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Pioneer biocrust communities prevent soil erosion in temperate forests after disturbances

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Abstract

Soil erosion continues to be one of the most serious environmental problems of our time, which is exacerbated by progressive climate change. Until now, forests have been considered an ideal erosion control in this regard. However, even minor disturbances of the forest floor for example from heavy vehicle used for timber harvesting can cause substantial sediment transport. An important countermeasure is the quick restoration of the uncovered soil surface by vegetation. In this context, biological soil crusts (biocrusts) can play a vital role, as they are known for their soil-protective effect. This study examined the natural succession of pioneer vegetation in skid trails on four soil substrates in a central European temperate forest and investigated their influence on surface runoff and sediment discharge. We applied rainfall simulation experiments on small-scale runoff plots and continuously surveyed vegetation during the same period, primarily to map biocrust development.

Skid trails on clayey substrates showed considerably higher biocrust cover and species richness. Biocrust cover was higher in center tracks than in wheel tracks, while there was no clear difference for biocrust species richness with regard to track position. Although biocrusts were quickly overtopped by vascular plants, they managed to coexist until their growth was restricted due to leaf litter fall. *Brachythecium rutabulum* and *Oxyrrhynchium hians* were the most important and persistent pioneer biocrust species, while *Dicranella schreberiana* and *Pohlia lutescens* were volatile and quickly disappeared after spreading in summer. Soil erosion was reduced with pioneer biocrust vegetation in summer, and again increased in winter. Total amount of sediment discharge was clearly site-dependent, indicating a high relevance of underlying substrates. Sediment discharge was 13.2 times higher in wheel tracks compared to undisturbed forest soil, and bare soil runoff plots produced 22-fold sediment discharge compared to undisturbed forest soil. Overall, bryophyte-dominated biocrusts contributed more to mitigating soil erosion than vascular plants. When soil coverage exceeded 50 %, biocrusts resulted in an average of 18 times less sediment loss compared to vascular plants.

1 Introduction

For decades, soil erosion has been a major environmental problem as it degrades the most productive soil layers, which threatens, among other things, food production worldwide. Although these effects have been known for a long time, there are still a variety of challenges to mitigating soil erosion in different ecosystems. As climate change progresses, the risk of soil loss increases, making the preparation of effective solutions an urgent matter (Olsson, 2019; Scholten and Seitz, 2019). Most prominent soil losses are appearing in agricultural environments and thus a considerable part of relevant research is conducted in those areas (Morgan, 2005; Maetens et al., 2012). In this context, soil erosion under forests has received comparably less attention by scientists, as undisturbed forest ecosystems generally exhibit the lowest soil erosion among all land use types (Blanco and Lal, 2008; Panagos et al., 2015b; Maetens et al., 2012) and are seen as a successful countermeasure to prevent the soil from being eroded (Panagos et al., 2015a; Wiśniewski and Märker, 2019).

However, soil erosion in forestlands can take important dimensions locally, for example in subtropical forest ecosystems (Goebes et al., 2015; Seitz et al., 2016). Even forest disturbances at smaller scale such as human-induced felling and skidding of individual trees or the construction of forest trail systems on sloped terrain have the potential to drastically increase soil loss (Blanco and Lal, 2008). Here, Sheridan and Noske (2007) showed that unsealed forest roads at the catchment scale contributed 50 t of the 1,142 t of total annual sediment discharge, accounting for 4.4 % of the total sediment load from the forest, even though they represented only 0.023% of the catchment area. The most important reason for this is soil compaction and reduced infiltration rates by heavy machines used for timber harvesting (Foltz et al., 2009; Jordán-López et al., 2009; Kastridis, 2020; Wemple et al., 2018). Results from Demir et al. (2007) revealed a significant higher soil bulk density ranging from 1.028 g cm^{-3} (0 – 5 cm soil depth) to 1.235 g cm^{-3} (5 – 10 cm soil depth) on skid trails, where soil compaction is caused by the direct overpassing with forestry equipment. Zemke (2016) measured 58 times higher erosion rates on unfortified forest roads (272.2 g m^{-2}) compared to undisturbed forest floor (4.7 g m^{-2}) in a temperate forest in western Germany. Also, already vegetated wheel tracks of skid trails showed a 5-fold higher soil erosion up to 21.4 g m^{-2}. Comparatively, Safari et al. (2016) reported an increase in erosion rates of a factor of 14 for bare wheel tracks of skid trails up to 301.65 g m^{-2} h^{-1} relative to the undisturbed forest floor.

These findings suggest, that it is not primarily the forest canopy which protects the soil against erosion, but an intact forest floor (Elliot et al., 1999; Li et al., 2019; Seitz et al., 2016; Shinohara et al., 2019). Several studies have also confirmed that soil erosion on skid trails was highest in the first year after logging and decreased significantly thereafter, primarily due to revegetation (Baharuddin et al., 1995; Jourgholami et al., 2017). Thus, the most important measure to counteract negative effects of soil erosion on the upper soil layer after skidding is a quick restoration of soil surface by vegetation (Zemke, 2016; Mceachran et al., 2018). Those protective soil covers consist either of leaf and conifer litter from surrounding trees (Li et al., 2014; Seitz et al., 2015) or understory vascular vegetation (Miyata et al., 2009; Liu et al., 2018). It also includes a cryptogamic plant layer within the first millimeters of the topsoil, referred to as biological soil crust (biocrust) (Weber et al., 2016). Especially when vascular plant growth is limited by edaphic conditions such as excessive drainage, acidity or low nutrient levels, biocrusts play a vital role as pioneer soil colonizers and stabilizers (Belnap and Büdel, 2016; Corbin and Thiet, 2020). In temperate climates, biocrusts occur primarily as an intermediate state of succession following disturbances such as deforestation (Seppelt et al., 2016), and bryophytes apparently constitute a larger component of mature biocrusts of temperate zones than in arid regions (Büdel et al., 2014; Corbin and Thiet, 2020).

Biocrusts in general, and especially bryophyte-dominate biocrusts, are known for their influence on hydrological processes (Eldridge et al., 2020) such as surface runoff (Bu et al., 2015; Xiao et al., 2015), infiltration (Li et al., 2016), and thus sediment discharge (Silva et al., 2019), which is inevitably related to their impressive water storage capacity, since bryophytes are able to absorb up to 20 times their dry weight (Proctor et al., 1998), with some *Sphagnum* species even reaching more than 50 times their dry weight (Wang and Bader, 2018). These mechanisms of water storage capacity are influenced by the complex 3D structure of bryophytes, composed of a variety of individual functional traits (e.g. leaf area, leaf frequency, leaf area per shoot length, leaf area index, total surface area, shoot length, shoot density), and their ability to form dense colony-level cushions (Thielen et al., 2021; Glime, 2017; Elumeeva et al., 2011). As the very most studies on the impact of biocrusts on soil erosion have been conducted in arid and semi-arid regions, their influence in humid climates is widely unknown (Weber et al., 2016; Eldridge et al., 2020). Previous studies in subtropical China proved an important erosion-reducing effect of bryophyte-dominated biocrusts within early-stage forest plantations after clear-cut (Seitz et al., 2017). It can be assumed that similar effects also occur under humid and temperate forest conditions.

Particularly in disturbed forest areas such as skid trails, where vascular plants are presumed to grow slowly due to harsh soil conditions, pioneer biocrust communities could benefit from special importance as erosion control agents. To date, few studies have addressed natural plant succession in skid trail recovery (Dearmond et al., 2021) and of those, the majority relate exclusively to vascular plants (Buckley et al., 2003; Wei et al., 2015). Recently, Mercier et al. (2019) observed on skid trails of different forest types in southern Germany that the species composition of vascular plants and bryophytes in the understory differed markedly from the forest interior. Further, these vegetation surveys showed that vascular plant species richness benefited from soil compaction in the skid trails, while bryophyte species richness was unaffected. Regarding this research gap, it is of high interest, how biocrust communities develop naturally after the passing over by forestry machines on different substrates, and how they accordingly affect soil erosion in these disturbed areas within temperate forests.

This study examined the natural succession of pioneer vegetation with a focus on biocrusts in skid trails on four different soil substrates in a central European temperate forest. Moreover, it investigated its influence on soil erosion processes, also considering the position of the tracks within the skid trails. We tested the following hypotheses:

1. **Composition, coverage and richness of pioneer vegetation vary depending on underlying substrate and track position**
2. **Soil erosion mechanisms differ with underlying substrate, vegetation cover and track position**
3. **Biocrusts are a major factor in mitigating soil losses after disturbances**

Therefore, we conducted rainfall simulation experiments using small-scale runoff plots (ROPs) to measure interrill erosion. Four rainfall simulation campaigns took place from March 2019 to February 2020 in the Schönbuch Nature Park in Southwest Germany, accompanied by parallel surveys of pioneer vegetation succession.

2 Material and methods

2.1 Study site

This study took place in the Schönbuch Nature Park in Southwest Germany, which is situated in Triassic hills consisting of sandstones, marlstones and claystones including some limestones and a few Lower Jurassic shales, sandstones and limestones at the tops. The Lower Jurassic plateaus are often covered with a loess layer (Einsele and Agster, 1986). Schönbuch Nature Park represents a low altitude (highest peak “Bromberg” at 583 m a.s.l), hilly (69 % with slopes ≤ 3° and 14 % with slopes >

15 %) and almost completely forested area (86 %) in the subatlantic temperate climate zone (Einsele and Agster, 1986; Arnold, 1986). While mean annual temperature is 8.3 °C , average amount of precipitation is 740 mm (mean annual values from 1979 to 1984 at the climate station in Herrenberg) (Dwd Climate Data Center, 2021c), which is comparable to the long-term average for Germany (Dwd Climate Data Center, 2021b, a).

For this research, four newly-established and unfortified skid trails in the Schönbuch Nature Park with different geological formations, soil properties and vegetation characteristics were selected (Table A1). All four skid trails consisted of two wheel tracks (WT) and a center track (CT) in between. They were created during logging operations conducted by the state forestry service of Baden-Württemberg (ForstBW) in Winter 2018/19 and represented an initial point of vegetation development when this study was commenced.

The four skid trails were distinguished according to their geological formation: Angulatensandstein (AS), Psilonotenton (PT), Löwenstein (LS) and Trossingen (TS). AS consists of thin, platy, fine-grained sandstones containing limestone in unweathered state, while PT is composed of pyrite-bearing shale clay, interstratified by beds of limestone. In comparison, TS consists of firm, fractured, unstratified claystones with lime nodules, whereas LS forms medium- to coarse-grained, banked sandstones interrupted by reddish marls (Einsele and Agster, 1986). The skid trail AS is located next to a loess plateau, which also determines soil properties. Since the Schönbuch Nature Park was extensively formed by periglacial processes, the geological formation does not represent the parent rock of soil formation in every case (Bibus, 1986).

In the surroundings of LS, a reforested conifer stand was determined with approximately 70-year-old *Pinus sylvestris* and 50-year-old *Picea abies*, where the former occurred with 50 % cover and the latter with 40 % cover in the highest tree layer. Furthermore, in a second tree layer, about 20-year-old *Fagus sylvatica* and *Carpinus betulus* have colonized, covering the forest floor with leaf litter over the entire area, so that a herb layer of about 10 - 20 % was formed, which was mainly restricted to sparse areas and dominated by grasses such as *Carex sylvatica* and *Brachypodium sylvaticum*. Additionally, a soil survey was carried out based on Ad-Hoc-Ag Boden (2005) and subsequently the soil types according to Iuss Working Group Wrb (2015) were derived using the WRB Tool for Geman Soil Data (Eberhardt et al., 2019). For LS, an Eutric Cambisol (Ochric) with typical moder was identified and the soil surface was covered with a moss layer up to 5 % in total. In comparison, the natural habitat of TS was dominated by young *Picea abies* (approx. 30 a), with 90 – 100 % of the soil surface covered with moss and in 5-10 % of the area a herb layer was formed. The soil survey revealed a Eutric Cambisol (Geoabruptic, Clayic, Ochric, Raptic, Protovertic), which was much deeper compared to WT in the skid trail and covered with a mull-like moder humus layer. The other two sites were characterized by deciduous tree species: While PT was formed primarily by beech trees (*Fagus sylvatica*) at different ages, developing a sparse tree layer and a very dense shrub layer, in AS a sparse tree layer of approximately 100-year-old *Quercus petraea* and a second level of younger *Fagus sylvatica* and *Carpinus betulus* were found. In PT, soil survey revealed an Eutric Calcaric Amphistagnic Cambisol (Loamic, Ochric) with a mull-like moder humus layer and in the vegetation survey a herb layer with a cover rate of less than 5 % was determined. In contrast, AS had a 20 % herb layer formed almost exclusively by *Quercus petraea* and *Carpinus betulus* seedlings and soil type was identified as Dystric Stagnic Regosol (Ochric) with L-mull.

2.2 Field and laboratory methods

To test for particular impacts of early successional post-disturbance forest floor vegetation on surface runoff and sediment discharge, rainfall simulations with micro-scale runoff plots (ROPs; 0.4 m × 0.4 m; cf. Seitz (2015)) were performed at four time steps (March 2019, July 2019, October 2019, February 2020) (Figure A1). ROPs are stainless steel metal frames connected with a triangular surface runoff gutter which are used to measure interrill erosion processes (Seitz, 2015). Four ROPs were placed in the WT and the CT in every skid trail (n = 32), and two ROPs in the undisturbed forest soil (UF) next to every skid trial site (n = 8). While rainfall simulations in the skid trails were conducted for every time step (n = 128), they were narrowed to the two last time steps in the UF (n = 16), which yields to a total number of 144 measurements.

Rainfall simulations were conducted with the Tübingen rainfall simulator (Iserloh et al., 2013; Seitz, 2015) which is equipped with a Lechler 460.788.30 nozzle and adjusted to a falling height of 3.5 m. Mean rainfall intensity was set at 45 mm, which refers to the duration of rainfall simulations of 30 minutes. In each run two ROPs (WT and CT) were irrigated simultaneously, with surface runoff and sediment collected in sample bottles (1 L). Prior to each rainfall simulation, soil moisture was determined next to every ROP using a Thetaprobe ML2 in combination with a HH2 Moisture Meter (Delta-T Devices, Cambridge, UK).

After soil erosion measurements, the total surface runoff for each ROP was gathered from the associated sample bottles marked with a milliliter measuring scale. To ascertain sediment discharge, the sample bottles were dried at 40 °C in a compartment drier and weighed in dry state. For determination of basic soil properties, bulk soil samples of the topsoil (0 – 5 cm) were collected in the surroundings of every ROP. While aggregate size was obtained by wet-sieving, which served as a basis for calculation of the mean weight diameter (MWD) (Tiulin 1933, Van Bavel 1950), grain size distribution was determined with an x-ray particle size analyser (Sedigraph III, Micromeritics, Norcross, GA, USA). Soil pH was measured with a pH-meter and Sentix 81 electrodes (WTW, Weilheim, Germany) in 0.01 M $CaCl_2$ solution. Additionally, soil organic carbon (SOC) and total nitrogen (N_t) were determined with an elemental analyser (element analyzer Vario EL II, Elementar Analysesysteme GmbH, Hanau, Germany). Core samples (100 cm^3) were taken to determine soil bulk density in the topsoil with the mass-per-volume method (Blake and Hartge, 1986). Slope was measured on both sides of every ROP using an inclinometer, while aspect for the entire skid trail sites was derived from a digital elevation model (DEM, Geobasisdaten © Landesamt für Geoinformation und Landentwicklung Baden-Württemberg) using a geographical information system (QGIS-Version 3.16.13-Hannover, (Qgis Development Team, 2020)). Furthermore, skid trail sites were examined for water repellency by applying the water drop penetration time test (WDPT) (Dekker et al., 2009).

To investigate the development of vegetation cover on the forest floor surface in every ROP, sampling campaigns took place in five time steps (April 2019, June 2019, July 2019, October 2019, February 2020) synchronized with in situ soil erosion measurements. Vascular plants and bryophytes were classified by eye and identified by morphological characteristics using a stereomicroscope (SteREO Discovery.V8, Carl Zeiss Microscopy Deutschland GmbH, Oberkochen, Germany) and a microscope (Leitz SM-Lux, Ernst Leitz GmbH, Wetzlar, Germany). Classification was carried out to the species level, wherever possible, using the following plant identification literature: Rothmaler (2005), Nebel et al. (2000), Nebel et al. (2001), Nebel et al. (2005) and Moser (1963). Nomenclature see Table 1 and Table 2. In addition, total vegetation and bryophyte cover were surveyed for each ROP, while Braun-Blanquet cover-abundance scale was used to determine coverages at the species level (Braun-Blanquet, 1964). Due to a further use of the skid trail TS after the rainfall simulation in March, it was not possible to survey the vegetation in the center track in April. Vascular plant cover was calculated as the difference between total vegetation cover and bryophyte cover. Furthermore, perpendicular photographs were taken of each ROP with a digital compact camera (Panasonic DC-TZ91, Osaka, Japan) to additionally assess total vegetation cover with a photogrammetric survey, which was processed with the grid quadrat method and using a digital grid overlay with 100 subdivisions (Belnap et al., 2001). Bare soil and vegetation covers were separated by hue distinction.

2.3 Statistics

All analyses were conducted with R 4.0.4 (R Core Team, 2021) on the level of individual samples. To screen for significant differences, Kruskal-Wallis tests were used in combination with post-hoc Wilcoxon Rank-Sum tests for independent measurements and Wilcoxon Signed-rank tests for related measurements. A nonparametric analysis of covariance was performed to compare nonparametric regression curves. Previously, normality was proofed with Shapiro-Wilk test, while homoscedasticity was verified using the Levene`s test. Significance was assessed at $p < 0.05$ in all cases. For all mean values described, the standard error of the mean value was also given (mean ± standard error of the mean).

3 Results and discussion

3.1 Composition, coverage and richness of pioneer vegetation vary depending on underlying substrate and track position

3.1.1 Biocrust species composition

Within the vegetation survey in five time steps, a total of 24 moss, two liverwort and two fungi species were found in the skid trails (Table 1), while 13 moss species occurred in the UF (Table 2). Therefore, a clear domination of biocrust communities by bryophytes and especially mosses could be stated and set the further focus of this study. The first moss species to recolonize the skid trails in April after skidding were *Brachythecium rutabulum* (53.1 % of ROPs) and *Oxyrrhynchium hians* (37.5 % of ROPs), and we observed protonema in 25 % of the ROPs. In June, the percentage of ROPs occupied by *Brachythecium rutabulum* and *Oxyrrhynchium hians* increased to 75 % and 40.6 %, respectively, while protonema was found in 31.3 % of the ROPs. Furthermore, *Plagiomnium undulatum* occurred in 25 % and *Thuidium tamariscinum* in 18.8 % of the ROPs. From July to February, *Oxyrrhynchium hians*, *Brachythecium rutabulum*, and *Plagiomnium undulatum* remained the most abundant moss species and the quantity of different moss species increased. Other moss species that developed on between 35 to more than 10 % of the ROPs during this time period were: *Atrichum undulatum*, *Calliergonella cuspidata*, *Dicranella schreberiana*, *Dicranella varia*, *Fissidens taxifolius*, *Apopellia endiviifolia (Schütz et al., 2016)*, *Pohlia lutescens*, *Thuidium tamariscinum* and *Trichodon cylindricus*. The other bryophyte and fungi species listed in Table 1 were sporadically present in the skid trails (in < 10 % of ROPs). In comparison, 13 moss species occurred in the UF (Table 2), eight of which were also present in the skid trails and five species just occupied the UF. 205

Table 1: Biocrust species list for skid trails (32 runoff plots) in the Schönbuch Nature Park in southwestern Germany, based on five vegetation surveys from April 2019 to February 2020

FAMILY	SPECIES		AUTHOR
	Liverworts		
Lophocoleaceae	*Lophocolea*	*bidentata*	*(L.) Dum.*
Pelliaceae	*Apopellia*	*endiviifolia*	*(Dicks.) Nebel & D.Quandt*
	Mosses		
Polytrichaceae	*Atrichum*	*undulatum*	(Hedw.) P. Beauv.
Pottiaceae	*Barbula*	*unguiculata*	Hedw.
Brachytheciaceae	*Brachythecium*	*rutabulum*	(Hedw.) Schimp.
Bryaceae	*Bryum*	*pseudotriquetrum*	(Hedw.) P.Gaertn., E.Mey. & Scherb.
Bryaceae	*Bryum*	*tenuisetum*	Limpr.
Pylaisiaceae	*Calliergonella*	*cuspidata*	(Hedw.) Loeske
Brachytheciaceae	*Cirriphyllum*	*piliferum*	(Hedw.) Grout
Dicranellaceae	*Dicranella*	*schreberiana*	(Hedw.) Dixon
Dicranellaceae	*Dicranella*	*varia*	(Hedw.) Schimp.
Pottiaceae	*Didymodon*	*fallax*	(Hedw.) R.H.Zander
Brachytheciaceae	*Eurhynchium*	*striatum*	(Hedw.) Schimp.
Fissidentaceae	*Fissidens*	*taxifolius*	Hedw.
Hypnaceae	*Hypnum*	*cupressiforme*	Hedw. s. str.
Brachytheciaceae	*Oxyrrhynchium*	*hians*	(Hedw.) Loeske
Mniaceae	*Plagiomnium*	*affine*	(Blandow ex Funck) T.J.Kop.
Mniaceae	*Plagiomnium*	*undulatum*	(Hedw.) T.J.Kop.
Mniaceae	*Pohlia*	*lutescens*	(Limpr.) H.Lindb.
Mniaceae	*Pohlia*	*melanodon*	(Brid.) A.J.Shaw
Mniaceae	*Pohlia*	*wahlenbergii*	(F.Weber & D.Mohr) A.L.Andrews
Brachytheciaceae	*Pseudoscleropodium*	*purum*	(Hedw.) M.Fleisch.
Hylocomiaceae	*Rhytidiadelphus*	*squarrosus*	(Hedw.) Warnst.
Hylocomiaceae	*Rhytidiadelphus*	*triquetrus*	(Hedw.) Warnst.
Thuidiaceae	*Thuidium*	*tamariscinum*	(Hedw.) Schimp.
Ditrichaceae	*Trichodon*	*cylindricus*	(Hedw.) Schimp.

Fungi			
Pyronemataceae	*Scutellinia*	*kerguelensis*	(Berk.) Kuntze
Pyronemataceae	*Scutellinia*	*umbrarum*	(Fr.) Lambotte

Table 2: Biocrust species list for undisturbed forest soil (4 runoff plots) in the Schönbuch Nature Park in Southwest Germany, based on one vegetation survey in February 2020

FAMILY	SPECIES		AUTHOR
Brachytheciaceae	*Brachythecium*	*rutabulum*	(Hedw.) Schimp.
Brachytheciaceae	*Brachythecium*	*salebrosum*	(F. Weber & D. Mohr) Schimp.
Bryaceae	*Bryum*	*rubens*	Mitt.
Dicranellaceae	*Dicranella*	*heteromalla*	(Hedw.) Schimp.
Brachytheciaceae	*Eurhynchium*	*angustirete*	(Broth.) T.J.Kop.
Brachytheciaceae	*Euryhnchium*	*striatum*	(Hedw.) Schimp.
Fissidentaceae	*Fissidens*	*taxifolius*	Hedw.
Hylocomiaceae	*Hylocomium*	*splendens*	(Hedw.) Schimp.
Hypnaceae	*Hypnum*	*cupressiforme*	Hedw.
Mniaceae	*Pohlia*	*melanodon*	(Brid.) A.J.Shaw
Polytrichaceae	*Polytrichastrum*	*formosum*	(Hedw.) G.L.Sm.
Hylocomiaceae	*Rhytidiadelphus*	*triquetrus*	(Hedw.) Warnst.
Thuidiaceae	*Thuidium*	*tamariscinum*	(Hedw.) B.S.G.

In our study area, *Brachythecium rutabulum* and *Oxyrrhynchium hians* have emerged as the most important pioneer species. Both species are widespread in Baden-Württemberg, Germany (Nebel et al., 2001) and known to colonize a wide range of habitats (Nebel et al., 2001; Atherton et al., 2010). While *Brachythecium rutabulum* is particularly common on wood and stones, growing also on soil and gravelly ground, *Oxyrrhynchium hians'* habitat is preferentially restricted to bare base-rich soils (Atherton et al., 2010), which renders both as very pioneer-friendly mosses (Nebel et al., 2001). Due to its competitive strength and broader distribution, *Brachythecium rutabulum* was even more frequent in the skid trails than *Oxyrrhynchium hians.* At a more advanced stage of succession, *Plagiomnium undulatum* and *Thuidium tamariscinum* also occurred, both of which grow mainly on forest soils (Nebel et al., 2001; Atherton et al., 2010). Furthermore, a clearly different species composition was found in the UF compared to the skid trails. The species composition in the UF showed an increased occurrence of more specialized species common in acidic woodlands such as *Hylocomium splendens*, *Polytrichastrum formosum* and *Dicranella heteromalla* (Atherton et al., 2010), which can be attributed to the lower pH in the UF (mean pH = 4.54 ± 0.07) compared to the skid trails (mean pH = 6.19 ± 0.07). Mercier et al. (2019) also observed a different species composition in skid trails of different forest types in northern Bavaria compared to the forest interior during their vegetation surveys of vascular plants and bryophytes, indicating that skid trails can contribute to higher species diversity in managed forests.

The vegetation succession developed differently in the four skid trails (Figure 1) in terms of biocrust and total vegetation coverage (Figure 2) and species richness of vascular plants and biocrusts (Figure 3) as well as species composition. At the beginning of vegetation succession after the disturbance due to skidding, we observed the development of protonema in AS and PT. Whereas protonema occurred in AS from April to July in 50 % of the ROPs, it was less frequent in PT but reached 50 % coverage in two ROPs in June. The most abundant pioneer species were *Brachythecium rutabulum* and *Oxyrrhynchium hians* in all skid trails, but *Oxyrrhynchium hians* was absent in TS. TS was clearly dominated by *Brachythecium rutabulum*, which occurs in almost every ROP, with the coverage being up to 50 % in CT, increasing constantly during the vegetation survey. *Brachythecium rutabulum* was present in all other skid trails, but mostly with little importance in terms of coverage. Furthermore, *Thuidium tamariscinum* occurred in TS in almost every ROP and in CT plots also with a considerably high coverage of up to 25 % in October or February, and did not colonize PT or AS, but was also abundant in LS with cover up to 5%. Liverwort species developed in PT, LS and TS, with *Apopellia endiviifolia* occurring in PT and LS, and *Lophocolea bidentata* found only in TS. While *Plagiomnium undulatum* did not occur in AS, it was very common in all other skid trails, with mostly low coverage (around 5 %). Generally, *Plagiomnium undulatum* development started early in summer (June or July) in PT and LS, and exclusively in fall in TS. Especially in July and October, *Dicranella schreberiana* was abundant in PT and in some ROPs up to a coverage of 50 %, while it did not grow in all other skid trails. Furthermore, *Oxyrrhynchium hians* achieved high coverage rates of up to 25 % in PT.

Brachythecium rutabulum has a wide variation of possible habitats (Nebel et al., 2001). In all skid trails it occurred as a pioneer species, however, while in PT, AS, and LS it associated with other moss species as succession progressed, in TS it was dominant in terms of coverage. Since *Brachythecium rutabulum* is known to be stimulated in growth by eutrophication (Nebel et al., 2001), high N_t in TS could be a possible explanation for its dominant occurrence there. In addition, TS was the only skid trail in which *Oxyrrhynchium hians* did not occur. On the one hand, this can be attributed to the fact that *Brachythecium rutabulum* is very competitive, especially on eutrophic sites, and suppresses other species (Nebel et al., 2001). On the other hand, TS had a low pH of 5.4 and since *Oxyrrhynchium hians* grows on base-rich soils, TS is not the preferred growing location. The absence of *Plagiomnium undulatum* in AS can be attributed to the fact that AS was clearly drier compared to the other sites and according to Nebel et al. (2001) *Plagiomnium undulatum* is a permanent moisture indicator. This is also shown by the fact that *Plagiomnium undulatum* occurred comparatively late in the year in TS: We assume that only the formation of a closed vegetation cover of vascular plants at this site developed a sufficiently shady and humid microclimate for *Plagiomnium undulatum* to establish there. In this context, Sedia and Ehrenfeld (2003) and Ingerpuu et al. (2005) demonstrated that vascular plants can promote a microhabitat more hospitable for moss growth. *Thuidium tamariscinum* occurred exclusively in skid trails surrounded by coniferous forests, which corresponds to its preferential distribution area (Nebel et al., 2001). According to Düll (1991), *Apopellia endiviifolia* is exclusively distributed at sites with neutral to alkaline pH, which is why it occurred in PT and LS in our study area, but not at the other two skid trails. It was also particularly interesting that the pioneer species *Dicranella schreberiana* and *Pohlia lutescens* were more volatile than expected, spreading only during summer and disappearing again during autumn.

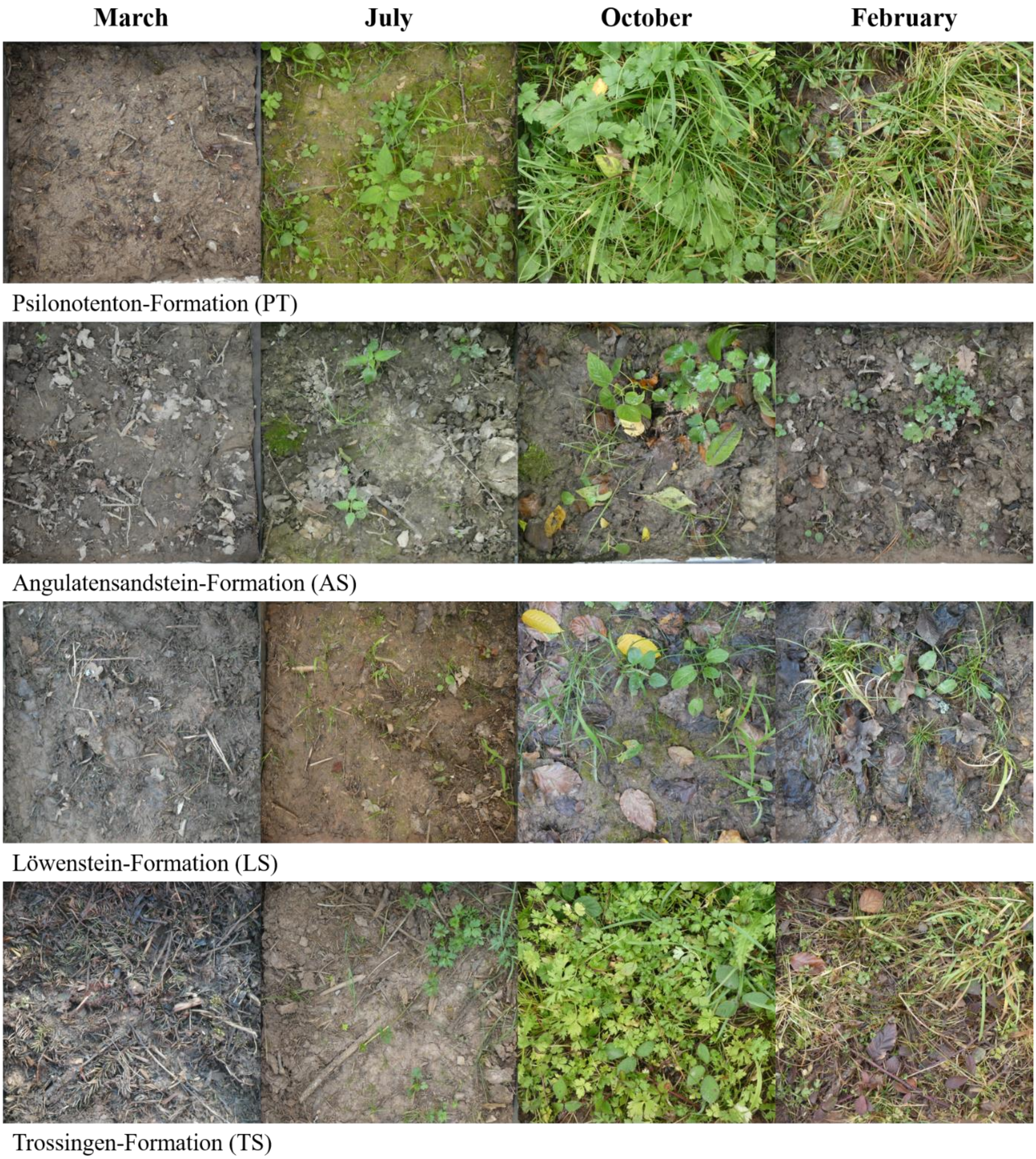

Figure 1: Vegetation succession of four examplary runoff plots in wheel tracks of the skid trails in Schönbuch Nature Park

3.1.2 Biocrust and total vegetation coverage

On average for all skid trail sites and vegetation surveys, biocrust coverage was higher in CT than in WT, which was also true for total vegetation coverage. With respect to the individual skid trails, the extent of biocrust cover varied widely (Figure 2). In AS and LS, biocrust coverage averaged no more than 12.00 %, while PT peaked at 33.33 % ± 6.67 in July and TS achieved 34.64 % ± 11.95 in February, with considerable variation in cover between WT and CT in the last two skid trails. PT showed a more pronounced development of biocrust cover in WT (up to 40 % from June to October), opposite to the preferential colonization of CT in TS (up to 60 % in February). While biocrust cover in PT decreased between October and February, this effect did not occur in TS.

Similar site-specific patterns of succession are reflected in total vegetation cover: In AS and LS, total vegetation coverage was lower than in the other two skid trails (Figure 2). Especially PT and TS were rapidly overgrown by vascular plants, however they did not displace biocrusts. This coexistence of vascular plants and biocrusts was also displayed in a positive correlation between their coverage rates (Spearman's correlation rho = 0.38, $P < 0.001$). While a closed vegetation cover developed in PT and TS until autumn in both CT and WT, no continuous pattern of growing emerged in AS and LS with clear differences between CT and WT. The latter developed a very sparse total vegetation cover in WT (about 5 %), and revealed a considerable higher coverage in CT.

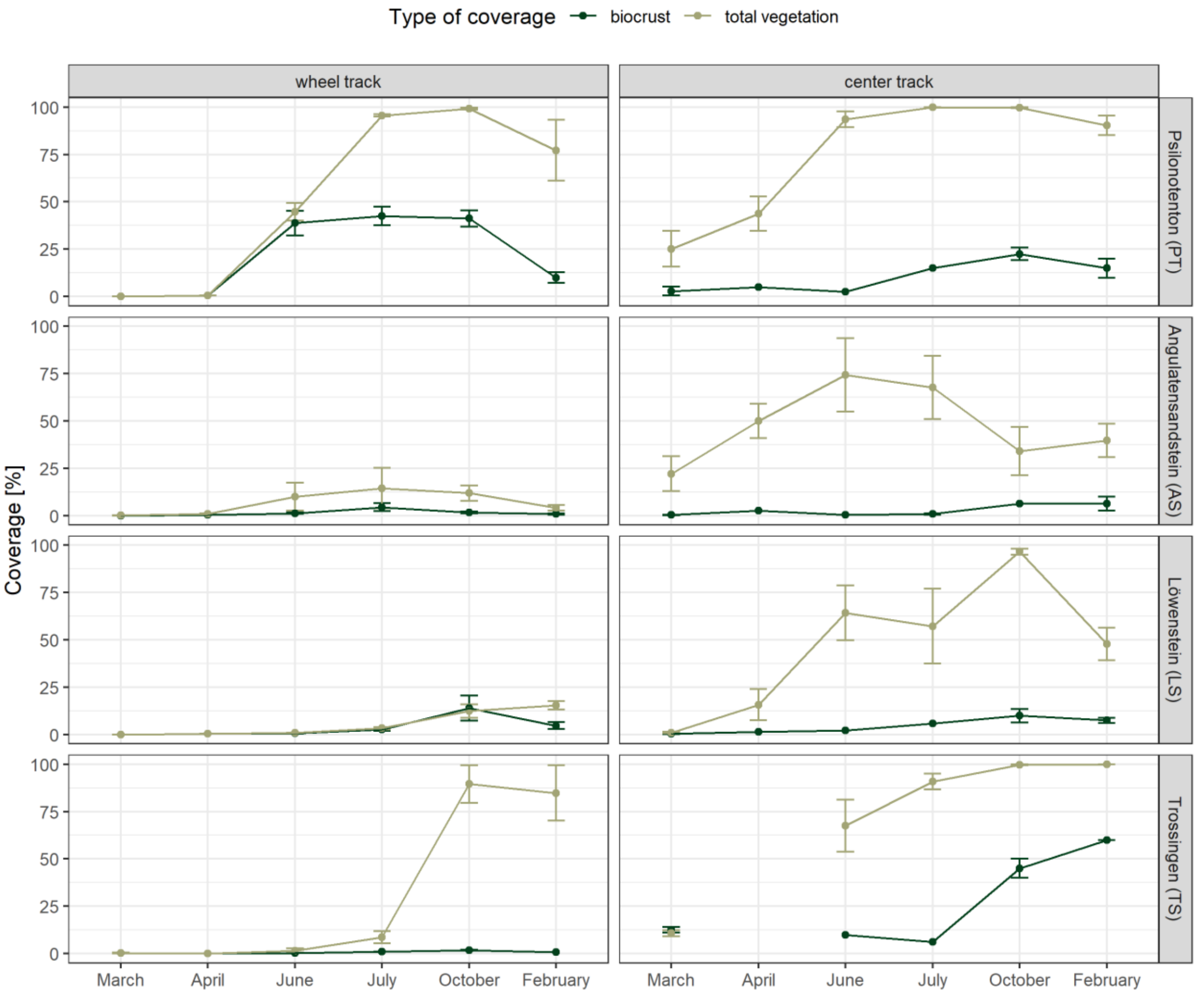

Figure 2: Development of biocrust and total vegetation coverage at the individual skid trail sites. Mean values are displayed as dots, error bars represent the standard error of the mean.

Generally, total vegetation and biocrust cover developed with a higher coverage rate in CT, indicating the inferior soil conditions in WT compared to CT. In this context, we found higher pH values in WT than in CT, with the difference being significant for AS, TS and LS. The importance of soil pH on the growth of vascular plants and bryophytes, as well as their composition and diversity, has also been highlighted in several studies (Löbel et al., 2006; Oldén et al., 2016; Hydbom et al., 2012). For example, Rola et al. (2021) showed that soils with a more acidic pH promoted a larger bryophyte coverage, which could explain, among other things, the generally higher bryophyte cover in CT in our study.

Furthermore, biocrusts were quickly overgrown by vascular plants in the course of the year. However, they could establish even with high total vegetation cover, which contradicts observations that vascular plants limit biocrust growth in different ecosystems (Corbin and Thiet, 2020; Bergamini et al., 2001; Fojcik et al., 2019). Ingerpuu et al. (2005) verified in a grassland experiment that vascular plants could actually facilitate moss growth, explaining this by the fact that vascular plants create a more favourable microclimate under their canopy. Likewise, positive correlations between vascular plant and moss cover have been reported for temperate forests, which are comparable to our results (Márialigeti et al., 2009; Rola et al., 2021). A decline in biocrust cover was observed for the first time in autumn on deciduous forest sites. For this reason, we assume that biocrust growth in our study area was limited by leaf litter fall rather than suppression by vascular plants. A negative effect of leaf litter was also reported in several other studies (Wu et al., 2020; Alatalo et al., 2020; Márialigeti et al., 2009; Fojcik et al., 2019; Mercier et al., 2019).

3.1.3 Biocrust and vascular plant species richness

In regard to biocrust and vascular plant species richness, we observed that more vascular plant species occur in CT compared to WT, while no significant difference between tracks was found for biocrust species richness (Figure 3). Furthermore, species richness varied in the skid trails: PT and LS showed, on average, considerably higher quantities of biocrust species compared to AS and TS. Concerning vascular plants, the highest species richness was achieved in PT, which was significantly higher than in AS and TS, but not different from LS. In comparison, AS, TS, and LS exhibited no differences among themselves with respect to vascular plant species richness. While biocrust species richness was positively correlated with pH (Spearman's correlation rho = 0.40, $P < 0.001$) and negatively correlated with silt content (Spearman's correlation rho = -0.35, $P < 0.001$), we could not find any clear associations between the soil parameters surveyed and vascular plant species richness.

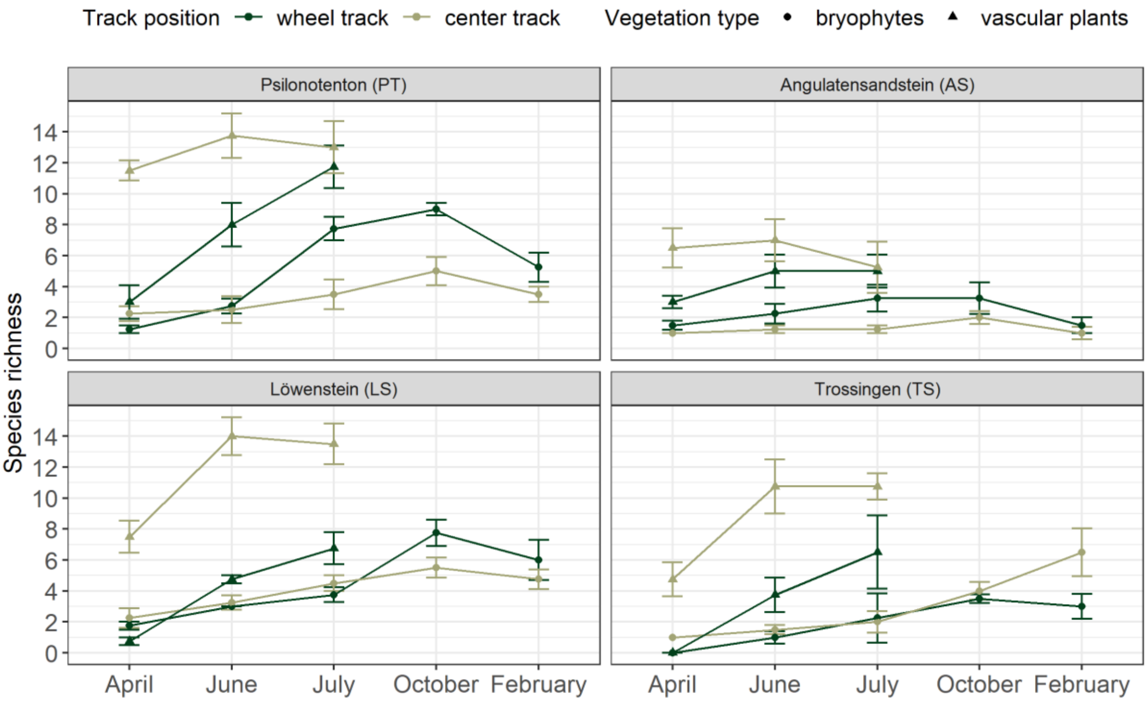

Figure 3: Species richness of bryophytes and vascular plants at the individual skid trail sites. Mean values are displayed as dots, error bars represent the standard error of the mean.

Our results revealed that development of total vegetation cover was not only slower and less pronounced in WT, but also that fewer vascular plant species could colonize there. Contrary to our expectations, biocrust species richness was not affected by track position. In this context, Müller et al. (2013) found that experimentally induced disturbances had no impact on bryophyte species richness, whereas diversity of annual plants benefited from disturbances. Minor disturbances, not exceeding 12 % bare ground, could still promote bryophyte species richness, while further disturbance were detrimental. Additionally, Mercier et al. (2019) discovered that soil compaction in skid trails had a positive effect on the species richness of vascular plants, while bryophyte species richness was not affected.

AS and LS, which showed particularly low levels of coverage and species richness, exhibited different underlying substrate (sandstone) in comparison with the other two skid trails (claystone), which was also why we found different soil conditions there. Regional variations in species richness of vascular plants and bryophytes due to different soil conditions have also been confirmed in a variety of studies (Müller et al., 2013; Filibeck et al., 2019; Klaus et al., 2013; Löbel et al., 2006), with pH in particular proving to be an important positive control variable for bryophyte species richness (Oldén et al., 2016; Tyler et al., 2018; Hydbom et al., 2012). Additionally, Tyler et al. (2018) discovered a significant influence of substrate type, soil depth and grazing intensity on overall bryophyte species richness, with pH remaining the most important factor in this study as well. Further factors influencing bryophyte species richness, such as light availability, CN ratio and bark water capacity were identified by Jagodziński et al. (2018) for 30-year old reforested areas on lignite mining spoil heaps.

3.2 Soil erosion mechanisms differ with underlying substrate, vegetation cover and track position

3.2.1 Soil erosion depending on track position

In total, mean sediment discharge reached 134.92 g m^{-2} ± 14.72 in the skid trails (WT + CT) and was 8.6 times higher than in the UF (15.68 g m^{-2} ± 3.84), with sediment discharge in the WT being 13.2 times higher and in the CT 4 times higher compared to the UF. Considering ROPs with bare soil separately, an average soil erosion of 341.53 g m^{-2} ± 68.20 was achieved, which corresponds to a 22-fold enhancement compared to the UF. Additionally, sediment discharge in WT was increased by a factor of 3.3 compared to CT. Mean surface runoff in the skid trails (WT + CT) achieved 27.30 L m^{-2} ± 1.30 and was 2 times higher than in the UF (13.75 L m^{-2} ± 3.84). While surface runoff in WT was higher than in UF by a factor of 2.8 and also increased by a factor of 2.4 compared to CT, there was no significant difference between CT and UF. The main driver of sediment discharge was surface runoff (Spearman's correlation rho = 0.80, $p < 0.001$), and other important influencing soil characteristics were soil bulk density (Spearman's correlation rho = 0.50, $p < 0.001$), SOC and N_t (both Spearman's correlation rho = -0.46, $p < 0.001$), and MWD (Spearman's correlation rho = -0.46, $p < 0.001$). Additionally, a negative correlation between soil erosion and clay content was identified (Spearman's correlation rho = -0.42, $p < 0.001$), and antecedent soil moisture and slope played a minor role in soil erosion.

These results show that skid trails are a major contributor to soil erosion in forest ecosystems, and that compacted WT in particular significantly increased sediment discharge, which has also been demonstrated in previous studies (Safari et al., 2016; Zemke, 2016). In line with our results, Safari et al. (2016) highlighted soil texture, soil bulk density, SOC and aggregate stability as the main soil parameter affecting runoff generation and soil erosion in skid trails. Based on these relationships, the significantly higher sediment discharge in skid trails is explained by the fact that the soil was disturbed and compacted by the timber harvesting machines, especially in WT, so that infiltration is reduced, which in turn leads to higher surface runoff and sediment transport (Zemke et al., 2019).

3.2.2 Soil erosion depending on underlying substrate and vegetation cover

On average for all skid trail sites, sediment discharge was highest in March on bare soil ROPs with a mean value of 201.80 g m^{-2} ± 39.82 and was considerably decreased in July to 74.13 g m^{-2} ± 16.16. Subsequently, sediment discharge increased significantly in October (97.77 g m^{-2} ± 21.16) and raised again to 165.03 g m^{-2} ± 29.75 in February. Considering the time progression of soil erosion individually in the skid trails, different erosion mechanisms and sediment loads were evident (Figure 4). Average sediment discharge was highest in AS with 243.63 g m^{-2} ± 37.30 and lowest in TS with 42.83 g m^{-2} ± 10.34, which represented a difference of 5.7 times. While all skid trails differed from each other in terms of sediment discharge, no significant difference could be detected between PT (151.62 g m^{-2} ± 32.57) and LS (99.26 g m^{-2} ± 15.76). With respect to the time progression of soil erosion in the skid trails, we could find a difference between the time steps for PT and LS, but not for AS and TS. In both cases, sediment discharge was significantly reduced from bare soil condition in March to an early successional stage of biocrust and vascular plant vegetation in July: PT showed a decrease of 89 % and LS a reduction of 59 %. The same pattern of soil erosion over the year was also observed in AS, but could not be statistically demonstrated.

While correlation between surface runoff and sediment discharge was particularly high on average for the first rainfall event (Spearman's correlation rho = 0.89, $p < 0.001$), the influence was distinctly reduced in the other events and especially in October (Spearman's correlation rho = 0.51, $p < 0.01$). In the subsequent rainfall events, vegetation cover was an additional factor influencing soil erosion: The negative relationship between total vegetation cover and sediment discharge increased considerably from the first to the third event in October (1. event in March: Spearman's correlation rho = -0.45, $p < 0.01$; 3. event in October: Spearman's correlation rho = -0.86, $p < 0.001$), and highest reduction of sediment discharge occurred in July.

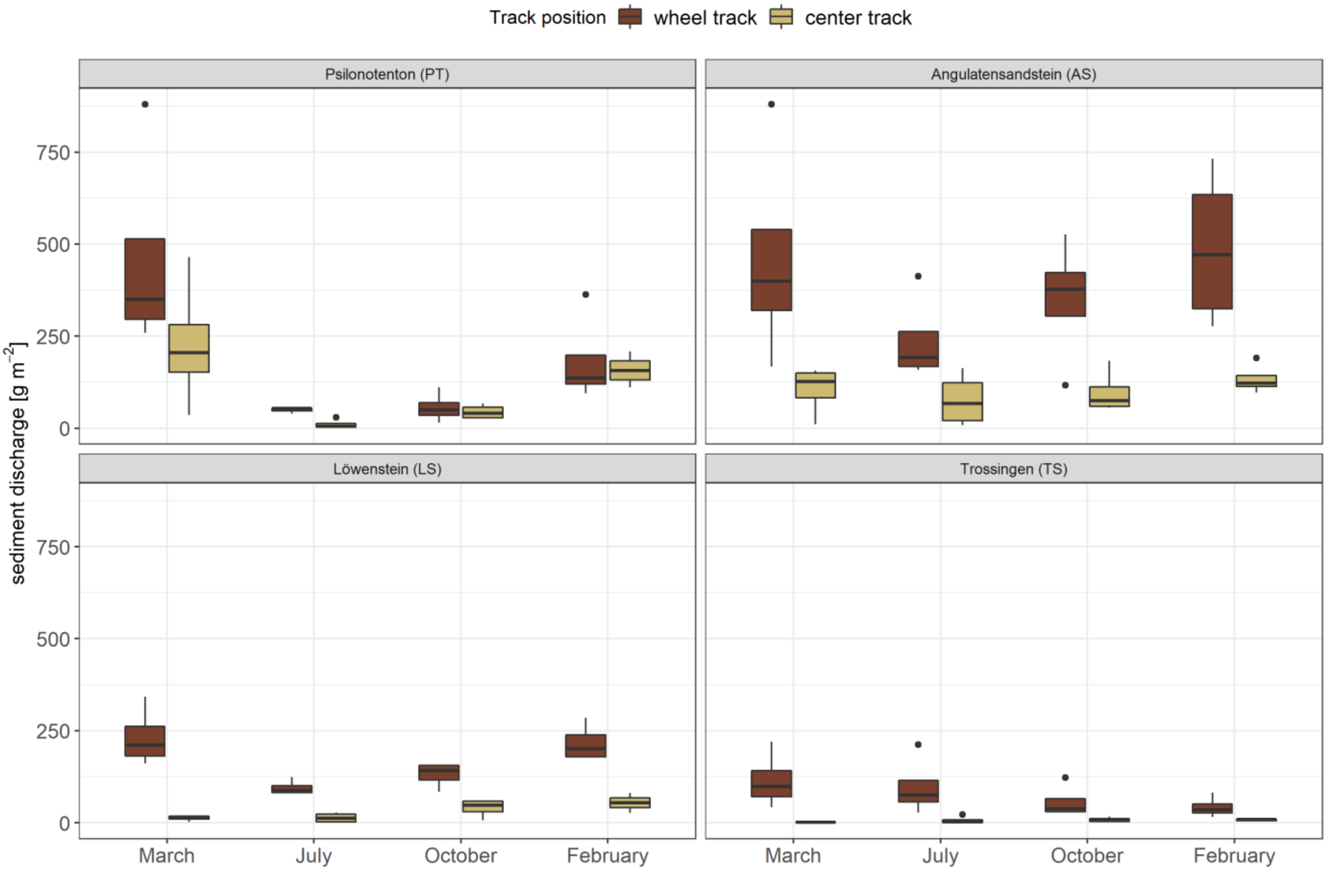

Figure 4: Sediment discharge in the wheel track (n = 4) and center track (n = 4) of the four skid trail sites for every rainfall simulation time step. The bottom and top of the box represent the first and third quartiles, and whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

Overall, the amount of discharged sediment clearly depended on the particular site, likely indicating an important effect of parent material on soil properties, adjunct vegetation development and thus on soil erosion. A high influence of parent material on soil erosion was confirmed by Rodrigo-Comino et al. (2018). Regardless of the amounts of sediment discharge, three skid trails showed comparable trends in soil erosion over time: In general, soil erosion was highest on bare soil, was reduced during the vegetation period, most with pioneer vegetation in July where biocrusts predominated, and then increased again in winter. This general trend was not observed in TS, which is probably related to the ecological structure of TS, since it was the only skid trial located in a clearing and was therefore clearly distinguished from the other skid trails in terms of vegetation succession. In addition, forest residues such as bark, small branches and needles were added to the topsoil in TS as a result of forestry use, which also had a stabilizing effect and certainly contributed to the low sediment discharge in this skid trail. An erosion-reducing effect of these types of mulching with forest residues had already been demonstrated in various studies (Prats et al., 2016; Prosdocimi et al., 2016) and Vinson et al. (2017) recently demonstrated that mulching strategies could also significantly reduce erosion rates in skid trails.

Several erosion studies in skid trails have already emphasized vegetation cover as one of the key control variables of soil erosion (Zemke, 2016; Mceachran et al., 2018; Malvar et al., 2017). Thereby, it was often observed that soil erosion was highest in the first year after skidding and decreased thereafter with increasing vegetation cover (Malvar et al., 2017; Baharuddin et al., 1995; Jourgholami et al., 2017). Martínez-Zavala et al. (2008) also reported a seasonality in their erosion measurements on forest road backslopes in southern Spain, with higher soil loss rates in winter despite vegetation cover, primarily attributed to higher soil moisture. However, they further found that this seasonal effect did not occur above a vegetation cover of 30 %. Additionally, Belnap et al. (2013) showed that antecedent moisture in biocrust-covered soils resulted in a higher sediment discharge and that the longer the soil was wet in advance, the more likely sediment discharge increased even in well-developed biocrusts. Thus, we hypothesize that, among other factors, higher soil moisture may have influenced increased winter soil erosion in our case as well, although we have not found significant correlations to support this theory.

3.3 Biocrusts are a major factor in mitigating soil losses after disturbances

Sediment discharge was distinctly negatively affected by total vegetation cover (Spearman's correlation rho = -0.61, $p < 0.001$). Furthermore, we discovered a stronger negative correlation between biocrust cover and sediment discharge (Spearman's correlation rho = -0.54, $p < 0.001$) than between vascular plant cover and sediment discharge (Spearman's correlation rho = -0.36, $p < 0.001$). For these correlations, all UF ROPs that were covered with leaf litter were extracted, because we assume that litter-covered soils have a different protective mechanism than soils with biocrusts or vascular plants (Silva et al., 2019; Wang et al., 2020).

To test for significant differences between cover types, we classified ROPs into bare, biocrust and vascular plant ROPs. In bare ROPs there was neither biocrust nor vascular plant cover (n = 14), biocrust ROPs were mainly covered by biocrusts (n = 27) and vascular plant ROPs were mainly covered by vascular plants and at the same time biocrust cover was lower or equal than 10 % (n = 58). All cover classes differed significantly from each other, with a reduction of 77 % being observed between bare ROPs and biocrust ROPs ($p < 0.001$) and a reduction of 59 % being observed between bare ROPs and vascular plant ROPs ($p < 0.005$). Biocrust ROPs produced 44 % less sediment discharge compared to vascular plant ROPs ($p < 0.05$). When ROPs were categorized into different cover classes, there was a non-significant trend for biocrusts to result in less sediment discharge compared to vascular plants (Figure 5). Especially with a cover of more than 50 % the erosion-reducing effect of biocrusts was more pronounced compared to vascular plants: There, for example, mean sediment discharge of biocrust ROPs was 3.27 g m^{-2} ± 1.50, while vascular plant ROPs still reached an average of 57.82 g m^{-2} ± 12.47, with a difference of 18-fold.

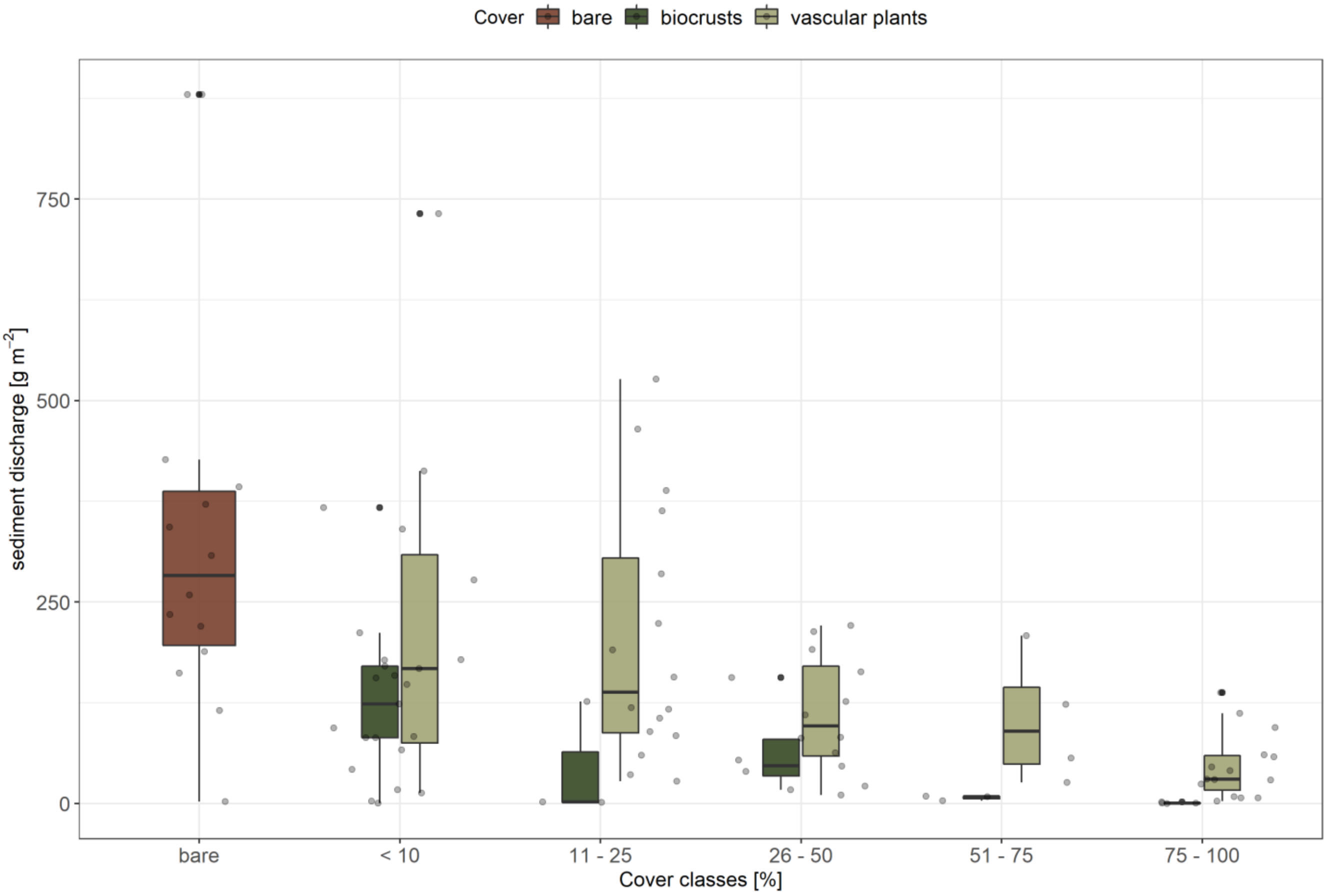

Figure 5: Sediment discharge for bare, biocrust and vascular plant runoff plots (ROPs) categorized into cover classes. The bottom and top of the box represent the first and third quartiles, and whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

Bryophyte-dominated biocrusts are known to stabilize soil surfaces and thus, being a protective agent against soil erosion (Belnap and Büdel, 2016; Seitz et al., 2017). The same applies to covers of vascular plants (Zuazo Durán and Rodríguez

Pleguezuelo, 2009), however, it has already been demonstrated during erosion experiments with a simulated scouring water flux on the Loess Plateau Region in China by Zhao and Xu (2013) that biocrusts have a stronger erosion-reducing effect compared to vascular plants. While plant canopies mitigated soil erosion by 10 % on 13-year and by 45 % on 4-year revegetated grassland, biocrusts resulted in a more than 90 % reduction with both scouring water of 12.0 L/min. Similar results were found by Bu et al. (2015) on the Loess Plateau: Bryophyte-dominated biocrusts achieved a reduction of soil erosion by 81 % compared to bare soil, whilst a mixture of vascular plants and biocrusts contributed significantly less to erosion control (0.7 - 0.3 % reduction depending on plant species). Contrary results were reported by Parsakhoo et al. (2012) who found that bryophyte-covered ROPs produced more sediment compared to ROPs with *Rubus hyrcanus*. However, it is still not clear which traits influence the stabilizing effect of biocrusts (Belnap and Büdel, 2016) and likewise there are still a number of unresolved questions regarding the bryophyte-soil interactions in water absorption and erosion processes (Thielen et al., 2021).

4 Conclusions

This study examined the initial development of pioneer biocrust and vascular plant cover, composition, and species richness in forest disturbance zones and their influence on soil erosion mechanisms. Regarding our hypotheses, the following conclusions were drawn:

(1) The succession of biocrust and vascular plant species varied by underlying substrate and track position in terms of coverage, species richness, and species composition. Generally, *Brachythecium rutabulum* and *Oxyrrhynchium hians* were the most important and persistent pioneer biocrust species, while *Dicranella schreberiana* and *Pohlia lutescens* were volatile and quickly disappeared after spreading in summer. Furthermore, we discovered a marked difference in biocrust species composition between undisturbed forest soil (UF) and skid trails, with specialized species in particular colonizing the UF. Skid trails on clayey substrates showed considerably higher vegetation cover and species richness, which applied to biocrusts and vascular plants. While vascular plants grew better in center tracks (CT) compared to wheel tracks (WT) in terms of both cover and species richness, there was no clear difference for biocrust species richness in this regard. Although biocrusts were quickly overtopped by vascular plants during vegetation succession, they managed to coexist until the end of the vegetation period and were then limited more likely due to leaf litter fall. The pH was identified as main influencing factor of biocrust cover and species richness.

(2) The total amount of sediment discharge and the general mechanisms of soil erosion were clearly site-dependent: While the amount of sediment was influenced by underlying substrate, soil erosion mechanisms were more likely determined by ecological aspects and mulching techniques. Soil erosion was reduced especially with the occurrence of pioneer biocrust vegetation in summer, and again increased in winter. In general, sediment discharge was 13.2 times higher in WT compared to UF, and bare soil runoff plots (ROPs) produced 22-fold sediment discharge compared to UF. Within the skid trail, sediment discharge was increased by a factor of 3.3 in WT compared to CT.

(3) Biocrusts are a major contribution to erosion control after disturbances in this temperate forest ecosystem. Bryophyte-dominated biocrusts contributed more to mitigating soil erosion than vascular plants and are of utmost importance to prevent soil degradation also in mesic areas. The erosion-reducing effect of biocrusts was particularly pronounced when soil cover was above 50 %: Here, vascular plant ROPs produced on average around 18 times more sediment compared to biocrust ROPs.

Based on these results, artificial inoculation of biocrusts as erosion control on bare forest soils, which often form a protective vegetation layer in nature only slowly, is assumed to be of particular interest for future research. In this context, Varela et al. (2021) recently published an approach of feasible artificial moss culture, which could be applied for environmental studies. Moreover, the question arises whether bryophyte-dominated biocrusts reduce soil erosion primarily through their protective layer effect or whether they also improve soil properties, which in turn enhances erosion control. Within this framework, it continues to be of special interest if there are different mechanisms of erosion control depending on particular bryophyte species and which of their structural traits affect soil erosion patterns.

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Table A1: Characteristics of studied skid trails.

	AS	**PT**	**LS**	**TS**
Series	Lower Jurassic	Lower Jurassic	Upper Triassic	Upper Triassic
Formation	Angulatensandstein (AS)	Psilonotenton (PT)	Löwenstein (LS)	Trossingen (TS)
Parent material	sandstone	shale clay	sandstone	claystone
Soil type (Ad-Hoc-Ag Boden, 2005)	Braunerde-Pseudogley	Pseudogley	Braunerde-Pelosol	Braunerde-Pelosol
Soil type (Iuss Working Group Wrb, 2015)	Dystric Leptosol (Ochric, Siltic, Stagnic)	Calcaric Albic Planosol (Clayic, Ochric, Raptic)	Calcaric Cambisol (Humic, Loamic, Protovertic)	Eutric Cambisol (Geoabruptic, Clayic, Ochric, Protovertic)
Soil texture	silt loam • sand: 6.89 % • silt: 67.99 % • clay: 25.33 %	silty clay loam • sand: 6.67 % • silt: 56.49 % • clay: 36.86 %	clay loam • sand: 25.91 % • silt: 40.78 % • clay: 33.20 %	silty clay loam • sand: 11.46 % • silt: 50.70 % • clay: 37.81 %
SOC	4.08 %	5.22 %	5.52 %	7.95 %
N_t	0.24 %	0.31 %	0.27 %	0.40 %
C/N	17	17	21	19
pH_{Ca}	5.6	6.9	6.9	5.4
Slope	4.6 °	7.2 °	10 °	11.3 °
Aspect	Southwest	South	West	Northwest
Sample site coordinates	Tübingen 48.553054 N 9.119053 E	Tübingen 48.557425 N 9.114462 E	Tübingen 48.557527 N 9.088098 E	Tübingen 48.556036 N 9.089313 E

Figure A1: Experimental setup: a) Tübingen rainfall simulator with protective tent, b) Skid trail in the Trossingen-Formation (TS) in July 2019, c) Runoff plots in the wheel track and the center track in the Angulatensandstein-Formation (AS) in October 2019

Code availability

The codes used in this study are available upon request.

Data availability

The dataset compiled and analysed in this study is available on figshare at https://doi.org/10.6084/m9.figshare.17206835.v2 (Gall et al., 2021).

Author contribution

StS, TS, DQ and MN designed the experiment. CG and StS carried out field measurements and CG was responsible for laboratory and data analyses. MN and CG conducted the vegetation surveys. CG and StS prepared the manuscript with contributions from all other co-authors.

Competing interests

The authors declare that they have no conflict of interest.

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