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Determinants of Microbial Respiration and Biomass across Global Drylands

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Summary

Soil microbes break down organic matter, and respire its carbon (C) constituents or utilize them in the formation of microbial biomass (C_{mic}). The main source of C-loss from soils is heterotrophic microbial respiration. Especially, in sensitive ecosystems such as global drylands, the parameters C_{mic} and microbial respiration are valuable, as microbes are sensitive to environmental changes and drylands are expected to be strongly affected by climate change. Agents affecting microbial activities, have, therefore, impact on decomposition processes, nutrient provision and C cycling in the soil. Drylands are heterogenic ecosystems characterized by aridity, which can be found at any latitudinal distribution. Covering 40 % of the earth's terrestrial surface and housing over 38 % of the worlds population, drylands are mostly managed as rangelands. The strength and size of global drylands is expected to increase with global change, thus more people need to be nourished and soil management will obtain even bigger importance. I hypothesized that high levels of aridity and locations close to the equator negatively affect microbial activity and grazing was assumed to have positive and negative impact on soil microbes; whereby possible outcomes can be compensated. Yet, it was assumed that chosen single factors interactively determine the soil microenvironment in each region. Microbial basal respiration was measured by water amendment (H_2O-BAS) via an automated electrolytic micro respiratory system. From this, C_{mic} and the respiratory quotient (qO_2) were calculated and the soil water content was determined. The data from this study was correlated to regional soil and climate data, from data bases. The results revealed a heterogenic distribution of C_{mic} and H_2O-BAS across global drylands. The distance from the equator had significant impact on C_{mic} and qO_2, while H_2O-BAS and soil water content were most significantly affected by effects between aridity and the distance from the equator. Grazing and all interactions were neglectable. The heterogeneity is assumed to evolve from the interplay of physical soil properties, climate conditions, biological processes and anthropogenic management. Soil texture and precipitation regime of a region are suggested to play a role in balancing or reinforcing the stress imposed on soil microbes. This hints, that with increasing aridity, due to changing climate, microbial activity and decomposition processes will be more frequently limited by moisture. The cycling of nutrients will be reduced, whereby plants, especially in cultivated areas, are affected too. Additionally, induction of basal respiration by water addition from dormant

microbes resulted in high respiration rates and, thereby, increased C loss from soils to the atmosphere. Yet, impacts of global warming will be controlled by an interplay of the specific soil and climate conditions of each region.

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1 Introduction

Global soils contain an enormous stock of terrestrial organic carbon (C) that is 3.1 times bigger than the atmospheric reservoir (Lal 2010). Its ability to act as a source (i.e. setting free carbon dioxide (CO_2)) or sink (i.e. depleting CO_2 from atmosphere) for environmental CO_2 is highly dependent on the structure and functioning of an ecosystem, taking factors like land use, temperature, water availability and vegetation cover into account (Slonczewski and Foster 2009). Carbon is fixed by photosynthesis of primary producers, such as plants, and via formation of inorganic calcium carbonates. Microorganisms break down organic matter and depending on their metabolism, then respire its carbon constituents in forms of CO_2 or utilize them in the formation of biomass. In consequence, they act as decomposers on the basis of the terrestrial carbon cycle (Bradford et al. 2019). Heterotrophic microbial respiration, as a result of metabolic stress, is one of the main sources for carbon loss from soils (Dacal et al. 2019; Schlesinger and Bernhardt 2013) and is predicted to increase with climate change (Frey et al. 2013). Such feedbacks are in turn expected to reinforce warming processes. The soil's role in acting as a source or a sink for green house gasses can therefore only be assessed by comparison of C-loss through heterotrophic respiration and C-fixation through biomass and litter production (Blume et al. 2016).

Lack of knowledge about how to treat soils appropriately might destroy ecosystems permanently (e.g. by shifting important environmental traits such as texture, water holding capacity and soil organism's habitats in general) with dramatic impacts on life and environmental processes on earth. Soil is the foundation of all global ecosystem and should accordingly be examined with particular interest. Furthermore, Rey and Pegoraro (2001) suggested that the carbon balance of dry ecosystems may be altered by deviations in temporal dynamics of soil respiration (and plant productivity). Factors like land degradation and altered precipitation regimes (i.e. drought events becoming more frequent and severe) (Solomon 2007), will have crucially adverse consequences for ecosystem functioning and sustainability (Rey et al. 2011), since most soil organisms are reliant on a water-saturated environment (Blankinship et al. 2011; Orchard and Cook 1983; Baldrian et al. 2010). This is because microorganisms take up nutrients by the process of diffusion, where nutrients need to be dissolved in an aqueous solution (J. Skopp, M. D. Jawson, J. W. Doran 1990).

Microbial biomass C (C_{mic}), which was initially defined by David Jenkinson as “the eye of the needle through which all organic matter entering the soil must pass”, (Powlson et al. 2016) is an important parameter in assessing soil fertility (Beck et al. 1997). It can be calculated from respiration responses after substrate induction (SIR) and acts as an indicator of microbial population size. To reliably predict outcomes of global change and calculate feedbacks of warming and expected land degradation, it is essential to collect comprehensive spatial data, especially in sensitive ecosystems such as global drylands. The UN Convention to Combat Desertification (CCD) defines land degradation in drylands (sometimes also referred to as ‘desertification’) as a series of processes involving soil erosion, sedimentation, alterations in natural fire cycles, the disruption of biogeochemical cycling, and a decline of native perennial plants, associated microbial and animal populations (United Nations Convention to Combat Desertification 1994). All these factors are expected to increase in intensity throughout global change.

Particularly in arid regions these effects and potential feedbacks of increased temperature and variations in precipitation patterns on soils are largely understudied and poorly understood (Dacal et al. 2019; Maestre et al. 2012b). The UN Environment Management Group assessed in 2011, that global drylands are likely to decline by 49-90 % in grassland productivity due to climate change (United Nations Environment Management Group 2011). Generally, drylands are highly diverse and vastly sensitive regions (Collins et al. 2008), characterized by the evapotranspirative demands the intense solar radiation and extreme temperatures impose. These features cannot be compensated by the relatively low overall precipitation in forms of rainfall or snow.

Covering 5.1 billion hectares, which is approximately 40 % of earth’s terrestrial surface, drylands can be found on all continents, harbouring over 38 % of the world’s total population. Correspondingly, the land is exposed to additional pressure (United Nations Environment Management Group 2011; Reynolds et al. 2007). For this reason, drylands are strongly connected to human well-being. In the context of global environmental change, the functional role of such areas is likely to be threatened and thus requires particular attention. One approach to define such regions was introduced by The United Nations Environmental Programme (UNEP): The *aridity index* (AI, ratio of mean annual precipitation and mean annual evapotranspiration) ranges from hyper-arid (AI < 0.05) to dry-subhumid (0.5 < AI < 0.65) and can be gradually subdivided into four distinct levels (Arnold 1992) (see methods). Soil litter decomposition is generally believed to be dependent on soil moisture, where decomposition rates increase with enhanced moisture and decline at moisture rates less than 30-50 % of soil dry mass(Haynes 1986). Since dryland soils as classified by the AI usually contain less than 30 % moisture, aridity is expected to operate as a limiting factor (Blume et al. 2016).

Furthermore, drylands can be found at any latitudinal distribution and therefore, encompass a wide range of different climatic conditions according to its distance from the equator. Prior studies have examined how microbial respiration rates, which are expressed at a common biomass, are higher in dryland soils from colder regions than from warmer regions when assayed at a common temperature. One reason is, that microbes coming from regions with colder annual temperature revealed more flexible enzymes than those coming from regions with warmer annual temperature. They accordingly express higher catabolic rates at higher laboratory assay temperatures (Dacal et al. 2019). Other studies suggested that microbes in equatorial latitudes experience a more stable environment (e.g. homogeneous climate conditions) and the decrease in stress factors enhances microbial productivity (Brown 2014).

These arid regions are mostly used as rangelands (>65%, United Nations Environment Management Group (2011)). Consequently, importance of collecting data about how herbivory and pasture influence soil microbial activity and abundance (and respectively ecosystem functioning) arises with regard to a vastly growing world population needing to be nourished. Asner et al. (2004) defined grazing as a key driver of the structure and functioning of rangelands with its manifold effects depending on identity, density and regime of grazers (Milchunas and Lauenroth 1993; Eldridge et al. 2016).

Some studies suggest that high levels of herbivory negatively impact soil microbial respiration and therefore, microbial biomass through direct and indirect factors. Direct factors might be the physical disturbance of the soil environment, such as soil compaction, erosion and poaching of the soil surface (Avni et al. 2006); (Lal 2009). Indirect factors are largely plant-dependent: By selectively feeding on plants high in nutrients, herbivores promote the succession of low-quality plants which produce low litter quality and, therefore, reduce substrate availability for soil organisms. This is mostly the case in unproductive grasslands (Ritchie et al. 1998). Other effects evolve from the accumulation of secondary metabolites in the leaves of the plants as a defense mechanism when experiencing foliar herbivory. Deposition of secondary metabolites reduces plant litter quality, thus reducing microbial activity as well (Bardgett and Wardle 2003).

On the contrary, positive effects of grazing have been monitored. Highly important, plant defoliation promotes plant carbon exudates via the roots in productive grasslands, adding substrate to the soil and alleviating carbon limitation. This improves microbial respiratory rates and likewise biomass formation (Bardgett et al. 1999). Further positive effects on microbial biomass and respiration result from ammonium influx from dung and urine coming from mammalian herbivores. Gains in ammonium concentration reverse nitrate limitation in the soils and, therefore, enhance microbial activity (Floate 1970).

Yet, ecosystems function as a whole and possible interactions between factors influencing soil microbial attributes in global drylands must be kept in mind. In turn, the three assayed determinants are expected to evolve from combined interactions of soil and climate agents. For example, the impacts of the aridity of a specific region on the soil microenvironment are closely related to soil structural characteristics, including soil texture (Bloor and Bardgett 2012). These effects are related to the water-holding capacity and nutrient availability of the soil resulting from variable soil particle sizes. As an example, sandy soils tend to dry out more quickly than clay soils (Blume et al. 2016), and therefore among others, textural characteristics of the investigated soils play an important role in the establishment of the soil microenvironment. Aside from that, other interactions are assumed. Similary, the impacts of grazing are modulated by additional climate stress and the stability of the soil's composition (McSherry and Ritchie 2013; Burke et al. 1989). Soils experiencing degradation and, thereby alterations in structure, tend to react more extreme to additional stress factors than soils employing a balanced structure. Furthermore, the distance from the equator as a determinant resembles a diverse set of present conditions from a variety of other correlated factors, such as temperature and precipitation regime, seasonality, total soil carbon content and soil pH. Thereby, the soils functions and the impacts on microorganisms are controlled. What this all amounts to is, that the evaluation of the cause for a factor determining soil microbial biomass in drylands is vital to properly understand how climate and soil agents interactively determine the impacts on the ecosystem, and are therefore taken into account for the interpretation of this study's findings.

In the following, I investigate how microbial biomass, found in soil sampled under vegetation cover, is determined by geographical factors: (I) aridity, (II) distance from equator (i.e. temperature, climate and seasonality), biotic factors like (III) different levels of grazing and additionally, and (IV) the interactions of named factors with correlating additional sets of present soil and climate traits. Accordingly, I hypothesized that

I) With increasing aridity soil microorganisms are negatively affected. Depending on moisture for their metabolic activity, less water availability decreases activity (i.e. respiration), therefore, slowing down decomposition and microbial biomass formation.

II) With reduced distance to the equator, the temperature regime increases, while seasonality decreases. Thereby the evapotranspiration potential is enhanced. Consequences are decreased soil moisture saturation, which negatively impacts microbial activity and biomass production respectively.

III) Grazing promotes microbial respiration up to a certain extent — and therefore positively affects microbial biomass — by factors like plant root feedback and ammonium influx from dung and urine. Alternatively, interactions with negative impacts of grazing have been previously monitored (i.e. soil degradation), whereby potential positive effects were compensated.

IV) A complex interplay between the investigated factors and the diverse present conditions and driving agents of the individual soils (textural soil attributes, climate and precipitation regime, soil pH, total carbon stock) control the diverging impacts of chosen factors on the soil microorganisms, giving the possibility of reinforcing or balancing impacts on the soil. Therefore, it is hypothesized, that the chosen single factors determining microbial biomass need to be broken down into smaller agents, which drive the composition and stability of the soil microenvironment in concert.

2 Methods

The study is part of the BIODESERT survey project, which is coordinated by Prof. Fernando T. Maestre (Dryland Ecology and Global Change Lab of Rey Juan Carlos University, Spain). Besides a description of the dryland sampling sites and the experimental set up, further details about the measuring/response variables (basal respiration, water-induced basal respiration, substrate-induced respiration, the respiratory quotient, calculation of microbial biomass and soil water content) are stated in the next paragraphs. Moreover, the statistical analyses are explicated.

2.1 Study Site and Soil Sampling

A set of 257 soil samples from 78 sites in 22 countries on six different continents (all except Antarctica) were studied (Maestre et al. 2012a). All sites showed environmental conditions classified as global drylands by the United Nations Environmental Programme (UNEP) (Arnold 1992), with the aridity index (AI; ratio of mean annual precipitation to mean annual potential evapotranspiration) ranging from hyper arid to dry sub-humid (Table 1). Some samples exceeded the AI (classified as 'humid').

Table 1: Classification of drylands by aridity index (Arnold 1992), $AI = \frac{P}{PET}$ (P=average annual precipitation, PET=potential evapotranspiration). Data was available for 249 out of 257 sites.

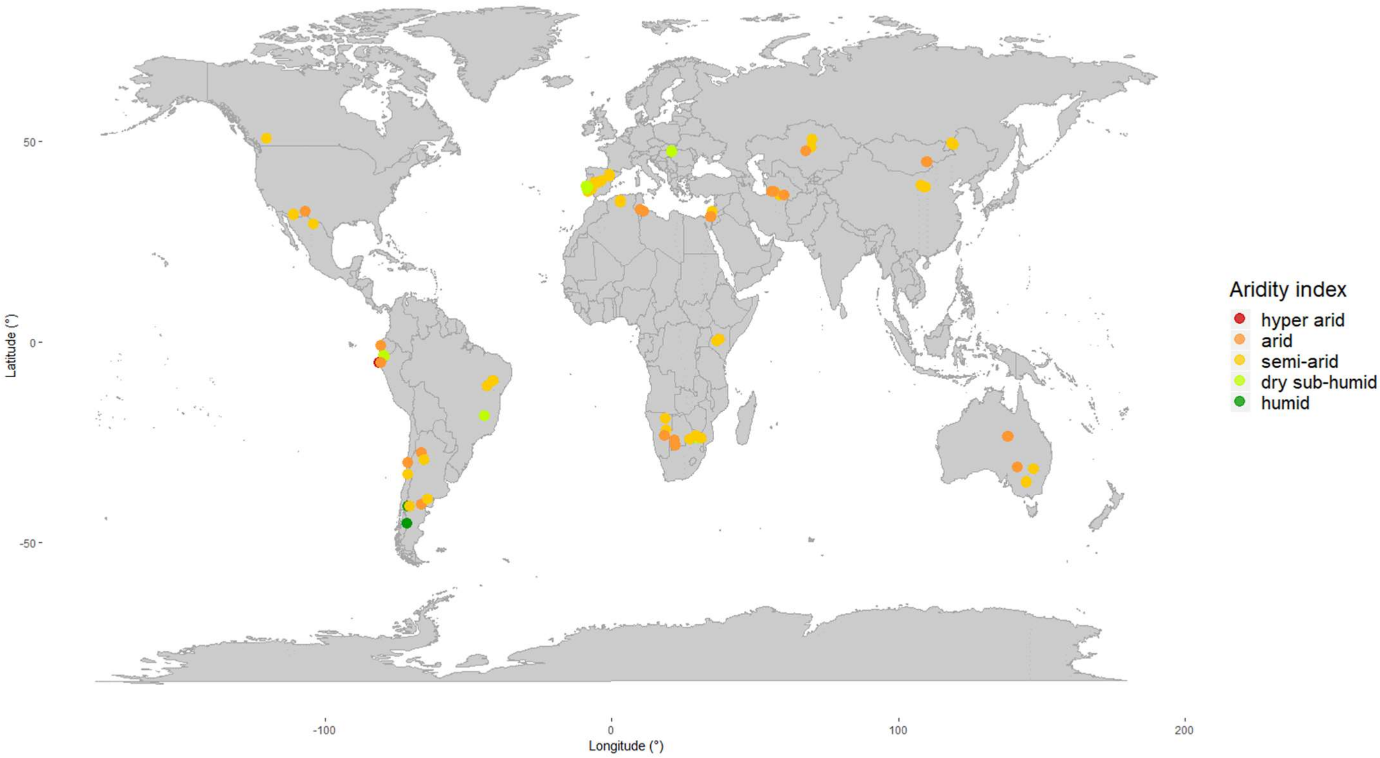
Classification	*AI*	*n samples*	*% samples*	*% Global land area*
Hyper arid	< 0.05	3	1.20	7.50
Arid	0.05 < AI < 0.20	81	32.53	12.10
Semi-arid	0.20 < AI < 0.50	134	53.82	17.70
Dry sub-humid	0.50 < AI < 0.65	25	10.04	9.90
Humid[1]	> 0.65	6	2.41	NA

[1]not included in UNEP classification system

The BIODESERT project comprises the investigation of three microsites: bare soil, soil with a biocrust and soil sampled under vegetation. In this study, all samples were from vegetated microsites. Each plot had four different levels of grazing ranging from one to four, with level one having high grazing activity and four having no grazing activity.

Sites were located at distances extending from 0.2 to 50.7 degrees from the equator and encompass a broad range of climate conditions and altitudes (Figure 1).

Figure 1: Sampling sites on the world map classified in aridity classes



Soil samples arrived in bags of approximately 10 g soil each, 9 g of which were used for the study. The samples were sieved and incubated under laboratory conditions. Different soils were observed to be morphologically diverse, differing in color, soil type, pore size, water content (only partial data from data bases).

2.2 Soil Microbial Respiration Measurements (SIR method)

2.2.1 Device Set Up

Generally, microorganisms consume O2 and produce CO2 by respiration. To examine the basal and substrate induced respiration of soil microorganisms via O2 consumption, an automated electrolytic microrespiratory system was used (Scheu 1992):

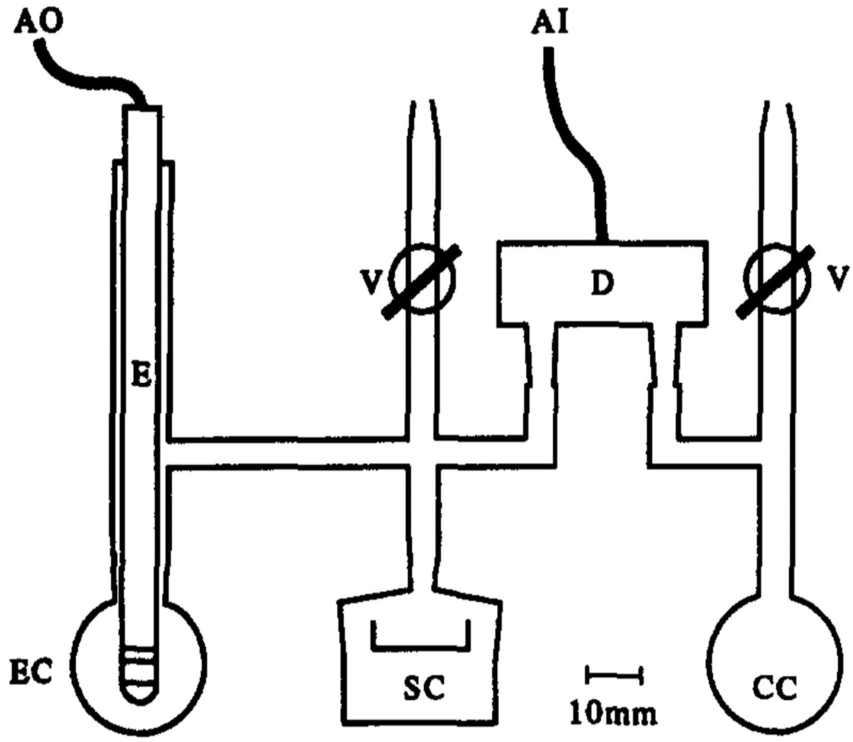


Figure 2: Set up of one measurement unit of an automated measurement of the respiratory response of soil microcompartiments (Scheu, 1992): (EC: Electrolytic chamber, E: electrode, AO: atmospheric pressure control system, SC: sample chamber, V: valve, D: detector, AI: amplifier, CC: control chamber)

The original system was modified to allow a set of 30 samples to be measured simultaneously by 30 independent measurement units. In the following study, two identical devices were employed in order to measure 60 samples at once. The general set up ensures a constant environment in terms of temperature by submersing the measurement units into a water bath set to 20°C. To prevent temperature fluctuations, the whole system was run in a temperature-controlled room at 18°C.

Each measurement unit consists of three chambers (Figure 2). The first one being an electrolytic chamber (EC) filled with saturated copper (II)-sulfate ($CuSO_4$) and an integrated electrode (E), secondly the vessel for the soil sample (SC), and thirdly a control chamber (CC). The soil vessel and the control chamber are connected via an electronic pressure detector (D), which measures pressure changes between both chambers. The control and soil units can be opened and closed by a valve (V) to adjust air supply and regulate air pressure. The chamber for the soil sample can easily be removed from the device and contains a lid with a small integrated vial for alkali (potassium hydroxide, KOH) addition. KOH acts as a CO_2-trap resulting in a decrease of the air pressure during O_2 consumption and CO_2 evolution. In the experiment, 0,2 ml KOH (2n) was added into the lid of each soil chamber and was renewed for each measurement. Attached to the detection unit, there is an amplifier (AI) connected to an analog digital converter. A control system maintains constant atmospheric pressure between the soil and the control chamber by sending pulses (AO) to the Pt electrode when a distinct difference in pressure has emerged, promoting the release of 0.83 µg O_2 per pulse from $CuSO_4$. The amount of pulses produced are used to calculate O_2 consumption (1).

$$\mathrm{O_2 - Consumption} = \frac{\mathrm{Pulses} \times 0.83\ \mu\mathrm{g}}{\mathrm{h}\ \times \mathrm{g\,dw}} \qquad (1)$$

2.2.2 Measurements of Respiration

Each respiratory measurement was divided into three parts: 1) basal respiration (BAS, µl O_2 h^{-1} g^{-1} soil dry weight) 2) water-induced basal respiration (H_2O-BAS, µl O_2 h^{-1} g^{-1} soil dry weight) and 3) substrate-induced respiration method (SIR, µl O_2 h^{-1} g^{-1} soil dry weight). SIR was then used to determine total microbial biomass (C_{mic}, µg C_{mic} g^{-1} soil dry weight) (Anderson and Domsch 1978). All three measurements were set up to record the O_2-uptake in hourly intervals for at least 22 h after 1 h of equilibration, where soil organisms acclimated to the temperature of the water bath. Basal respiration (BAS, H_2O-BAS) was calculated as the mean of the O_2-uptake rates of hours 10-19 after equilibration. Whereas, the SIR was used to asses total microbial biomass by inducing respiration through the addition of substrate (D-glucose) to saturate the catabolic activity of the soil microorganisms. Furthermore, the microbial respiratory quotient (qO_2, µl O2 µg^{-1} C_{mic} h $^{-1}$) was assessed, which gives information about the microbial respiration per unit biomass (Anderson and Domsch 1993). In this study, instead of BAS, H_2O-BAS was applied for all evaluations *(2).*

$$qO_2 = \frac{H2O\_BAS}{Cmic} \tag{2}$$

2.2.3 <u>Basal respiration and H_2O-induced basal respiration</u>

Plain dryland soils (without addition of substrate) were used to measure basal respiration. Samples were weighted into glass vessels and covered with a lid until attachment to the device. Since basal measurements constantly revealed no respiratory response, water was added to activate dormant microorganisms for the measurement of basal activity. However, the water absorptive capacity varied between the samples. The addition of an adequate amount of 1 ml of distilled water (aq. dest.) was approached by gradually adding H_2O in steps of 250 µl to all samples until saturation was achieved. Soils reacted disparately to addition of H_2O, i.e. clumping, hydrophobically repelling it or soaking it up instantly (no data). Homogeneous distribution was ensured by gently tapping the vessel until a thin water film was visible at the bottom side of the glass vessel.

2.2.4 <u>Substrate induced respiration and determination of microbial biomass</u>

After two days of measuring basal activity (BAS and H2O-BAS), SIR was measured. Considering the aridity of the samples, the fresh weight was equalized to the dry weight (9 g fresh weight = 9 g dry weight). 4 mg glucose per g dry weight soil (36 mg sample^{-1}) was pipetted onto each sample as 0.5 ml aqueous solution. A homogeneous distribution was ensured as described above. The average of the lowest three respiration values within hours 3-10 was assessed as the maximum initial respiratory response (MIRR; µl O_2 g^{-1} soil dry weight). Microbial biomass (C_{mic}, µg C_{mic} g^{-1} soil dry weight) was calculated after Beck as shown in (3) (Beck et al. 1997).

$$Cmic = \mathrm{MIRR} \times 0.7 \times 38 \tag{3}$$

2.2.5 Water content

Furthermore, the soil water content of the fresh weight (%) was determined by re-weighing samples that have been oven dried for 24 h at 75 °C (4).

$$H2O\ of\ dryweight\ \% \ = \frac{(Fresh\ weight - dry\ weight)\ \times 100}{Fresh\ weight} \qquad (4)$$

2.3 Statistical Analyses

To measure and statistically compare determinants of microbial biomass and microbial respiration, a model selection of linear mixed effect models (lme) (Winter 2013) was carried out. The response variables, H_2O-BAS, C_{mic}, qO_2, and the soil water-content (%), were modelled as a function of the selected fixed factors: distance from the equator, aridity and grazing. Moreover, the models involved random factors (the microrespiratory device and the sampling site), which were known to randomly influence the calculations and cannot be controlled experimentally.

From this an ANOVA was applied, where models were compared (Table 2) and model selection followed the lowest AIC-Values. Models 4-9 were more complex in terms of interactions and fixed factors. Both final models (M3, M5) contained the distance from the equator, yet, M5 took the interaction between the distance from the equator and aridity into account.

Table 2: Akaike information criterion (AIC) after model comparison for models testing the effect of different drivers on a) water-induced basal respiration, b) microbial biomass, c) respiratory quotient and d) soil water content. Soil water content was applied as a fixed factor for a), b), and c). For all of the models below, the respiratory device and the specific sampling site were applied as random factors. Models with lower AIC have a better model fit and were used for later discussion (marked in bold). ANOVA of selected models can be found in Table 4. AI: aridity index, X^2: Chi square, X Df: number of degrees of freedom added in comparisson to model 1.

a) Water-induced basal respiration and soil water content

Model	***Variables***	***AIC***	***X^2***	***X Df***	***p-value***
1	AI	829.46			
2	Grazing	834.75	0.00	0	1.00
3	Distance from the Equator	820.92	13.83	0	<.0001
4	AI + Grazing	831.38	0.00	1	1.00
5	**AI + Distance from the Equator**	**820.04**	**11.35**	**0**	**<0.0001**
6	Grazing + Distance from the Equator	822.86	0.00	0	1.00
7	AI + Grazing + Distance from the Equator	821.97	2.90	1	0.09
8	AI * Grazing	833.32	0.00	0	1.00
9	Distance from the Equator * Grazing	824.85	8.48	0	<0.0001
10	AI * Grazing * Distance from the Equator	828.93	3.91	4	0.42

b) Microbial Biomass and soil water content

Model	***Variables***	***AIC***	***X^2***	***X Df***	***p-value***
1	AI	3036.35			
2	Grazing	3038.91	0.00	0	1.00
3	**Distance from the Equator**	**3024.59**	**14.32**	**0**	**<0.0001**
4	AI + Grazing	3038.32	0.00	1	1.00
5	AI + Distance from the Equator	3025.79	12.52	0	<0.0001
6	Grazing + Distance from the Equator	3026.57	0.00	0	1.00
7	AI + Grazing + Distance from the Equator	3027.77	0.81	1	0.37
8	AI * Grazing	3039.43	0.00	0	1.00
9	Distance from the Equator * Grazing	3028.50	10.93	0	<0.0001
10	AI * Grazing * Distance from the Equator	3033.65	2.85	4	0.58

Continuation of table 2:

c) Respiratory quotient (qO2) and soil water content					
Model	***Variables***	***AIC***	***X^2***	***X Df***	***p-value***
1	AI	3036.30			
2	Grazing	3038.90	0.00	0	1.00
3	**Distance from the Equator**	**3024.60**	**14.32**	**0**	**<0.0001**
4	AI + Grazing	3038.30	0.00	1	1.00
5	AI + Distance from the Equator	3025.80	12.52	0	<0.0001
6	Grazing + Distance from the Equator	3026.60	0.00	0	1.00
7	AI + Grazing + Distance from the Equator	3027.80	0.81	1	0.37
8	AI * Grazing	3039.40	0.00	0	1.00
9	Distance from the Equator * Grazing	3028.50	10.93	0	<0.0001
10	AI * Grazing * Distance from the Equator	3033.70	2.85	4	0.58

d) Soil water content					
Model	***Variables***	***AIC***	***X^2***	***X Df***	***p-value***
1	AI	692.85			
2	Grazing	695.57	0.00	0	1.00
3	Distance from the Equator	695.60	0.00	0	1.00
4	AI + Grazing	694.73	2.87	1	0.09
5	**AI + Distance from the Equator**	**694.31**	**0.42**	**0**	**<0.0001**
6	Grazing + Distance from the Equator	697.45	0.00	0	1.00
7	AI + Grazing + Distance from the Equator	696.19	3.26	1	0.07
8	AI * Grazing	695.91	0.28	0	<0.0001
9	Distance from the Equator * Grazing	699.18	0.00	0	1.00
10	AI * Grazing * Distance from the Equator	702.45	4.73	4	0.32

To relate possible significant results to environmental variables, I correlated the response variables (H_2O-BAS, C_{mic}, qO_2, water content) with variables from data bases (Table 3). Therefore, the function *cor* from the *stats* package in R was used. It provides a spearman’s *rho* statistic correlation. To compute the correlation matrix, the *rcorr* function from the *Hmisc* package was used, whereof r and P values were extracted. All analyses were done with the statistical software R (version 3.6.0, R Development Core Team, http://www.Rproject.org).

Table 3: For the assessment of the relationship between the investigated factors, environmental variables were extracted from the data bases below

Variable	*Description*	*Unit*	*Source*	*Reference*
Carbon	Carbon concentration	%	SoilGRIDS - global soil information based on automated mapping	
clay	Clay concentration	%	SoilGRIDS - global soil information based on automated mapping	Hengl, T. et al. SoilGrids1km--global soil information based on automated mapping. PLoS One 9, e105992 (2014).
elevation	Elevation	m	GMTED2010 - Global Multi-resolution Terrain Elevation Data	Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) | The Long Term Archive. Available at: https://lta.cr.usgs.gov/GMTED2010. (Accessed: 6th December 2018)
land_cover	Land use types. Information about the coding can be retrieved at https://maps.elie.ucl.ac.be/CCI/viewer/ See documentation (below left) /Legend for LC Map v.2.0.7 or here: https://portal.idiv.de/nextcloud/index.php/s/d93GXqXQKoJDJdQ		ESA CCI - Global Land Cover database	European Space Agency. ESA - Land Cover CCI - Product User Guide Version 2.0. (2017).
land_cover_class	land_cover number translates into land cover type			Karger, D. N. et al. Climatologies at high resolution for the Earth land surface areas. Scientific data 1–19 (2017).
MAT	Mean annual temperature	°C	CHELSA - Climatologies at high resolution for the earth's land surface areas	Karger, D. N. et al. Climatologies at high resolution for the Earth land surface areas. Scientific data 1–19 (2017).
pet	Potential evapotranspiration		CGIAR-CSI - Global potential evapotranspiration database	Zomer, R. J., Trabucco, A., Bossio, D. A. & Verchot, L. V. Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. Agric. Ecosyst. Environ. 126,67–80 (2008). // van Straaten Oliver, Z. R. T. A. & Bossio, D. Carbon, land and water: A global analysis of the hydrologic dimensions of climate change mitigation through afforestation / reforestation. (IWMI, 2006).

Continuation of table 3:

Variable	Description	Unit	Source	Reference
soil.ph	Soil pH		SoilGRIDS - global soil information based on automated mapping	
prec	Mean annual precipitation	mm	CHELSA - Climatologies at high resolution for the earth's land surface areas	Hengl, T. et al. SoilGrids1km--global soil information based on automated mapping. PLoS One 9, e105992 (2014).
sand	Sand concentration	%	SoilGRIDS - global soil information based on automated mapping	Karger, D. N. et al. Climatologies at high resolution for the Earth land surface areas. Scientific data 1–19 (2017).
prec_sea	Coefficient of variation of precipitation. Shows how variable the climate in terms of precipitation is.		CHELSA - Climatologies at high resolution for the earth's land surface areas	Hengl, T. et al. SoilGrids1km--global soil information based on automated mapping. PLoS One 9, e105992 (2014).
silt	Silt concentration	%	SoilGRIDS - global soil information based on automated mapping	Karger, D. N. et al. Climatologies at high resolution for the Earth land surface areas. Scientific data 1–19 (2017).
temp_sea	Standard deviation of temperature. Shows how variable the climate in terms of temperature is.		CHELSA - Climatologies at high resolution for the earth's land surface areas	Hengl, T. et al. SoilGrids1km--global soil information based on automated mapping. PLoS One 9, e105992 (2014).
soil_type	Soil type		SoilGRIDS - global soil information based on automated mapping	Karger, D. N. et al. Climatologies at high resolution for the Earth land surface areas. Scientific data 1–19 (2017).
slope	slope			Hengl, T. et al. SoilGrids1km--global soil information based on automated mapping. PLoS One 9, e105992 (2014).

3 Results

The influence of selected factors, i.e. distance from the equator, grazing, and AI on microbial respiration (H_2O-BAS), microbial biomass (C_{mic}), the respiratory quotient (qO_2) and the soil water content was examined. Most fresh soils contained between 0 % and 6 % water (except for three samples with 11%, 12%, 23%). Basal respiration without the addition of water resulted in no respiration for 240 samples (Mean ± SD: 0±0 µl O_2 h^{-1} g^{-1} dry soil). Therefore, basal respiration was not realized for the remaining samples. After adding water, water induced basal respiration ranged from 0.46 µl O_2 h^{-1} g^{-1} dry soil (Brazil, semi-arid, high grazing intensity) to 13.53 µl O_2 h^{-1} g^{-1} dry soil (Israel, semi-arid, no grazing) with 2.75 ± 2.09 µl O_2 h^{-1} g^{-1} dry soil being the average. The maximum initial respiration rate (MIRR) was on average 9.077 ± 6.98 µg O_2 h^{-1} g^{-1} dry soil. Individual MIRR was then used to calculate the microbial biomass (3). The smallest microbial biomass was measured in Mongolia (23.72 µg C_{mic} g^{-1} dry soil; arid, low grazing intensity), while the greatest microbial biomass was found in Israel (902.36 µg C_{mic} g^{-1}, semi-arid, no grazing). On average, soils harbored 245.97 ± 185.74 µg C_{mic} g^{-1} dry soil, however, great variance was observed. The respiratory quotient (qO_2, µl O_2 µg^{-1} C_{mic} h^{-1}) was assessed as the specific respiration per unit biomass (2), providing indication of the soil quality. Values ranged from 0.00114 µl O_2 µg^{-1} C_{mic} h^{-1} to 0.15302 µl O_2 µg^{-1} C_{mic} h^{-1} with the overall mean being 0.0147 ± 0.0161 µl O_2 µg^{-1} C_{mic} h^{-1}. After model selection, the models containing the distance to the equator only, were the most parsimonious models for microbial biomass and qO_2 (M3). Models with joined interaction between aridity and the distance to the equator were significant for water-induced basal respiration and the soil water content (M5) (Table 2). However, the statistical output for the selected models revealed that the distance from the equator is also the only factor significantly affecting the basal respiration, while for qO2 and the soil water content, no significant factor within the interaction of AI and the distance from the equator could be identified (Table 4).

Increased distance to the equator had a significant positive effect on the basal respiration ($p=0.001$***) and resulted in elevated respiratory rates (Figure 3a; Table 4). Samples that were collected within ~25 ° latitudinal distance from the equator (tropic of cancer and tropic of capricorn) had lower respiratory rates than samples that were collected beyond ~25 ° distance from the equator. The highest respiratory responses were measured above the tropics at around 30 ° latitudinal distance from the equator, with 13.53 µl O_2 h^{-1} g^{-1} dry soil at 31.632°N being the highest value (see above: Israel; semi-arid no grazing). Principally, soils collected within 31° and 41° N and S of the equator had the highest respiratory responses.

Table 4: Statistical output final of linear mixed-effects models for a) water-induced basal respiration, b) microbial biomass, c) respiratory quotient, and d) soil water content. Additionally, the soil water content was used as a fixed factor for a), b) and c). An overview of the specific models can be found in Table 2. AI: aridity index, term: fixed factors, NumDF: Degrees of freedom of the numerator, DenDF: Degrees of freedom of the denumerator. Significant results are marked in bold.

a) Water-induced basal respiration and soil water content				
term	***NumDF***	***DenDF***	***F***	***p-value***
Soil water content	1	233.63	3.94	0.0484
AI	1	89.21	2.82	0.0968
Distance from the Equator	**1**	**78.71**	**11.76**	**0.0010**
b) Microbial Biomass and soil water content				
term	***NumDF***	***DenDF***	***F***	***p-value***
Soil water content	1	217.76	3.64	0.0576
Distance from the Equator	**1**	**81.05**	**15.11**	**0.0002**
c) Respiratory quotient (qO2) and soil water content				
term	***NumDF***	***DenDF***	***F***	***p-value***
Soil water Content	1	132.74	1.03	0.3117
Distance from the Equator	1	79.26	0.29	0.5946
d) Soil water content				
term	***NumDF***	***DenDF***	***F***	***p-value***
AI	**1**	**84.73**	**3.26**	**0.0745**
Distance from the Equator	1	77.40	0.51	0.4757

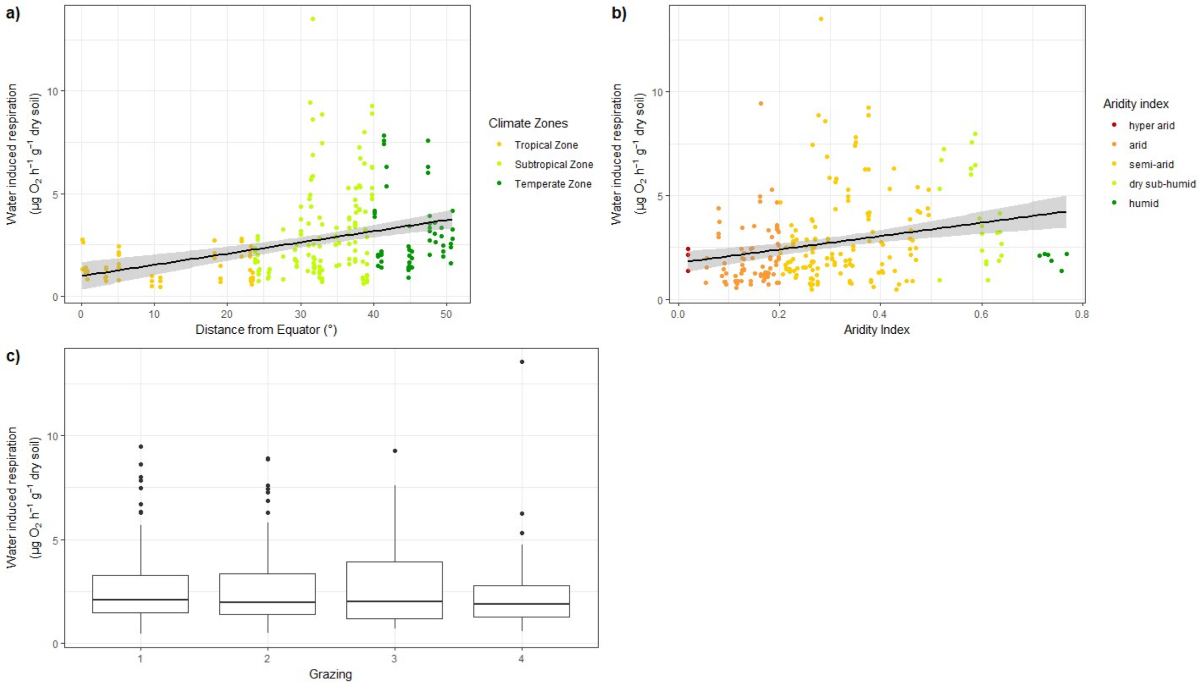


Figure 3: Relationship between water-induced basal respiration and a) the distance from the equator, b) linear regression the aridity index, and c) impacts of different intensities of grazing with 1 = high grazing, 2 = medium grazing, 3 = low grazing, 4 = no grazing activity. Dots were colored according to their climate zone in a) and their aridity index in b) to show the distribution across the different classes.

The correlation matrix comprising the relations between response variables and the different drivers showed, that the distance from the equator is closely negative related to the potential evapotranspiration (PET) (R^2= - 0.84) (Table 5). Overall, PET ranged from ~ 1800 ± 230 mm month^{-1} at the equator to 140 ± 46 mm month^{-1} in the temperate zone, with 1361 ± 345 mm month^{-1} being the average. Soils sampled within 31° and 41° N and S experienced moderate demands (1273 ± 190 mm month^{-1}).

Similarly, microbial biomass increased significantly (p=0.0002***) with the distance to the equator, whereas qO_2 was not significantly affected (p=0.5946) but revealed a slight increase with distance to the equator (Figure 5a, 6a; Table 4).

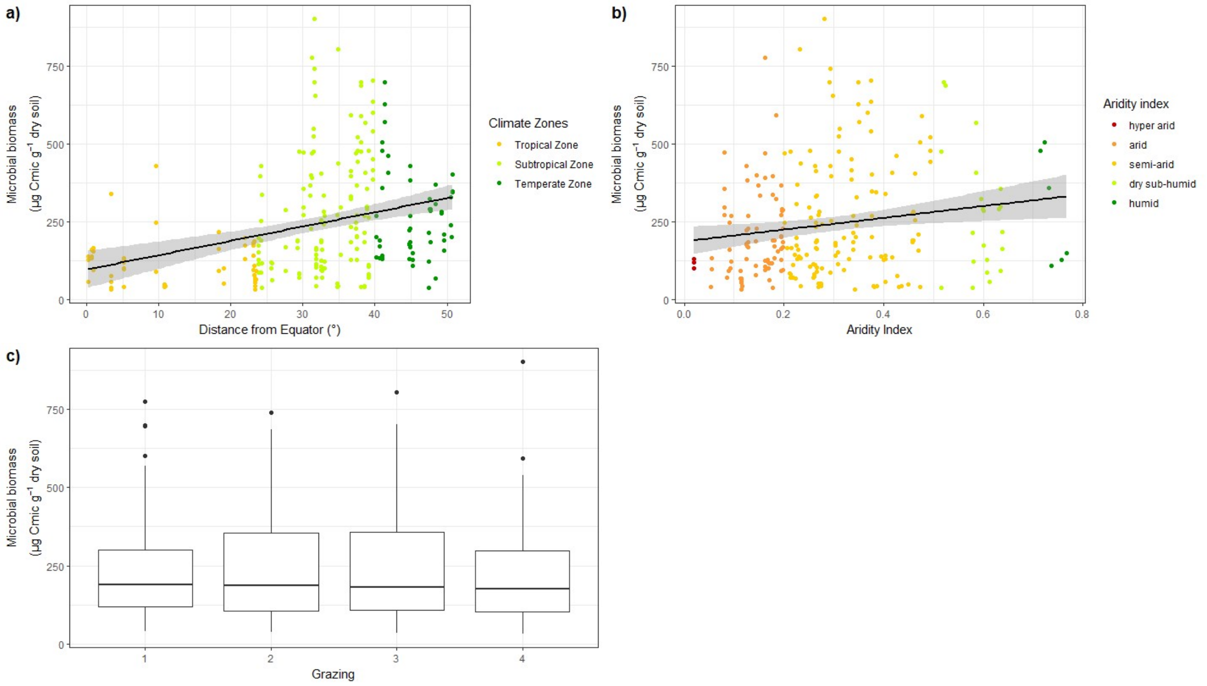


Figure 4: Relationship between microbial biomass and a) the distance from the equator, b) linear regression the aridity index, and c) impacts of different intensities of grazing with 1 = high grazing, 2 = medium grazing, 3 = low grazing, 4 = no grazing activity. Dots were colored according to their climate zone in a) and their aridity index in b) to show the distribution across the different classes.

The relationship between the distance from the equator and the soil water content was not significant (p=0.4757) (Table 2).

High aridity index values (i.e. lower aridity) increased the water-induced basal respiration (p=0.0968) and the soil water content (p=0.0745), whereas it had not affect on microbial biomass and qO_2 (Figure 4b, 5b; Table 4).

The factor grazing and all other interactions between response variables and drivers were non-significant (p=1).

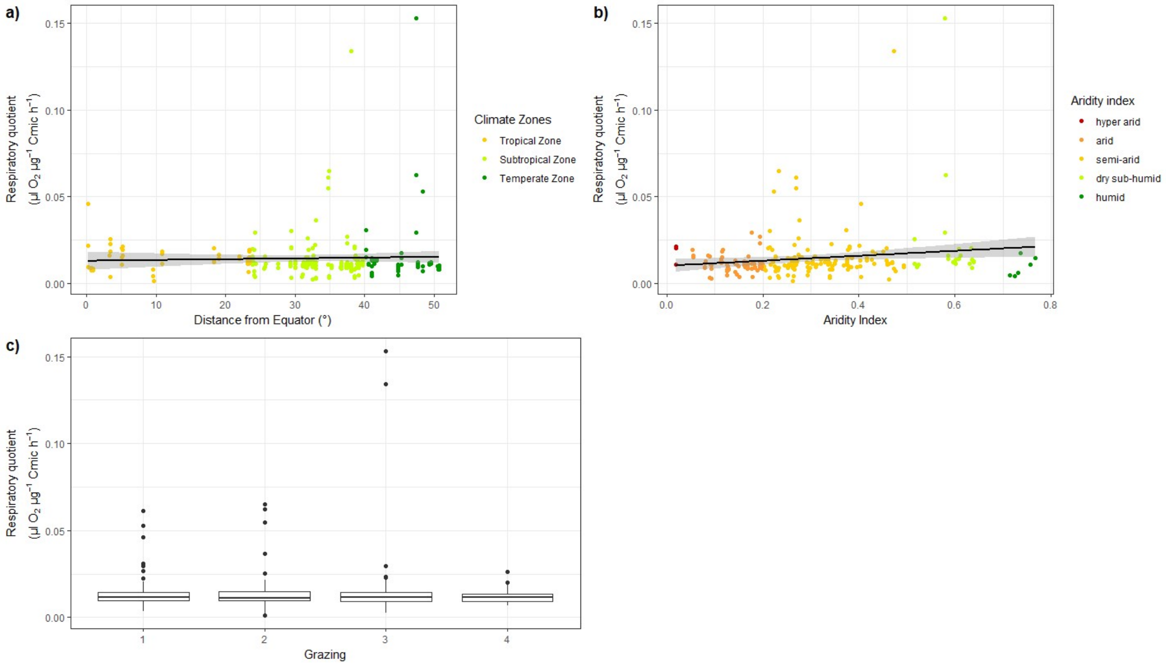


Figure 5: Relationship between qO_2 and a) the distance from the equator, b) linear regression the aridity index, and c) impacts of different intensities of grazing with 1 = high grazing, 2 = medium grazing, 3 = low grazing, 4 = no grazing activity. Dots were colored according to their climate zone in a) and their aridity index in b) to show the distribution across the different classes.

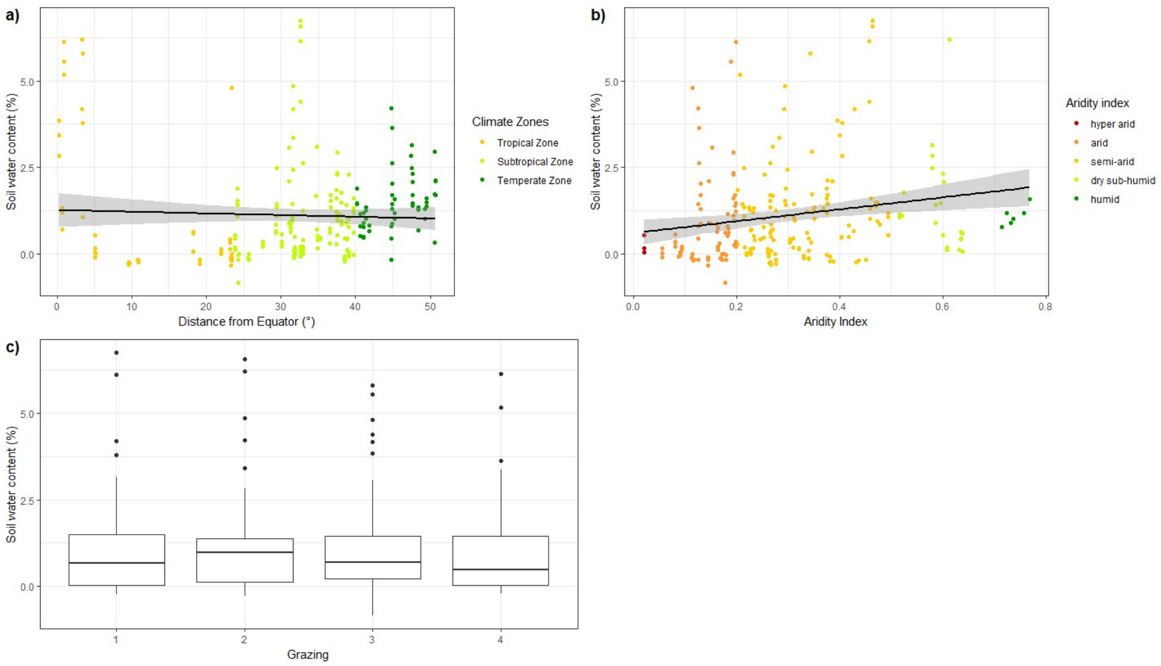


Figure 6: Relationship between water content and a) the distance from the equator, b) linear regression the aridity index, and c) impacts of different intensities of grazing with 1 = high grazing, 2 = medium grazing, 3 = low grazing, 4 = no grazing activity. Dots were colored according to their climate zone in a) and their aridity index in b) to show the distribution across the different classes

In addition, a variety of soil and climate data from public data bases (Table 3) was used to calculate a correlation matrix diagram (Appendix, Figure 7) together with the obtained data from this study (Table 5).

Factors strongly correlating ($p < 0.001$ ***) with the distance from the equator were: the potential evapotranspiration (PET) (R^2= -0.84), silt content (R^2= 0.52), sand content (R^2= -0.36), seasonal precipitation (R^2= -0.32), soil pH (R^2= 0.30) and the total carbon content (R^2=0.28). Of these factors, water-induced respiration correlated with the sand content (R^2= -0.46), the silt content (R^2= 0.41) and PET (R^2= -0.33). Microbial biomass revealed a close relation to the silt content (R^2= 0.39), the sand content (R^2= -0.38) and the PET (R^2= -0.32). The soil water content was found to be closely correlated to the sand content (R^2= -0.49), the clay content (R^2= 0.48), the silt content (R^2= 0.34) and the soil carbon stock (R^2=0.32). qO_2 did not show strong correlation (***) to the same factors correlating with the distance from the equator.

The aridity index correlated strongly with all investigated drivers. The strongest correlations were accounted to the amount of annual precipitation (R^2= 0.81), soil pH (R^2= -0.57), carbon stock (R^2= 0.53) and PET (R^2= -0.37), followed by soil texture attributes sand (R^2 = -0.3), clay (R^2= 0.26), silt (R^2= 0.23) and the seasonal amount of precipitation (R^2= -0.26).

The two response variables (water-induced respiration and soil water content), that fitted the combined interaction model (M5) of the distance from the equator and aridity were tested for correlations with factors related to aridity. Water-induced basal respiration responded strongly to the sand (R^2= -0.46), silt (R^2= 0.41) and clay content (R^2= 0.3), PET (R^2= -0.33), the annual amount of precipitation (R^2= 0.21), soil pH (R^2= -0.19**) and the soil carbon stock (R^2= 0.18**). The soil water content correlated the strongest to the sand (R^2= -0.49) and clay portions (R^2=0.48) of the soil, followed by silt (R^2= 0.34) and carbon (R^2= 0.32) and the annual amount of precipitation (R^2= 0.25). All significant correlations between aridity and the soil water content revealed also correlation with the distance from the equator (sand, clay, silt, carbon).

Grazing itself and all interactions between factors driving the impacts of grazing were neglected, since it was revealed to have no significant impact on the response variable (Table 2).

Table 5: Summary of applied data from the correlation matrix (Figure 7) showing the R^2-values for the correlation between response variables and driving factors. Correlation with *** marked in bold, p-values > 0.1 are marked n.s.

Response variables	*Drivers*							
	PET	Silt	Sand	Seasonal precipitation	Soil pH	Carbon	Annual precipitation	Clay
Distance from the Equator	**-0.84**	**0.52**	**-0.36**	**-0.32**	**0.3**	**0.28**	-0.19	n.s.
Aridity index	**-0.37**	**0.23**	**-0.3**	**-0.26**	**-0.57**	**0.53**	**0.81**	**0.26**
Water-induced basal respiration	**-0.33**	**0.41**	**-0.46**	-0.21	**-0.19**	**0.18**	**0.21**	0.3
Microbial biomass	**-0.32**	**0.39**	**-0.38**	-0.17	-0.13	n.s.	0.15	0.18
qO2	n.s.	n.s.	n.s.	-0.18	n.s.	n.s.	n.s	0.18
Soil water content	-0.19	**0.34**	**-0.49**	n.s.	n.s.	**0.32**	**0.25**	**0.48**

4 Discussion

Dryland soils and their productivity are characterized by the absence of moisture. The water content of the fresh samples ranged from 0 % up to 23 % but contained on average 1.10 ± 1.41 %. Since most soil organisms are dependent on a water saturated environment for their metabolic processes, microbial activity was non-existend before water amendment and microorganisms were in a dormant stage (Blankinship et al. 2011; Orchard and Cook 1983; Baldrian et al. 2010).

To evaluate soil quality, the respiratory quotient (qO_2) was used as an indicator. Low qO_2 values generally indicate a high biomass and low heterotrophic respiration, i.e. a higher carbon use efficiency, while a high qO_2 refers to a small biomass but high respiratory responses i.e. a lower carbon use efficiency in the microbial community. The findings of this study suggest, that qO_2-values increased with increasing distance to the equator. This connection is no surprise, since qO_2 is the ratio of basal respiration per unit biomass and both of the determinants revealed a positive correlation to the distance from the equator. Differences in qO_2 evolve through the composition of the soil microbial community or the ability of the present organisms to adjust to the environmental conditions. For instance, fungi tend to fixate C more efficiently than bacteria (Deruiter et al. 1993; Hunt, H. W., Coleman, D. C., Ingham, E. R. et al. 1987; Battaglia et al. 2011; Vries et al. 2012; Holtkamp et al. 2011), which can result in small qO_2 values. Alternatively, low qO_2 values are measured when soil microbial organisms are best adjusted to their environment. Efficient activity indicates an increased soil quality. Soils, which are characterized by small qO_2 values have a tendency to act as carbon sinks, since the ratio of the microbial biomass to the basal respiratory rates of the microorganisms is increased – meaning, more carbon is fixed than released into the atmosphere by soil microorganisms. In this study, dryland soils revealed heterogeneous results, though a positive trend for small qO_2-values in regions close to the equator was visible.

The analysis revealed, that in this study, the distance from the equator and partially, the strength of the region's aridity were the strongest determinants of soil microbial biomass, respiration, soil water content and the respiratory quotient.

4.1 Distance from the Equator

It was initially assumed that the distance from the equator impacts soil microbial activity through climatic differences in the latitudinal distribution around the globe. Following this, soils from dryland regions close to the equator were hypothesized to have lower respiratory rates and smaller microbial biomasses. The analysis showed that the distance from the equator had the strongest impact on the microbial biomass and significantly contributed to the respiratory rates. Furthermore, qO_2 and the soil water content were considerably influenced by the latitudinal distribution. The distance from the equator can be divided into climate zones with coherent climatic conditions.

Generally speaking, climate zones are circular, belt-shaped zones around the poles and range from 0° at the equator to 90 ° (N and S) at the poles. The categorical concept for dividing earth’s surface into climate zones evolves from the effects of the tilt of the earth’s axis and its angle to the sun. Throughout the year, the positions of earth to sun change, whereby the angle of incidence of the sunlight is altered. Each climate zone is characterized by certain traits such as temperature, amount of precipitation and superordinate trade winds (Table 6). In the tropics, the sun warms up the earth more powerfully than at the poles, whereby more water evaporates, raising the evapotranspirative demands exposed on landcover, soil and bodies of water. Causally, the air is often moist and a frequent and dense cloud cover reduces the effect of the strong radiation on the ground temperature (meteoScool 2016-2018). The tropical and subtropical zones are divided by the circles of latitude, namely tropic of Cancer and tropic of Capricorn at ~ 23.5 ° (N/S). Both tropics mark the northernmost/southernmost latitudes at which the sunlight reaches the ground perpendicularly. Beyond this zone the subtropics begin. The subtropics are characterized by receiving the highest radiation in summer, since the angle of the sun to the earth is almost vertical (like in the tropical zone), but the cloud cover is relatively thin. Less moisture is received due to the circulation of trade winds within the tropics.

In this study, soils from 0 ° to ~ 50 ° were evaluated. Specific features for each climate zone are summarized in Table 6. As evaluated in the results, the highest microbial biomasses and respiratory rates were measured in regions outside the tropics (i.e. in the subtropics and the temperate zone). The correlation data (Table 5) confirmed a close negative connection between the distance from the equator and the climatic factors PET and seasonal precipitation (although to a lesser extend). That implies, that regions close to the equator are strongly related to high evapotranspirative demands and seasonal rainfall, while regions further from the equator experience weaker potential evapotranspiration and a more balanced precipitation regime. A strong evaporational and transpirational pull decreases the water availability in the soil during the dry season, creating unfavorable conditions for decomposition processes and soil microorganisms in general. The cycling of carbon is therefore decelerated and both, microbial respiration and biomass formation are diminished. During the rainy season, tropical soils often become anaerobic due to temporary flooding, whereby nutrients are washed out as well. Similarly, as a result, microbial activity is diminished.

Furthermore, the content of sand and silt were strongly (negatively/positively) correlated to the distance from the equator (Table 5). I assumed that this hits, that the soil texture changes gradually from the equator to the poles, where sandy soils are mostly found close to 0°, while soils with increased silt fraction are likely to be found farther from the equator. Commonly, a soil's texture is characterized by the proportions of the different soil particle sizes. A distinction can be made between sand (2000-63 µm), silt (63-2 µm) and clay (< 2 µm), which fundamentally determine the water holding capacity, nutrient availability and aeration of the soil (Blume et al. 2016). While big particles provide for a better aeration through their large pore spaces, they also allow leaching. Consequently, the water holding capacity is weak in sandy soils, which negatively impacts the microorganism's ability to take up substances from their surrounding environment. In general, finer particles, such as clay and silt have bigger surfaces and, because of the adhesive force, they tend to have a higher capacity for water retention. Furthermore, clay is usually negatively charged and, therefore, attracts cationic soil nutrients which accumulate around the particles, preventing the nutrients from being recycled by soil organisms (Blume et al. 2016). In addition, the small particle size of clay decreases the pore sizes resulting in reduced aeration where clay soils often become anaerobic. However, a recycling of litter material to CO_2 or biomass can only be achieved under aerobic conditions. In the tropical zone, where extreme evapotranspirative demands are imposed on the land during the dry season, sandy soils lose moisture by evaporation and leaching. In the rainy season, nutrients cannot be kept in the soil and are washed out by heavy amounts of precipitation. Hence, the quality of the microbial soil environment, and therefore the functioning of the soil microorganisms, is highly dependent on the combination of soil texture and the regional climate.

Further factors significantly correlated to the distance from the equator were soil pH and carbon stock. Both factors were positively associated and increased with distance from the equator. A soils pH is dependent on the composition of soil minerals and has great influence on carbon and nutrient availability (KEMMITT et al. 2006; Andersson et al. 2000; Kemmitt et al. 2005), the solubility of metals (Flis et al. 1993) and soil organism's activity and composition (Rousk et al. 2009). Even when nutrients are sufficiently stored in the soil, their bioavailability is often directly controlled by a soil's pH. Depending on the pH, nutrients tend to react with other minerals to form compounds, which are less soluble and bioavailability is decreased. As a result, nutrient limitations arising from a shifted soil pH may affect microbial activity in dryland soils. The positive correlation between distance from the equator and the soil's carbon stock is interpreted to be accounted to an increased soil moisture in regions farther from the equator, whereby decomposition rates are accelerated, and carbon compounds are recycled and stored in the soil.

Table 6: Overview of different climate zones and associated features relevant for the study (meteoScool 2016-2018)

	Distance from Equator	*Day length (on 21st June)*	*Sun path*	*Temperature*	*Precipitation*	*Climate*	*Subdivisions*
Tropical zone	0 ° - 23.5 °	10 – 13.5 h	90 ° above the horizon at least once per year, never lower than 43 °	Max.: 40 °C Mean: > 20 - 30 °C Min.: 0 °C (no frost)	Rain, defined by seasonal shift of trade winds	Daily changes in temperature are bigger that the annual changes of daily averages	Humid (tropical rainforest), semi-humid (wet savannah, dry savannah), semi-arid (thorn savanna), arid (desert)
Subtropics	23.5 ° - 40 °	9 – 15 h	90 ° - 27 ° above the horizon, according to place and season	Max.: 66 ° C Mean.: > 20 °C – 35 °C Min.: -5 °C	Dry, winter humidity and always wet areas	Tropic summer, non-tropic winter	Dry subtropics, humid winter subtropics (Mediterranean climate), always wet subtropics
Temperate Zone	40 ° - 60 °	8 – 12 h	Maximum 73 °, minimum 0° (at Arctic Circle ~ 66 °)	Max.: 40 °C Mean: 0-20 °C Min.: -40 °C	300 – 2000 mm, average 800 mm	Warm and cold temperate	Humid subtropical climate, Mediterranean climate, oceanic climate, continental climate

4.2 Aridity

Contrary to the assumptions made in the introduction, aridity did not significantly influence microbial biomass across global drylands. Similar results were found for qO_2. Microbial respiration revealed to be determined by effects between previously itemized distance from the equator and aridity. As was the soil water content. Increased humidity benefited the water-induced microbial respiration and had positive impact on the soil water content.

The correlation of data base data and findings from this study revealed the closest relation between the AI and the annual amount of precipitation. This is no surprise, since the AI is the ratio of PET and the annual amount of precipitation. The second strongest agent was the soil pH, which was negatively correlated. This can be (at least partially) explained by previous findings (Blume et al. 2016). Since precipitation is decreased in arid regions, substances tend to be stored in dryland soils instead of being washed out. Accumulations of alkaline carbonates (e.g. $CaCO_3$, Na_2CO_3) coming from natural pedogenesis can result in an increase of the pH. Thereby a low AI (high aridity) is related to a high pH. In humid regions, rain is more frequent, thereby more protons are washed into the soil and released by chemical soil processes than soils can neutralize or utilize. For this reason, soils from wetter regions (high AI) become more acid (low pH). Rousk et al. (2009) found that increase in the pH of a soil was associated with higher respiratory rates and larger microbial biomasses. A possible expanation might be, that soils with a low pH are physiologically disadvantageous for most microorganisms, whereby their activity is decelerated. Another factor significantly related to the aridity index, was the carbon stock. A possible mechanism might be, as suggested above, that enhanced moisture again enhances decomposition processes, whereby carbon compounds are faster recycled and can be utilized for biomass formation. Again, other agents significantly correlated to the aridity, were the soil's proportions of sand, silt and clay. As expounded before, soil texture strongly determines the moisture content, whereby microbes are directly affected. Sandy soils are vulnerable to moisture loss, which is thriven by greater levels of aridity and as a result soil microbial activity is decelerated. This hints that physical soil traits can strongly compensate or reinforce the impacts of aridity on the soil microenvironment and should thus be integrated in further models as important variables.

4.3 Grazing

It was hypothesized that herbivory influences the soil environment and impacts should be measurable by investigating soil microbial properties such as microbial respiration and biomass production. Root exudates induced by defoliation and additional ammonium input coming from herbivory dung and urine were suggested to improve soil productivity. Especially in the tropical zone, where nutrient deficiencies are commonly monitored (Vitousek 1984; Matson et al. 1999), additional inputs were expected to improve microbial activity. Nevertheless, other impacts of grazing, like soil deformation and reduction of litter quality can decelerate such processes. Thus, the interplay between positive and negative effects determines the strength of these consequences imposed on soil processes by grazing activity. In this study, no significant impacts of different intensities of grazing were found. Positive impacts and compensatory negative ones may have canceled each other out. A possible reason might be the identity of the grazing activity. Cattle pasture should have stronger impacts on the soil textural properties than rodent or insect herbivory, due to the grazer's weight and movement pattern even if the intensity of herbivory is equal. Additionally, the amount and distribution of nutrient influx coming from the grazer's excrements is highly dependent on the identity of the grazer. Therefore, it is possible, that the samples from soils which experienced grazing activity might not be representative of the whole plot. A soil's tendency to experience compaction and shear stress, and therefore, a reduction in total pore space depends on its stability and texture. van Haveren (1983) previously examined the impacts of different intensities of grazing and soil type on bulk soil and found out, that soil density increases with increased grazing activity in fine-textured soils, while coarse-textured soils were not significantly affected. It was concluded, that soil compaction from grazing occurred mainly on fine-textured soils. Thereby, the availability of water and nutrients is reduced which directly impacts the microbial community. Hence, soil composition is assumed to strongly influence the strength of the impact of grazing on soil microbial productivity.

4.4 Interactions

Since it was assumed, that the previously examined single factors give insufficient information about the interplay of mechanisms, interactions between drivers underlying the investigated determinants of microbial activity were examined.

Aridity and distance from the equator coincided in significant correlations with drivers: PET, silt, sand, carbon, soil pH, seasonal precipitation (and annual precipitation). Although I did not include those possible important factors in the mixed models, interactions are likely and should be considered in further analyses. It was earlier discussed how microbial respiration and biomass and aridity, distance from the equator, climate conditions and soil texture are related, and how the strength of the impacts depends on the interplay of all factors.

In short; climate, soil texture and pH were revealed to act in concert. Microbial community composition and activity depends on the environment, which is driven by the composition of the soil texture, the availability of moisture and nutrients and chemical soil processes. These drivers interactively influence how the natural conditions imposed on the soil impact the activity of soil microorganisms.

5 Conclusion

Since respiratory responses and microbial biomass were highly diverse across global drylands, this study hints that more factors determining microbial activity have to be taken into account. The interplay between different physical soil properties (e.g. soil texture, pH, carbon stock and water-holding capacity), climate conditions (e.g. precipitation, seasonality, evapotranspirative demands), biological processes (e.g. soil microbial community composition, organism's adjustment competence, food web interactions, flora-fauna-interdependencies) and anthropogenic usage (e.g. cultivation and rangeland) is complex, which makes it difficult to calculate reliable predictions about specific regions within the dryland classification system. However, the data, which was used to calculate correlation, was extracted from public data bases and the spacial resolution was several square kilometers. Thereby valuable information may not be represented in the correlated data. In addition, no data about the date of sampling was available. Depending on seasonality, this may have also affected the respiratory measurements and the soil water content.

Yet, this study provides important comprehensive data which should be integrated into large-scale carbon models. Additionally, long term analysis of the selected sites can provide information about possible trends in a changing environment. This may facilitate a step forward in our ability to predict the global carbon balance – both, now and in a future climate. Additionally, the results suggests that there are various factors determining microbial respiration and biomass across global drylands. Interactions between named physical, biological and anthropogenic factors play a major role and should be taken into account for further evaluations of determinants of microbial biomass and respiration in drylands.

These results are highly valuable in times of global warming: The total global dryland area is expected to increase with increasing temperature and precipitation regimes and present drylands are predicted to increase in aridity. Thereby, even higher importance for reliable predictions about these areas evolve. The findings of this study suggest, that with increasing aridity, microbial activity and decomposition processes will be limited by moisture and thereby, also nutrient availability. With reduced decomposition, less dead organic matter can be recycled, whereby the nutrient availability is decreased. Thereby, microbial biomass is expected to be reduced. Likewise, plants are expected to experience nutrient limitations more frequently since nutrient influx from decomposition processes is stalled. As a result, the vegetation cover decreases or shifts to species which are better adapted to extreme conditions. Especially in cultivated areas, crop yields are assumed to be negatively impacted by increasing aridity as a result of the damaged microbial environment and are expected to be compensated by increased irrigation and fertilization, which further upsets the nutrient balance in the soil and wastes valuable water resources. Furthermore, floods are expected to happen more frequent due to global change (United Nations Convention to Combat Desertification 1994). This study suggests, that dormant microbes in the soil become highly active through water induction, which results in enhanced respiratory activity and therefore, increased carbon loss from soils to the atmosphere. However, impacts will be controlled by an interplay of the specific present soil and climate conditions.

Index of Abbreviations

Abbreviation	*Explanation*
AI	Aridity Index
AIC-value	Akaike information criterion
aq. dest.	distilled water
BAS	Basal respiration
C	Carbon
CO_2	Carbon dioxide
$CuSO_4$	Copper (II)-sulfate
dw	Soil dry weight
e.g.	*lat*: exempli gratia
H_2O-BAS	Water-induced basal respiration
i.e.	*lat*: id est
KOH	Potassium hydroxide
MAT	Mean annual temperature
MIRR	Maximal initial respiratory response
O_2	Oxygen
P	Precipitation
PET	Potential evapotranspiration
Prec	Precipitation
qO_2	Respiratory quotient
Sea_prec	Seasonal precipitation
SIR	Substrate induced respiration
UCC	United Nations Convention to Combat Desertification
UNEP	United Nations Environmental Programme

Appendix

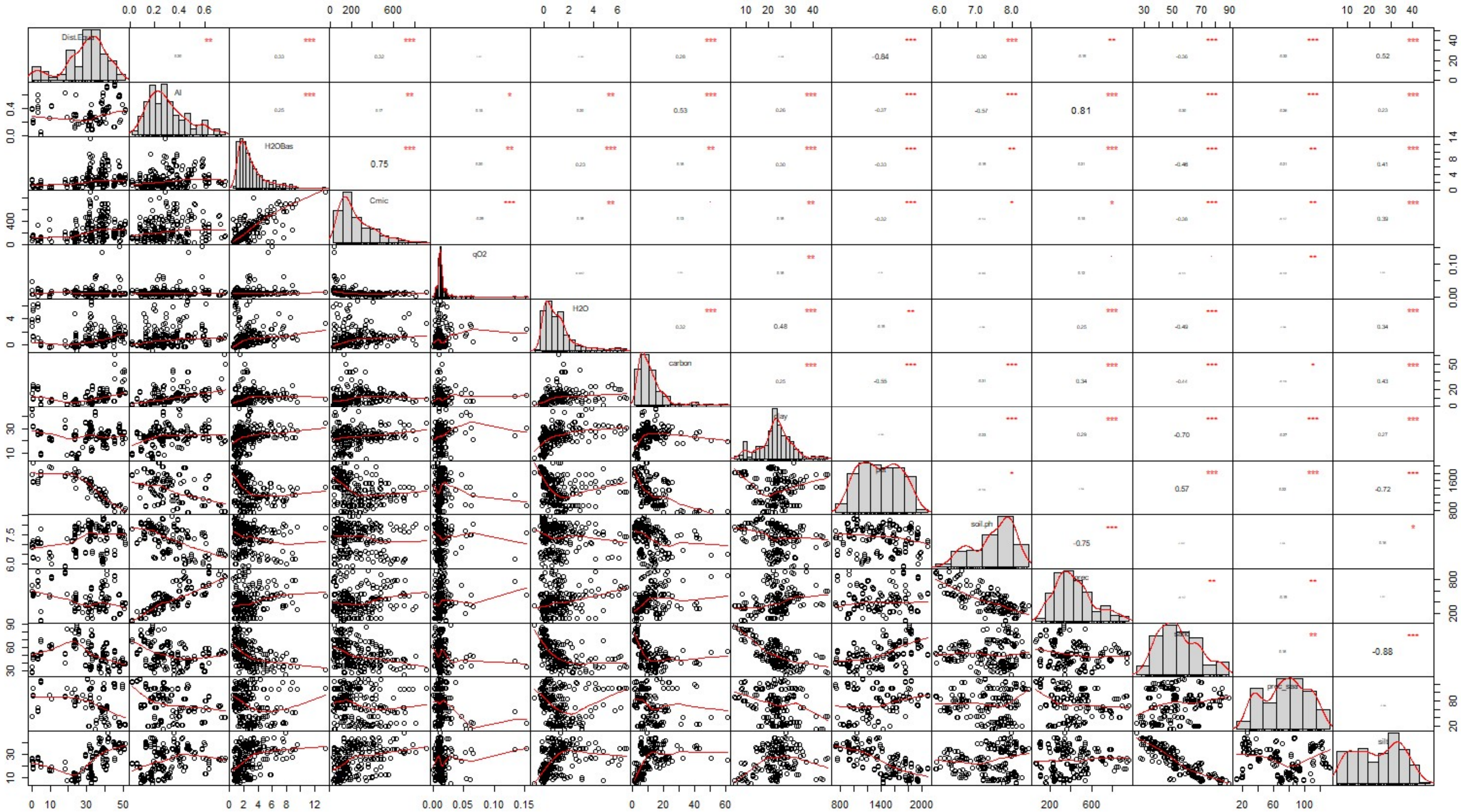


Figure 7: Correlation matrix comprising findings from this study with data from data bases (Table 3). Dist.Equa: distance from the equator, AI: aridity index, H2OBAS: water-induced basal respiration, Cmic: microbial biomass, qO2: respiratory quotient, H2O: soil water content, carbon: total soil carbon content, clay: amount of clay , pet: potential evapotranspiration, soil.ph: pH of the soil, prec: mean annual precipitation, sand: amount of sand, prec_sea: precipitation per season, silt: amount of silt. Significant correlations are marked with ***, **, * and R^2-values.

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