Quantification of biogeomorphic interactions between small-scale sediment transport and primary vegetation succession on proglacial slopes of the Gepatschferner, Austria

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Abstract
Proglacial slopes provide suitable conditions for observing the co-development of abiotic and biotic systems. The frequency and magnitude of geomorphic processes and plant composition govern this interplay, which is described in the model of biogeomorphic succession. In high mountain environments, this model has only been tested in a limited number of studies. The study aimed to quantify small-scale sediment transport via erosion plots along a plant cover gradient and to investigate the influence of sediment transport on plant communities. We aimed to generate quantitative data to test existing biogeomorphic models. Small-scale biogeomorphic interactions were investigated on 30 test plots of 2 × 3 m size on proglacial slopes of the Gepatschferner (Kaunertal) in the Austrian Alps during the snow-free summer months over three consecutive years. The experimental plots were established on slopes along a plant cover gradient. A detailed vegetation survey was carried out to capture biotic conditions, and specific sediment yield was measured at each plot. Species abundance and composition at each site reflected successional stages. Additional environmental parameters, such as terrain age, geomorphometry, grain size distribution, soil nutrients, and precipitation, were also included in the analyses. We observed two pronounced declines in geomorphic activity on plots with both above 30% and above 75% plant cover. Nonmetric multidimensional scaling showed distinct clusters of vegetation composition that mainly followed a successional gradient. Sites that were affected by high-magnitude geomorphic events showed different environmental conditions and species communities. Quantified process rates and observed species composition support the concept of biogeomorphic succession. The findings help to narrow down a biogeomorphic feedback window.

KEYWORDS
biogeomorphic succession, disturbance, erosion, primary succession, proglacial, sediment transport

1 | INTRODUCTION

Mountain landscapes are particularly prone to hydro-meteorological processes leading to high erosion rates and the formation of geomorphic hazards such as debris flows, floods, and landslides (Korup & Clague, 2009). Slope degradation and sediment output significantly affect downstream river systems and infrastructure (Lane et al., 2017). Biotic processes, in particular vegetation development,
have the ability to stabilize steep mountainous slopes (Dietrich & Perron, 2006). Increased vegetation cover affects slope stability by altering the hydrological regime (Moreau et al., 2008; Burolo et al., 2011) as plants modify soil moisture through interception loss and transpiration (Körner, 2003). Material detachment and transport are reduced due to a decrease in two parameters: (I) the kinetic energy of raindrops (Isselin-Nondedeu & Bédécarrats, 2007) and (II) transport energy by overland flow (Gurnell, 1997; Styczen & Morgan, 2003). Root density, branching, length, and volume also increase soil cohesion and leave soils less vulnerable to erosion processes (Graf et al., 2009; Fattet et al., 2011; Ghemst et al., 2013).

To utilize the stabilizing effect of vegetation, it is important to understand the interactions of biotic and abiotic processes. The expanding discipline of biogeomorphology is focused on the linkage of ecological and geomorphical processes and has the potential to provide knowledge for the application of Nature-based solutions in environmental management (Coombes, 2016; Larsen et al., 2020).

Several scholars (Corenblit et al., 2011; Rice et al., 2012; Steiger & Corenblit, 2012; Balke et al., 2014; Eichel et al., 2016; Schwarz et al., 2018; Stallins & Corenblit, 2018) have investigated the interacting development of abiotic and biotic systems and introduced conceptual approaches to describe the relationship of the abiotic–biotic feedback mechanism. The geoeocological model by Matthews (1992) highlighted a decrease in the relative importance of abiotic processes with a concurrent increase in the relative importance of biotic parameters over time. Corenblit et al. (2007b) focused on bidirectional interactions of abiotic and biotic parameters and introduced the conceptual model of “fluvial biogeomorphological succession,” which describes the connected evolution of river landforms and associated vegetation communities over time. The starting point is a highly dynamic geomorphic system (geomorphic stage) in which the morphodynamics determines the establishment of pioneer species (pioneer stage, Corenblit et al., 2007a, 2007b). Over time, ecosystem engineers establish and can modify, maintain, and create habitats for other species through interventions in the abiotic environment (biogeomorphic stage; Corenblit et al., 2015; Jones, 2012). As soon as a stability threshold is reached, abiotic processes decrease significantly (Eichel et al., 2016), after which biotic interactions start to dominate at late successional stages (ecologic stage: Corenblit et al., 2011).

Eichel et al. (2013), Eichel et al., (2016), and Eichel et al., (2018) were the first researchers to apply these conceptual ideas to high mountain environments. Proglacial landforms help us observe initial conditions for vegetation development in a highly active geomorphic surrounding on different scales (Matthews, 1992; Reinhardt et al., 2010) and to observe different stages of biogeomorphic succession (Eichel et al., 2013). After glacier recession, increased sediment reworking by slope processes (Curry et al., 2006; Drebing & Eichel, 2018; Eichel et al., 2018) and high sediment yields (Lane et al., 2017) can be observed, processes also referred to as para-glacial adjustment (Ballantyne, 2002). Several years after glacier retreat, vegetation develops and plant cover increases over time (Erschbamer et al., 2008; Robbins & Matthews, 2009; Matthews & Vater, 2015; Schumann et al., 2016). Eichel et al., (2016) narrowed down biogeomorphological interactions that stabilize slopes in the concept of “biogeomorphic feedback windows.” Within this concept, biogeomorphic interactions occur in a specific “envelope of conditions” that is determined by species traits in addition to the frequency and magnitude of geomorphic events (Eichel et al., 2016).

To transfer such conceptual knowledge into applicable management recommendations, one has to test these biogeomorphological models and see what generalized guidelines and thresholds can be deducted. Quantitative data concerning biotic and abiotic process rates allow for testing the concept of biogeomorphic succession (Corenblit et al., 2007a) and identifying drivers of biogeomorphic feedback mechanisms (Eichel et al., 2016) and the conditions under which these occur. Hence, this study aimed to explore the statistical relationship and development of biotic and abiotic variables by measuring rates of specific sediment yield (SSY) along a plant cover gradient on alpine slopes in the Austrian Alps. We aimed to answer several questions:

1. How does increasing plant cover influence SSY?
2. Is species community composition influenced by sediment transport?
3. Do observed rates of SSY and species community data along a plant cover gradient support the existing models of biogeomorphic succession and/or the biogeomorphic feedback window?

2 | STUDY AREA

The Gepatschferner in the upper Kaunertal is located in the crystalline Central Eastern Alps (Figure 1a). This is a showcase environment for the investigation of biogeomorphic interactions as the retreating glacier and highly active slope processes provide the grounds for different stages of ecological succession and promote high rates of sediment reworking within the proglacial deposits (Cavalli et al., 2019; Hilger et al., 2019; Morche et al., 2019; Vehling et al., 2019; Dusik, Leopold et al., 2019). The catchment is located at an altitude range of 2,000 to 2,800 m a.s.l. just above the local tree line (Figure 1b). The climate is representative of the dry Central Alpine region, with mean annual precipitation of 1,000 to 1,300 mm and mean annual air temperature of −0.17°C (Weißsee meteorological station, 2,470 m a.s.l.; 2007–2018; data courtesy of Tiroler Wasserkraft AG [TIWAG]). The Gepatschferner has lost more than 3 km in length due to rising temperatures since the end of the Little Ice Age (LIA, considered to be around 1850). Glacial melt has increased since 2000, with a mean annual retreat rate of 51 m (Lieb & Kellerer-Pirklbauer, 2019). Within the area of the LIA glacier extent (Figure 1c and d), there is a large amount of unconsolidated sediments (moraines, talus cones, and glaciofluvial deposits). Outside the LIA moraines, shallow landslides create patches of bare ground with loose sediment within the vegetation-covered slopes. Glaciogenic sediments are mainly derived from the predominant lithology that is para- and orthogneiss (Hammer, 1923). Slope wash, gully erosion, and debris flows are the main processes that transport these glacial sediments to the Fagge channel system (Morche et al., 2019), and paraglacial adjustment of the slopes is still ongoing (Dusik et al., 2019). Only about 4% of all sediment moving in the study area actually reaches the outlet (Hilger et al., 2019), indicating poor hillslope-channel coupling. Extreme precipitation events during summer play a dominant role in the morphodynamics, followed by temperature- and moisture-induced
snow slides during winter, whereas springtime offers important preparatory conditions for sediment transport as moraine material is softened through infiltration of snowmelt and precipitation (Dusik, Leopold, et al., 2019). Periglacial processes, namely thermokarst, permafrost creep, and thermal-contraction cracks, do occur in the valley. However, no obvious periglacial processes were observed in and around the test sites. This finding is in line with the permafrost map of Dusik, Leopold, et al. (2019), Dusik, Neugirg, et al. (2019). According to Temme et al., (2016), predominant soils are Leptosols in recently deglaciated locations and a mix of Regosols and Cambisols in locations that are deglaciated for longer time. Parts of the proglacial slopes are seasonally used as mountain pasture. Around 100 cows graze during summertime on the orographic left side of the Fagge River.

3 METHODS

We selected 10 sites with three plots each on drift mantled slopes along a plant cover gradient, which was divided into six classes with 0% to 5% up to >75% vegetation cover. The first four classes have six plot replicates each, while the last two classes have three replicates each (Figure 2). The smaller classes and higher number of replicates correspond to our increase in focusing on areas with low to medium vegetation cover as these areas should be prone to erosion (Thornes, 2010) and biogeomorphic interactions should be high (Eichel et al., 2016). Three plots per site was a prerequisite for the underlying applied research project aiming at testing a microbe-assisted seed mixture to reduce erosion. Site selection was guided by field-based visible estimation of plant cover and according to several criteria: (I) mean slope angle of 30–35°, (II) planar surface composed of fine-grained sediment without large boulders or sinks, and (III) evenly distributed aspect and elevation classes. All plots at one site were in one cover class.

Each plot was 2 × 3 m, fenced in with metal plates, and equipped with a metal funnel to guide surface runoff and transport sediment into two 60-litre polyvinylchloride (PVC) buckets. Controlled slope length results in a decreased potential for overland flow; hence, only splash and interrill processes that occur under natural rainfall conditions were covered (Boix-Fayos et al., 2006). To prevent enhanced SSY rates due to artificial disturbances immediately after plot construction and after maintenance work (Boix-Fayos et al., 2006; Kinnell, 2016), we waited at least 1 month for the plot surface to recover before continuing to take measurements. With regard to Kinnell’s (2016) study, we ensured that surface water was able to flow freely and was not obstructed by plot equipment, especially at the transition from plot surface to metal funnel.

The erosion plots were operated in the snow-free months between July and October in 2018–2020. This period roughly constitutes the potential vegetation period in the study area (Nagl & Erschbamer, 2010). We collected eroded material after extracting the water from the bucket with a thin hose and after at least 24 h without rainfall to give suspended sediments enough time to settle down at the bottom of the bucket. One-hundred ninety-six sediment samples were obtained over the course of three consecutive years (Figure 3). Eroded sediments were dried at 105°C, and weighed until no weight fluctuations between two consecutive measurements occurred. The latter was derived from unmanned aerial vehicle-derived ortho-images. SSY rates were analyzed separately per plot, as we considered each fenced area to be independent from the others.

We carried out a vegetation survey of each plot during peak season for plant activity in August 2018. Recorded parameters included overall vegetation cover, cover of nonwoody forbs, graminoids, woody plants, and individual cover for every vascular

FIGURE 1 (a) Location of the study area in western Austria. (b) Distribution of the sites according to their respective plant cover class on proglacial slopes of the Gepatschnerferner including glacier extents for the years 1850, 1922, and 1971. Orographic (c) right and (d) left side of the valley respectively. Data source: Land Tirol - data.tirol.gv.at for orthoimages; glacier extents based on Hartl (2010)
plant species per plot. The visually estimated cover of a species was defined as the proportion of ground occupied by vertical projection expressed as a percentage where the maximum cover is 100%. Taxonomy of species is based on Fischer et al., (2005). Based on flora indicativa indicator values (Landolt et al., 2010), cover abundance for individual species was summed for six modes of vegetative dispersal (below-ground runners, tussocks, creeping shoots or espaliers, no vegetative dispersal parts, basal lateral shoots, and others) and three classes of successional strategies, that is competitive, stress tolerant, and ruderal (Grime, 1979). Using a similar approach to that applied for vegetation abundances, we determined the open soil ratio as the total plot area minus plant cover, the percentage of coarse gravel larger than 10 cm, and the percentage of moss.

To assess terrain ages, we reconstructed past glacier extents using historical aerial imagery, topographical maps, and existing glacier inventories. Grain size and soil nutrient contents, namely carbon (C), nitrogen (N), and sulfur (S), were determined from one mixed topsoil sample (~5 cm) per site. We performed the analysis of C, N, and S with a Vario Macro Elementar Analyzer with a catalytic tube combustion technique. Additionally, pH values were determined for each of the samples. Fractions of sand, silt, and clay were determined in the laboratory using a laser diffraction particle size distribution analyzer (Retsch La-950). A weather station providing precipitation data in 10-min intervals was installed at a maximum distance of 1.6 km from the measurement sites.

Analyses were conducted in R, and figures were produced using the ggplot2 package (Wickham, 2011). For the species abundance data and the environmental parameters, Moran’s I autocorrelation coefficient test (Moran, 1950) based on geographic distance between plots using the R package ape (1,000 permutational steps, Paradis & Schliep, 2019) was used. For initial data exploration, a Pearson correlation analysis was conducted, and hierarchical clustering (Ward.D2) was implemented, aiming at clustering parameters based on dissimilarities (see Supplements for results; Figure A1). The applied Ward.D2 algorithm minimizes the dissimilarities within clusters and maximizes the dissimilarities between them (Castro-Insua et al., 2018). A set of 28 abiotic and biotic parameters were investigated (Table 1). The Wilcoxon–Mann–Whitney test (Wilcoxon, 1945) with the R package ggpubr (Kassambara & Kassambara, 2020) highlighted differences in SSY between the six plant cover classes. To investigate dissimilarities of species communities, we adopted the approach of Eichel et al., (2016) and used nonmetric multidimensional scaling (NMDS) (Kruskal, 1964; Bray–Curtis dissimilarity) with a Wisconsin double standardization, a maximum number of 100 iterations to find a stable solution, and 1,000 permutations to test the significance of constraints. The two-dimensional NMDS was carried out using metaMDS.
| Category      | Parameter          | Entity                     | Method                      | Remark (including references where appropriate)                                                                                                                                                                                                 |
|--------------|--------------------|----------------------------|-----------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Abiotic      | SSY                | g m\(^{-2}\) month\(^{-1}\) | Erosion plot                | Metal-fenced erosion plots, 2 × 3 m, with metal funnels and 60-liter PVC buckets designed according to the suggestion of Konz et al., (2012), Kinnell (2016), Parsons (2019). Measured monthly for the 2018 - 2020 summer months (a total of 128 measurements) and corrected for exact number of days between consecutive measurements and exact area of each plot. |
| Biotic       | Plant cover (total)| %                          | Cover-abundance approach    | Abundance is the cover per species in percent, species nomenclature for vascular plants based on (Braun-Blanquet, 1932).                                                                                                                                                               |
|              | Species number     | Count                      | Cover-abundance approach    | Number of different species per plot                                                                                                                                                                                                                                                                   |
|              | Plant functional groups | %                       | Cover-abundance approach    | Moss, forbs, graminoids, woody                                                                                                                                                                                                                                                                        |
|              | Vegetative dispersal | %                          | Literature-based indicator values - *flora indicativa*  | Cover of every species with a certain lifeform is summed up; types: below-ground runners, tussocks, creeping shoots or espaliers, no vegetative dispersal parts, basal lateral shoots, other (Landolt et al., 2010)                                                                 |
| Further parameter | Slope/aspect/elevation | °/dimension-less/m.a.s.l. | GIS analyses                | Derived from a digital elevation model - 1 m (data source Land Tirol - data.tirol.gv.at)                                                                                                                                                     |
|              | Solar Radiation     | WH/m\(^{2}\)              | GIS analyses                | Topographic wetness index                                                                                                                                                                                                                                                                         |
|              | Wetness             | dimensionless              | GIS analyses                | Terrain age is determined by the time of last glacier cover                                                                                                                                                                                                                                           |
|              | Age                 | Years before present      | glacier retreat data        | Stones with a diameter > 10 cm                                                                                                                                                                                                                                                                      |
|              | Soil skeleton (>10 cm) | %                        | Field measurement           | Fraction (in %) of clay, silt, and sand                                                                                                                                                                                                                                                               |
|              | Grain size (topsoil) | %                          | Particle Sizer              | Carbon, nitrogen, sulfur                                                                                                                                                                                                                                                                            |
|              | pH                  |                             | Laboratory analyses - pH Meter | 10-minute interval since August 2018                                                                                                                                                                                                                                                                |
|              | Nutrients (topsoil) | %                          | Laboratory - Macro elemental analyzer | 10-minute interval since August 2018                                                                                                                                                                                                                                                                |
|              | Precipitation       | mm                         | Automated climate station  | 10-minute interval since August 2018                                                                                                                                                                                                                                                                |
in the R package vegan (Oksanen et al., 2007). Hierarchical clustering was used to identify groups of dissimilarities (Bray–Curtis) for the species communities. This identification was done with hclust in the R package cluster (Maechler et al., 2013) using the Ward.D2 option (Murtagh & Legendre, 2014). To determine the main factors influencing vegetation composition, we used a post hoc correlation (Envfit in R package vegan). The settings for the post hoc correlations included a maximum of 100 starts and again 1,000 permutations for calculating the coefficient of determination ($R^2$) and significance ($p$-value). Rates of SSY were included into the NMDS ordination using ordisurf in the R package vegan (Oksanen et al., 2007). Ordisurf uses a smoothed surface of an environmental variable to fit it to an ordination plot using penalized splines (Wood, 2003). Values for all environmental parameters on the plot and site levels are presented in the Supplementary Material (Supplementary Material, Table A2).

4 | RESULTS

4.1 | Temporal variability of SSY

The highest monthly sums and highest number of days with more than 10 mm of precipitation were observed for August in the three consecutive years. After breaking down the monthly measurements, the data showed a decrease in SSY with increasing plant cover for each individual month. Furthermore, we observed an interseasonal trend, with the highest rates of SSY occurring at the start of the season and decreasing rates occurring in August and September. A minimum of 0 g m$^{-2}$ month$^{-1}$ was measured during all three seasons for the highest plant cover class (>75%), and a maximum of 572.9 g m$^{-2}$ month$^{-1}$ was measured for the lowest plant cover class (0–5%) in July 2018. Mean rates of SSY for all plots were highest in July for the three consecutive years with 214, 192, and 106 g m$^{-2}$ month$^{-1}$ for July 2018, 2019, and 2020, respectively. Monthly rates of precipitation did not correlate with SSY.

4.2 | Variability of SSY along a plant cover gradient

Cumulated SSY per plant cover class for the whole measurement period showed a decrease of SSY with increasing plant cover class (Figure 4) but at the same time a mean species number increase indicating a parallel increase in community complexity. Both the SSY mean and variance within each class decreased along the plant cover gradient. Pairwise comparison of samples between the cover classes using the Wilcoxon–Mann–Whitney test showed two significant reduction steps in SSY: (I) between cover class 15–30% and 30–50% ($p < 0.001$; $W = 806$, $n_1 = 35$, $n_2 = 29$) and (II) between cover class 50–75% and >75% ($p < 0.001$; $W = 667$, $n_1 = 26$, $n_2 = 27$). No significant influence of aspect or elevation on rates of SSY could be detected.

4.3 | Changes in vegetation composition along a plant cover gradient

Among the first pioneer species within early plant cover classes (0–5% and 5–15%), we observed Agrostis capillaris, Agrostis rupestris, and Carex curvula. Within the intermediate classes (15–30% and 30–50%), early successional species such as Lotus alpinus, Achillea moschata, and Salix herbacea can be found. In the highest plant cover classes (50–75% and >75%) vegetation stratification increases, and shrub species, such as Rhododendron ferrugineum and Calluna vulgaris, and graminoids, such as Nardus stricta, take over. For detailed information on species present at each site, a sorted species list is available in the supplementary material (Supplementary Material, Table A3). The clustered distribution of the 30 plots with sets of three plots per sites led to a strong spatial signal in the variation of community dissimilarities as revealed by tests for spatial autocorrelation (Bray–Curtis, Moran’s I 0.46; $p < 0.001$). Therefore, we aggregated the vegetation data using mean values per site. All analyses, including vegetation data, were based on these merged abundance values. Results of the NMDS analysis (two-dimensional stress of 0.071) showed well-separated centroids (for example, mean of species abundances per site) for the 10 sites (Figure 5). An additional hierarchical cluster analyses validated four clusters (A–D in Figure 5) as the optimal number of clusters for our vegetation dataset. All resulting clusters contained sites with neighboring plant cover classes, except for cluster D that contained sites with 0–5%, 5–15%, and 30–50% cover. The fitting of environmental parameters on the NMDS biplot (Figure 5) shows the strongest correlation of vegetation composition with the gradient of terrain age with NMDS1 ($R^2 = -0.81$, $p < 0.001$), followed by gradients of sand and silt in the topsoil ($R^2 = 0.67$, $p < 0.001$ and $R^2 = -0.68$, $p < 0.001$), gradients of N and C ($R^2 = -0.67$; $p < 0.001$ and $R^2 = -0.66$; $p < 0.01$, respectively), and the gradient of woody species ($R^2 = -0.54$; $p < 0.001$). For NMDS, two significant correlations were found for gradients of stress-resistant plants ($R^2 = 0.58$; $p < 0.001$), competitive plants...
F I G U R E 5 NMDS of the dissimilarity (Bray–Curtis) in plant community composition between n = 30 investigated plots. 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. The NMDS resulted in a two-dimensional stress of 0.072. Centroids per site (mean of three plots each) are represented as larger points of different shape and color reflecting results of the hierarchical clustering (a–d). Grey shapes around centroids indicate community composition for individual plots. Mean SSY (g m⁻² month⁻¹) rates per plot are shown as smooth surfaces indicating red contour lines over the ordination space. Arrows indicate environmental parameters that significantly (p < 0.001) influenced species community composition. Direction of the arrows indicates most rapid increase for the respective parameter, with the length of arrows being proportional to the strength of its relationship with the NMDS result ($R^2 = -0.47; p < 0.001$), and N ($R^2 = 0.52, p < 0.001$). The amount of mosses, graminoids, forbs, and the different modes of vegetative dispersal in addition to slope, coarse material >10 cm, amount of clay in the topsoil, pH value, radiation, wetness, and elevation did not show significant relationships with species composition. The smooth surface of SSY shows significant correlation with the ordination ($R^2 = -0.47$ for NMDS2; $p < 0.05$).

5 | DISCUSSION

5.1 | Temporal variability of SSY

The drop in SSY at levels above 75% plant cover was visible for all months under investigation (Figure 3); however, this drop did not occur in all months for plant cover above 30%. As previously reported, erosion rates in high mountain environments are subject to considerable variation over time (Alewell et al., 2015). Monthly SSY rates showed that the dynamic nature of geomorphic disturbances is probably related to local rainfall intensities (Placentini et al., 2018). Between the snow-free days from August 2018 to September 2020, we measured six events with more than 45 mm precipitation in 24 h with a maximum of 118 mm on 12 June 2019. Although we could not relate sediment output to single rainfall events, we observed that the highest rates of SSY did not occur during the month with highest total precipitation. This discrepancy between monthly precipitation and SSY in our observations may be caused by several factors: (I) soil moisture saturation due to snow melt leading to increased potential for surface runoff (Dusik, Neugirg, et al., 2019), (II) influences of vegetation characteristics, such as biomass increase, increase in surface roughness, and trapping of sediments by roots during the peak vegetation stage (August; Filipa et al., 2015), (III) a heavy precipitation event causing erosion, which did not show in monthly means, and/or (IV) surface disturbance after plot setup and repairs (Parsons, 2019), which we tried to reduce by introducing a delay between plot setup and the start of obtaining measurements.

5.2 | Variability of SSY along a plant cover gradient

We conclude that a dense plant cover combined with increased species diversity can lead to slope stabilization. The influence of vegetation on sediment transport is well known (Osterkamp et al., 2012). The relationship of increasing species richness with decreasing sediment transport has also been shown previously (Berendse et al., 2015). However, quantified sediment yields via plot measurements on slopes in high mountain environments are scarce (Konz et al., 2012). Although a linear trend between SSY and vegetation cover was observed for all measurement months under consideration (Figure 3), the relationship was not gradual. We observed two significant reductions in SSY at more than 30% and more than 75% plant cover. A similar plant cover threshold at 35% cover has been shown before (Eichel et al., 2016). Soil erosion research plot measurements also showed how vegetation cover thresholds influence sediment yield (Loch, 2000; Moreno-de Las Heras et al., 2009). However, to our knowledge, no study has related small-scale plot measurements of SSY to thresholds in plant cover in alpine environments. The relationship between cover and SSY suggests that the open soil ratio, which is inversely dependent on plant cover, may be a useful substitute for estimating sediment transport via remote sensing on larger spatial scales in high mountain environments (Vrieling et al., 2008). However, this deduction is limited as material properties (e.g., large grain sizes) on unvegetated terrain may prevent sediment movement (Matthews, 1992) and as periglacial processes (i.e., frost creep, solifluxion, and cryoturbation) may lead to sediment transport on fully vegetated slopes (Draebing & Eichel, 2017).

Regarding mechanical research setup, Parsons (2019) highlighted that various limitations of plot studies exist. Most importantly, it is only possible to cover processes that happen on the respective scale of investigation due to the semi-natural conditions at the areas with borders. Due to the small contributing area, the setup allowed for a comparison between different plots with changing biotic parameters to be made but did not show natural erosion rates (Konz et al., 2012; Parsons, 2019). Small erosion plots mainly cover splash and interrill processes as restricted slope lengths result in a decrease in potential for overland flow (Boix-Fayos et al., 2006). However, Parsons (2019) also argues that splash and interrill processes are major contributors to overall erosion as they provide sediment to larger-scale processes such as rill and gully erosion. Due to plot design and location, we excluded influences from large-scale topography (for example, slope angle and slope position) as influencing factors. The described setup can be considered to represent a trade-off between the disciplines of geomorphology and ecology as it allowed a sufficient number of replicates of plots for statistical tests and to capture sediment yield produced by small-scale erosion processes (Haussmann, 2011).
5.3 | Changes in vegetation composition along a plant cover gradient

The constant increase in species richness is in contrast to the general assumption that species number peaks in mid-succession and decreases in late successional stages (Matthews, 1992). However, different successional pathways are possible; hence, high species richness at late successional stages may still be the general trend on proglacial slopes in and around the Gepatscherferner glacier foreland (Burga et al., 2010; Fickert, 2017). Hierarchical clustering revealed four clusters of species communities. Clusters A, B, and C (Figure 5) separate sites with similar plant cover classes and show a gradient from low to high levels of plant cover. Sites within cluster A are further apart compared with sites in cluster C, indicating that species composition in later successional stages is more homogeneous compared with pioneer stages. This assumption is supported by Jones & Del Moral (2005), who showed that, although species richness increases, community heterogeneity decreases in later successional stages on larger scales due to the presence of shrub species. The identified plant cover gradient is in line with mean terrain ages for cluster A (13 years), B (100 years), and C (>170 years, plots are outside the glacier foreland). Soil nutrients, namely N and C, increase towards the glacier foreland. Soil nutrients, namely N and C, increase towards older sites. Raffl et al. (2006) showed that early successional species are adapted to low N levels, while nitrogen-fixing species in combination with atmospheric sources facilitate an increase in N levels in later successional stages. Soil organic C is closely related to the amount of organic matter in the soil and increases with increasing plant cover (Kabala & Zapart, 2012). Nitrogen fixation and increased amounts of organic matter usually occur with an increase in the amount of woody species (Fastie, 1995). At our sites, especially Rhododendron ferrugineum and Calluna vulgaris dominate these later successional stages. Material properties showed a trend from coarser sand-dominated sites in early successional stages to an increase in the amount of silt in later successional stages. This demonstrates the role of weathering (Burga et al., 2010) and downwashing of fine particles (Matthews, 1992) in altering the ratio of sand and silt during primary succession. The finer substrate in late successional stage also supports local water retention, which affects vegetation growth in a positive way (Nagl & Erschbamer, 2010).

A special case in terms of species composition is cluster D (Figure 5). Heterogeneity of plant cover classes and/or distance to other clusters with similar SSY rates do not support the above-mentioned successional trend for clusters A–C. This finding explains why the smoothed surface for SSY did not show a clear gradient and was separated into two groups of high SSY rates (Figure 5). When examining terrain ages for the three sites in cluster D, it appeared that plant cover for these sites was not as high as expected for their respective terrain age (>150 years). Field observations showed the past influence of shallow landslides and rockslide of blocky moraine materials. As species composition for sites within cluster D was different from sites in similar plant cover classes, we observed that comparably mature seed pools were available in close proximity to the respective sites due to high terrain ages. Therefore, we conclude that the available seed pool, rather than disturbances, and surrounding established vegetation define which species are readily available for succession on these geomorphologically overprinted sites. In an experimental setup, Cichini et al. (2011) showed that gaps within later successional stages are usually colonized through seed dispersal or clonal ingrowth. This local micro-succession depends on site conditions and the surrounding established vegetation. However, the rate of SSY probably slows down successional development on formerly disturbed sites, and SSY may influence which species from late successional species pools are capable of establishing themselves on disturbed areas (Matthews et al., 1998; Haugland & Beatty, 2005; Haugland, 2006; Eichel et al., 2013). The increase of competitor species (Figure 5) towards cluster D suggests that clonal ingrowth of late successional species dominates the respective sites. On the other hand, stress-tolerant species dominate early to mid-successional stages at our sites. Here, SSY as a source of disturbance may prevent less resilient species, such as shrubs, from establishing themselves (Matthews, 1992). For vegetation establishment during frequent disturbances, Lane et al. (2016) already demonstrated that species selection might be governed by disturbing events. Based on these findings, it is important to note that vegetation surveys in glacier forelands and surrounding areas must consider the geomorphological history of a site. The limited number of sites within this sampling approach compared with other studies (see Raffl et al., 2006) did not allow us to examine different successional pathways more thoroughly.

5.4 | Discussing concepts of biogeomorphic succession

We observed an overall change within our sites from low cover, low number of species, and high SSY rates to dense plant cover, an increase in species number, and almost no SSY. This switch is in line with the geoeological model by Matthews (1992) in which the interplay of abiotic and biotic importance is driven by successional time and environmental severity. In this model, the starting point is a system of geomorphic disturbance (Ballantyne, 2002) and low levels of nutrient availability (Hodkinson et al., 2003); thus, vegetation development is limited (Chapin et al., 1994). Early pioneer species are capable of establishing themselves under these conditions (Fickert & Grüninger, 2018) and facilitate an increase in species richness and plant cover (Chapin et al., 1994). Over time, vegetation development increases (Erschbamer et al., 2008) and leads to stabilization of slopes; concurrently, abiotic processes become less dominant (Moreau et al., 2008; Eichel et al., 2013; Klaar et al., 2015; Eichel et al., 2016). In contrast to the general geoeological model of Matthews (1992), we observed a rather stepwise stabilization of slopes. Hence, either biotic capability to stabilize changes increases (Corenblit et al., 2009) or abiotic processes diminish (Carrivick & Heckmann, 2017) in cases in which precipitation patterns do not change drastically (Nearing et al., 2005). The availability of sediments to be eroded was a prerequisite for our plots, hence we concluded that biotic processes play an important role in stabilizing small-scale sediment transport. The effects of certain plant species or thresholds of biotic influence were shown by Corenblit et al. (2007b). In their model of fluvial biogeomorphic succession, certain plants are capable of sustainably altering abiotic process regimes in reference to the ecosystem engineering concept by Jones et al. (1994). Eichel et al. (2016) showed that biogeomorphic succession in glacier forelands is dependent on the frequency and
magnitude of disturbance and on the establishment of ecosystem engineers. Within this study, it was possible to isolate one set of processes, namely rill and interrill erosion, and determine quantities of abiotic and biotic processes. Once plant cover rose above 30% and/or mean SSY decreased below 90 g m\(^{-2}\) month\(^{-1}\), the so-called engineering threshold was reached (Eichel et al., 2016). Eichel et al. (2016) found a similar value of 35% cover above which an engineering threshold was reached, and alpine dwarf shrubs potentially caused stabilization of slopes due to their resistance to disturbances and their stabilizing mat growth. They identified Dryas octopetala as an ecosystem engineer for lateral moraine slopes, which mostly occurs on calcareous substrate (Elkington, 1971). For the Gepatschferner glacier foreland and surrounding slopes, the dwarf shrubs Salix herbacea and Calluna vulgaris, which occur in mid to late successional stages, possess similar traits (D’amico et al., 2014; Wheeler et al., 2015). Once plant cover rises above 75% and the mean SSY decreases below 33 g m\(^{-2}\) month\(^{-1}\), only very limited abiotic activity occurred at our sites. We interpret this as the “competition threshold” (Eichel et al., 2016) in which stabilization of slopes is completed. Rhododendron ferrugineum is a shrub species that potentially starts to dominate (Pornon & Doche, 1995) and was also present in and around our late successional sites. However, due to sparse data on the above-named species, further research is needed to test their ecosystem engineering potential for proglacial slopes with crystalline substrate. As clusters of the vegetation communities for our data do not group according to the SSY thresholds (Figures 4 and 5), we argue that species composition already changes prior to the observed drops in SSY. Furthermore, as shown in the previous section, the situation is somewhat different for sites that were affected by high-magnitude geomorphic events as abiotic conditions of an early pioneer phase occurred within a set of mature seed pools. This finding shows that the gradual shift in dominance from abiotic to biotic processes along glacier retreat as proposed by Matthews (1992) may be valid for catchment-wide development (Klaar et al., 2015); however, it is challenged on a local scale (Burga et al., 2010). Locally, abiotic processes might reset environmental conditions to stages comparable to earlier paraglacial adjustment with high disturbance rates, low levels of nutrients, and coarser texture (Matthews, 1999; Eichel et al., 2019). However, a different successional pathway is started due to the proximity of a mature seed pool (Fastie, 1995; Cichini et al., 2011; Erschbamer & Caccianiga, 2016). This process has implications for the conceptual work of Miller & Lane (2018), who illustrated how gradients in environmental stress combined with successional time drive the balance between abiotic and biotic factors and ultimately determine successional pathways. We showed that successional time appears to be determined either by glacier retreat or by secondary disturbances.

6 | CONCLUSION

This study sets out to investigate small-scale sediment transport along a plant cover gradient. Quantified geomorphic process rates and the interpretation of small-scale sediment transport as a source of physical disturbance for plants in high mountain environments are scarce in biogeomorphological research. The data allowed the testing of conceptual models of biogeomorphic succession in a proglacial environment. We showed a stepwise stabilization of small-scale sediment transport on proglacial slopes with distinct species communities according to successional stage and/or geomorphological history. This biogeomorphic development could be related to existing conceptual models when discussing their assumptions in light of quantified data. The number and size of plots limited this study. Hence, the investigated areas show only a small proportion of the processes present in a proglacial environment. Nevertheless, the research design allowed us to incorporate quantitative methods from geomorphology and ecology and can be seen as a trade-off between these two disciplines. Whether these biogeomorphic processes are scale variant remains a topic for future analysis. Further work that incorporates quantified geomorphic process rates with detailed information on vegetation succession on larger scales needs to be done.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article or from the corresponding author upon request.

CONFLICT OF INTERESTS

The authors have no conflicts of interest.

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REFERENCES

<1994, Chapin_Mechanisms of Primary Succession Following Deglaciation.pdf>
Alewell, C., Egli, M. & Meusburger, K. (2015) An attempt to estimate tolerable soil erosion rates by matching soil formation with denudation in Alpine grasslands. Journal of Soils and Sediments, 15(6), 1383–1399. https://doi.org/10.1007/s11368-014-0920-6
Balke, T., Herman, P.M.J., Bouma, T.J. & Nilsson, C. (2014) Critical transitions in disturbance-driven ecosystems: identifying windows of opportunity for recovery. Journal of Ecology, 102(3), 700–708. https://doi.org/10.1111/1365-2745.12241
