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Biotic drivers of soil development: the contribution of biocrusts and roots to soil structure and organic matter formation in drylands

Kristina Harriet Marianne Witzgall

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Chair: Prof. Dr. Johannes Kollmann
Examiners: 1. Prof. Dr. Dr. h.c. Ingrid Kögel-Knabner
2. Prof. Dr. Carsten W. Mueller
3. Prof. Dr. Sebastian Dötterl

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I | Summary

Soil development is largely regulated by the intricate interplay between soil minerals, plants, and microorganisms. In sparsely vegetated dryland ecosystems, these interactions are often confined to heterogeneously distributed hotspots; either concentrated within the soil volume surrounding plant roots (rhizosphere), or within biological communities colonizing the soil surface (biocrusts). At these critical interfaces, nutrients are increasingly available—either derived from biota in the form of rhizodeposits and microbial exudates, or released through biogeochemical weathering processes driven by micro- and macroorganisms—which, in turn, stimulates microbial abundance and activity. Overall, the increased biotic activity, along with the associated gradual build-up of organic C and N, represent a fundamental starting point for the formation and potential stabilization of soil organic matter (SOM) into particulate OM (POM) and mineral-associated OM (MAOM). Fungal mycelium and cyanobacterial filaments further bind soil minerals, promoting the formation of subsurface soil structures and the aggregation of soil particles. These processes enhance water and nutrient retention and, over time, create a soil environment that facilitates further ecological succession, allowing for continued development toward more complex and diverse communities. However, despite their critical role for the development of the soil system, fundamental aspects of soil-biota interactions in the context of dryland ecosystems remain poorly understood—research has previously focused on more productive ecosystems. Adding to this, the focus has mainly been on higher plant systems, disregarding the relevance of biocrust-soil interactions for ecosystem functionality.

The main objective of this publication-based thesis is to investigate the role of biota as regulators and drivers of soil development in dryland ecosystems, with a particular emphasis on soil structures and SOM formation. This is approached in a set of experiments designed along a successional gradient, first encompassing interactions between primary and early successional biota (biocrusts) and soil at the soil surface (Studies I and II), and later expanding the scale to include interactions between higher plants and soil at the soil-root interphase, addressing both processes around living and decaying root systems (Study III). Overall, this approach allows us to distinguish the critical role of different biotic agents in the development of dryland soils, where overall biotic activity is otherwise limited.

In order to trace C fluxes in early successional biocrust-soil systems, a gas sampling system was developed with the overall aim to facilitate both CO_2 measurements and $^{13}CO_2$ labeling within a single setup (Study I). This methodological development was also a prerequisite for the subsequent measurements conducted in Study II. Given the low CO_2 fluxes typically expected in biocrust-soil systems—due to the generally low respiration rates of semi-arid soils and limited photosynthetic C uptake by lower organisms—we sought to design a system capable of obtaining larger sample volumes for reliable quantification while minimizing incubation and pressure effects on the soil system. Additionally, the system was designed to enable high sample throughput while minimizing the risk of cross-contamination between samples, as both Studies I and II involved the handling of $^{13}CO_2$ and $^{15}N_2$.

Following the developments of Study I, the focus of Study II was extended to determine the effect of changing climatic conditions on C and N pathways from biocrusts into the underlying sub-crust soil. This was realized in a phytotron incubation experiment, where intact biocrust-soil systems were exposed to experimental warming and drought. During incubation, pulse $^{13}CO_2$ and $^{15}N_2$ labeling was applied and CO_2 fluxes were monitored to determine photosynthetic C uptake and respiratory C losses. We then traced the allocation of biocrust-derived C and N into POM and MAOM and into microbial biomass both within the biocrust layer and the underlying 0-1 cm subsurface soil—an approach that allowed us to directly quantify biocrust effects extending into the mineral soil.

Finally, Study III broadened the context to the root-soil interphase where by mimicking the natural growth of a pioneer plant species in a semi-arid topsoil and subsoil during two incubation phases; a 'rhizosphere phase' involving living roots, followed by a 'detritusphere phase' focusing on the *in situ* decomposition plant and root litter. The main objective was hereby to determine the effect of root C inputs on soil aggregation, microbial community structures, and the fate of OM in living and decaying root systems. At the end of each phase, we traced the contribution of water stable aggregates to total C and N pools, followed the fate of OM in POM and MAOM, and determined microbial community structures via phospholipid fatty acid (PLFA) extractions.

Common across all studies is the emphasis on exploring the mechanisms regulating pathways of C and N through microbial transformation into OM pools of varying persistence. Thus, the separation of OM into POM and MAOM fractions by density was a core methodology applied

in all studies, providing deeper insights into the transformation and stabilization mechanisms underlying these processes. This was complemented by microbial community analyses (PLFA extractions) to determine the involvement of different microbial groups in the stabilization and destabilization of SOM. In summary, this dissertation provides a conceptual understanding of the multi-level effects of biota on fundamental soil development processes observed along a successional gradient, outlining a framework in which the contributions of early successional microbial communities to pioneer plants are disentangled.

II | Zusammenfassung

Die Bodenentwicklung wird weitgehend durch das komplexe Zusammenspiel von Bodenmineralen, Pflanzen und Mikroorganismen gesteuert. In spärlich bewachsenen Trockenland-Ökosystemen sind diese Wechselwirkungen häufig auf heterogen verteilte Hotspots beschränkt, die sich entweder im Bodenvolumen um Pflanzenwurzeln (Rhizosphäre) oder in an der Bodenoberfläche siedelnden biologischen Gemeinschaften (Biokrusten), konzentrieren. An diesen Grenzflächen stehen zunehmend Nährstoffe zur Verfügung, die entweder von Biota in Form von Rhizodepositionen und mikrobiellen Exsudaten bereitgestellt werden oder durch biogeochemische Verwitterungsprozesse, die von Mikro- und Makroorganismen gesteuert werden, freigesetzt werden. Die erhöhte Nährstoffverfügbarkeit stimuliert wiederum die mikrobielle Abundanz und Aktivität. Die erhöhte biotische Aktivität stellt, gemeinsam mit dem damit verbundenen Aufbau von organischem Kohlenstoff (C) und Stickstoff (N), den Ausgangspunkt für die Bildung und mögliche Stabilisierung von organischer Bodensubstanz (SOM) in partikulärer OM (POM) und mineralassoziierter OM (MAOM) dar. Pilzmyzel und filamentöse Cyanobakterien binden darüber hinaus Bodenminerale und fördern die Bildung der Bodenstruktur und die Aggregation von Bodenpartikeln. Diese Prozesse verbessern die Wasser- und Nährstoffspeicherung und schaffen im Laufe der Zeit eine Bodenumgebung, die die weitere ökologische Sukzession antreibt und eine kontinuierliche Entwicklung zu komplexeren und vielfältigeren Gemeinschaften ermöglicht. Trotz ihrer entscheidenden Rolle für die Entwicklung des Bodensystems sind die grundlegenden Wechselwirkungen zwischen Boden und Biota in Trockenlandökosystemen nach wie vor unzureichend verstanden, da sich die Forschung bislang vor allem auf produktivere Ökosysteme konzentriert hat. Zudem lag der Fokus überwiegend auf höheren Pflanzensystemen, während die Bedeutung der Wechselwirkungen zwischen Biokrusten und Boden für die Ökosystemfunktionalität weitgehend vernachlässigt wurde.

Das Hauptziel dieser publikationsbasierten Dissertation ist die Untersuchung der Rolle von Biota als Regulatoren und Triebkräfte der Bodenentwicklung in Trockenland-Ökosystemen, mit besonderem Schwerpunkt auf Bodenstruktur und SOM-Bildung. Dies wird in einer Reihe von Experimenten entlang eines Sukzessionsgradienten untersucht, die zunächst die Interaktionen zwischen dem Boden und primären und frühen Sukzessionsbiota (Biokrusten) an der Bodenoberfläche umfassen (Studien I und II) und anschließend auf die Interaktionen zwischen

höheren Pflanzen und dem Boden an der Boden-Wurzel-Grenzfläche erweitert werden, wo sowohl Prozesse rund um lebende als auch abgestorbene Wurzelsysteme untersucht werden (Studie III). Insgesamt ermöglicht uns dieser Ansatz, die kritische Rolle verschiedener biotischer Akteure bei der Entwicklung von Trockenlandböden zu unterscheiden, wo die biotische Gesamtaktivität sonst begrenzt ist.

Um die C-Flüsse während früher Sukzessionsstadien in Biokruste-Boden-Systemen zu verfolgen, wurde ein Gasentnahmesystem entwickelt, das sowohl CO_2-Messungen als auch $^{13}CO_2$-Markierungen in einem einzigen Aufbau ermöglicht (Studie I). Diese methodische Entwicklung war eine Voraussetzung für die nachfolgenden Messungen in Studie II. In Anbetracht der geringen CO_2-Flüsse, die in Biokrustensystemen zu erwarten sind—bedingt durch die allgemein niedrigen Respirationsraten semiarider Böden und die begrenzte photosynthetische C-Aufnahme durch niedere Organismen—wollten wir ein System entwickeln, mit dem größere Gasvolumen für eine zuverlässige Quantifizierung gewonnen werden können, während gleichzeitig die Auswirkungen von Inkubation und Druck auf das Bodensystem minimiert werden. Darüber hinaus wurde das System so gebaut, dass es einen hohen Probendurchsatz ermöglicht und gleichzeitig das Risiko einer Kreuzkontamination minimiert zwischen Proben, da sowohl in Studie I als auch in Studie II mit $^{13}CO_2$ und $^{15}N_2$ gearbeitet wurde.

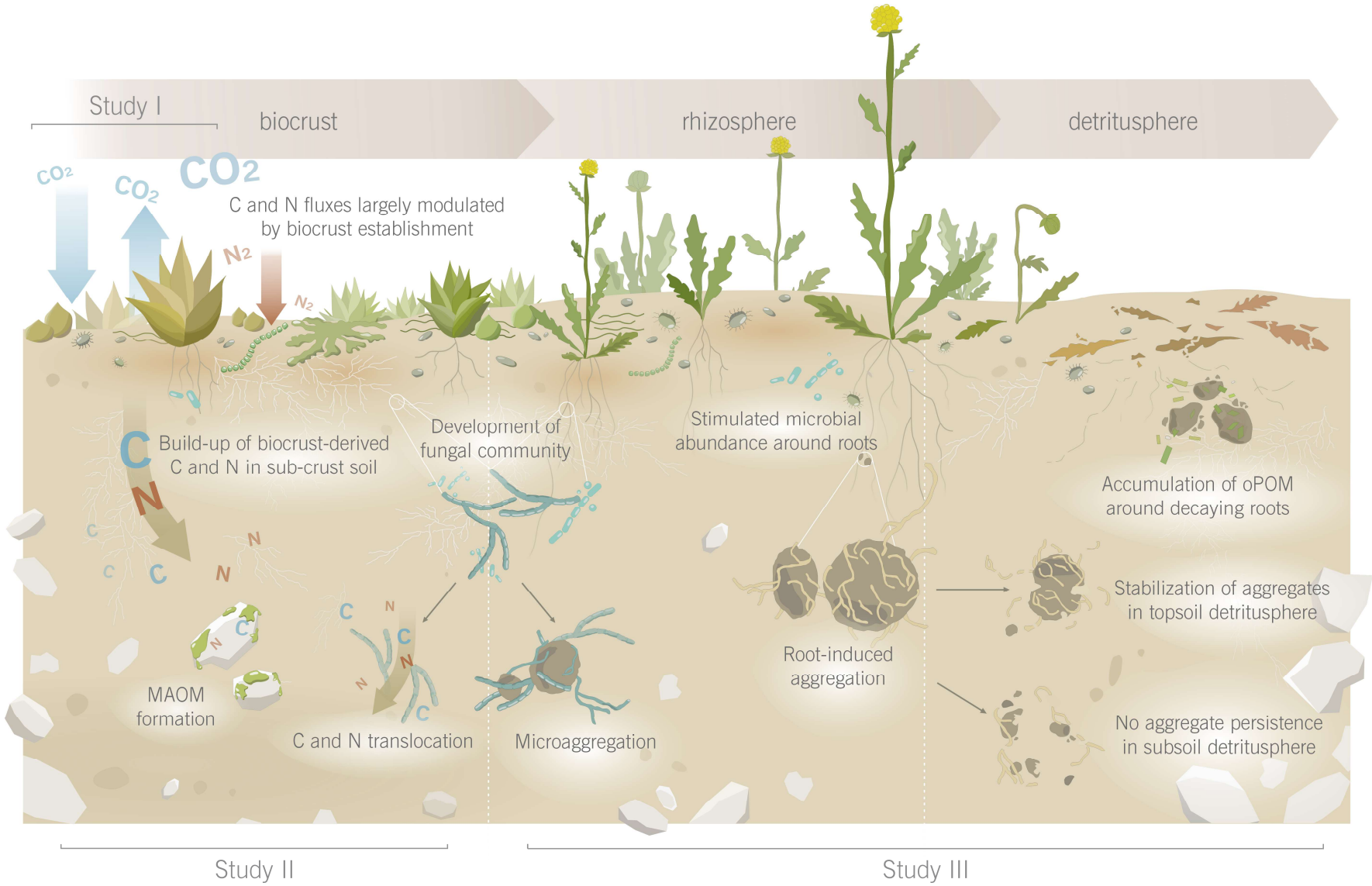
Basierend auf den Entwicklungen in Studie I wurde der Schwerpunkt von Studie II erweitert, um die Auswirkungen veränderter klimatischer Bedingungen auf die Übertragungswege von C- und N von Biokrusten in den darunter liegenden Boden zu ermitteln. Dies wurde in einem Phytotron-Inkubationsexperiment durchgeführt, bei dem intakte Biokruste-Boden-Systeme experimentell Erwärmung und Trockenheit ausgesetzt wurden. Während der Inkubation wurden $^{13}CO_2$- und $^{15}N_2$-Markierungpulse verabreicht und die CO_2-Flüsse überwacht, um die photosynthetische C-Aufnahme und C-Verluste durch Atmung zu bestimmen. Anschließend verfolgten wir die Verteilung des aus der Biokruste stammenden C und N über POM und MAOM und die mikrobielle Biomasse, sowohl innerhalb der Biokruste als auch in den darunter liegenden 0-1 cm Boden. Dieser Ansatz ermöglichte es uns, die Auswirkungen der Biokruste auf den Mineralboden direkt zu quantifizieren.

In Studie III wurde der Kontext schlussendlich auf die Wurzel-Boden-Grenzfläche ausgeweitet, indem das natürliche Wachstum einer Pionierpflanzenart in einem semiariden Ober- und

Unterboden während zweier Inkubationsphasen nachgeahmt wurde: eine „Rhizosphärenphase" mit lebenden Wurzeln, gefolgt von einer „Detritusphärenphase", die sich auf die *in situ*-Zersetzung von Pflanzen- und Wurzelreste konzentriert. Das Hauptziel bestand darin, die Auswirkungen des C-Eintrags von Wurzeln auf die Bodenaggregation, die Struktur der mikrobiellen Gemeinschaften und den Verbleib von OM in lebenden und verrottenden Wurzelsystemen zu bestimmen. Am Ende jeder Inkubationsphase quantifizierten wir den Beitrag wasserstabiler Aggregate zu den gesamten C- und N-Pools, verfolgten den Verbleib von OM in POM und MAOM und bestimmten die Struktur der mikrobiellen Gemeinschaft durch Extraktion von Phospholipidfettsäuren (PLFA).

Die Gemeinsamkeit aller Studien ist, dass der Forschungsschwerpunkt auf dem Verständnis der Mechanismen liegt, die den Weg von C und N durch mikrobielle Umwandlung in OM-Pools mit unterschiedlicher Persistenz regulieren. Die Trennung von OM in POM- und MAOM-Fraktionen nach Dichte war eine zentrale Methode, die in allen Studien angewandt wurde und tiefere Einblicke in die Umwandlungs- und Stabilisierungsmechanismen ermöglichte, die diesen Prozessen zugrunde liegen. Ergänzt wurde dies durch Analysen mikrobieller Gemeinschaften (PLFA-Extraktionen), um die Beteiligung verschiedener mikrobieller Gruppen an der Stabilisierung und Destabilisierung von SOM zu bestimmen. Zusammenfassend vermittelt diese Dissertation ein konzeptionelles Verständnis der mehrstufigen Auswirkungen von Biota auf grundlegende Bodenentwicklungsprozesse entlang eines Sukzessionsgradienten und skizziert einen Rahmen, der die Beiträge der mikrobiellen Gemeinschaften früher Sukzessionsstadien von denen der Pionierpflanzen unterscheidet.

III | Graphical summary



IV | List of abbreviations

ANOVA	One-way analysis of variance
Biocrust	Biological soil crust
$CO_{2\ headspace}$	CO_2 content in headspace after incubation
$CO_{2\ flush}$	CO_2 content or concentration of flush air
CP-MAS	Cross-polarization magic angle spinning
CuO	Cupric oxide
DFG	German Research Foundation
DOM	Dissolved organic matter
EA-IRMS	Elemental Analyzer-Isotope Ratio Mass Spectrometer
EC	Electric conductivity
EPS	Extracellular polymeric substances
FAME	Fatty acid methyl esters
FNR	Agency for Renewable Resources
fPOM	Free particulate organic matter
GC/C-IRMS	Gas chromatography-flame ionization detector
GC-MS	Gas chromatography-mass spectrometry
Gram+	Gram-positive bacteria
Gram−	Gram-negative bacteria
Gram+:gram−	Gram-positive:gram-negative bacteria ratio
HSD	Honestly significant differences (post-hoc test)
IRIS	Isotope Ratio Infrared Spectrometer
MAOM	Mineral-associated organic matter
$MAOM_{>63\mu m}$, $MAOM_{>63\mu m}$	Mineral-associated organic matter separated by size (63 µm)
NanoSIMS	Nano-scale secondary ion mass spectrometry
NDVI	Normalized difference vegetation index
NEE	Net ecosystem exchange
NEE_{light}	Net ecosystem exchange under light incubation
NEE_{dark}	Net ecosystem exchange under dark incubation
NPP	Net primary production
NMR	Nuclear magnetic resonance
OC	Organic carbon
OM	Organic matter
oPOM	Occluded particulate organic matter
$oPOM_{<20\mu m}$, $oPOM_{>20\mu m}$	Occluded particulate organic matter separated by size (20 µm)
PLFA	Phospholipid fatty acids
POM	Particulate organic matter
PPFD	Photosynthetic photon flux density
ROI	Region of interest
SOM	Soil organic matter
SOC	Soil organic carbon
SD	Standard deviation of means
VP-PDB	International Vienna Pee Dee Belemnite standard
VSC	Sum of vanillyl, syringyl and cinnamyl units
$\delta^{13}C_{respiration}$	$\delta^{13}C$ signal of respired CO_2
$\delta^{13}C_{headspace}$	$\delta^{13}C$ signal in headspace
$\delta^{13}C_{flush}$	$\delta^{13}C$ signal of flush air before incubation
Ac/Al, $(Ac/Al)_V$	Ratio between phenolic acids and corresponding aldehydes

V | List of studies

This publication-based doctoral dissertation is based on the following first-authored research articles:

Study I | Tracing low-CO_2 fluxes in soil incubation and ^{13}C labeling experiments: A simplified gas sampling system for respiration and photosynthesis measurements

Witzgall, K., Hesse, B. D., Seguel, O., Oses, R., Grams, T. E. E. & Mueller, C. W. 2023. *Journal of Geophysical Research: Biogeosciences*, 128(9). https://doi.org/10.1029/2023JG007410

Objectives

The primary objective of this study was to develop a gas sampling setup optimized for quantifying low soil CO_2 fluxes, particularly in early-stage soil ecosystems colonized by biocrusts. Specifically, the system was designed to facilitate both CO_2 measurements and *in situ* $^{13}CO_2$ labeling of biocrust-soil systems, ensuring high sample throughput while minimizing risks of cross-contamination and potential sampling effects on the studied systems.

Summary

We confirmed the suitability of the developed system for capturing small changes in headspace CO_2 concentration via repeated respiration and photosynthesis measurements of soil-biocrust systems. We were able to quantify fluxes down to 0.1 µmol CO_2 m^{-2} s^{-1} with high accuracy. Due to a balloon application, we successfully mitigated >70% of the negative pressure buildup during gas sampling, which effectively allowed for larger and more representative sample volumes for isotopic measurements. The developed system further facilitated one-step flushing and evacuation of the entire system which minimized contamination risks and allowed for convenient handling. In conclusion, we were able to implement a simple, cost-effective and straightforward solution for repeated gas measurements with high sample throughput, while using only easily accessible and exchangeable system components.

Contribution

I designed the experiment, collected the data, and performed the analyses with the support of B. D. Hesse. I processed and evaluated the data, wrote the manuscript, and handled the peer-review and publishing process.

Study II | Soil carbon and nitrogen cycling at the atmosphere-soil interface: quantifying the responses of biocrust-soil interactions to global change

Witzgall, K., Hesse, B. D., Pacay, N., Jansa, J., Seguel, O., Oses, R., Buegger, F., Guigue, J., Rojas, C., Grams, T. E. E., Rousk, K., Pietrasiak, N. & Mueller, C. W. 2024. *Global Change Biology*, 30(10), e17519. https://doi.org/10.1111/gcb.17519

Objectives

In this study, we aimed to trace the pathways of C and N from biocrusts into the underlying mineral soil, particularly into SOM pools and microbial biomass, as these processes remain largely unknown. Additionally, we sought to determine whether the underlying mechanisms are influenced by changing climatic conditions, particularly rising temperatures and drought.

Summary

We were able to show how biocrusts drive the accumulation of C and N not only as biomass within the biocrust layer, but also as soil C and N in the underlying soil. This downward elemental translocation was associated with the formation of $MAOM_{<63\mu m}$ and an increased dominance of fungi. We argue that both the redistribution of C and N and the formation of organo-mineral associations can be attributed to the extension of the fungal hyphae. However, these processes were not observed in systems exposed to warming and drought, where instead accelerated C turnover and higher microbial involvement in the mineralization of biocrust-derived C inputs offset biocrust effects on the underlying soil. Regardless of temperature, we determined net C uptake in biocrust systems that were not exposed to drought stress, confirming biocrusts as important primary producers in otherwise sparsely vegetated drylands. The measurements also confirmed moisture availability as a major constraint on CO_2 fluxes, where the photosynthetic C uptake were reduced by >80%, to the point where the total C balance in the systems was verging on net negative. This data overall showcases rapid biogeochemical responses to climate change, and how some of the most fundamental ecosystem services of biocrusts may be offset under future global change.

Contribution

I designed the experiment, collected the data, performed the analyses, processed and evaluated the data with the support of B. D. Hesse. I wrote the manuscript and handled the peer-review and publishing process.

Study III | Living and decaying roots as regulators of soil aggregation and organic matter formation—from the rhizosphere to the detritusphere

Witzgall, K., Steiner, F., Hesse, B. D., Riveras-Muñoz, N., Rodríguez, V., Teixeira, P. P., Mengmeng, L., Oses, R., Seguel, O., Seitz, S., Wagner, D., Scholten, T., Buegger, F., Angst, G. & Mueller, C. W. 2024. *Soil Biology and Biochemistry*, 109503.
https://doi.org/10.1016/j.soilbio.2024.109503

Objectives

This study aims to disentangle how C inputs from root systems drive soil aggregation, microbial community development, and the formation and fate of OM during the transition from the rhizosphere to the detritusphere. Furthermore, the study seeks to capture potential legacy effects from the living root system in shaping the conditions of the subsequent detritusphere, and to determine whether these processes vary depending on the stage of development of the soil substrate (topsoil and subsoil).

Summary

The two-phase incubation approach, in which the transition from growth to subsequent decay of the pioneer plant and root system was kept undisturbed, shows how roots drive the formation of macroaggregates in the rhizosphere regardless of soil substrate. However, the root-induced aggregation only persisted after plant death in the topsoil and not in subsoil. This underscores the requirement of a certain 'backbone' of native C for longer-term aggregate stabilization in the root detritusphere in arid soil systems and shows how continuous OM inputs may be required for maintaining aggregate persistence in otherwise C-poor subsoils. The results also show the importance of the root-associated microbiome, where fungal hyphae facilitate aggregation and gram+ bacteria drive the mineralization of complex C sources in the developing detritusphere. The buildup of occluded POM, fueled by the decaying root litter in the topsoil detritusphere, further emphasizes the importance of root residues for the formation and persistence of SOM.

Contribution

I collected the data and performed the analyses with the support of F. Steiner, processed and evaluated the data, wrote the manuscript, and handled the peer-review and publishing process.

1 | INTRODUCTION

1.1 Soil development in dryland ecosystems

The development of soils is driven by the dynamic interplay between physical, chemical, and biological processes. In early stages of soil formation, as the parent material undergoes weathering, nutrients are released which facilitates the colonization of primary biota such as fungi, algae, and cyanobacteria (Schulz et al. 2013). These pioneering micro- and macroorganisms further intensify weathering through both physical and chemical means, promoting the mobilization of plant nutrients and accumulation of organic matter (OM), hereby marking a fundamental starting point in the development of soil horizons (Chen et al. 2000; Raven and Edwards 2001; Mitchell et al. 2016). At the same time, fungal mycelium and cyanobacterial filaments bind soil minerals which contributes to the gradual formation of subsurface soil structures (Zhan et al. 2006). As ecological succession progresses, these processes pave way for the establishment pioneering plants with deeper roots that extend the biogeochemical weathering front and funnel C inputs deeper into the soil via root exudates or structural root litter inputs (Villarino et al. 2021; Gregory 2022).

In dryland ecosystems, where limited moisture availability constrains biogeochemical weathering and the associated pedogenesis, these primary biotic drivers are fundamental for the development of the soil ecosystem (Dunkerley 2011). The hyperarid, arid, and semiarid regions, characterized by abundant solar radiation, unevenly distributed precipitation, and high potential evapotranspiration, experience significant abiotic stressors which limits plant establishment and overall net primary production (Hou et al. 2021). Thus, soils are generally poorly developed and characterized by coarse texture, low availability and retention of nutrients, and low SOC contents (Lal 2004). The horizon differentiation between the soil profiles is typically very subtle compared to in humid areas, with shallow and light-colored A horizons and with occasional accumulation of soluble salts (Dunkerley 2011). The large areas of uncovered soil in the interspaces between vegetated patches are exposed to wind, solar radiation and precipitation, making the soil vulnerable to soil erosion and the physical breakdown of the soil structure (Plaza et al. 2018; Riveras-Muñoz et al. 2022). Exacerbated by the low SOM contents and reduced porosity in the bare soil interspaces, this exposure can over time create inorganic surface seals which significantly reduce water infiltration, further aggravating the water scarcity and potentially leading to 'pedogenic aridity' (Dunkerley 2011).

1.2 Biocrusts and pioneering plants in dry environments

Given the aforementioned abiotic stressors, dryland ecosystems are shaped by high environmental and anthropogenic pressures that fundamentally determine—and constrain—the establishment and growth of biota. Organisms capable of withstanding the harsh conditions in arid landscapes, including extreme temperatures, high UV radiation and prolonged desiccation, exhibit unique morphological and physiological adaptation strategies that enable survival in such extreme climatic environments (Green and Proctor 2016; Abd El-Ghani et al. 2017; Tariq et al. 2024). Vegetation is these areas is typically limited to scarce and heterogeneously distributed patches of lower shrubs, bushes, and herbaceous plants, while biological soil crusts (biocrusts hereafter) colonize the soil surface in the interspaces (Belnap et al. 2016; Abd El-Ghani et al. 2017; Maurice et al. 2023). These macro- and microbial communities form thin, well-aggregates surface layers composed of non-vascular photoautotrophs and microbial heterotrophs in intimate association with soil mineral particles and can comprise over 70% of the living cover (Belnap and Lange 2001). The photoautotrophic components of biocrusts, *i.e.,* non-vascular cryptograms such as cyanobacteria, bryophytes and algae, play a crucial role in dryland biogeochemical cycles by fixing atmospheric CO_2 and N_2 (Johnson et al. 2007; Weber et al. 2022). At the ecosystem level, their biological fixation of C and N influences nutrient cycling, soil food web structures and soil microbial communities (Belnap et al. 2016; Bates et al. 2010; Mager and Thomas 2011). On a global scale, these processes significantly contribute to biogeochemical fluxes with implications for global C and N cycles (Finger-Higgens et al. 2022; Weber et al. 2022).

Within the biocrust layer, filamentous cyanobacteria, moss rhizoids and fungal hyphae enmesh soil particles, and the release of extracellular polymeric substances (EPS) further promotes the formation of aggregated soil structures (Barger et al. 2006; Mager and Thomas 2011; Chenu and Consentino 2011; Costa et al. 2018). These processes are critical for soil surface stabilization (Pietrasiak et al. 2013; Felde et al. 2018), water infiltration (Chamizo et al. 2012; Kidron et al. 2022) and soil erosion protection (Belnap and Büdel 2016; Faist et al. 2017). The accumulation of organic C and N in the biocrust layer can reach the sub-crust soil through processes such as leaching of dissolved nutrients (Dümig et al. 2014; Young et al. 2022), translocation of litter from decomposing biocrust components biomass (Hagemann and Moroni 2015), or release of microbial exometabolites into the underlying soil (Swenson et al. 2018)—processes that can be amplified by channeling effects of moss stems and rhizoids (Kidron et al. 2010). These

processes can accelerate soil formation in the underlying soil substrate, *e.g.,* through enhanced mineral weathering due to OC accumulation and acidification caused by the stimulated biological activity (Chen et al. 2009; Dümig et al. 2014; Agnelli et al. 2021). As such, alongside stimulated OM formation, microbial activity, and the resulting increased mineral weathering, biocrusts drive the development of the soil towards conditions that support the growth of more complex and diverse plant communities (Beyschlag et al. 2008). Moreover, this initial formation of soil structure, including soil aggregates and biopores, may enhance the infiltration and preferential flow of rainwater and dissolved OM (DOM), which in turn can create critical hotpots for microbial activity and continued soil development (Hagedorn et al. 2000; Schaaf et al. 2011). Given that dryland soils are characterized by low organic C and N contents, the release of EPS in the significantly contributes to the buildup of SOC and SON—with EPS potentially comprising up to 70% of the total SOC stock (Mager 2010; Mager and Thomas 2011). This accumulation of OM in turn stimulates the development and diversification of soil microbial communities and results in the buildup of C and N not only within the crust layer but also in the underlying soil (Bates et al. 2010; Hagemann and Moroni 215; Young et al. 2022).

The colonization and development of biocrusts communities in drylands also play a key role in modulating the continued ecological succession, paving way towards the establishment of higher plant communities with deeper root systems, including pioneering herbaceous plants (Esperschütz et al. 2011; Tariq et al. 2024; Wang et al. 2024). Like biocrusts, dryland plants are highly adapted to extreme environmental constraints and resource shortages. In response, they exhibit a wide range of adaptive strategies, such as developing deep root systems, reducing specific leaf area, and optimizing photosynthetic efficiency—strategies that collectively reflect an exceptionally high functional diversity compared to less constrained environments (Noy-Meir 1973; Peguero-Pina et al. 2020; Cao et al. 2024) and is commonly referred to as the "functional paradox of drylands" (Maestre et al. 2021). The influence of plants on the soil processes varies greatly depending on specific plant traits, such as root morphology and litter production, as well as on factors like climate and land use (Van der Putten et al. 2016), Yet, overall, plant establishment enhances the complexity and spatial dimension of the effects on soil and soil-forming processes (Bardgett et al. 1999). A significant portion of these processes are concentrated at the root-soil interface, *i.e.,* within the rhizosphere, where soil minerals are physically altered by the growing roots, and the release of organic acids by root-associated microorganisms drives the mobilization of essential soil nutrients (Uroz et al. 2009; Gregory

2022). Rhizodeposits, such as root mucilage, may act as glue-like binding agents that help aggregate soil particles, directly promoting the formation of soil structure (Baumert et al. 2018; Rötzer et al. 2023). Moreover, rhizodeposits can indirectly support soil aggregation—labile rhizodeposits, such as glucose and amino acids which are easily metabolized by microorganisms, stimulate the production of EPS, further binding soil particles and stabilizing soil aggregates (Paterson et al. 2007). These processes, in conjunction with the decomposition of plant and root litter, represent critical inputs of C and N and mark the starting point for the formation of SOM and its gradual accumulation in deeper soil layers (Villarino et al. 2021). However, much of our understanding of plant-soil interactions stems from studies in humid or subhumid environments, leaving the processes specific to marginal and extreme environments poorly understood.

1.3 The characteristics of dryland soil C and N cycles

The constraining environmental conditions in drylands fundamentally control biogeochemical cycles and shape the dynamics and distribution of SOM. The availability of C and N varies greatly across the landscape, often concentrated within so called "fertility islands" that are typically found beneath plant patches, strongly modulated by biotic processes such as photosynthesis and atmospheric N fixation by microorganisms (Hadley and Szarek 1981; Schlesinger 1997; Lal 2004; Elbert et al. 2012). Net primary production is mainly limited by prolonged periods of desiccation, resulting in overall slower C turnover and C cycles. Photosynthetic activity tends to be concentrated during "hot moments" within irregularly occurring precipitation pulses, during which biological activity is accelerated (Jenerette et al. 2008; Leon et al. 2014; Kannenberg et al. 2020). In addition to water limitations, the deficiency of N imposes a major constraint on biomass production, impacting both plant establishment and rooting depth (Hooper and Johnson, 1999; Lal 2004). In addition to limiting biomass production, the sparse establishment vegetation—and the absence of roots through which C can be allocated into the subsurface soil—is a dominant control on the vertical distribution of SOC (Jobbágy and Jackson 2000; Albaladejo et al. 2013). As a result, SOM tends to be concentrating at the soil surface, leaving soil C and N more exposed to variations in abiotic conditions.

The slower biogeochemical cycles and biotic processes in these systems have contributed to the misconception that drylands are less influential in global C and N cycles compared to humid biomes. This perspective is misleading; for example, restricted photosynthetic rates do not automatically equate to lower net C uptake than in more "productive" ecosystems (Schimel 2010). Research by Rotenberg and Yakir (2010) demonstrates that dryland forests can in fact exceed the net C uptake rates of average European pine forests due to the lower respiratory C losses under low soil moisture conditions, thereby enhancing the system's C storage efficiency. Biocrusts are another example of the significance of the drylands on a larger scale—while their absolute C and N fixation rates are typically lower than those of higher plants in humid environments, due to their vast geographical coverage they account for 7% of total net C uptake and 50% of terrestrial N_2 fixation, thereby constituting a fundamental contribution to global biogeochemical cycles (Elbert et al. 2012; Finger-Higgens et al. 2022; Weber et al. 2022). In total, drylands are estimated to store around 300 Pg C, representing ~16% of the total terrestrial SOC pool found in the uppermost 1 m of the soil (Lal 2004; Jobbágy and Jackson, 2000; Ahlström et al. 2015) and account for approximately 40% of the global net primary production (Grace et al. 2006).

1.4 Dryland biogeochemical cycles in a changing climate

Given the significance of drylands in the global C cycle, the impact of climate change on SOC sensitivity in these regions has gained increasing research attention. The intensification of climate change is projected not only to accelerate global desertification and the expansion of drylands, but also to profoundly affect their inherent functionality—potentially more intensely than in temperate or humid biomes (Huang et al. 2016; Burrell et al. 2020). Studies have shown how temperature increases driven by global warming over the last century have been most pronounced in arid regions, with stronger heating effects compared to biomes with higher precipitation (Guan et al., 2015; Zhou et al. 2015; Huang et al. 2017a). Additionally, dryland biomes are considered to be particularly vulnerable to climatic change. Their functionality and ecosystem productivity are closely tied to their high taxonomic, endemic and functional biotic diversity (García-Palacios et al. 2018; Maestre et al. 2021). Given that these systems are already operate under challenging environmental conditions, even small changes in precipitation can drastically alter system functionality, with significant implications for biogeochemical cycles

(Huang et al. 2017b). However, predicting these effects of future climate change on biogeochemical cycles is challenging, with the response of the C cycle being one of the greatest sources of uncertainty (Ballantyne et al. 2012). Since dryland C stocks are typically concentrated in the upper layers of the soil profile—due to the restricted microbial activity and plant growth—this further exacerbates their vulnerability to climatic change compared to soils where C stocks are allocated in deeper soil layers (Batjes 1996; Albaladejo et al. 2013).

The challenge of predicting effects of climatic change in drylands is further compounded by the fact that rising aridity impacts ecosystems on multiple non-linear levels. For instance, warming soil temperatures and reduced soil moisture can disrupt gross primary production and the associated C and N pathways into the soil, decrease photosynthesis rates and accelerate respiratory C losses, which may fundamentally disrupt the overall capacity of the system to sequester atmospheric CO_2 (Maestre et al. 2013; Hoover et al. 2015). Rising aridity can also reduce and alter the composition and diversity of vegetation and biocrusts, potentially leaving larger areas of bare soil vulnerable to erosion-induced SOC losses and soil degradation (Ravi et al. 2010; Maestre et al. 2013; Rodriguez-Caballero et al. 2018; Lal 2019; Finger-Higgens et al. 2022). As such, increased soil degradation and compromised primary production following increasing abiotic stressors can fundamentally alter ecosystem functions and services (Finzi et al. 2011; Delgado-Baquerizo et al. 2013), and interacting effects with other factors, such as intensified grazing pressure and fire, add further complexity to projections (Maestre et al. 2022; Gross et al. 2024).

1.5 Objective of thesis

The overarching goal of this publication-based thesis was to investigate the effects of early successional vegetation on SOM dynamics and soil aggregate formation in dryland ecosystems. The three publications included in the dissertation focused on two key biotic drivers; biocrusts and herbaceous plants. In two main simulation experiments, these drivers were introduced to a natural semiarid soil, representing a soil ecosystem with limited prior vegetation influence. This approach allowed direct observation of biotic influences in two different contexts: a biocrust-soil system (Studies I and II) and a plant-soil system, specifically within the soil volume around the roots (Study III). The interactions between the studied biota, microorganisms, and mineral soil were investigated through various biogeochemical and

microbiological analyses, exploring changes in SOM formation, microbial community structures, and C and N dynamics. Furthermore, Study II addressed the effects of changing climatic conditions on these processes. The thesis is organized into two main chapters, following the continuum of biotic succession from biocrusts to vascular plants. The first chapter contains two studies, where Study I was a methodological development and a prerequisite for the experiment presented in Study II.

Chapter 1: Early pioneer biocrust (Studies I and II)

This chapter addresses:

i) The development of an appropriate sampling setup for monitoring CO_2 fluxes and apply isotopic labeling in early soil systems colonized by biocrusts (Study I)

ii) How biocrusts regulate C and N cycles in dryland systems, focusing on elemental pathways from the biocrusts into specific OM pools in the underlying mineral soil (Study II)

iii) The fate of biocrust-derived OM into POM and MAOM within the biocrust and in the sub-crust soil (Study II)

iv) The influence of changing climatic conditions (drought and elevated temperature) on C and N fluxes (Study II)

Chapter 2: Later pioneer plant and its associated root system (Study III)

This chapter addresses:

i) The effects of root-derived C inputs on soil aggregate formation in topsoil and subsoil

ii) Changes in the rhizo-microbial community during the establishment of roots and during the later transition from a rhizosphere to a detritusphere

iii) The fate and composition of root-derived C into POM and MAOM at the root-soil interface in living and decaying root systems

iv) Capture potential legacy effects of the rhizosphere shaping the conditions in the subsequent detritusphere

2 | MATERIAL & METHODS

2.1 Study site and soil sampling

The EarthShape program includes four research sites spanning over a 1300 km gradient along the Chilean Coastal Cordillera, encompassing arid deserts (Pan de Azúcar), semiarid shrublands (Santa Gracia), Mediterranean forests (La Campana), and temperate-humid forests (Nahuelbuta). For this dissertation, we worked with soil material collected from semiarid Santa Gracia Natural Reserve in the Coastal Cordillera of Chile (−71.166, −29.757). This soil is characterized by sparse vegetation (shrub) cover, low OM content, and a shallow, weakly structured A horizon (Oeser et al. 2018). Given the limited vegetation, this site is ideal for quantifying the effect of biota, across the early successional biocrusts to pioneer plants, on the development of the soil system.

Santa Gracia is located in the Coquimbo region, near the city of La Serena. The area receives 89 mm of annual precipitation and the mean annual temperature is 13.7 °C (Ministerio de Obras Públicas, 2017). The vegetation is dominated by smaller and sparsely distributed shrubs (*e.g., Proustia cuneifolia, Balbisia peduncularis* and *Cordia decandra*; Bernhard et al. 2018) and classified as Interior Mediterranean desert scrub (Luebert and Pliscoff, 2006). Up to 15% of the soil surface is covered by biocrusts (*e.g.*, *Riccia* spp., *Placidium* sp., and *Acarospora* spp.; Bernhard et al. 2018). Grazing by goats has been reported within the reserve by local authorities, which has led to a degraded, shrub-dominated vegetation (Bahre 1979; Armesto et al. 2007; Figure 1).

Figure 1 | Santa Gracia Natural Reserve, located in the Coastal Cordillera of Chile (29°44'26.3"S, 71°09'01.2"W), from where the soil material used in all studies was collected.

Five representative subplots, each located within a 500 m radius, were selected for sampling. Subplots were selected based on their shared slope position (all located on a south-facing top slope) and similar surrounding vegetation. The soil across all subplots was classified as a Cambisol according to the WRB (IUSS Working Group WRB, 2015), featuring a shallow and weakly aggregated A horizon (~0-3 cm) and a brownish, white-spotted B horizon (~3->25 cm; Table 1). A detailed description of the sampling procedures is provided in section 2.1.1 and 2.1.2.

Table 1 | Coordinates, elevation, and the magnitude of the horizons in each of the five subplots.

	Coordinates		Elevation (masl)	A horizon	B horizon	C horizon
Subplot 1	29°45'22.7"S	071°10'03.4"W	720	0-3 cm	3-25 cm	25 cm-
Subplot 2	29°45'24.4"S	071°09'59.4"W	711	0-3 cm	3-25 cm	25 cm-
Subplot 3	29°45'09.1"S	071°10'00.8"W	720	0-2 cm	2-40 cm	25 cm-
Subplot 4	29°45'08.3"S	071°10'02.8"W	724	0-3 cm	3-40 cm	40 cm-
Subplot 5	29°45'08.1"S	071°10'03.3"W	725	0-3 cm	3-30 cm	40 cm-

2.1.1 Sampling for Studies I and II

The soil material used in Studies I and II was collected from two depths; 0-1 cm (representing part of the A horizon) and 3-5 cm (representing part of the B horizon) using sterilized spatulas (Figure 2). Prior to sampling, biocrusts were carefully removed to ensure the collection of mineral soil only. After sampling, the soil was sieved (<2 mm), homogenized into composite samples for each depth increment and air-dried. The material from these two depth layers were later used to reconstruct a quasi-natural soil profile in the mesocosms setup used during incubation, with the B horizon material in the bottom of the mesocosm and the A horizon material on top (this is described in detail in the following chapters).

Figure 2 | Sampling of soil material for Studies I and II from 0-1 and 3-5 cm depths.

The basic soil properties as well as texture of the soil material before incubation is included in Table 2.

2.1.2 Sampling for Study III

The soil material used in Study III was sampled directly from the profile walls of the five subplots (Figure 3). The material from 0-3 cm (A horizon) and 5-~30 cm (B horizon) was sieved (<2 mm) and homogenized into composite samples for each depth increment. The two depth increments are referred to as "topsoil" and "subsoil" hereafter.

Figure 3 | The soil material for Study III was collected directly from the profile walls of the A horizon (0-3 cm) and the B horizon (5- ca 30 cm) across five subplots. The sample material from the subplots was then homogenized into two composite samples for each depth increment. The horizon boundaries depicted in the image are for illustrative purposes only; actual horizon designations were determined in the field.

Visible plant residues and seeds were removed to prevent unwanted germination during incubation, and the material was air-dried until further processing. The basic soil properties as well as texture of the soil material before incubation is included in Table 2.

Table 2 | a Basic soil properties and **b** soil texture of homogenized and sieved (<2 mm) soil material before incubation. The soil material was sampled either from 0-1 and 3-5 soil depth in Studies I and II or from 0-3 and 5-~30 cm in Study III.

a

	Studies I and II		Study III	
Basic soil properties	0-1 cm	3-5 cm	Topsoil (A horizon)	Subsoil (B horizon)
EC [µS cm^{-1}]	14.0	14.2	86.0	24.5
pH*	5.9	6.0	7.0	7.5
GWC [g g^{-1}]	*n.a.*	*n.a.*	0.2	0.1
C [mg g^{-1}]	4.8	3.9	7.9	4.5
N [mg g^{-1}]	0.5	0.4	0.8	0.4
C:N	9.9	9.4	10.4	10.8
δ^{13}C-VPDB‰	-25.8	-24.9	-25.9	-24.4
δ^{15}N-AIR‰	7.5	8.7	7.8	7.2

*pH was determined with $CaCl_2$ in Studies I and II and with H_2O in Study III, contributing to the higher values in Study III.

b

	Studies I and II		Study III	
Texture (mass%)	0-1 cm	3-5 cm	Topsoil (A horizon)	Subsoil (B horizon)
Medium and coarse sand (>250 µm)	56.3	61.6	53.8	55.2
Fine sand (250-53 µm)	21.1	15.1	24.9	22.3
Silt (53-2 µm)	12.7	12.2	9.2	9.6
Clay (<2 µm)	9.9	11.1	12.1	12.9

2.2 Experimental setup and incubation procedure (Studies I and II)

2.2.1 Sample preparation

For both Studies I and II, 5 x 8 cm mesocosms (h x d; polyvinyl chloride) were filled with composite B horizon material up until 4 cm and with composite A horizon material in the top 1 cm (1.6 g cm^{-3} bulk density according to field conditions; Riveras-Muñoz et al. 2022). A strip of sterilized Teflon foil was placed between the layers to facilitate their separation after incubation. The mesocosms were sealed with Ø30 µm mesh from below and arranged on elevated metal grids inside glass incubation vessels (Figure 4).

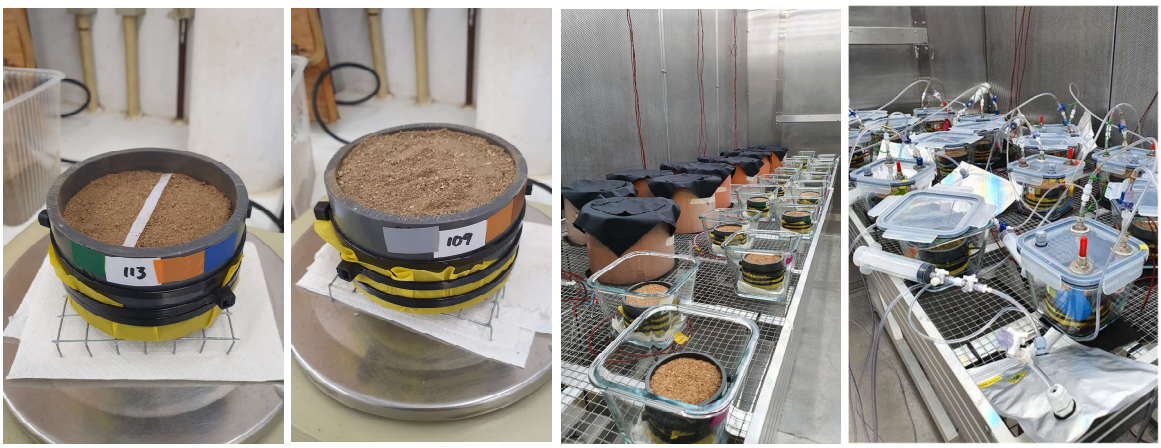


Figure 4 | Polyvinyl chloride mesocosms sealed at the bottom with a Ø30 µm mesh. A strip of Teflon foil separates two depth layers, with B horizon material (filled up to 4 cm) and A horizon material (top 1 cm). All samples were placed on elevated metal grids inside glass incubation vessels during incubation, which were later sealed during gas measurements (described in section 2.4.1).

2.2.2 Experimental design and phytotron incubation

The 133-day incubation of the biocrust-soil systems was conducted in two phytotron chambers (TUM*mesa*; TUM School of Life Sciences, Freising, Germany; Jákli et al. 2021). One chamber was set to resemble the weather conditions at the sampling site (according to climate data recorded in Santa Gracia; 10.5-21.5°C; Übernickel et al. 2020) while the second chamber was set to simulate a continuous +5°C temperature increase (15.5-26.5°C) in accordance with the IPCC RCP 8.5 scenario (Rogelj et al. 2012). Both chambers were set to a 14h photoperiod, with the photosynthetic photon flux density (PPFD) ranging from 65 to 425 µmol m^{-2} s^{-1} (Figure 5).

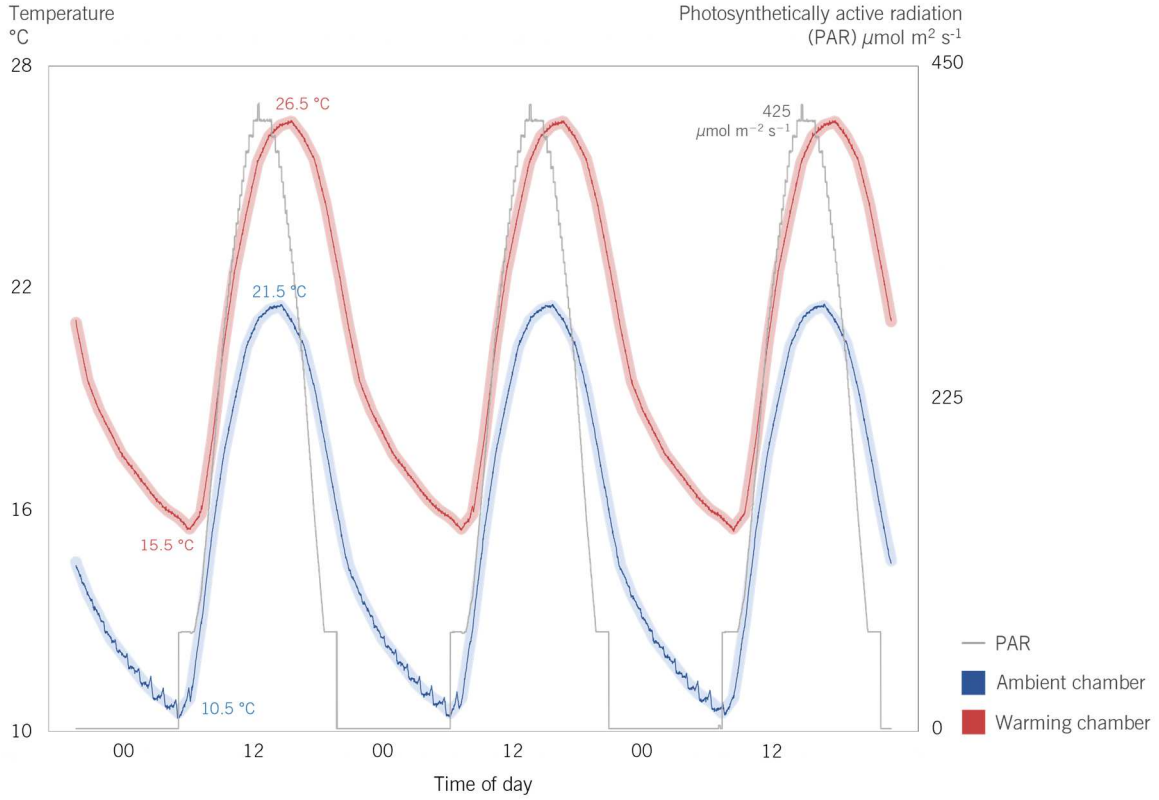


Figure 5 | Temperature (°C) and light (µmol m^{-2} s^{-1}) gradients during day and nighttime in the two phytotron chambers with a photoperiod of 14 h. The faded color represents the set temperature in the chamber program and the darker color represents the measured temperature.

While biocrusts were let to establish spontaneously in half of the samples, the photosynthetic active radiation (PAR) was blocked in the other half via shading to prevent biocrust growth (bare soil controls, hereafter). During the first 43 days of incubation, 6 mL of autoclaved deionized H_2O was added to each sample to promote the development of the biocrusts. During the remaining 90 days, water was given according to field conditions (1 mL per day) and decreased to 0.5 mL per day in half of the samples to simulate drought. This ultimately resulted in 8 treatments; systems with or without biocrusts (2 levels), ambient and warming temperatures (2 levels), and normal water and reduced water (drought hereafter) conditions (2 levels; Figure 6). Study I did not include the warming treatment, resulting in a total of 6 treatments.

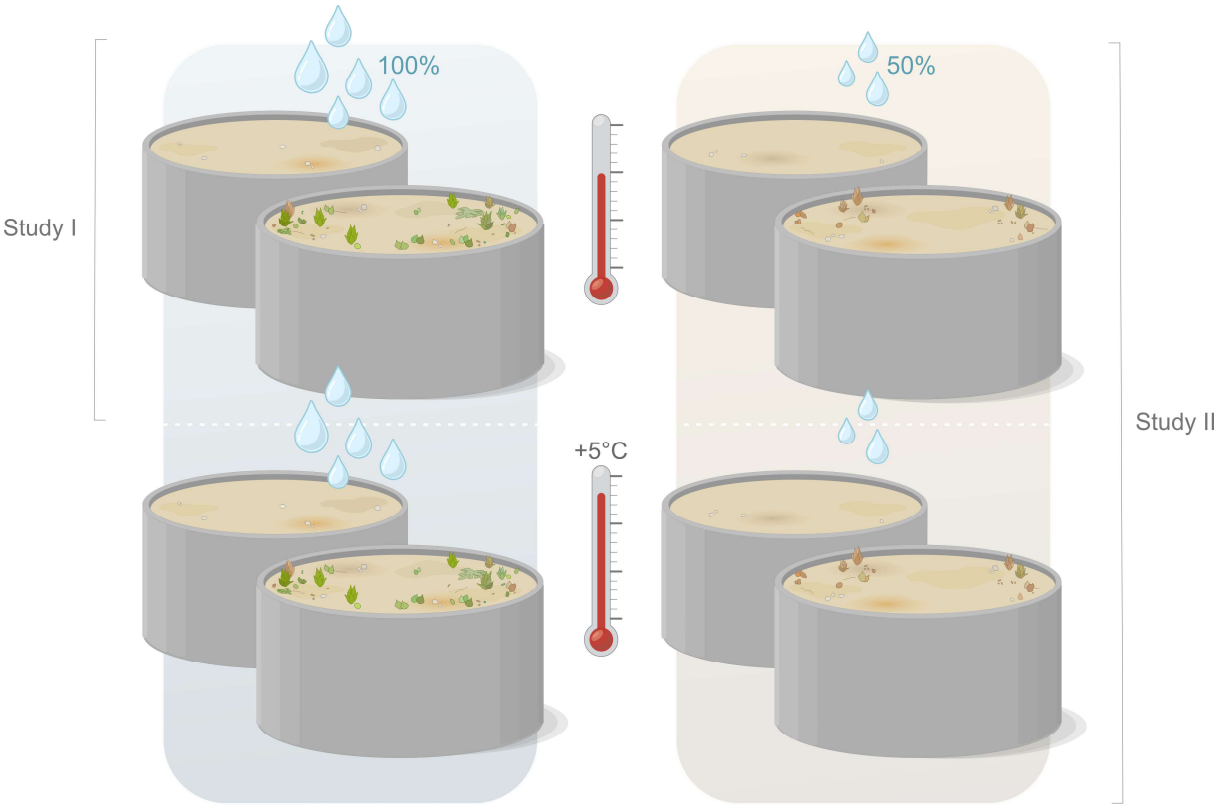


Figure 6 | Graphical overview of the experimental design of Studies I and II, where treatments included experimental warming (+5°C), drought (−50% water reduction), either with or without biocrusts (*n*=8 independent replicates per treatment). The warming treatment was not included in Study I, resulting in a total of 6 treatments.

2.2.3 Sample harvest after incubation

After incubation, the mesocosms were divided into three depths; the biocrust was separated by lifting off the aggregated surface layer, including the adhering soil. In addition, the surface of the remaining soil in the mesocosm was scraped off and added to the biocrust layer in order to collect potential biocrust residues. The underlying 1 cm soil was then collected down to the Teflon foil (referred to as 0-1 cm soil hereafter) followed by the subsequent 1.5 cm (1-2.5 cm hereafter). To minimize the effect of natural heterogeneity between samples, incubation replicates were pooled by two, resulting in 4 composite replicates from the original 8 for subsequent analyses. Samples for elemental analyses and fractionation were air-dried and stored at room temperature, while samples for microbial analyses were immediately freeze-dried and stored at −20°C until further analysis.

2.3 Experimental setup and incubation procedure (Study III)

2.3.1 Sample preparation and greenhouse incubation

The composite topsoil and subsoil material was weighed separately into 350 cm^3 pots. In half of the samples, pre-germinated seeds of (*Helenium aromaticum (Hook.) L. H. Bailey*) were added on top, while the other half remained free of plants as bare soil controls. The pots were incubated under greenhouse conditions for 70 days during an initial incubation period, referred to as the 'rhizosphere phase'. At the end of this phase, half of the samples were harvested, while the remaining half were put in darkness for an additional 100 days, referred to as the 'detritusphere phase'. During this phase, the decomposition of the plant-root system was left undisturbed, with above-ground biomass left to decompose on the soil surface. Throughout both incubation phases, all samples received 6 mL of rainwater each day. In total, there were 6 treatments; topsoil or subsoil, systems with or without plants (controls), and with living (rhizosphere) or decaying (detritusphere) roots (Figure 7). Each treatment had 12 independent replicates per treatment (48 pots in total), which were later pooled in pairs, resulting in 6 composite replicates per treatment for subsequent analyses.

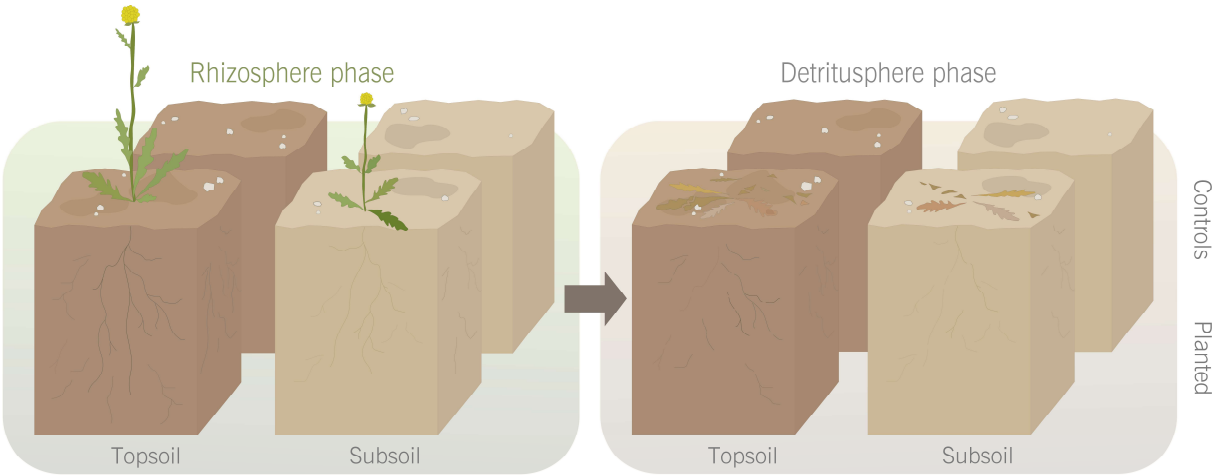


Figure 7 | Graphical overview of the experimental design of Study III, where the topsoil and subsoil material was incubated either with or without plants, in two incubation phases; the rhizosphere phase with living plant-root systems followed by a detritusphere phase with decaying plant-root systems.

2.3.2 Sample harvest after incubation

After incubation, plants and roots were separated from the bulk soil. The uppermost 0-1 cm soil in the pots was discarded to minimize the effect of biocrusts growing on the surface. Soil sticking to the roots was separated as 'root-adhering soil' and the remaining soil in the pots was defined as either 'rhizosphere soil' or 'detritusphere soil'. Due to the progressed decomposition of the roots in the detritusphere phase, we were not able to separate 'root-

adhering soil' during this phase. Plant and root materials were immediately frozen in liquid N and a homogenized aliquot of each soil sample was freeze-dried and stored at −20 °C for microbial analyses. The remaining soil was air-dried at room temperature until further analyses.

2.4 Gas measurements, isotopic labeling and imaging (Studies I and II)

2.4.1 CO_2 measurements (Studies I and II)

In preparation for the gas measurements reported in Studies I and II, and using the system developed in Study I, the samples were given water >2 h before to avoid CO_2 spikes and then flushed with air for >15 min (405 ppm; −38.3‰ $\delta^{13}C$ V-PDB) to achieve a defined concentration at the start of incubation. The incubation vessels were then closed for 45 min incubation, either in darkness (respiration) or in light (photosynthesis). During photosynthesis measurements, the PPFD was set to 600 µmol m^{-2} s^{-1} to account for the PAR transmittance of the lids of the incubation vessels (73.8±0.3%). During respiration measurements, all handling was carried out under green light (PPFD<15 µmol m^{-2} s^{-1}).

After the 45 min incubation, gas samples were collected and analyzed with a Delta Ray Isotope Ratio Infrared Spectrometer TMURI (Thermo Fisher Scientific, Bremen, Germany; Qtegra™ ISDS 2.3.1487.49 software). The ideal gas law was used to convert the spectrometer output (µmol CO_2 mol^{-1}) to µmol CO_2, from which the fluxes were then calculated as:

$$CO_2\ flux = \frac{CO_{2_{headspace}} - CO_{2_{flush}}}{A * t}$$

with

CO_2 flux: net ecosystem exchange of CO_2 (in µmol m^{-2} s^{-1})

$CO_{2\ headspace}$: CO_2 content in the headspace after incubation (in µmol)

$CO_{2\ flush}$: CO_2 content before incubation (here: ~16.8 µmol)

A: surface area of sample (in m^2)

t: time of incubation (in s)

Net photosynthesis was calculated by subtracting the respiration from the gross photosynthesis.

2.4.2 Dual isotopic labeling (Study II)

All biocrust-soil systems in Study II underwent dual isotopic labeling. We applied four $^{13}CO_2$ pulses by adding H_2SO_4 in excess to 7.5 mg of 99%$Na_2{}^{13}CO_3$ (Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany) for 5 h (achieving ~80 atom% ^{13}C in the headspace). Furthermore, one pulse of 99%$^{15}N_2$ (Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany) was added for 8 h (achieving ~23 atom% ^{15}N in the headspace). During labeling, the PPFD was set to 600 µmol m^{-2} s^{-1} to account for the shading effects of the plastic lids of the incubation vessels, similar to in the photosynthesis measurements as described earlier.

2.4.3 Gas sample system testing (Study I)

The core of Study I was to develop a gas sampling and labeling setup suitable to accommodate CO_2 flux measurements of arid biocrust-soil systems. As part of this work, the functionality and reliability of the system was tested in a range of feature tests.

Airtightness. The airtightness of the system was tested by adding 2 mg 99% $Na_2{}^{13}CO_3$ and 2 M H_2SO_4 in excess (~48,300‰ $\delta^{13}C$ V-PDB in the headspace) in the incubation vessels (n=5) and placing them in airtight plastic bags filled with defined air (−38.3‰ $\delta^{13}C$ V-PDB) for 3 h. The surrounding air was measured at the start and end of the incubation from which the relative source proportions of the air leaking from the incubation vessel and the surrounding air was determined with a two-end-member mixing model (Phillips et al. 2005).

Storage effects. The sample bags in which the gas samples were collected and stored were tested to determine possible storage effects. Therefore, sample bags (n=5) were filled with 500 mL with a defined concentration and isotopic signature (1,850 ppm, −76‰ $\delta^{13}C$ V-PDB) and continuously measured at start and after 2, 8, and 24 h (n=4 analytical replicates).

Pressure effects during sampling. The effectivity of the installed balloons in counterbalancing pressure changes in the headspace during sampling was tested by continuously removing 60 mL of gas until a total volume of 660 mL had been collected (representing ~66% of the headspace volume). The pressure changes in the headspaces of vessels with or without balloons (n=5) was compared.

Furthermore, test CO_2 flux measurements were conducted on the soil-biocrust systems as reported in section 2.4.1.

2.4.4 VNIR Hyperspectral imaging (Study II)

Directly after incubation, hyperspectral images of the soil surfaces were recorded using a Hyspex VNIR-1800 camera (Norsk Elektro Optikk, Oslo, Norway) as a means to estimate biocrust cover. The field of view was 9 cm (53×53 µm^2 per pixel) and the light reflectance intensity was recorded for 186 bands (400–990 nm; spectral resolution of 3.17 nm per band). The spectral intensity (I) was normalized to a 50% reflectance calibration target for each wavelength (λ) and pixel (x):

$$R_{Sample,\lambda,x} = \frac{I_{Sample,\lambda,x}}{I_{Target,\lambda,x}} \cdot R_{Target,\lambda,x}$$

The images were then cropped with a standard circle, resulting in a total area of 43.2 cm^2 per sample (1537844 pixels). Regions of interest (ROIs) were chosen from bryophytes, microbial biocrust, or bare soil with no visible biocrust cover, from which the spectral signatures for each of the three groups were isolated (Figure 8).

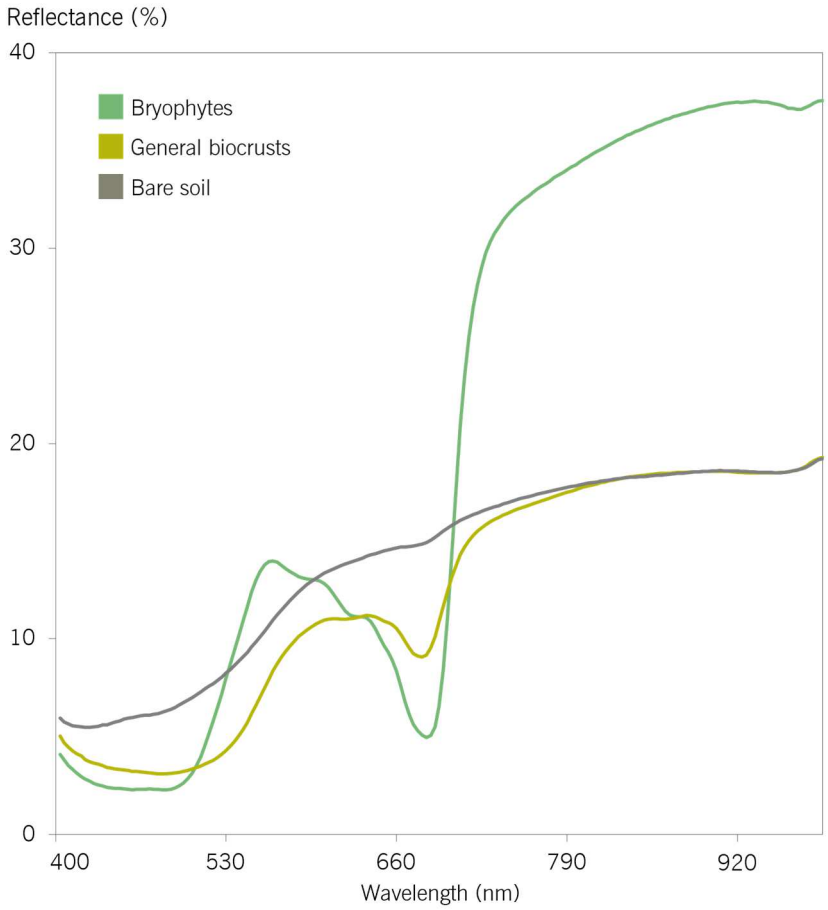


Figure 8 | Spectral signatures of the manually selected regions of interests from pixels associated with bryophytes, general microbial biocrust or bare soil without visible biocrust cover. Based on these, distinct spectral features in each group were identified from which suitable ratios and thresholds from an automated classification were established.

From the spectral signatures of the manually selected ROIs, suitable ratios and thresholds for an automated classification were identified based on distinct spectral features of the different groups. Pixels were classified as 'bryophytes ' if normalized difference vegetation index (NDVI) was ≥0.33, the sum of the RGB band's reflectance was >5, the ratio of bands 87/48 (680.9/556.7 nm) was <0.9, and the ratio of bands 60/50 (594.9/563.1 nm) was <1.1. The NDVI was computed (Kriegler et al. 1969) as:

$$NDVI = \frac{R_{NIR} - R_{RED}}{R_{NIR} + R_{RED}}$$

where R_{NIR} and R_{RED} are the reflectance of the near infrared (849.7–881.5 nm) and red (636.3–674.5 nm) bands. The pixels that did not meet the criteria for bryophytes were classified as 'general biocrusts' if the sum of RGB band's reflectance was >5, the ratio of bands 87/77 (680.9/649.0 nm) was <0.95, and the ratio of bands 60/50 (594.9/563.1 nm) was ≥1.1.

2.5 Soil analyses (Studies II and III)

Since Study I focused on the development and testing of the gas and labeling setup, this chapter is dedicated to Studies II and III, with an overview of the soil analyses from both studies provided in Table 3.

Table 3 | Overview of the soil analyses conducted in Studies II and III.

	Study II			Study III		
	Biocrust layer	0-1 cm soil layer	1-2.5 cm soil layer	Plant/root biomass	Root-adhering soil	Bulk soil
C and N contents	✓	✓	✓	✓	✓	✓
^{13}C and ^{15}N contents	✓	✓	✓	✓	✓	✓
Aggregate fractionation	×	×	×	×	×	✓
Density fractionation	✓	✓	×	×	×	✓
^{13}C NMR Spectroscopy	×	×	×	✓	×	✓
PLFA extraction	✓	✓	×	×	×	✓
Lignin extraction	×	×	×	×	×	✓

2.5.1 Physical fractionation (Studies II and III)

Between 20-50 g of air-dried soil (20-30 g in Study II and 30-50 g in Study III) was saturated with sodium polytungstate solution ($Na_6[H_2W_{12}O_{40}]$; 1.8 g cm^{-3}) for 12 h. Free floating particulate OM (fPOM) was then separated using a vacuum pump. Ultrasonic dispersion (440 J ml^{-1}; Amelung and Zech 1999; Mueller et al. 2014) was applied to release occluded POM (oPOM) from aggregated soil structures, and the fraction was separated into oPOM and $oPOM_{<20\mu m}$ by sieving (20 µm). The remaining heavier mineral fraction was sieved into two mineral-associated OM fractions; $MAOM_{<63\mu m}$ and $MAOM_{>63\mu m}$. After separation, all fractions were washed and pressure filtered below an electrical conductivity of <5 µS cm^{-1}. Finally, washed fractions were freeze-dried and milled for further analyses.

In Study III, the fractions fPOM, oPOM, $oPOM_{<20\mu m}$, $MAOM_{<63\mu m}$, and $MAOM_{>63\mu m}$ were separated. In Study II, however, a clean fPOM fraction could not be separated as the free floating biocrusts in the saturated polytungstate solution were intertwined with soil minerals. As such, a combined POM fraction was retrieved after ultrasonification, yielding POM, $MAOM_{<63\mu m}$, and $MAOM_{>63\mu m}$ fractions in Study II.

2.5.2 Aggregate fractionation (Study III)

For the separation of water stable aggregates, 5 g of re-wetted soil was gently placed on a sieve tower (mesh size: 250 and 53 µm, diameter: 100 mm) in a beaker containing 2 L deionized water. The sieve tower was slowly moved up and down for 130 cycles (30 min), during which the soil material was submerged in water at all times (Baumert et al. 2018), yielding three aggregate size classes: macroaggregates (2000-250 µm), large microaggregates (250-53 µm) and small microaggregates including silt and clay particles (<53 µm). The <53 µm fraction was retained via pressure filtration (0.45 µm) and freeze-dried while the other two fractions were dried at 40 °C until further analyses.

2.5.3 ^{13}C Nuclear Magnetic Resonance Spectroscopy (Study III)

The chemical composition of plant/root biomass as well as the three POM fractions of Study III was determined via solid state ^{13}C CP-MAS NMR spectroscopy (Bruker DSX 200, Bruker BioSpin GmbH, Karlsruhe, Germany). Samples were placed in placed in 7-mm zirconium dioxide rotors and spun at 6.8 kHz (0.01024 s acquisition time and 1.0 s delay time for plant/root

biomass and 0.4 delay time for POM fractions). The baseline was manually corrected after the relative abundance of alkyl C (−10-45 ppm), O alkyl C (45-110 ppm), aromatic C (110-160 ppm), and carbonyl/carboxyl C (160-220 ppm) were quantified, including spinning side bands. Furthermore, the alkyl C/O alkyl C ratio (−10-45/45-110 ppm) according to Baldock et al. (1997) and the O alkyl C/methoxyl C and N alkyl C ratio (70-75/52-57 ppm) according to Bonanomi et al. (2013) were used as proxies for the stage of decomposition. Finally, all spectra were modeled using the molecular mixing model (Nelson and Baldock 2005; Prater et al. 2020) to quantify the relative abundance of carbohydrates, proteins, lignins, lipids, and carbonyls.

2.5.4 Lignin extraction fractionation (Study III)

Lignin-derived phenols were extracted from plant/root biomass samples through cupric oxide (CuO) oxidation (Angst et al. 2017). Samples with at least 5 mg of C were placed in pressure digestion vessels, along with 50 mg of ammonium iron (II) sulfate hexahydrate, 300 mg of CuO, and 2M NaOH in excess. The samples were then shaken for 3 h (155 °C) after which the NaOH solution was separated by centrifugation, acidified with 6M HCl, and lastly extracted with ethyl acetate. The resulting solution was filtered over Na_2SO_4 and evaporated under a stream of N_2. The sum of vanillyl, syringyl, and cinnamyl units (VSC) was used to estimate total lignin content. The ratios of lignin-derived phenolic acids to their corresponding aldehydes were computed for vanillyl ($(Ac/Al)_V$) and for the total lignin units (Ac/Al).

2.5.5 Microbial community analyses (Studies II and III)

As a means to quantify changes in microbial community structures, PLFA patterns were recorded according to the method of Frostegård et al. (1993) and Quideau et al. (2016) with modifications by Kramer et al. (2013). Between 4 and 12 g of freeze-dried soil was vortexed with Bligh & Dyer solution [methanol, chloroform, citrate buffer (pH = 4±0.1), 2:1:0.8, v/v/v]. Phospholipids were separated from glycolipids and neutral lipids by solid phase extraction over silica tubes (SPE DSC-Si, 500 mg, Discovery®, Sigma-Aldrich, Taufkirchen, Germany) and later converted to fatty acid methyl esters (FAMEs) via alkaline methanolysis. Lastly, FAMEs were quantified relative to the internal standard via gas chromatography coupled to a flame ionization detection (Thermo Scientific Trace 1310, Waltham, MA, USA). In Study II, the isotopic enrichment of the selected FAMEs was further determined using a Rtc-5 60 m/0.25 mmID/1

µm coated column (Restek, Bellefonte, PA, United States) coupled to a Delta V Advantage mass spectrometer via GC Isolink (Thermo Fisher Scientific, Bremen, Germany). All FAMEs were thereby converted to CO_2, from which the $^{13}C/^{12}C$ ratios in the carrier gas stream could be determined (López-Mondéjar et al. 2018).

Some improvements were made to the PLFA extractions protocol between Studies II and III. In Study II, the soil samples were spiked with an internal standard at the start of the extraction (C19:0; Avanti Polar Lipids, Birmingham, UK). This approach had two main advantages: first, the addition of a PLFA standard at the beginning of the extraction procedure, rather than as an ester at the end, allowed for direct accounting of differences in extraction success between samples. In the previous protocol (Study III), the extraction efficiency for all samples was assumed based on the extractions of an external standard soil (air-dried agricultural soil, Ap horizon). Secondly, by adding the standard during the beginning of the protocol instead of at the very end, we were able to account potential samples losses or other mistakes throughout the entire extraction process. The selection of markers differed slightly between the two studies (Table 4).

Table 4 | The selection and designation of phospholipid fatty acid (PLFA) markers to different microbial groups in Studies II and III.

	Study II	Study III
C14:0	unspecified	unspecified
iC15:0	gram+	gram+
aC15:0	gram+	gram+
C15:0	bacteria	bacteria
iC16:0	gram+	gram+
C16:0	×	unspecified
C16:1ω7	gram−	gram−
10MeC16:0	actinomycetes	×
iC17:0	gram+	gram+
aC17:0	bacteria	×
cy17:0	×	gram−
C17:0	gram+	bacteria
10MeC17:0	actinomycetes	×
C18:1ω7	×	unspecified
C18:1ω9	×	fungi
C18:2ω6,9	fungi	fungi
C18:0	unspecified	unspecified
10MeC18:0	actinomycetes	×
cy19:0	bacteria	gram−
C19:0	int. standard	int. standard
C20:5ω3	fungi	×
20:3ω3	cyanobacteria	×
C20:0	unspecified	unspecified

2.5.6 Elemental analyses (Studies II and III)

The C, N, ^{13}C, and ^{15}N contents of biocrust/soil layers, and OM fractions in Study II, as well as of plant/root biomass, OM fractions, aggregate fractions, and bulk soil in Study III, were determined by dry combustion using an isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Bremen, Germany) coupled to an elemental analyzer (Euro EA, Eurovector, Milan, Italy). A laboratory standard (acetanilide) was used for calibration and to determine the isotope linearity of the system. To check for the presence of $CaCO_3$, samples were treated with 0.5 M HCl. Since their elemental composition remained unchanged, $CaCO_3$ could be ruled out. Consequently, total C content was assumed equal to OC contents.

2.6 Calculations and statistical analyses

2.6.1 ^{13}C and ^{15}N calculations (Study II)

From the isotopic signatures ($\delta^{13}C$ ‰ V-PDB and $\delta^{15}N$ ‰ air N_2) of the biocrust/soil samples and OM fractions in study II, the atom% was derived and used to calculate the adjusted molar mass of C and N (according to Teixeira et al. 2023):

$$M_{\mathrm{C}}\ [\mathrm{g\ mol^{-1}}] = (M_{13\mathrm{C}} \cdot \frac{^{13}C_{atom\,\%}}{100}) + (M_{12\mathrm{C}} \cdot (1 - \frac{^{13}C_{atom\,\%}}{100})$$
$$M_{\mathrm{N}}\ [\mathrm{g\ mol^{-1}}] = (M_{15\mathrm{N}} \cdot \frac{^{15}N_{atom\,\%}}{100}) + (M_{14\mathrm{N}} \cdot (1 - \frac{^{15}N_{atom\,\%}}{100})$$

where M_C and M_N represent the adjusted molar mass for C and N. The molar mass of ^{13}C (M_{13C}) was set at 13.00335, of ^{12}C (M_{12C}) at 12, ^{15}N (M_{15N}) at 15.000109 and ^{14}N (M_{14N}) at 14.003074 g mol^{-1}.

To correct for the natural abundance of ^{13}C and ^{15}N, the excess isotopic enrichment was calculated:

$$^{13}\mathrm{C}_{\mathrm{enrichment}}\ [\%] = \ ^{13}\mathrm{C}_{\mathrm{atom\%\ biocrust}} - {}^{13}\mathrm{C}_{\mathrm{atom\%\ bare\ soil}}$$
$$^{15}\mathrm{N}_{\mathrm{enrichment}}\ [\%] = \ ^{15}\mathrm{N}_{\mathrm{atom\%\ biocrust}} - {}^{15}\mathrm{N}_{\mathrm{atom\%\ bare\ soil}}$$

from which then the excess content of ^{13}C and ^{15}N was determined:

$$^{13}\mathrm{C}_{\ concentration}\ [\mu\mathrm{g\ g^{-1}}] = \frac{^{13}\mathrm{C}_{\mathrm{enrichment\%}}}{100} \cdot \mathrm{C}_{\mathrm{soil}} \cdot \frac{M_{13\mathrm{C}}}{M_{\mathrm{C}}} \times 1000$$
$$^{15}\mathrm{N}_{\ concentration}\ [\mu\mathrm{g\ g^{-1}}] = \frac{^{15}\mathrm{N}_{\mathrm{enrichment\%}}}{100} \cdot \mathrm{N}_{\mathrm{soil}} \cdot \frac{M_{15\mathrm{N}}}{M_{\mathrm{N}}} \times 1000$$

where C_{soil} and N_{soil} represent the total C and N contents in the biocrust/soil samples and OM fractions.

2.6.2 Statistical analyses

The statistical testing for all studies was carried out in the R statistical environment (version 4.2.1 or 4.2.2, R Development Core Team 2008) in RStudio (version 2022.07.2+576 or 2022.12.0+353, RStudio Team 2015). All data was tested for homogeneity of variances (Levene test, package: car, version: 3.1-2) and normality of the residuals (Shapiro test/qq-plots). The data was log transformed if the assumption of normality and homoscedasticity was not met.

Study I. A lme model A mixed effect model (lme, package: nlme version: 3.1-157; Pinheiro et al. 2006) was used to test for differences in pressure changes in the incubation vessels and the CO_2 flux and $\delta^{13}C$ data. For the pressure changes, the air volume removed from the vessels and the presence of the ballon (yes vs no) were used as fixed effects whereas box ID was set as a random effect. For the CO_2 and $\delta^{13}C$ data, treatment (normal water vs drought) and biocrust vs control were used as fixed effects while the chamber was set as a random effect. In cases where significant effects were determined in the mixed effect model, a post-hoc test with the emmeans function and Tukey correction was carried out (package: emmeans, version: 1.3.1).

Study II. The CO_2 fluxes data was tested with an ANOVA with the treatments (ambient vs. warming) and drought (normal water vs. drought) as fixed effects for the samples with biocrusts only. A mixed effect model (lme, package: nlme version: 3.1-157; Pinheiro et al. 2006) was used to test for differences between C, N, ^{13}C and ^{15}N contents of the biocrust/soil samples and OM fractions, with the treatment, drought and biocrust (yes vs no) as fixed effects and the sample ID as a random effect. The PLFA data was also tested with the lme model with treatment, drought, and the depth (biocrust vs top soil layer) as fixed effects and ID again as a random effect. Post-hoc tests were carried out for all models: Tukey's test for ANOVA and emmens test (package: emmeans version: 1.8.8; Lenth 2023) for the lme model. The correlations between single parameters was carried out using the chat.correlation function (package: PerformanceAnalytics, version: 2.0.4; Peterson and Carl 2020) and the spearman method.

Study III. Differences between the plant/root biomass data were tested with a one-way ANOVA with Tukey's post-hoc test. The rest of the data was analyzed with a mixed-effect model (package:nlme) with the soil material (topsoil vs subsoil) and the incubation phase (rhizosphere vs detritusphere) as fixed factors and sample ID as a random effect.

All errors reported in text and displayed in graphics refer to the standard deviation of the mean (SD).

3 | RESULTS & DISCUSSION

3.1 Soil C and N dynamics and formation of SOM in biocrusted and rooted systems

3.1.1 Sampling system for CO_2 flux measurements and *in situ* ^{13}C labeling

The closed static chamber (non-flow-through) system developed in Study I provided a convenient and effective setup. Its design, incorporating one-directional check valves, allowed for easy handling during system flushing, evacuation, and subsequent sampling (Figure 9).

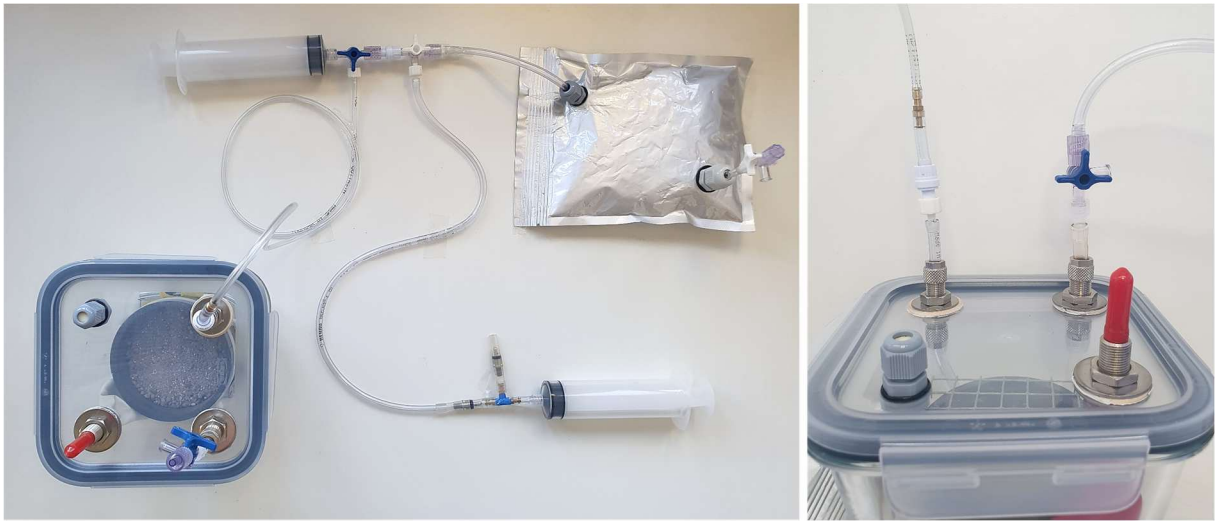


Figure 9 | An overview of the developed gas system, where one-directional check valves enabled convenient handling both before and during sampling. The integration of two syringes—one for evacuation of residual air residing in sample bags and other system compartments, and another for gas sampling—allowed all steps to be conducted within one single setup, without the need to attach or detach any system components.

Furthermore, and most importantly, the system demonstrated adequate sensitivity and precision for the reliable quantification of small-scale CO_2 fluxes. While limiting closure times during gas measurements to minimize the artifacts caused by changing headspace conditions (Rochette and Hutchinson 2005), the system effectively captured both respiratory CO_2 release and fixation in the soil-biocrust samples. For instance, in drought-exposed bare soil controls samples, where the lowest microbial activity was expected, fluxes as small as 0.1 µmol CO_2 m^{-2} s^{-1} were successfully quantified during respiration measurements (Figure 3 in Study I and Figure 10). Both the measured respiration and net photosynthesis rates aligned with, or fell slightly below, values reported in field studies of comparable biocrust systems (Bowling et al. 2011; Chamizo et al. 2021), further reinforcing the system's the accuracy and reliability.

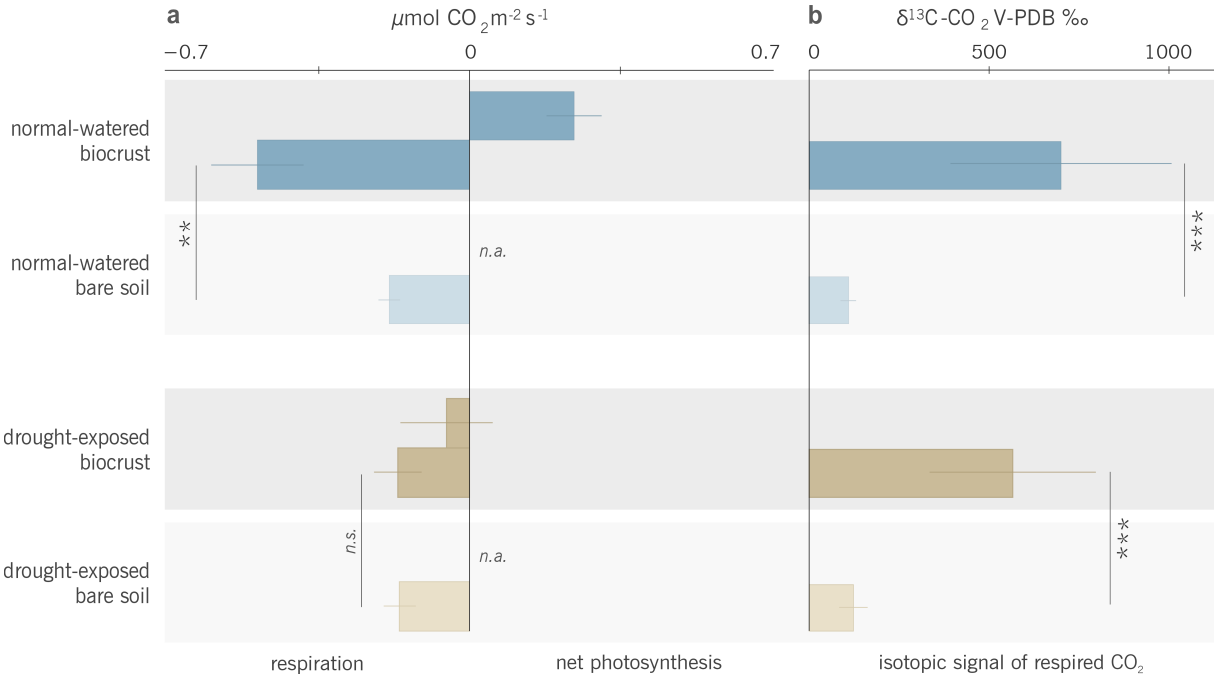


Figure 10 | a Respiration and net photosynthesis (in µmol CO_2 m^{-2} s^{-1}) in soils with biocrusts and bare soil controls, either under normal water conditions (blue) or under drought (brown), and **b** the isotopic signal of the respired CO_2 (in $\delta^{13}C$ V-PDB‰). Data are presented as means ± SD (n = 4), with asterisks indicating significant differences between biocrust samples and their respective controls. Figure modified from Study I.

Capturing small CO_2 fluxes in the biocrust-soil systems posed a significant methodological challenge in designing the sampling system. On one hand, the headspace volume of the incubation vessel needed to be kept small to allow for sufficient CO_2 buildup within a given (limited) incubation time. On the other hand, a larger sample volume was necessary to facilitate both flushing of the analyzer and for analytical replication (Boudoire et al. 2020). Besides, we needed the sample volumes to be large enough to accurately represent the true headspace mean, rather than just accounting for a small fraction of the headspace volume. This posed a challenge, as withdrawing larger sample volumes from a static chamber causes underpressure, which may not only harm the research sample but also draw air with high CO_2 concentration from internal pore spaces, thus distorting the measurement results (Fang & Moncrieff, 1996). To solve this, a balloon was installed open to the outside, to directly counterbalance the underpressure during sampling. This modulation reduced under pressure by 72% when collecting a sample volume corresponding to approximately 36% of the headspace volume (Figure 11).

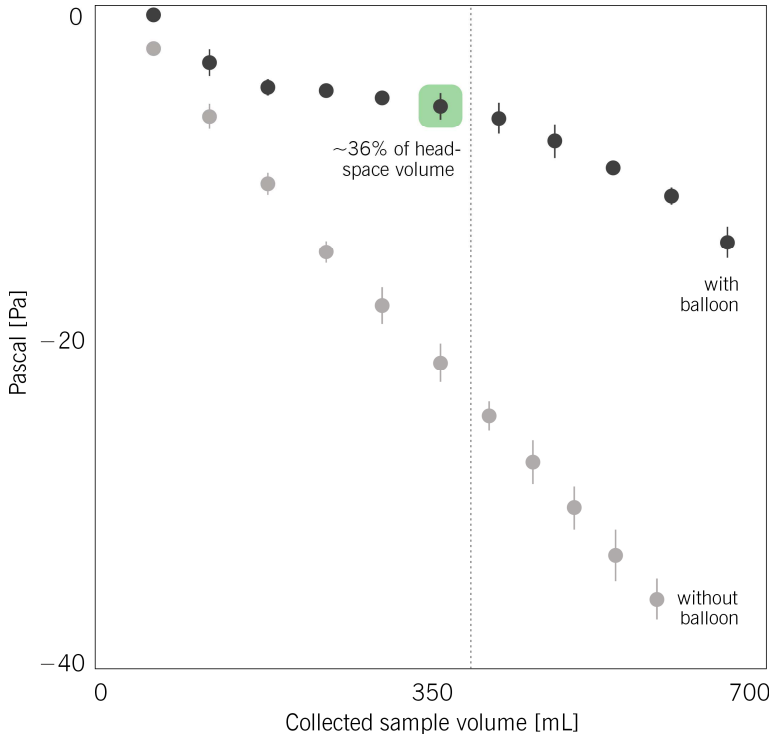


Figure 11 | Pressure changes in the incubation chamber headspace (Pa) as a function of collected gas sample volume (mL). The differences between systems with and without balloon was significant in all measurement points (P<0.001). The green box marks the selected sample volume used in Studies I and II (360 mL, corresponding to 36% of headspace volume). Data are presented as means ± SD (n=5). Figure modified from Study I.

The system was also designed to accommodate a high sample throughput while minimizing the risks of cross-contamination between samples, leakages or human error. This was especially important during the measurements following isotopic labeling, as highly enriched samples were processed alongside unlabeled samples at natural abundance. For this reason, the system compartments were designed and mounted in a way so that the entire system (including gas sample bags) could be flushed in one step without having to attach or detach any compartments, after which the residual air residing in sample bags and the system could be directly removed using an evacuation syringe. In addition, check valves were installed that guaranteed one-directional gas flow between all system compartments to further facilitate the handling (Figure 1 in Study 1). Taken together, this setup provided a low-cost and accessible solution facilitating the measurements conducted in Study II.

3.1.2 Carbon fluxes in soil-biocrust systems

Using the developed gas sampling system, we were able to confirm the distinct role of biocrusts in regulating C fluxes (Study I and Study II). The measurements of both photosynthetic C uptake and stimulated respiration in biocrusted soils not only emphasizes their significant role in mediating C fixation and release in dryland ecosystems, but also demonstrate how the establishment of these early communities can fundamentally alter C fluxes within relative short time frames (Castillo-Monroy et al. 2011). Similar to in Study I, the measured photosynthetic C uptake in Study II (>0.4 µmol CO_2 m^{-2} s^{-1} in samples with the highest biocrust cover; Figure 1a in Study II) was consistent with, or slightly below, field observations from comparable systems (0.5-2 µmol CO_2 m^{-2} s^{-1}; Bowling et al. 2011; Darrouzet-Nardi et al. 2015). This discrepancy—where measured values were slightly below those reported in natural settings—may be attributed to the short duration of the incubation (approximately 4.5 months) compared to reported growth and development rates of natural biocrust systems (Weber et al. 2016).

In Study II, the measured respiration and net photosynthesis in biocrusted samples were positively correlated, emphasizing the strong link between the primary production by biocrust autotrophs and microbial heterotrophs (Table S4 in Study II; Tucker et al. 2020). Biocrusts are widely reported to stimulate soil respiration (*e.g.,* Grote et al 2010; Wilske et al. 2008; Feng et al. 2014). This interdependence is largely ascribed to the release of organic C by photoautotrophic biocrust components (*e.g.,* mosses and lichens), which alleviates the otherwise C-limited conditions, thereby stimulating the metabolic activity of heterotrophic organisms both within the biocrust layer and in the underlying soil (Su et al. 2023). These findings nicely underscore the interplay between autotrophic and heterotrophic activity within biocrusts as well as their collective role in driving soil C cycling.

The C fluxes were strongly modulated by changing climatic conditions (temperature and moisture availability)—although in different ways. Overall, moisture availability proved to be the primary constraint on the measured CO_2 fluxes, reducing both photosynthetic activity and respiration across all biocrust systems studied (Studies I and II). The drought-induced reduction in photosynthetic C fixation (>80% reduction) resulted in an almost net negative C balance in the systems overall, despite also decreasing respiratory C losses (Figure 3a in Study I; Figure 1a in Study II). This shows how even brief periods of drought reduces the metabolism and primary production of biocrusts to the extent that constrains their contribution to a positive C balance in the system (Figure 12).

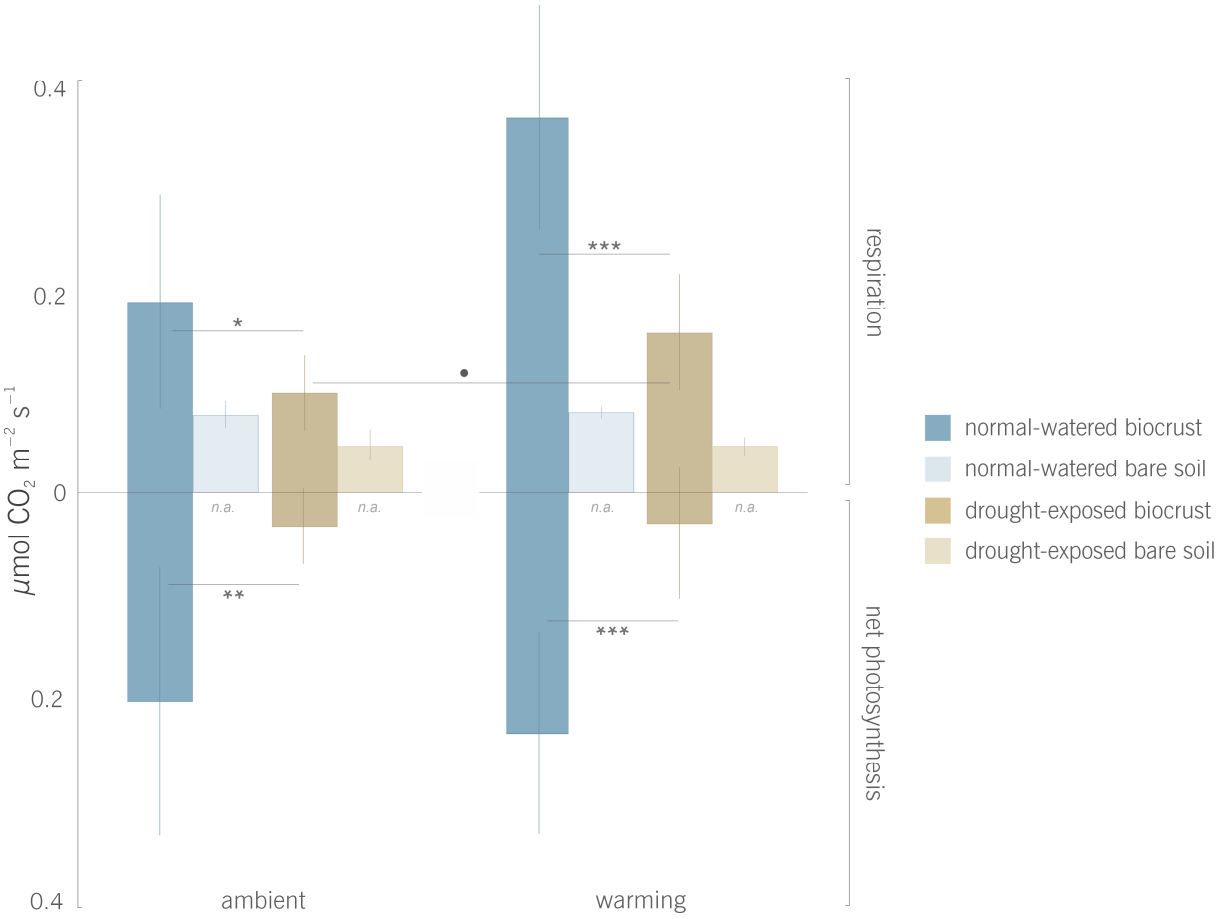


Figure 12 | Respiration and net photosynthesis (µmol CO_2 m^{-2} s^{-1}) in soils with biocrusts (bold colors) or in bare soil controls (faded colors), either under normal water conditions (blue) or drought (brown). The two moisture levels are depicted in blue respectively brown colors, and 'ambient' represents temperatures according to field conditions, and 'warming' a +5 °C throughout the incubation. The net photosynthesis represents the total CO_2 flux in the biocrust–soil system and is therefore equivalent to net ecosystem exchange. Photosynthesis could be excluded in all bare soil controls ("*n.a.*"). Data are presented as means ± SD (n = 8), where asterisks denote significant differences between biocrusts and bare soil controls (•P<.05, *P<.05, **P<.01, ***P<.001). Figure modified from Study II.

Contrary to drought, there was no clear effect of temperature on the net C balance in any of the studied systems (Study II). Despite accelerated respiratory C losses in due to warming, *e.g.,* caused by increased kinetic energy of enzymes and diffusion rates (Davidson et al. 2006), we found no differences in net C uptake between the temperature treatments (Figure 12). Instead, the accelerated losses in the warmed systems were counterbalanced by higher gross photosynthesis rates, evidently caused by the greater biocrust cover in the systems exposed to warming (Table S3 in Study II). These findings revealed an interesting difference in the dynamic of the biocrusts caused by the temperature regime; C gains and losses were greater under the warmer temperature, with increased C throughput from photoautotrophs as indicated by higher ^{13}C contents in microbial biomass compared to under ambient conditions (Figure 6 in Study II). This points to enhanced microbial involvement in the processing and turnover of

biocrust-derived C. However, when compared to the ambient system, where C fluxes were overall smaller, there was no difference in the total C gain to the system (Figure 13). It is important to note, as mentioned earlier, that the duration of the incubation is relatively short compared to the relatively slow natural growth and establishment of biocrusts. Especially in regards to these non-linear effects of climate change and how they evolve over time, future studies could provide valuable insights by extending incubation periods, exposing biocrusts to prolonged periods of drought and warming—thus, conditions that may more closely align with the long-term impacts of climate change in natural ecosystems.

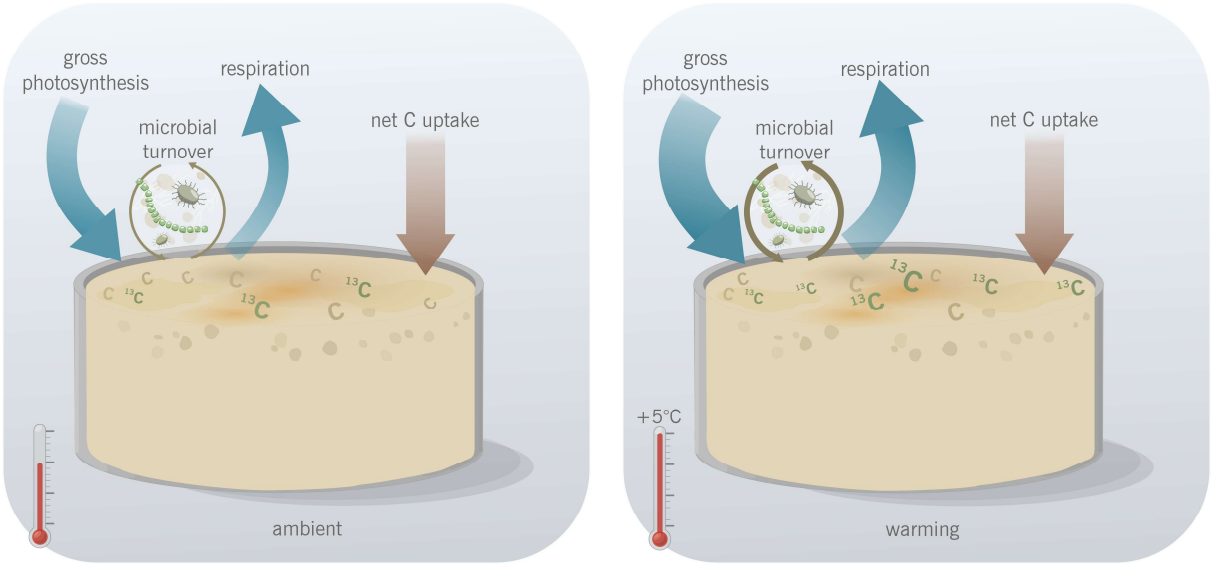


Figure 13 | The difference in temperature impacted the overall C cycling dynamic in the studied systems. In the ambient system, CO_2 fluxes were generally lower compared to in the warming chamber, but the total net C uptake was the same between the temperatures. The accelerated fluxes under warming were associated with a higher microbial involvement in the processing of biocrust-derived C, indicated by higher ^{13}C contents.

3.1.3 Biocrusts as drivers of C and N translocation into the mineral soil

The differences in net C balances in the systems under the different moisture treatments, and the coherency between the temperature treatments, was directly reflected in the elemental composition of the biocrust layer. The buildup of C and N within the layer was similar between temperature treatments, but distinctively lower in systems exposed to drought (Figure 14).

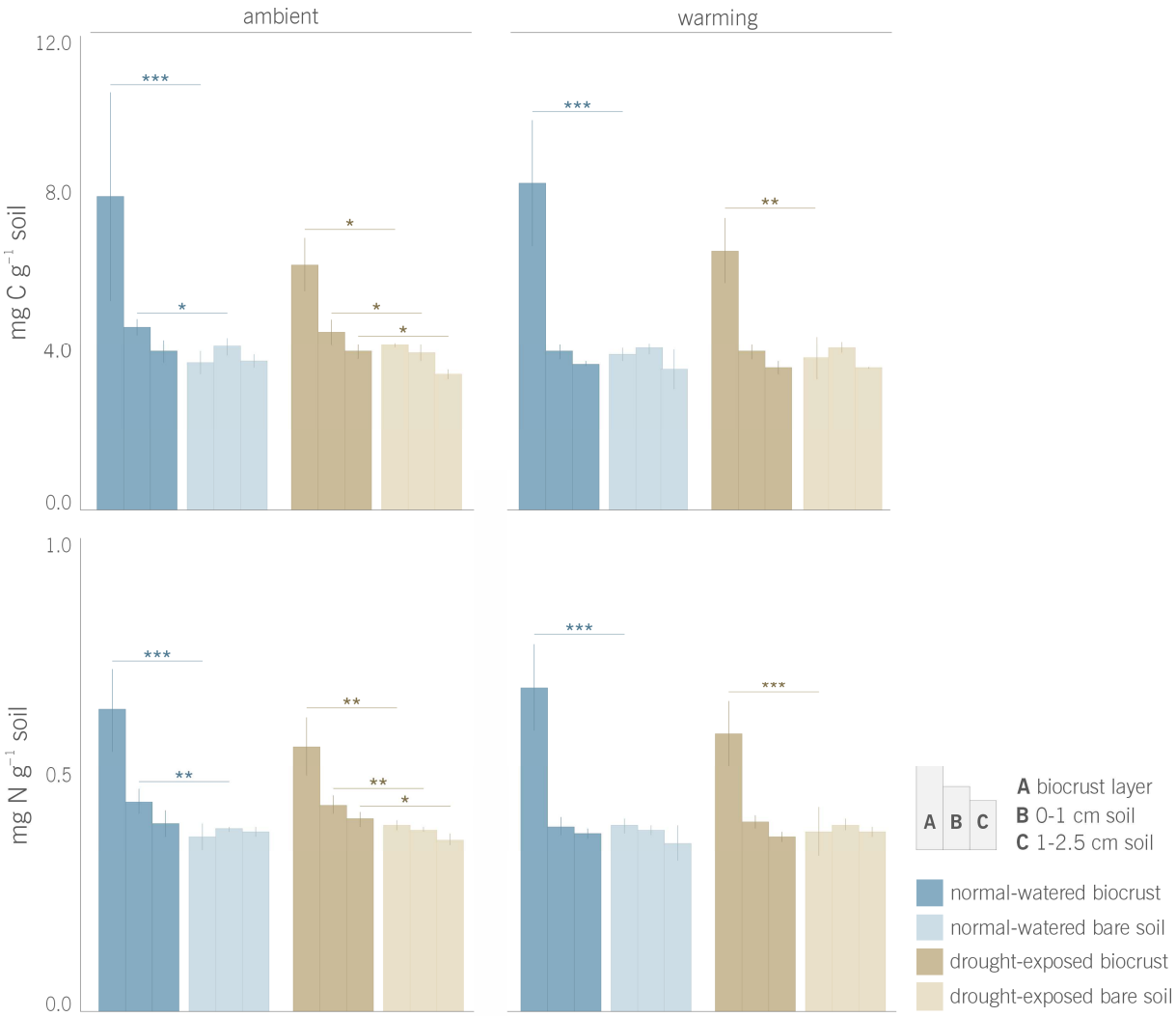


Figure 14 | The contents of C and N (in mg g^{-1} soil) across the three depth increments; biocrust layer and underlying top (0-1 cm) and sub (1-2.5 cm) soil layers. Biocrusted samples are depicted in bold colors and the corresponding bare soils faded colors. The two moisture levels are depicted in blue respectively brown colors, and 'ambient' represents temperatures according to field conditions, and 'warming' a +5 °C throughout the incubation (means, SDs displayed with error bars, $n = 3$ independent replicates). Asterisks denote significant differences between biocrusts and bare soil controls (*P<.05, **P<.01, ***P<.001). Figure modified from Study II.

While the composition of the biocrust layer remained consistent across temperature treatments, there were differences in the underlying mineral soil (Figure 14). In fact, only in systems maintained at ambient temperature there was an accumulation of C and N in the 0-1 cm soil layer, regardless of moisture availability, while the contents in the soil beneath warming-exposed biocrusts remained consistent with the bare soil controls. These findings suggests that mechanisms involved in the downward translocation of C and N are sensitive to temperature. While the exact mechanisms involved in the movement of C and N from biocrusts remain largely unknown, studies suggest that biocrusts may enhance elemental translocation via increased infiltrability through channels created by moss stems and rhizoids or via increased leaching of DOC into the sub-crust soil (Kidron et al. 2010; Chamizo et al. 2012; Dümig et al.

2014; Young et al. 2022). Although it is speculative, the differences observed in Study II may stem from temperature-driven variations in biocrust species and composition, which could, in turn, influence infiltrability and leaching dynamics.

3.1.4 The influence of biocrusts and roots on particulate and mineral-associated OM

In contrast to the direct effects of biocrusts on the C and N contents within the biocrust layer and in the underlying soil in Study II, no such changes were observed in the presence of roots in Study III—neither in the rhizosphere or detritusphere. Contrary to our expectations, we observed no differences in the elemental composition of the bulk soil around roots in either topsoil or subsoil (Figure S3 in Study III). Given the widely accepted scientific consensus of the contribution of plant roots to soil OM pools, the absence of quantifiable effects was unexpected. Potentially, root-derived inputs may have been masked by the inherent soil C and N pools, or inputs may have been processed by the stimulated microbial activity in the rhizosphere prior to sampling (Figure 3 in Study III; Cheng 2009). It should also be noted that the rhizosphere and detritusphere soil material was collected from the entire pot, meaning that it cannot be ruled out that potential elemental changes within the immediate soil volume around the roots were diluted in the larger sampling volume (Marschner et al. 2012).

The absence of root-induced changes concluded in the bulk C and N contents was also true for the separated OM fractions. Here, both C and N contents and the chemical composition of POM and MAOM fractions remained consistent with those of the bare soil controls in both topsoil and subsoil (Figure S6 and S8 in Study III). However, occluded C as $oPOM_{<20\mu m}$ and the contribution of the $oPOM_{<20\mu m}$ fraction to the total C and N content in the soil were clearly affected by the roots—albeit, in different ways between the rhizosphere and the detritusphere (Figure 2 in Study III). In the topsoil rhizosphere, occluded C ($oPOM_{<20\mu m}$) slightly decreased compared to the controls, indicating that aggregate breakdown processes occurred in the vicinity of the living roots (Six et al. 2004). While roots are commonly associated with direct or indirect aggregate formation (*e.g.,* Gale et al. 2000; Gould et al. 2016; Baumert et al. 2018), these findings instead point to enhanced aggregate turnover in the presence of roots, promoting the destruction of aggregates more than their formation. Ultimately, this can be attributed to the increased decomposition intensity of inherent rhizosphere SOM, driven by the stimulated growth and activity of root-associated microorganisms in comparison to the

root-free soil, which exposes physically protected SOM within aggregates (Helal and Sauerbeck 1989; Villarino et al. 2021). The increased destruction of aggregates in the rhizosphere has previously been shown to be tightly linked to the rhizosphere priming effect (Kuzyakov et al. 2002; Cheng 2009). Interestingly, as the rhizosphere transitioned to a detritusphere, the influence of the roots on the SOM fractions changed. Around the decaying roots in the topsoil, an increased accumulation of occluded POM ($oPOM_{<20\mu m}$) was determined, reversing the pattern observed in the rhizosphere (Figure 4d in Study III). These observations are in line with previous studies (*e.g.,* Sanaullah et al. 2011) and point to the fact that C inputs from decaying roots are preferentially stored as occluded POM within the detritusphere (Mueller et al. 2024). Furthermore, this underscores how decaying litter surfaces are at the core of aggregate formation, representing functional soil components that contribute to longer-term C stabilization (Witzgall et al. 2021).

In Study II, we were unfortunately unable to separate the POM fraction into free and occluded OM, as was done in Study III, which limits the direct comparison between biocrust and root effects on POM to speculations. However, we can conclude that their contribution to MAOM formation differed significantly. We found no changes in the elemental, isotopic, or chemical composition of either $MAOM_{>63\mu m}$ nor $MAOM_{<63\mu m}$ in the rhizosphere or detritusphere (Figures S6, S8 and S9 in Study III). The absence of root effects on the MAOM fractions in the rhizosphere was surprising, given the well-established role of root-derived organic compounds in directly adsorbing onto mineral surfaces as well as indirectly driving the formation of organo-mineral assemblages via microbial EPS production and necromass in the vicinity of roots (Sokol and Bradford 2019; Liang et al. 2020; Neurath et al. 2021; Teixeira et al. 2024). The fact that neither total amount of mineral-associated C nor the total C content in the bulk soil was unchanged by rooting does not necessarily rule out the incorporation of root-derived C into the MAOM fractions. Instead, the absence of detectable changes may be due to root exudates driving the desorption of organic compounds from their protective association with mineral surfaces (Keiluweit et al. 2015) or due to accelerated turnover of mineral-associated C in the rhizosphere (Neurath et al. 2021). In the study by Neurath et al. 2021, the authors suggest that while the total C content associated with mineral surfaces is maintained the roots, native non-root-derived C in the MAOM fraction is replaced with newly formed root-derived C, introducing the concept that MAOM turnover occurs more rapidly within the rhizosphere than in the bulk soil. To better understand the processes at play in Study III, and to detect potential

small-scale changes occurring in the immediate soil volume surrounding roots, future studies could benefit from ^{13}C labeling of the plants in combination with a more narrowed and precise sampling approach of the immediate soil around the roots (Neurath et al. 2021; Teixiera et al. 2024). Lastly, the absence of changes in MAOM in the developing detritusphere was expected, as root litter inputs are known to preferentially accumulate as POM (as discussed previously).

In contrast to the observations in rooted soils, biocrusts had a substantial influence on MAOM. We found that C and N accumulated as $MAOM_{<63\mu m}$ both within the biocrust and in the underlying 0-1 cm mineral soil under ambient conditions (Figure 4 in Study II). These changes could be attributed to the filamentous growth of cyanobacteria and moss rhizoids, which are known to enmesh soil minerals (Weber et al. 2022), potentially driving the formation of biologically active biogeochemical interfaces at the surfaces of soil minerals and thereby promoting MAOM formation (Mager and Thomas 2011; Vidal et al. 2021; Witzgall et al. 2021). Additionally, the increase in $MAOM_{<63\mu m}$ in the underlying soil was strongly correlated with the fungi:bacteria ratio, suggesting that fungi played a key role in MAOM formation (this will be discussed in detail in section 3.4.2).

As research on the effects of biocrust on OM dynamics is still in its early stages, the mechanisms involved in MAOM formation in biocrust-soil systems are still largely unknown. To date, only one study has separated OM fractions in biocrust-soil systems (Díaz-Martínez et al. 2023), emphasizing the need for further research to fully disentangle the processes involved. While our study provides a novel finding—reporting MAOM formation in separated sub-crust soils for the first time—additional field-based studies are needed to validate and expand on these findings. Future research under natural conditions will be essential to better understand the interactions between biocrusts, the associated microbiome, and soil minerals surfaces, and to unravel the broader implications of MAOM formation for OM dynamics in dryland ecosystems.

3.2 Soil microorganisms under biocrusts and at the soil-root interface

3.2.1 Microbial growth and abundance in biocrusts and around roots

The establishment of biocrusts, along with the corresponding increase of biologically fixed C and N, was linked to distinct changes in the microbiome (Figure 4 in Study II). In the biocrust layer, the microbial abundance was strongly enhanced in all studied systems—up to a factor of 8 compared to the bare soil controls. Similarly, the introduction of plant roots to the soil

system (Study III) resulted in a clear increase in total microbial abundance in the topsoil rhizosphere, likely driven by the increased OM availability from root exudates or sloughed-off root cells (Holz et al. 2018). These findings reinforce the well-established concept that both biocrusts and plant roots play a crucial role in stimulating microbial growth in the otherwise nutrient depleted dryland soils (Kramer and Gleixner, 2008; Esperschütz et al. 2011; Fanin et al. 2014). The microbial colonization induced by biota represents a foundational contribution to the continued development of dryland soils, setting the stage for further ecological succession and the subsequent establishment of more complex biotic communities (Rodríguez et al. 2024). However, these results also underscore the limitations provided by the soil substrate. Microbial colonization and growth were notably constrained around the roots grown in the subsoil, illustrating how the soil material dictates, and constrains, microbial development (Figure 15). Several factors, including overall lower root growth in the subsoil and the chemical composition of the root tissue, arguably contributed to the restricted microbial growth and abundance in the subsoil rhizosphere (Table 1 in Study III). Firstly, the limited plant and root growth in the subsoil systems likely resulted in reduced rhizodeposition, decreasing the input of essential substrates that can stimulate and maintain microbial growth (Baptist et al. 2015). Secondly, the nutrient limitations in the subsoil, such as the lower N contents (Table S1 in Study III), may alter the composition of the root exudates. Specifically, this could reduce the exudation of more labile compounds, such as amino acid, while increasing the release organic acids (Vives-Peris et al. 2020). Moreover, the chemical composition of the roots grown in subsoil, characterized by a higher lignin:N ratio, indicated lower litter quality compared to the roots grown in topsoil. This difference is known to affect decomposability of the root tissue, *e.g.,* through cross-linkages between lignin and labile N, for example, through cross-linkages between lignin and labile nitrogen, which reduce microbial access to N and hinder mineralization (Aber et al. 1990; Talbot et al. 2012; Walela et al. 2014). As such, reduced substance availability may have further contributed to the restriction on microbial growth, preventing the establishment of larger microbial communities in the subsoil. Overall, these difference between the topsoil and subsoil rhizosphere underline how the influence of roots on the rhizo-microbial development is largely regulated by the soil material in which the roots grow.

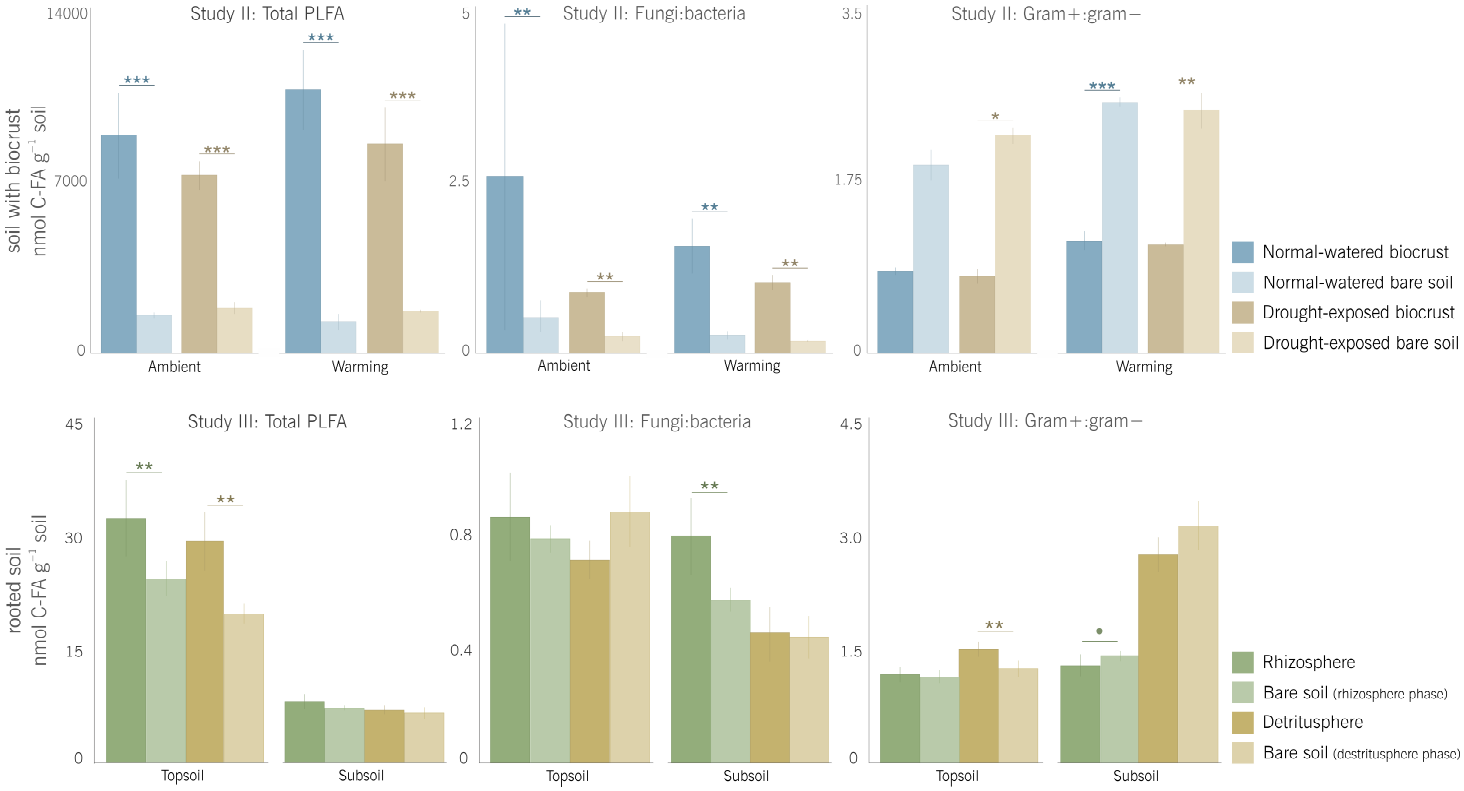


Figure 15 | The total abundance of phospholipid fatty acids (in nmol C-FA FA g^{-1}), fungi:bacteria ratio and gram+:gram− ratio in Study II (upper panel) and Study III (lower panel). For Study II, the biocrusted samples are shown in bold colors and the bare soils in faded colors. The two moisture levels are shown in blue and brown colors respectively, and 'ambient' represents temperatures according to field conditions, and 'warming' represents a +5 °C throughout the incubation. For Study III, rooted samples are shown in bold colors and the bare soils in faded colors. The living root phase ('rhizosphere phase') is shown in green and the dead root phase ('detritusphere phase) in brown. Bars represent means±SDs (n = 3 independent replicates in Study II and n = 6 independent replicates in Study III). Asterisks denote significant differences between biocrusts and bare soil controls ($^{\bullet}P$<.05, $^{*}P$<.05, $^{**}P$<.01, $^{***}P$<.001). Figure modified from Studies II and III.

3.2.2 Microbial community structure and succession induced by biota

The structural changes within the microbial community differed between the biocrust and root systems. The establishment of biocrusts led to a distinct shift towards increased dominance of fungi (reflected in higher fungi:bacteria ratios) and of gram− bacteria (higher gram+:gram− ratios; Figure 4 in Study II), indicative of an ongoing microbial succession driven by the establishment of the biocrust. In contrast, the rooted topsoil (the soil substrate from Study III which is most comparable to that used in Study II) did not display such changes in community composition (Figure 3 in Study III). Both fungal and bacterial abundance increased in a similar manner in the topsoil rhizosphere, leaving the overall community structure around the roots unchanged, and also showed no notable changes in the gram+:gram− ratios. The latter was unexpected, as we anticipated a similar increase in gram− bacteria in the rhizosphere as was observed in the biocrust systems; this shift is indicative of increased availability of labile and

easily-available C sources (Kramer and Gleixner, 2008; Fanin et al. 2014). The same was true for the subsoil rhizosphere, where again no significant changes in bacterial groups were observed (Figure 15). Instead, we observed a pronounced community shift towards a higher relative abundance of fungi (Figure 3 b in Study III and Figure 15). This differentiation in the subsoil rhizosphere can be attributed to the ability of fungi to adapt to assimilating more complex and heterogeneously distributed C sources (Poll et al. 2006). Our observations are also consistent with Baumert et al. 2021, who show how rooting drives the increased dominance of fungi in subsoil rhizospheres compared to in topsoil. These findings hereby emphasize fungi as key players in the assimilation of root-derived C sources in subsoils.

Contrary to in the topsoil rhizosphere, the shift towards gram+ bacteria in the developing detritusphere, as the system transitioned from a living to a decaying root system, followed the expected patter. Here, the relative increased dominance of gram+ bacteria pointed to an increased complexity of the resources available for microbial uptake as decomposition progressed over time. This shift is likely caused by the shift from low molecular weight compounds to increasingly complex litter-derived C sources in the detritusphere. The increased complexity and progressed decomposition of the remaining root litter in the detritusphere was further supported by increasing $(Ac/Al)_V$ ratios and increasing concentration of lignin as estimated by the molecular mixing model (Table 1 in Study III; Kögel-Knabner et al. 1988). The changes in the microbiome were further associated with an increased bacterial dominance around the decaying roots (reflected in lower fungi:bacteria ratios in Figure 3 in Study III), pointing to the increased importance of bacteria in the involvement in litter decomposition in the detritusphere, which is supported by the findings of Herman et al. 2012. At a larger scale, given the nutrient-depleted and moisture-limited conditions in dryland soils, it remains uncertain whether microbial responses to temporarily increased nutrient availability around decaying roots at all influence SOM processed. Since microorganisms are typically C-starved, any newly accessibly substrates are likely to be rapidly metabolized regardless of microbial community composition. This suggests that shifts in microbial diversity are more likely a response to changes in moisture or substrate availability rather than a direct driver of SOM processing (Schimel 2010).

When directly comparing the microbial community patterns between Studies II and III, it is important to take into account that both field sampling and later sampling for analyses differed between the studies. In Study II, soil material was sampled from 0-1 cm depth in the field and

the PLFA profiles of the biocrusts were later derived from the top few millimeters of the mesocosms' biocrust layer after incubation. In contrast, in Study III, soil material was collected from the entire A horizon (0-3 cm), and the PLFA profiles were recorded from a much larger soil volume, representing the entire rooted pot. This discrepancy in the sampling and soil material does constrain the direct comparison between the biocrust-specific and root-associated microbial communities. As the effects of roots on microbial abundance has been shown to concentrate within 1-2 mm around the roots, it is possible that certain root effects might have been overseen, or diluted, due to the larger sampling volumes (Marschner et al. 2012). In order to directly determine differences in the microbial community dynamics between the systems, more coherent and standardized sampling approaches could be adopted in future studies. Additionally, investigating the interactions between biocrusts and plants through microbial mediators, such as fungi and other root-associated microorganisms involved in nutrient exchange, could provide deeper insights. Such integrative approaches would help disentangle how biocrusts and plant-associated microbes influence each other, potentially revealing broader ecosystem-level processes (Dettweiler-Robinson et al. 2020).

3.2.3 Fungal hyphae as vectors in C and N translocation

The downward transfer of C facilitated by fungi into deeper soil layers has been demonstrated across various systems (*e.g.,* Frey et al. 2003; Witzgall et al. 2021). The apical growth properties of fungal mycelium enable the bidirectional mobilization of C sources throughout the fungal colony, thereby driving the redistribution into the soil (Poll et al. 2006; Brand et al. 2009). In Study II, we build on this concept, demonstrating the role of fungi in the buildup—and potential stabilization—of C in the sub-crust soil under biocrusts. These findings highlight fungi not only as essential biocrust components within the biocrust layer itself (States et al. 2001; Abed et al. 2013), but also as key regulators of biogeochemical processes in the sub-crust soil. Although the translocation observed in Study II was spatially limited to 1 cm within the short timeframe of the incubation, it still represents an important initial step in the downward movement of C away from the soil surface into deeper horizons. Over longer timescales, this initial redistribution of C, facilitated by the fungal networks, may thus serve as a precursor to more extensive and deeper C transfers over longer timescales.

3.3 Soil structure formation at the soil-root interphase

3.3.1 Soil aggregation in the rhizosphere and comparison to biocrusted soil

In Study III, we observed how living roots induced a clear shift in aggregation within the topsoil and subsoil rhizosphere, where both the mass contribution of water stable macroaggregates as well as the allocation of C and N within macroaggregates increased significantly (Figure S5, Figure 1 c and d in Study II). Roots as important vectors for the formation of coarser aggregates is widely recognized (*e.g.,* Tisdall and Oades 1982; Six et al. 2004). Thus, our findings only reinforce the notion of the importance of root-induced soil structure formation—either directly via the excretion of root-derived gluing agents, the physical entanglement of soil particles by the roots, or indirectly via promoted microbial activity in the rhizosphere that build up biofilm patches which, in turn, function as gluing agents (Oades 1982; Chenu and Jaunet 1999; Angst et al. 2018; Rabbi et al. 2020).

Aggregate fractionation was not performed in Study II, as it fell outside the main scope of the study. Therefore, we can only speculate on whether biocrust establishment influenced soil structure in a manner to similar or contrasting from the effects observed in the rhizosphere systems of Study III. Just like roots, biocrusts are known to enhance soil aggregation through the physical enmeshment of soil particles—instead of root hairs and in addition to fungal hyphae, this process is mediated by moss rhizoids, cyanobacterial strands and algal filaments, which can intertwine soil minerals into aggregates (States et al. 2001; Belnap 2006). Additionally, similar to the processes observed within the rhizosphere, the enhanced microbial activity within biocrusts and the exudation of EPS and other organic gluing agents has been shown to stimulate soil aggregation (Barger et al. 2006; Mager and Thomas 2011; Riveras-Muñoz et al. 2022). However, as these processes are concentrated within the uppermost millimeters or centimeters of the soil, while roots extend deeper into the soil profile, their effect on the development of soil structure, although similar, are spatially separated. And although biocrusts are widely recognized as important contributors to soil aggregation, their effect on aggregate size distribution is still largely unknown. In a recent contribution by Zenouzi et al. 2024, the authors show how biocrust-mediated processes, including enhanced calcium carbonates and OM contents, especially drive the adhesion of fine silt, contributing to the formation of sandy microaggregates. Overall, this underlines the interplay between physical and biogeochemical mechanisms, which are regulated by biocrusts, for the structure formation at the soil surface.

3.3.2 Fungal involvement in microaggregation in the subsoil rhizosphere

Processes involved in the root-induced aggregation within the rhizosphere apparently differed depending on the soil substrate in which the roots grew. While the increased macroaggregation around the roots was, as described earlier, observed in both the topsoil and subsoil rhizosphere, we also found an increase in the large microaggregation fraction in the subsoil rhizosphere (Figure 1 a and b in Study III). Here, C and N contents were elevated compared to the bare soil controls. This difference was associated with increased fungal abundance (PLFA structure), and it is possible that this shift contributed not only to the macroaggregation, but also the microaggregation around the roots. If so, this underscores fungi as important players in the assimilation of root-derived C compounds in the subsoil and the allocation of C and N into both macro- and microaggregates (Frey et al. 2003; Baumert et al. 2018). These findings hereby not only reinforce the well-established and widely reported concept of how soil mineral particles are enmeshed by fungal hyphae into stable macroaggregates (Tisdall et al. 1997; Baumert et al. 2018; Bucka et al. 2021), but also provide insights into fungal-induced microaggregation—a process for which evidence still remains scarce (Vidal et al. 2018). Taken together, the findings in Studies II and III emphasize fungi as key contributors to several biogeochemical processes, including the involvement in nutrient translocation (Study II) and aggregate formation (Study III) along the biocrust-root-soil nexus. As such, these observations point to the diverse functionality of fungi in the studied dryland system.

3.3.3 Root legacy effects on soil structure in the rhizosphere-detritusphere transition

The dynamics of the root-induced aggregation in the topsoil and subsoil rhizosphere shifted after plant death, when the rhizosphere transitioned into a detritusphere. Root-induced macroaggregation, which developed in the rhizosphere, showed contrasting stability between the topsoil and subsoil detritusphere. In the topsoil, newly formed macroaggregates around the roots persisted after plant death, contributing to the structural integrity of the detritusphere. In the C-poor subsoil, however, these aggregates disintegrated during root decay (Figure 1 in Study III), suggesting that aggregates formed within the subsoil rhizosphere are only loosely connected. Differences in the mechanical stability of macroaggregates have been found to be lower in initial soils compared to mature soils (Felde et al. 2020; Bucka et al. 2021), supporting the differences we observed between topsoil and subsoil. As such, the lower

aggregate stability in the subsoil detritusphere emphasizes continuous C inputs as a prerequisite to maintain aggregate persistence in C restricted soil systems, and further indicate that a certain backbone of native C may be required for more long-term stabilization of aggregates formed around roots in dryland systems.

The persistence of the aggregates after plant death further provides importance evidence of root legacy effects in the topsoil. Root legacy was also observed beyond structural changes; microbial abundance, initially stimulated by the living roots in the rhizosphere, persisted into the detritusphere, apparently sustained by the litter-derived C from the decaying roots. Both the structural and microbial legacies observed in Study III point to the importance of including the succession from a living to a decaying root system in experimental design of studies, instead of studying the rhizosphere and detritusphere as two separate systems. Only then, the conditions manifested around the roots which persist beyond the lifetime of the plant, thereby regulating processes in the detritusphere, can be fully accounted for (Wurst and Ohgushi 2015).

3.4 Climate change impacts on dryland functionality

3.4.1 Climate change impacts on biocrust functionality and C-N decoupling

In Study II, drought and warming were introduced as additional treatments to explore the effects of climate change on biocrust-soil interactions. The results revealed that biocrust functionality was significantly affected by the changing climatic conditions. Specifically, when photosynthetic fluxes were normalized to biocrust cover, used as a proxy to express biocrust functionality, the data showed that C fixation was no longer solely constrained by drought (as shown in the total flux data; Figure 12 and Figure 1 in Study II), but was also substantially reduced by experimental warming, with net C uptake decreasing by almost 50% (Figure 16 a). This suggests that while the overall net C flux balance in the system remained unaffected by warming, the elevated temperature impaired the capacity—or efficiency—of the photoautotrophs to fix CO_2. The reduced C fixation potential of biocrusts may be attributed to several factors, such as shorter hydration periods due to accelerated desiccation in the warming chamber (Lange 2001), or compositional changes within the biocrusts that affect primary production (Escolar et al. 2012; Maestre et al. 2015; Finger-Higgens et al. 2022). But regardless of the direct driver of these functional changes—especially if related to biocrust composition, which was beyond the scope of this study—our data provide concerning evidence that

biocrusts may no longer effectively sustain net C uptake as climate change intensifies (Maestre et al. 2013; Darrouzet-Nardi et al. 2015; Tucker et al. 2020).

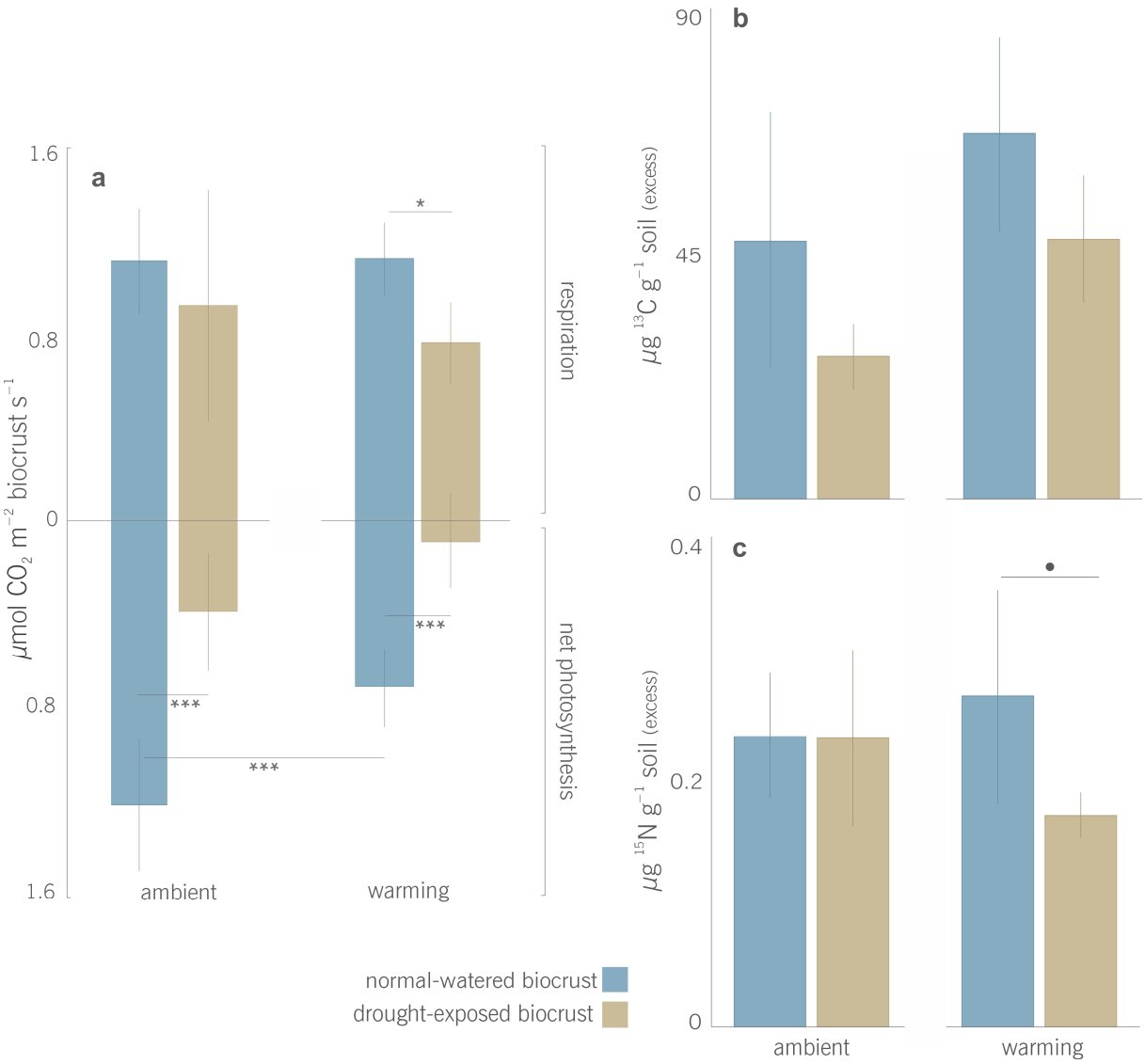


Figure 16 | a Respiration and net photosynthesis as a function of biocrust cover (µmol CO_2 m^{-2} biocrust s^{-1}; *n*=8). Biocrust-derived **b** ^{13}C and **c** ^{15}N (µg g^{-1}, excess; *n*=3) within the biocrust layer, where the isotopic signatures of the bare soil controls were used to calculate the excess isotopic content. In **a**, controls are excluded as biocrust cover could be ruled out. Asterisks denote significant differences between biocrusts and bare soil controls (•*P*<.05, **P*<.05, ***P*<.01, ****P*<.001). Figure modified from Study II.

A further effect of climate change on the system functionality was observed in the contents of biocrust-derived ^{15}N. While the distribution of ^{13}C mirrored the patterns of the bulk C data, showing clear effects of drought alone (Figure 16 b), excess ^{15}N remained stable under drought at ambient temperatures but decreased significantly under combined drought and warming (Figure 16 c). This suggests an interactive effect of drought and warming that specifically

constrains biological N fixation. Moisture is widely recognized as a primary environmental factor controlling N fixation in biocrusts (Barger et al. 2016; Rousk et al. 2018), and warming may further reduce the cover of N-fixing biocrusts, thereby limiting the N uptake potential (Finger-Higgens et al. 2022). In Study II, the biocrust cover was only estimated via hyperspectral imaging, but our data does not show signs of a stronger cover decline induced by drought only in the warmer chamber. Instead, our data suggests that declined N fixation under climate change is not necessarily caused by shrinking biocrust cover, but could stem from reduced nitrogenase and overall functionality within the inherent biocrust. As shown by Johnson et al. 2005, warming can also accelerate the oxidation of recently fixed $^{15}N_2$, which may further contribute to the observed decline. It is important to note that we cannot rule out that the observed climate effect may have been intensified by shifts in the species composition of the biocrusts, potentially reducing the abundance of N fixators (Maestre et al. 2013; Ladrón de Guevara et al. 2018; Finger-Higgens et al. 2022). Certainly, more detailed taxonomic analyses would have been valuable to disentangle this, though this was beyond the primary scope of Study II. Overall, and regardless of species composition, we can conclude that these findings indicate a risk of decreased N availability under increasing aridity and warming, which may disrupt the system balance by limiting primary productivity and thereby impacting both C and N dynamics (Johnson et al. 2007; Finzi et al. 2011).

Moreover, the fact that ^{13}C did not show the same pattern under drought and warming as ^{15}N suggests that biocrust and microbial components, or related biogeochemical processes, exhibited differing sensitivities to the applied climatic stressors. This could have led to the accumulation or depletion of specific pools and thereby contributing to the different pattens observed. The observed differences are indicative of biogeochemical decoupling between biologically controlled C and N, a phenomenon which has previously been observed in other systems (*e.g.,* Delgado-Baquerizo et al. 2013; Evans and Burke 2013; Ehtesham and Bengtson 2017). Although the C-N decoupling was clearly driven by the interactive effect of drought and warming, we were unable to distinguish these changes in the bulk C and N contents (Figure 2 in Study II). This could either reflect a general resolution issue, where subtle changes could only be distinguished through isotopic labeling, or suggest that C-N decoupling is a specific response to the conditions emerging later in the incubation period when the $^{15}N_2$ pulse was applied. If the latter is true, it would imply that either the decoupling only represents a transient response in the observed biogeochemical processes, rather than a long-term shift, or the

duration during which the biocrusts were exposed to the climatic stressors was too short to see larger-scale changes in the C and N contents. Regardless, extending the incubation duration and applying multiple $^{15}N_2$ pulses would be an interesting adaptation for future studies.

3.4.2 C and N translocation and associated MAOM formation under warming and drought

As noted in section 3.1.4, our data show how processes contributing to $MAOM_{<63\mu m}$ formation in the subsurface soil are sensitive to increases in both temperature and aridity. Specifically, the buildup of MAOM in the mineral soil was observed only under ambient conditions, with no accumulation detected in systems exposed to warming or drought (Figure 4 in Study II). Several factors may have contributed to this distinction. As previously discussed, the total accumulation of bulk C and N in the mineral soil was associated with greater fungal dominance and occurred only under ambient conditions (Figure 5 in Study II). This suggest that changing climatic conditions disrupted processes that facilitate the elemental translocation, such as the expansion of fungal hyphae. Under warming and drought, the negative effects on the presumed fungal-mediated elemental pathways into the subcrust soil may be linked to the changes observed in the MAOM fraction. This interpretation is supported by the positive correlation between the C and N contents in $MAOM_{<63\mu m}$ and the fungi:bacteria ratio in the 0-1 cm soil layer (Table S6 in Study II). Consequently, reduced substrate availability in the mineral soil under warming and drought likely limited microbial assimilation, and, in turn, the synthesis of microbial extracellular and necromass compounds—key precursors for MAOM formation (Liang et al. 2017).

In addition to pathways directly mediated by fungi or microbial transformation, other mechanisms may have contributed to the observed changes in the MAOM fraction. For example, downward movement of DOM through leaching into the mineral soil can lead to the direct sorption of low molecular weight compounds onto uncolonized mineral surfaces, thereby fostering the formation of organo-mineral associations independently of microbial involvement in the subcrust soil (Guggenberger and Kaiser 2003; Kalbitz et al. 2005). Generally, leaching of dissolved organic compounds has been shown to constitute a key pathway for the vertical movement of C, N, and other nutrients in comparable biocrust systems (Young et al. 2022). However, the extent of the translocation is largely controlled by the availability of percolating water (Kaiser and Kalbitz 2012), which could help explain the differences in MAOM between the temperature treatments. Specifically, higher evaporation rates in warming-

exposed systems likely reduced the amount of downward-moving water, diminishing DOM leaching and, consequently, the potential for DOM-based pathways to contribute to MAOM formation in warming scenarios.

Another important factor likely influencing not only the magnitude but also the composition of the leachate is the composition of the biocrust (Young et al. 2022). In this study, biocrust cover was estimated through hyperspectral imaging, allowing us to broadly classify biocrust types into bryophytes and unspecified biocrusts (Table S3 in Study II). The warmer climatic conditions appeared to favor, or accelerate, the development of district biocrust communities, indicated by an overall higher biocrust cover and bryophyte cover (Table S3 in Study II). As such, having a more precise measure of the general species composition would have allowed for a clearer separation of direct climatic effects on DOM leaching and MAOM formation processes from indirect effects driven by shifts in biocrust composition—a differentiation that would have been interesting to develop also in regard to several of the other studied parameters. Additionally, quantifying DOC contents in the soil solution, or at least measuring water-extractable C in the samples before and after incubation, might have helped gain a more comprehensive understanding of the underlying processes behind the observed MAOM formation (Kleber et al. 2015; Cotrufo and Lavallee 2022).

4 | CONCLUSION & OUTLOOK

Drylands, which cover nearly half of Earth's terrestrial surface, remain underrepresented in scientific research relative to other, more productive ecosystems. This underrepresentation is counterintuitive given the fundamental importance of drylands to global biogeochemical cycles and how nearly half of the terrestrial land surface and contain some of the most biodiverse, yet fragile, ecosystems. Consequently, key knowledge gaps persist regarding their functioning, including dryland C fluxes (Bond-Lamberty and Thomson 2010), linkages between biodiversity or vegetation composition and ecosystem processes (Maestre et al. 2012; Biancari et al. 2024), growth and reproduction traits of dryland plant species (Thomas et al. 2020) and the impacts of global change (Schimel 2010). Ultimately, even fundamental soil-biota interactions that underpin ecosystem development are understudied.

The overarching goal of this thesis was to explore soil-biota interactions in the context of dryland soil development, particularly focusing on the role of early-colonizing organisms at the onset of ecological succession. We demonstrate that during early soil colonization, as biocrusts establish at the soil surface, C and N fluxes are significantly impacted, with both net photosynthesis and respiration stimulated by biocrust (Figure 17 a and b). This establishment also contributes to a substantial build-up of biocrust-derived C, N, and MAOM in the underlying mineral soil (Figure 17 c and d). Along with the increased microbial abundance observed both within and beneath the biocrust layer, these represent critical steps in the redistribution of C into the mineral soil and the initial development of the soil profile.

As ecological succession progresses—and the system transitions from a biocrust-dominated community to one increasingly shaped by higher plants—the scale of soil-biota interactions extends deeper into the soil. The root system broadens this interaction zone, establishing new pathways for C inputs and stimulated microbial activity throughout the soil profile. Our work confirms the role of roots as vectors for soil structure development (Figure 17 h), but also shows how the fate of the newly formed aggregates around roots differs depending on the soil environment. In the studied topsoil, a clear root legacy effect was imprinted as newly formed aggregates persisted after plant death (Figure 17 I and j). A microbial legacy in the topsoil was also determined, as the stimulated abundance of root-associated microorganisms persisted after plant death. This underlines how the effects of roots on shaping the soil environment extend beyond the life time of the plant, influencing physical, chemical, and biological

conditions that may affect, and facilitate, future plant establishment. Fungi were identified as key components across all studied systems, facilitating downward C and N translocation from the biocrust into the soil as well as in driving aggregate formation around the roots (Figure 17 e-g). Ultimately, these represent critical processes for the stabilization of SOM within the mineral soil.

However, we also observe how some of the most crucial biogeochemical processes are vulnerable to changing environmental conditions. Our work demonstrates that biocrust-soil systems are highly susceptible to changes in temperature and moisture, highlighting the fragility of biocrust-mediated soil development under climate change. This is evident in how the systems lost their net C uptake and in the complete disruption of C and N pathways into more persistent SOM pools (MAOM) in systems exposed to climate change. This shows that while already the early establishment of macro- and microbial communities can fundamentally modulate CO_2 fluxes and the overall development of the uppermost soil, these interactions are highly sensitive to climatic stressors—even to the point where the C balance is at stake, which may have detrimental repercussions for overall C and N cycles in dryland ecosystems.

Despite being conducted under laboratory conditions, which inherently limits the ability to directly translate experimental results to natural environments, these findings provide valuable insights into the complex interactions among plants, macro- and microorganisms, and soil particles in dryland soil environments. They highlight the importance of biota in driving ecosystem development and emphasize the need for integrative studies that account for temporal dynamics, such as the rhizosphere-to-detritusphere transition. Incorporating such transitions into experimental designs, along with approaches that consider the interplay between biocrusts and higher plant communities, is essential for capturing the multifaceted nature of soil-biota interactions. A more holistic approach that mirrors natural conditions and addresses these interactive processes will be key to advancing our understanding of the mechanisms driving soil and ecosystem development in drylands.

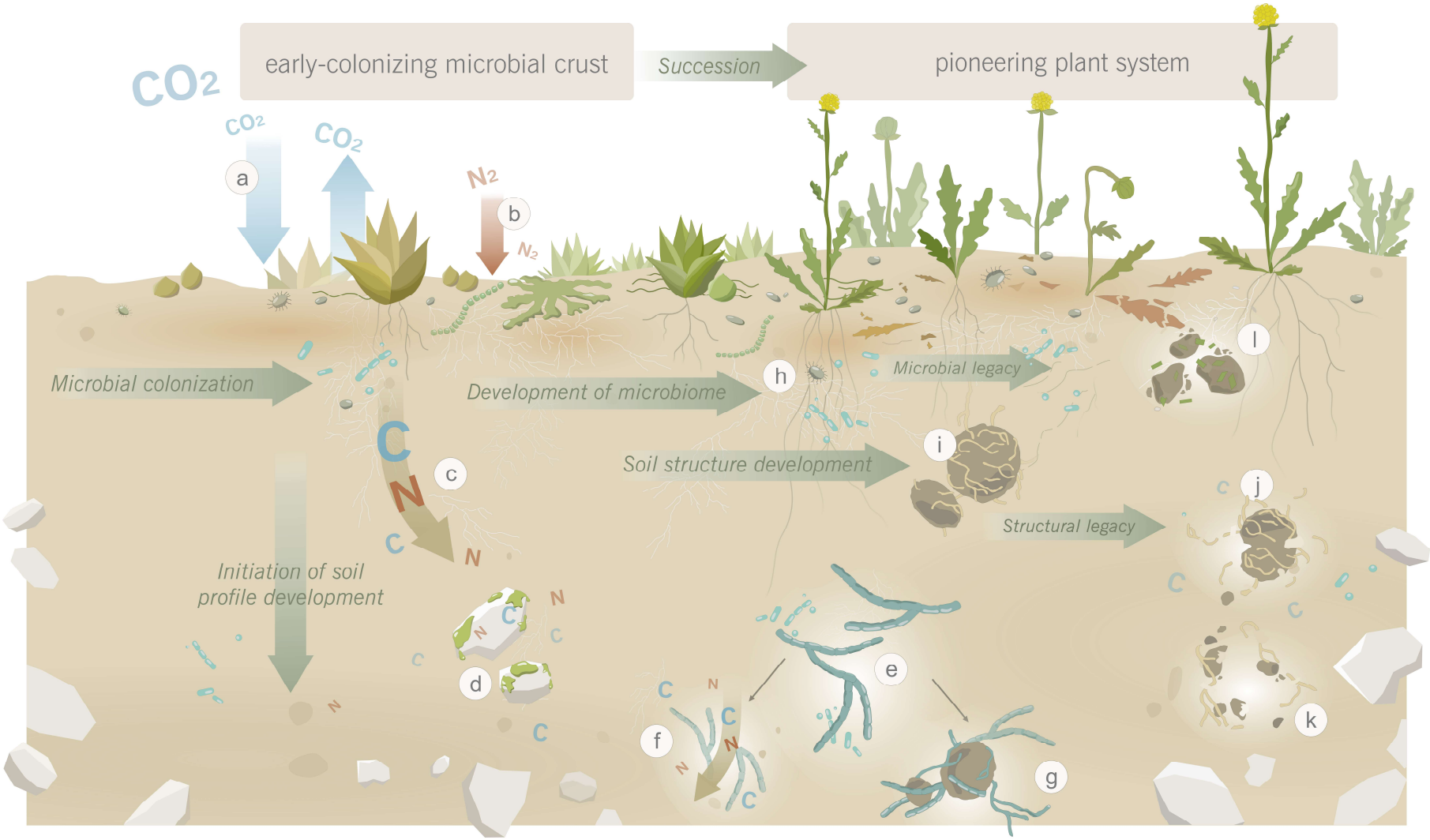


Figure 17 | A conceptual overview over the impact of biota (early-colonizing biocrusts and pioneer plants) on the development of a dryland soil system. During the early establishment of biota, as biocrusts colonize the soil surface, **a** C fluxes are significantly altered, with both net photosynthesis and respiration being directly regulated by the growth of the biocrust and associated microorganisms. However, limited moisture availability significantly constrains net C uptake, and when coupled with increasing temperatures, also limits **b** N fixation. These combined factors hinder the **c** build-up of C and N in the sub-crust soil, ultimately influencing the further development of the soil profile. Only in biocrust-soil systems unaffected by climate change, the accumulation of biocrust-derived C and N drives the formation of mineral-associated OM (MAOM) in the underlying mineral soil, a process likely promoted by fungal hyphae. The critical role of **e** fungi in the system also extends to the rhizosphere. While fungal hyphae promote the **f** downward C and N translocation in the sub-crust soil in the biocrust system, their increased dominance in the rhizosphere of C-restricted subsoils supports the **g** formation of microaggregates in the vicinity of roots. The introduction of biocrusts and plants to the system also drives microbial community development. While the effect of biocrusts and pioneer plants on microbial community structures differ, both contribute to the **h** increase in total microbial abundance and the build-up of microbial biomass. Furthermore, the introduction of roots fosters to the development of soil structure, leading to **i** increased macroaggregation in the rhizosphere. Macroaggregates formed around roots persist in the **j** topsoil detritusphere even after plant death, leaving a lasting legacy of root activity. In the developing subsoil detritusphere, however, **k** newly formed aggregates are not maintained. As roots decay, they further influence the allocation of **l** C and N into particulate organic matter (POM) pools, however slightly differently deending on the soil substrate; in the topsoil detritusphere, root litter facilitates the occlusion of POM into aggregates (oPOM), whereas in the microbially restricted subsoil environment, fresh C inputs instead remain highly bioavailable as free POM (fPOM).

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To my family, to my friends. And of course—**to music**.

Tack så mycket!
Kristina

APPENDIX

A | Studies

Study I

Study I is published as follows:

Witzgall, K., Hesse, B. D., Seguel, O., Oses, R., Grams, T. E. E. & Mueller, C. W. (2023). Tracing low-CO_2 fluxes in soil incubation and ^{13}C labeling experiments: A simplified gas sampling system for respiration and photosynthesis measurements. *Journal of Geophysical Research: Biogeosciences*, 128(9).

https://doi.org/10.1029/2023JG007410

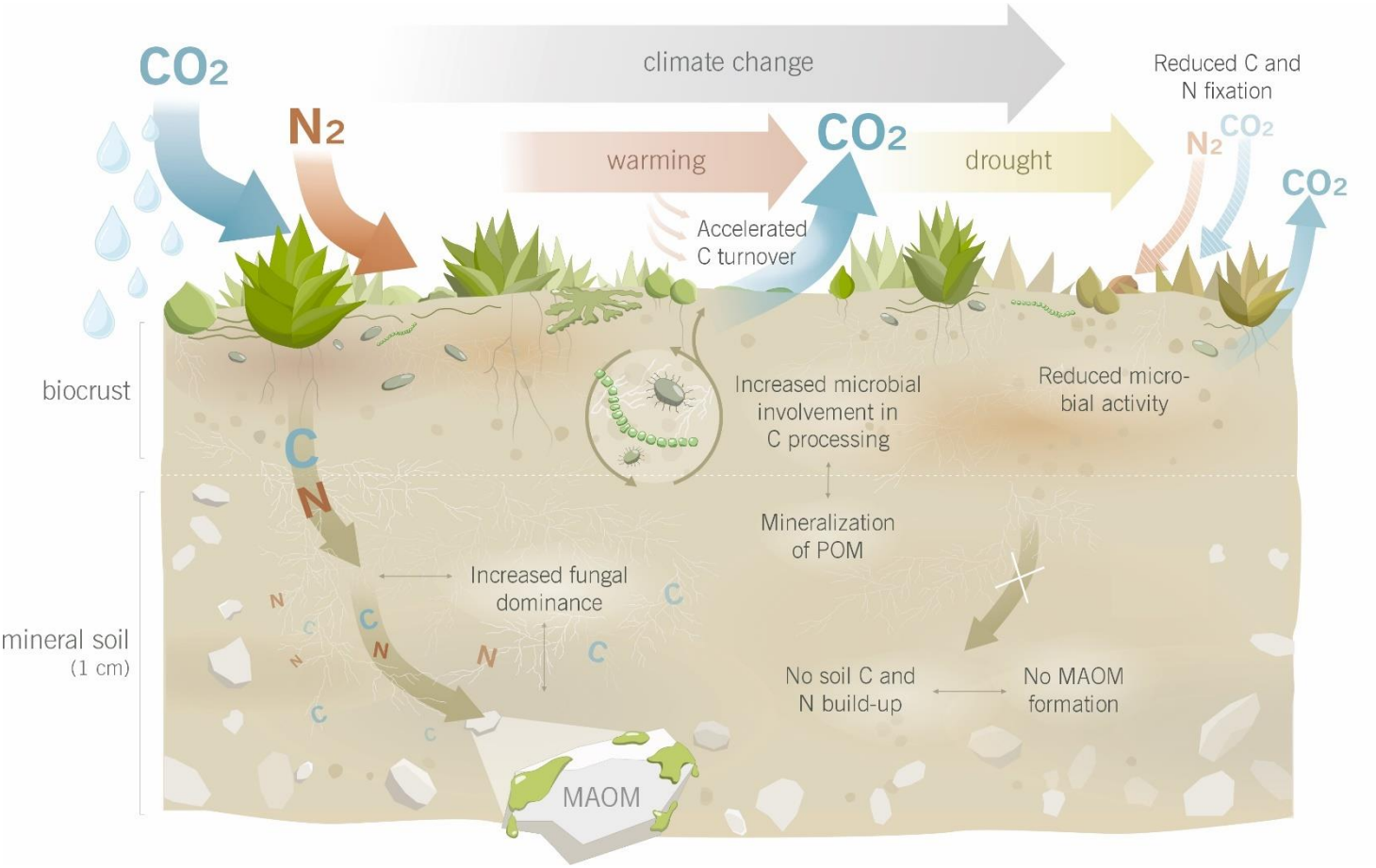
Study II

Study II is published as follows:

Witzgall, K., Hesse, B. D., Pacay, N., Jansa, J., Seguel, O., Oses, R., Buegger, F., Guigue, J., Rojas, C., Grams, T. E. E., Rousk, K., Pietrasiak, N. & Mueller, C. W. 2024. Soil carbon and nitrogen cycling at the atmosphere-soil interface: quantifying the responses of biocrust-soil interactions to global change. *Global Change Biology*, 30(10), e17519.

https://doi.org/10.1111/gcb.17519

Graphical abstract:



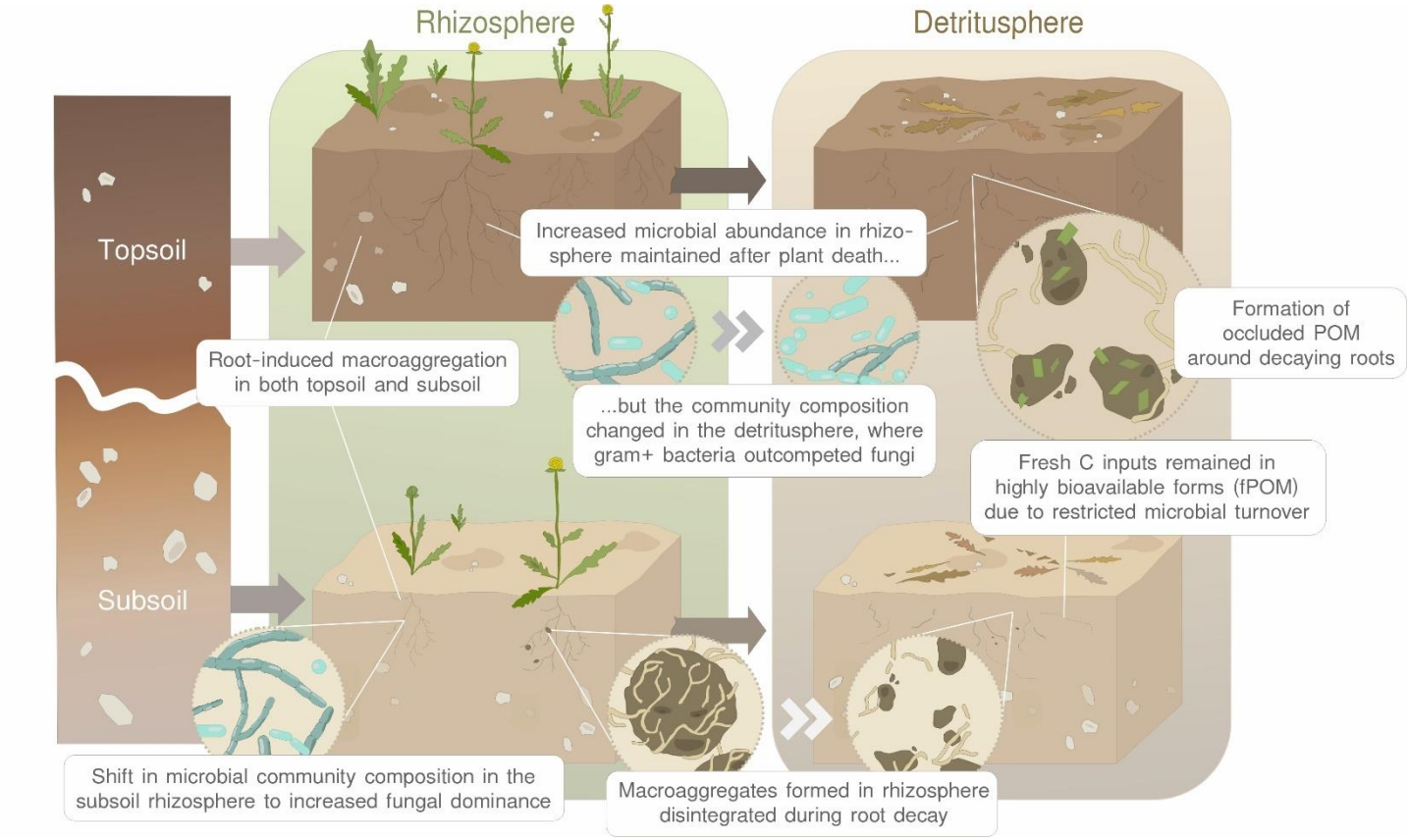
Study III

Study III is published as follows:

Witzgall, K., Steiner, F., Hesse, B. D., Riveras-Muñoz, N., Rodríguez, V., Teixeira, P. P., Mengmeng, L., Oses, R., Seguel, O., Seitz, S., Wagner, D., Scholten, T., Buegger, F., Angst, G. & Mueller, C. W. 2024. Living and decaying roots as regulators of soil aggregation and organic matter formation—from the rhizosphere to the detritusphere. *Soil Biology and Biochemistry*, 109503.

https://doi.org/10.1016/j.soilbio.2024.109503

Graphical abstract:



B | Affidavit

I, Kristina Witzgall, declare in lieu of oath that the work presented to the degree-awarding institution School of Life Sciences (Weihenstephan) of TUM and entitled "Biotic drivers of soil development: the contribution of biocrusts and roots to soil structure and organic matter formation in drylands" was completed under the guidance and supervision of Prof. Dr. Dr. h.c. Ingrid Kögel-Knabner and Prof. Dr. Carsten W Mueller without any other assistance and using only those aids specified in § 7(6) and (7) of the doctoral regulations.

☒ I have not engaged any organization that seeks supervisors for the preparation of dissertations in return for payment, or that takes care of all or part of the duties incumbent upon me with regard to examination requirements.

☒ I have not submitted the dissertation in this or a similar form as an examination requirement in any other examination process.

☒ I have not yet earned nor have I irreversibly failed in a previous doctoral examination process for the doctoral degree I am seeking.

☒ I am not aware of any criminal investigation of science-related offenses against me or of any lawful criminal conviction related to my scientific work.

☒ I am aware of the publicly accessible doctoral regulations, as well as the guidelines for ensuring good scientific practice and for dealing with scientific misconduct of TUM. In particular, I have taken note of the meaning of § 27 PromO (Invalidation of the Doctoral Degree) and § 28 PromO (Revocation of the Doctoral Degree). I am aware of the consequences of filing a false affidavit.

☒ I permit my personal data to be stored in the TUM alumni database.

Place, Date, Signature

C | Scientific contributions

Peer-reviewed publications

Witzgall, K., Vidal, A., Schubert, D. I., Höschen, C., Schweizer, S. A., Buegger, F., Pouteau, V., Chenu, C. & Mueller, C. W. 2021. Particulate organic matter as a functional soil component for persistent soil organic carbon. *Nature Communications*, 12, 4115.

Sauter, L., Schwerdhelm, C., Samuels, T., **Witzgall, K.**, Hampl, F. J., Mueller, C. W. & Bryce, C. 2021. Changes in the bioavailability of iron (III) for microbial reduction along a precipitation gradient. *Goldschmidt2021*.

Riveras-Muñoz, N., Seitz, S., **Witzgall, K**., Rodríguez, V., Kühn, P., Mueller, C. W. & Scholten, T. 2022. Biocrust-linked changes in soil aggregate stability along a climatic gradient in the Chilean Coastal Range. *Soil Discussions*, 1–28.

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Rodríguez, V., Bartholomäus, A., **Witzgall, K.**, Riveras-Muñoz, N., Oses, R., Liebner, S. & Wagner, D. 2024. Microbial impact on initial soil formation in arid and semiarid environments under simulated climate change. *Frontiers in Microbiology*, 15, 1319997.

Witzgall, K., Steiner, F., Hesse, B. D., Riveras-Muñoz, N., Rodríguez, V., Teixeira, P. P., Menmeng, L., Oses, R., Seguel, O., Seitz, S., Wagner, D., Scholten, T., Buegger, F., Angst, G. & Mueller, C. W. 2024. Living and decaying roots as regulators of soil aggregation and organic matter formation—from the rhizosphere to the detritusphere. *Soil Biology and Biochemistry*, 109503.

Witzgall, K., Hesse, B. D., Pacay, N., Jansa, J., Seguel, O., Oses, R., Buegger, F., Guigue, J., Rojas, C., Grams, T. E. E., Rousk, K., Pietrasiak, N. & Mueller, C. W. 2024. Soil carbon and nitrogen cycling at the atmosphere-soil interface: quantifying the responses of biocrust-soil interactions to global change. *Global Change Biology*, 30(10), e17519.

First-authored conference contributions

Witzgall, K., Hesse, B. D., EE Grams, T., Pietrasiak, N., Seguel, O., Oses, R., Jansa, J., Guigue, J., Rojas, C., Rousk, K. & Mueller, C. W. 2023. Soil carbon and nitrogen cycling at the atmosphere-soil interface: quantifying the response of biocrust-soil interactions to climate change. *EGU General Assembly Conference*, Vienna, Austria. Oral presentation.

Witzgall, K. Hesse, B. D., Grams, T. E. E., Seguel, O., Oses, R., Pietrasiak, N., Rousk, K. & Mueller, C. W. 2022. How biocrusts determine soil carbon and nitrogen cycling in a changing climate. *World Congress of Soil Science*, Glasgow, Scotland. Poster presentation.

Witzgall, K., Vidal, A., Schweizer, S., Pouteau, V., Chenu, C. & Mueller, C. W. Mutual interactions between decaying plant litter, soil microorganisms and mineral particles, controlled by soil texture. 2019. *7th International Symposium on Soil Organic Matter*, Adelaide, Australia. Oral presentation.