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Bioturbation enhances C and N contents on near-surface soils in resource-deficient arid climate regions but shows adverse effects in more temperate climates

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Abstract

Bioturbating animals can affect physical and chemical soil properties on near-surface soil by either foraging for food or constructing suitable habitats. Thereby, bioturbation can influence the soil texture either sorting or mixing the different grain sizes clay, silt and sand during burrowing. Additionally, bioturbating animals can increase the macronutrients carbon (C), nitrogen (N) and phosphorus (P) through the transport of nutrients by vertically mixing the soil column and the addition of the bioturbators' feces to the soil surface. To date, it is not clear how the effects of bioturbation on soil properties vary along an ecological gradient. Therefore, we compared the physical properties clay, silt and sand and the chemical contents of the macronutrients C, N and P for soil samples from mounds and the surrounding area as controls in three different climatic regions (arid, semi-arid and Mediterranean) of coastal Chile. To do so, we calculated the difference between the concentrations of paired mound and control samples. When comparing soil texture, we did not find significant differences between mound and control soil samples. For the macronutrient contents, the difference between mound and control C and N contents increased in the arid site and decreased in the two other research sites with increasing vegetation cover. Since we aimed to cover bioturbation patterns on a broader scale, we additionally compared our findings to other bioturbation studies performed in different biomes. Thereby, we found that other studies also show small differences in soil properties caused by bioturbation which are already sufficient to increase soil fertility.

Keywords: bioturbation, soil physical and chemical properties, macronutrients, soil fertility, climate gradient

1. Introduction

Bioturbating animals act as ecosystem engineers, as they physically and chemically alter their environment by foraging for food or constructing suitable habitats and dens (Day et al., 2003). Thereby, bioturbators, ranging in size from beetles and lizards to gophers and badgers, create a variety of above- and belowground soil patterns, particularly an increase in the proportion of fine soil compartments and macronutrients near the surface (Eldridge and Rath, 2002; Gutterman, 1997; Mallen-Cooper et al., 2019; Zaitlin and Hayashi, 2012).

Bioturbation can physically affect soil properties, mainly soil texture, through the vertical translocation of sediments (Phillips, 2001; Phillips and Lorz, 2008). Bioturbators transport the fine soil particles (< 2 mm) such as clay, silt or sand from deeper soil layers to the near-surface soil through digging along the soil column, which increases the proportion of these components in mounds created by bioturbators. This process also leads to an increased mixing of the vertical soil column (Eldridge, 2004; Hagenah and Bennett, 2013; Yurkewycz et al., 2014). In contrast and depending on body size, larger and heavier gravels cannot be vertically transported and hence, remain at the surface at the near-surface soil (Johnson, 1989; Ross et al., 1968; Wilkinson et al., 2009). Both, the sorting in fine and coarse-grained soil components, and the mixing of the fine-grained soil fraction due to bioturbation, was shown to

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enhance soil quality by increasing contents of soil nutrients and water holding capacity (Clark et al., 2018a; Moorhead et al., 1988; Wilkinson et al., 2009).

Beside these effects, bioturbation can also affect chemical soil properties, especially the availability of macronutrients such as carbon (C), nitrogen (N) and phosphorus (P) (Bardgett, 2010; Carlson and Whitford, 1991; Contreras et al., 1993; Eldridge and Whitford, 2014). This is mainly attributed to the transport of soluble nutrients to the near-surface soil during the active mixing of the vertical soil column (Abaturov, 1972). Several studies reported a positive correlation between bioturbation activity and C content in the near-surface soil (Faiz et al., 2018; Nkem et al., 2000; Yurkewycz et al., 2014; Platt et al., 2016; Frouz, 2020). Such an enrichment of C is possible since the C within the organic layer on the surface is exposed and unprotected to disturbances such as bioturbation and can easily be transported by bioturbators (Jandl et al., 2007; Zakharova et al., 2014). Consequently, bioturbation causes C fluxes between the different soil layers (Arai et al., 2007; Fröberg et al., 2005) leading to an increased C supply of the near-surface soil and accordingly to an accumulation of organic matter (OM) (Yurkewycz et al., 2014; Platt et al., 2016; Faiz et al., 2018). Further, bioturbation increases total N at the near-surface soil directly through the bioturbators' physical digging and thereby mixing of the soil layer bringing up the N from deeper soil layers (Lara et al.,2007; Laycock and Richardson, 1975; Hagenah and Bennett, 2013). This increase of N contents due to bioturbating animals is indirectly caused through the removal of N-enriched plants from the soil surface to either feed on them or to create burrows and dens (Tardiff and Stanford, 1998). At the same time, bioturbating animals regularly leave their urine and feces in the burrows (Mulder and Keall, 2001; Eldridge and Rath, 2002; Gervais et al., 2010; Whitford and Steinberger, 2010; Kurek et al., 2014; Yu et al., 2017). In that way, OM is trapped and its' decomposition results in higher N contents in the burrows and dens and the bioturbating animals then vertically transport this soil to the near-surface (James et al., 2009, 2011). In a similar way, bioturbation leads to increased P content near the surface as the decomposition of fecal and skeletal materials in burrow systems as well as the upward transport of caliche and deep soil material promote P enrichment on the near-surface soil (Carlson and White, 1988; Kelt, 2011; Willott et al., 2000).

However, while these general patterns with increasing soil nutrient contents have been observed primarily in arid climates (Nkem et al., 2000; Eldridge and Rath, 2002; Hagenah and Bennett, 2013), studies in temperate climates also showed a decrease in macronutrient contents on the near-surface soil (Sherrod and Seastedt, 2001; Eldridge and Mensinga, 2007; Lara et al., 2007; Eldridge and Koen, 2008). For example, Kurek et al. (2014) found that mounds created by badgers and foxes contained significantly less total N than the surrounding soil in a temperate climate zone. Such unexpected effects may appear due to the variable bioturbation activity depending on climate: It has been shown that bioturbation decreases from resource-limited, arid, to temperate climate regions which provide more resources such as food and habitat associated with ubiquitous vegetation (Kraus et al., 2022; Übernickel et al., 2021). This translates in animals needing to invest less energy into digging in areas with more resources, e.g. temperate regions. In turn, this means that burrowing is a beneficial strategy for animals living in resource-limited areas (Carlson and Whitford, 1991; Eldridge and Whitford, 2014; Ladegaard-Pedersen et al., 2005). Here, we aim to analyze the magnitude of the impact of bioturbation on chemical soil properties may be associated with climate and the associated varying vegetation cover. We therefore predicted that the magnitude of bioturbation on macronutrient contents is smaller in resource-rich in comparison to resource-limited climate regions where bioturbation activity and its' effects will appear on a larger scale. However, up until now, there are few analyses comparing the impact of bioturbation on soil properties comparing different climate regions.

To investigate this research gap, we compared the effects of bioturbation on soil physical and chemical properties along a climate and vegetation gradient ranging from the arid desert to the Mediterranean forest with comparable topography, size and geology in Chile. More specifically, we measured clay, silt and sand as physical soil properties and the macronutrients C, N and P as chemical soil properties for soil samples taken from mounds and surrounding area as unaffected controls. We compared the presented results to other studies in a literature review including publications of the influence of bioturbation on soil properties in different climate zones. This approach allows us to test the following hypotheses:

(1) Bioturbating animals affect soil texture, increasing the proportion of fine-grained soil compartments such as either clay, silt or sand at the near-surface soil, in comparison to undisturbed soil, especially in the arid research site.

(2) Bioturbation increases the C, N and P contents at the near-surface soil due to the decomposition of OM at the surface plus the accumulation of bioturbators' excrements, especially in the arid research site.

(3) The magnitude of bioturbation impacting the macronutrient contents (C, N, P) is greater in the resource-limited arid region than in the more humid regions harboring denser vegetation due to the food and shelter need of the bioturbating animals.

2. Materials and methods

2.1 Study area

Our study was performed within the EarthShape project investigating the effect of biota shaping Earth surface (https://esdynamics.geo.uni-tuebingen.de/earthshape/index.php?id=129). The study was conducted at three research sites along the Chilean Coastal Cordillera which were chosen due to their comparability in topography, size and geology since we aim to focus on the climatic influences on bioturbating animals (Table 1). All research sites (NP Pan de Azúcar, private reserve Santa Gracia , NP La Campana) are situated at a distance < 80 km of the coast and offer opposite north- and south-facing hillslopes. The general lithological compositions of the sites are similar, located in Cretaceous, Jurassic, and Permo-Carboniferous granitoid lithologies (Oeser et al., 2018). The vegetation cover is lowest in the arid desert (8.3%), followed by 34% in the semi-arid site, while in the Mediterranean site the cover is highest with up to 83.8% (Grigusova et al., 2022). In the semi-arid research site there were goats and in the Mediterranean research site there were cows acting as disturbances of this ecosystem (Armesto et al., 2007; Rundel and Weisser, 1975). However, these disturbances should not affect our analyses since we considered conducting our plots in areas not frequently visited by these animals (Table S1).

2.2 Study design

In the first field campaign, conducted in autumn of the southern hemisphere (March to April 2019), we established twelve 10 m x 10 m plots at each research site with a distance of at least 30 m between plots. In a second field campaign, conducted in spring of the southern hemisphere (September to November 2019), we complemented eight additional plots at each site, resulting in a total of 20 plots per site. The plots were evenly distributed across two opposing hillsides, 10 on the north- and 10 on the south-facing hillslope, but randomly distributed on each of the hillslopes.

All plots were examined for visible excavated mounds created through bioturbation. We applied a pairwise design: if multiple mounds occurred in one plot, a maximum of six soil samples were taken from randomly selected mounds, and the same amount of soil samples was taken from the surrounding, visually undisturbed soil as controls. If there was no mound detected within a plot, this plot was not included in our analysis.

2.3 Data collection

The soil samples were taken via an equal volume cylinder (100 cm³ volume) with a height of 5.1 cm. We drove the cylinder from the surface into the soil until we reached the appropriate depth when the upper part of the cylinder was in line with the soil surface. We collected 306 paired soil samples in total: 134 samples in 15 plots in Pan de Azúcar, 126 samples in twelve plots in Santa Gracia, 46 samples in nine plots in La Campana (Table 1).

We used mound density as a proxy for bioturbation activity (Nkem et al., 2000; Clark et al., 2018). Therefore, we counted the number of visible mounds in each plot by identifying excavated soil next to burrows, which appeared darker in colour than the surrounding soil.

To examine bioturbation in relation to climate and vegetation, we included additional characteristic features of each climate zone (arid, semi-arid, Mediterranean) such as hillside elevation, hillslope, and vegetation cover in our study. The variables elevation and hillslope were derived from high resolution Lidar data (Kügler et al., 2022). Vegetation cover was estimated at the plot level using unmanned aerial vehicle which created red-green-blue images on which land cover was classified (Grigusova et al., 2021). We calculated the ratio of pixels classified as any plant type (herbs, shrubs, cacti, trees) to the total amount of all pixels per plot.

2.4 Laboratory methods for soil properties

All soil samples were analyzed in the laboratory for soil analysis at the Department of Geography at the University of Marburg (Germany). This study comprises 302 soil samples since for four out of 306 samples (two samples from Pan de Azúcar and two samples from La Campana) we had no data due to failed measurements.

Soil texture data was produced using the standard procedure DIN ISO 11277:2002 with the goal to differentiate course from fine grained sediment (determine the proportions of clay, silt and sand in %). First, we detected and excluded particles larger than 2 mm. Then, the Pario device (Soil Particle

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Analyzer PARIO, METER Group, Germany) was used to further differentiate the grain size distribution of the fine-grained soil < 2 mm. This allows the determination of the proportion of clay and silt. We used 25 g of the soil sample for this analysis adding hydrogen peroxide and heating the sample afterwards to remove organic material. Then we added sodium pyrophosphate as a dispersant and afterwards transferred the suspension to a measuring cylinder to fill it up with distilled water to receive an overall volume of one liter. We stirred the suspension and inserted the Pario sensor into the liquid. After the Pario measurement, we determined the sand proportion by wet-sieving manually. We then incorporated the determined weight of the sand into the Pario program. As a final step, we calculated the percentages of clay, silt and sand and identified texture classes. Our sample size was reduced to n = 300 due to measurement failure in two samples.

To determine the concentrations of C and N (in %), we used a C/N analyzer (Vario El cube elemental analyzer, Elementar, Germany). For this analysis, we used 5 mg of the fine-grained portion of each soil sample. We transferred this sample into a tin ship and weighted the sample as well as the tin ship to enter the correct sample volume into the C/N analyzer. We then folded, closed and placed the tin ship into the C/N analyzer. We extrapolated the amount of C and N to a 5 mg soil sample considering the measurement deviations.

To quantify the concentration of P (in ppm), we used inductively coupled plasma mass spectrometry (ICP-MS), an elemental analysis technology capable of detecting most of the periodic table of elements at milligram to nanogram levels (Amman, 2007). Following the procedure DIN EN 16174, the fine-grained soil of each sample was first digested with aqua regia. For this, we mixed 1 g of soil sample with 15 ml of 37% hydrochloric acid and 65% nitric acid and cooked the sample for two hours for digestion. Afterwards, we filtered the cooled mixture and diluted it to a ratio of 1:50. Prior measurement, we again diluted the sample to a ratio of 1:50 and then measured with the ICP-MS (XSeriesII, ThermoFisher, Germany) following DIN EN ISO 17294-2: 2017-01 and DIN EN ISO 17294-2: 2005-02.

2.5 Statistical analyses

We used generalized linear mixed effect models (GLMMs) to analyze the effect of bioturbation on physical and chemical soil properties along the climate gradient. For that reason, we used physical soil properties (clay, silt and sand content) and chemical soil properties (C, N, P) as response variables. To compare properties between mounds and control, we calculated the difference between the content in physical (clay, silt, sand) and chemical properties (C, N, P) in mound and control soil samples which resulted in a variable characterizing the difference of the two samples. We used site, mound density, hillslope, hillside elevation, season and vegetation cover as fixed predictors while we used the study plots as a random factor (Table 2). Since we aim to understand the effect of bioturbation along our climate gradient, we included interaction terms between site and all other fixed predictor variables. We standardized the fixed predictor hillside elevation since it could not be assigned to each site separately without standardization. In order to approximate normality, we $\log_{10}$-transformed the fixed predictor variable mound density. This analysis includes 36 plots in which we could obtain soil samples (134 samples in 15 plots in Pan de Azúcar, 126 samples in twelve plots in Santa Gracia, 46 samples in nine plots in La Campana) from our both field campaigns (the first conducted in the southern-hemispheric autumn, the second conducted in the southern-hemispheric spring). We additionally checked for possible correlations by depicting all possible combinations between the response variables using the Pearson test.

All statistical analyses were performed using the R statistical environment (version 1.3.1093). We employed the *buildmer* (Voeten, 2019) function for the GLMMs to perform backward stepwise selection and additionally calculated the AIC. To determine the proportion of variation explained by the model in total including fixed and random effects, we calculated R-squared for the fitted models using the *rsq* command from the *rsq* package (Zhang, 2020).

2.6 Literature review

To compare the input of physical (clay, silt, sand) and chemical (C, N, P) soil properties and its' effect on ecosystem functioning, we screened papers from different climate settings which performed similar analysis to ours quantifying the effects of bioturbation. Out of these papers, we filtered the amount of clay, silt, sand, C, N, P for mound and control soil, calculated the percentual input and listed the impacts of bioturbation mentioned in the studies (Table S10) for comparison to our study.

3. Results

The proportions of the physical soil properties clay, silt and sand did not vary significantly between mound and control soil samples in all three research sites, as well as across sites (Fig. 1,Table S2). The content of the chemical soil properties C and N increased along the climate gradient from Pan de Azúcar to La Campana both in mound and control samples while P content remained constant across all three research sites (Fig. 2,Table S2). Mound samples showed higher contents in C, N and P than control samples across all research sites: Considering just the mean of the macronutrient samples from mound and control, the C content was 20% higher in Pan de Azúcar, 28% higher in Santa Gracia and 52% higher in La Campana for mound than control samples. Mound samples contained 25% more N in Pan de Azúcar, 10% more N in Santa Gracia and 44% more N in La Campana than control samples. The P content was 12% higher in Pan de Azúcar, 14% higher in Santa Gracia and 21% higher in La Campana for mound than control soil samples (Table S2).

It is important to note that similar patterns may be observed because some of the dependent variables show correlations among each other. This is why we calculated all possible combinations between the response variables and since some of these variables are correlated (Table S3), we present just silt, C and N here.

When fitting GLMMs for the physical soil properties, only the model for silt contained significant predictors with the fixed predictor hillslope and the interaction between mound density and the site Pan de Azúcar explaining 5% of the model variation (AIC = -79.7, $p < 0.1$, Supplementary Table S5). The silt content increased in Pan de Azúcar with increasing mound density while it decreased in Santa Gracia and La Campana (Fig. 3A). In all research sites, the silt content increased with increasing hillslope (Fig. S1A).

Out of the GLMMs for the chemical soil properties, the models for C and N contained significant predictors with the fixed predictors mound density, vegetation cover and hillslope explaining 31% of the

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variation in the response variable (AIC = 730.6, $p < 0.001$, Supplementary Table S7) within the fitted model for the chemical soil property C content. Within the fitted GLMM for N, the fixed predictors vegetation cover and hillside elevation explained 6% of the model variation (AIC = 148.2, $p < 0.01$, Supplementary Table S8). The C content decreased in Pan de Azúcar and La Campana and remained constant in Santa Gracia (Fig. 3B) due to bioturbation. For both macronutrients, C and N, the same trends occurred in the fitted models (Fig. 4): C and N contents were positively associated with increasing vegetation cover in Pan de Azúcar but negatively associated in Santa Gracia and La Campana. C content was positively associated with hillslope in La Campana but remained constant in Pan de Azúcar and Santa Gracia (Fig. S1B). N content decreased with increasing hillside elevation in La Campana but remained constant in the two northern research sites (Fig. S2). When considering the relationship between soil properties and mound density, the physical soil property silt did not change with increasing mound density (Fig. 5A) whereas the chemical C content decreased with increasing mound density across all research sites (Fig. 5B).

4. Discussion

In our study, bioturbation increased the contents of C and N with increasing vegetation cover on the near-surface soil in the arid research site. In contrast, C and N contents decreased with increasing vegetation cover in the two other research sites. Neither the macronutrient P content nor the physical soil properties of the near-surface soil were related to bioturbation activity. Additionally, we found that near-surface soil contents of all investigated properties affected by the bioturbators did not increase with increasing mound density which we interpreted as a proxy for bioturbation activity (see section “2.3 data collection” in methods). This finding clearly shows that bioturbation did not always lead to an input but had only small effects on soil properties.

Overall, we observed similar patterns for C and N contents in our study when comparing the difference in absolute concentration between mound and control samples in comparison to other studies (see Table S10 “% input (mound-control)”). For instance, the C input in our study was 20% in the arid zone (and 28 % in the semi-arid zone) which is concomitant to findings of Nkem et al. (2000) with 18% C input due to bioturbation within the arid climate zone. In contrast, in the Mediterranean climate zone C input was 52% while another study showed a lower C input of 9% (Yurkewycz et al., 2014). The N input in the arid climate zone contained 25% (and 21% in the semi-arid zone) in our study in contrast to another finding of Eldridge and Koen (2008) showing a decrease in N of 45%. Within the Mediterranean climate zone, N input of our study with 21% was similar compared to 8% N input found by Yurkewycz et al. (2014). In summary, even though the input of C and N contents caused by bioturbation in previous studies and our study is small, it can be significant: already low N input stimulates plant growth while C input leads to an increased C uptake by the plants which can contribute to the mitigation of climate change (Ciais et al., 2008; Pregitzer et al., 2008; Reay et al., 2008; Thomas, 2010). Consequently, the observed C and N input associated with vegetation cover in the desert due to bioturbation in our study might improve soil fertility and through this enhance plant growth in near-surface soils (Mulder and Keall, 2001; Eldridge and Rath, 2002; Gervais et al., 2010; Whitford and Steinberger, 2010; Kurek et al., 2014; Yu et al., 2017).

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In contrast to our first hypothesis we found no enrichment of clay, silt or sand particles in mound samples. One possible explanation for this observation is that over a longer time period, the small, and easily erodible clay, silt or sand particles were transported (eroded) by water (Simkin et al., 2004) or wind (Ravi et al., 2007) from the exposed soil in animal mounds, and subsequently redistributed on surfaces nearby, which will be in a later time subject to burrowing. This process would reduce differences between mounds and controls, and lead to an equalization of fine soil particles on the hillslope. This would mean that, if bioturbation occurs to a greater extend, the near-surface soil becomes in time so homogenized through the burrowing process that differences minimalize (Dostál et al., 2005; Johnson, 1989). Such patterns have been found elsewhere, e.g. in temperate Slovakia where ant bioturbation led to the homogenization of the soil (Dostál et al., 2005).

With regards to the macronutrients, our second hypothesis stating that bioturbation increases C, N and P contents was not supported for the whole climate gradient since C and N contents did not increase in the semi-arid and Mediterranean research sites. However, within the arid research site, C and N contents were higher for mound than for control samples. This small scale heterogeneity is in line with many other studies, which argue that animals incorporate plant derived C, and N from feces through burrowing activity. This process is commonly associated with improvement of soil fertility through macronutrient input, and an increase in soil and vegetation heterogeneity at small scales (Jouquet et al., 2017; Yurkewycz et al., 2014b). This has been found to lead to a positive influence of bioturbation on plant growth, establishing indigenous plant species, and even sometimes protecting semi-arid ecosystems from disturbance events such as fire or erosion (Dostál et al., 2005; Eldridge and Koen, 2008; Clark et al., 2018). In contrast to the macronutrients C and N, the P content in all three research sites did not change due to bioturbation (Garkaklis et al., 2003; Hagenah and Bennett, 2013). This is surprising, as most previous studies revealed an increased P content with bioturbation, which has been shown to increase plant abundance and diversity (Carlson and Whitford, 1991; Dostál et al., 2005; Nkem et al., 2000). A possible explanation for the steady P content in our study is that higher bioturbation activity might speed up leaching of susceptible macronutrients such as P in contrast to the more resistant C and N (Garkaklis et al., 2003; Mohr et al., 2005). Like already mentioned for the soil texture, the soil P content might also remain constant since the near-surface soil becomes homogenized if bioturbation occurs to a greater extent (Dostál et al., 2005; Johnson, 1989).

Our observation of different C and N patterns along the climate gradient due to bioturbation is concomitant with our third hypothesis stating that the influence of bioturbating animals on the macronutrient inputs differs depending on the climate region and the concomitant available resources. Previous studies confirmed that bioturbation activity depends on the different climate concomitant with varying vegetation patterns (Don et al., 2019; Eldridge and Whitford, 2014; Jouquet et al., 2017; Kraus et al., 2022; Wilkinson et al., 2009; Yu et al., 2017). One reason therefore is that in arid climate regions bioturbation occurs due to the loss of shelter like plants protecting the animals from the sun or predation which explains that burrowing animals in the desert prefer digging next to the occurring sparse vegetation and during this process, they bury plants or plant parts resulting in higher C and N contents within bioturbated soils (Raymond P. Yurkewycz et al., 2014; Platt et al., 2016; Faiz et al., 2018). In contrast, C and N contents in this and other studies did not significantly change in bioturbated compared

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to unaffected soils in climate regions providing more resources where digging is not as necessary (Dostál et al., 2005; Eldridge and Koen, 2008; Clark et al., 2018). In a previous study, we showed that bioturbation patterns are distributed more patchy in the arid research site than in the two other ones which might additionally explain why the macronutrients are distributed more homogeneously in the semi-arid and Mediterranean sites (Grigusova et al., 2021). An additional explanation for the differing macronutrients patters along the climate gradient is that the macronutrient content largely depends on the occurring vegetation (Carlson and Whitford, 1991; Eldridge and Whitford, 2014). Thereby, in regions with greater vegetation cover than in deserts, bioturbating animals can cause the destruction of plants or plant parts while burrowing (Contreras et al., 1993) which could also explain the observed decrease in C and N contents in the semi-arid and Mediterranean regions in our study. This is supported by previous research which showed that tunneling through bioturbation reduces 20 – 50% of vegetation cover over active burrows (Contreras et al., 1993). Another reason for the deficiency of C and N contents in the climate regions with denser vegetation than the arid climate zone is the C and N uptake by plants: both macronutrients, C and N, are crucial for several cellular plant functions (Zheng, 2009). Hence, C is used as an energy source for photosynthesis or assimilated by vegetation and later transferred as plant litter to the soil as soil OM (Bassham and Calvin, 1960). N is an important component of chlorophyll involved in photosynthesis as well as a major component of amino acids for protein building (Evans, 1989; Stocking and Ongun, 1962). Therefore, the depletion of C and N in the research sites with more vegetation cover such as semi-arid and Mediterranean might occur due to the uptake of these macronutrients by plants. In our study, we saw similar effects of bioturbation for both, C and N, since these two macronutrients are often intertwined because C and N immobilization by plants controls soil development (Walker and Moral, 2003).

5. Conclusion

Our study revealed that the effects of bioturbation on soil macronutrient contents of C and N vary with climate. While bioturbation leads to an increase of C and N contents associated with increasing vegetation cover in the arid zone, it leads to a decrease of C and N contents in the semi-arid and Mediterranean zones. This is likely because animals depend heavily on the resources they gain from the occurring vegetation such as food and shelter. Because of the observed C and N inputs due to burrowing animals we support that bioturbation impacts ecosystem functioning by improving soil fertility as well as mitigating climate change by contributing to C increase and thereby C uptake by plants. For an overarching understanding of the effects of bioturbation on soil properties, further studies should explore all existing climate regions as well as further exploring the various effects of bioturbation on ecosystem functions.

Supplementary material

Code availability

The R code and the datasets generated and analyzed within the current study are available from the corresponding author on reasonable request.

Author contributions

Diana Kraus: Investigation, Data curation, Formal analysis, Writing- Original draft, preparation, Visualization

Roland Brandl: Resources, Funding acquisition, Methodology, Conceptualization, Writing-Reviewing and Editing

Jörg Bendix: Resources, Funding acquisition, Methodology, Conceptualization, Writing-Reviewing and Editing

Paulina Grigusova: Data curation, Funding acquisition, Writing-Reviewing and Editing

Sabrina Köhler: Data curation, Formal analysis

Annegret Larsen: Resources, Funding acquisition, Methodology, Conceptualization, Writing-Reviewing and Editing

Patricio Pliscoff: Project administration, Writing-Reviewing and Editing

Kirstin Übernickel: Project administration, Writing-Reviewing and Editing

Nina Farwig: Resources, Funding acquisition, Methodology, Conceptualization, Writing-Reviewing and Editing

Competing interests

The authors declare that they have no conflict of interest.

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References

Abaturov, B.: The role of burrowing animals in the transport of mineral substances in the soil, Pedobiologia (Jena)., 12, 261–266 [online] Available from: https://cir.nii.ac.jp/crid/1573668925545645824 (Accessed 26 October 2022), 1972.

Arai, H., Tokuchi, N. and Koba, K.: Possible Mechanisms Leading to a Delay in Carbon Stock Recovery after Land Use Change, Soil Sci. Soc. Am. J., 71(5), 1636–1638, doi:10.2136/SSSAJ2005.0309, 2007.

Bardgett, R.: The Biology of Soil: A community and ecosystem approach., 2010.

Bassham, J. A. and Calvin, M.: The path of carbon in photosynthesis, Die CO2-Assimilation / Assim. Carbon Dioxide, 884–922, doi:10.1007/978-3-642-94798-8_30, 1960.

Carlson, D. C. and White, E. M.: Variations in Surface-Layer Color, Texture, pH, and Phosphorus Content Across Prairie Dog Mounds, Soil Sci. Soc. Am. J., 52(6), 1758–1761, doi:10.2136/SSSAJ1988.03615995005200060044X, 1988.

Carlson, S. R. and Whitford, W. G.: Ant Mound Influence on Vegetation and Soils in a Semiarid Mountain Ecosystem, Am. Midl. Nat., 126(1), 125, doi:10.2307/2426157, 1991.

Clark, K. L., Branch, L. C. and Farrington, J.: Bioturbation by mammals and fire interact to alter ecosystem-level nutrient dynamics in longleaf pine forests, PLoS One, 13(8), e0201137, doi:10.1371/JOURNAL.PONE.0201137, 2018a.

Clark, K. L., Branch, L. C. and Farrington, J.: Bioturbation by mammals and fire interact to alter ecosystem-level nutrient dynamics in longleaf pine forests, PLoS One, 13(8), e0201137, doi:10.1371/JOURNAL.PONE.0201137, 2018b.

Contreras, L., … J. G.-R. C. and 1993, undefined: Ecological relevance of subterranean herbivorous rodents in semiarid coastal Chile, rchn.biologiachile.cl [online] Available from: http://rchn.biologiachile.cl/pdfs/1993/3/Contreras_1993.pdf (Accessed 28 March 2022), n.d.

Contreras, L. C., Gutierrez, J. R., Valverde, V. and Cox, G. W.: Ecological relevance of subterranean herbivorous rodents in semiarid coastal Chile , Rev. Chil. Hist. Nat., (66), 357–368 [online] Available from: http://rchn.biologiachile.cl/pdfs/1993/3/Contreras_1993.pdf (Accessed 26 October 2022), 1993.

Day, R. L., Laland, K. N. and Odling-Smee, J.: Rethinking adaptation: the niche-construction perspective, Perspect. Biol. Med., 46(1), 80–95, doi:10.1353/PBM.2003.0003, 2003.

Don, A., Hagen, C., Grüneberg, E. and Vos, C.: Simulated wild boar bioturbation increases the stability of forest soil carbon, Biogeosciences, 16(21), 4145–4155, doi:10.5194/BG-16-4145-2019, 2019.

Dostál, P., Březnová, M., Kozlíčková, V., Herben, T. and Kovář, P.: Ant-induced soil modification and its effect on plant below-ground biomass, Pedobiologia (Jena)., doi:10.1016/j.pedobi.2004.09.004, 2005.

Eldridge, D. J.: Mounds of the American Badger (Taxidea Taxus): Significant Features of North American Shrub-Steppe Ecosystems, J. Mammal., 85(6), 1060–1067, doi:10.1644/BEH-105.1, 2004.

Eldridge, D. J. and Koen, T. B.: Formation of nutrient-poor soil patches in a semi-arid woodland by the European rabbit (Oryctolagus cuniculus L.), Austral Ecol., 33(1), 88–98, doi:10.1111/J.1442-9993.2007.01793.X, 2008.

Eldridge, D. J. and Mensinga, A.: Foraging pits of the short-beaked echidna (Tachyglossus aculeatus) as small-scale patches in a semi-arid Australian box woodland, Soil Biol. Biochem., doi:10.1016/j.soilbio.2006.11.016, 2007.

Eldridge, D. J. and Rath, D.: Hip holes: kangaroo (Macropus spp.) resting sites modify the physical and chemical environment of woodland soils, Austral Ecol., 27(5), 527–536, doi:10.1046/J.1442-9993.2002.01212.X, 2002.

Eldridge, D. J. and Whitford, W. G.: Disturbances by desert rodents are more strongly associated with spatial changes in soil texture than woody encroachment, Plant Soil, doi:10.1007/s11104-014-2142-5, 2014.

Evans, J. R.: The allocation of protein nitrogen in the photosynthetic apparatus: Costs, consequences, and control Dual-purpose crops View project, [online] Available from: https://www.researchgate.net/publication/285010849 (Accessed 26 October 2022), 1989.

Faiz, A. H., Fakhar-I-Abbas and Faiz, L. Z.: Burrowing activity of rodents alter soil properties: A case study on the short tailed mole rat (Nesokia Indica) in Pothwar Plateau, Punjab, Pakistan, Pak. J. Zool., 50(2), 719–724, doi:10.17582/JOURNAL.PJZ/2018.50.719.724, 2018.

Fröberg, M., Kleja, D. B., Bergkvist, B., Tipping, E. and Mulder, J.: Dissolved organic carbon leaching from a coniferous forest floor - A field manipulation experiment, Biogeochemistry, 75(2), 271–287, doi:10.1007/S10533-004-7585-Y, 2005.

Frouz, J.: Soil biodiversity conservation for mitigating climate change, Clim. Chang. Soil Interact., 1–19, doi:10.1016/B978-0-12-818032-7.00001-1, 2020.

Garkaklis, M. J., Bradley, J. S. and Wooller, R. D.: The relationship between animal foraging and nutrient patchiness in south-west Australian woodland soils, Soil Res., 41(4), 665–673, doi:10.1071/SR02109, 2003.

Gervais, J. A., Griffith, S. M., Davis, J. H., Cassidy, J. R. and Dragila, M. I.: Effects of Gray-tailed Vole Activity on Soil Properties, https://doi.org/10.3955/046.084.0205, 84(1), 159–169, doi:10.3955/046.084.0205, 2010.

Grigusova, P., Larsen, A., Achilles, S., Klug, A., Fischer, R., Kraus, D., Übernickel, K., Paulino, L., Pliscoff, P., Brandl, R., Farwig, N. and Bendix, J.: Area-wide prediction of vertebrate and invertebrate hole density and depth across a climate gradient in chile based on uav and machine learning, Drones, 5(3), 86, doi:10.3390/drones5030086, 2021.

Grigusova, P., Larsen, A., Achilles, S., Brandl, R., del Río, C., Farwig, N., Kraus, D., Paulino, L., Pliscoff, P., Übernickel, K. and Bendix, J.: Time-Of-Flight monitoring reveals higher sediment redistribution rates related to burrowing animals than previously assumed, Earth

Surf. Dyn. Discuss., 1–43, doi:10.5194/ESURF-2021-104, 2022.

Gutterman, Y.: Ibex diggings in the Negev Desert highlands of Israel as microhabitats for annual plants. Soil salinity, location and digging depth affecting variety and density of plant species, J. Arid Environ. (United Kingdom), doi:10.3/JQUERY-UI.JS, 1997.

Hagenah, N. and Bennett, N. C.: Mole rats act as ecosystem engineers within a biodiversity hotspot, the Cape Fynbos, J. Zool., doi:10.1111/j.1469-7998.2012.00958.x, 2013.

James, A. I., Eldridge, D. J. and Hill, B. M.: Foraging animals create fertile patches in an Australian desert shrubland, Ecography (Cop.)., 32(5), 723–732, doi:10.1111/j.1600-0587.2009.05450.x, 2009.

James, A. I., Eldridge, D. J., Koen, T. B. and Moseby, K. E.: Can the invasive European rabbit (Oryctolagus cuniculus) assume the soil engineering role of locally-extinct natives?, Biol. Invasions, 13(12), 3027–3038, doi:10.1007/s10530-011-9987-9, 2011.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D. W., Minkkinen, K. and Byrne, K. A.: How strongly can forest management influence soil carbon sequestration?, Geoderma, 137(3–4), 253–268, doi:10.1016/J.GEODERMA.2006.09.003, 2007.

Johnson, D. L.: Subsurface Stone Lines, Stone Zones, Artifact-Manuport Layers, and Biomantles Produced by Bioturbation via Pocket Gophers (Thomomys Bottae), Am. Antiq., 54(2), 370–389, doi:10.2307/281712, 1989.

Jouquet, P., Caner, L., Bottinelli, N., Chaudhary, E., Cheik, S. and Riotte, J.: Where do South-Indian termite mound soils come from?, Appl. Soil Ecol., 117–118, 190–195, doi:10.1016/J.APSOIL.2017.05.010, 2017.

Kelt, D. A.: Comparative ecology of desert small mammals: A selective review of the past 30 years, J. Mammal., 92(6), 1158–1178, doi:10.1644/10-MAMM-S-238.1, 2011.

Kraus, D., Brandl, R., Achilles, S., Rg Bendix, J., Grigusova, P., Larsen, A., Pliscoff, P., Bernickel, K. U. ¨ and Farwig, N.: Vegetation and vertebrate abundance as drivers of bioturbation patterns along a climate gradient, edited by T. Bhadauria, PLoS One, 17(3), e0264408, doi:10.1371/JOURNAL.PONE.0264408, 2022.

Kügler, M., Hoffmann, T. O., Beer, A. R., Übernickel, K., Ehlers, T. A., Scherler, D. and Eichel, J.: (LiDAR) 3D Point Clouds and Topographic Data from the Chilean Coastal Cordillera, , doi:10.5880/FIDGEO.2022.002, 2022.

Kurek, P., Kapusta, P. and Holeksa, J.: Burrowing by badgers (Meles meles) and foxes (Vulpes vulpes) changes soil conditions and vegetation in a European temperate forest, Ecol.

Res., doi:10.1007/s11284-013-1094-1, 2014.

Ladegaard-Pedersen, P., Elberling, B. and Vesterdal, L.: Soil carbon stocks, mineralization rates, and CO2 effluxes under 10 tree species on contrasting soil types, Can. J. For. Res., 35(6), 1277–1284, doi:10.1139/X05-045, 2005.

Lara, N., Sassi, P. and Borghi, C. E.: Effect of Herbivory and Disturbances by Tuco-Tucos (Ctenomys Mendocinus) on a Plant Community in the Southern Puna Desert, [online] Available from: https://bioone.org/journals/arctic-antarctic-and-alpine-research/volume-39/issue-1/1523-0430_2007_39_110_EOHADB_2.0.CO_2/Effect-of-Herbivory-and-Disturbances-by-Tuco-Tucos-Ctenomys-Mendocinus/10.1657/1523-0430(2007)39[110:EOHADB]2.0.CO;2.full (Accessed 26 October 2022), n.d.

Laycock, W. A. and Richardson, B. Z.: Long-Term Effects of Pocket Gopher Control on Vegetation and Soils of a Subalpine Grassland, J. Range Manag., 28(6), 458, doi:10.2307/3897222, 1975.

Mallen-Cooper, M., Nakagawa, S. and Eldridge, D. J.: Global meta-analysis of soil-disturbing vertebrates reveals strong effects on ecosystem patterns and processes, Glob. Ecol. Biogeogr., 28(5), 661–679, doi:10.1111/GEB.12877, 2019.

Mohr, D., Cohnstaedt, L. W. and Topp, W.: Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel, Soil Biol. Biochem., 37(4), 693–700, doi:10.1016/J.SOILBIO.2004.10.002, 2005.

Moorhead, D. L., Fisher, F. M. and Whitford, W. G.: Cover of spring annuals on nitrogen-rich kangaroo rat mounds in a Chihuahuan Desert grassland, Am. Midl. Nat., 120(2), 443–447, doi:10.2307/2426018, 1988.

Mulder, C. P. H. and Keall, S. N.: Burrowing seabirds and reptiles: Impacts on seeds, seedlings and soils in an island forest in New Zealand, Oecologia, 127(3), 350–360, doi:10.1007/s004420000600, 2001.

Nkem, J. N., Lobry De Bruyn, L. A., Grant, C. D. and Hulugalle, N. R.: The impact of ant bioturbation and foraging activities on surrounding soil properties, Pedobiologia (Jena)., doi:10.1078/S0031-4056(04)70075-X, 2000.

Oeser, R. A., Stroncik, N., Moskwa, L. M., Bernhard, N., Schaller, M., Canessa, R., van den Brink, L., Köster, M., Brucker, E., Stock, S., Fuentes, J. P., Godoy, R., Matus, F. J., Oses Pedraza, R., Osses McIntyre, P., Paulino, L., Seguel, O., Bader, M. Y., Boy, J., Dippold, M. A., Ehlers, T. A., Kühn, P., Kuzyakov, Y., Leinweber, P., Scholten, T., Spielvogel, S., Spohn, M., Übernickel, K., Tielbörger, K., Wagner, D. and von Blanckenburg, F.: Chemistry and microbiology of the Critical Zone along a steep climate and vegetation gradient in the Chilean Coastal Cordillera, CATENA, 170, 183–203, doi:10.1016/J.CATENA.2018.06.002, 2018.

Phillips, J. D.: Contingency and generalization in pedology, as exemplified by texture-contrast soils, Geoderma, 102(3–4), 347–370, doi:10.1016/S0016-7061(01)00041-6, 2001.

Phillips, J. D. and Lorz, C.: Origins and implications of soil layering, Earth-Science Rev., 89(3–4), 144–155, doi:10.1016/J.EARSCIREV.2008.04.003, 2008.

Platt, B. F., Kolb, D. J., Kunhardt, C. G., Milo, S. P. and New, L. G.: Burrowing through the literature: The impact of soil-disturbing vertebrates on physical and chemical properties of soil, Soil Sci., 181(3–4), 175–191, doi:10.1097/SS.0000000000000150, 2016a.

Platt, B. F., Kolb, D. J., Kunhardt, C. G., Milo, S. P. and New, L. G.: Burrowing Through the Literature, Soil Sci., doi:10.1097/ss.0000000000000150, 2016b.

Ravi, S., D’Odorico, P., Zobeck, T. M., Over, T. M. and Collins, S. L.: Feedbacks between fires and wind erosion in heterogeneous arid lands, J. Geophys. Res. Biogeosciences, 112(G4), doi:10.1029/2007JG000474, 2007.

Ross, B. A., Tester, J. R. and Breckenridge, W. J.: Ecology of Mima-Type Mounds in Northwestern Minnesota, Ecology, 49(1), 172–177, doi:10.2307/1933579, 1968.

Sherrod, S. K. and Seastedt, T. R.: Effects of the northern pocket gopher (Thomomys talpoides) on alpine soil characteristics, Niwot Ridge, CO, Biogeochem. 2001 552, 55(2), 195–218, doi:10.1023/A:1010621102330, 2001.

Simkin, S. M., MICHENER, W. K. and WYATT, R.: Mound Microclimate, Nutrients and Seedling Survival, https://doi.org/10.1674/0003-0031(2004)152[0012:MMNASS]2.0.CO;2, 152(1), 12–24, doi:10.1674/0003-0031(2004)152, 2004.

Stocking, C. R. and Ongun, A.: THE INTRACELLULAR DISTRIBUTION OF SOME METALLIC ELEMENTS IN LEAVES, Am. J. Bot., 49(3), 284–289, doi:10.1002/J.1537-2197.1962.TB14939.X, 1962.

Tardiff, S. E. and Stanford, J. A.: Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability, Ecology, 79(7), 2219–2228, doi:10.1890/0012-9658, 1998.

Übernickel, K., Ehlers, T. A., Ershadi, M. R., Paulino, L., Fuentes Espoz, J.-P., Maldonado, A., Oses-Pedraza, R. and von Blanckenburg, F.: Time series of meteorological station data in the EarthShape study areas in the Coastal Cordillera, Chile, [online] Available from: https://dataservices.gfz-potsdam.de/panmetaworks/showshort.php?id=d4691c94-1d01-11eb-9603-497c92695674 (Accessed 2 November 2021), 2020.

Übernickel, K., Pizarro-Araya, J., Bhagavathula, S., Paulino, L. and Ehlers, T. A.: Reviews and syntheses: Composition and characteristics of burrowing animals along a climate and ecological gradient, Chile, Biogeosciences, 18(20), 5573–5594, doi:10.5194/BG-18-5573-2021, 2021.

Voeten, C. C.: Using “buildmer” to automatically find & compare maximal (mixed) models, 2019.

Walker, L. R. and Moral, R. del: Primary succession and ecosystem rehabilitation / Lawrence R. Walker and Roger del Moral. [online] Available from: https://books.google.de/books?hl=en&lr=&id=fkfr24g-PCkC&oi=fnd&pg=PR12&dq=Walker+and+del+Moral,+2003&ots=LdsN6PfTjT&sig=xC_FJGq-P1To1qYt5lZrnSDxo4Q&redir_esc=y#v=onepage&q&f=false (Accessed 26 October 2022), 2003.

Whitford, W. G. and Steinberger, Y.: Pack rats (Neotoma spp.): Keystone ecological engineers?, J. Arid Environ., 74(11), 1450–1455, doi:10.1016/J.JARIDENV.2010.05.025, 2010.

Wilkinson, M. T., Richards, P. J. and Humphreys, G. S.: Breaking ground: Pedological, geological, and ecological implications of soil bioturbation, Earth-Science Rev., doi:10.1016/j.earscirev.2009.09.005, 2009.

Willott, S. J., Miller, A. J., Incoll, L. D. and Compton, S. G.: The contribution of rabbits (Oryctolagus cuniculus L.) to soil ferility semi-arid, Biol. Fertil. Soils, 31(5), 379–384, doi:10.1007/s003749900183, 2000.

Yu, C., Zhang, J., Pang, X. P., Wang, Q., Zhou, Y. P. and Guo, Z. G.: Soil disturbance and disturbance intensity: Response of soil nutrient concentrations of alpine meadow to plateau pika bioturbation in the Qinghai-Tibetan Plateau, China, Geoderma, 307, 98–106, doi:10.1016/J.GEODERMA.2017.07.041, 2017.

Yurkewycz, R. P., Bishop, J. G., Charles, ·, Crisafulli, M., Harrison, J. A., Gill, R. A., Yurkewycz, R. P., Harrison, J. A., Bishop, J. G., Crisafulli, C. M. and Gill, R. A.: ECOSYSTEM ECOLOGY-ORIGINAL RESEARCH Gopher mounds decrease nutrient cycling rates and increase adjacent vegetation in volcanic primary succession, Oecologia, 1, 1135–1150, doi:10.1007/s00442-014-3075-7, 2014.

Zaitlin, B. and Hayashi, M.: Interactions between soil biota and the effects on geomorphological features, Geomorphology, 157–158, 142–152, doi:10.1016/J.GEOMORPH.2011.07.029, 2012.

Zakharova, A., Midwood, A. J., Hunt, J. E., Graham, S. L., Artz, R. R. E., Turnbull, M. H., Whitehead, D. and Millard, P.: Loss of labile carbon following soil disturbance determined by measurement of respired ∂13CO2, Soil Biol. Biochem., 68, 125–132, doi:10.1016/J.SOILBIO.2013.10.001, 2014.

Zhang, D.: Rsq: R-Squared and Related Measures. R package, 2020.

Zheng, Z. L.: Carbon and nitrogen nutrient balance signaling in plants, https://doi.org/10.4161/psb.4.7.8540, 4(7), 584–591, doi:10.4161/PSB.4.7.8540, 2009.

Table 1

Coordinates and characteristics of the research sites arranged by latitude (from north to south). Depicted are the coordinates, elevation, mean annual temperature, mean annual precipitation, number of plots with mounds (out of 20 randomly-selected plots) and the number of paired samples per research site (Pan de Azúcar, Santa Gracia, La Campana). The mean temperature and annual precipitation of the year 2019 was obtained from weather stations created within the EarthShape project (Übernickel et al., 2020). We chose to show the temperature and precipitation for 2019 since the study was conducted during this year.

	Pan de Azúcar	Santa Gracia	La Campana
Center coordinate lat	S26° 10.749	S29° 22.878	S32° 41.202
Center coordinate long	W70° 34.782	W71° 9.516	W70° 50.346
Elevation [m. a. s. l.]	667 - 795	637 - 742	441 - 740
Annual temperature [°C]	14.6	14.4	14.9
Annual precipitation [mm]	9.4	20.8	63.8
Sampled plots	15	12	9
Total number of samples	134	126	46

Table 2

Summary of physical and chemical response variables as well as the fixed predictors site, mound density, hillslope, hillside elevation, season and vegetation cover used in all GLMMs. Depicted are the minimum and maximum values for all predictors except for site (Pan de Azúcar, Santa Gracia, La Campana) and season (autumn and spring) since there are no minimum and maximum values. The response variables were the difference of the particular characteristic between mound and control. As a random factor we used 59 plots.

Response variables	Minimum	Maximum	Mean
Clay content (mound - control) [%]	-0.73	0.38	-0.0021
Silt content (mound - control) [%]	-0.53	0.55	-0.016
Sand content (mound - control) [%]	-0.57	0.62	0.019
C content (mound - control) [%]	-4.75	13.68	0.95
N content (mound - control) [%]	-0.64	2.55	0.087
P content (mound - control) [ppm]	-1.94	2.04	0.1
Fixed predictors			

Site	no ranking: Pan de Azúcar, Santa Gracia, La Campana		
Mound density [No/ 100 m²]	1	44	8.56
Hillslope [°]	8.35	41.08	22.59
Hillside elevation [m a. s. l.]	441.3	795.4	688.3
Season	no ranking: autumn, spring		
Vegetation cover [%]	0.18	96.65	22.27

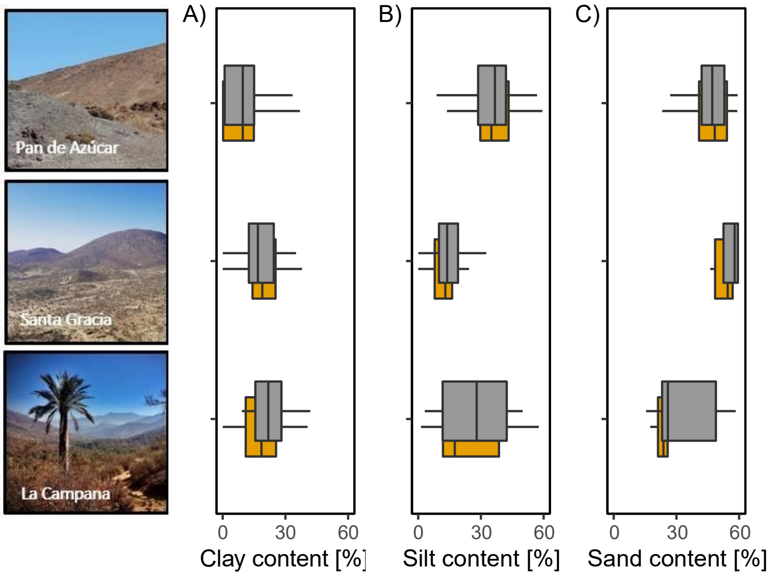

Fig. 1. Physical soil properties of mound (orange) and control (grey) soil samples in the research sites Pan de Azúcar (arid), Santa Gracia (semi-arid) and La Campana (Mediterranean). A): median clay [%], B): median silt [%], C): median sand [%].

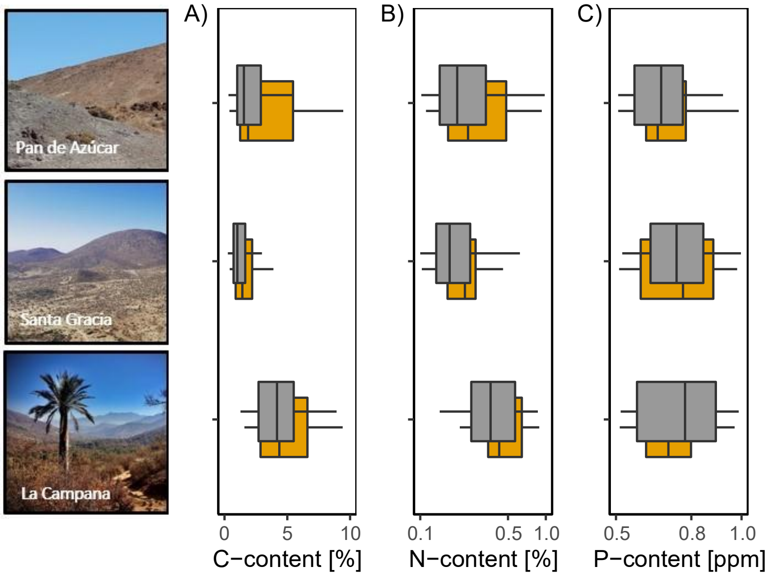

Fig. 2. Chemical soil properties of mound (orange) and control (grey) soil samples in the research sites Pan de Azúcar (arid), Santa Gracia (semi-arid) and La Campana (Mediterranean). A): median C [%], B): median N [%], C): median P [ppm]. Note that the x-axis in B) was $\log_{10}$-scaled for illustrative reasons.

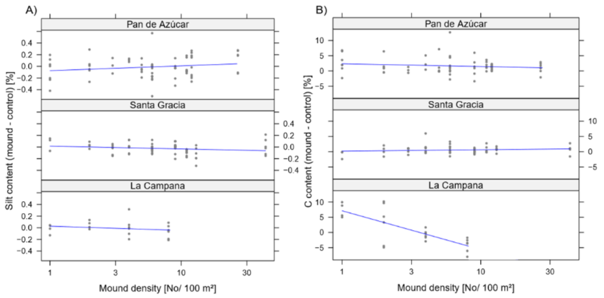

Fig. 3. Effect plots for the fixed effect mound density at each research site (arid Pan de Azúcar, semi-arid Santa Gracia, Mediterranean La Campana). A) Fitted relationships between mound density [No/ 100 m²] and silt content [%], B) fitted relationship between mound density [No/ 100 m²] and C content [%]. Note that the x-axis for A) and B) was $\log_{10}$-transformed.

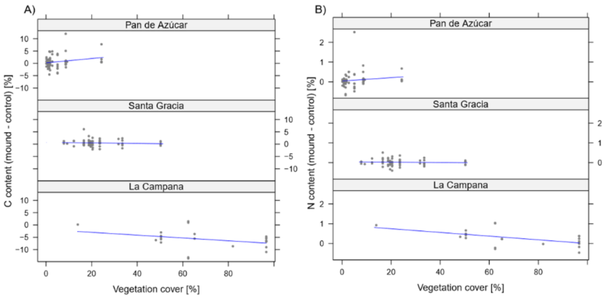

Fig. 4. Effect plots for the fixed effect vegetation cover at each research site (arid Pan de Azúcar, semi-arid Santa Gracia, Mediterranean La Campana). A) Fitted relationships between vegetation cover [%] and C content [%], B) fitted relationship between vegetation cover [%] and N content [%].

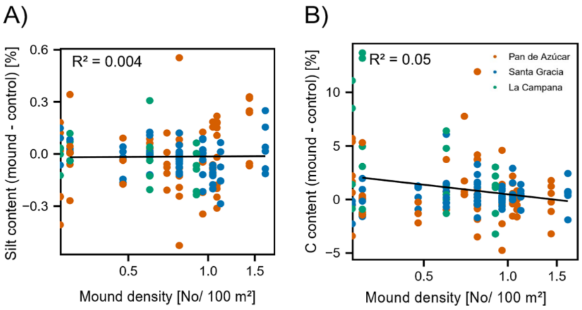

Fig. 5. Relationship between the physical soil property silt and the macronutrient C and mound density in the three research sites Pan de Azúcar (arid), Santa Gracia (semi-arid) and La Campana (Mediterranean). A) Relationship between silt content and mound density. B) Relationship between C content and mound density. For illustrative reasons we included the coefficient of determination R². Note that the x-axes in A) and B) were $\log_{10}$-transformed.