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ARTICLE

Ecology of Critical Zones

Similar vegetation-geomorphic disturbance feedbacks shape unstable glacier forelands across mountain regions

Jana Eichel[1] | **Daniel Draebing**[1,2] | **Stefan Winkler**[3] | **Nele Meyer**[4]

[1]Department of Physical Geography, Utrecht University, Utrecht, The Netherlands

[2]Chair of Geomorphology, University of Bayreuth, Bayreuth, Germany

[3]Department of Geography and Geology, University of Würzburg, Würzburg, Germany

[4]Department of Soil Ecology, University of Bayreuth, Bayreuth, Germany

Correspondence
Jana Eichel
Email: j.eichel@uu.nl

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Abstract

Glacier forelands are among the most rapidly changing landscapes on Earth. Stable ground is rare as geomorphic processes move sediments across large areas of glacier forelands for decades to centuries following glacier retreat. Yet, most ecological studies sample exclusively on stable terrain to fulfill chronosequence criteria, thus missing potential feedbacks between geomorphic disturbances and vegetation colonization. By influencing vegetation and soil development, such vegetation-geomorphic disturbance feedbacks could be crucial to understand glacier foreland ecosystem development in a changing climate. We surveyed vegetation and environmental properties, including geomorphic disturbance intensities, in 105 plots located on both stable and unstable moraine terrain in two geomorphologically active glacier forelands in New Zealand and Switzerland. Our plot data showed that geomorphic disturbance intensities permanently changed from high/moderate to low/stable when vegetation reached cover values of around 40%. Around this cover value, species with response and effect traits adapted to geomorphic disturbances dominated. This suggests that such species can act as "biogeomorphic" ecosystem engineers that stabilize ground through positive feedback loops. Across floristic regions, biogeomorphic ecosystem engineer traits creating ground stabilization, such as mat growth and association with mycorrhiza, are remarkably similar. Nonmetric multidimensional scaling revealed a linked sequence of decreasing geomorphic disturbance intensities and changing species composition from pioneer to late successional species. We interpret this linked geomorphic disturbance-vegetation succession sequence as "biogeomorphic succession," a common successional pathway in unstable river and coastal ecosystems across the world. Soil and vegetation development were related to this sequence and only advanced once biogeomorphic ecosystem engineer species covered 40%–45% of a plot, indicating a crucial role of biogeomorphic ecosystem engineer stabilization. Different topoclimatic conditions could explain variance in biogeomorphic succession timescales and ecosystem engineer root traits between the glacier forelands. As glacier foreland ground is widely unstable, we propose to consider glacier forelands as "biogeomorphic ecosystems" in which ecosystem structure and function are shaped by geomorphic disturbances and their feedbacks with adapted plant species, similar to rivers and coasts.

KEYWORDS
biogeomorphic ecosystem, biogeomorphic succession, biogeomorphology, chronosequence, critical zone, ecogeomorphology, ecosystem engineering, geomorphic disturbances, glacier forefield, paraglacial processes, plant traits, vegetation succession

INTRODUCTION

Around the world, retreating glaciers expose hundreds of square kilometers of new terrain each year. As organic material is usually absent in glacial sediments, glacier forelands are perfect areas to study primary vegetation succession, with ongoing research for over a century (Coaz, 1887; Cooper, 1916). To investigate which mechanisms drive vegetation succession and soil development in time, chronosequence approaches were used that replace time with space and thereby create areal chronologies (Jenny, 1941; Matthews, 1992). Chronosequence studies strongly advanced fundamental understanding of primary succession and identified terrain age as main driver of successional change in glacier forelands (e.g., Fischer et al., 2019; Hodkinson et al., 2003; Raffl et al., 2006). Successional trends and trajectories were often explained by biotic interactions, such as facilitation, tolerance, and inhibition (Clements, 1928; Connell & Slatyer, 1977), or plant strategies (Grime, 1977). Other studies have highlighted the importance of seed availability, dispersal, and establishment conditions for vegetation succession (e.g., Erschbamer et al., 2001; Franzén et al., 2019; Jones & Del Moral, 2009).

Yet, chronosequence approaches require similar abiotic conditions and site history to be valid (Johnson & Miyanishi, 2008). To fulfill these criteria, many ecologic studies in glacier forelands sample exclusively on stable ground (e.g., Hodkinson et al., 2003), avoiding setbacks of succession caused by geomorphic disturbances. However, this stable ground is typically rare, as glacier forelands are among the most rapidly changing landscapes on Earth (e.g., Carrivick & Heckmann, 2017; Knight & Harrison, 2009). Sediment exposed by retreating glaciers is usually highly unstable and prone to be redistributed by different geomorphic processes during the so-called "paraglacial adjustment" (Ballantyne, 2002). Immediately following glacier retreat, intense sediment reworking caused by melting dead ice (Ewertowski & Tomczyk, 2015), gullying and debris flows (Curry et al., 2006; Jäger & Winkler, 2012), landsliding (Cody et al., 2020; Emmer et al., 2020), and meltwater erosion (Lane et al., 2017) cause high geomorphic disturbance intensities. Disturbance intensities decrease after several decades when lower magnitude soil erosion and periglacial processes start to dominate on hillslopes (Draebing & Eichel, 2017; Eichel et al., 2018) and channel patterns change from braided to single thread (Gurnell et al., 2000). When sediment is depleted or stabilized by vegetation after decades to centuries, geomorphic disturbances cease (Ballantyne, 2002; Matthews et al., 1998).

Significant paraglacial geomorphic disturbance effects on vegetation and soil development have been described in many studies (Burga et al., 2010; Matthews, 1999; Stawska, 2017; Wojcik et al., 2021). Still, ecological studies often consider geomorphic disturbances as neglectable, "erratic" processes (Fischer et al., 2019) or do not consider them at all. In a similar way, geomorphic studies focus on unvegetated glacier foreland terrain (e.g., Neugirg et al., 2016) and often disregard vegetation colonization and its stabilizing effects on the landscape. Yet, recent "biogeomorphic" studies detected strong feedbacks between geomorphic disturbances, vegetation, and microbial succession in glacier forelands (Cowie et al., 2014; Eichel et al., 2013; Haselberger et al., 2021; Roncoroni et al., 2019). The prostrate shrub species *Dryas octopetala* L. was identified as a "biogeomorphic" ecosystem engineer plant species sensu Phillips (2016). Once slopes have sufficiently stabilized for *D. octopetala* to establish (Eichel et al., 2016, 2018), it decreases geomorphic disturbance intensities and creates habitats for other species through adapted "geomorphic" responses and effect engineer traits (Eichel et al., 2017). While key engineer traits have been identified for *D. octopetala* in the European Alps, comparative studies to assess similarities in engineer traits and resulting vegetation-geomorphic disturbance feedbacks across glacier forelands are lacking.

Yet, understanding of vegetation-geomorphic disturbance feedbacks in glacier forelands is crucial in today's changing climate. The current global mass loss of glaciers (Hugonnet et al., 2021) will result in vastly expanding glacier forelands. These new areas offer habitats for potentially threatened alpine and arctic species requiring geomorphologically unstable habitats (Gentili et al., 2020), but only as long as they remain unstable (Bollati et al., 2020). Thus, we need to understand how long vegetation-geomorphic disturbance feedbacks take to stabilize ground in glacier forelands and what controls their mechanisms and timescales. This requires studies across mountain and floristic regions.

We used a comparative study in two contrasting mountain regions, the European Alps and the Southern Alps of New Zealand, to test the following three hypotheses:

> **Hypothesis 1.** Biogeomorphic ecosystem engineer species possess similar geomorphic response traits, effect traits, and ground stabilization effects across floristic regions.

> **Hypothesis 2.** Similar vegetation-geomorphic disturbance feedbacks, influencing vegetation and soil development, characterize geomorphologically active glacier forelands across mountain regions.

> **Hypothesis 3.** Topoclimatic conditions influence vegetation-geomorphic disturbance feedback timescales and mechanisms.

In both geomorphologically active glacier forelands, selected for their different established glacial chronologies, topoclimatic settings, and floristic regions, we applied a similar plot-based sampling approach to assess vegetation and environmental properties across stable and unstable ground.

METHODS

Study sites

We investigated vegetation-geomorphic disturbance feedbacks in Mueller glacier foreland (Southern Alps, New Zealand) and Turtmann glacier foreland (European Alps, Switzerland; Figure 1). Within Mueller glacier foreland (Figure 1a), about 75% of the terrestrial ground within its Little Ice Age (LIA) maximum extent (ca. 1730/1735 CE; Winkler, 2004) is geomorphologically active with disturbance to vegetation. The entire glacial chronology of this Holocene glacier foreland extends back to terrain ages of 3400 years or even 6400 years if an isolated moraine remnant outside our map is included (Winkler, 2018). The area received up to 4000 mm of annual precipitation between 2014 and 2017, including individual precipitation events >300 mm in 24 h (Environment Canterbury, 2020). Mean annual air temperatures (MAATs) of around 8.5°C between 2014 and 2017 (Environment Canterbury, 2020) preclude permafrost and periglacial processes.

In Turtmann glacier foreland (Figure 1b), about 60% of its ground is geomorphologically disturbed (Eichel et al., 2013). Maximum terrain age is 170 years, corresponding to the maximum glacier extent during the LIA (1850; Eichel et al., 2013; Tscherrig, 1965). Between 2014 and 2017, the annual rainfall was around 800 mm per year with individual rainfall events of maximum 49 mm in 24 h (MeteoSwiss, 2017). Though located below the lower limit of permafrost (Kenner et al., 2019), the low MAAT around 3°C permits active periglacial processes in the glacier foreland (Draebing & Eichel, 2017; Eichel et al., 2020). We focused our sampling on the geomorphologically active lateral and laterofrontal moraines (Figure 1). Except for introduced species (e.g., *Anthoxanthum odoratum* L.), no species are shared between the study sites.

Vegetation and environmental plot surveys

To select plots (2 × 2 m) for vegetation and environmental surveys, we used a random stratified sampling approach based on normalized difference vegetation index (NDVI) values. We derived NDVI classes roughly representing known successional stages from Swisstopo FCIR (2011; Turtmann) or Sentinel-2 imagery (2018; Mueller) and selected 10–15 plots per class. In Mueller glacier foreland, we surveyed 55 plots with 125 species in total in February 2018, using the smartphone-based VegApp (S. Schmidtlein, www.vegapp.de) to note field observations. In Turtmann glacier foreland, we surveyed 50 plots with 121 species in total in July and August 2015 using a paper-based survey. We visually determined individual species cover as well as tree, shrub, herb, bare ground, and total cover (Appendix S1: Table S2). Our survey focused on vascular plants, however, we included two prominent *Racomitrium* moss species with dominant cover (up to 90%) in Mueller glacier foreland (cf. Burrows, 1973). In Turtmann glacier foreland, moss cover was <10% and not included in further analyses. Nomenclature follows Lauber and Wagner (2018) for Turtmann and Breitwieser et al. (2010) for Mueller glacier foreland.

Based on our observations of visible landforms and active sediment transport, we noted which geomorphic processes (gullying, debris flow, interrill erosion, debris sliding, wind erosion, wash, cryoturbation, and solifluction) disturb or recently disturbed plot vegetation (Figure 1c, Table 1). Using known magnitude and

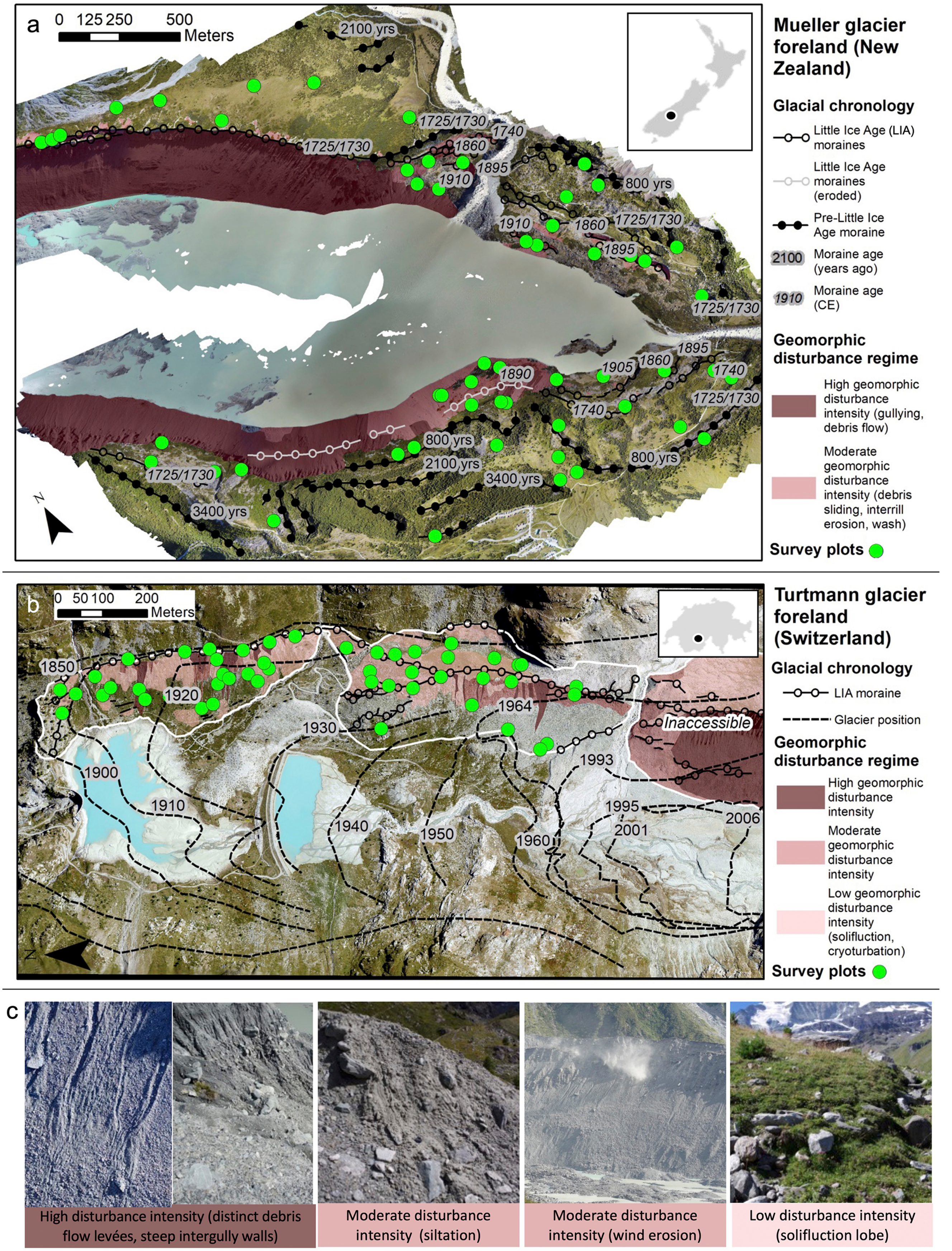

FIGURE 1 Legend on next page.

TABLE 1 Geomorphic disturbance intensity classification based on process magnitude and frequency following Eichel et al. (2016) with indicative landforms/field observations.

Geomorphic disturbance intensity	Description (magnitude/frequency)	Indicative landforms/observations	References
High disturbance intensity (4)	*Magnitude*: Debris flow and/or gullying processes with effective sediment transport and large mechanical stresses in plot. *Frequency*: Multiple times per year during snow-free period depending on high-intensity rainfall activity.	Gullies, steep intergully walls, distinct levées and other unreworked debris flow deposits	Curry et al. (2006), Deline et al. (2021), van Woerkom et al. (2019)
Moderate disturbance intensity (3)	*Magnitude*: Interrill erosion, debris sliding, wind erosion and/or wash processes with intermediate sediment transport rates. *Frequency*: Multiple times per year during snow-free period depending on rainfall and wind activity.	Rills, siltation, splash impact craters, observed eolian sediment transport, observed clast movement	Wolman and Miller (1960), Toy et al. (2002)
Low disturbance intensity[a] (2)	*Magnitude*: Cryoturbation and solifluction processes with low sediment transport rates and short movement distances occur. *Frequency*: Seasonally during winter freezing and spring thawing.	Irregular soil surface, sorted clasts, solifluction steps/lobes/terraces	Rapp (1960), Matsuoka (2001)
Stable (1)	No geomorphic processes occur.	...	

Note: Process sediment transport, mechanical stress, and frequency were used as proxies for disturbance intensity. Numerical values assigned to disturbance intensities for statistical analyses are given in brackets. See Figure 1c for landform examples.
[a]Only present in Turtmann glacier foreland.

frequency for identified geomorphic processes in general (Flageollet, 1996; Otto & Dikau, 2004; Rapp, 1960) and on moraine slopes (Curry et al., 2006; van Woerkom et al., 2019), we assigned a geomorphic disturbance intensity to each plot based on the most intense geomorphic process that disturbed the plot (Table 1; Eichel et al., 2016). Thereby, geomorphic disturbance intensities became comparable across glacier forelands.

Nature conservation restrictions only allowed a non-invasive approach to investigate soil development in Mueller glacier foreland. Here, we visually determined the percentage of plot area covered by organic soil. For Turtmann glacier foreland, we could strengthen this qualitative indication of soil development using quantitative methods. Here, we measured O (i.e., organic layer) and A (i.e., weathered mineral soil with accumulation of humus) horizon thicknesses and took soil samples in each plot using a 100-cm^3 steel corer (0–4 cm depth, two replications), for which soil organic carbon and nitrogen content were measured in the laboratory (Appendix S1: Table S2).

FIGURE 1 Maps of unstable glacier forelands in which vegetation and environmental surveys were conducted: (a) Mueller glacier foreland, New Zealand and (b) Turtmann glacier foreland, Switzerland. For both forelands, plot locations are shown. Moraine ridges and their ages (Mueller; Winkler, 2004, 2018) or glacier positions (Turtmann; Eichel et al., 2013; Tscherrig, 1965) illustrate glacial chronology. Spatial distribution of geomorphic disturbance intensities, including dominant geomorphic processes, is shown. In Turtmann glacier foreland, the sampled lateral moraines are highlighted by white polygons. (c) Examples of geomorphic disturbance intensities with indicative landforms. See Appendix S1: Table S1 for further details on the study sites. CE, common era; LIA, Little Ice Age; yrs, years.

To assign a maximum terrain age to each plot, we used dated moraines in Mueller glacier foreland (Winkler, 2004, 2018), a glacier position map (Tscherrig, 1965; see Figure 1b), and aerial imagery in Turtmann glacier foreland.

For our analyses, we created three datasets: (1) a species dataset containing individual species cover values; (2) a combined species-disturbance dataset containing presence–absence values for all species and geomorphic disturbance processes; and (3) an abiotic–biotic dataset containing plot geomorphic, biotic, and soil properties (see Appendix S1: Table S2). All statistical analyses were carried out in R version 1.3.959 (R Development Core Team, 2020).

Data analyses

To investigate if biogeomorphic ecosystem engineer species possess similar geomorphic disturbance–adapted traits and geomorphic effects across floristic regions (Hypothesis 1), we first identified potential ecosystem engineer species in the species datasets. To be considered, a species needed to be present in a site (i.e., plot) with a moderate or high disturbance intensity and reach cover values above 35%. This is a biogeomorphic "ecosystem engineering threshold" found by Eichel et al. (2016), conforming with measured decrease in sediment transport above 30%–55% vegetation cover (Haselberger et al., 2021; Snelder & Bryan, 1995). Though *Coriaria angustissima* Hook.f. did not occur with moderate or high geomorphic disturbance intensities in our data, we included this species as we observed that it forms large stable patches with very dense cover and extensive rhizome systems in Mueller glacier foreland. We then determined the most important geomorphic disturbance–adapted response and effect traits using existing information on previously identified "biogeomorphic" ecosystem engineer species (Eichel et al., 2017) and geomorphologically relevant plant traits (cf. Burylo et al., 2014; Stokes et al., 2009). We assessed identified traits for each species in literature and the TRY trait database (Kattge et al., 2020). Species were only included in further analyses if their geomorphic effects had previously been reported in literature. Finally, we plotted geomorphic disturbance intensities and potential biogeomorphic ecosystem engineer species' cover along a vegetation cover gradient.

To assess the role of vegetation-geomorphic disturbance feedbacks for vegetation and soil development (Hypothesis 2), we first determined which species grew with which geomorphic disturbance processes by classifying the species-disturbance dataset (isopam packages, distance Jaccard; Schmidtlein et al., 2010). We then conducted a nonmetric multidimensional scaling (NMDS) for the species-disturbance dataset to unravel linked changes between species composition and geomorphic disturbance processes (metaMDS in R vegan; distance Jaccard, three dimensions, maximum 100 runs; Oksanen et al., 2020). We only considered species and geomorphic processes occurring more than once. Subsequently, we used post hoc correlations with measured biotic and abiotic variables to relate linked species-geomorphic disturbance changes to variables indicating vegetation and soil development (envfit, factorfit, and ordisurf in R vegan; 1000 permutations; Oksanen et al., 2020). We only considered significant correlations ($p < 0.001$).

To assess the role of biogeomorphic ecosystem engineering for slope stabilization and soil development, we fitted smooth surfaces of total engineer cover on the ordinations (ordisurf, 1000 permutations), along with overlays of geomorphic disturbance intensities and selected soil properties. To assess the role of topoclimatic conditions for vegetation-geomorphic disturbance feedback timescales and mechanisms (Hypothesis 3), we finally compared our results from the Turtmann and Mueller glacier forelands.

RESULTS

Potential biogeomorphic ecosystem engineer species, traits, and geomorphic effects

In Mueller glacier foreland, we identified *C. angustissima* Hook.f., *Muehlenbeckia axillaris* (Hook.f.Endl.), and *Racomitrium pruinosum* (Wilson) Müll. Hal. as potential biogeomorphic ecosystem engineers. *Anthyllis vulneraria* L., *D. octopetala*, *Salix hastata* L., *Salix serpillifolia* Scop, and *Thymus praecox* Opiz are potential engineer species in Turtmann glacier foreland (Table 2). Considered important engineer response traits include burial tolerance, resprouting capacity, clonal growth, and lateral spread. Growth habit, vegetative height, root system type, rooting depth, and symbiosis with mycorrhiza were considered as important effect traits (Table 2).

In both glacier forelands, prostrate shrub and shrub growth forms dominated for potential biogeomorphic ecosystem engineer species (Table 2). Except for moss species *R. pruinosum* (Mueller) and *S. hastata*, all identified species can resprout from stems or grow clonally, and most species are able to spread laterally. Half of all potential engineer species are tolerant to burial (*M. axillaris*, *A. vulneraria*, *D. octopetala*, and *S. serpillifolia*). No information was available for the other species. Common geomorphic effect traits included formation of low-lying (<0.2 m) mats and

TABLE 2 Potential ecosystem engineer species with their key response and effect traits and reported geomorphic effects retrieved from TRY trait database (Kattge et al., 2020) and literature.

		Response traits				Effect traits				
Species	**Growth form**	**Burial tolerance**	**Resprouting capacity**	**Clonal growth**	**Lateral spread**	**Growth habit and vegetative height**	**Root system and depth**	**Mycorrhiza**	**Geomorphic effects**	**References**
Mueller										
Coriaria angustissima	Shrub	NA	Regeneration from cuttings	NA	NA	Close-set stems, partly creeping, dense patches, <0.5 m	Rhizome, short, vigorous formation	Yes, nitrogen fixating	Binds rock, gravel, and soil, traps fines	1, 2, 3
Muehlenbeckia axillaris	Prostrate shrub	Yes	Produces stems from exposed roots	NA	Yes	Mat forming with creeping stems, <0.1 m, patches up to 4 m wide	Rhizome, adventitious roots	No	Binds soil, stabilizes open ground	4, 5, 6, 7
Racomitrium pruinosom	Pleuro-carpous (moss)	NA	No	NA	NA	Mat forming, dense patches	No roots	No, but itself nitrogen fixating	High water storage capacity, large cover	8, 9, 10, 11
Turtmann										
Anthyllis vulneraria	Herb	Yes	Poor tolerance against cutting	Root splitter[a]	No[a]	Rosette forming, <0.6 m	Tap root with thick root stock, <0.3 m	Yes, nitrogen fixating	Decreases wind-induced soil loss	12, 13, 14, 15, 16
Dryas octopetala	Prostrate shrub	Yes	Yes	Epigeogenous stems and root splitter clonal growth[a]	Yes[a], 0.01–0.25 m/year	Mat forming, creeping stems, thick organic mat, patches >2 m^2, <0.05 m	Woody root stock, adventitious roots, <0.4 m	Yes	Scree-coverer, stabilizes moving debris, traps organic material	12, 17, 18, 19, 20
Salix hastata	Shrub	NA	No	No	No	Erect or low lying, strongly branching, thicket forming, <1.5 m	Cluster roots[a], <0.3 m[a]	Yes	Erosion control, rockfall and surface protection, shallow reinforcement	16, 21, 22
Salix serpillifolia	Prostrate shrub	NA	Yes	Epigeogenous and above ground stems clonal growth[a]	Yes[a], 0.01–0.25 m/year[a]	Mat forming with creeping stems, forms patches, <0.2 m	Tap root, adventitious roots, <0.4 m	Yes	Scree-dammer, traps fines and organic material	12, 20, 23, 24, 25
Thymus praecox	Prostrate shrub	Yes	Yes	Root splitter clonal growth[a]	Yes[a], 0.01–0.25 m/year	Mat forming with creeping stems, forms patches, <0.15 m	Tap root	No	Traps and stabilizes the soil	12, 26, 27

Note: For species' traits marked with NA, no information could be found. Numbers in the References column are: 1, Daly et al. (1972); 2, Burrows (1995); 3, Walker et al. (2003); 4, Wardle (1972); 5, Burrows (1973); 6, Wiser et al. (2010); 7, Foo et al. (2011); 8, Vitt and Marsh (1988); 9, Buxton et al. (2005); 10, Michel et al. (2013); 11, Klarenberg et al. (2022); 12, Klimešová and Bello (2009); 13, Erschbamer and Mayer (2011); 14, Krautzer et al. (2011); 15, Burri et al. (2013); 16, Lauber and Wagner (2018); 17, Schröter et al. (1926); 18, Elkington (1971); 19, Wookey et al. (1995); 20, Kutschera et al. (1997); 21, Norris et al. (2008); 22, Craine et al. (2009); 23, Rauh (1939); 24, Körner (2003); 25, Kosiński et al. (2019); 26, Harley and Harley (1987); and 27, Burylo et al. (2014).

[a]Kattge et al. (2020).

patches through prostrate shrubs' creeping stems. Other growth habits included close-set stems or strongly branching, partly creeping or low-lying stems (*C. angustissima* and *S. hastata*), or rosettes (*A. vulneraria*). In Mueller glacier foreland, rhizomes dominated, whereas in Turtmann glacier foreland, tap root and cluster root systems dominated with rooting depths up to 0.4 m. Except for *T. praecox*, all prostrate shrubs in both glacier forelands can develop adventitious roots. All potential biogeomorphic engineer species in Turtmann glacier foreland, except *T. praecox*, are associated with mycorrhiza. *A. vulneraria* can additionally fix nitrogen. In Mueller glacier foreland, only *C. angustissima* is associated with mycorrhiza. Both *C. angustissima* and *Racomitrium lanuginosum* can fix nitrogen.

Reported geomorphic effects included binding and trapping of soil, fines, gravel, and organic material for all prostrate shrubs and *C. angustissima* (Mueller), reduction in wind-induced soil loss for *A. vulneraria* (Turtmann), and erosion control and rockfall protection for *S. hastata* (Turtmann).

For both glacier forelands, we found that geomorphic disturbance intensities decreased with increasing vegetation cover (Figure 2a,b). Below 40% vegetation cover, high to moderate geomorphic disturbance intensities (debris flows, gullying, debris sliding, interrill erosion, wind erosion, and wash) dominated, whereas plots with more than 40% vegetation cover were either characterized by low disturbance intensities (solifluction and cryoturbation; only Turtmann) or stable. The switch to lower geomorphic disturbance intensities happened once potential biogeomorphic ecosystem engineer species' cover increased from <5%–25% to 25%–50%. Cover especially increased for *R. pruinosum* (from <25% to up to 100%) in Mueller glacier foreland and prostrate shrub (*M. axillaris*, *D. octopetala*, and *S. serpillifolia*) and shrub species (*C. angustissima* and *S. hastata*) in both forelands (Figure 2c,d). In Turtmann glacier foreland, prostrate shrub *D. octopetala* reached very high cover (75%–100%) in plots with low disturbance intensities or stable plots, whereas erect *S. hastata* shrubs showed very high cover (75%–100%) mostly in stable plots. While potential biogeomorphic ecosystem engineer species often made up the main share of vegetation cover around 40% cover, they only had low shares for low (5%–25%) total vegetation cover and often lower shares for very high (75%–100%) total vegetation cover.

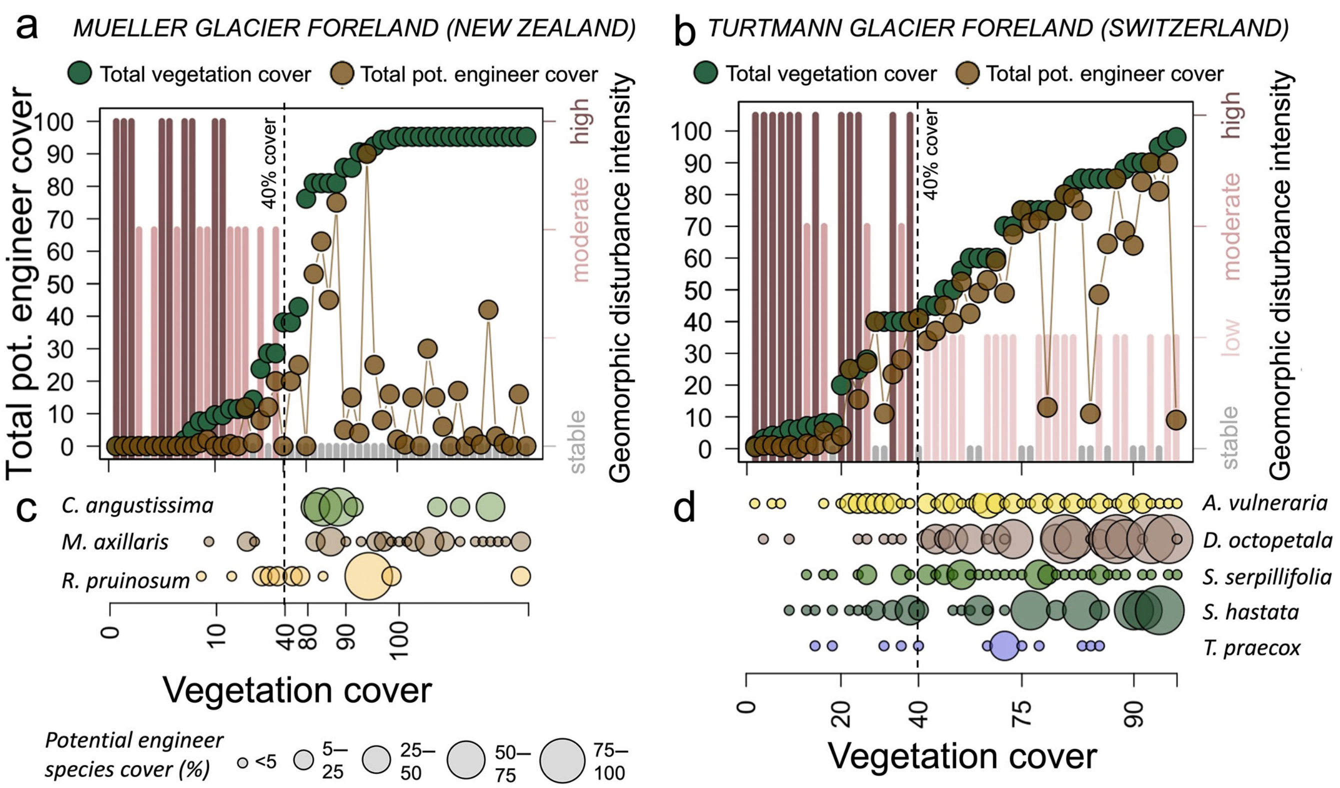

FIGURE 2 Geomorphic disturbance intensities and total potential (pot.) biogeomorphic ecosystem engineer species' cover plotted with increasing vegetation cover for Mueller (a) and Turtmann (b) glacier foreland (c, d). Individual potential engineer species' cover plotted with increasing vegetation cover (a, b).

Relationships between species composition, geomorphic disturbance processes, soil, and biotic properties

We identified six vegetation-geomorphic disturbance classes in Mueller and three in Turtmann glacier foreland (Figure 3a,b; Appendix S1: Tables S5 and S6). They summarize linked changes in species composition and occurring geomorphic processes and range from disturbance classes with no plants to late successional shrub and tree classes. For both glacier forelands, vegetation-disturbance classes were arranged along the main NMDS axes, revealing a vegetation-geomorphic disturbance gradient (Figure 3a,b). Abiotic and biotic variables indicating vegetation and soil development were related to this gradient and notably proceeded once total potential engineer cover exceeded 40%–45% (Figure 3c,d).

In Mueller glacier foreland, the highest geomorphic disturbance intensity ($r^2 = 0.69$) and bare ground cover ($r^2 = 0.78$) were related to a disturbance class with debris sliding, wash, and interrill erosion processes (lower right side of diagram in Figure 3a). The highest vegetation ($r^2 = 0.78$) and organic soil cover ($r^2 = 0.44$) were related to herb-shrub (*Holcus lanatus* L., *C. angusstissima*), grass-prostrate shrub (*A. odoratum* L., *L. fraseri*, and *M. axillaris*), and shrub-tree classes (*Podocarpus laetus* Hooibr. Ex Endl., *Griselinia littoralis* [Raul] Raul; all upper left side in Figure 3a). The highest species number ($r^2 = 0.61$) and herb cover ($r^2 = 0.36$) were additionally related to the herb-shrub and grass-prostrate shrub classes (upper diagram center in Figure 3a), whereas the highest litter ($r^2 = 0.51$), tree ($r^2 = 0.27$), and shrub cover ($r^2 = 0.49$) were related to the shrub-tree class (left side of diagram in Figure 3a). Fitting of total biogeomorphic ecosystem engineer cover on the ordination showed that ground stabilized and organic soil cover strongly increased once total engineer cover exceeded about 45% (Figure 3c).

In Turtmann glacier foreland, the highest geomorphic disturbance intensities ($r^2 = 0.58$) and bare ground cover ($r^2 = 0.76$) related to a pioneer-disturbance class characterized by *S. aizoides*, *L. alpina*, debris sliding, and debris flow (lower right side of diagram in Figure 3b). The highest total vegetation cover ($r^2 = 0.70$), A- ($r^2 = 0.20$) and O-horizon ($r^2 = 0.36$) thicknesses, and soil nitrogen content ($r^2 = 0.40$) related to solifluction-prostrate shrub (*S. serpillifolia*, *D. octopetala*, *Elyna myosuroides* [Vill. Fritsch], solifluction) and stable herb-shrub classes (*Epilobium fleischeri*, *Festuca alpina* Suter; left side of Figure 3b). The highest shrub cover ($r^2 = 0.33$) was additionally related to the stable shrub-herb class (upper left in Figure 3b), whereas the highest herb cover ($r^2 = 0.57$) and soil organic carbon content ($r^2 = 0.30$) related to the solifluction-prostrate shrub class (lower left in Figure 3b). When potential biogeomorphic ecosystem engineer cover exceeded 40% and geomorphic disturbance intensities were low or stable, A-horizon thickness and soil nitrogen content strongly increased (Figure 3d). Terrain age is related to vegetation-geomorphic disturbance gradients in both glacier forelands (Mueller: $r^2 = 0.28$, $p < 0.001$; Turtmann: $r^2 = 0.33$, $p < 0.002$).

DISCUSSION

Biogeomorphic ecosystem engineer traits create a positive feedback loop leading to ground stabilization

We found that geomorphic disturbance intensities decreased when vegetation cover exceeded 40%. At this point, potential biogeomorphic ecosystem engineers dominated (Figure 2), supporting our hypothesis that identified species indeed stabilize glacier foreland ground, similar to bryophytes and associated soil crusts (Haugland & Beatty, 2005; Jones & Henry, 2003). We expect that identified engineer response and effect traits (Table 2) can create a positive biogeomorphic feedback loop between decreasing geomorphic disturbance intensities, engineer establishment, and growth (Figure 4), which results in gradual ground stabilization from plant scale to slope scale (Figure 5).

Response traits, such as burial tolerance and resprouting capacity (Table 2), can act as filters determining establishment and growth success (Figure 4). They enable engineer species to establish once high disturbance intensities have decreased and despite ongoing moderate-intensity erosion processes (Figure 2; Burylo et al., 2012, 2014). Once established, engineer prostrate shrub and moss mats decrease water and wind erosion through hydrological and hydraulic effects, such as intercepting rainfall, obstructing runoff, and storing moisture (Figure 5; Annandale & Kirkpatrick, 2017; Michel et al., 2013; Schröter et al., 1926). Developing engineer root systems, often associated with mycorrhiza (Table 2), can add mechanical reinforcement against erosion (Burri et al., 2013; Graf et al., 2019; Stokes et al., 2009; Vannoppen et al., 2015). Prostrate shrubs' creeping stems and adventitious roots binding gravel additionally protect against debris sliding (Table 2). Thereby, sediment transport by wind, water, and gravity can decrease locally at the plant scale (Figure 5; Burylo et al., 2011, 2012).

We expect that engineer cover can quickly increase (Figure 2) through clonal growth and lateral spread (Table 2, Figure 5). *M. axillaris* and *R. pruinosum*, for

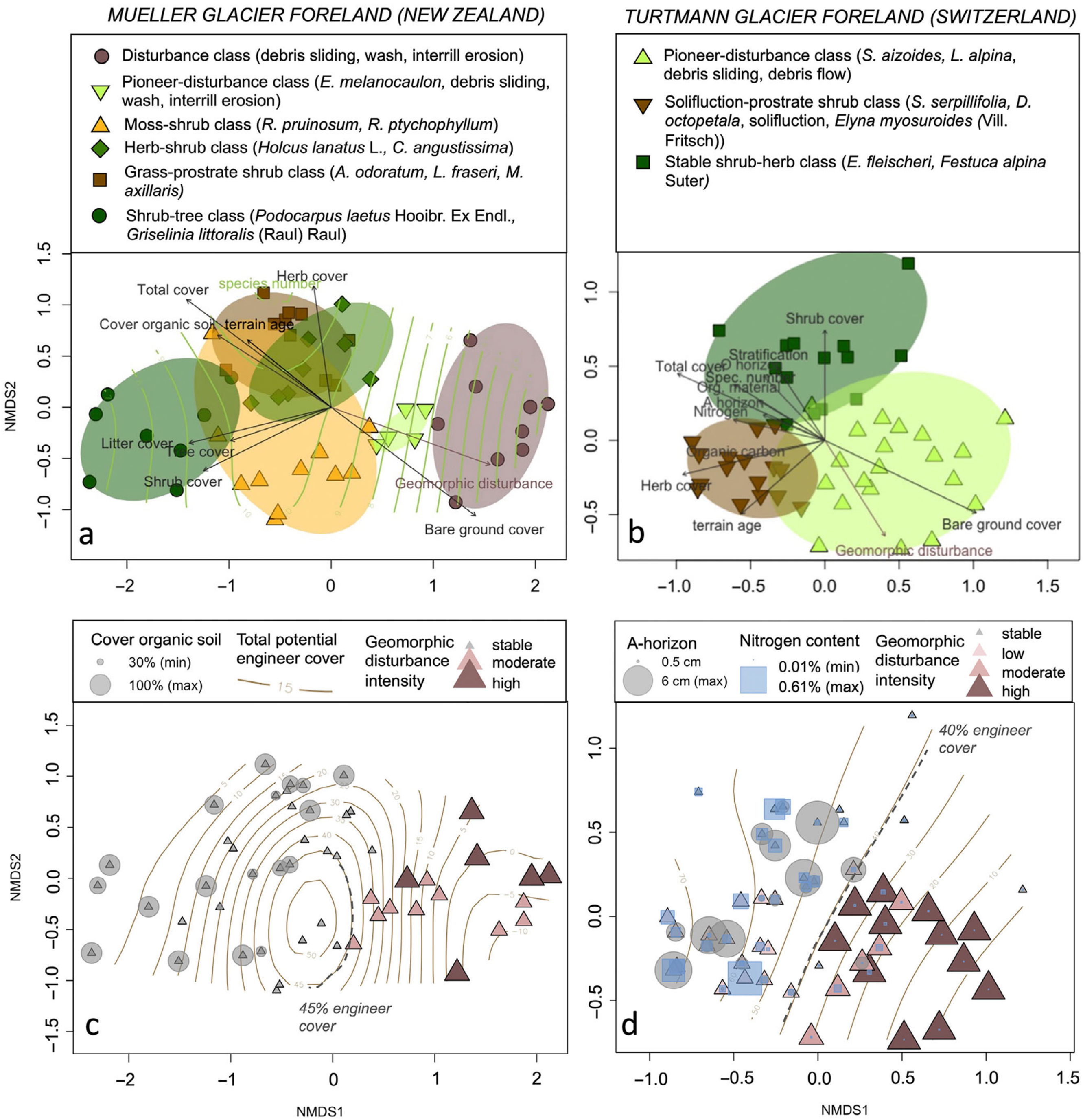

FIGURE 3 Nonmetric multidimensional scaling (NMDS) results for species-disturbance dataset from Mueller (a, c) and Turtmann (b, d) glacier forelands. (a, b) NMDS results with vegetation-disturbance classes (polygons encompassing all points per class) and post hoc correlation results (arrows, contour lines with an interval of one) for biotic and abiotic variables. Main indicators (species [spec.] or geomorphic processes) for each vegetation-disturbance class are given in brackets in the legend. (c, d) NMDS results with fitted total potential biogeomorphic ecosystem engineer cover (contour lines: 5% cover) and overlay with total organic soil cover and geomorphic disturbance intensities (c) or fitted total potential biogeomorphic ecosystem engineer cover (contour lines: 10% cover), A-horizon thickness, soil nitrogen content, and geomorphic disturbance intensities (d). For all shown variables $p < 0.001$. See Appendix S1: Tables S3 and S4 for all post hoc correlation results. NMDS stress is 0.12 for Mueller data (a, c) and 0.16 for Turtmann data (b, d). max, maximum; min, minimum.

example, can multiply their biomass 10-fold in three years (Buxton et al., 2005; Foo et al., 2011). Resulting positive feedbacks (Figures 4 and 5) can explain the transition to low geomorphic disturbance intensities or stable ground above 40% vegetation cover (Figure 5; cf. Haselberger et al., 2021; Snelder & Bryan, 1995), which we observed at

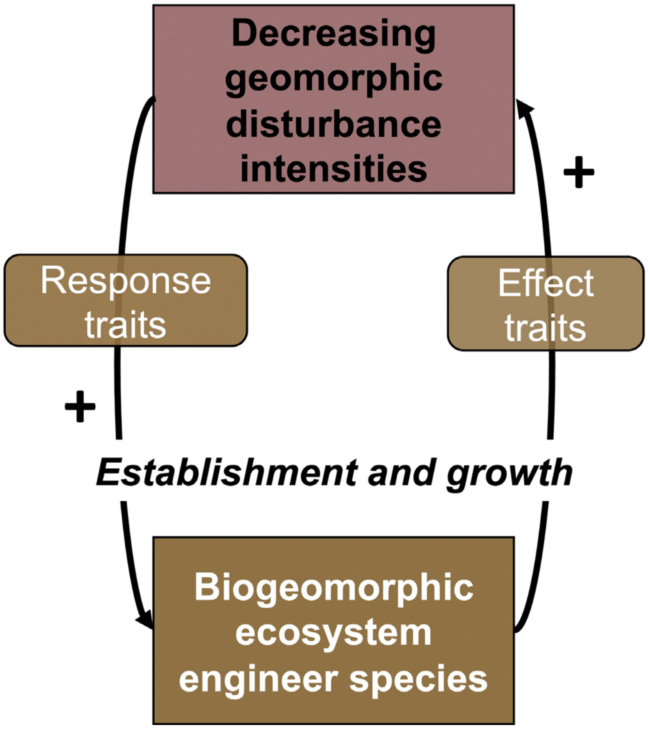

FIGURE 4 Conceptual illustration of the positive biogeomorphic feedback loop between decreasing geomorphic disturbance intensities and biogeomorphic ecosystem engineer establishment and growth. Response traits filter disturbance effects on engineer species, while effect traits determine their impact on disturbance intensities.

plot scale (Figure 2). Complementary stabilization effects by erect shrub species (Figure 2) with close-set stems and vigorous rhizomes (*C. angustissima*; Daly et al., 1972) or thicket-forming branches and cluster roots (*S. hastata*; Lautenschlager-Fleury & Lautenschlager-Fleury, 1994) could explain stable ground associated with high to very high (50%–100%) engineer cover, especially in Mueller glacier foreland (Figure 2). Thus, about 40% cover (Figures 2, 3, and 5) seems to be a community level-stabilization threshold, which gets reinforced at higher cover values by complementary engineer traits of erect shrub species that create slope-scale ground stabilization.

Biogeomorphic ecosystem engineer species' traits were remarkably similar between floristic regions (Table 2), for example, clonal growth, burial tolerance, and resprouting capacity. These traits are also shared with ecosystem engineer plants along water-terrestrial interfaces (Corenblit et al., 2015). Therefore, our results support trait convergence due to similar geomorphic constraints (Corenblit et al., 2015; Fukami et al., 2005) and suggest common geomorphic disturbance adaptations across geomorphologically disturbed ecosystems from the mountains to the coast.

"Biogeomorphic succession" on unstable glacier foreland ground

Our classification and NMDS results (Figure 3) demonstrate that vegetation-geomorphic disturbance feedbacks are a main driver of vegetation and soil development in unstable, geomorphologically active glacier forelands. Vegetation-geomorphic disturbance classes with distinct geomorphic process-species combinations arranged along the main NMDS gradients (Figure 3) indicate synchronization of decreasing geomorphic disturbance intensities with changing species composition and proceeding vegetation succession. Corenblit et al. (2007) termed a similar sequence of reciprocal coupling between hydromorphological and vegetation succession processes in rivers "fluvial biogeomorphic succession." Based on changing abiotic–biotic feedbacks, this sequence can be divided into four phases: geomorphic, pioneer, biogeomorphic, and ecologic. These phases also show up in our ordered, distinct vegetation-geomorphic disturbance classes (Figure 3).

We interpret the disturbance class with bare ground and high to moderately intense geomorphic processes in Mueller glacier foreland (Figure 3a) as a "geomorphic phase" (Figure 6). In this phase, landsliding, running water, and wind intensely move sediments and remove seeds and seedlings before they can sufficiently establish (cf. Balke et al., 2014). Consequently, vegetation colonization and soil development are inhibited (Betz et al., 2019; Curry et al., 2006; Temme & Lange, 2014; Wojcik et al., 2021; Figure 6c). Pioneer-disturbance classes with moderate-intensity disturbance processes and pioneer species (Figure 3a,b) indicate a "pioneer phase." In this phase, recruitment and establishment become possible for ruderal strategists tolerating sediment movement, such as *Epilobium melanocaulon* Hook., *Linaria alpina* (L.) Mill, and *Saxifraga aizoides* L. (Figure 6; Cannone & Gerdol, 2003; Jenny-Lips, 1930; Sommerville et al., 1982). Geomorphic disturbances and initial habitat conditions filter dispersal, recruitment, and establishment in this phase (Corenblit et al., 2015), for example, by transporting and depositing diaspores and plant material (Erschbamer et al., 2001; Raffl et al., 2006; Stöcklin & Bäumler, 1996). Biogeomorphic ecosystem engineer species, growing with cover values <45% in association with pioneer-disturbance classes (Figure 3) in this phase, will likely establish within "Windows of Opportunity" between higher intensity disturbances (Balke et al., 2014) or at safe sites (Jumpponen et al., 1999).

When total engineer cover exceeded 40%–45%, organic soil cover (Mueller), A-horizon thickness, and soil nitrogen contents (Turtmann) were distinctly higher, while disturbance intensities changed to low (Turtmann)

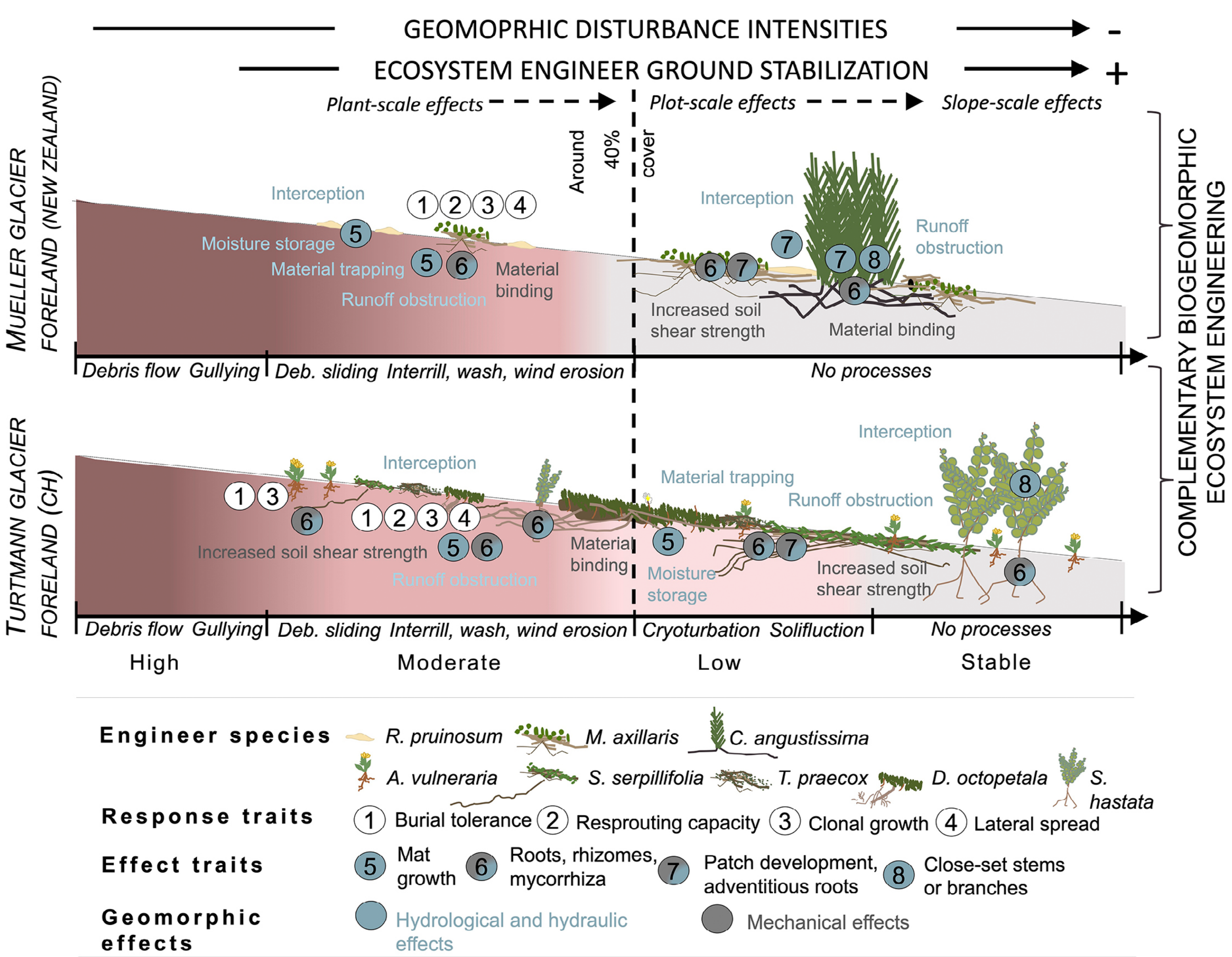

FIGURE 5 Illustration of gradual ecosystem engineer ground stabilization in Turtmann and Mueller glacier foreland. Common geomorphic disturbance–adapted response and effect traits are linked to hydrological, hydraulic, and mechanical geomorphic effects, which increase from plant scale to slope scale. Response and effect traits are assigned to individual engineer species based on Table 2 using numbers; number colors indicate their roles for illustrated hydrological and hydraulic (blue) or mechanical (gray) effects. Decrease in geomorphic disturbance intensities due to changing or ceasing geomorphic disturbance processes is shown. CH, Switzerland; Deb., debris.

or stable (both glacier forelands; Figure 3c,d) in engineer-disturbance classes. Fine and organic material accumulation in dense engineer mats, for example, as reported for *D. octopetala* (McGraw, 1985), could explain increased organic soil cover and horizon development. Observed increase in nitrogen contents could be explained by nitrogen fixation through engineer species (cf. Table 2). Thus, stable habitat creation and soil development associated with engineer plants seem to go hand in hand and facilitate establishment for other species, as indicated by the highest species numbers (Figure 3a,b). Consequently, we interpret engineer-disturbance classes as a biogeomorphic phase (Figure 6).

For Mueller glacier foreland, NMDS results furthermore show that biogeomorphic ecosystem engineer cover and species numbers decrease with increasing litter, shrub, and tree species cover in a stable shrub-tree class (Figure 3a). Characteristic *Podocarpus* spp. and *G. littoralis* (Raul) Raul typically require stable conditions (Burrows, 1973; Wardle, 1972), indicating an "ecologic phase" (Figure 6) with absent geomorphic disturbances. Competition and trophic interactions act as filters for establishment and maturation (Corenblit et al., 2015) in this phase, explaining lower species numbers (Figure 3a) and exclusion of less competitive biogeomorphic ecosystem engineer species (Chapin et al., 1994; Tscherko et al., 2005). In Turtmann glacier forelands, typical late successional trees species (*Pinus cembra* L., and *Larix decidua* Mill.) are mostly absent on sampled lateral moraines. However, erect *Salix* shrub species dominating

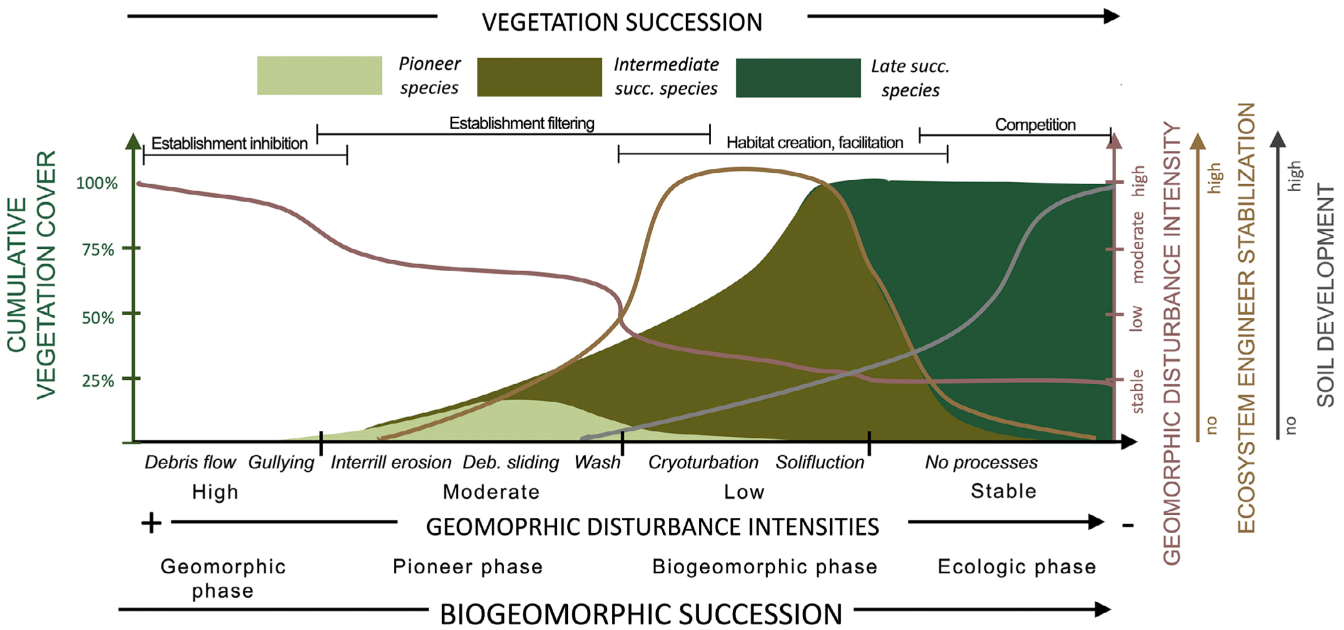

FIGURE 6 Conceptual model of biogeomorphic succession in unstable glacier forelands with decreasing geomorphic disturbance intensities (red line) and proceeding vegetation succession (green graphs) and soil development (gray line), made possible by biogeomorphic ecosystem engineer ground stabilization (brown line). Deb., debris; succ., successional.

on stable ground (Figure 3b) can exclude disturbance-adapted prostrate shrubs (Eichel et al., 2017) and therefore indicate a transition from biogeomorphic to ecologic phase.

While we focused on moraine slopes, similar sequences of synchronized vegetation and geomorphic disturbance development were observed on active glaciofluvial floodplains (Cowie et al., 2014; Gurnell et al., 2000; Moreau et al., 2008) and unstable glacier foreland valley floors (Haugland, 2006; Haugland & Beatty, 2005). Thus, given dominantly unstable ground in many glacier forelands (Carrivick & Heckmann, 2017; Knight & Harrison, 2009), biogeomorphic succession may well be a main successional pathway in glacier forelands, missed by frequently applied chronosequence approaches.

Topoclimatic conditions influence timescales of biogeomorphic succession and biogeomorpic ecosystem engineer traits

Contrasting topoclimatic conditions and resulting differences in geomorphic disturbance intensities and processes (Figure 1) could explain biogeomorphic differences between the two glacier forelands (Figure 3, Table 2). Exceptionally high and intense rainfall (4000 mm/year, >300 mm in 24 h) triggers high-intensity geomorphic disturbances in Mueller glacier foreland, such as gullying and debris flows (Winkler, 2015). These frequent and intense geomorphic disturbances limit engineer establishment (Figures 2 and 3) and thereby delay biogeomorphic succession. Thus, geomorphic processes can still disturb terrain that was deglaciated more than thousand years ago (Figure 1).

However, once engineer species managed to establish and grow over 40% cover in Mueller glacier foreland, geomorphic disturbance intensities changed directly from moderate to stable (Figure 2). Dominant rhizome root systems (Table 2) could explain this direct stabilization, as they enable quick lateral spreading while at the same time fixing the moving debris. In Turtmann glacier foreland, rhizome root systems are notably absent (Table 2). This could be explained by periglacial disturbances permitted by sufficiently low MAATs (3°C). Solifluction movement, most intense in the upper centimeters of the soil (millimeters to centimeters per year; Matsuoka, 2001), could destroy rhizomes growing in this soil layer and favor prostrate engineer shrubs that grow their stems securely on top of the moving soil and are able to adapt their root growth to downslope soil movement (e.g., *D. octopetala*; Eichel et al., 2017; Kutschera et al., 1997). This adaptation of engineer traits to dominant geomorphic processes could indicate eco-evolutionary feedbacks (Corenblit et al., 2015; Odling-Smee et al., 2013).

Overall, ongoing biogeomorphic successions over centuries (Turtmann) to millennia (Mueller) suggest that unstable terrain and resulting geomorphic habitat diversity (Bollati et al., 2020) could persist well into the future, securing unstable glacier forelands as valuable microrefugia for disturbance-adapted alpine species (Losapio et al., 2021).

CONCLUSIONS: UNSTABLE GLACIER FORELANDS AS BIOGEOMORPHIC ECOSYSTEMS

Our results show strikingly similar vegetation-geomorphic disturbance feedbacks in two unstable glacier forelands with contrasting topoclimatic conditions and floristic regions. We found that:

1. Biogeomorphic ecosystem engineer species possess similar traits and create similar positive biogeomorphic feedback loops to stabilize moving ground.
2. Vegetation-geomorphic disturbance feedbacks play a key role for soil and vegetation development during biogeomorphic succession dynamics.
3. Topoclimatic conditions can influence biogeomorphic succession timescales and select biogeomorphic ecosystem engineer species root traits by controlling dominant geomorphic processes.

Collectively, our results suggest that vegetation-geomorphic disturbance feedbacks control ecosystem structure and function in unstable glacier forelands across mountain regions, which makes them “biogeomorphic ecosystems” similar to rivers, coasts, and coastal dunes (Corenblit et al., 2015).

We believe that interdisciplinary research approaches and the utilization of a biogeomorphic ecosystem perspective could strongly improve our capacity to manage and conserve ecosystems not only in globally vastly expanding glacier forelands but also in other alpine ecosystems strongly affected by intrinsic geomorphic disturbances, such as talus and solifluction slopes, rock glaciers, and alluvial fans (cf. Gentili et al., 2013; Pierce et al., 2007).

AUTHOR CONTRIBUTIONS

Jana Eichel developed the research setup and led field surveys. Jana Eichel, Daniel Draebing, Stefan Winkler, and Nele Meyer collected the data. Jana Eichel processed and analyzed the data with inputs from Daniel Draebing, Stefan Winkler, and Nele Meyer. Jana Eichel led the writing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Eichel et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.7d7wm3803.

ORCID

Jana Eichel https://orcid.org/0000-0001-6116-084X
Daniel Draebing https://orcid.org/0000-0001-6379-4707
Stefan Winkler https://orcid.org/0000-0002-0650-1207
Nele Meyer https://orcid.org/0000-0002-1378-4786

REFERENCES

Annandale, B., and J. B. Kirkpatrick. 2017. “Diurnal to Decadal Changes in the Balance between Vegetation and Bare Ground in Tasmanian Fjaeldmark.” *Arctic, Antarctic, and Alpine Research* 49: 473–86.

Balke, T., P. M. Herman, and T. J. Bouma. 2014. “Critical Transitions in Disturbance-Driven Ecosystems: Identifying Windows of Opportunity for Recovery.” *Journal of Ecology* 102: 700–8.

Ballantyne, C. K. 2002. “Paraglacial Geomorphology.” *Quaternary Science Reviews* 21: 1935–2017.

Betz, S., V. Croce, and M. Becht. 2019. “Investigating Morphodynamics on Little Ice Age Lateral Moraines in the Italian Alps Using Archival Aerial Photogrammetry and Airborne LiDAR Data.” *Zeitschrift für Geomorphologie* 62: 231–47.

Bollati, I. M., B. C. Lenz, and V. Caironi. 2020. “A Multidisciplinary Approach for Physical Landscape Analysis: Scientific Value and Risk of Degradation of Outstanding Landforms in the Glacial Plateau of the Loana Valley (Central-Western Italian Alps).” *Italian Journal of Geosciences* 139: 233–51.

Breitwieser, I., P. J. Brownsey, W. A. Nelson, and A. D. Wilton. 2010. “Flora of New Zealand Online.” www.nzflora.info.

Burga, C. A., B. Krusi, M. Egli, M. Wernli, S. Elsener, M. Ziefle, T. Fischer, and C. Mavris. 2010. “Plant Succession and Soil Development on the Foreland of the Morteratsch Glacier (Pontresina, Switzerland): Straight Forward or Chaotic?”

Flora-Morphology, Distribution, Functional Ecology of Plants 205: 561–76.

Burri, K., C. Gromke, and F. Graf. 2013. “Mycorrhizal Fungi Protect the Soil from Wind Erosion: A Wind Tunnel Study.” *Land Degradation & Development* 24: 385–92.

Burrows, C. J. 1973. “Studies on some Glacial Moraines in New Zealand—2.” *New Zealand Journal of Geology and Geophysics* 16: 831–56.

Burrows, C. J. 1995. “Germination Behaviour of the Seeds of Four New Zealand Species of Coriaria (Coriariaceae).” *New Zealand Journal of Botany* 33: 265–75.

Burylo, M., T. Dutoit, and F. Rey. 2014. “Species Traits as Practical Tools for Ecological Restoration of Marly Eroded Lands.” *Restoration Ecology* 22: 633–40.

Burylo, M., F. Rey, E. Bochet, and T. Dutoit. 2011. “Plant Functional Traits and Species Ability for Sediment Retention during Concentrated Flow Erosion.” *Plant and Soil* 353: 135–44.

Burylo, M., F. Rey, N. Mathys, and T. Dutoit. 2012. “Plant Root Traits Affecting the Resistance of Soils to Concentrated Flow Erosion.” *Earth Surface Processes and Landforms* 37: 1463–70.

Buxton, R. P., J. Stanley, P. Alspach, C. Morgan, and C. Ross. 2005. “Mosses and Other Early Colonizers: Pioneers for Revegetating Mine Waste Rock Dumps and Rock Walls.” *Journal of the American Society of Mining and Reclamation.* 22: 170–81.

Cannone, N., and R. Gerdol. 2003. “Vegetation as an Ecological Indicator of Surface Instability in Rock Glaciers.” *Arctic, Antarctic, and Alpine Research* 35: 384–90.

Carrivick, J. L., and T. Heckmann. 2017. “Short-Term Geomorphological Evolution of Proglacial Systems.” *Geomorphology* 287: 3–28.

Chapin, F., L. Walker, C. Fastie, and L. Sharman. 1994. “Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska.” *Ecological Monographs* 64: 149–75.

Clements, F. E. 1928. *Plant Succession and Indicators: A Definitive Edition of Plant Succession and Plant Indicators*. New York: The Wilson Company.

Coaz, J. 1887. “Erste Ansiedlung Phanerogamer Pflanzen auf vom Gletscher Verlassenem Boden.” *Mittheilungen der Naturforschenden Gesellschaft Bern*: 3–12.

Cody, E., B. Anderson, S. McColl, I. Fuller, and H. Purdie. 2020. “Paraglacial Adjustment of Sediment Slopes during and Immediately after Glacial Debuttressing.” *Geomorphology* 371: 107411.

Connell, J. H., and R. O. Slatyer. 1977. “Mechanisms of Succession in Natural Communities and their Role in Community Stability and Organization.” *The American Naturalist* 111: 1119–44.

Cooper, W. S. 1916. “Plant Successions in the Mount Robson Region, British Columbia.” *The Plant World* 19: 211–38.

Corenblit, D., A. Baas, T. Balke, T. Bouma, F. Fromard, V. Garófano-Gómez, E. González, et al. 2015. “Engineer Pioneer Plants Respond to and Affect Geomorphic Constraints Similarly along Water–Terrestrial Interfaces World-Wide.” *Global Ecology and Biogeography* 24: 1363–76.

Corenblit, D., E. Tabacchi, J. Steiger, and A. M. Gurnell. 2007. “Reciprocal Interactions and Adjustments between Fluvial Landforms and Vegetation Dynamics in River Corridors: A Review of Complementary Approaches.” *Earth-Science Reviews* 84: 56–86.

Cowie, N. M., R. D. Moore, and M. A. Hassan. 2014. “Effects of Glacial Retreat on Proglacial Streams and Riparian Zones in the Coast and North Cascade Mountains.” *Earth Surface Processes and Landforms* 39: 351–65.

Craine, J. M., A. J. Elmore, M. P. M. Aidar, M. Bustamante, T. E. Dawson, E. A. Hobbie, A. Kahmen, et al. 2009. “Global Patterns of Foliar Nitrogen Isotopes and their Relationships with Climate, Mycorrhizal Fungi, Foliar Nutrient Concentrations, and Nitrogen Availability.” *New Phytologist* 183: 980–92.

Curry, A. M., V. Cleasby, and P. Zukowskyj. 2006. “Paraglacial Response of Steep, Sediment-Mantled Slopes to Post-‘Little Ice Age’ Glacier Recession in the Central Swiss Alps.” *Journal of Quaternary Science* 21: 211–25.

Daly, G. T., B. E. Smith, and S. Chua. 1972. “Carbon and Nitrogen Fixation in Rhizomatous Species of Coriaria.” *Proceedings (New Zealand Ecological Society)* 19: 65–74.

Deline, P., S. Gruber, F. Amann, X. Bodin, R. Delaloye, J. Failletaz, L. Fischer, et al. 2021. “Chapter 15—Ice Loss from Glaciers and Permafrost and Related Slope Instability in High-Mountain Regions.” In *Snow and Ice-Related Hazards, Risks, and Disasters*, 2nd ed., edited by W. Haeberli and C. Whiteman, 501–40. Waltham, MA: Elsevier.

Draebing, D., and J. Eichel. 2017. “Spatial Controls of Turf-Banked Solifluction Lobes and their Role for Paraglacial Adjustment in Glacier Forelands.” *Permafrost and Periglacial Processes* 28: 446–59.

Eichel, J., D. Corenblit, and R. Dikau. 2016. “Conditions for Feedbacks between Geomorphic and Vegetation Dynamics on Lateral Moraine Slopes: A Biogeomorphic Feedback Window.” *Earth Surface Processes and Landforms* 41: 406–19.

Eichel, J., D. Draebing, T. Kattenborn, J. A. Senn, L. Klingbeil, M. Wieland, and E. Heinz. 2020. “Unmanned Aerial Vehicle-Based Mapping of Turf-Banked Solifluction Lobe Movement and its Relation to Material, Geomorphometric, Thermal and Vegetation Properties.” *Permafrost and Periglacial Processes* 31: 97–109.

Eichel, J., D. Draebing, L. Klingbeil, M. Wieland, C. Eling, S. Schmidtlein, H. Kuhlmann, and R. Dikau. 2017. “Solifluction Meets Vegetation: The Role of Biogeomorphic Feedbacks for Turf-Banked Solifluction Lobe Development.” *Earth Surface Processes and Landforms* 42: 1623–35.

Eichel, J., D. Draebing, and N. Meyer. 2018. “From Active to Stable: Paraglacial Transition of Alpine Lateral Moraine Slopes.” *Land Degradation & Development* 29: 4158–72.

Eichel, J., D. Draebing, S. Winkler, and N. Meyer. 2022. “Similar Vegetation-Geomorphic Disturbance Feedbacks Shape Unstable Glacier Forelands across Mountain Regions.” Dryad. Dataset. https://doi.org/10.5061/dryad.7d7wm3803.

Eichel, J., M. Krautblatter, S. Schmidtlein, and R. Dikau. 2013. “Biogeomorphic Interactions in the Turtmann Glacier Forefield, Switzerland.” *Geomorphology* 201: 98–110.

Elkington, T. T. 1971. “*Dryas octopetala* L.” *Journal of Ecology* 59: 887–905.

Emmer, A., J. Klimeš, D. Hölbling, L. Abad, D. Draebing, P. Skalák, P. Štěpánek, and P. Zahradníček. 2020. “Distinct Types of Landslides in Moraines Associated with the Post-LIA Glacier

Thinning: Observations from the Kinzl Glacier, Huascarán, Peru." *Science of The Total Environment* 739: 139997.

Environment Canterbury. 2020. *Climate Data for Mount Cook, 2010–2018*. Kaikōura: Environment Canterbury Regional Council, Kaunihera Taiao ki Waitaha.

Erschbamer, B., E. Kneringer, and R. N. Schlag. 2001. "Seed Rain, Soil Seed Bank, Seedling Recruitment, and Survival of Seedlings on a Glacier Foreland in the Central Alps." *Flora* 196: 304–12.

Erschbamer, B., and R. Mayer. 2011. "Can Successional Species Groups be Discriminated Based on their Life History Traits? A Study from a Glacier Foreland in the Central Alps." *Plant Ecology & Diversity* 4: 341–51.

Ewertowski, M. W., and A. M. Tomczyk. 2015. "Quantification of the Ice-Cored Moraines' Short-Term Dynamics in the High-Arctic Glaciers Ebbabreen and Ragnarbreen, Petuniabukta, Svalbard." *Geomorphology* 234: 211–27.

Fischer, A., T. Fickert, G. Schwaizer, G. Patzelt, and G. Groß. 2019. "Vegetation Dynamics in Alpine Glacier Forelands Tackled from Space." *Scientific Reports* 9: 13918.

Flageollet, J.-C. 1996. "The Time Dimension in the Study of Mass Movements." *Geomorphology* 15: 185–90.

Foo, C. L., K. C. Harrington, and M.-A. B. MacKay. 2011. "Weed Suppression by Twelve Ornamental Ground Cover Species." *New Zealand Plant Protection* 64: 149–54.

Franzén, M., P. Dieker, J. Schrader, and A. Helm. 2019. "Rapid Plant Colonization of the Forelands of a Vanishing Glacier Is Strongly Associated with Species Traits." *Arctic, Antarctic, and Alpine Research* 51: 366–78.

Fukami, T., T. M. Bezemer, S. R. Mortimer, and W. H. van der Putten. 2005. "Species Divergence and Trait Convergence in Experimental Plant Community Assembly." *Ecology Letters* 8: 1283–90.

Gentili, R., S. Armiraglio, S. Sgorbati, and C. Baroni. 2013. "Geomorphological Disturbance Affects Ecological Driving Forces and Plant Turnover along an Altitudinal Stress Gradient on Alpine Slopes." *Plant Ecology* 214: 571–86.

Gentili, R., C. Baroni, C. Panigada, M. Rossini, G. Tagliabue, S. Armiraglio, S. Citterio, A. Carton, and M. C. Salvatore. 2020. "Glacier Shrinkage and Slope Processes Create Habitat at High Elevation and Microrefugia across Treeline for Alpine Plants during Warm Stages." *Catena* 193: 104626.

Graf, F., A. Bast, H. Gärtner, and A. Yildiz. 2019. "Effects of Mycorrhizal Fungi on Slope Stabilisation Functions of Plants." In *Recent Advances in Geotechnical Research. Springer Series in Geomechanics and Geoengineering*, edited by W. Wu, 57–77. Cham: Springer.

Grime, J. P. 1977. "Evidence for the Existence of Three Primary Strategies in Plants and its Relevance to Ecological and Evolutionary Theory." *The American Naturalist* 111: 1169–94.

Gurnell, A. M., P. J. Edwards, G. E. Petts, and J. V. Ward. 2000. "A Conceptual Model for Alpine Proglacial River Channel Evolution under Changing Climatic Conditions." *Catena* 38: 223–42.

Harley, J. L., and E. L. Harley. 1987. "A Check-List of Mycorrhiza in the British Flora." *The New Phytologist* 105: 1–102.

Haselberger, S., L.-M. Ohler, R. R. Junker, J.-C. Otto, T. Glade, and S. Kraushaar. 2021. "Quantification of Biogeomorphic Interactions between Small-Scale Sediment Transport and Primary Vegetation Succession on Proglacial Slopes of the Gepatschferner, Austria." *Earth Surface Processes and Landforms* 46: 1941–52.

Haugland, J. E. 2006. "Short-Term Periglacial Processes, Vegetation Succession, and Soil Development within Sorted Patterned Ground: Jotunheimen, Norway." *Arctic, Antarctic, and Alpine Research* 38: 82–9.

Haugland, J. E., and S. W. Beatty. 2005. "Vegetation Establishment, Succession and Microsite Frost Disturbance on Glacier Forelands within Patterned Ground Chronosequences." *Journal of Biogeography* 32: 145–53.

Hodkinson, I. D., S. J. Coulson, and N. R. Webb. 2003. "Community Assembly along Proglacial Chronosequences in the High Arctic: Vegetation and Soil Development in North-West Svalbard." *Journal of Ecology* 91: 651–63.

Hugonnet, R., R. McNabb, E. Berthier, B. Menounos, C. Nuth, L. Girod, D. Farinotti, et al. 2021. "Accelerated Global Glacier Mass Loss in the Early Twenty-First Century." *Nature* 592: 726–31.

Jäger, D., and S. Winkler. 2012. "Paraglacial Processes on the Glacier Foreland of Vernagtferner (Ötztal Alps, Austria)." *Zeitschrift für Geomorphologie, Supplementary Issues* 56: 95–113.

Jenny, H. 1941. *Factors of Soil Formation*. New York: McGraw-Hill.

Jenny-Lips, H. 1930. "Vegetationsbedingungen und Pflanzengesellschaften auf Felsschutt: Phytosoziologische Untersuchungen in den Glarner Alpen." Doctoral Thesis, ETH Zurich.

Johnson, E. A., and K. Miyanishi. 2008. "Testing the Assumptions of Chronosequences in Succession." *Ecology Letters* 11: 419–31.

Jones, C. C., and R. Del Moral. 2009. "Dispersal and Establishment both Limit Colonization during Primary Succession on a Glacier Foreland." *Plant Ecology* 204: 217–30.

Jones, G. A., and G. H. R. Henry. 2003. "Primary Plant Succession on Recently Deglaciated Terrain in the Canadian High Arctic." *Journal of Biogeography* 30: 277–96.

Jumpponen, A., H. Vare, K. G. Mattson, R. Ohtonen, and J. M. Trappe. 1999. "Characterization of "Safe Sites" for Pioneers in Primary Succession on Recently Deglaciated Terrain." *Journal of Ecology* 87: 98–105.

Kattge, J., G. Bönisch, S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, S. Tautenhahn, G. D. Werner, T. Aakala, and M. Abedi. 2020. "TRY Plant Trait Database–Enhanced Coverage and Open Access." *Global Change Biology* 26: 119–88.

Kenner, R., J. Noetzli, M. Hoelzle, H. Raetzo, and M. Phillips. 2019. "Distinguishing Ice-Rich and Ice-Poor Permafrost to Map Ground Temperatures and Ground Ice Occurrence in the Swiss Alps." *The Cryosphere* 13: 1925–41.

Klarenberg, I. J., C. Keuschnig, A. J. Russi Colmenares, D. Warshan, A. D. Jungblut, I. S. Jónsdóttir, and O. Vilhelmsson. 2022. "Long-Term Warming Effects on the Microbiome and nifH Gene Abundance of a Common Moss Species in Sub-Arctic Tundra." *New Phytologist* 234: 2044–56.

Klimešová, J., and F. D. Bello. 2009. "CLO-PLA: The Database of Clonal and Bud Bank Traits of Central European Flora." *Journal of Vegetation Science* 20: 511–6.

Knight, J., and S. Harrison. 2009. "Sediments and Future Climate." *Nature Geoscience* 2: 230.

Körner, C. 2003. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Cham: Springer, Berlin, Heidelberg.

Kosiński, P., K. Sękiewicz, Ł. Walas, A. Boratyński, and M. Dering. 2019. "Spatial Genetic Structure of the Endemic Alpine Plant *Salix serpillifolia*: Genetic Swamping on Nunataks Due to Secondary Colonization?" *Alpine Botany* 129: 107–21.

Krautzer, B., W. Graiss, G. Peratoner, C. Partl, S. Venerus, and B. Klug. 2011. "The Influence of Recultivation Technique and Seed Mixture on Erosion Stability after Restoration in Mountain Environment." *Natural Hazards* 56: 547–57.

Kutschera, L., E. Lichtenegger, and M. Sobotik. 1997. *Bewurzelung von Pflanzen in Verschiedenen Lebensräumen*. Linz: OÖ Landesmuseum.

Lane, S. N., M. Bakker, C. Gabbud, N. Micheletti, and J.-N. Saugy. 2017. "Sediment Export, Transient Landscape Response and Catchment-Scale Connectivity Following Rapid Climate Warming and Alpine Glacier Recession." *Geomorphology* 277: 210–27.

Lauber, K., and G. Wagner. 2018. *Flora Helvetica*. Bern: Haupt Verlag.

Lautenschlager-Fleury, D., and E. Lautenschlager-Fleury. 1994. *Die Weiden von Mittel- und Nordeuropa: Bestimmungsschlüssel und Artbeschreibungen für die Gattung Salix L.*, 2nd ed. Basel: Birkhäuser.

Losapio, G., B. E. L. Cerabolini, C. Maffioletti, D. Tampucci, M. Gobbi, and M. Caccianiga. 2021. "The Consequences of Glacier Retreat Are Uneven between Plant Species." *Frontiers in Ecology and Evolution* 8: 616562.

Matsuoka, N. 2001. "Solifluction Rates, Processes and Landforms: A Global Review." *Earth-Science Reviews* 55: 107–34.

Matthews, J. A. 1992. *The Ecology of Recently-Deglaciated Terrain: A Geoecological Approach to Glacier Forelands*. Cambridge: Cambridge University Press.

Matthews, J. A. 1999. "Disturbance Regimes and Ecosystem Response on Recently-Deglaciated Terrain." In *Ecosystems of Disturbed Ground*, edited by L. R. Walker, 17–37. Amsterdam: Elsevier.

Matthews, J. A., R. A. Shakesby, M. S. Berrisford, and L. J. McEwen. 1998. "Periglacial Patterned Ground on the Styggedalsbreen Glacier Foreland, Jotunheimen, Southern Norway: Micro-Topographic, Paraglacial and Geoecological Controls." *Permafrost and Periglacial Processes* 9: 147–66.

McGraw, J. B. 1985. "Experimental Ecology of *Dryas octopetala* Ecotypes: Relative Response to Competitors." *New Phytologist* 100: 233–41.

MeteoSwiss. 2017. "Climate Data Station Turtmann, 2014–2017." Provided by MeteoSwiss, the Swiss Federal Office of Meteorology and Climatology. https://www.meteoswiss.admin.ch/services-and-publications/applications/measurement-values-and-measuring-networks.html.

Michel, P., I. J. Payton, W. G. Lee, and H. J. During. 2013. "Impact of Disturbance on above-Ground Water Storage Capacity of Bryophytes in New Zealand Indigenous Tussock Grassland Ecosystems." *New Zealand Journal of Ecology* 37: 114–26.

Moreau, M., D. Mercier, D. Laffly, and E. Roussel. 2008. "Impacts of Recent Paraglacial Dynamics on Plant Colonization: A Case Study on Midtre Lovénbreen Foreland, Spitsbergen (79° N)." *Geomorphology* 95: 48–60.

Neugirg, F., A. Kaiser, A. Huber, T. Heckmann, M. Schindewolf, J. Schmidt, M. Becht, and F. Haas. 2016. "Using Terrestrial LiDAR Data to Analyse Morphodynamics on Steep Unvegetated Slopes Driven by Different Geomorphic Processes." *Catena* 142: 269–80.

Norris, J. E., A. Di Iorio, A. Stokes, B. C. Nicoll, and A. Achim. 2008. "Species Selection for Soil Reinforcement and Protection." In *Slope Stability and Erosion Control: Ecotechnological Solutions*, edited by J. E. Norris, A. Stokes, S. B. Mickovski, E. Cammeraat, R. van Beek, B. C. Nicoll, and A. Achim, 167–210. Dordrecht: Springer Netherlands.

Odling-Smee, J., D. H. Erwin, E. P. Palkovacs, M. W. Feldman, and K. N. Laland. 2013. "Niche Construction Theory: A Practical Guide for Ecologists." *The Quarterly Review of Biology* 88: 4–28.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, et al. 2020. "vegan: Community Ecology Package." https://cran.r-project.org/web/packages/vegan/vegan.pdf.

Otto, J.-C., and R. Dikau. 2004. "Geomorphic Analysis of a High Mountain Valley in the Swiss Alps." *Zeitschrift für Geomorphologie, N.F.* 38: 323–41.

Phillips, J. D. 2016. "Biogeomorphology and Contingent Ecosystem Engineering in Karst Landscapes." *Progress in Physical Geography* 40(4): 503–26.

Pierce, S., A. Luzzaro, M. Caccianiga, R. M. Ceriani, and B. Cerabolini. 2007. "Disturbance Is the Principal α-Scale Filter Determining Niche Differentiation, Coexistence and Biodiversity in an Alpine Community." *Journal of Ecology* 95: 698–706.

R Development Core Team. 2020. *The R Project for Statistical Computing*. Vienna: R Development Core Team. http://www.r-project.org/.

Raffl, C., M. Mallaun, R. Mayer, and B. Erschbamer. 2006. "Vegetation Succession Pattern and Diversity Changes in a Glacier Valley, Central Alps, Austria." *Arctic, Antarctic, and Alpine Research* 38: 421–8.

Rapp, A. 1960. "Recent Development of Mountain Slopes in Kärkevagge and Surroundings, Northern Scandinavia." *Geografiska Annaler* 42: 65–200.

Rauh, W. 1939. "Über polsterförmigen Wuchs. Ein Beitrag zur Kenntnis der Wuchsformen der höheren Pflanzen." *Nova Acta Leopold* 7: 272–505.

Roncoroni, M., J. Brandani, T. I. Battin, and S. N. Lane. 2019. "Ecosystem Engineers: Biofilms and the Ontogeny of Glacier Floodplain Ecosystems." *WIREs Water* 6: e1390.

Schmidtlein, S., L. Tichý, H. Feilhauer, and U. Faude. 2010. "A Brute-Force Approach to Vegetation Classification." *Journal of Vegetation Science* 21: 1162–71.

Schröter, C., H. Brockmann-Jerosch, M. C. Brockmann-Jerosch, A. Günthart, P. Vogler, and G. Huber-Pestalozzi. 1926. *Das Pflanzenleben der Alpen*. Zürich: Albert Raustein.

Snelder, D. J., and R. B. Bryan. 1995. "The Use of Rainfall Simulation Tests to Assess the Influence of Vegetation Density on Soil Loss on Degraded Rangelands in the Baringo District, Kenya." *Catena* 25: 105–16.

Sommerville, P., A. F. Mark, and J. B. Wilson. 1982. "Plant Succession on Moraines of the Upper Dart Valley, Southern South Island, New Zealand." *New Zealand Journal of Botany* 20: 227–44.

Stawska, M. 2017. "Impacts of Geomorphic Disturbances on Plant Colonization in Ebba Valley, Central Spitsbergen, Svalbard." *Quaestiones Geographicae* 36: 51–64.

Stöcklin, J., and E. Bäumler. 1996. "Seed Rain, Seedling Establishment and Clonal Growth Strategies on a Glacier Foreland." *Journal of Vegetation Science* 7: 45–56.

Stokes, A., C. Atger, A. G. Bengough, T. Fourcaud, and R. C. Sidle. 2009. "Desirable Plant Root Traits for Protecting Natural and Engineered Slopes against Landslides." *Plant and Soil* 324: 1–30.

Temme, A. J. A. M., and K. Lange. 2014. "Proglacial Soil Variability and Geomorphic Activity—The Case of Three Swiss Valleys." *Earth Surface Processes and Landforms* 39: 1492–9.

Toy, T. J., G. R. Foster, and K. G. Renard. 2002. *Soil Erosion: Processes, Prediction, Measurement, and Control*. New York: John Wiley & Sons.

Tscherko, D., U. Hammesfahr, G. Zeltner, E. Kandeler, and R. Böcker. 2005. "Plant Succession and Rhizosphere Microbial Communities in a Recently Deglaciated Alpine Terrain." *Basic and Applied Ecology* 6: 367–83.

Tscherrig, A. 1965. "Turtmanngletscher. Situations-Plan der Gletscher-Veränderungen 1850–1964, Forstdepartement des Kantons Wallis, Gemeinde Ober-Ems (1965)." Unpublished Records.

van Woerkom, T., J. F. Steiner, P. D. A. Kraaijenbrink, E. S. Miles, and W. W. Immerzeel. 2019. "Sediment Supply from Lateral Moraines to a Debris-Covered Glacier in the Himalaya." *Earth Surface Dynamics* 7: 411–27.

Vannoppen, W., M. Vanmaercke, S. De Baets, and J. Poesen. 2015. "A Review of the Mechanical Effects of Plant Roots on Concentrated Flow Erosion Rates." *Earth-Science Reviews* 150: 666–78.

Vitt, D. H., and C. Marsh. 1988. "Population Variation and Phytogeography of *Racomitrium lanuginosum* and *R. pruinosum*." *Nova Hedwigia* 90: 235–60.

Walker, L. R., B. D. Clarkson, W. B. Silvester, and B. R. Clarkson. 2003. "Colonization Dynamics and Facilitative Impacts of a Nitrogen-Fixing Shrub in Primary Succession." *Journal of Vegetation Science* 14: 277–90.

Wardle, P. 1972. "Plant Succession on Greywacke Gravel and Scree in the Subalpine Belt in Canterbury, New Zealand." *New Zealand Journal of Botany* 10: 387–98.

Winkler, S. 2004. "Lichenometric Dating of the 'Little Ice Age' Maximum in Mt Cook National Park, Southern Alps, New Zealand." *The Holocene* 14: 911–20.

Winkler, S. 2015. "Observations of Paraglacial Processes on Glacier Forelands in Aoraki/Mount Cook National Park, Southern Alps, New Zealand." Geophysical Research Abstracts. 1492 pp.

Winkler, S. 2018. "Investigating Holocene Mountain Glaciations: A Plea for the Supremacy of Glacial Geomorphology when Reconstructing Glacier Chronologies." *Erdkunde* 72: 215–34.

Wiser, S. K., R. P. Buxton, B. R. Clarkson, S. J. Richardson, G. M. Rogers, M. C. Smale, and P. A. Williams. 2010. "Climate, Landscape and Microenvironment Interact to Determine Plant Composition in Naturally Discrete Gravel Beach Communities." *Journal of Vegetation Science* 21: 657–71.

Wojcik, R., J. Eichel, J. A. Bradley, and L. G. Benning. 2021. "How Allogenic Factors Affect Succession in Glacier Forefields." *Earth-Science Reviews* 218: 103642.

Wolman, M. G., and J. P. Miller. 1960. "Magnitude and Frequency of Forces in Geomorphic Processes." *The Journal of Geology* 68: 54–74.

Wookey, P. A., C. H. Robinson, A. N. Parsons, J. M. Welker, M. C. Press, T. V. Callaghan, and J. A. Lee. 1995. "Environmental Constraints on the Growth, Photosynthesis and Reproductive Development of *Dryas octopetala* at a High Arctic Polar Semi-Desert, Svalbard." *Oecologia* 102: 478–89.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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