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Primary succession and its driving variables – a holistic approach applied in three proglacial areas in the upper Martell Valley (Eastern Italian Alps)

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Abstract. Climate change and the associated glacier retreat lead to considerable enlargement and alterations of the proglacial systems. The colonisation of plants in this ecosystem was found to be highly depending on terrain age, initial site conditions and geomorphic disturbances. Although the explanatory variables are generally well understood, there is little knowledge on their collinearities and resulting influence on proglacial primary succession. To develop a holistic understanding of vegetation development, a more interdisciplinary approach was adopted. In the proglacial area of Fürkele-, Zufall-, and Langenferner (Martell Valley/Eastern Italian Alps), totally 65 plots of 5 × 2 m were installed to perform the vegetation analysis on vegetation cover, species number, and species composition. For each of those, 30 potential explanatory variables were collected, selected through an extensive literature review. To analyse and further avoid multicollinearities, 26 of the explanatory variables were clustered via Principal Component Analysis (PCA) to five components. Subsequently, generalised additive models (GAM) were used to analyse the potential explanatory factors of primary succession. The results showed that primary succession patterns were highly related to the first component (‘elevation and time’), the second component (‘solar radiation’), and the third component (‘south-eastness’) as well as snow free freeze-thaw days, and landforms. In summary, the analysis of all explanatory variables together provides an overview of the most important influencing variables and their interactions, and thus a basis for the debate on future vegetation development in a changing climate.

1 Introduction

Due to climate change and the associated glacier retreat, proglacial areas, which are defined as landscapes that became deglaciated since the high stand glacier extent of the Little Ice Age (LIA, mid-19th century, e.g., Carrivick et al., 2019 and references therein), undergo considerable enlargement and structural changes. The extent and rate of change in proglacial areas (e.g., primary succession) are influenced by different variables. According to the geoscientific concept of spheres (Sintubin, 2008; Stötter et al., 2014), these variables can be assigned to different spheres (Biosphere, Atmosphere, Cryosphere as part of the Hydrosphere, Relief sphere, Pedosphere, and Anthroposphere). Sintubin (2008) and Stötter et al. (2014) outlined that these spheres are interconnected and influence each other, to varying degrees, which has been supported by a large number of studies. The main interactions are highlighted in Figure 1. Primary succession in the proglacial area is profoundly affected by variations in temperature and solar radiation (Kaufmann, 2002; Raffl et al., 2006; Schumann et al., 2016). However, due to the interconnection of the spheres, which are all significantly modified by climate warming, proglacial vegetation development is further indirect influenced in diverse ways (Wojcik et al., 2021, and references therein). Atmospheric changes have strongly altered the temporal and spatial distribution of (sub)surface frost and ice occurrences (high mountain cryosphere); (Hock et al., 2019). As a result the time-depending processes, in dependency of e.g. deglaciation and the encompassing site conditions and geomorphic processes are constantly modified by changes of the cryosphere (Wojcik et al., 2021 and references therein). In addition, the climate driven changes of the mountain cryosphere directly impact both, the hydrological system (Wehren et al., 2010) and the relief sphere (Beniston, 2006), leading to substantial variations of microclimatic and microtopographic

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patterns. All these factors in turn control the dynamics of soil formation and alteration, and they are closely related to the spatial variability of vegetation development and plant diversity. The distinct changing vegetation patterns in the proglacial area during landscape evolution, in turn, modify the microclimatic regime (i.e., temperature and humidity) due to changes in surface albedo and in evapotranspiration (Larcher, 1984) and increase the aggregate stability of soils and lead to changes in sediment fluxes. The mutual reaction between the stabilising effects of vegetation traits and geomorphic processes is investigated e.g. by Eichel et al. (2013, 2016, 2018) and presented as a conceptual model in Wojcik et al. (2021). Furthermore, also the anthropogenic impact on the system has to be mentioned, not only by the effect of global climate change but also by livestock grazing and/or trampling, practiced up to the proglacial areas (Theurillat et al., 1998).

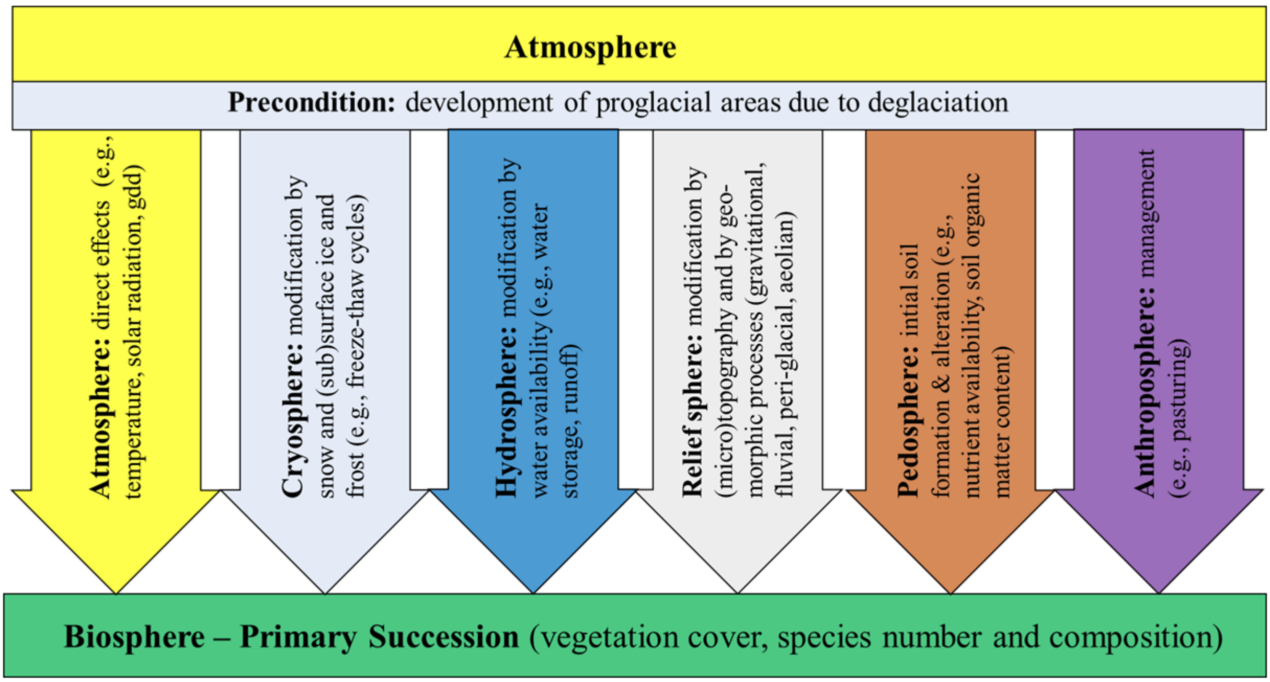

Figure 1: The main direct and indirect effects of atmospheric forcing on primary vegetation succession in proglacial systems (e.g., Hock et al., 2019; Wojcik et al., 2021).

The interaction of these variables leads to a spatially heterogenic pattern and development of the proglacial area which optically can be detected very clearly via the vegetation conditions on a small scale. In order to explain patterns of proglacial vegetation succession, it is necessary to include as many potential explanatory variables from different spheres as possible. The comprehension of these interaction processes will help to predict how the proglacial areas will develop under future climate change. Scientists currently assume an increase in mean temperature with a stronger increase for the summer (Kotlarski et al.,

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2022), depending on the climate scenario, season, and region. Also a shift from solid to liquid precipitation due to higher temperature can be observed (Serquet et al., 2011; Kotlarski et al., 2022).

As summarised in Table 1, a large number of studies exist on primary succession in proglacial areas worldwide (e.g. European Alps: Raffl and Erschbamer, 2004; Fickert, 2020; Himalaya: Jiang et al., 2018; Andes: Llambí et al., 2021), although most of them only consider a few potential explanatory variables in their analyses. Although already Matthews (1992) recommended a multidisciplinary approach, to our knowledge only the study of Schumann et al. (2016) considers the influence of potential explanatory variables that covering all the spheres mentioned above. But even this study neglects some of the potential explanatory variables such as snow and (perennial) frost, which are expected to significantly change the patterns of primary succession in the face of climate change (Kaufmann and Raffl, 2002; Marcante et al., 2012).

In our study, we aimed to explain primary succession on proglacial areas in the Eastern Italian Alps by an approach as holistic as possible. We analysed the impact of as many potential explanatory variables as available, categorised according to the geoscientific concept of spheres. Our objectives were: (1) We conducted a comprehensive literature review on potential explanatory variables known to influence vegetation development in proglacial areas. (2) We investigated primary succession on three proglacial areas in the Eastern Italian Alps by recording total vegetation cover and plant species number. (3) We used the from literature known potential explanatory variables to test the following hypotheses: i) Many of the known potential explanatory variables are correlated and can be summarised to a few numbers of components using a Principal Component Analysis (PCA). ii) The most important explanatory variables for vegetation cover development include years since deglaciation, elevation, and climatic variables. iii) Disturbances such as geomorphic disturbance and grazing/trampling reduce cover and species number and thus changes also species composition. iv) We expected that there are no single potential explanatory variables, and we will provide a better understanding of primary succession for prediction of future development.

2 Study area

The studied proglacial areas of the once united contiguous glaciers Fürkele-, Zufall-, and Langenferner are located within the Ortles-Cevedale group in the Upper Martell Valley (46.46 °N, 10.64 °E, Fig. 2a), Autonomous Province of Bozen/Bolzano, Italy. The study area extends from 2367 m above sea level (a.s.l.) to 2881 m a.s.l. and is NE-SW orientated. Totally 65 plots (Fig. 2c), first described by Knoflach et al. (2021), were located on the ground and lateral moraines at the proglacial areas along the elevation gradient. The study area is mainly characterised by chlorite-secerite leading micaschist consisting of alluvial and glacial deposits (Martin et al., 2009), which exhibit spatially very heterogeneous soil formations (Martin et al., 2009). Additionally, deposits of quartzite and marble can be found (Martin et al., 2009). The study area is located in the Central Alps within the tundra climate (ET) (Kottek et al., 2006) with a mean daily air temperature of 10-12 °C in July (Station Zufritt; based on data from the 3PCLIM-project; source: www.3pclim.eu), and maximum precipitation of 76-100 mm in July (Station Zufritt; based on data form the 3PCLIM-project; source: www.3pclim.eu).

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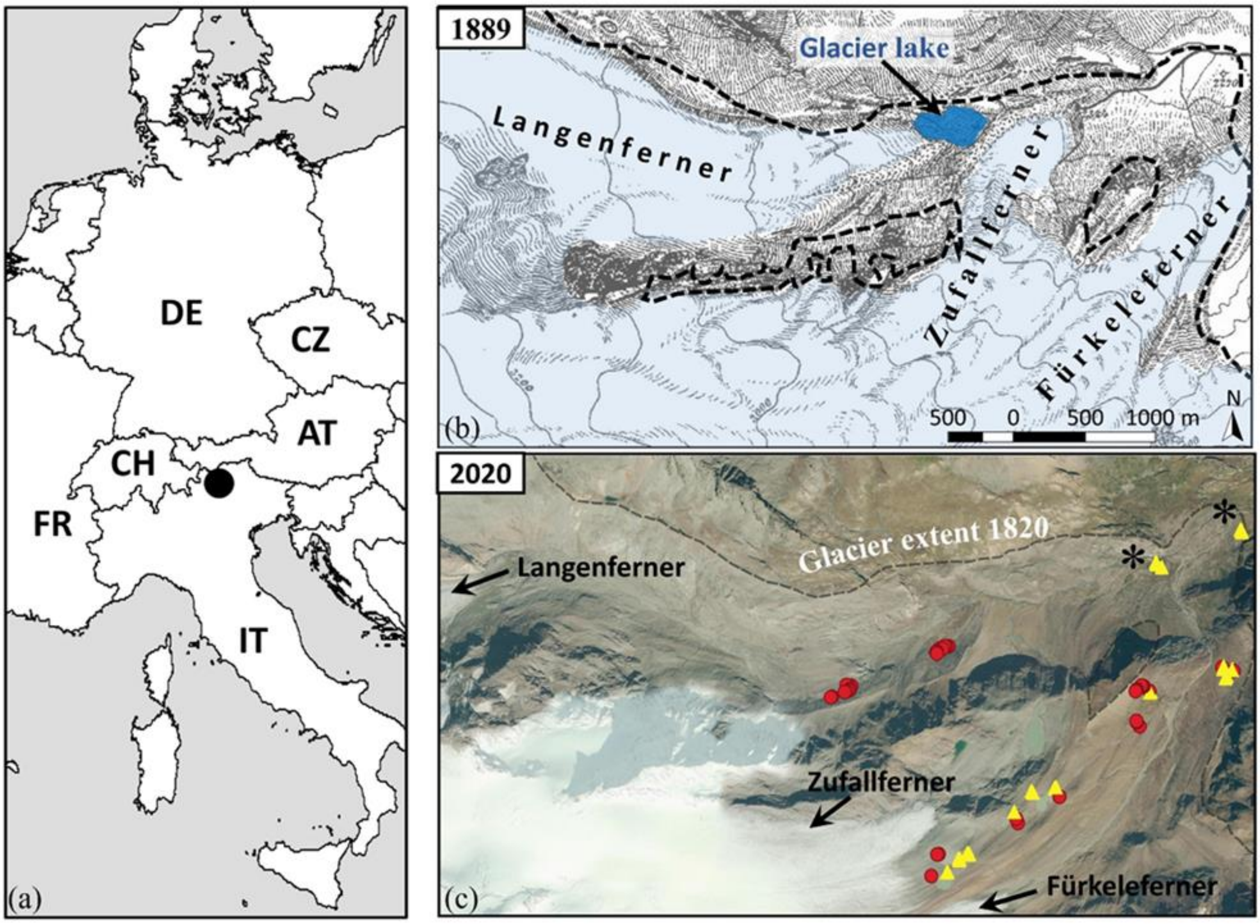

Figure 2: (a) Study area and (b) glacier tongues of Fürkele-, Zufall-, and Langenferner in 1889 (Finsterwalder, 1890); modified) with the glacier extent around 1820 (Ivy-Ochs et al., 2009; Kinzl, 1932) (end of the LIA = black dashed line), (c) distribution of the vegetation plots in the proglacial area of Fürkele-, Zufall-, and Langenferner with the glacier extent around 1820 (Ivy-Ochs et al., 2009; Kinzl, 1932) (end of LIA = black dashed line; * = plots influenced by glacier lake outburst). Source of orthophoto: Autonomous Province of Bozen/Bolzano, Italy 2020 (red dots = geomorphologically disturbed plots, yellow triangles = stable plots).

3 Material and methods

The study consists of two steps: in the first step, a literature review was performed for defining the potential explanatory variables. In a second step, as many potential explanatory variables as possible were collected from the three proglacial areas of Fürkele-, Zufall- and Langenferner and implemented in a Principal Component Analysis (PCA) and Generalised Additive Models (GAM) as well as a nonmetric multidimensional scaling to investigate their influence on primary succession.

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3.1 Literature review: Definition of the potential explanatory variables

As a preselection of potential explanatory variables for primary succession for primary succession (in particular, vegetation cover, species number, and species composition) in the proglacial area, we conducted a systematic review of existing literature (google scholar on 15/12/2021). To find articles which relate to vegetation analyses in proglacial areas, the search term had to contain vegetation- and glacier-related strings (intitle:vegetation OR intitle:plant OR intitle: succession AND intitle: glacier OR intitle:proglacial). Additionally, we added the string 'alps' to limit the search to alpine areas. From 176 publications, all non-scientific articles (only peer-reviewed journals and books written in English or German language were considered), and those not focusing on primary vegetation succession in proglacial areas (e.g., studies on rock glaciers) were excluded manually. All remaining articles (n = 45) were considered (listed in the Supplement, Table S1). In total, 39 potential explanatory variables emerged from these articles (Fig. 3b). From these 39 potential explanatory variables we excluded variables only mentioned once or twice (e.g., wind exposure, snow depth, or soil type), except they could be relevant due to climate change, or variables not available for this study (e.g., soil depth, soil colour or soil texture). Therefore, we ultimately used 31 potential explanatory variables and three dependent variables in our study.

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Table 1: Dependent and potential explanatory variables and assignment to the spheres as a result of the literature review, and details of the data sources and collection methods used in this study calculated for the entire year and the growing season (gs). Some parameters were generated with the Water Flow and Balance Simulation Model WaSiM (Schulla and Jasper, 2019) and averaged for the years 2018/19 (*).

Sphere	**Dependent variables**	**Literature source**	**Data source**	**Methodical information**
Biosphere	Total vegetation cover (%)	1, 2, 4-6, 9, 11, 12, 14-17, 20-22, 24, 25, 27, 29, 31, 35-39, 41-45	Own field data from 2019/20	
	Total species number (n)	1, 3-7, 9, 11-13, 15, 18-22, 25-27, 29, 31, 34, 35, 37-42, 44, 45	Own field data from 2019/20	
	Successional stages	1, 3, 4, 9, 12, 14, 20-24, 26, 28, 29, 32, 34-38, 40, 41, 44, 45	(Knoflach et al., 2021)	Nonmetric Multidimensional Scaling (NMDS), Two Way INdicator SPecies ANalysis (TWINSPAN)
Sphere	**Potentially explanatory variables**	**Literature source**	**Data source**	**Methodical information**
Atmosphere	Solar radiation, annual (W m^{-2} d^{-1}) *	1, 6, 9, 10, 20, 26, 28, 33, 35, 37, 39	WaSiM	corrected for inclination and aspect (Oke, 1987)
	Solar radiation, gs (W m^{-2} d^{-1}) *		WaSiM	corrected for inclination and aspect (Oke, 1987)
	Mean max. temperature, annual (°C) *		WaSiM	mean daily temperature maxima, corrected for daily sunshine duration, aspect and local zenith angle (Schulla and Jasper, 2019)
	Mean max. temperature, gs (°C) *		WaSiM	mean daily temperature maxima, corrected (see above)
	Mean temperature, annual (°C) *	9, 13, 22	WaSiM	mean daily temperature means, corrected (see above)
	Mean temperature, gs (°C) *		WaSiM	mean daily temperature means, corrected (see above)
	Mean min. temperature, annual (°C) *		WaSiM	mean daily temperature minima, corrected (see above)
	Mean min. temperature, gs (°C) *		WaSiM	mean daily temperature minima, corrected (see above)
	Snow free gdd (n) *	47	WaSiM	calculated following Francon et al. (2021), Carlson et al. (2017), and Molau (1993)
Cryosphere	Years since deglaciation (n)	1-13, 15-17, 19-45	See supplement Table2	
	Terrain age (n)		Own data	years since glacial melt or last debris flow deposition or lake outburst
	Distance to glacier (m)	4, 5, 13, 16, 18, 36, 43	Orthophoto 2020 (©Autonome Provinz Bozen-Südtirol)	Derived with the ‚near‘ function in ArcGIS10.6®
	Snow free freeze-thaw days (n) *		WaSiM	calculated following Schmidlin et al.(1987)
	Days with snow cover (n) ‘	39	WaSiM	calculated following Hofmeister et al. (2022)
Hydrosphere	Topographic wetness index (TWI)	1, 5, 10	Derived from DTM (2019) (© Physical geography, KU Eichstätt-Ingolstadt)	calculated in ArcGIS 10.6®
	Sum precipitation, annual (mm d-1)	1, 26	WaSim	

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	Sum precipitation, gs (mm d-1)		WaSiM	
Relief sphere	Landforms	5, 6, 8, 36, 40	(Elsner et al., unpublished)	
	Inclination (°)	1, 4, 5, 10, 15, 20, 21, 26, 28, 33, 34, 37, 38, 40, 45	Derived from DTM (2019) (© Physical Geography, KU Eichstätt-Ingolstadt)	calculated in ArcGIS 10.6®
	Aspect (northness/eastness)	1, 4, 5, 9, 10, 15, 20, 21, 26, 33, 37, 38, 40, 44	Derived from DTM (2019) ((© Physical Geography, KU Eichstätt-Ingolstadt)	aspect calculated in ArcGIS 10.6®, converted to northness/eastness according to Dial (2017)
	Elevation	1, 2, 4, 6-12, 15, 20, 21, 26, 28, 32, 33, 35-38, 40, 45	Derived from DTM (2019) ((© Physical Geography, KU Eichstätt-Ingolstadt)	
	Curvature		Derived from DTM (2019) ((© Physical Geography, KU Eichstätt-Ingolstadt)	calculated in ArcGIS 10.6®
	Disturbance (Stream power index SPI)		Derived from DTM (2019) ((© Physical Geography, KU Eichstätt-Ingolstadt)	calculated according to Florinsky (2017) in ArcGIS 10.6®
	Disturbance	1, 6, 11, 20, 22, 36, 40, 43, 45	Own field data from 2019/20	Observations in the field (small gullies, visible instability)
Pedosphere	Soil humus, community weighted mean (m_w_H)	22	Own field data from 2019/20	gradient from humus poor soils (1) to humus rich soils (5) (Landolt et al., 2010)
	Soil nutrients, community weighted mean (m_w_N)	22	Own field data from 2019/20	gradient from nutrient poor soils (1) to nutrient rich soils (5) (Landolt et al., 2010)
	Soil reaction, community weighted mean (m_w_R)	22	Own field data from 2019/20	gradient from acidic soils (1) to carbonate containing alkaline soils (5) (Landolt et al., 2010)
	Soil moisture, community weighted mean (m_w_F)	22	Own field data from 2019/20	Gradient from very dry (1) to flooded/under water (5) (Landolt et al., 2010)
	Scree cover (%)	1, 5, 6, 14, 15, 21, 23, 26, 31, 34, 36, 40, 41	Own field data from 2019/20	Estimated in the field during vegetation surveys (1 class)
Anthroposphere	Anthropogenic impact through grazing/trampling (yes/no)	26	Own field data from 2019/20	Estimated in the field (Observation of livestock faces or trampling)

[1]Haselberger et al. (2021), [2]Knoflach et al. (2021), [3]Losapio et al. (2021), [4]Wei et al. (2021), [5]Wietrzyk-Pelka et al. (2021), [6]Wojcik et al. (2021), [7]Llambí et al. (2021), [8]Bayle (2020), [9]Fickert (2020), [10]Lambert et al. (2020), [11]Eichel (2019), [12]Fischer et al. (2019), [13]Franzén et al. (2019), [14]Szymański et al. (2019), [15]Fickert and Grüninger (2018), [16]Wietrzyk et al. (2018), [17]Mazhar et al. (2018), [18]Cazzolla Gatti et al. (2018), [19]Jiang et al. (2018), [20]D'Amico et al. (2017), [21]Fickert (2017), [22]Fickert et al. (2017), [23]Sitzia et al. (2017), [24]Göransson et al. (2016), [25]Erschbamer and Caccianiga (2016), [26]Schumann et al. (2016), [27]Tampucci et al. (2017), [28]Carlson et al. (2014), [29]D'Amico et al. (2014), [30]Fischer (2013), [31]Burga

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et al. (2010), [32]Robbins and Matthews (2010), [33]Jones and del Moral(2009), [34]Dolezal et al. (2008), [35]Raffl et al. (2006), [36]Mizuno (2005), [37]Caccianiga and Andreis (2004), [38]Raffl and Erschbamer (2004), [39]Kaufmann and Raffl (2002), [40]Andreis et al. (2001), [41]Burga (1999), [42]Frenot et al. (1998), [43]Mizuno (1998), [44]Vetaas (1994), [45]Matthews and Whittaker (1987)

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3.2 Dependent variables: Vegetation indicators (Biosphere)

The vegetation surveys in the three glacier forelands of Fürkele-, Zufall-, and Langenferner were carried out in July/August of 2019 and 2020 (n = 65) (Fig. 2c). For each of the study plots with a size of 5 m × 2 m, the total vegetation cover, all individual vascular species, and their cover (%) were recorded. The nomenclature of the species follows Fischer et al. (2008). Mosses and lichens were considered as own functional groups. According to the change in species composition along the chronosequence, Knoflach et al. (2021) discriminated four successional stages: (i) a pioneer stage, (ii) an early successional stage, (iii) a late successional stage with snowbed and grassland communities, and (iv) a climax stage with dwarf shrub, by performing a Nonmetric MultiDimensional Scaling (NMDS) and a Two Way Indicator Species Analysis (TWINSPAN).

3.3 Potential explanatory variables

3.3.1 Atmosphere

Based on the meteorological data from different weather stations (Supplement, Table S2), distribution maps (25 m × 25 m) of daily temperature (maxima, mean, and minima), and topographically corrected solar radiation were generated by the fully distributed Water Flow and Balance Simulation Model (WaSiM) (Schulla and Jasper, 2019). We spatially interpolated the meteorological variables temperature, wind speed, and humidity with an elevation dependent regression algorithm. Precipitation and solar radiation were interpolated with an inverse divergence weighting (IDW) method. The model setup and parameterisation published by Hofmeister et al. (2022) was used. The beginning and the end of the growing season were defined, following Bishop and Bishop (2014), by the mean temperature of 0 °C for four consecutive days (above 0 °C: start of the season; below 0 °C: end of the season) and the simultaneous absence of snow cover. Following Molau (1993), Carlson et al. (2017), and Francon et al. (2021), the number of annual snow free growing degree days (gdd) was defined as number of days with a mean daily air temperature above 0 °C. This was chosen because, especially in high alpine environments, germination and growth are possible at temperatures just above 0 °C (Kost, 2014). The calculation was done for the years 2018 and 2019 as the youngest plots were at least deglaciated since 2018. All atmosphere-related variables are listed in Table 1.

3.3.2 Cryosphere

In order to determine the temporal exposure of the study plot to non-glacial conditions, a high-resolution glacial reconstruction was carried out based by using (i) hill shade maps created from Airborne Laser Scanning (ALS) digital elevation models, (ii) aerial images, (iii) historical maps and photographs, and (iv) field investigations (Supplement, Table S3). The primary succession of some experimental plots was restarted after glacier lake outburst floods (Fig. 2b). Historical documents show that "The Martell Valley was affected by water catastrophes in the past two years (1888 and 1889), which in their magnitude and peculiarity as well as the intital reason for their causes, are likely to attract the interest of wider circles. […] […] in an unusual place an exalted glacier snout had formed, from which the water must in all probability have poured out. […]" (Finsterwalder, 1890): 21; translated from German).

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Seven study plots (*, Fig. 2c) are located in this lower proglacial area which was affected by outburst floods of these ice-dammed lakes.(Fig. 1b)Further outburst floods of the ice-dammed lakes were reported from 1891 (DOeAV, 1891) and 1895 (DOeAV, 1895). Since these plots were affected by these high impact disturbances and the succession was restarted, the actual terrain age (time zero of succession) was considered as a further variable in the analyses (Table 1).

The parameter 'distance to the glacier front' was determined as the shortest distance from every single study plot to the glacier tongue using the 'near' function in ArcGIS 10.6®. Information on the number of days with snow cover was derived from WaSiM (Schulla and Jasper, 2019) for the years 2018/19 by Hofmeister et al. (2022). Snowmelt is simulated with the energy balance method, which computes the energy fluxes on the top of the snowpack. In addition, snow redistribution processes based on gravitational slides and wind were also considered in the simulation results. For the parametrisation of WaSiM (Schulla and Jasper, 2019) we used the same model configuration and parametrisation as recently published by (Hofmeister et al., 2022) The distinction between no snow and snow cover was defined by a threshold of 5 mm snow water equivalent. The number of snow free freeze-thaw days was defined following Schmidlin et al. (1987) as days with a maximum temperature > 0 °C and a minimum temperature < -2.2 °C.

3.3.3 Hydrosphere

The two hydrosphere-related variables were the precipitation and the TWI. Based on the meteorological data from different weather stations (Supplement, Table II), distribution maps (25 m × 25 m) of the daily precipitation sums were also generated with the WaSiM model (Schulla and Jasper, 2019). The calculation was done using the years 2018 and 2019 as the youngest plots were at least deglaciated since 2018 (Table 1). The TWI was determined in ArcGIS 10.6® using the ALS derived Digital Terrain Model (DTM) acquired during a flight campaign (9th August 2019) with the VP1 (VuxSys LR) mobile laser scanner (Riegl.com) (Operator: Chair of Physical Geography, Catholic University of Eichstätt-Ingolstadt) and the calculation methods after Beven and Kirkby (1979).

3.3.4 Relief sphere

Topographical parameters (elevation, inclination, curvature, and aspect) were based also on the ALS derived DTM of 2019. As aspect is a circular variable it had to be transformed into the linear variables eastness and northness by computing the sine and cosine, respectively (Table 1).

A geomorphological landform map provided by Elsner et al. (unpublished) was utilised to assign the study plots to the categories 'ground moraine' (n = 42) 'lateral/end moraines' (n = 18), and 'other landforms' (n = 5) e.g., lacustrine plain and active flood plain, active river channel, displaced landslide mass. In addition, the Stream Power Index (SPI) was calculated according to Florinsky (2017) to provide a proxy for geomorphic disturbance by flowing water. To verify this modelled parameter, the study plots were also classified in terms of disturbance estimated in the field: (i) more stable (n = 27) and (ii) disturbed plots (n = 38), based on observations of small gullies due to erosion or other visible instability (for more details see Supplement, Fig. S1; the mean SPI values of the two classes were significantly different with $p < 0.0001$).

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3.3.5 Pedosphere

To examine the influence of different soil parameters on vegetation succession, the community weighted mean (m_w_) of the Landolt indicator values (Landolt et al., 2010) humus (H), level of nutrients (N), soil reaction (R), and soil moisture (F) was obtained based on the single species cover on the plot. The suitability of indicator values as proxies for soil parameters was described among others by e.g., Anschlag et al. (2017), Descombes et al. (2020), and Simon et al. (2020). Previous studies were mainly concerned with the suitability of the indicator values for vegetation communities on already mature soils. Therefore, several soil analyses were carried out and compared with the indicator values to ensure that the Landolt indicator values (Landolt et al., 2010) are appropriate for soils in our study area. Soil analyses were performed on soil samples derived from three sampling points (0-10 cm soil depth) for a subsample of the 65 study plots (n = 15). The samples were taken in July and August 2019. During transportation, the samples were cooled down with cooling aggregates in order to keep the samples in a thermal condition as natural as possible. In field-moist condition, the samples were sieved at 2 mm in the laboratory and then stored at -20 °C. Field-moist subsamples were used for determination of microbial carbon (Cmic µgCmic-Cg^{-1} soil dw^{-1}) by substrate induced respiration of microbes using an infra-red gas analyser (EGA60 Multisample soil respiration system; ADC BioScientific Ltd., Global House, Geddings Road, Hoddesdon, Herts EN11 0NT, UK) measuring the microbial carbon, and the photometrical determination of plant available ammonia (NH_4^+, µg NH_4^+-Ng^{-1} soil dw^{-1}) after extraction with 1 M KCl. Subsamples for chemical analyses were dried at 60 °C for five days. Soil pH was determined in 0.01 M $CaCl_2$ as well as in H_2O. After drying the soil for 8 h at 105 °C, soil organic matter content (SOM, grav. %) was determined by loss-on-ignition after 4 h at 430 °C. Furthermore, the soil water potential was measured with MicroLog V3A dataloggers (EMS Brno) for a subsample of the 65 study plots (n = 6). The high correlations between measured and calculated soil parameters showed that the community weighted mean indicator values are also suitable for characterising primary initial soils in proglacial areas (see Supplement, Table S4). Finally, the estimated cover of coarse-grained material (scree cover) in the field was used as an additional independent variable (scree cover).

3.3.6 Anthroposphere

Through conversations with local farmers, information on livestock grazing as the most important human influence on proglacial ecosystems in the study area was retrieved and added in the list of independent variables. Signs of livestock grazing and/or trampling were determined as dichotomous variable (yes/no) for each plot and described in the following as anthropogenic impact.

3.4 Data analysis

Since many of the environmental variables are closely correlated, a PCA with varimax rotation and using the Kaiser's criterion of 1 was performed to avoid multicollinearity. The 26 variables were reduced to 5 rotated components (RC1 – RC 5). The factor scores of the rotated components (RC) were obtained from the PCA with the package psych (Revelle, 2021) in R (R Core Team, 2019) and calculated for each sampling plot.

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GAM were then run using the R package mgcv (V.1.8-34; Wood (2011)). The independent variables were the factor scores of the RCs derived from the PCA as well as the variables excluded from the PCA after the Kaiser-Meyer-Olkin (KMO)-test limit of 0.5 (SPI, TWI) and the variables with a loading below the threshold of 0.5 in the PCA (snow free freeze-thaw days and days with snow cover.). These variables, excluded from the PCA or not significant in the PCA, are additional explanatory variables for the GAM. Furthermore, the categorical variables (landforms and anthropogenic impact) were added. Due to their non-linear relationship with the dependent variable for the variables RC1, RC2, and RC3 the non-parametric smooth function was applied in the GAM. For the model of total species number, the smooth function was applied for RC1. The smooth function uses a thin plate regression spline basis for each and automatically selects the effective degrees of freedom (Wood, 2022).

The GAM model for total vegetation cover was fitted using a beta distribution, as this is appropriate for dependent variables with values between 0 and 1 (Ferrari and Cribari-Neto, 2004). Therefore, total vegetation cover was converted to values between 0 and 1 using the formula

Equ. (1):

$$y^{cov} = \frac{y*(n-1)+0.5}{n} \quad (1)$$

Where y^{cov} the transformed ratio of the vegetation cover, y is the percentage of cover divided by 100, and n is the number of plots (Smithson and Verkuilen, 2006).

The equation for the smooth function (f) is defined as,

Eq. (2):

$$f(x) = \sum_{j=1}^{k} \beta_j b_j(x1) \quad (2)$$

where β_j is a coefficient, $b_j\, x(1)$ is a basis function using by default a thin plate regression spline using which are smooths without knots and optimal low ranked. (Wood, 2022)

The equation of the final GAM for the analysis of the total vegetation cover was,

Eq. (3):

$$g(E[y^{cov}]) = \beta_0 + f_1 * RC1 + f_2 * RC2 + f_3 * RC3 + \beta_1 * RC4 + \beta_2 * RC5 + \beta_3 * SPI + \beta_4 * TWI + \beta_5 * Snow\ free\ freeze - thaw\ days + \beta_6 * Days\ with\ snow\ cover + \beta_7 * Landform + \beta_8 * Anthropogenic\ impact \quad (3)$$

where $g()$ is the link function, E the expectation, y^{cov} the transformed ratio of the vegetation cover, β_0 the overall intercept, β_i the intercept, and f_i the smooth function.

For the analysis of the species number, the GAM model was fitted using a Poisson distribution. The equation for the final model for the analysis of the species number was,

Eq. (4):

$$g(E[y^{num}]) = \beta_0 + f_1 * RC1 + \beta_1 * RC2 + \beta_2 * RC3 + \beta_3 * RC4 + \beta_4 * RC5 + \beta_5 * SPI + \beta_6 * TWI + \beta_7 * Snow\ free\ freeze - thaw\ days + \beta_8 * Days\ with\ snow\ cover + \beta_9 * Landforms + \beta_{10} * Anthropogenic\ impact \quad (4)$$

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where $g()$ is the link function, E the expectation, y^{num} the species number, β_0 the overall intercept, β_i the intercept, and f_i the smooth function.

Following Schröder and Reineking (2004)and Dormann (2011) the residuals of the models were tested for spatial autocorrelation using the Moran's I in the R package DHARMa (Hartig, 2022).

To analyse the influence of environmental variables on species composition, a NMDS was performed using the package vegan version 2.5.6 (Oksanen et al., 2020) based on square root transformation of the in-situ observations and Bray-Curtis dissimilarity. Plots without vegetation (n = 2) had to be excluded from the analysis. The environmental variables were fitted to show their influence on the species composition.

4 Results

4.1 Literature review: Definition of the dependent and potential explanatory variables

The most frequently analysed vegetation-related variables (biosphere) in the literature were total species number (n = 31), total species cover (n = 30), and species composition (n = 24; Fig. 3a). Significantly less studies addressed the cover of individual species (n = 2) (e.g., Wietrzyk et al., 2018), functional groups (n = 2) (e.g., Kaufmann and Raffl, 2002), individual strategy types (n = 2) (e.g., Fickert et al., 2017), or the development of the Normalised Difference Vegetation Index (NDVI) (n = 5) (e.g., Fischer et al., 2019; Lambert et al., 2020; Knoflach et al., 2021). In order to ensure a solid basis for comparing our results, we limited our analyses to the most frequently used dependent variables total vegetation cover, species number, and species composition for our further analyses.

The potentially explanatory variables derived from literature research were assigned to the different spheres, following the geoscientific concept of spheres (Sintubin, 2008; Stötter et al., 2014): atmosphere (n = 5), cryosphere (n = 4), hydrosphere (n = 4), relief sphere (n = 7), pedosphere (n = 18), and anthroposphere (n = 1) (Fig. 2b). In total, 39 potential explanatory (independent) variables were mentioned in the 45 articles considered (Fig. 3b). Most studies included solar radiation (n = 11) (e.g., Caccianiga and Andreis, 2004; D'Amico et al., 2017; Fickert, 2020; Lambert et al., 2020), years since deglaciation (n = 43) (e.g., Fickert and Grüninger, 2018; Jiang et al., 2018; Franzén et al., 2019; Knoflach et al., 2021; Wei et al., 2021), soil moisture (n = 9) (e.g., Matthews and Whittaker, 1987; Andreis et al., 2001; Raffl and Erschbamer, 2004; Szymański et al., 2019; Fickert, 2020), elevation (n = 22) (e.g., Carlson et al., 2014; Schumann et al., 2016; Llambí et al., 2021; Wei et al., 2021), inclination (n = 15) (e.g., D'Amico et al., 2017; Haselberger et al., 2021; Wietrzyk-Pelka et al., 2021), aspect (n = 14) (e.g., Caccianiga and Andreis, 2004; Raffl and Erschbamer, 2004; Fickert, 2017; Lambert et al., 2020; Wietrzyk-Pelka et al., 2021), and disturbance (n = 9) (e.g., Matthews and Whittaker, 1987; Andreis et al., 2001; Eichel, 2019) as well as soil-related parameters such as organic carbon (n = 16) (e.g., D'Amico et al., 2014; Jiang et al., 2018; Wietrzyk et al., 2018; Losapio et al., 2021), nitrogen (n = 14) (e.g., Raffl et al., 2006; Burga et al., 2010; Fickert, 2020; Wei et al., 2021), and pH (n = 15) (e.g., Raffl et al., 2006; Burga et al., 2010; D'Amico et al., 2017; Fickert, 2020; Wietrzyk-Pelka et al., 2021) (Fig. 3b). Variables that received the least attention, with only one mention, include annual temperature (Tampucci et al., 2017) and summer temperature (June/July/August) (Knoflach et al., 2021), wind exposure (Andreis et al., 2001), duration of snow cover (Kaufmann and Raffl, 2002), snow depth (Matthews and Whittaker, 1987), flow accumulation as a proxy for areas where water accumulates (Lambert et al., 2020), soil type (Matthews and Whittaker, 1987), soil colour (Andreis et al., 2001), and anthropogenic impact (Schumann et al., 2016) (Fig. 3b).

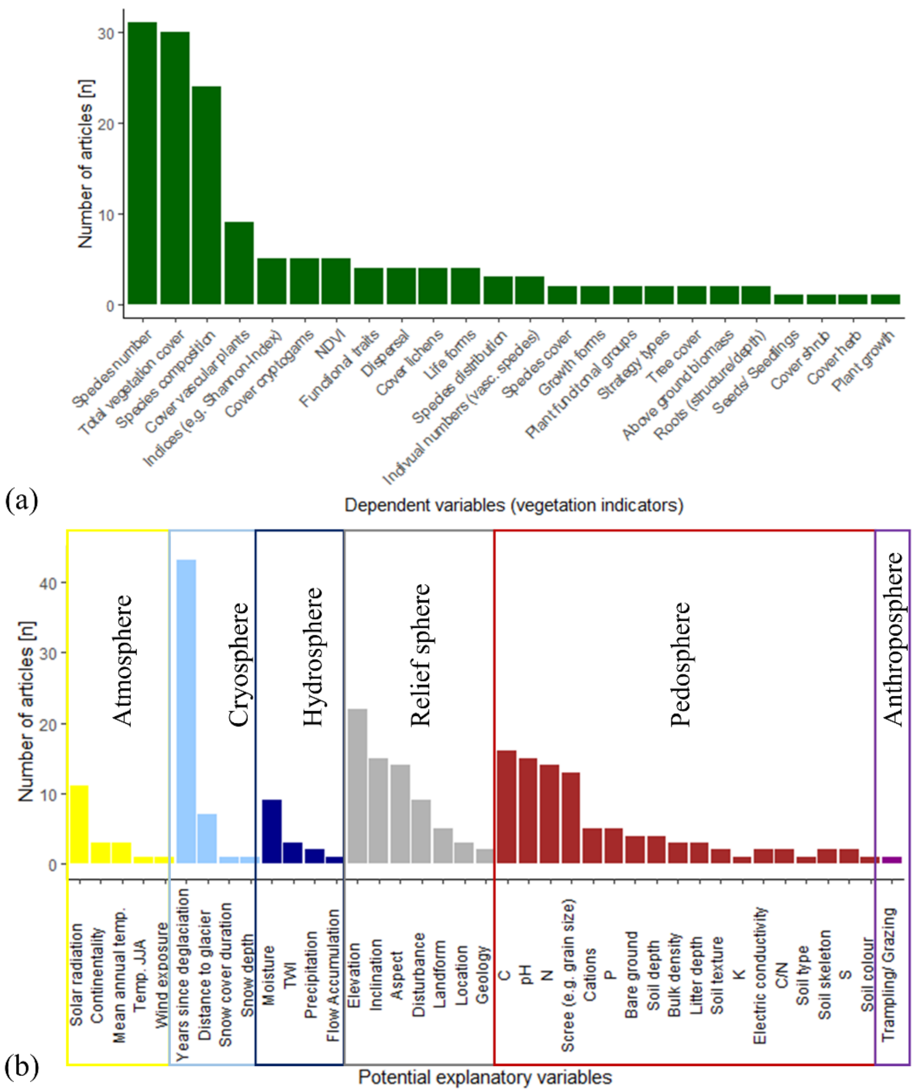

Figure 3: Results of the literature research. Frequency of mentioned (a) vegetation indicators (dependent variables), and (b) potential explanatory variables. Colours indicate to which sphere the variable has been assigned.

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Although the potential explanatory variable temperature was considered less in literature, it was included in this analysis as it is important in times of changing climate. Furthermore, we decided to include the atmospheric variables (solar radiation for the growing season (gs), max. temperature, min. temperature, snow free gdd, and the temperature values for gs). Kaufmann and Raffl (2002) and Kreyling et al. (2007), for example, showed the relevant impact of the number of days with snow cover and the snow free freeze-thaw days on vegetation. Therefore, we included also these two variables although they were only mentioned once or even not found in our literature review. For the hydrosphere, this study included precipitation (annually and for gs) as they are also relevant due to climate change. In our study, community weighted means of the Landolt indicator values (Landolt et al., 2010) were used instead of measured soil parameters.. Thus, 31 potential explanatory variables remained for the analyses: nine variables were assigned to the atmosphere, five to the cryosphere, two to the hydrosphere, seven to the relief sphere, five to the pedosphere, and one to the anthroposphere. For geomorphic disturbance, only the SPI was used for the analyses (Table 1).

4.1.1 Reduction of potential explanatory variables to components

Twenty-six potential explanatory variables were reduced to five components. The five components (RC1 – RC5) explained 83 % of the variance. RC1 accounted for 46 % of the variance, RC2 for 16 %, RC3 for 6 %, RC4 for 7 %, and RC5 for 8 % respectively (Supplement, Table S5).

RC1 included, among others: years since deglaciation (0.87), elevation (-0.92), annual temperature as well as temperature during the growing season, sum of precipitation (annual and during the growing season), and soil moisture (0.82) (Table 2). Therefore, RC1 summarised key elevation-related climate parameters and variables connected with them, such as years since deglaciation, distance to glacier tongue or soil humus content; it will be referred to 'elevation and time'. RC2 included the solar radiation (0.94 and 0.90) and the snow free gdd (Table 2). This component will be designated as 'solar radiation'. RC3 was related to eastness (0.83) and northness (-0.72) (Table2). This component will be referred to 'south-eastness'. RC4 was negatively correlated with soil nutrients (-0.88), and positively with curvature (0.60) (Table 2). A positive curvature value indicates flow (run off) acceleration and therefore also higher nutrient leaching. Therefore, this component will be designated as 'high leaching'. RC5 refers to inclination (-0.79), and mean number of days with snow cover (Table 2), hence this component will be referred to as 'low inclination'. Two of the variables (snow free freeze-thaw days and days with snow cover) with factor loading < 0.5 remained as additional variables.

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Table 2: Results of the PCA for our included driving variables in the proglacial area. The rotated factor loadings > 0.5 for the single components (RC) are given. Parameters which did not load sufficiently in any component (loading < 0.5) are highlighted in grey (gs = growing season, m_w_H = soil humus, m_w_F = soil moisture, m_w_R = soil reaction, m_w_N = soil nutrients).

Parameters	RC1	RC2	RC3	RC4	RC5
Mean max. temperature gs	0.97				
Mean max. temperature annual	0.96				
Mean temperature gs	0.95				
Mean min. temperature gs	0.95				
Mean temperature annual	0.95				
Mean min. temperature annual	0.94				
Elevation	-0.92				
Years since deglaciation	0.87				
Scree cover	-0.82				
m_w_H	0.82				
Terrain age	0.80				
Sum precipitation annual	-0.73	-0.58			
Distance to glacier	0.72	-0.65			
m_w_F	-0.67				
m_w_R	-0.61				
Sum precipitation gs	0.59				
Snow free freeze-thaw days					
Sum solar radiation annual		0.94			
Sum solar radiation gs		0.90			
Snow free gdd	0.56	0.64			
Eastness			0.83		
Northness			-0.72		
m_w_N				-0.88	
Curvature				0.60	0.51
Inclination					-0.79
Days with snow cover					

4.2. Effects of years since deglaciation, elevation, and climate on vegetation cover

In the GAM for total vegetation cover 97.4 % of the variance was explained by the model. The effect of the smoothed parameter, ‘elevation and time’ s(RC1) was highly significant ($p < 0.0001$) (Fig. 4a), i.e., total vegetation cover increases with increasing RC1.

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But also, RC5 had a significantly positive effect on vegetation cover, i.e., low inclination ($p < 0.0001$) and the number of snow free freeze-thaw days ($p = 0.020$) (Table 4a) as well as the smoothed parameters s(RC2), solar radiation ($p < 0.0001$), and s(RC3), south-eastness ($p < 0.0001$) (Table 3b) increased vegetation cover. For the anthropogenic impact, a significant negative impact of livestock grazing and/or trampling ($p < 0.0001$) on total vegetation cover was calculated (Table 3a, Fig. 3b). Regarding the different landforms, total vegetation cover was significantly higher on lateral/end moraines ($p = 0.012$) and other landforms ($p < 0.0001$) in comparison to ground moraines (Table 3a, Fig. 4c). Morans'I for the residuals of the model was not significant ($p = 0.15$), thus it was not necessary to account for spatial autocorrelation.

Table 3: (a) Effects of the analysed components and the additional potential explanatory variables (excluded from the PCA) on the total vegetation cover with the estimate, the standard error (SE), and the p-value. (b) Effects of the smoothed terms with their approximate significance and their estimated degrees of freedom (edf), the reference degrees of freedom (Ref df) the Chi sq, and the p-value on the total vegetation cover. The significant variables are highlighted with bold numbers.

(a) Parametric coefficients.

	Estimate	**SE**	**p-value**
(Intercept)	-2.99	2.77	0.280
RC4	0.0158	0.0886	0.858
RC5	0.685	0.147	**<0.0001**
SPI	-0.00002	-0.00002	0.488
TWI	0.072	0.058	0.219
Snow free freeze-thaw days	0.169	0.073	**0.020**
Number of days with snow cover	-0.001	0.011	0.918
Lateral/end moraine	0.712	0.282	**0.012**
Other landforms	1.11	0.313	**<0.0001**
Grazing/trampling, yes	-1.15	0.240	**<0.0001**

(b) Approximate significance of smooth terms.

	edf	Ref df	Chi sq	p-value
s(RC1)	7.066	8.029	212.75	**< 0.0001**
S(RC2)	3.824	4.662	67.12	**< 0.0001**
S(RC3)	5.368	6.448	16.61	**0.0178**

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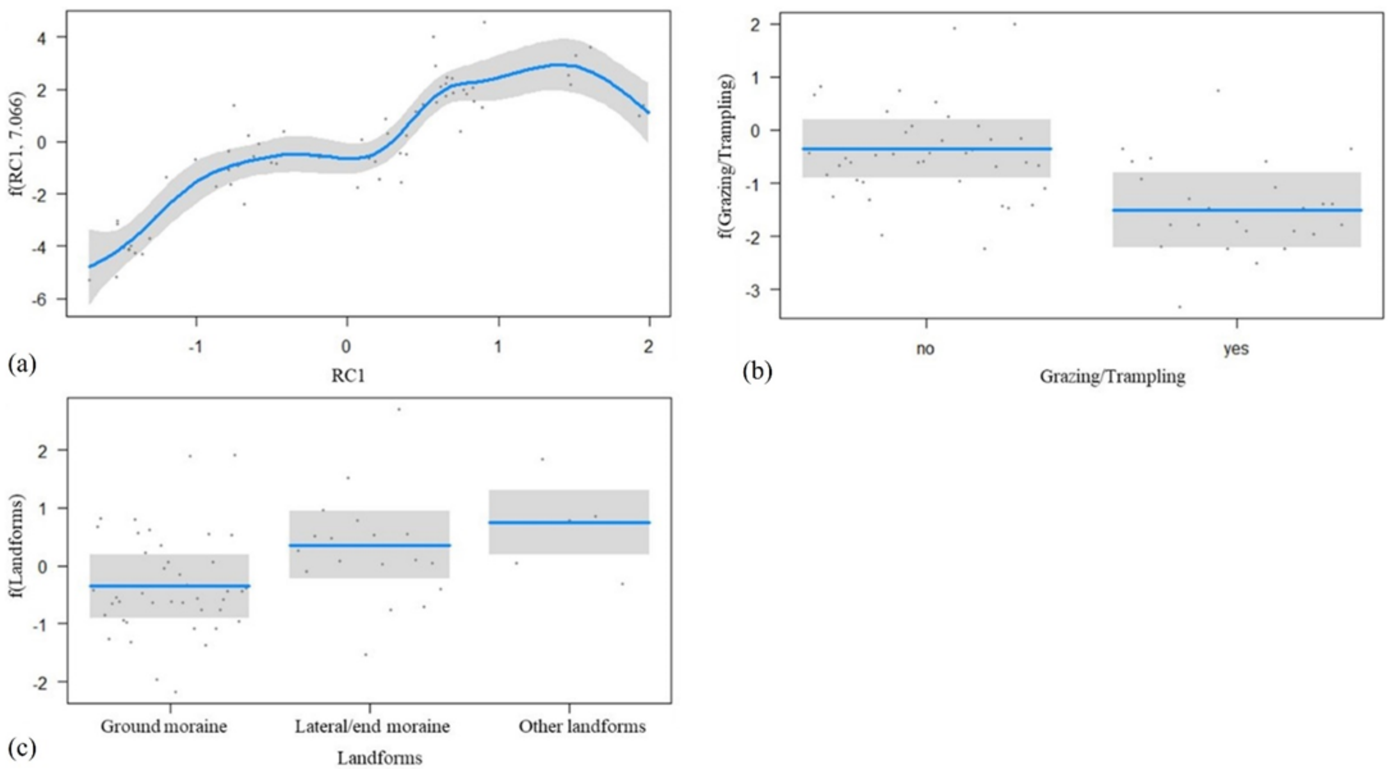

Figure 4: Partial effect plot (a) for RC1 (p < 0.0001) and the partial effect plots for (b) anthropogenic impact (grazing/trampling) (p < 0.0001), and (c) Landforms (p < 0.0001).

4.3 Important drivers for species number and composition

The utilised variables explained 85.1 % of the model variance. The proxy for geomorphic disturbance, SPI, had a weak negative effect ($p = 0.051$) (Table 4a). Grazing and/or trampling had no significant ($p = 0.835$) effect on total species number (Table 4a, Fig. 5c). The model showed also a significantly positive effect of solar radiation (RC2, $p < 0.0001$), high leaching (RC4, $p = 0.0038$), low inclination (RC5, $p = 0.038$), and snow free freeze-thaw days ($p = 0.0003$) (Table 4a). On other landforms total species number was significantly higher ($p = 0.039$) in comparison to ground moraines; for lateral/end moraines the effect was not significant (Table 4a, Fig. 5b). Furthermore, there is a highly significant effect ($p < 0.0001$) for the smoothed term s(RC1). This indicates that species numbers are higher at lower elevations and ice-free for longer times (RC1) (Table 4b, Fig. 5a). Morans'I for the residuals of the model was not significant ($p = 0.913$). Thus, it was not necessary to account for spatial autocorrelation.

Table 4: (a) Effects of the analysed components and driving variables on the total species number with the estimate, standard error (SE), and the p-value. (b) Effects of the smoothed term s(RC1) with their approximate significance and their estimated degrees of freedom (edf), the reference degrees of freedom (Ref df), the Chi sq, and the p-value on the total vegetation cover. Significant variables in bold.

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(a) Parametric coefficients.

	Estimate	SE	p-value
(Intercept)	1.11	0.742	0.136
RC2	0.214	0.049	< **0.0001**
RC3	0.057	0.045	0.204
RC4	0.124	0.043	**0.004**
RC5	0.124	0.060	**0.038**
SPI	-0.00002	0.00001	**0.051**
TWI	0.013	0.027	0.627
Snow free freeze-thaw days	0.104	0.029	**0.0003**
Days with snow cover	0.003	0.003	0.257
Lateral/end moraine	0.159	0.126	0.206
Other landforms	0.296	0.144	**0.039**
Grazing/trampling, yes	0.020	0.097	0.835

(b) Approximate significance of smooth term s(RC1).

	edf	Ref df	Chi sq	p-value
s(RC1)	7.522	8.47	154	< **0.0001**

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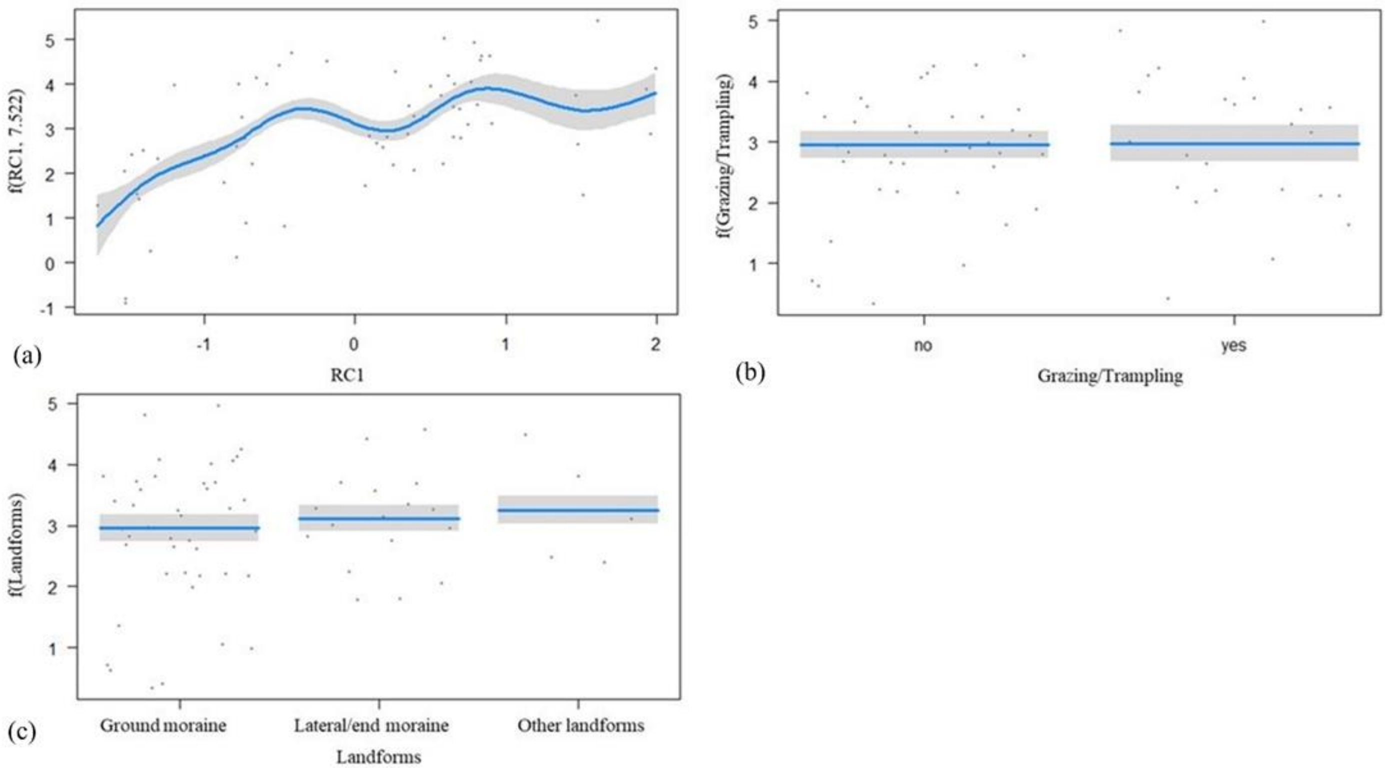

Figure 5: Partial effect plot (a) for RC1 ('elevation and time') and the partial effect plots for (b) anthropogenic impact (grazing/trampling) and (c) landforms.

The NMDS (Fig. 6) clearly showed the relationships between the drivers and the successional stages, representing different species compositions. The pioneer stage is positively correlated with scree cover, annual precipitation, and pH, as well as with snow free freeze-thaw days, soil moisture, and elevation. Geomorphic disturbance correlates mainly with the early successional stages while anthropogenic impact in form of grazing and/or trampling by livestock is more common in the dwarf shrub stage. Solar radiation corresponded with the early successional stage with the transition to grassland. The snowbed community occurs mainly on areas with higher number of days with snow cover and SPI, and the transition to grassland on areas with more snow free gdd as well as precipitation during the growing season. The dwarf shrub stage was highly correlated with an increasing number of years since deglaciation, higher temperature values, higher values of soil humus content, and negatively with increasing elevation.

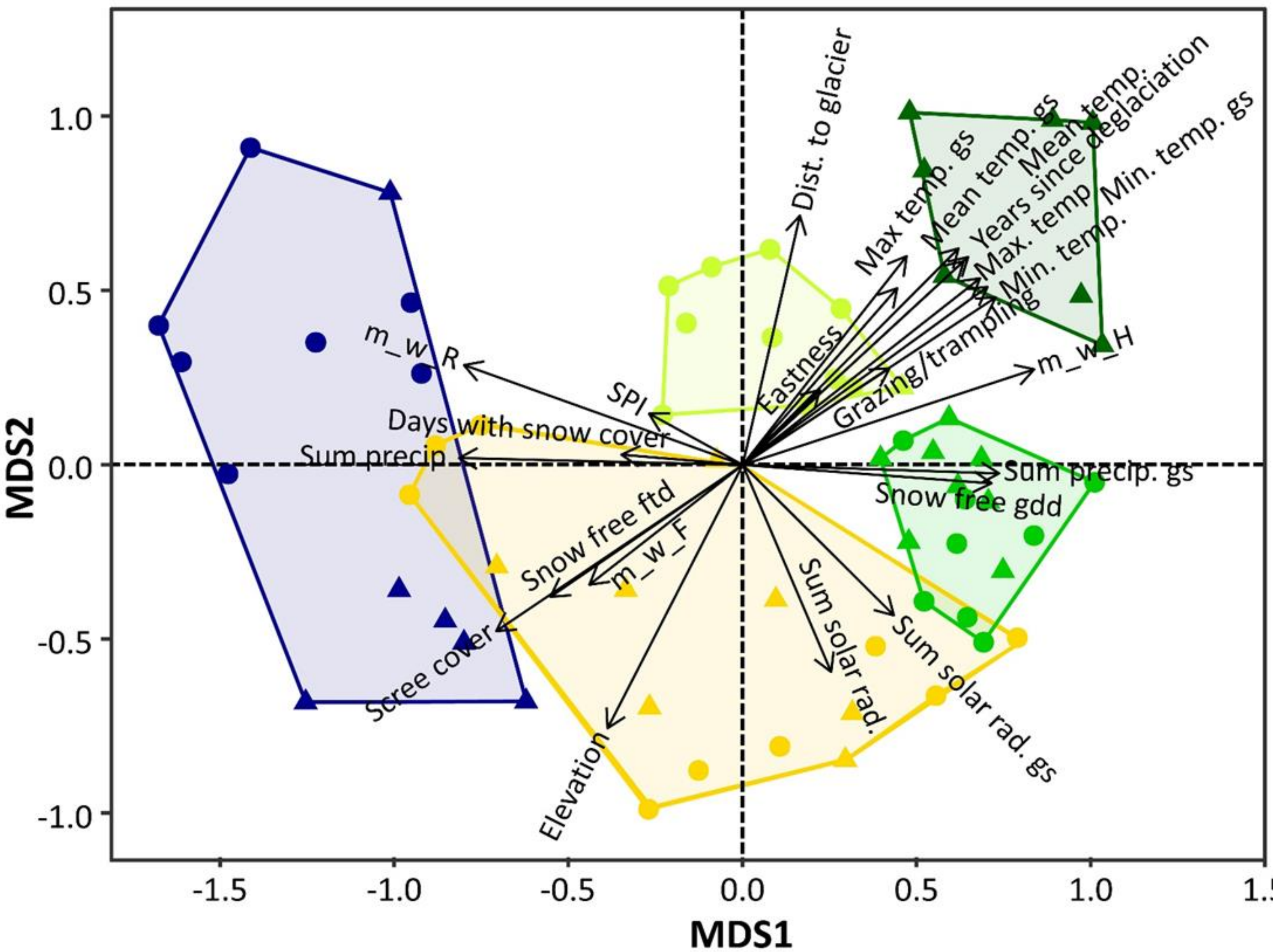

Figure 6: Successional stages on the proglacial areas of Fürkele-, Zufall-, and Langenferner. The results are shown as a NMDS of the sampling plots. In the NMDS, the coloured dots (geomorphic disturbed), triangles (more stable), and polygons indicate the different species communities: blue = pioneer stage, yellow = early successional stage, yellowish green = late successional stage (snowbed community), light green = late successional stage (transition to grassland), and dark green = dwarf shrub stage. The length of the black arrows shows the high significant correlation between the driving variables on species composition (temp. = temperature, precip. = precipitation, dist. = distance, ftd = freeze-thaw days, gs = growing season, gdd = growing degree days, SPI = stream power index, m_w_F = community weighted mean of the indicator value for moisture, m_w_H = community weighted mean of the indicator value for humus, and m_w_R = community weighted mean for the indicator value soil reaction).

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5 Discussion

Primary succession in the proglacial area is well studied and many drivers of succession have been suggested in the literature. However, most of the studies included only a few potential explanatory variables that in many cases do not cover all spheres (e.g., Knoflach et al., 2021; Fickert, 2020; Cazzolla Gatti et al., 2018; Robbins and Matthews, 2010; Mizuno, 2005; Andreis et al., 2001). This study stresses that many potential explanatory variables outlined in the literature are strongly correlated with each other and thus reflect the same phenomenon (statistically the same principal component). To prove this, we used as many known potential explanatory variables from as many spheres as possible in our approach. The set of 26 potential explanatory variables could be reduced to five components due to multicollinearities. The first component RC1 (‘elevation and time’) is correlated with years since deglaciation, elevation, temperature, precipitation, community weighted means of the Landolt indicator values for humus, moisture, and soil reaction, and scree cover. Several studies listed the variables summarised in our study in RC1 as important for the development of vegetation in the proglacial area: e.g., Andreis et al. (2001) and Wei et al. (2021) named years since deglaciation as well as elevation, Fickert (2020) concluded that years since deglaciation, elevation and temperature have an influence on vegetation development in the proglacial area. Similarly, e.g. Schumann et al. (2016), Haselberger et al. (2021), and Wietrzyk-Pelka et al. (2021) stated that years since deglaciation, scree cover, soil reaction, or soil moisture have an impact on vegetation development. Other studies (e.g, Schumann et al., 2016; Lambert et al., 2020) took solar radiation as separate variable into account whereas in our study this variable is combined with snow free gdd in the component RC2. The relevance of the snow free gdd for enhanced vegetation development was shown by Carlson et al. (2017) in the French Alps. RC3 (‘south-eastness’) is linked with aspect as a continuous variable, south-east being favourable for vegetation development. In contrast to this study other authors used the aspect as categorical variable (e.g., Caccianiga and Andreis, 2004; Schumann et al., 2016; Fickert, 2020). The fourth component (RC4, ‘high leaching’) is correlated with curvature and soil nutrients. The correlation of curvature and nutrients was already shown by (Franz, 1979). Most of the previous studies analysed the effect of total nitrogen and associated it directly with years since deglaciation (e.g., Göransson et al., 2016; Wietrzyk-Pelka et al., 2021; Wei et al., 2021). In contrast to these publications, our study revealed that nutrients are more dependent on the microtopography and not only on time as also shown by Temme and Lange (2014). Finally, RC5 is correlated with inclination and weak with number of days with snow cover. In comparison to flat terrain steeper slopes have less snow cover or are free of snow (Schmidt et al., 2009). Many studies took inclination into account (e.g., Dolezal et al., 2008; Schumann et al., 2016; Lambert et al., 2020) but only one publication considered the snow cover duration (Kaufmann and Raffl, 2002). With our analyses we confirmed hypothesis (i) of variables collinearity and outlined an example of variable aggregation to fewer components.

5.1 Drivers for development of vegetation cover

For total vegetation cover we hypothesised that the most important drivers influencing the development in the proglacial area are: years since deglaciation, elevation, and climatic variables. This hypothesis was based on previous studies in which years since deglaciation (e.g., Matthews and Whittaker, 1987; Raffl et al., 2006; Erschbamer and Caccianiga, 2016; Schumann et al., 2016;

Llambí et al., 2021), elevation (e.g., Raffl and Erschbamer, 2004; Lambert et al., 2020), temperature (e.g., Fickert et al., 2017; Franzén et al., 2019; Fickert, 2020), and precipitation (e.g., Schumann et al., 2016; Haselberger et al., 2021) resulted as essential drivers of vegetation development. In our study, we have now demonstrated that – contrary to our initial expectation – a series of other variables correlates with our hypothesised three variables, jointly described by the components RC1 ('elevation and time'), RC2 ('solar radiation'), RC3 ('south-eastness'), and RC5 '(low inclination'). Thus, hypothesis (ii) that the most important explanatory variables for vegetation cover development include years since deglaciation, elevation, and climatic variables, cannot be confirmed. RC1 includes scree cover and pH for which the impact is also shown by e.g., Dolezal et al. (2008), Burga et al. (2010), or Schumann et al. (2016) as well as community weighted means of the Landolt indicator values for humus, moisture, and soil reaction also used by Fickert (2020). In addition, we showed that also snow free freeze-thaw days, landforms, and anthropogenic impact constitute a significant impact. Rydgren et al. (2014) and Schumann et al. (2016) also suggested the positive effect of solar radiation on vegetation cover, which, by the way, correlated with the snow free gdd in our study. At the same time, succession in proglacial areas is positively associated with enhanced rate of soil formation (Rech et al., 2001). The significant effect of the aspect ('south-eastness') found in our study was also mentioned by e.g., Schumann et al. (2016). We found that vegetation development was positively correlated with 'low inclination' (RC5), an effect also observed by Schumann et al. (2016) by their generalised linear model (GLM) for cover of mosses and lichens. The positive effect of low inclination can be based on high deposition of fine materials and nutrients, improving soil properties. The significantly positive effect of snow free freeze-thaw days on vegetation cover can be interpreted by its positive effects on mineralisation of organic carbon (Grogan et al., 2004; Wipf et al., 2015) and thus enhanced plant growth (Kreyling et al., 2007). Higher mineralisation a is associated with higher concentrations of ammonium, nitrate and dissolved organic carbon, and lower C:N ratio in the soil (Freppaz et al., 2019; Zhou et al., 2011).

The development of vegetation cover was found to differ significantly between landforms. We observed higher vegetation cover on lateral/end moraines as well as on flat areas with high material deposition (summarised under 'other landforms') not primarily driven by glacier retreat. Ground moraines often have a shorter time of deglaciation in comparison to the lateral/end moraines. So far, our results underline that landforms are important in context with primary succession in proglacial areas (see also, Moreau et al., 2008). Another less investigated driver in previous studies was the impact of livestock grazing. With our study we demonstrated that trampling and grazing slowed down the development of vegetation cover. Similar results were published by Schumann et al. (2016).

5.2 Drivers for development of species number and species composition

For species number and species composition we hypothesised in particular that geomorphic and anthropogenic disturbances reduce species number compared to undisturbed areas and thus also change species composition. Of course, the species number and composition are also influenced by the same components as the vegetation cover such as RC1 ('elevation and time'), RC2 ('solar radiation'), RC5 ('low inclination'), and snow free freeze-thaw days. Contrary to the drivers of vegetation cover, the species number was significantly affected by RC3 ('high leaching') but not by RC4 ('south-eastness'). With respect to our hypothesis (iii) on the effect of disturbances, the results are not clear. The stream power index (SPI) had a weak but significant effect on species number, grazing and/or trampling showed no significant correlation. Most of the studies in the literature came to the conclusion that geomorphic disturbance has an impact on species composition (D'Amico et al., 2017; Andreis et al., 2001; Matthews and Whittaker, 1987) but not on species number. Only Fickert and Grüninger, 2018) noticed that individuum number and also species number decreased with disturbance in an early successional stage. Thereby, geomorphic disturbance controls succession not only by erosion but also by modification of the relief and relocation of sediments (Ballantyne, 2002). The modification of the relief (microtopography, and grain size composition) can further lead to changes in microclimate, water and nutrient availability, and shading (Ballantyne, 2002). As grain-size has an impact on vegetation development (Burga et al., 2010), the relocation of sediments by geomorphic processes is important for the entire primary succession pathway. Andreis et al. (2001) showed a negative impact of disturbance on species composition but they included surface runoff as well as grazing and/or trampling in one factor.

6 Conclusion

Considering all variables used in this study and with a view to future development, we note that most of these variables are significantly influenced by advancing climate change. For example, through the ongoing climate change, the growing season will be prolongated and the growing conditions will be generally improved. Theurillat et al. (1998) suggested that per every increased degree in mean air temperature, the length of growing season will be enhanced by 16 to 17 days. Regarding precipitation, the ratio of snow relative to liquid precipitation shows a decreasing trend since the 1960s and 1970s in the Alps (Serquet et al., 2011), implicating less snowfall also in high elevations. Changes in snow cover can affect snow bed communities due to earlier melt or can also cause frost damages (Theurillat et al., 1998).

Our results clearly reveal that many drivers for primary succession found in literature refer to the same phenomenon (principal component), which reflects the interaction of spheres. Main drivers are the components elevation and time (RC1), solar radiation (RC3), and low inclination (RC5). It was demonstrated that vegetation cover, species number (diversity), and species composition are not always affected by the same set of drivers. The main difference is that vegetation cover is correlated with south-eastness (RC4) and species number with high leaching (RC3). However, in order to substantiate these results, further studies of a similar nature must follow, also in geologically different areas.

Data availability

All raw data can be provided by the corresponding authors upon request.

Author Contributions:

KR, BK, CG, BEr, JS and ET did the conceptualization- KR, B., BEl, FHo, FHa, TH, LP, CR, ST, MW, JS and ET did the data curation.; KR, BK, JS, and ET analysed the data and developed the methodology. CG, BEr, JS and ET did the funding acquisition and project administration. KR, BK, and ST conducted the field work and data collection. CG, BEr., JS, and E.T did the validation..;KR, BK, and ET did the visualisation.

KR and BK wrote the manuscript draft. BEl, BEr, FHo., FHa., TH, LP, CR, ST, MW, CG, JS and ET reviewed and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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