Beyond plants: How soil alterations shape restoration success in alpine grasslands

Mehr als Pflanzen: Wie Bodenveränderungen den Renaturierungserfolg in alpinen Grasländern beeinflussen

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Abstract

Alpine ecosystems face increasing disturbances from construction activities, prompting restoration efforts to mitigate soil erosion and biodiversity loss. We investigated the short-term outcomes of alpine grassland restoration measures at Curtinella, Corvatsch (canton of Grisons, Switzerland), comparing vegetation composition, soil properties, and soil bacterial communities of two restored sites – one seeded (2017) and one restored by turf transplantation (2020) – against an undisturbed reference site.

Vegetation analysis revealed significant floristic differences between restored and undisturbed sites. Seeded plots showed reduced species diversity, richness, and dominance by non-native and competitively strong species, whereas turf transplantation plots demonstrated improved establishment of native species but featured considerable vegetative gaps indicative of slow recovery. Restoration substantially modified soil properties: shallower soils with higher gravel cover, elevated pH, and lower microbial biomass, likely influencing long-term vegetation patterns.

Microbial community analyses using 16S rRNA gene sequencing indicated distinct bacterial community shifts due to restoration measures, with increased diversity linked to altered soil conditions. Eight bacterial genera were identified as putative bioindicators for undisturbed alpine soils. These findings underscore the critical importance of topsoil conservation during alpine restoration.

We recommend prioritizing spontaneous vegetation establishment over extensive seeding, limiting seeding primarily to erosion control, and preserving topsoil to sustain alpine biodiversity. Future research should explore microbial-plant interactions further and include additional taxonomic groups to strengthen ecological assessments and restoration practices in alpine regions.

Keywords: amplicon sequencing, detrended correspondence analysis, PERMANOVA, soil microbial biomass, Ward clustering

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Global biodiversity is declining rapidly, driven predominantly by climate change, pollution, and extensive anthropogenic land-use changes (IPBES 2019). By 2019, human activities had modified over 75% of terrestrial habitats, putting up to one million species at risk of extinction worldwide (IPBES 2019). Switzerland is no exception, showing measurable negative trends across habitats, species, and genetic diversity (BAFU 2017). Alpine ecosystems, harboring over 20% of the country's native plant species, are disproportionately affected by climate changes, thus highlighting Switzerland's international responsibility to protect alpine biodiversity (BAFU 2017, 2019, Vitasse et al. 2021).

Historically, the intricate mosaic of natural and cultural landscapes in the Alps, coupled with extensive agricultural practices, has fostered species-rich alpine pastures and meadows, now covering approximately one-third of Switzerland's agricultural land (BFS 2019). However, these ecosystems face increasing pressures from land abandonment in remote regions, intensified agricultural practices, and growing recreational use (BAFU 2017). Although the number of alpine ski lifts has slightly decreased since the 1990s, artificial snowmaking infrastructure has notably expanded, with over half of Swiss ski slopes now relying on artificial snow (Seilbahnen Schweiz 2024). Such developments typically disturb accessible alpine grasslands, which regenerate slowly due to short growing seasons and primarily vegetative reproduction strategies (Delarze et al. 2015).

To mitigate biodiversity loss and protect habitats, ecological restoration has become increasingly important. The United Nations' declaration of 2021–2030 as the "Decade of Ecosystem Restoration" underscores the urgency of halting habitat degradation (UNO 2021). In Switzerland, restoration measures, particularly outside designated construction zones, are standard practice, holding developers accountable for ecological restoration (Kägi et al. 2002). Alpine restoration methods, such as turf transplantation and initial planting with mulching, have demonstrated promising results yet are labor-intensive and limited in scale (Bay & Ebersole 2006, Mehlhoop et al. 2018, Roberts & Seastedt 2019). Although current restoration practices often successfully establish vegetation cover and mitigate erosion, they rarely restore the original floristic composition. Instead, seeded species typically remain dominant for extended periods, suppressing native plant recovery (Isselin-Nondedeu & Bedecarrats 2009, Güsewell & Klötzli 2012, Rydgren et al. 2016). Thus, restoration efforts frequently fail to achieve adequate floristic quality, emphasizing the need for more effective methods and clear ecological benchmarks (Ruiz-Jaen & Mitchell Aide 2005).

Microorganisms, particularly soil bacteria, significantly influence ecosystem functions, including nutrient cycling, soil formation, and plant growth (Berendsen & Schlaeppi 2019, Wagg et al. 2019). Alpine soil bacteria represent a well-studied group known for their sensitivity to environmental disturbances, making them suitable indicators for assessing ecological impacts of restoration activities (Hermans et al. 2017, Jones et al. 2021). Recent advances in molecular ecology, especially high-throughput 16S rRNA gene amplicon sequencing, offer new opportunities to evaluate restoration effectiveness by capturing comprehensive microbial diversity alongside traditional vegetation surveys and soil analyses (Hart et al. 2015, Soliman et al. 2017, Holderegger et al. 2019).

This study investigates recently restored alpine grasslands at Corvatsch, canton of Grisons, Switzerland, to evaluate differences in vegetation composition, diversity, and soil bacterial communities between restored and undisturbed reference sites. By integrating traditional vegetation assessments with soil chemical analyses and molecular methods, we

aim to identify key factors influencing restoration outcomes, explore soil structural and chemical differences between restored and reference sites, and develop practical recommendations for improving alpine restoration practices and biodiversity conservation efforts.

2. Methods

2.1 Study area

The study was conducted in the ski area of Piz Corvatsch, located in the Upper Engadine region of the canton of Grisons (Switzerland). The investigated area lies on the northwestern slope of the Corvatsch massif (Fig. 1), near the upper station of the recently constructed Curtinella chairlift (2535 m a.s.l.), accessible from the valley station at Surlej (2087 m a.s.l.).

The landscape is characterized by a mosaic of alpine and subalpine vegetation types, shaped by the region's high topographic and geological heterogeneity. Dominant communities include *Nardion strictae* grasslands and *Caricion curvulae* sedge meadows, interspersed with wind-exposed grasslands (*Elynion myosuroides*) and snowbed communities on siliceous substrates (*Salicion herbaceae*). Scattered stands of subalpine larch-Swiss stone pine forests (*Larici-Pinetum cembrae*) occur on more stable terrain. The area is subject to both summer grazing by cattle and intensive winter tourism use, including artificial snow production.
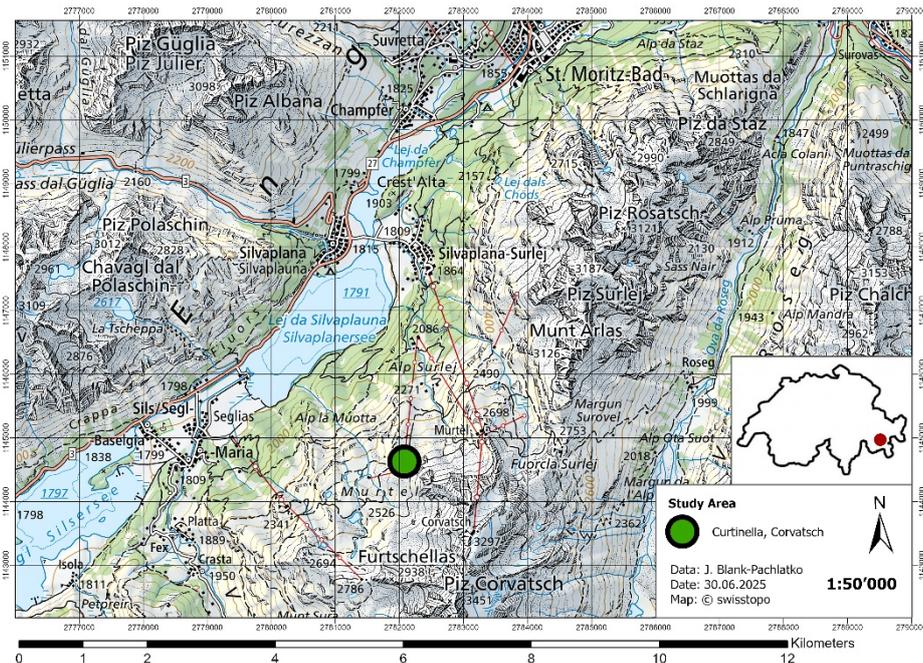

Fig. 1. Location of the study area at the top station of the Curtinella chairlift in the Corvatsch ski area, Upper Engadine, canton of Grisons, Switzerland (map source: swisstopo, 2025).

Abb. 1. Lage des Untersuchungsgebiets an der Bergstation der Curtinella-Sesselbahn im Skigebiet Corvatsch (Oberengadin, Kanton Graubünden, Schweiz) (Kartenquelle: swisstopo, 2025).

Major earthworks associated with the chairlift construction (2016) and snowmaking infrastructure (2017) led to extensive soil disturbance, which was followed by restoration measures in accordance with the guidelines for high-altitude restoration by the 'Working Group for high altitude restoration' (Peters et al. 2019). These measures included seeding and turf translocation. Additional restoration was implemented in 2020 along the decommissioned track of the former drag lift. As part of the same construction project, the restoration work around the valley station of the lift, completed a year earlier and located at a lower elevation (2087 m a.s.l.), was later recognized as "best practice" by the Swiss Association for Ecological Engineering (Edelkraut 2021). In summer 2021, restored and adjacent undisturbed reference sites were surveyed using vegetation plots and soil sampling to assess restoration outcomes.

2.2 Study design and sampling

The study compared three distinct areas near the Curtinella chairlift summit station (2535 m a.s.l.) at Piz Corvatsch, Graubünden (CH), differing in restoration status (Table 1). The "Seeding" site was restored in 2017 through seeding along a snowmaking pipeline. A seed mixture adapted to altitude and soil conditions with high-altitude ecotypes was used (K. Edelkraut, pers. commun.). The "Turf" site comprises areas restored by turf transplantation in 2020 following the dismantling of a former ski lift track. The "Reference" site, located directly adjacent to the restored areas at the same elevation, served as an undisturbed control featuring native vegetation.

In each site, nine vegetation plots were placed across similar elevation gradients (±100 m) under homogeneous conditions, yielding 27 plots in total (Fig. 2). Vegetation surveys and soil sampling for physicochemical and microbial analyses, including bacterial 16S rRNA gene amplicon sequencing (NGS), were conducted on 12, 14, and 16 July 2021.

Table 1. Overview of the three study sites near the top station of the Curtinella chairlift at Corvatsch. Site "Reference" represents undisturbed reference plots located in close proximity to the restored areas.

Tabelle 1. Übersicht der drei Teilflächen nahe der Bergstation des Sesselliftes Curtinella am Corvatsch. Die Teilfläche "Referenz" stellt unveränderte Vergleichsflächen in unmittelbarer Nähe dar.

Site	Year of Intervention	Restoration Method	Description
Seeding	2017	Seeding	Snowmaking pipeline trench
Turf	2020	Turf translocation	Former ski lift track
Reference	None	None	Undisturbed grassland

2.2.1 Vegetation survey

Vascular plant species and percent cover (%) were recorded following the EDGG protocol (Dengler et al. 2016). In deliberate deviation from the recommended square plots, we used standardized circular plots (10 m², radius 1.78 m) at all sites to ensure homogeneous microsite conditions and to facilitate relocation. Plots were randomly located within homogeneous stands, avoiding transitional zones. The flora was surveyed both in the generative and in the vegetative state (Lauber et al. 2018, Eggenberg & Möhl 2020, Eggenberg et al. 2022). Bryophytes and lichens were excluded. The nomenclature of vascular plants follows Juillerat et al. (2017). Plant community assignment follows Phytosuisse (Prunier et al. 2019). The relative cover of cryptogams, litter, bare soil, gravel (2–63 mm), stones (> 63 mm), and fine soil (<2mm) was also estimated. Environmental variables per plot included coordinates, altitude, slope, aspect and soil depth. Plots were geo-referenced using buried magnets for re-identification (coordinates provided in Supplement E2). The vegetation data was incorporated into the EDGG-affiliated GrassPlot database (Dengler et al. 2018).

Fig. 2. Distribution of the 27 vegetation plots across three study sites (9 plots per site) near the top station of the Curtinella chairlift (2500 m a.s.l.) on Corvatsch (Grisons, Switzerland). The grey trail shown was constructed after the survey (map source: swisstopo, 2025).

Abb. 2. Verteilung der 27 Vegetationsaufnahmen auf drei Untersuchungsflächen (je 9 Aufnahmen) nahe der Bergstation des Sessellifts Curtinella (2500 m ü. M.) am Corvatsch (Kanton Graubünden, Schweiz). Der breite Wanderweg (grau) wurde erst nach den Erhebungen angelegt.

2.2.2 Soil sampling and laboratory analysis

Soil samples were collected from each vegetation plot as a pooled sample of ten soil cores (5–15 cm depth), sieved (2 mm), and kept cool during transport (Agroscope 2020c, d). For microbial biomass determination (FE-C_{mik}), samples were fresh sieved (2 mm), moisture-adjusted to 50% water-holding capacity with deionized water (Agroscope 2020a) and incubated at 20 °C light-protected for seven days (Agroscope 2020e). Microbial biomass was then assessed via chloroform fumigation-extraction (Agroscope 2020b), with 24 h fumigation in chloroform vapor under light-protected conditions followed by extraction with 0.5 M K_2SO_4. The dissolved organic carbon (DOC) in the extracts was quantified with a TOC analyzer (Shimadzu TOC-L CSH) and microbial biomass C (C_{mic}) was calculated as DOC_fum − DOC_unfum (per g dry soil). Soil carbon, hydrogen, nitrogen, and organic carbon content (C, H, N, C_{org}) were measured using a TruSpec Macro Analyzer (LECO) after drying, sieving, and grinding soil samples. Samples were combusted according to standard protocols at 950 °C (C, H, N) and 550 °C (organic carbon). Soil pH and electrical conductivity were determined from dried samples using a 1:2.5 soil-to-solution ratio with 0.01 M $CaCl_2$ for pH and distilled water for conductivity measurements (Agroscope 2020f).

2.2.3 Soil DNA extraction

The samples for molecular biological analysis were transferred on site from the mixed soil samples into sterile Falcon tubes (15 ml). Kept cold in cool bags during sampling, the samples were frozen (-18 °C) on the same evening. For the determination of soil bacteria, total genomic DNA was extracted

from 0.25 g of soil using the DNeasy PowerLyzer PowerSoil Kit (Qiagen GmbH, Germany) according to the manufacturer's instructions, and DNA quality and quantity were verified by UV/VIS spectrophotometry. The DNA then served as template for PCR, in which the V3–V4 region of the 16S rRNA gene was amplified with primers 341F (5′-CCTACGGGNGGCWGCAG-3′) and 805R (5′-GACTACHVGGGTATCTAATCC-3′) (Herlemann et al. 2011, Klindworth et al. 2013). PCR reactions (25 μL) contained 12.5 μL KAPA HiFi HotStart ReadyMix, 0.75 μL of each primer (10 μM), 2.5 μL template DNA, and 8.5 μL nuclease-free water. Initial denaturation was at 95 °C for 3 min, followed by 30 cycles of 98 °C for 20 s, 53 °C for 30 s, and 72 °C for 30 s, with a final extension at 72 °C for 60 s. The PCR product was purified with the CleanNGS kit (LABGENE Scientific SA, Switzerland) and indexed in a second PCR using the Nextera XT Index Kit v2 (Illumina, USA). The second PCR had a reaction volume of 25 μL consisting of 12.5 μL KAPA HiFi HotStart ReadyMix, 2.5 μL per index, and 2.5 μL of the purified amplicon. This PCR started with denaturation at 95 °C for 3 min, followed by 12 cycles of 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 30 s, and ended with a final elongation at 72 °C for 5 min.

Indexed samples were purified and normalized using a SequalPrep plate (Thermo Fisher Scientific, USA). Normalization (i.e., DNA concentration) was verified on 15 samples with a Fluo 100 fluorometer (Hangzhou Allsheng Instruments Co., China), and samples were then pooled in equal volumes. The pool was prepared for sequencing according to the "Illumina Denature and Dilute Libraries Guide" (2018). Paired-end sequencing was performed on a MiSeq (Illumina, USA) using a v2 300-cycle micro cartridge (2 × 150) (loading concentration: 8 pM, 10% 12.5 pM PhiX spike-in). Resulting reads were provided in FASTQ format.

Using the dada2 package (Callahan et al. 2016) in R, we assessed the quality of paired-end reads and filtered them to a minimum length of 120 bp. Due to the limited read length, reads were concatenated without overlap (using an artificial bridge of 10 Ns), and identical reads were collapsed into sequences with relative abundances. Chimeras were subsequently removed (mean 18%), and amplicon sequence variants (ASVs) were inferred. Taxa were assigned using dada2 (SILVA v132). Raw 16S rRNA gene amplicon reads were deposited in the NCBI Sequence Read Archive (SRA) under accession number PRJNA1309041.

2.3 Statistical analyses

2.3.1 Vegetation & soil

Statistical analyses were conducted using R (R Core Team 2025, Version 4.5.1) and RStudio (RStudio Team 2025, Version 2025.05.0), with data organization facilitated by the R packages tidyverse and data.table (Wickham et al. 2019, Dowle & Srinivasan 2025). Weighted ecological indicator values according to Landolt (2010) and Shannon diversity indices were calculated using Vegedaz software (Küchler 2021). Additionally, species frequencies and φ-values were determined (Chytrý et al. 2002).

Vegetation data were analyzed using cluster analysis (Euclidean distance, Ward's method), with the optimal number of clusters identified via the elbow method (package factoextra; Kassambara & Mundt 2025). Differences among the subplots regarding vegetation and soil parameters were assessed using one-way ANOVA (significance level $\alpha = 0.05$). Model assumptions were verified visually and statistically through Levene's and Shapiro-Wilk tests. Non-homogeneous variances were improved by applying square root or logarithmic transformations where necessary. Differences among subplots were further examined using Tukey's tests (package stats & car; Fox & Weisberg 2019).

Detrended Correspondence Analysis (DCA) was performed with reduced weighting of rare species (package vegan; Oksanen et al. 2025). Species with frequency ≥ 5 (across all plots) were plotted; additionally, species with high ecological significance, defined as diagnostic value $\varphi \geq 0.30$ or clear habitat fidelity, were included. Environmental variables were projected onto the ordination through multiple regression.

Moreover, we used an information-theoretic framework (AICc) to rank a priori linear models with fixed transforms ($\sqrt{}$ gravel; log10 soil depth) from a global set (herbaceous cover, gravel cover, soil depth, pH, fine soil cover, site, snowmaking). Models within ΔAICc < 2 were treated as equivalently

supported; we report the parsimonious model and provide full-average model-averaged estimates with unconditional 95% CIs. Model quality was checked via residual diagnostics, VIF, and K-fold cross-validation (RMSE, R^2_{CV}).

2.3.2 Soil bacterial community

Genus-level ASVs were agglomerated, and subplot alpha diversity (Shannon) was compared by Welch's ANOVA followed by Games-Howell post-hoc tests. Assumptions were checked with Levene's test. We visualized compositional differences of bacterial communities using non-metric multidimensional scaling (NMDS; $k = 2$) based on Bray-Curtis distances computed from Hellinger-transformed relative abundances (package phyloseq & vegan; McMurdie & Holmes 2013, Oksanen et al. 2020). Prior to testing, we assessed homogeneity of multivariate dispersions with PERMDISP (9999 permutations). Group differences were analysed by PERMANOVA (9999 permutations). Post-hoc contrasts used pairwise PERMANOVAs with Holm correction. Environmental vectors (soil pH, soil depth, gravel cover, total vegetation cover) were fitted to the NMDS using envfit (9999 permutations) after gentle transformations (log or square-root where appropriate) and screening for collinearity; p-values were Benjamini-Hochberg adjusted and only non-redundant predictors were shown in the main figure (full table in Supplement E5). Differential bacterial taxa among treatments were screened with a linear discriminant analysis (package MicrobioataProcess, Xu et al. 2023). We applied Kruskal-Wallis tests across treatments (BH-adjusted) and computed linear discriminant scores (LDA) as effect sizes.

3. Results

3.1 Vegetation composition

A total of 89 vascular plant species (including three identified only at genus level) were recorded across 27 vegetation plots (Supplement E1), representing typical acidic alpine grassland (class: *Caricetea curvulae*). *Poa alpina*, *Ligusticum mutellina*, and *Festuca rubra* aggr. were most frequent, found in over 80% of plots, while *Polygonum viviparum*, *Leontodon helveticus*, and *Potentilla aurea* appeared in about 70% of plots.

Cluster analysis (Ward's method, Euclidean distance, cophenetic correlation c = 0.85) clearly separated the plots into three groups corresponding closely to field classifications (Fig. 3). Group "Seeding" was characterized by *Achillea millefolium* and an unidentified *Leucanthemum* sp., both present in all plots with high fidelity ($\varphi \geq 0.73$), indicating that these species occurred almost exclusively in this subplot. Group "Turf" featured *Trifolium pallescens* consistently, alongside *Poa alpina*, *Festuca rubra* aggr. and *Polygonum viviparum*. In contrast, plots of the undisturbed reference area consistently contained *Helictotrichon versicolor*, *Anthoxanthum alpinum*, *Selaginella selaginoides*, *Vaccinium gaultherioides* and *Pulsatilla vernalis*, with notably higher species richness (mean = 28 ± 6 species) and vegetation cover (mean = 87%) compared to restored areas (C17: 14 ± 5 species, 59% cover; C20: 23 ± 5 species, 28% cover).

3.2 Beta-Diversity of vascular plants

Detrended correspondence analysis (DCA) revealed clear differences in plant community composition among areas (Fig. 4; Axis 1 eigenvalue = 0.73, length = 4.74 SD). The first and second axes explain 38.3% and 19.1% of the total variance, respectively. Key drivers explaining differentiation along axis 1 were gravel content ($r^2 = 0.47$), soil pH ($r^2 = 0.46$), microbial biomass ($r^2 = 0.58$), and soil depth ($r^2 = 0.70$), all representing soil parameters notably altered by restoration activities, thus highlighting significant environmental gradients influencing plant community structure.

Fig. 3. Ward's cluster analysis of vegetation plots based on Euclidean distance (cophenetic correlation coefficient: c = 0.85). Cluster heterogeneity (cophenetic distance) is represented on the Y-axis (scaled 0–3). The three resulting clusters – Seed (blue), Turf (red), and Reference (green) – closely match the field-defined plot classification.

Abb. 3. Ward-Clusteranalyse der Vegetationsaufnahmen auf Basis der euklidischen Distanz (kophenetischer Korrelationskoeffizient: c = 0,85). Die Heterogenität der Cluster (kophenetische Distanz) ist auf der Y-Achse dargestellt (Skalierung 0–3). Die drei resultierenden Cluster – Ansaat (blau, Seed), Rasenziegel (rot, Turf) und Referenz (grün, Reference) – entsprechen weitgehend der feldbasierten Zuordnung der Untersuchungsflächen.

3.3 Differences in site-related parameters

Soil parameters differed significantly among the three areas, excluding stone cover. Restored areas had notably lower vegetation am cryptogam cover, shallower soil depth, and higher gravel content compared to undisturbed sites. Organic carbon, total nitrogen, and soil electrical conductivity were highest in reference plots, correlating positively with soil depth. Soil pH was significantly lower in undisturbed plots compared to restored areas.

Specifically, the Shannon diversity index for plants was significantly higher in undisturbed plots than in restored plots (Ref-Seed: p_{adj} = 0.001, Ref-Turf: p_{adj} = 0.001, Turf-Seed: p_{adj} = n.s.) (Fig. 5). Similarly, soil electrical conductivity was significantly greater in reference plots compared to restored plots (Ref-Seed: p_{adj} = 0.0001, Ref-Turf: p_{adj} = 0.0001, Turf-Seed: p_{adj} = n.s.). Microbial biomass also significantly differed (Ref-Seed: p_{adj} = 0.0001, Ref-Turf: p_{adj} = 0.0001, Turf-Seed: p_{adj} = n.s.) as well as organic carbon (Ref-Seed: p_{adj} = 0.0001, Ref-Turf: p_{adj} = 0.0001, Turf-Seed: p_{adj} = n.s.).

Within our dataset, plant diversity (Shannon) was best explained by an AICc-selected additive model with vegetation cover and √gravel cover (R^2 = 0.57; 10-fold R^2_{CV}=0.45; ΔAICc = 0.3 vs. the interaction model). Shannon diversity increased with vegetation cover and declined with gravel cover, indicating that restoration influenced Shannon indirectly via its effects on substrate and cover (Supplement E3 and E4).

Fig. 4. Detrended Correspondence Analysis (DCA) of species composition across the three study sites. Axis 1 and Axis 2 explain 38.3% and 19.1% of the total variance, respectively. The gradient length of Axis 1 (4.74 standard deviation units) indicates substantial species turnover along the main ecological gradient. Together, the first four axes account for 86.9% of the total variation, indicating a robust ordination. Environmental variables are shown as vectors (gravel content, pH, FE-Cmic) or as a surface overlay (soil depth). The 27 plots are symbolized by subplot (Seeding: blue triangles; Turf: red squares; Reference: green circles), and 46 ecologically distinctive species are labeled with black dots. Abbreviation: FE-Cmic = microbial biomass.

Abb. 4. Detrended Correspondence Analysis (DCA) der Artenzusammensetzung in den drei Untersuchungsflächen. Achse 1 und 2 erklären 38,3 % bzw. 19,1 % der Gesamtvarianz. Die Gradientenlänge von Achse 1 (4,74 Standardabweichungseinheiten) weist auf einen deutlichen Artenumsatz entlang des Hauptgradienten hin. Insgesamt erfassen die ersten vier Achsen 86,9 % der Variabilität in den Artendaten, was auf eine robuste Ordination hinweist. Umweltvariablen sind als Vektoren (Kiesanteil, pH-Wert, FE-Cmik) bzw. als Oberflächengradient (Bodentiefe) dargestellt. Die 27 Plots sind nach Teilfläche symbolisiert (Ansaat: blaue Dreiecke; Rasenziegel: rote Quadrate; Referenz: grüne Kreise); 46 ökologisch charakteristische Arten sind als beschriftete Punkte markiert. Abkürzung: FE-Cmik = mikrobielle Biomasse.

3.4 Soil bacterial communities

The 16S rRNA gene amplicon sequencing yielded a total of 1 024 004 high-quality sequences, clustered into 26 042 ASVs. On average, samples contained 37 926 sequences and 1818 ASVs. The mean number of sequences and ASVs per sample was 35 194 and 1765 in Seeding plots, 40 973 and 2144 in Turf plots, and 37 612 and 1545 in Reference plots, respectively. Soil bacterial diversity was notably higher in restored areas compared to the undisturbed reference ($p = 0.002$) (Fig. 6). Games-Howell post-hoc tests showed Turf-Reference ($p_{adj} = 0.001$) and Seeding-Reference ($p_{adj} = 0.010$), whereas Turf vs Seeding was not significant ($p_{adj} = 0.184$). Phyla Proteobacteria, Verrucomicrobia, and Acidobacteria dominated all sites, collectively representing approximately 77% of sequences (Fig. 7).

Fig. 5. Shannon indices of vascular plants, soil solution conductivity, microbial biomass (square-root transformed), and organic carbon content (log$_{10}$ transformed) for the three study sites: Seeding, Turf, and Reference. Boxplots show the median (horizontal line), interquartile range (box), minimum and maximum values (whiskers), and individual data points. Horizontal bars and asterisks indicate statistically significant differences between groups based on pairwise *t*-tests. *n* = number of samples; *** *p* < 0.001.

Abb. 5. Shannon-Indizes der Gefäßpflanzen, elektrische Leitfähigkeit der Bodenlösung, mikrobielle Biomasse (Wurzeltransformation) und organischer Kohlenstoff (log$_{10}$-transformiert) in den drei Untersuchungsflächen: Ansaat, Rasenziegel und Referenz. Die Boxplots zeigen Median (horizontale Linie), Interquartilsabstand (Box), Minimal- und Maximalwerte (Whisker) sowie Einzelwerte. Horizontale Balken und Sternchen kennzeichnen statistisch signifikante Unterschiede zwischen den Gruppen auf Basis paarweiser *t*-Tests. *n* = Stichprobengröße; *** *p* < 0,001.

Non-metric multidimensional scaling (NMDS) showed a clear tendency to separate undisturbed and restored soils, suggesting treatment-related differences in bacterial composition (Fig. 8). PERMDISP indicated no difference in multivariate dispersion among treatments ($F = 0.65$, $p = 0.54$). PERMANOVA revealed strong differences in community composition ($F = 6.66$, $R^2 = 0.357$, $p = 0.0001$). Pairwise PERMANOVAs (Holm-adjusted) showed Reference vs Turf ($F = 10.83$, $R^2 = 0.404$, $p_{adj} = 0.0002$) and Reference vs Seeding ($F = 8.42$, $R^2 = 0.345$, $p_{adj} = 0.0004$) to be significant, whereas Turf vs Seeding was not ($F = 1.12$, $R^2 = 0.065$, $p_{adj} = 0.283$). Because dispersion was homogeneous, these differences reflect centroid (location) shifts rather than dispersion effects. Environmental fitting indicated strong alignment of soil pH ($R^2 = 0.408$, $p_{(BH)} = 0.0003$) and soil depth ($R^2 = 0.353$, $p_{(BH)} = 0.0003$) with the ordination, followed by gravel cover ($R^2 = 0.211$, $p_{(BH)} = 0.0032$) and total vegetation cover ($R^2 = 0.078$, $p_{(BH)} = 0.028$).

Fig. 6. Shannon indices of bacterial communities in soil samples from the three sites Seeding, Turf, and Reference. Boxplots display the median (horizontal line), interquartile range (box), minimum and maximum values (whiskers), and individual data points. Horizontal bars and asterisks indicate statistically significant differences between groups based on pairwise t-tests. n = number of samples; *** $p < 0.001$, ** $p < 0.01$.

Abb. 6. Shannon-Indizes der bakteriellen Gemeinschaften in Bodenproben aus den drei Untersuchungsflächen: Ansaat, Rasenziegel und Referenz. Die Boxplots zeigen Median (horizontale Linie), Interquartilsabstand (Box), Minimal- und Maximalwerte (Whisker) sowie Einzelwerte. Horizontale Balken und Sternchen kennzeichnen statistisch signifikante Unterschiede zwischen den Gruppen auf Basis paarweiser t-Tests. n = Stichprobengröße; *** $p < 0,001$; ** $p < 0,01$.

Fig. 7. Relative abundance of Phyla and Orders of the 20 most common ASVs (aggregated by genus) sorted by sites (seeding, turf, reference). Orders that could not be taxonomically assigned are listed as NA (gray).

Abb. 7. Relative Abundanz von Phyla und Ordnungen der 20 häufigsten ASV (aggregiert auf Gattung) geordnet nach Teilflächen (Ansaat, Rasenziegel, Referenz). Ordnungen welche taxonomisch nicht zugeordnet werden konnten sind als NA (grau) aufgeführt.

Fig. 8. NMDS of bacterial communities (Bray-Curtis on Hellinger-transformed data; stress = 0.067). Points are samples (colors/shapes = Sites); ellipses show 68% confidence envelopes. Arrows denote significant environmental vectors after BH adjustment: soil pH, soil depth, gravel cover, and total vegetation cover. PERMDISP: $F = 0.65$, $p = 0.54$. PERMANOVA: $F = 6.66$, $R^2 = 0.357$, $p = 0.0001$. Pairwise PERMANOVA (Holm): Reference vs Turf, $p_{adj} = 0.0002$; Reference vs Seeding, $p_{adj} = 0.0004$; Turf vs Seeding, $p_{adj} = 0.283$.

Abb. 8. NMDS der Bakteriengemeinschaften (Bray-Curtis auf Hellinger-transformierten Daten; Stress = 0,067). Punkte zeigen Proben (Farben/Formen = Standort); Ellipsen geben 68 %-Konfidenzen an. Pfeile: signifikante Umweltvektoren nach BH-Korrektur: Boden-pH, Bodentiefe, Kiesdeckung und Gesamtvegetationsdeckung. PERMDISP: $F = 0,65$; $p = 0,54$. PERMANOVA: $F = 6,66$; $R^2 = 0,357$; $p = 0,0001$. Paarweise PERMANOVA (Holm): Referenz vs Turf, $p_{adj} = 0,0002$; Referenz vs Seeding, $p_{adj} = 0,0004$; Turf vs Seeding, $p_{adj} = 0,283$.

Linear discriminant analysis identified eight bacterial genera significantly associated with undisturbed soils (Fig. 9): The genera *Roseiarcus* and *Nitrobacter*, along with the genus complex *Burkholderia-Caballeronia-Paraburkholderia*, belong to the phylum Proteobacteria. The genera "Candidatus *Udaeobacter*" and "Candidatus *Xiphinematobacter*" belong to the phylum Verrucomicrobia, while the genus *Acidothermus* is classified within Actinobacteria. Additionally, the genera *HSB_OF53-F07* and *JG30a-KF-32*, assigned to the phylum Chloroflexi, have not yet been fully described or cultured. These taxa may serve as bioindicators for soil integrity in alpine restoration projects.

4. Discussion

Restoration measures play a crucial role in the recovery of alpine ecosystems disturbed by construction activities and in mitigating soil erosion (Meusburger & Alewell 2014, Zerbe & Wiegleb 2016). To effectively conserve alpine biodiversity, restoration practices must closely replicate the native vegetation and preserve soil integrity (Peters et al. 2019). Our short-term study at Curtinella, Corvatsch, highlighted pronounced differences in vegetation composition, soil properties, and bacterial communities between restored and undisturbed reference plots, underscoring the need for refinement in current alpine restoration strategies.

Fig. 9. Differences per subplots of eight bacterial genera. In this dataset, the genera serve as indicators for undisturbed soils (reference) in the study area. Boxplots display the median (horizontal line), interquartile range (box), minimum and maximum values (whiskers), and individual data points. Horizontal bars and asterisks indicate statistically significant differences between groups based on pairwise *t*-tests. *** $p < 0.001$, ** $p < 0.01$.

Abb. 9. Unterschiede pro Teilfläche von acht Bakterien-Gattungen. Die Gattungen dienen im vorliegenden Datenset als Indikatoren für ungestörte Böden (Referenz) im Untersuchungsgebiet. Die Boxplots zeigen den Median (horizontale Linie), den Interquartilsabstand (Box), Minimal- und Maximalwerte (Whisker) sowie Einzelwerte. Horizontale Balken und Sternchen markieren statistisch signifikante Unterschiede zwischen den Gruppen auf Basis paarweiser *t*-Tests. *** $p < 0,001$; ** $p < 0,01$.

4.1 Vegetation patterns reflecting restoration technique

The undisturbed reference area (Reference) exhibited typical alpine grassland vegetation classified within the *Caricetea curvulae*, characterized by high species richness, diversity, and the presence of characteristic alpine species such as *Arnica montana* and *Geum montanum* (Delarze et al. 2015, Prunier et al. 2019). In contrast, seeded restoration sites (Seeding) significantly deviated from the reference community, being dominated by competitively strong, often non-native species such as *Phleum pratense* aggr. This resulted in reduced species richness, diversity, and vegetation cover (Conrad & Tischew 2011, Waldén & Lindborg 2016, Hudek et al. 2020). These results align with other studies demonstrating the long-term dominance of seeded species, inhibiting the establishment of target alpine species (Prach & Pyšek 2001, Conrad & Tischew 2011). This underscores the importance of prioritizing spontaneous revegetation wherever erosion control allows.

Conversely, restoration by turf transplantation (Turf) facilitated a better establishment of native species than seeding. However, these species occurred only at low cover values and were interspersed with extensive vegetation-free gaps. While such open patches can promote seedling establishment from surrounding vegetation in alpine environments (Briceño et al. 2015, Margreiter et al. 2021), and turf transplants have generally yielded promising results (Trueman et al. 2007), the development of full vegetation cover (including cryptogams) is likely to take several more years due to the inherently slow vegetative growth at this Elevation. In addition, grasses appeared more resilient to transplantation, potentially disadvantaging slower-establishing herbaceous species (Conlin & Ebersole 2001). Although turf transplantation achieved relatively high floristic similarity to reference conditions, its success strongly depends on the quality of turf removal and reinstallation. In practice, complete coverage is often unachievable, and topsoil layers may be lost or insufficiently replaced (Rydgren et al. 2013, Peters et al. 2019). This highlights the critical importance of careful handling of vegetation mats and soil during restoration operations (Heneghan et al. 2008).

4.2 Soil properties and restoration implications

Soil analyses revealed substantial differences between restored and reference sites, notably in microbial biomass, electrical conductivity, nutrient concentrations, and soil depth. Restored sites exhibited significantly shallower soils with reduced fine soil fractions, increased gravel content, and altered nutrient concentrations. These changes can adversely affect soil water retention, nutrient availability, and consequently vegetation composition (Fu & Shen 2016, Guo et al. 2021, Kwaku et al. 2021). Furthermore, despite lower total nitrogen and carbon content, restored soils exhibited a lower carbon-to-nitrogen ratio than the reference plots, potentially facilitating increased nitrogen availability, favoring competetive plant species, and affecting long-term community structure (Janssens et al. 1998, Güsewell 2004).

Lower soil pH values in undisturbed reference areas correlated strongly with deeper soil profiles and coincided with higher organic carbon (C_{org}). Consistent with acidifying influences of organic matter (organic acids, CO_2 from decomposition), such lower pH conditions can limit nutrient availability (Tibbett et al. 2019, Barlow et al. 2020). Across ordinations, microbial biomass emerged as a key correlate of plant community composition. In our DCA, the FE-C_{mic} vector aligned with the principal species-turnover axis and pointed towards the reference plots, indicating that the construction works severely altered the initial microbacterial conditions in the soil for the plants. This finding highlights the importance of

soil depth and structure in sustaining native plant communities, emphasizing the critical role of topsoil preservation during construction activities. Given the slow rate of soil formation in alpine environments, the loss of topsoil represents a significant and irreversible constraint on biodiversity recovery (Heneghan et al. 2008, She et al. 2022).

4.3 Soil bacterial communities and bioindicator potential

Bacterial community analysis revealed distinct shifts in community structure between restored and reference soils. Phyla Acidobacteria, Verrucomicrobia, and Proteobacteria were consistently dominant, aligning with findings from similar alpine studies (Lipson & Schmidt 2004, Adamczyk et al. 2019, Jiang et al. 2021). Notably, "Candidatus *Udaeobacter*", a genus associated with hydrogen cycling, emerged as highly abundant across all sites (Willms et al. 2020). Restoration raised soil pH and likely increased bacterial diversity, and pH emerged as the dominant NMDS gradient, aligned with broad evidence that pH is a primary determinant of soil bacterial communities (Fierer & Jackson 2006, Lauber et al. 2009, Rousk et al. 2010, Kim et al. 2013, Choi et al. 2017). While soil depth and gravel cover serve as indicators of fine soil capacity and water retention capacity in NMDS, vegetation cover reflects surface exposure and vegetation structure, which is consistent with the treatment differences observed in PERMANOVA.

Importantly, our analysis identified eight bacterial genera serving as potential bioindicators for undisturbed alpine soils, such as the genus *Nitrobacter*, suggesting that stable, minimally disturbed soils have distinctive microbial fingerprints (Poly et al. 2008, Attard et al. 2010, Bayranvand et al. 2020). These bacterial indicators hold promise for monitoring and evaluating the ecological integrity of alpine restoration projects. However, the ecological roles and functional significance of these indicators remain largely unexplored, necessitating further research into their specific contributions to ecosystem processes and vegetation dynamics.

4.4 Comparative context and broader ecological considerations

Our findings align with numerous studies underscoring the challenges of replicating native alpine communities through conventional restoration methods (Waldén & Lindborg 2016, Hudek et al. 2020). Turf transplantation showed greater floristic similarity to reference conditions at the time of survey, yet neither method fully achieves reference site conditions within short time frames. The dominance of competitive, non-native species observed in seeded areas may persist, potentially altering long-term successional trajectories and reducing biodiversity value (Conrad & Tischew 2011).

Moreover, soil microbial community alterations following restoration are widely reported but poorly understood regarding long-term ecological consequences. The correlations we saw in the NMDS suggest that microbiome responses to restoration are mediated chiefly by pH as well as substrate and cover; steering communities toward reference-like states will likely require rebuilding organic matter and microbial biomass. Seasonal variations and nutrient availability, particularly related to snowmelt dynamics, significantly influence alpine bacterial community structures, indicating the necessity of incorporating temporal dimensions into future research (Lipson & Schmidt 2004, Lazzaro et al. 2015).

4.5 Practical implications and future recommendations

Given these insights, several key practical recommendations emerge. Preservation and careful management of topsoil during alpine restoration are paramount due to its irreplaceable ecological value and slow formation rates. Restoration practices should minimize soil disturbances, prioritize spontaneous revegetation processes, and reserve seeding primarily for erosion control rather than biodiversity enhancement (Prach & Pyšek 2001, Conrad & Tischew 2011).

Furthermore, our methodological framework, integrating traditional vegetation analyses with advanced molecular microbial assessments, tentatively identified putative indicator genera – best viewed as hypothesis-generating given amplicon biases, thereby helping to refine restoration monitoring. Expanding this methodological approach to include additional organism groups (e.g., fungi, insects) could further enrich biodiversity evaluations and strengthen restoration assessments. The complexity and limited understanding of soil biological dynamics in alpine ecosystems represent significant knowledge gaps. Further research should focus on comprehensively characterizing soil microbial communities, elucidating their ecological functions, and understanding their interactions with alpine plant communities. Additionally, more detailed and temporally resolved studies on microbial indicators are necessary to inform adaptive management strategies effectively.

Given ongoing biodiversity loss and climate change pressures, robust, evidence-based restoration practices are essential for alpine ecosystem conservation. Comprehensive ecological monitoring and interdisciplinary research remain imperative to guide effective restoration interventions, safeguard alpine biodiversity, and maintain ecosystem resilience.

Erweiterte deutsche Zusammenfassung

Einleitung – Alpine Ökosysteme gelten als Hotspots der Biodiversität und sind besonders anfällig für anthropogene Störungen (BAFU 2017, IPBES 2019). In der Schweiz machen alpines und subalpines Grasland einen beträchtlichen Teil der landwirtschaftlichen Fläche aus und beherbergen zahlreiche endemische und gefährdete Arten (Delarze et al. 2015, BFS 2019). Im Zuge von Infrastrukturbauten, insbesondere im alpinen Wintertourismus, kommt es häufig zu massiven Bodenbewegungen, die eine spontane Wiederbesiedlung verhindern. Hochlagenbegrünungen verfolgen das Ziel, erosionsgefährdete Flächen rasch zu stabilisieren und eine standorttypische Vegetation wiederherzustellen (Peters et al. 2019). Bisherige Studien zeigen jedoch, dass Ansaatflächen oft dauerhaft von konkurrenzstarken Arten dominiert bleiben und das Ziel einer floristisch hochwertigen Vegetation nur unzureichend erreichen (Conrad & Tischew 2011, Güsewell & Klötzli 2012). Vor diesem Hintergrund wurde am Corvatsch (GR, CH) eine Untersuchung zur Wirksamkeit von Hochlagen-Renaturierungen durchgeführt, die vegetationsökologische und bodenchemische Parameter integriert bewertet.

Untersuchungsgebiet – Das Untersuchungsgebiet befindet sich an der Bergstation der Curtinella-Sesselbahn im Skigebiet Corvatsch (2535 m ü. M.). Die Region ist geprägt von artenreichen Borstgrasrasen (*Nardion strictae*), Krummseggenrasen (*Caricion curvulae*) sowie Schneetälchen- und Windrasen-Gesellschaften (vgl. Abb. 1). Die untersuchten Flächen umfassen eine Ansaatfläche (Renaturierung 2017), eine Fläche mit Rasenziegeln (2020) sowie eine ungestörte Referenzfläche in räumlicher Nähe auf derselben Höhenstufe. Die massiven Bodenbewegungen im Rahmen der Bauarbeiten führten zu drastischen Veränderungen im Oberbodenprofil, welche die Ausgangsbedingungen für die Renaturierung prägten.

Methode – Insgesamt wurden 27 Vegetationsaufnahmen (9 pro Fläche, jeweils 10 m², rund) erhoben (angelehnt ans EDGG-Protokoll; Dengler et al. 2016) und ergänzt durch Bodenproben sowie Umweltparameter (u. a. pH-Wert, Bodentiefe, Feinerde- und Kiesanteil) (Tab. 1, Abb. 2). Die Arten-

zusammensetzung wurde analysiert mittels Clusteranalyse und Detrended Correspondence Analysis (DCA; Abb. 3 und 4), Diversitätsmaße (Shannon-Index), sowie ökologischen Zeigerwerten nach Landolt (2010). Die Bodenproben wurden unter anderem auf pH, Leitfähigkeit, Corg, Ntot und mikrobielle Biomasse (FE-C$_{mik}$) untersucht.

Ergebnisse – *Vegetation*: Insgesamt wurden 89 Gefäßpflanzenarten erfasst, wobei die Referenzflächen eine signifikant höhere Artenzahl (Ø = 28 Arten), Deckung (Ø = 87 %) und Diversität (Shannon-Index Ø = 2.2) zeigten als die renaturierten Flächen (Ansaat: 14 Arten, 59 %, Index = 1.4; Rasenziegel: 23 Arten, 28 %, Index = 1.3; vgl. Abb. 5). In der Ansaatfläche dominierten konkurrenzstarke Gräser wie *Phleum pratense* aggr., während in der Rasenziegelfläche eine höhere floristische Nähe zur Referenzgesellschaft erkennbar war, aber mit großen vegetationsfreien Lücken. Die Clusteranalyse bestätigte eine deutliche Trennung der Vegetationsgruppen entsprechend den Eingriffsflächen (Abb. 3). Die DCA ordnete die Hauptunterschiede entlang eines Gradienten von Kiesanteil, pH-Wert sowie Bodentiefe und mikrobielle Biomasse ein (Abb. 4).

Bodenparameter: Renaturierte Flächen wiesen im Vergleich zur Referenz signifikant geringere Bodentiefe, höheren Grobanteil, niedrigere elektrische Leitfähigkeit und reduzierte organische Kohlenstoff- und Stickstoffgehalte auf. Der pH-Wert war auf gestörten Flächen deutlich erhöht (Abb. 5). Die mikrobielle Biomasse (FE-C$_{mik}$) war in den gestörten Flächen um mehr als die Hälfte reduziert (Referenz: 47 mg C/kg; Ansaat/Rasenziegel: je ca. 20 mg C/kg). Ein multiples Regressionsmodell zeigte, dass die tiefere pflanzliche Diversität (Shannon) in den renaturierten Flächen mit einem erhöhten Kiesanteil und einer tieferen Vegetationsdeckung einherging; beides Faktoren, die durch die Eingriffe in den Boden direkt beeinflusst wurden.

Diskussion – Die Studie belegt, dass die untersuchten Renaturierungsmassnahmen in kurzer Zeit keine vollständige Wiederherstellung der alpinen Vegetation ermöglichen. Besonders die Ansaatfläche zeigte eine dauerhafte Dominanz eingesäter, meist nicht-standorttypischer Arten, was mit anderen Studien übereinstimmt (Conrad & Tischew 2011, Rydgren et al. 2016). Rasenziegel schnitten besser ab, allerdings behinderten Lücken und langsames Wachstum die Wiederherstellung der vollen Vegetationsdeckung (Margreiter et al. 2021). Entscheidender als die gewählte Methode erwies sich jedoch der Umgang mit dem Boden: Der Verlust der organisch reichen Oberbodenschicht, erhöhte pH-Werte und veränderte physikalische Eigenschaften erschwerten die Etablierung der Zielvegetation nachhaltig (Heneghan et al. 2008, Guo et al. 2021). Der Schutz des Oberbodens, insbesondere der Feinerde, ist daher essenziell für langfristigen Renaturierungserfolg im Hochgebirge.

Schlussfolgerung – Die Ergebnisse zeigen, dass technische Massnahmen wie Rasenziegeltransplantation kurzfristig Vorteile gegenüber Ansaaten bieten, jedoch beide Verfahren die natürliche Vegetationsentwicklung nicht vollständig wiederherstellen. Zentrale Herausforderung bleibt der Schutz und die Wiederherstellung bodenökologischer Bedingungen. Der Aus- und Wiedereinbau von Rasenziegeln sollte sorgfältig geplant und fachlich eng begleitet werden, idealerweise mit gezielter Instruktion der ausführenden Maschinenführer. Spontane Sukzession ist – wo immer es die Erosionsgefahr zulässt – als bevorzugte Option gegenüber der Ansaat zu prüfen. Diese sollten auf erosionsgefährdete Bereiche beschränkt bleiben. Weiter ist der vorhandene Oberboden möglichst vollständig zu erhalten und schonend zu behandeln. Eine Integration bodenökologischer Kriterien in Monitoring und Planung sollte künftig Standard werden, um die Biodiversität in alpinen Lagen effektiv zu sichern.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Species cover data for all 27 plots including constancy and fidelity values per site.

Anhang E1. Artenliste und Deckungsgrade für alle 27 Plots inklusive Stetigkeiten und Treuewerte pro Teilfläche.

Supplement E2. Header data of all 27 plots including coordinates, indicator values, environmental parameters and soil data.

Anhang E2. Kopfdaten aller 27 Plots inklusive Koordinaten, Zeigerwerten, Umweltparameter und Bodendaten.

Supplement E3. Candidate linear models ranked by AICc for plant diversity (Shannon index).

Anhang E3. Kandidatenmodelle der linearen Regression sortiert nach AICc für Pflanzenvielfalt (Shannon-Index).

Supplement E4. Final linear model for plant diversity (Shannon-index) in the collected data set.

Anhang E4. Finales lineares Modell für Pflanzenvielfalt (Shannon-Index) im erhobenen Datenset.

Supplement E5. Results of fitting environmental variables to the NMDS ordination.

Anhang E5. Ergebnisse der Anpassung von Umweltvariablen an die NMDS-Ordination.

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Supplement E1. Species cover data for all 27 plots including constancy and fidelity values per site. Abbreviations: Sum DG = Sum of Cover values, Freq = frequencies, Fid = Fidelity.

Anhang E1. Artenliste und Deckungsgrade für alle 27 Plots inklusive Stetigkeiten und Treuewerte pro Teilfläche. Abkürzungen: Sum DG = Summe der Deckungsgrade, Freq = Frequenzen, Fid = Treue.

Species list	Sed.1	Sed.2	Sed.3	Sed.4	Sed.5	Sed.6	Sed.7	Sed.8	Sed.9	Turf.1	Turf.2	Turf.3	Turf.4	Turf.5	Turf.6	Turf.7	Turf.8	Turf.9	Ref.1	Ref.2	Ref.3	Ref.4	Ref.5	Ref.6	Ref.7	Ref.8	Ref.9	Count	Freq Total %	Sum DG	SumDG-Sed	SumDG-Turf	SumDG-Ref	FreqSed %	FreqTurf %	FreqRef %	FidSed	FidTurf	FidRef
Ligusticum mutellina		0.01	5	0.5	0.5				0.1	0.04	0.3	0.5	0.001	0.1		0.05	0.05	0.05	15	0.05	20	2	7	25	3	3	2	23	85.2	84.8	6.6	1.1	77.1	66.7	88.9	100.0	-0.37	0.07	0.29
Leontodon helveticus			1			0.05	0.05		0.5	0.01	0.1	0.4	0.03	0.05			0.05	0.01	0.1	0.05	4	4	3	1	1	0.05	1	20	74.1	16.5	1.6	0.7	14.2	44.4	77.8	100.0	-0.48	0.06	0.42
Polygonum viviparum	1					2			1	0.03	0.1	0.3	0.5	0.5	0.1	0.05	0.5	3	0.3	0.05	3	3	2	2	2	0.5	0.5	21	77.8	22.4	4.0	5.1	13.4	33.3	100.0	100.0	-0.76	0.38	0.38
Luzula lutea				2		2				1		0.3	0.05	15	1	5	1		1	0.03	0.02	5	5	1	1	4	1	18	66.7	45.4	4.0	23.4	18.1	22.2	77.8	100.0	-0.67	0.17	0.50
Homogyne alpina				0.1	0.1					0.05		0.01		0.1		0.01			0.05	0.04	1	8	1	0.1	0.5	0.5	0.1	15	55.6	11.7	0.2	0.2	11.3	22.2	44.4	100.0	-0.47	-0.16	0.63
Poa alpina	15	12	5	3	10	0.3	1		10	13	15	7	25	15	15	20	20	15	2		5	10	15	20	1	2	0.5	25	92.6	256.8	56.3	145.0	55.5	88.9	100.0	88.9	-0.10	0.20	-0.10
Gentiana punctata			1	0.1	0.1	0.1			3					1					5		2	15	2	1	1	5	1	14	51.9	37.3	4.3	1.0	32.0	55.6	11.1	88.9	0.05	-0.58	0.52
Leucanthemopsis alpina ssp. alpina				0.5	0.01				0.5	0.03			0.01	0.01	0.01	0.01			0.03		0.01	0.1	1	0.2	0.05	0.01	0.05	16	59.3	2.5	1.0	0.1	1.5	33.3	55.6	88.9	-0.37	-0.05	0.43
Carex curvula ssp. curvula						0.001	0.01		0.5	0.01			0.001	0.01	0.1			0.01	12	0.1	0.01		3	2	0.5	3	0.5	16	59.3	21.8	0.5	0.1	21.1	33.3	55.6	88.9	-0.37	-0.05	0.43
Senecio incanus ssp. carniolicus		0.01					0.01			0.01	0.03			0.03	0.05		0.01	0.001	0.1	0.01	0.5		3	0.1	0.5	0.05	0.1	16	59.3	4.5	0.0	0.1	4.4	22.2	66.7	88.9	-0.53	0.11	0.43
Helictotrichon versicolor								7											10	2	15		3	5	8	10	1	9	33.3	61.0	7.0	0.0	54.0	11.1	0.0	88.9	-0.33	-0.50	0.83
Potentilla aurea			3		0.1	0.5			0.5	0.03	0.2	0.1	0.1		0.1	0.01	2	0.05	15		10	10	2	15	25	0.5		19	70.4	84.2	4.1	2.6	77.5	44.4	88.9	77.8	-0.40	0.29	0.11
Salix herbacea	0.001								0.5	0.3										0.05	10	5	0.05	1	20		30	10	37.0	66.9	0.5	0.3	66.1	22.2	11.1	77.8	-0.22	-0.38	0.60
Selaginella selaginoides		0.001																	0.001	0.001		0.05	0.05	0.05	0.02		0.1	8	29.6	0.3	0.0	0.0	0.3	11.1	0.0	77.8	-0.29	-0.46	0.75
Ranunculus montanus													3	0.01		0.3	0.01	1	0.5		0.5	5	1	3	12	0.5	2	13	48.1	28.8	0.0	4.8	24.0	0.0	66.7	77.8	-0.68	0.26	0.42
Bartsia alpina										0.05				0.1	0.1	0.05				2	1	1	3	0.1	3	1	0.1	11	40.7	10.5	0.0	0.3	10.2	0.0	44.4	77.8	-0.59	0.05	0.53
Anthoxanthum alpinum																1			5		0.05	15		3	3	1	0.5	7	29.6	28.6	0.0	1.0	27.6	0.0	11.1	77.8	-0.46	-0.29	0.75
Vaccinium gaultherioides																			0.1	0.1		1	3		0.3	20	35	7	25.9	59.5	0.0	0.0	59.5	0.0	0.0	77.8	-0.42	-0.42	0.84
Pulsatilla vernalis																			0.05	1	0.05		1	4			0.1	7	25.9	6.5	0.0	0.0	6.5	0.0	0.0	77.8	-0.42	-0.42	0.84
Sempervivum montanum	0.001	0.001	0.001							0.1	0.05						0.001	0.01	0.01		1	0.01	0.1	0.1	0.5			13	48.1	1.9	0.0	0.2	1.7	33.3	44.4	66.7	-0.21	-0.05	0.26
Soldanella alpina																				0.05	0.3	0.1	0.1	0.1			0.05	8	29.6	0.7	0.0	0.0	0.7	0.0	0.0	66.7	-0.11	-0.46	0.57
Hieracium piliferum aggr.										0.01	0.1			0.03			0.01	0.01	0.1		0.05	0.01		0.2	0.5	0.5		11	40.7	1.5	0.0	0.2	1.4	0.0	55.6	66.7	-0.59	0.21	0.37
Festuca rubra aggr.	25	30	20	20	18	25	45	10	20	1	0.5	0.05	0.05	1	0.1		1	1		12		20	0.5	1			0.05	22	81.5	251.3	213.0	4.7	33.6	100.0	88.9	55.6	0.34	0.13	-0.47
Geum montanum						0.3	0.05		0.05	0.1	0.03	0.5			0.05				0.1		0.5		2		0.2	0.1	0.1	12	44.4	3.9	0.4	0.7	2.8	33.3	44.4	55.6	-0.16	0.00	0.16
Loiseleuria procumbens						0.05				0.001				0.05					40	25	5			10			3	8	29.6	83.1	0.1	0.1	83.0	11.1	22.2	55.6	-0.29	-0.11	0.40
Leontodon hispidus									0.01		0.03								0.5		0.3		0.5	0.1			0.05	7	25.9	1.5	0.0	0.0	1.5	11.1	11.1	55.6	-0.24	-0.24	0.48
Myosotis alpestris										0.01	0.1	0.01	0.01	0.1			0.01				0.2	1	0.05	0.3	2			11	40.7	3.8	0.0	0.2	3.6	0.0	66.7	55.6	-0.59	0.37	0.21
Erigeron uniflorus											0.05									0.002		0.1	0.01	0.1	0.05			6	22.2	0.3	0.0	0.1	0.3	0.0	11.1	55.6	-0.38	-0.19	0.57
Campanula scheuchzeri										0.01	0.001	0.001	0.001	0.001			0.001	0.01			0.1		0.05	0.001	0.03			11	40.7	0.2	0.0	0.0	0.2	0.0	77.8	44.4	-0.59	0.53	0.05
Elyna myosuroides										10	8										3		4					4	14.8	25.0	0.0	0.0	25.0	0.0	0.0	44.4	-0.29	-0.29	0.59
Lloydia serotina																				0.5			0.01	0.01	0.001			4	14.8	0.5	0.0	0.0	0.5	0.0	0.0	44.4	-0.29	-0.29	0.59
Pedicularis rostratospicata ssp. helvetica																					1			5	5		0.5	4	14.8	11.5	0.0	0.0	11.5	0.0	0.0	44.4	-0.29	-0.29	0.59
Androsace obtusifolia		0.001																	0.001	0.001					0.001			4	14.8	0.0	0.0	0.0	0.0	11.1	0.0	33.3	-0.07	-0.29	0.37
Primula integrifolia													0.01						0.01	0.3								4	14.8	0.4	0.0	0.0	0.4	11.1	0.0	33.3	-0.07	-0.29	0.37
Gentiana brachyphylla															0.01						0.1			0.01	0.01			4	14.8	0.1	0.0	0.0	0.1	0.0	11.1	33.3	-0.29	-0.07	0.37
Plantago alpina				0.3			2	1	2							1					2						0.1	7	25.9	8.4	5.3	1.0	2.1	44.4	11.1	22.2	0.30	-0.24	-0.06
Gnaphalium norvegicum						0.001	0.01		0.001		0.2				0.04	0.1					0.04			2				8	29.6	2.4	0.0	0.3	2.0	33.3	33.3	22.2	0.06	0.06	-0.11
Gentiana acaulis										0.04			0.1											0.1			0.1	4	14.8	0.3	0.0	0.1	0.2	0.0	22.2	22.2	-0.29	0.15	0.15
Primula glutinosa																	0.1				0.3			0.8				3	11.1	1.2	0.0	0.1	1.1	0.0	11.1	22.2	-0.25	0.00	0.25
Saxifraga bryoides																	0.05							0.05	0.1			3	11.1	0.2	0.0	0.1	0.2	0.0	11.1	22.2	-0.25	0.00	0.25
Silene acaulis															0.05						2			0.5				3	11.1	2.6	0.0	0.1	2.5	0.0	11.1	22.2	-0.25	0.00	0.25
Phleum rhaeticum	20		5				1	15																	1			5	18.5	42.0	41.0	0.0	1.0	44.4	0.0	11.1	0.47	-0.34	-0.13
Arabis caerulea	0.01	1	0.05										0.01	0.001										0.001				7	25.9	1.1	1.1	0.0	0.0	33.3	33.3	11.1	0.12	0.12	-0.24
Draba hoppeana	0.001	0.03	0.01											0.001									0.001					4	14.8	0.0	0.0	0.0	0.0	33.3	0.0	11.1	0.37	-0.29	-0.07
Silene vulgaris	0.05					1																	0.05					3	11.1	1.1	1.1	0.0	0.0	22.2	0.0	11.1	0.25	-0.25	0.00
Veronica alpina			0.01							0.01			0.001	0.01	0.01										0.01			6	22.2	0.1	0.0	0.0	0.0	11.1	44.4	11.1	-0.19	0.38	-0.19
Sibbaldia procumbens								0.01					0.001				0.01					0.01						4	14.8	0.0	0.0	0.0	0.0	0.0	22.2	11.1	-0.07	0.15	-0.07
Juncus jacquinii										0.1			0.01	0.01	0.01				0.03									5	18.5	0.2	0.0	0.1	0.0	0.0	44.4	11.1	-0.34	0.47	-0.13
Lotus corniculatus aggr.												0.05			0.05		0.001								0.5			4	14.8	0.6	0.0	0.1	0.5	0.0	33.3	11.1	-0.29	0.37	-0.07
Salix reticulata														0.05				0.03	0.01									3	11.1	0.1	0.0	0.1	0.0	0.0	22.2	11.1	-0.25	0.25	0.00
Veronica bellidioides										0.01														0.01				2	7.4	0.0	0.0	0.0	0.0	0.0	11.1	11.1	-0.20	0.10	0.10
Gentiana verna												0.05												0.01				2	7.4	0.1	0.0	0.1	0.0	0.0	11.1	11.1	-0.20	0.10	0.10
Salix serpillifolia												0.05										10						2	7.4	10.1	0.0	0.1	10.0	0.0	11.1	11.1	-0.20	0.10	0.10
Botrychium lunaria												0.001												0.01				2	7.4	0.0	0.0	0.0	0.0	0.0	11.1	11.1	-0.20	0.10	0.10
Nardus stricta																			20									1	3.7	20.0	0.0	0.0	20.0	0.0	0.0	11.1	-0.14	-0.14	0.28
Saussurea alpina																								0.5				1	3.7	0.5	0.0	0.0	0.5	0.0	0.0	11.1	-0.14	-0.14	0.28
Anthyllis vulneraria ssp. carpatica																								0.1				1	3.7	0.1	0.0	0.0	0.1	0.0	0.0	11.1	-0.14	-0.14	0.28
Saxifraga oppositifolia																								0.1				1	3.7	0.1	0.0	0.0	0.1	0.0	0.0	11.1	-0.14	-0.14	0.28
Saxifraga paniculata																									0.05			1	3.7	0.1	0.0	0.0	0.1	0.0	0.0	11.1	-0.14	-0.14	0.28
Polygala alpina																									0.05			1	3.7	0.1	0.0	0.0	0.1	0.0	0.0	11.1	-0.14	-0.14	0.28
Minuartia sedoides																									0.03			1	3.7	0.0	0.0	0.0	0.0	0.0	0.0	11.1	-0.14	-0.14	0.28
Rhododendron ferrugineum																									0.01			1	3.7	0.0	0.0	0.0	0.0	0.0	0.0	11.1	-0.14	-0.14	0.28
Arnica montana																											0.3	1	3.7	0.3	0.0	0.0	0.3	0.0	0.0	11.1	-0.14	-0.14	0.28
Achillea millefolium aggr.	0.5	1	2	3	0.5	2	15	3	5			0.5	0.5	0.05			0.5											13	48.1	33.6	32.0	1.6	0.0	100.0	44.4	0.0	0.73	-0.05	-0.68
Leucanthemum	0.3	0.05	0.5	2	1	0.5	1	0.5	0.5	0.01							0.5	0.05										12	44.4	7.4	6.9	0.5	0.0	100.0	33.3	0.0	0.79	-0.16	-0.63
Phleum pratense				25	23	25	35	15							4													6	22.2	127.0	123.0	4.0	0.0	55.6	11.1	0.0	0.57	-0.19	-0.38
Sagina saginoides	0.05	0.01	0.03		0.01					0.5	0.1	0.05	0.01	0.01			0.01	0.01										12	44.4	0.8	0.1	0.7	0.0	44.4	88.9	0.0	0.00	0.63	-0.63
Taraxacum		0.03			0.1	0.1			0.1	0.1				0.03	0.05	0.01		0.1										8	29.6	0.5	0.3	0.2	0.0	44.4	44.4	0.0	0.23	0.23	-0.46
Trifolium pallescens	0.001		2			0.03				10	10	2	4	0.3	0.1	3	3	7										12	44.4	41.4	2.0	39.4	0.0	33.3	100.0	0.0	-0.16	0.79	-0.63
Plantago serpentina	0.3				0.1	0.01																						3	11.1	0.4	0.4	0.0	0.0	33.3	0.0	0.0	0.50	-0.25	-0.25
Agrostis schraderiana						5					0.05				5	0.1	0.1	0.01										6	22.2	10.3	5.0	5.3	0.0	11.1	55.6	0.0	-0.19	0.57	-0.38
Tussilago farfara				0.5													0.05											2	7.4	0.6	0.5	0.1	0.0	11.1	11.1	0.0	0.10	0.10	-0.20
Poa annua				5																								1	3.7	5.0	5.0	0.0	0.0	11.1	0.0	0.0	0.28	-0.14	-0.14
Luzula multiflora aggr.																		0.05										1	3.7	0.1	0.1	0.0	0.0	0.0	11.1	0.0	0.28	-0.14	-0.14
Trifolium alpinum																		0.01										1	3.7	0.0	0.0	0.0	0.0	11.1	0.0	0.0	0.28	-0.14	-0.14
Trifolium thalii															0.05	2	1	10										4	14.8	13.1	0.0	13.1	0.0	0.0	44.4	0.0	-0.25	0.59	-0.29
Salix foetida										0.3				0.5	0.03													3	11.1	0.8	0.0	0.8	0.0	0.0	33.3	0.0	-0.25	0.50	-0.25
Cirsium spinosissimum													0.1		10	0.1												3	11.1	10.2	0.0	10.2	0.0	0.0	33.3	0.0	-0.25	0.50	-0.25
Epilobium angustifolium														0.05	0.1	3												3	11.1	3.2	0.0	3.2	0.0	0.0	33.3	0.0	-0.25	0.50	-0.25
Plantago atrata													0.05				0.01											2	7.4	0.1	0.0	0.1	0.0	0.0	22.2	0.0	-0.20	0.40	-0.20
Salix helvetica										0.3																		1	3.7	0.3	0.0	0.3	0.0	0.0	11.1	0.0	-0.14	0.28	-0.14
Sedum montanum														0.01														1	3.7	0.0	0.0	0.0	0.0	0.0	11.1	0.0	-0.14	0.28	-0.14
Aster alpinus													0.05															1	3.7	0.1	0.0	0.1	0.0	0.0	11.1	0.0	-0.14	0.28	-0.14
Alchemilla vulgaris aggr.															0.05													1	3.7	0.1	0.0	0.1	0.0	0.0	11.1	0.0	-0.14	0.28	-0.14
Festuca pratensis																0.05												1	3.7	0.1	0.0	0.1	0.0	0.0	11.1	0.0	-0.14	0.28	-0.14
Trifolium badium																	0.05											1	3.7	0.1	0.0	0.1	0.0	0.0	11.1	0.0	-0.14	0.28	-0.14
Trifolium pratense ssp. nivale																		0.05										1	3.7	0.1	0.0	0.1	0.0	0.0	11.1	0.0	-0.14	0.28	-0.14
Salix																		0.01										1	3.7	0.0	0.0	0.0	0.0	0.0	11.1	0.0	-0.14	0.28	-0.14
Species richness	14	10	16	11	12	22	15	8	22	28	21	28	26	30	18	15	23	20	24	26	25	24	36	36	36	21	28												
Total Vegetation cover	62.21	44.09	35.45	67.5	46.33	72.86	100.6	32.01	66.33	27.06	27.05	15.2	30.25	52.78	21.63	30.4	30.9	38.25	96.48	78.71	90.25	97.61	87.14	89.09	89.99	71.32	80.3												

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Supplement E2.1. Header data of all 27 plots: Coordinates and spatial context.

Anhang E2.1. Kopfdaten aller 27 Plots: Koordinaten und räumlicher Bezug.

id	municipality	date	x	y	geometry	altitude_gps	locality_descript	plot_name	surface	plot_form	remark
1	Silvaplana	12.07.2021	9.80724044	46.42752094	POINT(9.8072	2545	Unter erster Schneelanze von oben	Seed.1	10	round	Kiesig, lückig
2	Silvaplana	12.07.2021	9.80720926	46.42771483	POINT(9.8072	2541	Unterhalb Station, zwischen 1. und 2. Masten	Seed.2	10	round	Beschneiungsleitung
3	Silvaplana	12.07.2021	9.80713047	46.42806332	POINT(9.807	2534	Vor Schneekanone, zwischen 2. und 3. Masten von oben	Seed.3	10	round	Beschneiungsleitung, lückig
4	Silvaplana	14.07.2021	9.80711505	46.42838338	POINT(9.807	2533	Beschneiungsleitung, zw. 2. und 3. Masten von oben, unterhalb S	Seed.4	10	round	Viel Streu
5	Silvaplana	14.07.2021	9.80717473	46.42898514	POINT(9.807	2524	Neben Weg, zw. 2. und 3. Masten von oben	Seed.5	10	round	Viel Streu
6	Silvaplana	14.07.2021	9.80728226	46.42925959	POINT(9.8072	2520	Neben Weg, zw. 2. und 3. Masten von oben	Seed.6	10	round	Viel Streu
7	Silvaplana	16.07.2021	9.80717573	46.42961324	POINT(9.807	2510	Westlich 3. Masten von oben, neben Schachtdeckel	Seed.7	10	round	Beschneiungsleitung, viel Streu
8	Silvaplana	16.07.2021	9.80714221	46.42980759	POINT(9.807	2510	Unterhalb Weg auf Höhe des 3. Masten	Seed.8	10	round	Beschneiungsleitung, viel Streu
9	Silvaplana	16.07.2021	9.8071982	46.43009344	POINT(9.807	2502	Etwas unterhalb 3. Masten und Weg bei Schachtdeckel	Seed.9	10	round	Beschneiungsleitung, viel Streu
10	Silvaplana	12.07.2021	9.8076022	46.42740862	POINT(9.8076	2549	Altes Trassee, unter neuer Liftstation	Turf.1	10	round	Lückig mit Ziegel
11	Silvaplana	12.07.2021	9.80773229	46.42771367	POINT(9.807	2550	Altes Trassee	Turf.2	10	round	Steinig, lückig
12	Silvaplana	12.07.2021	9.8078611	46.42804931	POINT(9.8078	2538	Altes Trassee, zwischen 2. und 3. Masten von oben	Turf.3	10	round	Steinig, lückig
13	Silvaplana	14.07.2021	9.80793245	46.42830689	POINT(9.8079	2535	Altes Trassee, zw. 1. und 2. Masten	Turf.4	10	round	Steinig, lückig
14	Silvaplana	14.07.2021	9.8080213	46.42849199	POINT(9.8080	2529	Altes Trassee, zw. 1. und 2. Masten von oben	Turf.5	10	round	Steinig, lückig
15	Silvaplana	14.07.2021	9.80811652	46.42881021	POINT(9.808	2525	Altes Trassee, zw. 2. und 3. Masten von oben	Turf.6	10	round	Steinig, lückig
16	Silvaplana	16.07.2021	9.80826505	46.42916747	POINT(9.8082	2519	Altes Trassee, zw. 2. und 3. Masten von oben	Turf.7	10	round	Steinig, lückig
17	Silvaplana	16.07.2021	9.80830025	46.42944455	POINT(9.8083	2518	Altes Trassee, zw. 2. und 3. Masten von oben	Turf.8	10	round	Lückig
18	Silvaplana	16.07.2021	9.80836596	46.42967702	POINT(9.8083	2513	Altes Trassee, etwas oberhalb 3. Masten von oben	Turf.9	10	round	Steinig, lückig
19	Silvaplana	12.07.2021	9.80810847	46.42741371	POINT(9.808	2556	Östlich altem Trassee, zwischen 1. und 2. Masten von oben	Ref.1	10	round	Weidecharakter
20	Silvaplana	12.07.2021	9.80785567	46.42767831	POINT(9.8078	2550	Neben altem Trassee, zwischen 1. und 2. Masten von oben	Ref.2	10	round	Leicht windkuppig
21	Silvaplana	12.07.2021	9.80799146	46.42813218	POINT(9.8079	2538	Östlich vom alten Trassee, zwischen 2. und 3. Masten von oben	Ref.3	10	round	Leicht windkuppig
22	Silvaplana	14.07.2021	9.80817787	46.42828401	POINT(9.808	2534	Östlich altem Trassee, zw. 2. und 3. Masten von oben	Ref.4	10	round	Weidecharakter
23	Silvaplana	14.07.2021	9.808143	46.4285641	POINT(9.808	2529	Östlich altem Trassee, zw. 1. und 2. Masten von oben	Ref.5	10	round	Weidecharakter, felsig
24	Silvaplana	14.07.2021	9.80829991	46.42883401	POINT(9.8082	2525	Östlich altem Trassee, zw. 2. und 3. Masten von oben	Ref.6	10	round	Weidecharakter
25	Silvaplana	16.07.2021	9.80833612	46.42903298	POINT(9.8083	2521	Östlich altem Trassee, mittig zw. 2. und 3. Masten von oben	Ref.7	10	round	Weidecharakter
26	Silvaplana	16.07.2021	9.80882932	46.42941127	POINT(9.8088	2514	Östlich altem Trassee, zwischen Felsen, oberhalb 3. Masten von	Ref.8	10	round	Felsig
27	Silvaplana	16.07.2021	9.80867576	46.42982815	POINT(9.808	2510	Östlich altem Trassee, leicht unterhalb 3. Masten von oben, felsig	Ref.9	10	round	Felsig, Weidecharakter

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Supplement E2.2. Header data of all 27 plots: Environmental parameters.

Anhang E2.2. Kopfdaten aller 27 Plots: Umweltparameter.

id	plot_name	species_number	Shannon	total_cover	trees_cover	bushes_cover	herbaceous_height	herbaceous_cover	crypto_cover	litter_cover	stones_cover	gravel_cover	fine_soil_cover	soil_depth_mean	pH_mean	tivity_mean
1	Seed.1	14	1.2	60	0	0	12	55	5	40	30	60	10	9	6.4	155
2	Seed.2	10	0.8	45	0	0	20	45	2	5	50	40	10	13	6.7	122
3	Seed.3	16	1.4	35	0	0	16	35	1	8	30	60	10	11	6.9	138
4	Seed.4	11	1.8	95	0	0	11	95	2	60	30	20	50	7	5.3	216
5	Seed.5	12	1.1	45	0	0	12	45	1	40	35	40	25	8	5.1	154
6	Seed.6	22	1.6	65	0	0	13	65	1	35	1	4	95	11	5.0	153
7	Seed.7	15	1.3	85	0	0	9	85	3	50	10	30	60	9	6.0	189
8	Seed.8	8	1.4	30	0	0	5	50	1	60	30	20	50	7	6.3	111
9	Seed.9	22	2.0	65	0	0	21	65	3	15	15	10	65	11	4.1	124
10	Turf.1	28	1.3	25	0	0	22	25	10	0.5	40	30	30	9	4.1	127
11	Turf.2	21	1.1	25	0	0	20	25	8	0.3	50	15	35	10	4.4	145
12	Turf.3	28	1.8	10	0	0	24	10	3	0.5	40	20	40	8	4.3	131
13	Turf.4	26	0.7	30	0	0	13	30	10	0.01	35	30	35	11	5.6	219
14	Turf.5	30	1.9	50	0	0	35	50	10	3	25	5	70	9	6.2	168
15	Turf.6	18	1.1	20	0	0	23	20	1	0.01	25	25	50	10	6.5	187
16	Turf.7	15	1.1	30	0	0	8	30	1	0.001	25	5	70	9	6.7	187
17	Turf.8	23	1.4	30	0	0	13	30	1	0.001	2	3	95	9	4.8	131
18	Turf.9	20	1.6	35	0	0	15	35	1	0.01	15	15	70	7	6.4	146
19	Ref.1	24	2.2	80	0	0	19	80	25	0.5	5	1	94	22	3.5	346
20	Ref.2	26	1.6	75	0	0	15	75	60	1	25	1	74	14	5.5	278
21	Ref.3	25	2.1	75	0	0	17	75	70	0.05	15	2	83	18	3.5	250
22	Ref.4	24	2.5	85	0	0	27	85	70	0.5	10	5	85	16	4.0	232
23	Ref.5	36	2.7	65	0	0	29	65	50	1	35	2	63	16	5.5	372
24	Ref.6	36	2.2	85	0	0	31	85	70	0.5	5	5	90	17	4.5	260
25	Ref.7	36	2.5	80	0	0	24	80	65	0.5	5	0	95	24	4.6	267
26	Ref.8	21	2.0	70	0	0	24	70	80	0.5	15	1	84	17	3.4	325
27	Ref.9	28	1.6	70	0	0	22	70	75	0.05	25	1	74	20	3.5	304

Supplement E2.3. Header data of all 27 plots: Weighted indicator values and soil data.

Anhang E2.3. Kopfdaten aller 27 Plots: Gewichtete Zeigerwerte und Bodendaten.

id	plot_name	Corg	Ctot [%]	Htot [%]	Ntot[%]	Corg/Ntot	Cmic eff	orientation [°]	slope [°]	litter_cover_I	soil_cover_I	rocks_cover_I	water_cover_I	gew.Feuchte	gew.Licht.Z	gew.Reaktion	gew.Humus.Z	gew.Nutrient.	gew.Kont.Z	gew.Temp.Z	gew.Durchluft.
1	Seed.1	1.020	2.460	0.715	0.241	4.2	111	341	11	40	30	30	0	3	4	3	3	4	3	2	3
2	Seed.2	0.506	1.315	0.672	0.151	3.4	92	352	18	5	25	50	0	4	4	3	3	4	3	1	3
3	Seed.3	0.795	2.654	0.715	0.507	1.6	167	355	9	8	30	30	0	3	4	3	3	4	3	3	2
4	Seed.4	8.935	5.575	1.215	0.480	18.6	1645	353	16	60	35	30	0	3	4	3	3	4	3	3	3
5	Seed.5	2.593	2.950	0.882	0.404	6.4	433	353	14	40	15	35	0	3	4	3	3	4	3	3	3
6	Seed.6	2.419	2.830	0.946	0.288	8.4	687	348	18	35	10	1	0	3	4	3	3	4	3	3	3
7	Seed.7	1.622	1.935	0.806	0.237	6.8	549	350	13	50	5	10	0	3	4	3	3	4	3	3	3
8	Seed.8	2.430	2.965	0.894	0.285	8.5	401	345	12	60	20	30	0	3	4	3	3	4	3	3	3
9	Seed.9	2.247	2.590	0.925	0.312	7.2	533	334	14	15	3	15	0	3	4	3	3	3	3	2	3
10	Turf.1	2.689	3.015	1.100	0.338	8.0	319	21	19	1	20	40	0	3	4	3	2	3	3	2	4
11	Turf.2	3.277	3.615	1.120	0.376	8.7	421	20	16	1	50	50	0	3	4	3	2	3	3	2	4
12	Turf.3	2.231	2.605	0.965	0.334	6.7	480	11	15	1	40	40	0	3	4	3	3	3	3	2	3
13	Turf.4	3.505	3.955	1.025	0.336	10.4	770	11	16	0	40	35	0	3	4	3	3	4	3	2	3
14	Turf.5	1.489	2.060	0.846	0.249	6.0	292	4	19	3	30	25	0	3	4	3	4	3	3	2	3
15	Turf.6	1.395	1.960	0.819	0.229	6.1	273	9	7	0	70	25	0	3	4	3	3	4	3	2	3
16	Turf.7	2.072	2.790	0.853	0.234	8.9	479	11	14	0	30	25	0	3	4	3	3	3	3	2	3
17	Turf.8	2.864	3.250	0.957	0.269	10.7	641	15	7	0	65	2	0	3	4	3	3	3	3	2	3
18	Turf.9	0.919	2.780	0.721	0.212	4.3	240	5	4	0	70	15	0	3	4	3	3	3	3	2	3
19	Ref.1	13.970	14.150	2.425	0.964	14.5	4044	3	1	1	15	5	0	3	4	2	3	2	3	2	3
20	Ref.2	7.537	7.810	1.515	0.631	11.9	1951	352	25	1	8	25	0	2	5	3	4	1	4	1	4
21	Ref.3	6.117	6.385	1.460	0.473	12.9	1574	348	12	1	1	15	0	3	4	2	4	2	3	2	3
22	Ref.4	7.121	7.300	1.485	0.619	11.5	1993	18	26	1	0	10	0	3	4	2	3	2	3	2	3
23	Ref.5	10.705	10.900	1.820	0.825	13.0	2182	4	22	1	1	35	0	3	4	2	4	3	3	1	3
24	Ref.6	6.046	6.295	1.330	0.539	11.2	1503	18	4	0	1	5	0	3	4	2	3	3	3	2	3
25	Ref.7	7.131	7.760	1.475	0.600	11.9	2139	11	11	0	3	5	0	3	4	3	4	2	3	2	3
26	Ref.8	10.710	11.100	1.985	0.777	13.8	1944	75	4	0	5	15	0	3	4	2	4	2	2	1	2
27	Ref.9	9.020	9.365	1.915	0.661	13.6	2825	4	5	0	5	25	0	3	4	2	4	2	2	1	1

Supplement E3. Candidate linear models ranked by AICc for plant diversity (Shannon index). Shown are model id, *df*, logLik, AICc, ΔAICc, and Akaike weight. Models within ΔAICc < 2 were treated as similarly supported; the parsimonious additive model was retained for inference.

Anhang E3. Kandidatenmodelle der linearen Regression sortiert nach AICc für Pflanzenvielfalt (Shannon-Index). Dargestellt sind ModellID, *df*, logLik, AICc, ΔAICc und Akaike-Gewicht. Modelle innerhalb von ΔAICc < 2 wurden als ähnlich unterstützt behandelt; das parsimonische additive Modell wurde für die Inferenz beibehalten.

Model ID	*df*	logLik	AICc	delta	weight
138	5	-5.577	24.010	0.000	0.08745
12	5	-6.094	25.046	1.036	0.05210
74	6	-4.739	25.679	1.668	0.03797
76	6	-4.739	25.679	1.668	0.03797
142	6	-4.769	25.739	1.729	0.03685

Supplement E4: Final linear model for plant diversity (Shannon-index) in the collected data set. Ordinary least squares coefficients (±SE), classical t statistics and p values, plus HC3 heteroskedasticity-robust SE and tests. P values are reported descriptively; primary inference follows an AICc information-theoretic framework.

Anhang E4: Finales lineares Modell für Pflanzenvielfalt (Shannon-Index) im erhobenen Datenset. Koeffizienten der OLS (±SE), klassische t-Statistiken und p-Werte sowie robuste HC3 SE und Tests. P-Werte werden deskriptiv angegeben; die primäre Inferenz folgt einem informationstheoretischen AICc-Rahmen.

Term	Estimate	SE	t-value	p-value	SE HC3	t HC3	p HC3
Intercept	1.574	0.267	5.894	0.000	0.311	5.056	0.000
Vegetation cover	0.008	0.003	2.610	0.015	0.004	2.241	0.035
√Gravel cover	-0.118	0.035	-3.338	0.003	0.037	-3.223	0.004

Supplement E5. Results of fitting environmental variables to the NMDS ordination. Shown are variable, applied transformation, correlation (r) and coefficient of determination (R^2), raw p and BH-adjusted p ($p_{(BH)}$). Variables in bold type are shown in the main figure.

Anhang E5. Ergebnisse der Anpassung von Umweltvariablen an die NMDS-Ordination. Aufgeführt sind Variablenname (englische Bezeichnung), angewandte Transformation, Korrelation (r) und Bestimmtheitsmaß (R^2), Roh-p und BH-korrigiertes p ($p_{(BH)}$). Fettgedruckte Variablen sind in der Hauptabbildung dargestellt.

Environmental Variable	Transformation	r	R^2	p	p_{BH}
Total H	log-transformed	0.7428	0.5517	0.0001	0.0003
Total C	log-transformed	0.6998	0.4897	0.0001	0.0003
Organic C	log-transformed	0.6827	0.4661	0.0001	0.0003
Cryptogam cover (%)	square root	0.6798	0.4622	0.0001	0.0003
Microbial Biomass	log-transformed	0.6787	0.4606	0.0001	0.0003
Soil pH	**not transformed**	**0.6386**	**0.4079**	**0.0001**	**0.0003**
Total N	log-transformed	0.6104	0.3726	0.0001	0.0003
Soil depth (cm)	**log-transformed**	**0.5942**	**0.3531**	**0.0001**	**0.0003**
Shannon Diversity	not transformed	0.4750	0.2256	0.0007	0.0016
Gravel cover (%)	**square root**	**0.4590**	**0.2106**	**0.0010**	**0.0020**
Fine soil cover (%)	square root	0.4091	0.1674	0.0021	0.0035
Conductivity (u/cm)	log-transformed	0.4085	0.1669	0.0021	0.0035
Species richness	not transformed	0.3059	0.0936	0.0137	0.0211
Herb cover (%)	square root	0.2833	0.0802	0.0192	0.0274
Total vegetation cover (%)	**square root**	**0.2793**	**0.0780**	**0.0216**	**0.0283**
Rock/stone cover (%)	square root	0.2732	0.0747	0.0226	0.0283
Herb height (cm)	log-transformed	0.2243	0.0503	0.0473	0.0556
Litter cover (%)	square root	0.2162	0.0468	0.0569	0.0632
Tree cover (%)	square root	0	0	1	1
Shrub cover (%)	square root	0	0	1	1