazinska et al., 2018; Yuan et al., 2017); whereas in a worldwide study of grasslands, plant diversity was found to predict beta but not alpha diversity of bacterial and fungal communities (Prober et al., 2015). Coinciding with the latter, we found that the microbial beta diversity between plots was shaped by plant community parameters. Plants can shape soil microbial composition by changing belowground environmental conditions through their species-specific impact on resource quantity and quality as well as pH by providing different carbon sources and root exudates (Grigulis et al., 2013; Mitchell et al., 2010; Strecker et al., 2015). Because this effect is facilitated by high redundancy of traits between plant species, a diverse vegetation is therefore an important driver of soil ecosystem functions (Le Bagousse-Pinguet et al., 2019). This is also reflected in our finding that microbial communities were influenced by plant composition and both above- and belowground plant trait distribution. We also found that plant communities with high plant cover were associated with an increase in specific microbial families. In sites with higher plant cover there was a clear increase in abundance of Glomeraceae and Serendipitaceae, both families that include mycorrhiza-forming fungi known for symbiotic relationships with a wide variety of host plants (Ray, Lakshmanan, Labbé, & Craven, 2020). This is also in line with the occurrence of low SRL in high-cover plant communities, which is a trait shown to be more likely associated with mycorrhiza (Bergmann et al., 2020; Kramer-Walter et al., 2016). Mycorrhizal interactions with plant roots are also a crucial force in driving soil aggregation processes (Faucon, Houben, & Lambers, 2017). The increasing abundance of nitrogen-fixing Rhizobiaceae and Hyphomicrobiaceae, which are known for having plant growth-promoting properties, may be explained by the increasing demand for growth factors and

mineral elements exhibited by the higher number of plants. The increase in methylotrophic bacteria of the Methylocystaceae family may be an indication of the larger input of organic plant material in high cover sites, including different types of organic compounds available for the bacteria to metabolise (Pershina et al., 2015). Another positive effect of a diverse and dense vegetation on erosion processes is the facilitation of soil aggregation and therefore soil stability through the introduction of diverse root exudates and organic material to the soil and the associated increase in microbial biomass (Bardgett et al., 2014; Faucon et al., 2017). Microorganisms feed on the additional resources and in turn may produce polysaccharides that further promote the formation of soil aggregates (Costa, Raaijmakers, & Kuramae, 2018; Vannoppen et al., 2015). On the other hand, soil erosion itself can negatively affect below-ground microbial communities by altering soil characteristics and associated vegetation, which has negative impacts on nutrient cycling and soil functionality (Qiu et al., 2021). Plants are therefore a key factor in mediating negative effects of erosion processes on the soil microbiome and soil functions. Although with this study we are not able to show the direct relationship between the soil microbiome and erosion, our data clearly indicate possible interactions between soil erosion, plants, and microorganisms. A better understanding and further investigations of the complex interactions between microbial communities and plant traits are necessary for future investigations in the context of soil erosion to link this data.

The identification of plant community characteristics that are beneficial for slope protection is of large relevance for revegetation purposes to mitigate erosion. However, many of these efforts are utilising mono-specific vegetation, which are ecologically less valuable and inefficient in reducing soil erosion because of their simple canopy and root system composition (Zhu et al., 2015). We demonstrated in our study that the most relevant feature of a plant community associated with slope stabilisation is a high overall plant cover, which is tightly coupled with certain traits related to growth strategies and stress-resistance as well as with a high trait diversity, supported by a larger number of plant species. A dense vegetation supported by diverse plant species with certain beneficial traits can be therefore preferable for restoration purposes as it may facilitate the plants' important role in the ecosystem function of slope stabilisation. Our results may inspire additional research investigating causalities and confirm our observational findings. In particular, experimental studies are needed where the effects of plant traits and cover can be investigated independently from each other, which was not possible under natural field conditions.

Author contributions

All authors contributed to conceptualization and methodology. SK, RRJ and JCO managed the project administration. LMO and SH performed the investigation. LMO, RRJ and SJ performed the analyses. LMO wrote the original draft

with contributions of RRJ. All authors reviewed and edited the final manuscript.

Appendix A. Supplementary data Supplementary data associated with this article can be found, in the online version, at XXXXX. Bacterial and fungal sequences can be accessed in fastq files deposited in the European Nucleotide Archive (ENA) under the accession number ERP133205.

Declaration of Competing Interest

The authors declare no competing interests.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.bae.2023.05.008](https://doi.org/10.1016/j.bae.2023.05.008).

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