The positive link between geo- and biodiversity reflected in bioturbation patterns along a climate gradient

Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften (Dr. rer. nat.)

vorgelegt am Fachbereich Biologie der Philipps-Universität Marburg

von Diana Kraus

aus Karabulak, Kasachstan

Marburg an der Lahn, Februar 2023

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Illustration page: A fox (*Lycalopex culpaeus*) digging in soil in Pan de Azúcar, Chile. This drawing was recreated by Maria Giovanna Eva Papadopoulos referenced to a photo taken by Diana Kraus.

Die vorliegende Dissertation wurde von Februar 2019 bis Februar 2023 am Fachbereich Biologie der Philipps-Universität Marburg unter Leitung von Prof. Dr. Nina Farwig angefertigt.

Vom Fachbereich Biologie der Philipps-Universität Marburg (Hochschulkennziffer 1180) als Dissertation angenommen am

Erstgutachterin: Prof. Dr. Nina Farwig
Zweitgutachter: Prof. Dr. Roland Brandl

Tag der Disputation:

To my beloved grandmother Larissa Petrovna
Andrejewa who has always encouraged, supported and
believed in me despite the distance

Моей любимой бабушке Ларисе Петровне
Андреевой, которая всегда ободряла, поддерживала
и верила в меня, несмотря на расстояние

"To forget how to dig the earth and to tend the soil is to forget ourselves."

Mahatma Gandhi (1967): "The Mind of Mahatma Gandhi"

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Declaration of the author contributions

The thesis 'The positive link between geo- and biodiversity reflected in bioturbation patterns along a climate gradient' is based on the work I carried out from February 2019 to February 2023 at the Philipps University of Marburg, under the supervision of Prof. Dr. Nina Farwig and Prof. Dr. Roland Brandl. **Chapters 2 - 4** of this thesis include three independent scientific manuscripts, each with co-authorship, and have been published or will be published. The contributions of the authors for each manuscript or project is stated as following:

Chapter 2 – Meta-analysis: The positive link between terrestrial geo- and biodiversity and the importance of scales

(not published)

Diana Kraus, Rafaella Canessa, Roland Brandl, Jörg Bendix, Paulina Grigusova, Annegret Larsen, Nina Farwig

DK: Investigation, Data curation, Methodology, Investigation, Formal analysis, Writing-Original draft, preparation, Visualization
RC: Methodology, Formal analysis, Writing- Original draft, preparation
RB: Resources, Funding acquisition, Supervision, Methodology, Conceptualization, Writing-Reviewing and Editing
JB: Resources, Funding acquisition, Conceptualization, Writing-Reviewing and Editing
PG: Writing-Reviewing and Editing
AL: Resources, Funding acquisition, Writing-Reviewing and Editing
NF: Resources, Funding acquisition, Supervision, Methodology, Conceptualization, Writing-Reviewing and Editing

Chapter 3 – Vegetation and vertebrate abundance as drivers of bioturbation patterns along a climate gradient

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Diana Kraus, Roland Brandl, Sebastian Achilles, Jörg Bendix, Paulina Grigusova, Annegret Larsen, Patricio Pliscoff, Kirstin Übernickel, Nina Farwig

DK: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – Reviewing & Editing
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PG: Investigation, Writing – Reviewing & editing
AL: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Writing – Reviewing & Editing
PP: Project administration, Writing – Reviewing & Editing
KÜ Methodology, Project administration, Writing – Review & Editing
NF: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – Reviewing & Editing

Chapter 4 – Bioturbation enhances C and N contents on near-surface soils in resource-deficient arid climate regions but shows adverse effects in more temperate climates

(not published)

Diana Kraus, Roland Brandl, Jörg Bendix, Paulina Grigusova, Sabrina Köhler, Annegret Larsen, Patricio Pliscoff, Kirstin Übernickel, Nina Farwig

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PG: Data curation, Funding acquisition, Writing-Reviewing and Editing
SK: Data curation, Formal analysis
AL: Resources, Funding acquisition, Methodology, Conceptualization, Writing-Reviewing and Editing
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Summary

In present times, climate change, pollution or the overexploitation of the natural environment cause a global decline in biodiversity. To maintain biodiversity, ecosystem management is crucial. Therefore, first, a general understanding of the prevailing biodiversity is needed to develop appropriate conservation strategies to prevent biodiversity losses. Recent research has suggested the idea to use easily available geodiversity data as a surrogate for biodiversity data. Thereby, geodiversity can determine the availability and diversity of ecological conditions and resources facilitating the coexistence of species. An example of such a positive link between geo- and biodiversity is reflected in bioturbation patterns along a climate gradient.

Bioturbation offers an important ecosystem engineering mechanism because burrowing animals biologically rework soils and sediments shaping the environment for themselves and other species. Through this, bioturbators affect crucial ecosystem processes such as sediment transport, soil formation, nutrient availability, and soil water cycles. As a result, bioturbation promotes geodiversity by improving habitat and soil conditions for the bioturbators as well as for other species.

In this thesis, I performed a meta-analysis with 90 studies from 51 publications investigating the relationship and determinants of the link between geo- and biodiversity. To complement my research on the positive link between geo- and biodiversity, I additionally investigated the drivers of bioturbation patterns along a climate gradient in Chile. Therefore, I installed 80 plots distributed in four research sites (in arid, semi-arid, Mediterranean, and humid climates). In addition, I analyzed the effects of bioturbators on the ecosystem processes soil formation and nutrient availability incorporating data from the arid, semi-arid and Mediterranean research sites.

My thesis shows that (i) geodiversity is positively associated with biodiversity. However, this relationship is influenced by many complex features such as spatial scale, climate zone, or taxa which should be considered to adequately predict biodiversity with geodiversity. In terms of bioturbation patterns, (ii) climate, vegetation and the abundance of vertebrates are the significant drivers. Here, (iii) the magnitude of bioturbation varies along the climate gradient with the strongest effect in arid regions, where it produces a macronutrient enrichment and improves soil fertility.

This thesis expands our understanding of geodiversity and biodiversity positive links while raising awareness of the intricate relationships among them. Further, I provide bioturbation

patterns and effects in different environments by covering a broad climatic gradient. Thereby, this study highlights especially the role of bioturbation as an important mechanism enhancing chemical soil properties via macronutrient input. Thus, this thesis supports the role of bioturbation as a potential driver of local geodiversity.

Chapter 1: General introduction

In present times, global climate change, pollution or the overexploitation of the natural environment lead to worldwide biodiversity loss (Bálint et al., 2011; Chapin et al., 2000; McNeely, 1992; Schmeller et al., 2016). To be able to prevent such biodiversity loss, appropriate conservation strategies are needed (Dawson et al., 2011; McClanahan et al., 2008). In order to develop such strategies, first, a general understanding of the prevailing biodiversity is crucial (Tilman, 1999).

However, the estimation of biodiversity is often difficult. One reason is that biologists often work on rather small scales (Parks & Mulligan, 2010; Serrano & Flano, 2007), for instance, at the plot scale (Barthlott et al., 1999), which limits our understanding of overall species richness. In addition, the sampling of biological data can be time-, cost- and labor-intensive (Müller et al., 2004). A solution for these problems is the use of geodiversity as a surrogate for biodiversity: Previous research showed that geodiversity can determine the availability and variability of ecological conditions and resources facilitating the coexistence of species (Gray, 2004). Thus, geo-referred data can be used to explain and predict biodiversity and ecosystem processes. Because geodiversity incorporates an integrative perspective, combining abiotic or environmental elements (e.g. soil types, elevation) as well as their spatial variation (Gray, 2004; Parks & Mulligan, 2010), biodiversity hotspots might be indicated through high geodiversity (Lawler et al., 2015). Further, in contrast to biodiversity data, geodiversity data can be more easily accessed through remote sensing techniques such as drone flights or satellite images and additionally covers larger spatial scales (Comer et al., 2015; Parks & Mulligan, 2010).

Yet, the strength and shape of the links between geo-and biodiversity may depend on various parameters, such as taxa, climate or spatial scale. Different taxa have different resource requirements and accordingly, their diversity may be driven by different geo-parameters. For example, plants need fertile soil and light, and thus, plant diversity directly depends on soil and hydrological aspects (Araújo et al., 2004). In comparison, most vertebrate animals often directly depend on vegetation or other animals as their main food resource (Litvaitis & Pearl, 2000; MacArthur & MacArthur, 1961). In addition, the strength of the correlation between geo- and biodiversity might be affected by latitudes. In latitudes with stressful climates, e.g. deserts, biodiversity is more limited by climate and less by topography, soil and geology resulting in a potentially weaker correlation between geo- and biodiversity. On the contrary, in latitudes harboring mild biomes with only intermediate disturbances, e.g. temperate regions, the link between geo- and biodiversity might appear stronger (Connell, 1978). In terms of spatial scales,

the depiction of biodiversity through geodiversity appears to work best on intermediate to large scales (Bailey et al., 2017; Hjort et al., 2012). A possible reason is that species richness, which is often used as a biodiversity measure, is dependent on climate, which can be better depicted at larger spatial scales (Hawkins et al., 2003). However, up until now, research investigating the existence of positive links between geo- and biodiversity and integrating taxa, latitudes and spatial scales is scarce.

Although this link between geo- and biodiversity has often been used unidirectional for geodiversity promoting biodiversity, considering the complexity of this relationship, it can be seen as bidirectional. This likely means that biodiversity can also predict geodiversity and a process reflecting this is bioturbation. Thereby, through the physical movement of soils and sediments, bioturbating animals create and maintain habitats for themselves and other biota (Darwin, 1881; Jones et al., 1994) . Through this, burrowing animals may promote geodiversity and affect crucial ecosystem functions (Jones et al., 1994) such as sediment transport and soil formation (Eldridge & Mensinga, 2007; Hagenah & Bennett, 2013), soil water cycles (Valentine et al., 2017) or nutrient availability (Kurek et al., 2014; Yu et al., 2017).

When considering the body size of bioturbators, terrestrial bioturbators range from small invertebrates such as earthworms, ants or termites (Dangerfield et al., 1998; Darwin, 1881; Nkem et al., 2000; Ruiz et al., 2015) to medium-sized vertebrates like gophers or foxes (Gabet, 2000; Klaas et al., 1998; Kurek et al., 2014). Thereby, smaller invertebrates have a higher "bioturbation activity", i.e. a higher number of burrowed holes, due to their greater abundance compared to bigger vertebrates (Platt et al., 2016). In contrast, vertebrates, have higher energy costs to dig holes that are big enough for themselves. Thus, vertebrates prefer to reuse holes built by previous bioturbators resulting in a lower overall bioturbation activity (Newsome & Corbett, 1975; Roper, 1992; Vleck, 1981). In terms of the soil volume, the "excavated soil volume" or "bioturbation quantity", is larger for bigger vertebrates compared to smaller invertebrates (Abaturov, 1972; Ellison, 1946; Kalisz & Stone, 1984; Platt et al., 2016; Polis et al., 1986; Yair & Rutin, 1981).

To investigate the geo-biodiversity links considering the impact of bioturbators on ecosystem functioning, it is important to first understand which environmental features affect bioturbating animals. Previous research showed that bioturbation is related to climate (Holmgren et al., 2006; Jimenez et al., 1992; Lima et al., 1999; Milstead et al., 2007) because the burrowing animal abundance and composition depend on the prevailing climate conditions (Crawford et al., 1993;

Gerrard et al., 1996). While mammals and ants are the most present bioturbators in arid areas, earthworms are the dominating bioturbating animals in humid areas (Wilkinson et al., 2009).

Further, bioturbators are closely linked to vegetation. Especially in resource-limited environments, such as semi-arid and arid regions, burrowing animals are positively correlated to vegetation cover (Eldridge & Whitford, 2014). Here, the restricted access to food supply or shelter on the soil surface drives animals to burrow for belowground resources (Price & Podolsky, 1989; Vleck, 1981). Accordingly, changes in the vegetation cover influence the abundance and composition of bioturbating animal communities directly by changing food availability (Kelt et al., 2004; Muñoz et al., 2009), and indirectly by changing habitat availability (Kerley et al., 1997). Furthermore, bioturbation might increase vegetation cover by promoting the distribution and, with this, the establishment of seedlings (Valentine et al., 2017). On the contrary, bioturbators may also cause a decrease in vegetation cover by feeding on or destroying plants or plant parts by burrowing (Carlson & Whitford, 1991; Eldridge & Whitford, 2014).

In terms of ecosystem functions affected by bioturbation, one of them is soil formation because bioturbators might change physical soil properties such as soil texture. Thereby, burrowing animals mix and sort soil vertically and, through this, bring up finer soil compartments to the near-surface soil (i.e. the first few centimeters covering the organic soil layer and the upper part of the A-horizon) (Phillips, 2001; Phillips & Lorz, 2008). This leads to an increase of fine soil particles on the near-surface soil and thereby to the improvement of the water-holding capacity of the soil surface. As a result, the soil surface becomes more susceptible to water infiltration through the created burrows (Gervais et al., 2010). With this, bioturbation might impact not only soil texture but also vegetation (Dodd et al., 2002; Noy-Meir, 1979; Woinarski et al., 1999) because vegetation cover might increase due to better water holding capacity of the finer soil (Bucini & Hanan, 2007).

Another important ecosystem function influenced by bioturbation is nutrient availability. Bioturbators may affect chemical soil properties such as the macronutrients carbon (C), nitrogen (N) and phosphorus (P) on the near-surface soil (Bardgett, 2010; Carlson & Whitford, 1991; Contreras et al., 1993; Eldridge & Whitford, 2014). During the active mixing of the vertical soil column by bioturbators, these macronutrients are transported to the near-surface soil (Abaturov, 1972). By this, C is especially exposed to disturbances by bioturbation since the organic layer is C-enriched and thus, C can be easily transferred to the near-surface soil (Jandl et al., 2007; Zakharova et al., 2014). Through this, C is accumulated as organic matter (OM) on

the near-surface soil (Yurkewycz et al., 2014; Platt et al., 2016; Faiz et al., 2018). In addition, the soil surface is enriched with N and P contents by the incorporation of plant material or feces moved during the burrowing (Eldridge & Rath, 2002; Gervais et al., 2010; Kurek et al., 2014; Mulder & Keall, 2001; Tardiff & Stanford, 1998; Whitford & Steinberger, 2010; Yu et al., 2017).

These effects of bioturbation on soil formation, soil water cycles and nutrient availability elucidate the crucial role of bioturbators as ecosystem engineers modifying their environment not only for themselves but also for other biota (Jones et al., 1994) such as plants. By increasing physical and chemical soil properties as well as the soil water holding capacity, bioturbating animals promote soil fertility which leads to increased plant growth on the near-surface soil (Eldridge & Rath, 2002; Gervais et al., 2010; Kurek et al., 2014; Mulder & Keall, 2001; Whitford & Steinberger, 2010; Yu et al., 2017).

1.1 Aims of the thesis

With this thesis, I investigate (i) if there is a general positive link between geodiversity and biodiversity and what are the main factors affecting this relationship. Additionally, I aim to provide a comprehensive understanding of (ii) the bioturbation patterns of vertebrates and invertebrates and their drivers along a climate gradient ranging from arid to humid as well as (iii) their effects on ecosystem functioning regarding physical and chemical soil properties.

Since geodiversity is better depicted at larger spatial scales and additionally, bioturbation patterns depend on climate conditions and accordingly vegetation, I compare different climates at four different research sites in Chile, South America. These research sites are part of the German–Chilean priority program EarthShape (Earth Surface Shaping by Biota, https://esdynamics.geo.uni-tuebingen.de/earthshape/index.php?id=129). To minimize anthropogenic disturbances, three of the sites are located within national parks and one is located within a private reserve. The research sites (from North to South) include the arid Atacama Desert, located in Pan de Azúcar National Park ($\sim 26°$ S), a semi-arid shrubland in the private reserve Santa Gracia ($\sim 30°$ S), a Mediterranean forest in La Campana National Park ($\sim 33°$ S) and a humid rainforest in Nahuelbuta National Park ($\sim 38°$ S). These research sites were chosen due to their comparability. All four sites 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 northernmost research site Pan de Azúcar National Park is characterized by arid climate with a mean annual temperature (MAT) of 16.8 °C and a mean annual precipitation (MAP) of 12 mm (Fick & Hijmans, 2017). While the elevation is 330 m a.s.l., the vegetation cover is the lowest out of the four research sites with < 10% (Grigusova et al., 2021; Oeser et al., 2018). The predominating soil is classified as Regosol and the soil texture a sandy loam (Bernhard et al., 2018).

The second northernmost research site is a semi-arid private reserve Santa Gracia with a MAT of 13.7°C and a MAP of 66 mm (Fick & Hijmans, 2017). The elevation there is about 680 m a.s.l. and the vegetation covers 30 % - 40 % (Grigusova et al., 2021; Oeser et al., 2018). The soil is classified as Cambisol and the predominating soil texture is sandy loam (Bernhard et al., 2018). In this research site, goats are grazing on and thereby reducing the vegetation cover acting as disturbances of this ecosystem (Armesto & Arroyo, 2007).

The Mediterranean La Campana National Park has a MAT of 14.1°C and a MAP of 367 mm (Fick & Hijmans, 2017). The predominating elevation is about 730 m a.s.l. while the mean vegetation cover is up to 84% (Grigusova et al., 2021) and can reach 100% in some areas (Oeser et al., 2018). The soil in La Campana is classified as Cambisol and the general soil texture is sandy loam (Bernhard et al., 2018). Grazing cows are known for disturbances in this ecosystem (Rundel & Weisser, 1975).

The southernmost research site Nahuelbuta National Park is classified as humid with a MAT of 6.6°C and a MAP of 1469 mm (Fick & Hijmans, 2017). The elevation there is about 1240 m a.s.l. and the vegetation cover is up to 100% (Grigusova et al., 2021; Oeser et al., 2018). The predominating soil is classified as Umbrisol while the soil texture is mostly sandy-clay loam (Bernhard et al., 2018). There are grazing cows as known disturbances in this ecosystem (Zamorano-Elgueta et al., 2012).

In chapter 2, I expected a positive link between geo- and biodiversity. I also assumed that plant diversity is mostly affected by soil richness while animal diversity is driven by vegetation heterogeneity. Further, I expected that the link between geo- and biodiversity is impacted by climates and that this link is stronger at larger spatial scales.

In chapter 3, I expected that the activity of bioturbating animals will decrease from arid to humid. Further, I assumed that seasonal changes will affect bioturbation activity since the soil gets softer during rainy seasons reducing the digging costs for bioturbators. In addition, I

expected that increasing vegetation cover enhances the bioturbating activity of vertebrates whereas invertebrates' bioturbating activity will decrease.

In chapter 4, I expected that, on the one hand, bioturbation increases the fine-soil compartments clay, silt and sand. On the other hand, I assumed that bioturbators increase the contents of the macronutrients C, N and P on the near-surface soil compared to undisturbed soil. Furthermore, I hypothesized that just as bioturbation activity, the magnitude of bioturbation on C, N and P contents differs along the climate gradient.

Because this is a cumulative dissertation, chapters 2 - 4 can be read independently as the scientific background, methods and the results are presented and discussed independently in each chapter. Please consider that even though here I refer to the work done by me and write in first person, the three chapters are the result of collaborations with other researchers. The author contributions for each chapter can therefore be found within the section "Declaration of the author contributions".

Chapter 2: Meta-analysis: The positive link between terrestrial geo- and biodiversity and the importance of scales

2.1 Abstract

The concept of geodiversity was developed around 25 years ago and inspired by the concept of biodiversity. Geodiversity is commonly assessed by the elements topography, geology, soil richness and hydrology and sometimes additionally by climate. It has been suggested that geodiversity can serve as a surrogate for biodiversity assessment in cases where biological data is difficult to assess. Many studies suppose a positive link between geo- and biodiversity so that high geodiversity might indicate biodiversity hotspots and thereby help to develop conservation strategies. In this review, we conducted a meta-analysis and investigated the links between geo- and biodiversity across 51 scientific publications. For that, we investigated which geodiversity elements, e.g. geomorphology, soil richness, rock richness, are related to biodiversity measures, e.g. species richness, Shannon index. In addition, we tested whether latitude and the spatial resolution (depicted via the grain and extent of studies) affected the correlation between geo- and biodiversity. We found mostly positive correlations between geo-and biodiversity, however, most of these correlations were small (mean $r_s = 0.26$). The link between geo- and biodiversity was mostly affected by spatial aspects (grain, latitude, extent) whereas geodiversity elements were less important: Although three elements of geodiversity (soil richness, vegetation, rock richness) could partially explain the positive correlation, our study underlines to be cautious when using geodiversity as a surrogate for biodiversity.

2.2 Introduction

Geodiversity is a concept that has been around 25 for years (Sharples, 1993) referring to the natural variation in geological, geomorphic and soil features within an area (Gray, 2004, 2008). Recent approaches have also expanded the concept to include climate variability (Zarnetske et al., 2019). The notion of geodiversity was inspired by that of biodiversity, i.e. the variability among living organisms, including diversity within species, between species and of ecosystems (Rio de Janeiro Convention, 1992). Although the assessment of geodiversity has a value on its own as it provides cultural, provisioning and regulating services (Hjort et al., 2015), geodiversity can be used to predict biodiversity (Hunter et al., 1988; Lawler et al., 2015). Geodiversity is thereby supposed to indicate the diversity of conditions and resources that are relevant for organisms resulting in a positive link to biodiversity and thus, a high geodiversity can indicate biodiversity hotspots (Lawler et al., 2015; Parks & Mulligan, 2010). Consequently, the awareness and expanded understanding of geodiversity might help to find strategies for the

long-term conservation of biodiversity as well as of ecosystem functions and services (Fox et al., 2020; Knudson et al., 2018; Turner, 2019).

In the current context of biodiversity loss due to, among others, climate change and habitat loss, a clear understanding of the relationships between biodiversity and geodiversity is considered instrumental as it may help identifying conservation priorities (Zarnetske et al., 2019). Consequently, in recent years, an increasing number of studies has investigated whether geodiversity can effectively predict biodiversity and ecosystem functions (Alahuhta et al., 2019; Muellner-Riehl, 2019).

The basic hypothesis tested by these studies is the existence of a positive correlation between geo- and biodiversity. To a certain extent, similar to the concept of habitat diversity commonly used in ecology, geodiversity incorporates an integrative perspective that involves a combination of abiotic elements (e.g. soil types, nutrient availability, elevation) as well as their temporal and spatial variation. Geodiversity can thus determine the availability and diversity of ecological conditions and resources that allow the coexistence of species (Gray, 2004; Parks & Mulligan, 2010). In general, organisms depend on food, habitat or shelter (Parks & Mulligan, 2010). However, the main needs differ among taxa: Plant diversity directly depends on soil and hydrological aspects since plants need, among others, nutrients and light (Araújo et al., 2004), whereas most vertebrate animals often directly depend on vegetation or other animals as a main food resource (Litvaitis & Pearl, 2000; MacArthur & MacArthur, 1961). These examples demonstrate that different elements of geodiversity may be relevant to different taxa, likely affecting the strength and shape of geo- and biodiversity links.

Table 2.1: Most common elements used for the assessment of geodiversity.

Element of geodiversity	Typical variables used for characterizing geodiversity elements
Topography	Roughness, elevation, slope, aspect
Geology	Geological units, landscape complexity
Soil richness	Organic matter (OM), pH, nutrient availability, soil texture
Hydrology	Variation of hydrological elements in rivers, ponds or lakes

Just like biodiversity elements differ in their scope and focus (e.g. species vs. gene diversity, different biodiversity measures such as Simpson index, Shannon index or species richness), geodiversity assessments differ widely in the variables used for the characterization of geodiversity elements (Crisp et al., 2021, Table 2.1). Most studies consider either one or a

combination of topographical (roughness, elevation, slope, aspect), geological (geological diversity, landscape complexity), soil (OM, pH, nutrient availability) or hydrological (variation of hydrological elements such as rivers, ponds, lakes) elements. While some studies additionally include climate using the variables temperature, precipitation, evapotranspiration, water balance and solar radiation, others explicitly exclude climate in their concept of geodiversity (Gray, 2004; Parks & Mulligan, 2010; Tukiainen et al., 2017). With the idea of developing a standard methodology that allows geodiversity to be compared across studies, Serrano and Flano developed the so-called "Geodiversity index", that considers several of the previously mentioned elements simultaneously (Serrano & Flano, 2007). However, only a low proportion of studies uses this index, and it is unclear whether it represents a good proxy for biodiversity or any of its measures (e.g. species richness or Shannon Indices). To date, no study has examined which elements or combination of elements of geodiversity can sufficiently predict the biodiversity of various taxa.

The development of large global datasets via remote sensing and models for topographic, climatic and other relevant variables has enabled scientists to assemble useful data and obtain geodiversity measures at different spatial and temporal scales (Comer et al., 2015; Parks & Mulligan, 2010). Importantly though, when the correlation between geodiversity and biodiversity is assessed, the scale and grain size should be similar for comparing geo- and biodiversity data. This is, however, not easy to achieve, as biologists and geoscientists work often across different scales (Serrano & Flano, 2007). Even though there are some global datasets for biodiversity, the sampling of biological data such as genetic diversity within species or the diversity of soil organisms is often time-, cost- and labor-consuming and thereby such studies are scarce (Müller et al., 2004).

Besides, biodiversity measures using a particular taxon do not capture all characteristics of the underlying variation of living organisms since it has been shown that between-group diversity relationships are very weak (Gaston, 1996). As a result, the diversity in one family is hardly representative of biodiversity in another family (Parks & Mulligan, 2010). This is why species richness (defined as the number of species in an area) is limited because it ignores the abundance (number of individuals per species) or dominance (species with high abundance relative to other species) within the community (Parks & Mulligan, 2010; Wolters et al., 2006). This is where non-biological geodiversity surrogates for biodiversity can be useful to fill such gaps in taxonomic or geographical knowledge (Ferrier & Watson, 1997; Hoekstra et al., 2005). However, for some taxa (e.g. insects), species richness is the most common measure whereas

for vascular plants, species abundance or dominance within the community is also typically measured (Harper & Hawksworth, 1995). These variable assessments of biodiversity may also affect the correlations with geodiversity, leading to variable results and interpretations.

Geodiversity indices seem to be more suitable surrogates for biodiversity at intermediate to large spatial scales (Bailey et al., 2017; Hjort et al., 2012). A possible explanation for this is the strong climatic control of species richness over large spatial extents (Hawkins et al., 2003). In terms of biodiversity measures, species richness is best represented at scales from 1 km² or more (Wolters et al., 2006). The differences in scales between geo- and biodiversity have led to assessments conducted at variable scales (e.g. Hjort et al., 2012; Tukiainen et al., 2022). However, there is only scarce information at which scale geo- and biodiversity are strongly linked. This scale-dependent relationship might, additionally, be taxa-dependent: For instance, it is already known that terrestrial animals choose the size of their activity range area, which is described by latitude, elevation, and other geographic variables, depending on their body size and their metabolic needs (Lindstedt et al., 1986).

In order to understand which elements of geodiversity are related to which elements of biodiversity, and under which conditions both diversities are correlated, we conducted a meta-analysis and investigated the potential links between geo- and biodiversity across 51 scientific publications. We tested the following hypotheses:

H1: Overall, the link between geo- and biodiversity is positive and can be used as a surrogate for biodiversity since geodiversity determines the availability and variety of ecological niches.

H2: Plant diversity is strongly associated with soil diversity while animal diversity depends on the heterogeneity of vegetation, a surrogate for conditions (habitat, shelter) and resources (food).

H3: Latitude affects the correlation between geo- and biodiversity: In latitudes with stressful climates (e.g. desert, arctic), biodiversity is limited by climate rather than topography, soils or geology, while in more mild biomes the correlation between geo- and biodiversity is stronger than in harsh biomes.

H4: The correlation between geo- and biodiversity is stronger for studies on intermediate to large scales than on small to intermediate scales.

2.3 Methods

2.3.1 Data acquisition

We based our study on a systematic literature review of the links between geo- and biodiversity. Therefore, we searched the database "Web of Science" using the following search strings: "geodiversity and biodiversity", "environmental heterogeneity and biodiversity", "linking environmental heterogeneity", "geodiversity" "biodiversity", "species diversity" "habitat diversity", "environmental heterogeneity" "species richness" (Fig. 2.1). Because geodiversity is a term mainly used in the geosciences, we also considered "habitat diversity" and "environmental heterogeneity" as alternatives, as they typically describe similar environmental features and are more often used in older studies, particularly studies with a biological background (Menge & Sutherland, 1976; Tilman, 1994). After screening the results for duplicates, we listed a total of 962 publications. We then excluded those involving oceanic islands and marine studies since these ecosystems are influenced by different processes, e.g. on islands with increasing size there is a steeper increase in niche variety and population size than on continents (MacArthur & Wilson, 1967). Because of that, they differ in species abundance and composition from terrestrial ecosystems (Carr et al., 2003; Denny, 1993). When assessing their eligibility for our analysis, we checked all publications, screening for either correlation coefficients between geo- and biodiversity or for data or figures with data representing these correlations. In the last case, we extracted the data points with the program WebPlotDigitizer-4.5.exe and then calculated the Spearman correlation coefficients with R statistical software (version 4.0.3) using the cor command. It is important to note that the Spearman correlation coefficient (r_s) just measures the strength and direction of association between two ranked measures (Spearman, 1905). Publications were categorized as suitable if there was either a Spearman correlation coefficient or available data on the correlation between geodiversity and biodiversity. After our screenings, we considered 51 suitable publications (Fig. 2.1). Thereby, some publications included information on geo- and biodiversity links for either different regions or different taxa, which resulted in 90 correlation coefficients in total (Table S2.1), hereinafter referred as "studies". Even though our data acquisition did not cover all available studies on geo- and biodiversity coefficients, it can serve as an extrapolation of the link between the two disciplines.
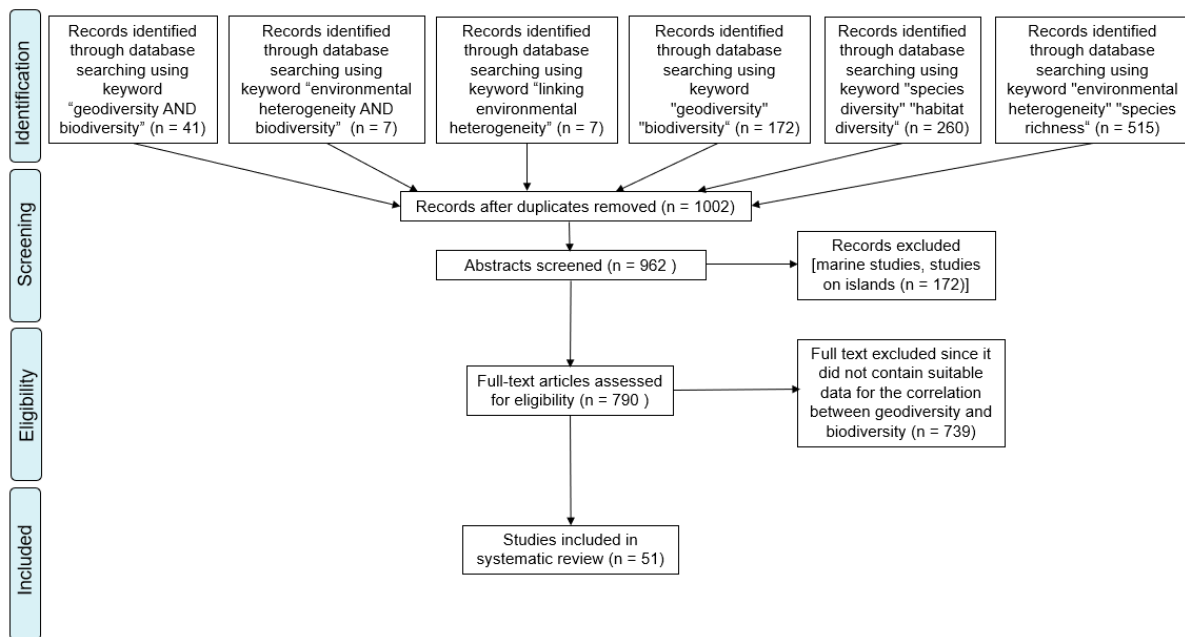
Fig. 2.1: Flow diagram representing systematic literature search.

2.3.2 Definition and category allocation of moderators

After identifying all available Spearman correlation coefficients for geo- and biodiversity links, we created a dataset listing the relevant moderators to be tested in the meta-analysis. Therefore, further information was extracted from the corresponding publications.

2.3.3 Assignment of studies to locations

We then created a map depicting the location of studies performed in different countries. Therefore, we used the R package "rworldmap" (South, 2011).

2.3.4 Geodiversity

Because we included publications that used not only "geodiversity", but also similar traditional terms such as "habitat diversity" and "environmental heterogeneity", we identified which geological diversity concept was used in each study. We then categorized studies based on the specific elements (Table 2.1) that were used for the geodiversity assessment. We incorporated the following elements of geodiversity in our analysis: geomorphology, soil richness, rock richness, climate, vegetation, habitat, and geodiversity (Table 2.2). In a stricter sense, vegetation and habitat are no elements of geodiversity (Table 2.1). However, we decided to incorporate these elements to compare the typical elements of geodiversity to habitat and vegetation as well as to have a sufficient amount of studies. But one should be aware of the fact that there are more studies available that use these elements than found by our search strings. We joined topographical units into the category "geomorphology" since geomorphology can be defined as the study of the origin and evolution of topographic features by physical, chemical

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or biological processes (Stetler, 2014). Accordingly, we included the correlations using slope and elevation into the summarized element "geomorphology". We integrated the parameters temperature, precipitation, solar radiation and diffuse light index within the category "climate". We decided to include climate as one component of geodiversity even though there is an ongoing discussion about whether climate represents geodiversity or not (Zarnetske et al., 2019). Since we excluded papers from marine environments to focus on terrestrial geodiversity, we excluded "hydrology" as a main geodiversity element from our analysis. However, when referring to "hydrology" we here mean that we excluded this geodiversity element in the broader sense of marine environments still involving precipitation within the geodiversity element "climate". In addition, we listed whether studies used the so-called "geodiversity index" (Serrano & Flano, 2007), a multi-element index.

Table 2.2: Elements of geodiversity and their variable assessment used for our meta-analysis.

Element of geodiversity	Variables used for characterizing geodiversity elements
Geodiversity	All variables from other possible elements
Geomorphology	Roughness, elevation, slope, aspect
Soil richness	OM, pH, N content, total wetness index, soil depth
Rock richness	Geological units, landscape units
Climate	Temperature, precipitation, solar radiation, diffuse light index
Vegetation	Canopy cover, vegetation height, tree density,
Habitat	Habitat units

2.3.5 Biodiversity

For each study, we recorded which biodiversity measure was assessed. Three main categories were found: "Species richness" (i.e. the count of species), "Shannon index" (a measure of diversity at different levels such as from genes and populations to whole species and ecosystems) and "GI biodiversity indicator". The GI (green infrastructure) biodiversity indicator (defined as "the interconnected green space network incorporating natural areas and open spaces to provide multiple benefits for people and wildlife green infrastructure" ((Benedict & McMahon, 2012)) was used in one paper (Fernández et al., 2020) but did not include a specific definition on how it was calculated.

In addition, we identified which taxa were included for a particular relationship. We used the following categories: plants (including vascular and nonvascular plants), birds, other

vertebrates (mammals, reptiles, amphibians), invertebrates (molluscs, arachnids as well as insects such as ants, butterflies, orthopterans and heteropterans).

2.3.6 Geographical and scale moderators

For all the investigated studies we incorporated also the latitude, climate zone, grain and extent in our analysis. For each correlation, we included the latitude of the study area by taking the average latitude of the different sampling sites. By using available information about the locations of the studies, we additionally assigned a climate zone to each study. In addition, we listed the grain, i.e. the square scale where one measurement was complemented in km², and the extent, i.e. the grain (in km²) multiplied by the number of measurements. Then, we $\log_{10}$-transformed the moderators for grain and extent to approximate normality.

2.3.7 Statistical analyses

As a first step, we calculated the effect sizes for geodiversity-biodiversity correlation coefficients. This was done by using the "escalc" function of the "metafor" package (Viechtbauer, 2010) in the R statistical environment. We thereby considered the number of data points used to calculate the correlation. Even though the usual measure to take for this function is "ZCOR", the Fisher's r-to-z transformed correlation coefficient (Fisher, 1921), we used the original correlation coefficient ("COR"). The use of the z-transformed correlation coefficient as well as the raw coefficient led to almost identical results (weighted mean for soil richness within the full model with ZCOR $r_s = 0.0243$; with COR $r_s = 0.0132$). However, the use of the raw correlation coefficient facilitates the interpretation of the figures.

To investigate the relevance of the different moderators on the correlation coefficients of geo- and biodiversity links across studies, we conducted a meta-analysis via a multivariate linear mixed-effects model, using the "rma.mv" function of the same metafor package. Overall, our dataset contained seven moderators: latitude, climate, grain, extent, geodiversity measures, biodiversity measures and taxon. We, therefore, created categories for the moderators climate, geodiversity measures, biodiversity measures and taxon. The moderator climate included the categories polar, subpolar, temperate, Mediterranean, subtropical, tropical, cross-zonal (cross-climatic zones of continental extent). Within the moderator geodiversity measures we included the categories geodiversity, geomorphology, soil richness, rock richness, climate, vegetation and habitat. If two different categories were involved in one study, we included both. Within the moderator biodiversity measures we incorporated species richness, Shannon diversity and GI geodiversity indicator. The moderator taxon consisted of the following categories: plants, birds, other vertebrates and invertebrates. Because some publications contained more than one

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correlation coefficient, we used the publication number (ranging from 1 to 51) as a random effect. From the model outcome of the meta-regression, we obtained the effect sizes of the different moderators and with this, created a forest plot with all different levels for taxon, biodiversity measures and climate zones. Afterwards, we extended our analysis to test if plants are strongly associated with soil while animals are depending on vegetation by using the interactions geodiversity x taxon.

We tested some additional models exclusively investigating our specific hypotheses. Hereby, we first studied the interactive effects of biodiversity and geodiversity measures on the correlation coefficients of all studies. For that, we used the package "metacart" (Dusseldorp et al., 2014) which is able to identify interactions between multiple moderators. With this, we created a meta-regression tree including the biodiversity and geodiversity as moderators. We also performed a model selection using the glmulti package (Calcagno & Mazancourt, 2010) which compares all possible combinations between the moderators and depicts the best model.

2.4 Results

2.4.1 Description of used data

51 out of the 962 screened publications evaluated correlations between geo- and biodiversity conducted between 1969 and 2022. From these 51 publications, we extracted 90 correlation coefficients (representing 90 studies). We found 22 studies using the search string "geodiversity" that were published in the years 2012-2020, 17 studies using the search string "habitat diversity" that were published in the years 1969-2018 and 51 studies using "habitat heterogeneity" published in the years 1997-2022 (Table S2.2).

When looking at the biodiversity indices used in the different studies, most of them (80) used species richness, followed by Shannon index (7) while GI biodiversity indicator was used only once (Table S2.2). In twelve of the incorporated 90 studies, more than one biodiversity index was used, typically species richness and Shannon index (seven times) or species richness, Shannon index and Simpson index (five times) .

Considering the different elements of geodiversity, most studies used habitat (21), followed by vegetation (19) and geomorphology and soil richness (both 14). In contrast, geodiversity (10), climate (7) and rock richness (3) were used more rarely (Table S2.2). Some studies used more than one element such as the combination of geomorphology and soil (two times) as well as the combination of vegetation and habitat or soil and habitat (both one time).

Out of the 90 considered studies, 48 included plants and 42 included animals for their biodiversity assessment. Further, among the studies including animals, 13 used birds, 12 used other vertebrates and 17 included invertebrates (Table S2.2).

The studies on the link between geo-and biodiversity were performed in North and South America, Europe, Africa, Asia and Australia, yet the majority were done in Europe, North and South America. Particularly, most studies were conducted in Finland, the USA and China (Fig. 2.2). Our review incorporated studies from all climate zones, ranging from polar (two studies in Canadian polar climate) to tropical (e.g. in Brazil or Kenya). Overall, most of the studies we integrated were performed in temperate and subpolar climates (Table S2.2).
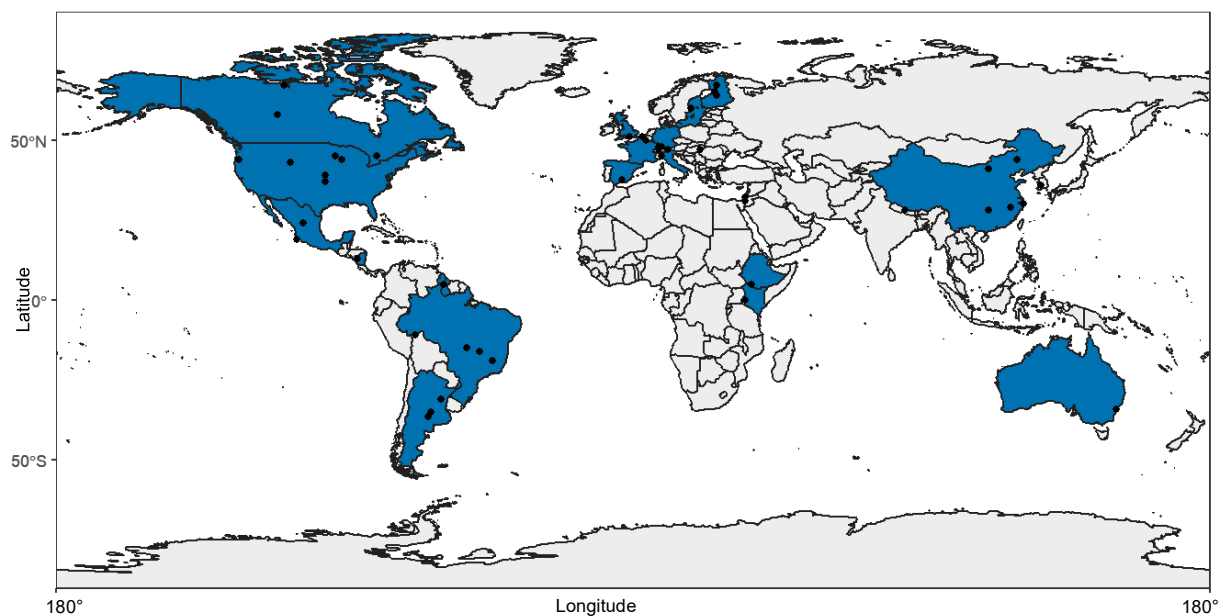
Fig. 2.2: World map depicting the investigated countries on the geodiversity-biodiversity links.

There was no clear trend of correlation coefficients for geodiversity-biodiversity links along latitudes, but the majority of studies were done within the range of 30-40° or over 60° (Fig. 2.3A). Considering the extent of the studies, most of them were either carried out on extents of one or less km² or in very large extents of about 10000 km². Thereby, most studies done over greater latitudes and extent contained a higher sample number (Fig. 2.3B). On average, the studies were carried out on about 20860 ± 46080 km².
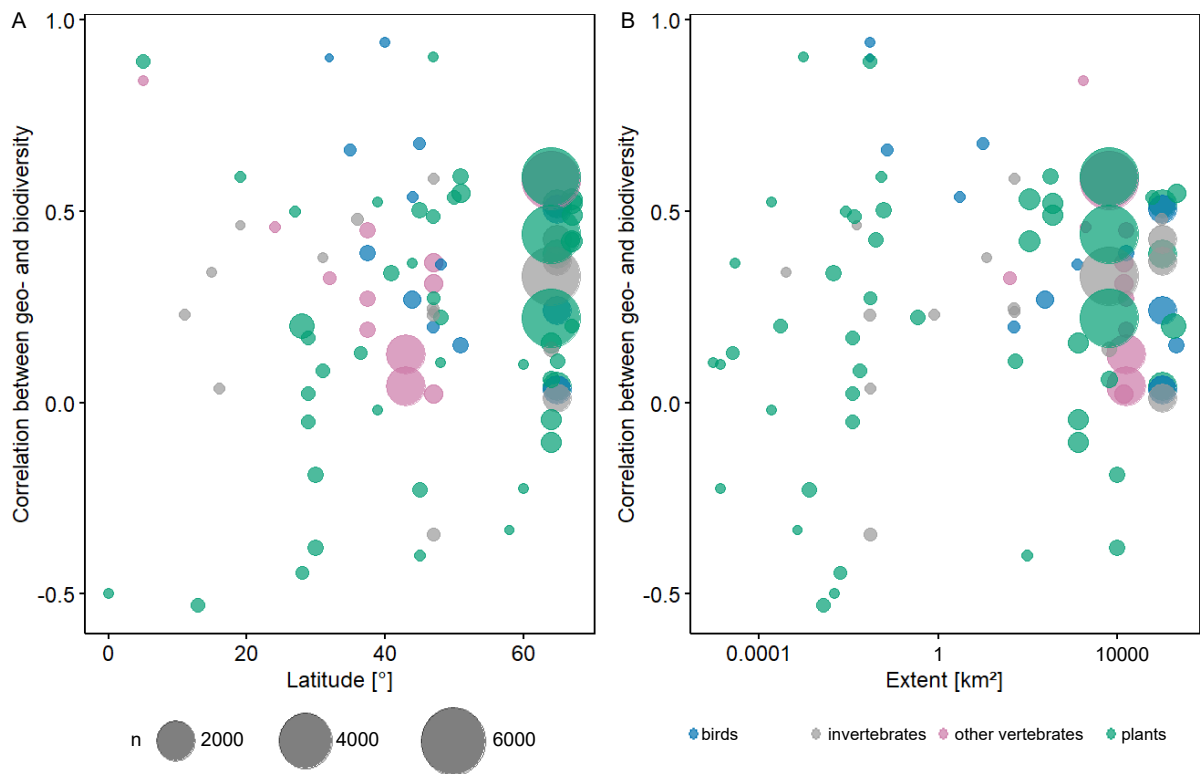
Fig. 2.3: Rank correlation coefficients of geodiversity and biodiversity plotted against (A) latitude and (B) study extension (log₁₀-transformed) for 90 studies identified in the current meta-analysis. The colors indicate the different taxa (blue: birds, grey: invertebrates, pink: other vertebrates; green: plants) while the point size indicates the sample number (n) used for the calculation of the correlation.

2.4.2 Meta-analysis

The average sample size used for calculating the correlation coefficients between geo- and biodiversity was n = 617 with a minimum of n = 5 and a maximum of n = 6571. Geo- and biodiversity were significantly correlated (p < 0.0001) across the studies included in our analysis. Correlation values varied from -0.53 to 0.94 and averaged 0.26 (weighted average). Overall, 86% (77 studies) found significantly positive correlations, whereas 14% (13 studies) found negative correlations. Specifically, the geodiversity elements "vegetation" and "geomorphology" for the taxa birds and plants, respectively, achieved high (r_s > 0.8) correlations (Fig. S2.1). Looking at the full model (i.e. with all moderators) for all 90 studies, the meta-analysis investigating the link between geo- and biodiversity showed a high level of heterogeneity (I^2 = 98.8 %, Q = 4083, p < 0.0001). Thereby, all moderators incorporated in the model explained 80% of the deviation (Table S2.3). Within the full model, the categories soil richness, vegetation and rock richness and the taxon "other vertebrates" were the significant moderators (Table S2.4). The funnel plot for the studies used in this meta-analysis showed that about half of the studies fall outside of the funnel area, indicating partially biased data (Fig. S2.2).
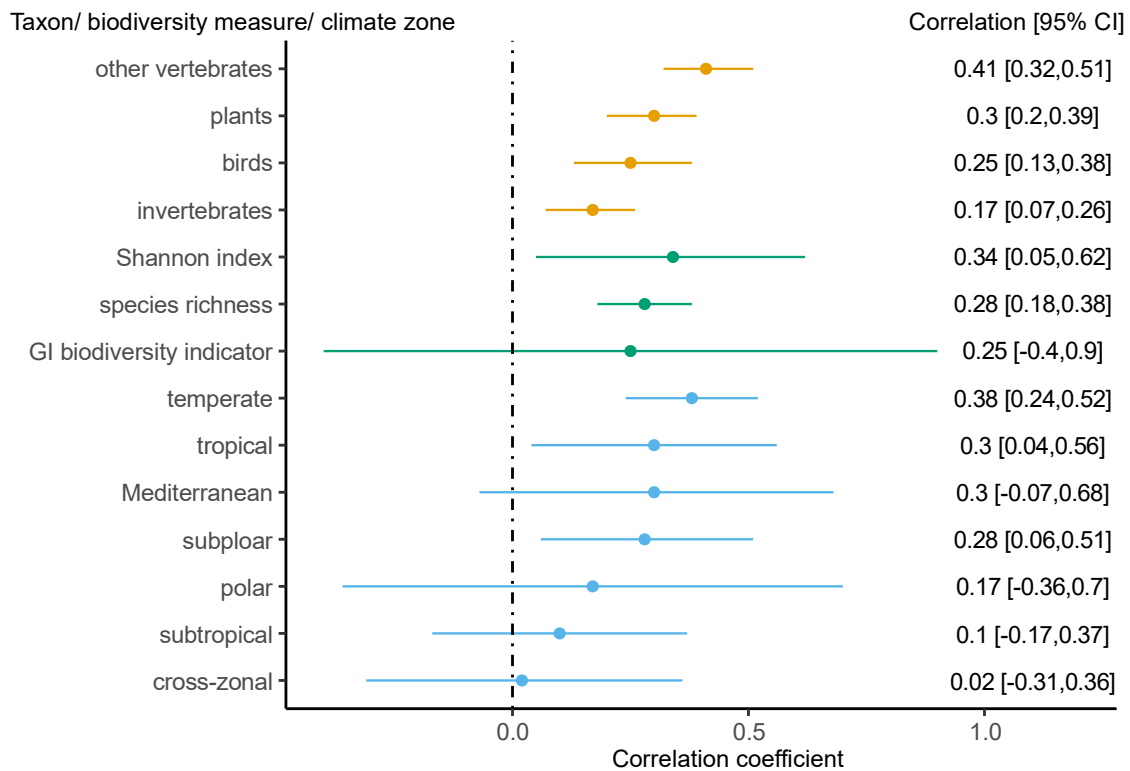
Fig. 2.4: Forest plot with the weighted mean correlation coefficients for each taxon, biodiversity measure and climate zone after a meta-analysis. The correlation coefficients for the different moderators are sorted in decreasing order. The bars around the correlation coefficients denote 95% confidence intervals. The colors represent the different moderators (orange: taxon; green: biodiversity measure; blue: climate zone).

Correlation coefficients were significantly positive for the taxon "other vertebrates" (weighted average rs = 0.41), whereas for birds, invertebrates and plants they were low and non-significant (Table S2.4, Fig. 2.6). Biodiversity indicators were not a significant moderator in the full model (Table S2.4). However, the Shannon biodiversity index showed the highest correlation coefficient (rs = 0.34), whereas the GI biodiversity indicator, used by only two studies, showed the lowest (Fig. 2.4). For the interaction between geodiversity elements and taxon, other vertebrates were depending on vegetation, geodiversity, geomorphology, habitat and soil richness. The taxon "plants" was depending on soil richness, habitat, geomorphology and rock richness whereas "invertebrates" were depending on geomorphology (Table S2.5). Significant correlation coefficients were observed only for the temperate climate zones, where the highest (rs = 0.38) coefficients were found (Fig. 2.4, Table S2.6). When testing the influence of scales within the full model via meta-regression, neither grain nor extent, did significantly affect the correlation between geodiversity and biodiversity (Table S2.7).

The meta-regression tree used to test the interaction of the moderators geodiversity and biodiversity, showed a significant interaction: we saw that their relationship is complicated

(Table S2.8). In the model averaging method, grain was the most important moderator followed by latitude, extent, biodiversity measure and taxon whereas geodiversity measure was the least important moderator (Table S2.9).

2.5 Discussion

Overall, we found positive correlations between geodiversity and biodiversity in most of the investigated studies. Thereby, we found that, for geodiversity elements, only soil richness, vegetation and rock richness significantly modulated this relationship between geo- and biodiversity. Further, grain, latitude, biodiversity and taxon appeared to also be relevant moderators for the correlation between geo- and biodiversity. However, these correlation coefficients were low. Several reasons may explain these results including the use of variable taxa, climates and scales, which was evaluated by our following hypotheses.

Even though our analysis showed overall positive correlations between geo- and biodiversity concomitant with our first hypothesis, these correlations were, however, explained only by a few elements of geodiversity. Thereby, one of the three geodiversity elements appearing as a suitable surrogate for biodiversity was soil richness which incorporates important information for soil biota and climate and thereby determines the availability of resources and conditions (Bardgett et al., 2002; Nielsen et al., 2011). Vegetation was also a significant predictor for the relation between geo- and biodiversity concomitant with the fact that biota is dependent on vegetation as food and shelter source (Harrington et al., 1999; Webb & Bartlein, 1992). However, in general, vegetation itself belongs to the biotic environment and thereby also represents biodiversity and is not a proxy for geodiversity, but potentially for "habitat" and only for taxa other than plants (Fischer & Lindenmeyer, 2007). Even though the element rock richness remained as suitable for biodiversity prediction, it is important to recognize that rock richness was used in fewest studies. The low correlation between geo- and biodiversity might also be explained by the fact that species richness was used in most of the investigated studies even though this measure is not suitable for correlations as it is not representative for the overall biodiversity within a community (Wolters et al., 2006).

The geodiversity index developed by Serrano and Flano (Serrano & Flano, 2007) did not serve as a sufficient surrogate for the correlation between geo- and biodiversity. A reason therefore is that there is no unification for such an index on how to assess data for it to calculate an appropriate predictor for biodiversity as also shown by previous research (Wallis et al., 2021). For instance, many other studies, especially older ones, use other approaches that appear to be suitable as well: for example, Nieto (2001) considered the number and variability of geological

units as basic parameters for the qualitative and quantitative assessment of geodiversity. Another approach of calculating geodiversity was developed by Kozlowski (2004) who assigned five levels of geodiversity ranging from very high to very low to quantitatively evaluate given areas. Jonasson et al. (2005) established the relationship between geodiversity (mainly landform diversity) and habitat diversity for three different spatial scales (large, intermediate, small). In line with this, we assumed that habitat was one of the most used elements of geodiversity in our review. Hence, for habitat diversity, it is important to examine how exactly this element was assessed, since the definition of "habitat" can be subjective: some studies involved other elements of geodiversity than habitat itself such as vegetation or geomorphology when addressing the term "habitat diversity" (Celada & Bogliani, 2009; Honnay et al., 1999; Shen et al., 2018) which might be the reason why habitat was not a good surrogate of the geodiversity-biodiversity relationship.

Contradicting our assumption that geomorphology incorporates many different features describing the environment such as slope, elevation and roughness, and thereby appears to be suitable to predict biodiversity patterns (Alexander, 1991; Walsh et al., 1998), this element was not a good surrogate. Climate was as well not suitable as a predictor which is concomitant with the fact that many previous studies decided to exclude this element as a geodiversity surrogate (Gray, 2004; Parks & Mulligan, 2010). One might assume that these findings are contradicting the assumption that more variable environments offer sufficient possibilities for species coexistence leading to higher biodiversity (Gray, 2004; Parks & Mulligan, 2010). An explanation therefore is that most studies we included only used one single element of geodiversity in their analysis. However, the actual purpose of geodiversity is a combination of several elements to obtain a "holistic" concept and suitably depict geodiversity (Tukiainen et al., 2022).

Our second hypothesis stating that plants are more depending on soil richness while animals are more depending on vegetation heterogeneity due to their resource needs could be extended by our study: We found that other vertebrates not only rely on vegetation but also on geodiversity, geomorphology, habitat and soil richness whereas plants depend on soil richness as well as habitat, geomorphology and rock richness. This finding highlights that the relationships between biota and their environments are more complex and thereby animals as well as plants cannot depend on only one but may rely on more than one element of geodiversity. For instance, species distribution is affected by climate (Hodkinson, 1999) while geomorphology may be an important driver for biotic changes and by that, influencing

biodiversity (Harris, 1987; Van Devender, 1990). As for invertebrates, only geomorphology seemed to be of importance, we assume this outcome is due to the fact that geodiversity elements are taken on larger spatial extents than the smaller spatial scales invertebrates operate on (Kremen et al., 1993). This finding draws attention to the fact that matching spatial scales are an important feature to consider when predicting biodiversity through geodiversity data.

Regarding our third hypothesis stating that latitude affects the correlation between geo- and biodiversity, we found that the correlation was highest in temperate climates. Although our analysis included studies from contrasting climate zones (from polar to tropical areas), to some extent, we did not find an equal amount of studies for all climates: most of the literature available focused on temperate and subpolar climates. In contrast, literature in the tropical and polar climate zones was scarce. This is why we recommend broadening the research on geo- and biodiversity in these and other underrepresented climate zones. However, in general, the influence of latitude on biodiversity followed the intermediate disturbance hypothesis: Like we assumed, in latitudes with mild climates (temperate ones) the link between biodiversity and geodiversity should be stronger since intermediate disturbance promotes higher biodiversity. In contrast, in latitudes or climates with more extreme stressful conditions such as tropical or polar ones, this link is less abundant because high disturbance reduces biodiversity while geodiversity remains unaffected (Connell, 1978).

Our fourth hypothesis, stating that studies covering wider spatial scales show a stronger correlation between geo- and biodiversity, was not supported by the main model. However, when considering spatial scales for biodiversity assessments, it has been shown that the extent of study areas has an effect on biodiversity. This effect is known as the species-area curve, where larger study areas depict higher species richness (with a slope ranging from 0.15 to 0.39) (MacArthur & Wilson, 1967; Preston, 1962). Thus, grain and extent affect geo- and biodiversity relationships. This likely means that only by depicting a large enough extent of study areas where geo- and biodiversity are assessed, the true biodiversity can be predicted. This is in line with previous studies which demonstrated that geodiversity indices are better surrogates for biodiversity at intermediate to large scales (Bailey et al., 2017; Hjort et al., 2012; Wallis et al., 2021). It is possible that the lack of studies at variable extents influenced the outcome of our model. In fact, the model averaging depicted that grain and extent could be significant factors on the link between geo- and biodiversity.

Another relevant aspect of the species-area curve is the difference in the slope of the relationship between continents and islands. As the species richness of an area can be predicted in terms of the balance between immigration and extinction rates (MacArthur & Wilson, 1967), the dispersal capacity of species relies on the habitat (the location and shape of an area) (Ney-Nifle & Mangel, 2000). In contrast to continents, islands harbor fewer species due to their small size and geographic isolation. This is why with increasing island size there is an increase in niche variety and population size (MacArthur & Wilson, 1967). As a result, species-area curves for islands are steeper and represented in higher slopes than continents (Connor & McCoy, 1979; Guo et al., 2015). This reinforces the idea of performing separate analyses for continents and islands when assessing biodiversity patterns.

Considering the effect of environmental heterogeneity on the species area, there is an assumption called "the area-heterogeneity tradeoff" (Allouche & Kadmon, 2009; Kadmon & Allouche, 2007). This likely means that with increasing environmental heterogeneity, the available area for species decreases. This is because the niche width of all species is limited due to the negative effect on the average population sizes and the positive effects on extinction rates with increasing environmental heterogeneity (Allouche et al., 2012). However, this is only valid for small to intermediate scales because with increasing scales this effect can be mitigated (Allouche et al., 2012) accordingly to our hypothesis that geodiversity is better depicted at larger scales.

Even though we considered geodiversity influencing biodiversity, a scenario vice versa in which biodiversity may also affect geodiversity is possible. Accordingly, a diversity of organisms may modify their environment through a diversity of processes and thereby influence geodiversity. One example are microorganisms modifying the soil composition and aggregation (Tisdall, 1994), or plant roots altering soil chemical and physical properties (Read et al., 2003). Another example are bioturbators acting as ecosystem engineers and thereby modifying the predominating conditions and through that influencing soil richness or even geomorphology (Corenblit et al., 2011; Grigusova et al., 2022, 2023; Meysman et al., 2006).

2.6 Conclusion

We found a positive relation between geo- and biodiversity which is affected by only some elements of geodiversity such as soil richness and vegetation. However, this relationship is weak, likely because there were only a few studies considering the combination of several geodiversity elements, even though such a holistic approach for the assessment of geodiversity

is needed. With our findings we provide new insights of the importance of taxa, grain, extent and climate when considering doing assessments of geodiversity elements as surrogates for biodiversity. These aspects should be considered in future studies assessing the concept of geodiversity as a tool for biodiversity conservation. To broaden the understanding of the intricate relationship between geo-and biodiversity, further studies that deepen our knowledge of the mechanisms supporting this link are needed. Additionally, more communication between those two disciplines before data assessment would help to develop appropriate methods.

Data Availability

All relevant data are within the manuscript and its Supplementary Material files.

Competing interests

The authors have declared that no competing interests exist.

Chapter 3: Vegetation and vertebrate abundance as drivers of bioturbation patterns along a climate gradient

3.1 Abstract

Bioturbators shape their environment with considerable consequences for ecosystem processes. However, both the composition and the impact of bioturbator communities may change along climatic gradients. For burrowing animals, their abundance and composition depend on climatic and other abiotic components, with ants and mammals dominating in arid and semiarid areas, and earthworms in humid areas. Moreover, the activity of burrowing animals is often positively associated with vegetation cover (biotic component). These observations highlight the need to understand the relative contributions of abiotic and biotic components in bioturbation in order to predict soil-shaping processes along broad climatic gradients. In this study, we estimated the activity of animal bioturbation by counting the density of holes and the quantity of bioturbation based on the volume of soil excavated by bioturbators along a gradient ranging from arid to humid in Chile. We distinguished between invertebrates and vertebrates. Overall, hole density (no/ 100 m²) decreased from arid (raw mean and standard deviation for invertebrates: 14 ± 7.8, vertebrates: 2.8 ± 2.9) to humid (invertebrates: 2.8 ± 3.1, vertebrates: 2.2 ± 2.1) environments. However, excavated soil volume did not follow the same clear geographic trend and was 300-fold larger for vertebrates than for invertebrates. The relationship between bioturbating invertebrates and vegetation cover was consistently negative whereas for vertebrates both, positive and negative relationships were determined along the gradient. Our study demonstrates complex relationships between climate, vegetation and the contribution of bioturbating invertebrates and vertebrates, which will be reflected in their impact on ecosystem functions.

3.2 Introduction

Bioturbation, the biological reworking of soils and sediments (Darwin, 1837; Meysman et al., 2006), shapes the environment and thus has considerable consequences for ecosystem processes (Jones et al., 1994) such as sediment transport, soil formation (Eldridge & Mensinga, 2007; Hagenah & Bennett, 2013), soil water cycles (Valentine et al., 2017), litter decomposition (Hayward et al., 2016), and nutrient availability (Kurek et al., 2014; Yu et al., 2017). Soil excavating animals range from small invertebrates such as ants (Lobry de Bruyn & Conacher, 1994; Nkem et al., 2000) and earthworms (Plaas et al., 2019; Ruiz et al., 2015) to medium-sized vertebrates such as gophers (Klaas et al., 1998; Vleck, 1981) and beavers (Larsen et al., 2021; Persico & Meyer, 2009). Generally, bioturbating animals have distinct adaptations to environmental conditions but recent studies reveal that bioturbating animals are intentionally

able to modify their environment (Corenblit et al., 2011, 2021; Viles et al., 2021). Thus, assessments of the relative contributions of bioturbators to soil-shaping processes across larger climate gradients, must consider both the composition of bioturbator communities and their relationships to the abiotic and biotic environment. Previous studies indicate that:

1. The abundance and composition of burrowing animal communities depend on climatic (=abiotic) factors such as temperature and humidity (Crawford et al., 1993; Gerrard et al., 1996; Holmgren et al., 2006; Jimenez et al., 1992; Lima et al., 1999; Milstead et al., 2007). Ants and mammals are the most important bioturbators in semiarid and arid areas, and earthworms (Lumbricidae) dominate in humid areas (Wilkinson et al., 2009). Local soil characteristics affect bioturbating activity, which is highest after rainfall because the soil softens and the energy cost of digging is accordingly reduced (Marsh, 1988) as shown for burrowing mammals (Price & Podolsky, 1989) and in the nest site selection of ants (Jimenez et al., 1992).

2. Burrowing animals are closely associated with biotic components of the environment, especially vegetation which affects the abundance of bioturbators directly by providing food (Kelt et al., 2004; Muñoz et al., 2009) and indirectly by providing habitat (Kerley et al., 1997). In humid regions with dense vegetation cover, food resources are generally abundant and thus mammals have less need to dig for food. Vegetation also provides shelter further reducing the need to dig. In resource-limited environments, such as semi-arid and arid regions, the activity and quantity of bioturbating mammals correlate positively with vegetation cover, because of those animals' need to seek subterranean food and shelter (Eldridge & Whitford, 2014). By contrast, invertebrates such as earthworms do not rely on surface resources offered by vegetation cover as they live entirely belowground, where they feed on dead roots in the soil (Armour-Chelu & Andrews, 1994).

Those studies demonstrate, that both, abiotic and biotic components influence bioturbation patterns, with the relationships between bioturbators and their environment varying between animal groups (Platt et al., 2016). Detailed insights into the relative contributions of those groups can be obtained by associating them with their burrows, such as based on the diameter of the holes they create. A previous study has collected data on burrowing animals along a climate gradient and used a threshold of 2.5 cm to differentiate between vertebrates and invertebrates (Übernickel et al., 2021).

However, most studies have thus far focused either on the burrowing activity and quantity of single species (mostly vertebrates), or on individual climatic regions (Übernickel et al., 2021). Studies on the overall patterns of bioturbation along broad climatic gradients are rare. To close this research gap, we examined the interaction of abiotic and biotic components along a broad climatic and vegetational gradient in Chile. For this purpose, we measured the abundance of burrow entrances (hole density) and the amount of soil excavated by burrowing animals (excavated soil volume) as parameters for bioturbation activity and quantity across seasons. Taking into account the available literature, we hypothesized that:

H1: Bioturbating activity decreases from arid to humid regions because climate drives the abundance of burrowing animals and the contribution of invertebrates and vertebrates to bioturbation patterns.

H2: Seasonal changes affect bioturbation with a higher activity of burrowing animals during rainy seasons, when the soil is softer, and the energetic cost of digging is therefore reduced.

H3: With increasing vegetation cover, the bioturbating activity of many invertebrates (including most earthworms) decreases, due to the subterranean food supply provided by fine roots in the soil independent of soil surface vegetation, while that of vertebrates increases, due to the increased availability of food and shelter.

3.3 Methods

3.3.1 Study area

Our study was conducted at four sites representing a climate gradient along the coastal range of Chile (26°S-38°S), extending from an arid desert with a mean annual temperature of 16.8 °C and mean annual precipitation of 12 mm to a temperate humid rainforest with a mean annual temperature of 6.6 °C and mean annual precipitation of 1469 mm (Fick & Hijmans, 2017): arid Atacama Desert, located in Pan de Azúcar National Park, semi-arid shrubland in the private reserve Santa Gracia, a Mediterranean forest in La Campana National Park and a humid rainforest in Nahuelbuta National Park. All approvals from the relevant authorities, i.e. the Chilean National Forest Commission (CONAF), were obtained in advance to our study and granted access to the research sites. In 2019, the year of our field campaigns, the mean temperature in the arid desert was 14.6 °C and the mean precipitation was 9.4 mm while in the humid rainforest, the mean temperature was 7.3 °C and the mean precipitation was 1885 mm (Übernickel et al., 2020).

To sample each research site representatively, we established 12 10 m × 10 m plots with a distance of at least 30 m between them during the first field campaign, conducted in autumn of the southern hemisphere (March to April 2019). In a second field campaign conducted in spring of the southern hemisphere (September to November 2019) we established eight additional plots at each site to cover possible variation, resulting in a total of 20 plots per site. The 20 plots per research site were evenly distributed across two opposing hillsides, 10 on the north- and 10 on the south-facing hillslope.

3.3.2 Assessment of bioturbation activity and quantity

To evaluate bioturbation activity, we counted the number of all visually detectable burrow entrances on the soil surface (hole density) of each plot. We calculated the amount of soil excavated by burrowing animals (excavated soil volume) as an indicator of bioturbation quantity by using a caliper to measure the vertical (d_v) and horizontal (d_h) diameters. In addition, we defined the depth of each hole entrance (d_e) as the distance to the first barrier encountered by the caliper and measured this parameter. Raw data of burrow measurements can be obtained from S3.7 Table. Following (Gabet, 2000; Richards et al., 2011; Übernickel et al., 2021), we calculated the (minimal) excavated soil volume assuming that the measured burrows were cone-shaped:

$$excavated\ soil\ volume = \frac{1}{3} * \left[\frac{d_v + d_h}{4}\right]^2 * \pi * d_e.$$

To distinguish between the burrows of invertebrates and vertebrates, burrows with a hole-entrance diameter < 2.5 cm were assumed to be created by invertebrates and burrows with a hole-entrance diameter ≥ 2.5 cm by vertebrates (Übernickel et al., 2021).

3.3.3 Assessment of vegetation data

Vegetation cover was estimated using unmanned aerial vehicle (UAV) red green blue (RGB) images and land cover classification (Grigusova et al., 2021). For each plot, we calculated the ratio of pixels classified as any plant type (herbs, shrubs, cacti, trees) to the amount of all pixels. Following (Horn, 1981), the average elevation (hillside elevation) and the hillslope of each plot were estimated based on high resolution Lidar data (Kügler et al., 2022).

3.3.4 Statistical analyses

For the burrows of invertebrates and vertebrates we analyzed the allometric relationship between their depth (d_e) and their diameter (mean of d_v and d_h). We regressed the mean diameter of the entrance versus the depth using the log_{10}-transformed values of both variables and then determining the slope. In an isometric relationship, the log-transformed variables should be

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linearly related to a slope of one (Huxley, 2005). Since diameter and depth were measured with roughly equal error, in addition to an ordinary least squares (OLS) regression, we estimated the slope using a reduced major axis (RMA) regression (Harper, 2014). To assess a deviation from a slope of one, we used the offset argument available in most regression functions. With the diameter serving as the independent variable and the offset, the estimate tests for deviations from one. For the slope of the RMA regression, we used the standard error and a t-test to test for deviations from one. The same approach was applied to the regression between excavated soil volume and hole density.

Table 3.1: Summary of all variables used in the GLMM. Depicted are the response variables, fixed predictors (abiotic and biotic) and the random factor.

Response variable	Abiotic fixed predictors	Biotic fixed predictors	Random factor
Hole density or excavated soil volume	Site Season Hillside elevation Hillslope	Vegetation cover Animal group	Plot number

To analyze the interaction of abiotic and biotic components in bioturbation activity and quantity, we applied generalized linear mixed effect models (GLMMs). We used hole density or excavated soil volume as response variables, site, season, hillside elevation and hillslope as abiotic fixed predictors and vegetation cover and animal group as biotic fixed predictors. The study plots were used as a random factor (Table 3.1). All data of the GLMM parameters can be obtained from Table S3.7. We also included interaction terms between site and all other fixed predictor variables and between vegetation cover and taxon. We standardized the fixed predictor hillside elevation for each site because it varied and could not be assigned separately to each of the sites. We performed GLMMs for the 12 plots within each site (total of 48 plots) in the first field campaign, conducted in the southern-hemispheric autumn, and in the 20 plots within each site (total of 80 plots) during the second campaign conducted in the southern-hemispheric spring. Separation of the hole density of invertebrates and vertebrates resulted in 256 measurements ($2 \times (48 + 80)$).

For the GLMM of the excavated soil volume, we $\log_{10}$-transformed data for hole density and excavated soil volume to achieve normality of the residuals. For the $\log_{10}$-transformation, we only considered plots with a hole density > 0 [no/ 100 m²]. Thus, 46 plots without holes were not included in the GLMM for excavated soil volume, resulting in 210 valid measurements.

Additionally, we integrated the interaction between hole density and taxon as another fixed predictor.

All statistical analyses were performed using the R statistical environment (version 1.3.1093). We used the *lmodel2* package (Legendre, 2018) for OLS and RMA regression analysis. For the GLMM, we employed the *buildmer* function (Voeten, 2019) of the *lme4* package (Bates et al., 2021) to perform backward stepwise selection. 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). We additionally performed an ANOVA between all possible combinations of fixed predictors retained within the fitted model to evaluate the significance of certain combinations between predictors using the *anova* command and performing a Chi-square test (Chambers & Hastie, 2017).

3.4 Results

First, we investigated the allometric relationships by examining the relationship between the mean diameter and mean depth of the burrows and between the hole density and excavated soil volume. While the respective estimates of the slope are presented herein, our focus is on the RMA slopes. For both, invertebrates and vertebrates, the slopes showed a positive allometric relationship (Fig 3.1A, Table 3.2) that was maintained also in the single-season analysis (Fig. S3.1, Table S3.2). However, note that the statistical tests evaluating burrow characteristics and the excavated soil volume were not strictly independent, as the former parameter was used to calculate the latter.
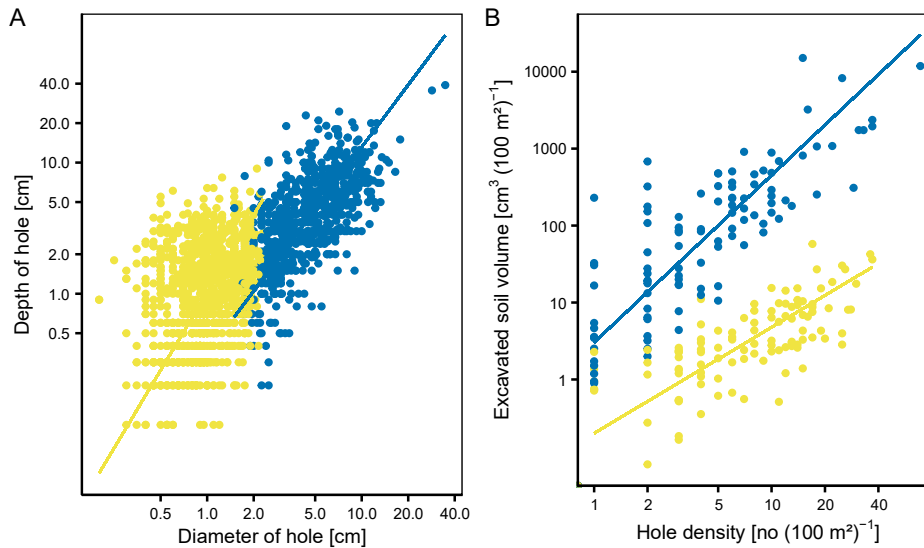
Fig 3.1: Relationships between burrow parameters and bioturbation parameters created by burrowing invertebrates (yellow) and vertebrates (blue). (A) Relationship between the depth and mean diameter of the holes, (B) relationship between the excavated soil volume and hole density. The regression lines are derived from the reduced major axis analysis. Note that both axes in (A) and (B) were log_{10}-scaled. Data from both field campaigns and all sites were used.

Hole density was always greater for invertebrates than for vertebrates (Fig 3.2A). For invertebrates, hole density decreased continuously from the arid site Pan de Azúcar (raw mean and standard deviation: 14 ± 7.8 no/ 100 m^{-2}) to the humid site Nahuelbuta (2.8 ± 3.1 no/ 100 m^{-2}) while hole density for vertebrates was highest in the semi-arid site Santa Gracia (9.1 ± 9.7 no/ 100 m^{-2}) and remained similar in the other three sites (Pan de Azúcar: 2.8 ± 2.9 no/ 100 m^{-2}, La Campana: 5.6 ± 8.7 no/ 100 m^{-2}, Nahuelbuta: 2.2 ± 2.1 no/ 100 m^{-2}, Fig. S3.1).

Table 3.2: Ordinary least squares (OLS) and reduced major axis (RMA) regression analyses of the relationships between the depth and mean diameter of the holes and between the excavated soil volume and hole density for invertebrates and vertebrates (all variables $\log_{10}$-transformed). A slope of one represents an isometric relationship. Depicted are statistical method, correlation coefficient, slope, standard error (SE) and p-value (p) of the offset. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001. Data from both field campaigns and all sites were used. Further information on the statistical analysis is provided in the Methods section.

		invertebrate				vertebrate			
Relation	method	r	slope	SE	p	r	slope	SE	p
Depth and diameter	OLS (mixed model)	0.31	0.729	0.053	<0.001***	0.44	0.996	0.045	0.93
	OLS	0.32	0.628	0.057	<0.001***	0.66	1.04	0.043	0.3
	RMA	0.61	1.97	0.057	<0.001***	0.53	1.57	0.43	<0.001***
Excavated soil volume and hole density	OLS (mixed model)	0.55	0.933	0.10	0.5	0.66	1.76	0.13	<0.001***
	OLS	0.69	0.955	0.10	0.64	0.81	1.77	0.13	<0.001***
	RMA	0.48	1.38	0.10	<0.001***	0.66	2.17	0.13	<0.001***
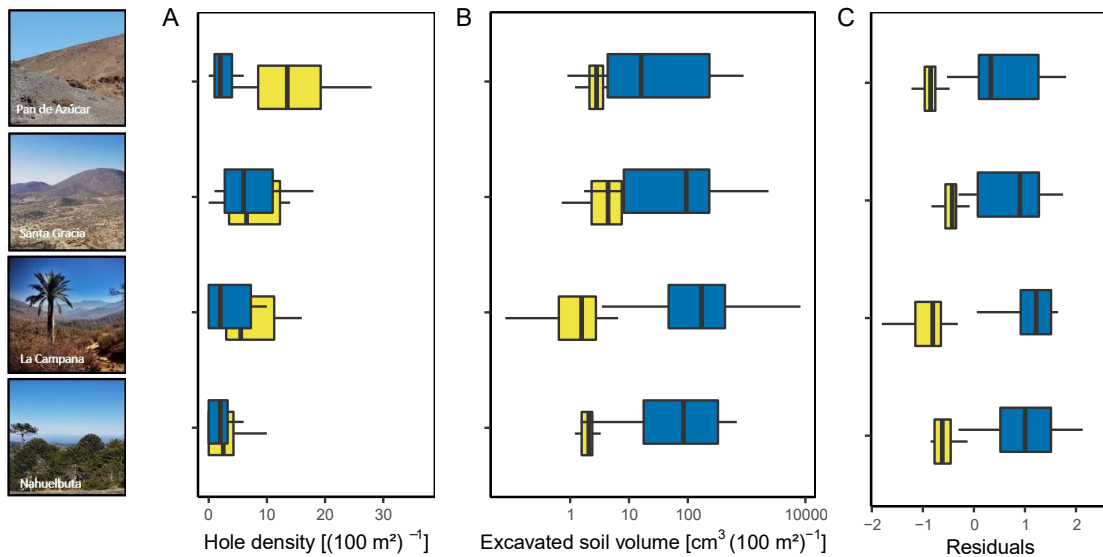
Fig 3.2: Bioturbation patterns of invertebrates (yellow) and vertebrates (blue) in each site (Pan de Azúcar, Santa Gracia, La Campana, Nahuelbuta). (A) Median hole density based on the raw data, (B) median excavated soil volume of holes, (C) the residuals of the excavated soil volume ($\log_{10}$-transformed) after correcting for hole density ($\log_{10}$-transformed) using separate regressions for the two animal groups. Note that the x-axis in (B) and (C) was $\log_{10}$-scaled. Data from the field campaign from September to November were used.

Overall, the pattern of excavated soil volume from arid to humid was hump-shaped for vertebrates (largest in La Campana), whereas for invertebrates we could not determine a clear geographic pattern along the gradient (Fig 3.2B). In each site, the soil volume excavated by vertebrates was larger. This difference between the two groups of bioturbators was especially clear in the Mediterranean site La Campana (raw mean and standard deviation for invertebrates: 0.00019 ± 0.00016 m³ ha^{-1}, for vertebrates: 0.06 ± 0.18 m³ ha^{-1}) and the humid site Nahuelbuta (invertebrates: 0.00015 ± 0.00022 m³ ha^{-1}, vertebrates: 0.012 ± 0.02 m³ ha^{-1}, Fig. S3.1). Correcting the amount of excavated soil volume for the number of holes, the geographic pattern revealed by the residuals was similar to that obtained based on the analysis of the raw data (Fig. 3.2C); thus, the excavated soil volume was larger for vertebrates than for invertebrates, especially large at the two southern sites.
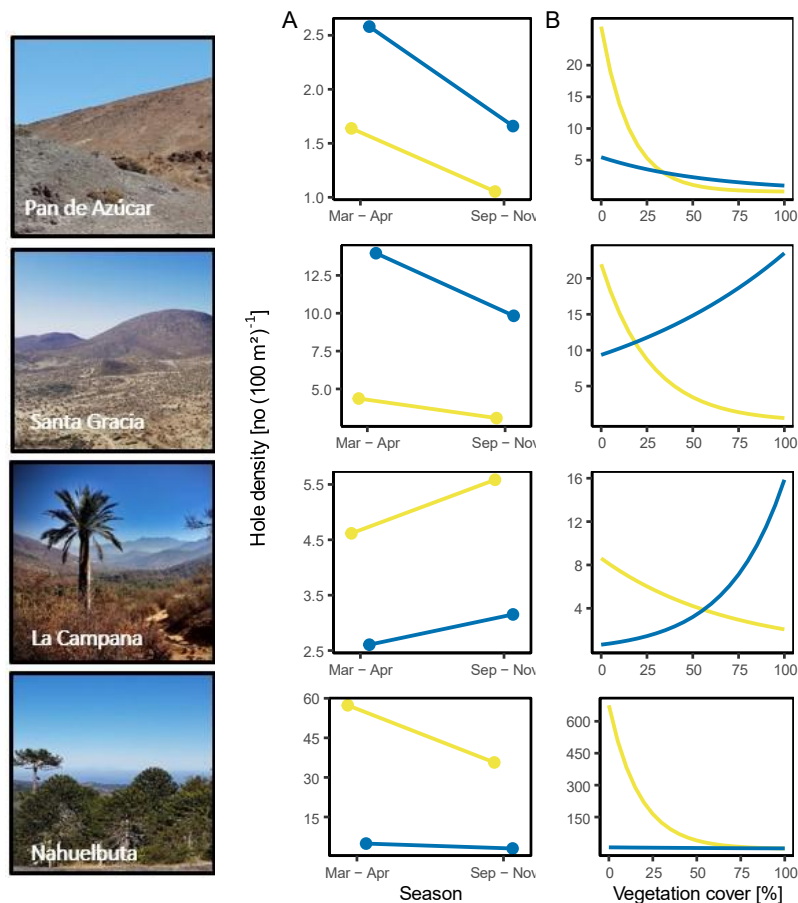
Fig 3.3: Fitted relationship between the hole density and fixed effects for invertebrates (yellow) and vertebrates (blue) at each site (Pan de Azúcar, Santa Gracia, La Campana, Nahuelbuta). (A) Season (autumn: March-April/ spring: September-November), (B) vegetation cover [%]. Data from both field campaigns were used.

All predictors for the response variable hole density were significant in the GLMM, with the fixed predictors explaining 48% and the random predictor plot number explaining 39% of the variation (AIC = 2030.7, p < 0.001, Tables S3.3 and S3.5). The overall hole density was higher in Santa Gracia and Nahuelbuta during the field campaign from March to April than during the field campaign from September to November while in Pan de Azúcar there was no difference between the two seasons (Fig 3.3A). For invertebrates, hole density decreased at all sites with increasing vegetation cover. The hole density of vertebrates was positively associated with increasing vegetation cover in Santa Gracia and La Campana (Fig 3.3B). Overall, there was no clear trend in the relationship between the hole density of invertebrates and increasing vegetation cover whereas vertebrates' hole density increased with increasing vegetation cover (Fig. S3.2A).

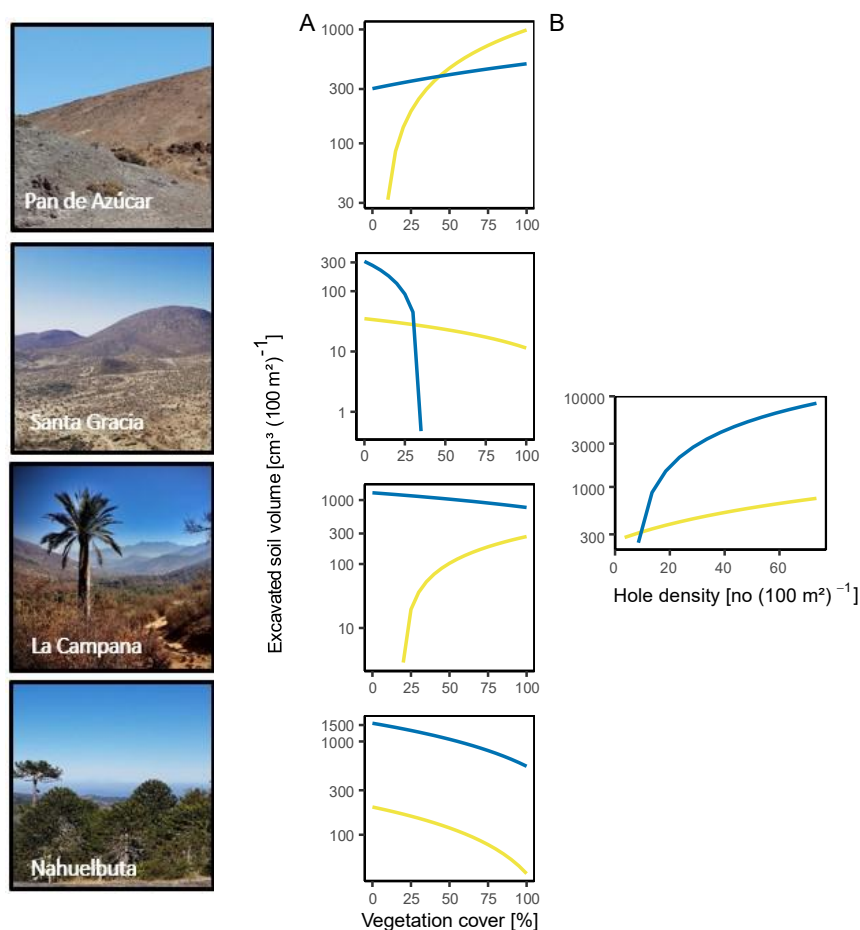**Fig 3.4: Fitted relation between excavated soil volume (log₁₀-transformed) and fixed effects for invertebrates (yellow) and vertebrates (blue) at each site (Pan de Azúcar, Santa Gracia, La Campana, Nahuelbuta).** (A) Vegetation cover [%], (B) hole density (log₁₀-transformed). Data from both field campaigns were used.

After the exclusion of non-significant independent variables, the fixed predictors season, vegetation cover, hole density and hillside elevation within the fitted GLMM for excavated soil

volume explained 85% of the model variation (AIC = 296.67, $p < 0.001$, Tables S3.4 and S3.6). The patterns of excavated soil volume varied for invertebrates and vertebrates with increasing vegetation cover along the climate gradient (Fig 3.4A). The raw data revealed another trend, as the excavated soil volume increased with increasing vegetation cover for both, invertebrates and vertebrates (Fig. S3.2B). In addition, the excavated soil volume increased disproportionally with increasing hole density, with a larger increase for vertebrates than for invertebrates (Fig. 3.4B).

3.5 Discussion

Our study showed that while hole density decreased from arid to humid environments, no clear pattern could be discerned for the excavated soil volume along the investigated environmental gradient. However, the contribution of vertebrates to excavated soil volume was larger than that of invertebrates. For the latter, the relationship to the vegetation cover along the climate gradient was consistently negative while for vertebrates it was partly positive.

Before discussing the general results, a few comments should be made on the allometric relationships of the burrow characteristics. Based on the RMA analysis regressions, these relationships were not isometric, as the relative depth of a burrow increased with the increasing diameter of the entrance. This finding suggests that, for bioturbators, larger animals dig deeper into the soil (White, 2005). This relationship presumably reflects the anti-predator behavior of larger animals: with increasing body size animals want to keep their entrance as small as possible to exclude predators (Milne & Bull, 2000), but on the same time minimize burrowing cost (Vleck, 1981) on one hand, but have a comfortable nest site (White, 2005) on the other hand. Our data do not allow a test of this hypothesis, but further analyses of these allometric relationships are likely to provide a rich source of biological and behavioral information, particularly in studies comparing a large number of animal groups.

Our first hypothesis, that bioturbating activity decreases from arid to humid regions (Crawford et al., 1993; Gerrard et al., 1996; Holmgren et al., 2006; Jimenez et al., 1992; Lima et al., 1999; Milstead et al., 2007), was supported by our results for invertebrates, as their hole density decreased from arid to humid climates. Vertebrates, however, created fewer holes in arid than in semi-arid regions. Burrowing vertebrates are, on average, larger than invertebrates (White, 2005) such that fewer holes are consistent with a decline in animal density with increasing body size (Peters & Wassenberg, 1983). Accordingly, vertebrates were presumably less frequent in the arid region of our study than in the other climatic zones, such that fewer vertebrate than invertebrate burrows were present over a given area. Similarly, the higher hole density of

invertebrates all along the climate gradient can be attributed to the generally higher abundance of invertebrates (Platt et al., 2016). However, it is also the case that most invertebrates create their own new burrows while some vertebrates use previously existing burrows as an energy-saving strategy (Newsome & Corbett, 1975; Roper, 1992). In particular, larger animals, in our case vertebrates, invest more energy in burrowing effort than smaller invertebrates. Previous investigations showed that the energy cost of burrowing is directly proportional to the amount of soil moved by the bioturbator. Consequently, larger vertebrates, which need to move larger soil amounts to create a burrow of adequate size, will burrow fewer holes (Vleck, 1981).

The excavated soil volume did not follow a clear pattern across the climatic gradient and it differed between invertebrates and vertebrates in our study. Similar results were obtained in a recent study measuring the excavated soil volume of bioturbators along the same environmental gradient (Übernickel et al., 2021). The authors found that the excavated soil volume was greater in the semi-arid (0.56 m³ ha^{-1} yr^{-1}) and Mediterranean (0.93 m³ ha^{-1} yr^{-1}) than in the arid (0.34 m³ ha^{-1} yr^{-1}) and humid (0.09 m³ ha^{-1} yr^{-1}) climate zones and that the excavation rates were higher for vertebrates (0.01-56 m³ ha^{-1} yr^{-1}) than for invertebrates (0.01-37 m³ ha^{-1} yr^{-1}).

These findings are in line with several studies showing that, due to their larger body size, vertebrates excavate considerably larger volume of soil (1 - 5 m³ ha^{-1} yr^{-1}) than invertebrates (<1 m³ ha^{-1} yr^{-1}) (Abaturov, 1972, 1972; Ellison, 1946; Humphreys, 1989; Formanowicz & Ducey, 2011; Kalisz & Stone, 1984; Platt et al., 2016; Polis et al., 1986; Yair & Rutin, 1981) as well as our findings. Those studies together with our own demonstrate the importance of vertebrates as bioturbators along a climate gradient.

Our second hypothesis, that bioturbation activity and quantity respond to seasonal changes (Jimenez et al., 1992; Price & Podolsky, 1989), was supported by the higher hole density during autumn than spring of the southern hemisphere, as observed at both the semi-arid and humid site. In the arid desert, with a consistent lack of rainfall events, there was no difference between seasons. This is in agreement with previous studies and with the observation that in the southern hemisphere the bioturbation season ends in autumn (Yair, 1995). Moreover, the climate in Central Chile during the study period in 2019 was drier than usual (Garreaud et al., 2020), which may have lessened the differences in bioturbation activity and quantity between seasons. While the relationship between seasons and bioturbation patterns is no doubt, our study suggests that, at least in Chile, the impact of bioturbation is largest in semi-arid and humid climate zones after the autumn rainfall.

The absence of a clear trend between vegetation cover and either bioturbation activity or quantity along the climate gradient was consistent with previous studies examining the distribution of burrow entrances as a function of vegetation (Eldridge et al., 2012; Whitford & Kay, 1999). However, we were able to show that the bioturbation patterns of invertebrates and vertebrates differed. The consistently negatively association of invertebrates with vegetation cover supported our hypothesis that some invertebrates are entirely independent of surface resources due to their permanently belowground lifestyle (Armour-Chelu & Andrews, 1994). By contrast, because vertebrates rely on a resource supply from the surface (Eldridge & Whitford, 2014), a positive association with vegetation cover occurred only in the middle of the geographic gradient, as in the arid region the vegetation cover is sparse. Vertebrates living in regions of extreme temperatures characterized by limited resource must invest their energy in digging for food as well as shelter from extreme temperatures in such resource-limited habitats (Giovanni, 1965). Furthermore, there is often no vegetation near freshly created burrows, because burrowing typically destroys the vegetation at and possibly adjacent to the burrow (Gabet, 2000; Kaczor & Hartnett, 1990). This may have introduced a biased estimate of vegetation cover within plots with fresh burrows and would explain the absence of either a positive or a negative association between burrowing vertebrates and vegetation cover in the humid region. Nonetheless, in general, vegetation cover was shown to be positively associated with vertebrates with a complex influence on bioturbation patterns along the climate gradient.

3.6 Conclusion

Our study showed that climatic conditions and vegetation cover drive the activity and quantity of bioturbation as well as the amount of burrowing by different animal groups. The contribution of vertebrates to bioturbation quantity is large and only bioturbating vertebrates had a positive association, albeit a partial one, with vegetation cover. In its examination of the interaction of abiotic and biotic components, our study demonstrated the intricate relationships between climate, vegetation and the contribution of bioturbating invertebrates and vertebrates. These results provide further insights into the patterns that occur along broad climatic gradients and therefore into the impact of ecosystem engineers on ecosystem processes such as sediment transport, soil water cycling and nutrient availability. In a further study, we will therefore compare physical and chemical soil properties in areas with soil affected and unaffected by bioturbation along the same climatic gradient. Additionally, our findings support the importance of examining impacts of bioturbation on ecosystem processes on a broader climatic scale and thereby encourage similar further studies like the assessment of sediment redistribution rates caused by bioturbation (Grigusova et al., 2022).

Data Availability

All relevant data are within the manuscript and its Supplementary Material files.

Competing interests

The authors have declared that no competing interests exist.

Chapter 4: Bioturbation enhances C and N contents on near-surface soils in resource-deficient arid climate regions but shows adverse effects in more temperate climates

4.1 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.

4.2 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 & Rath, 2002; Gutterman, 1997; Mallen-Cooper et al., 2019; Zaitlin & Hayashi, 2012).

Bioturbation can physically affect soil properties, mainly soil texture, through the vertical translocation of sediments (Phillips, 2001; Phillips & 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 & 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 enhance soil quality by increasing contents of soil nutrients and water holding capacity (Clark et al., 2018; 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 & Whitford, 1991; Contreras et al., 1993; Eldridge & 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.,2006; Laycock and Richardson, 1975; Hagenah & 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 & Stanford, 1998). At the same time, bioturbating animals regularly leave their urine and feces in the burrows (Mulder & Keall, 2001; Eldridge & Rath, 2002; Gervais et al., 2010; Whitford & 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 & 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 & Rath, 2002; Hagenah & Bennett, 2013), studies in temperate climates also showed a decrease in macronutrient contents on the near-surface soil (Sherrod & Seastedt, 2001; Eldridge & Mensinga, 2007; Lara et al., 2006; Eldridge & 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 & Whitford, 1991; Eldridge & 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:

H1: 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.

H2: 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.

H3: 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.

4.3 Materials and methods

4.3.1 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 & 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 S4.1).

4.3.2 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.

4.3.3 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 4.1).

Table 4.1: 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

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.

4.3.4 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 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.

Table 4. 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

4.3.5 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 4.2). 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).

4.3.6 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 S4.10) for comparison to our study.

4.4 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. 4.1, Table S4.2). 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. 4.2, Table S4.2). 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 S4.2).
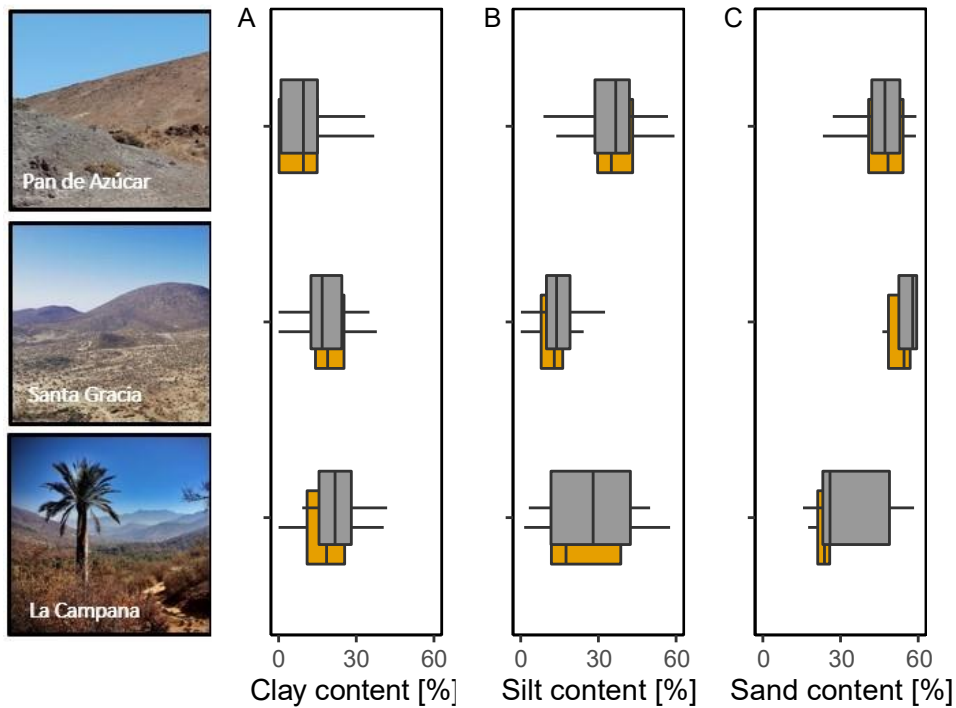
Fig. 4.1.: Physical soil properties of mound (orange) and control (grey) soil samples in the research sites Pan de Azúcar (arid), Santa Gracia (semi-arid) and La Campana (Mediterranean). (A): median clay [%], (B): median silt [%], (C): median sand [%].
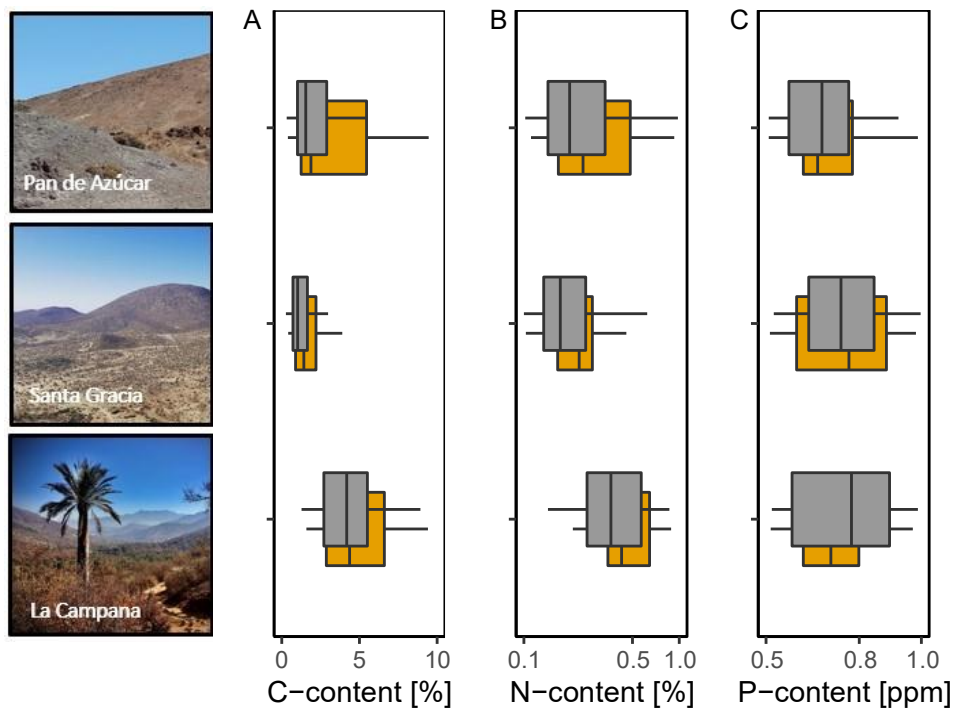
Fig. 4.2.: Chemical soil properties of mound (orange) and control (grey) soil samples in the research sites Pan de Azúcar (arid), Santa Gracia (semi-arid) and La Campana (Mediterranean). (A): median C [%], (B): median N [%], (C): median P [ppm]. Note that the x-axis in B) was $\log_{10}$-scaled for illustrative reasons.

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 S4.3), we present just silt, C and N here.
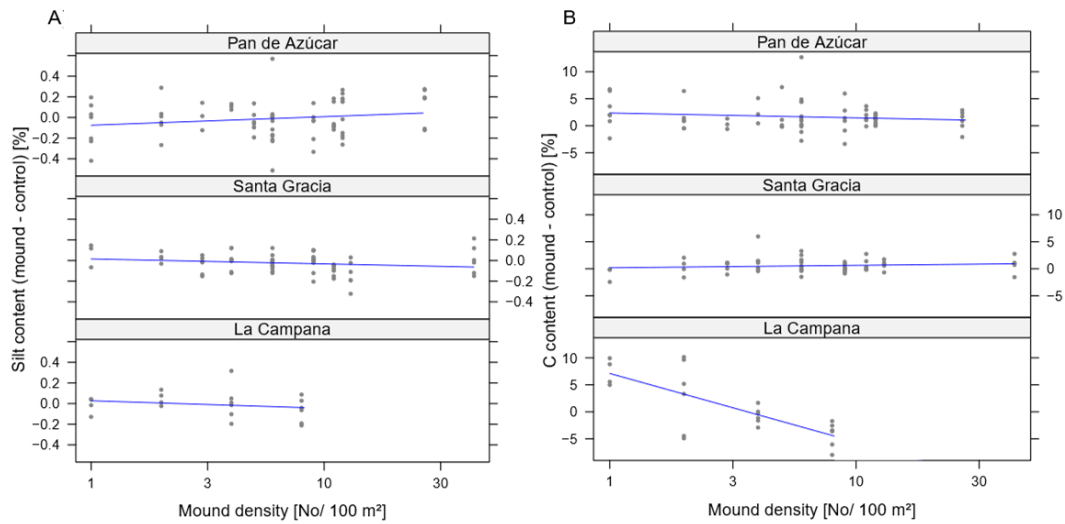
Fig. 4.3: Effect plots for the fixed effect mound density at each research site (arid Pan de Azúcar, semi-arid Santa Gracia, Mediterranean La Campana). (A) Fitted relationships between mound density [No/ 100 m²] and silt content [%], (B) fitted relationship between mound density [No/ 100 m²] and C content [%]. Note that the x-axis for (A) and (B) was $\log_{10}$-transformed.

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 S4.5). The silt content increased in Pan de Azúcar with increasing mound density while it decreased in Santa Gracia and La Campana (Fig. 4.3A). In all research sites, the silt content increased with increasing hillslope (Fig. S4.1A).
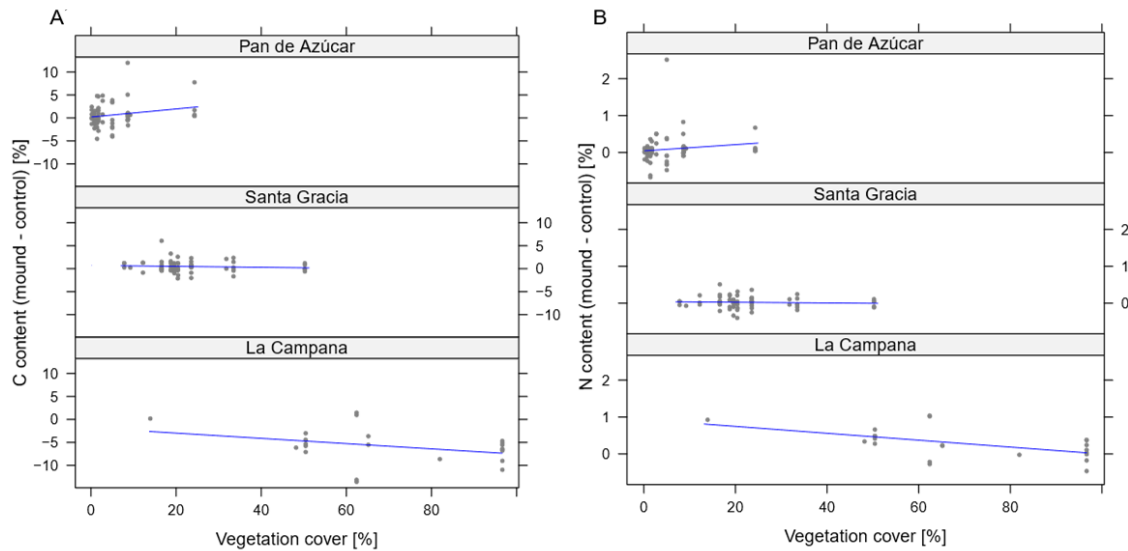
Fig. 4.4: Effect plots for the fixed effect vegetation cover at each research site (arid Pan de Azúcar, semi-arid Santa Gracia, Mediterranean La Campana). (A) Fitted relationships between vegetation cover [%] and C content [%], (B) fitted relationship between vegetation cover [%] and N content [%].
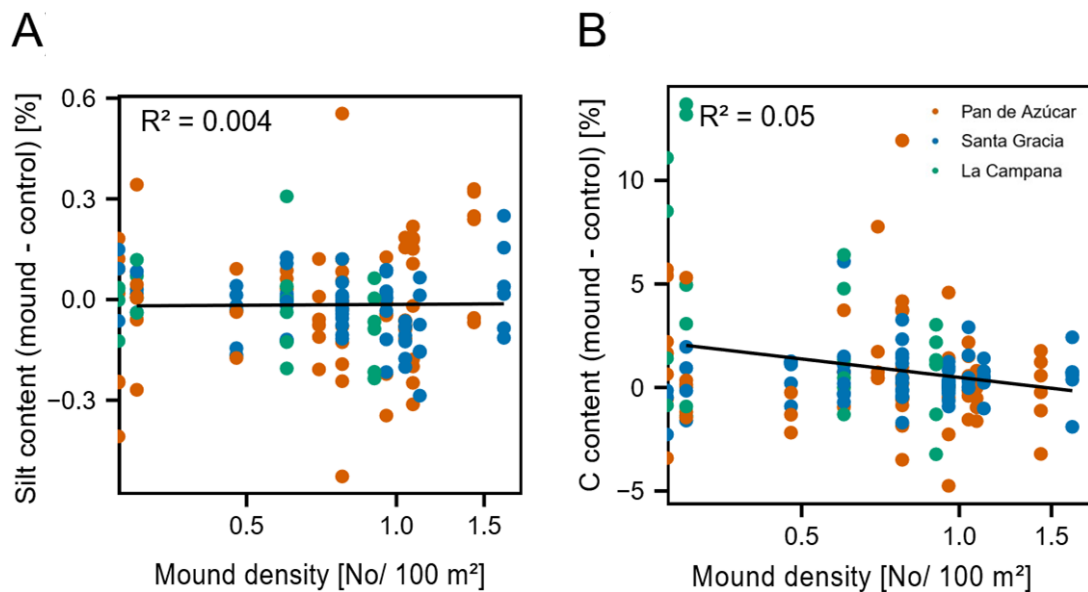
Fig. 4.5: Relationship between the physical soil property silt and the macronutrient C and mound density in the three research sites Pan de Azúcar (arid), Santa Gracia (semi-arid) and La Campana (Mediterranean). (A) Relationship between silt content and mound density. (B) Relationship between C content and mound density. For illustrative reasons we included the coefficient of determination R^2. Note that the x-axes in (A) and (B) were log_{10}-transformed.

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 variation in the response variable (AIC = 730.6, $p < 0.001$, Supplementary Table S4.7) 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 S4.8). The

C content decreased in Pan de Azúcar and La Campana and remained constant in Santa Gracia (Fig. 4.3B) due to bioturbation. For both macronutrients, C and N, the same trends occurred in the fitted models (Fig. 4.4): 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. S4.1B). N content decreased with increasing hillside elevation in La Campana but remained constant in the two northern research sites (Fig. S4.2). When considering the relationship between soil properties and mound density, the physical soil property silt did not change with increasing mound density (Fig. 4.5A) whereas the chemical C content decreased with increasing mound density across all research sites (Fig. 4.5B).

4.5 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 "4.3.3 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 S4.10 "% 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

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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 & Keall, 2001; Eldridge & Rath, 2002; Gervais et al., 2010; Whitford & Steinberger, 2010; Kurek et al., 2014; Yu et al., 2017).

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., 2014). 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 & 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 & 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 & 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 & 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 (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 to unaffected soils in climate regions providing more resources where digging is not as necessary (Dostál et al., 2005; Eldridge & 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 & Whitford, 1991; Eldridge & 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 & 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 & 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 & Moral, 2003).

4.6 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.

Data Availability

All relevant data are within the manuscript and its Supplementary Material files.

Competing interests

The authors declare that they have no conflict of interest.

Chapter 5: Synthesis

As ecosystem management is important for the maintenance of biodiversity, my thesis found a positive link between geo- and biodiversity which might help to predict biodiversity for conservation management through geo-referred data in future studies. In addition, this work increases the understanding of the drivers of bioturbation patterns as well as the bioturbators' effects along a climate gradient. In particular, this thesis highlights the importance of bioturbation for the ecosystem service C sequestration leading to climate regulation.

5.1 The link between geodiversity and biodiversity

Comparing previous studies in chapter 2, I found a link represented in a positive correlation between geo- and biodiversity. This correlation was explained by the geodiversity elements soil richness, vegetation and rock richness which promote sufficient niches for species coexistence and thereby higher biodiversity (Gray, 2004; Parks & Mulligan, 2010). However, the correlations of the analyzed studies appear rather small. One possible explanation for these low correlations linking geo- and biodiversity are the complex relationships between biota and their environments. Consequently, different taxa may depend on more than one element of geodiversity. For instance, climate affects species distribution (Hodkinson, 1999) while geomorphology is an important driver for biotic changes (Harris, 1987; Van Devender, 1990). Besides, climate is also a significant driver of the geo-biodiversity relationships because in mild climates, i.e. temperate ones, the link between geodiversity and biodiversity appears stronger since intermediate disturbance promotes higher biodiversity. In contrast, in climates with more extreme stressful conditions, i.e. tropical or polar ones, this link is less abundant as high disturbance reduces biodiversity while geodiversity remains unaffected (Connell, 1978). Another reason for the low correlation between geo- and biodiversity are scales since geodiversity indices work as better predictors at larger scales (Bailey et al., 2017; Hjort et al., 2012). Further, most of the existing studies use only one geodiversity element instead of the combination of several elements to treat geodiversity as a holistic concept (Tukiainen et al., 2022) which may additionally explain the low geo-biodiversity correlation. Consequently, when predicting biodiversity via geodiversity, it is important to develop standards for the measurement of geodiversity elements incorporating the significant taxa, climates and scales.

5.2 The drivers of bioturbation patterns and bioturbator community composition along a climate gradient

In chapter 3 I showed that bioturbation activity decreases from arid to humid in Chile because burrowing animal communities depend on temperature and humidity (Crawford et al., 1993; Gerrard et al., 1996; Jimenez et al., 1992). Further, in any climate zone, bioturbation activity for invertebrates is higher due to their generally higher abundance (Platt et al., 2016). This is in line with my finding that the energy costs of burrowing are directly proportional to the amount of soil moved by the bioturbator. As a consequence, larger-sized vertebrates need to move larger soil amounts to create a burrow of adequate size and due to that, burrow fewer holes than invertebrates (Vleck, 1981). In terms of burrow costs, burrowing animals try to reach an equilibrium between minimized burrow costs and comfortable nest sites (Peters & Wassenberg, 1983; Vleck, 1981). Thereby, the animals want to keep their burrow entrance as small as possible to protect it from predators (Milne & Bull, 2000). Regarding seasonal effects, bioturbation patterns can respond to seasonal changes, i.e. more bioturbation activity is associated with softer soil due to rainfall. However, such seasonal effects do not occur in sites with no or rather small rainfall events (Yair, 1995). For the relation between bioturbation activity and vegetation cover, there is no clear trend. However, vertebrates and invertebrates behave distinctively different in response to increasing vegetation cover: Vertebrates rely on surface resources and conditions (Eldridge & Whitford, 2014) whereas invertebrates are independent of such due to their permanently belowground lifestyle (Armour-Chelu & Andrews, 1994). In summary, the patterns of bioturbation are driven by complex relations between climatic conditions, vegetation cover and the abundance of vertebrates.

5.3 The effect of bioturbation on soil chemical and physical properties

Even though bioturbation can enrich finer-sized soil compartments on the near-surface soil for a short time (Phillips, 2001; Phillips & Lorz, 2008), I found no significant changes in the finer-sized soil compartments in chapter 4. This is because, over longer time periods, finer soil particles are eroded from the surface through either wind (Simkin et al., 2004) or water (Ravi et al., 2007). In addition, when bioturbation occurs to a great extent, the finer and coarse particles are mixed to an extent where the soil texture becomes homogenized (Dostál et al., 2005; Johnson, 1989). In contrast to physical properties, I showed significant effects of bioturbation on macronutrient inputs: Like the varying patterns of bioturbation driven by different climates (Wilkinson et al., 2009; Yu et al., 2017), the effects of bioturbators on macronutrients are diverging along the climate gradient (Clark et al., 2018; Dostál et al., 2005).

Thereby, especially in arid climates with limited resources such as food and conditions like habitats or shelter from the sun or predation, bioturbation is mandatorily necessary to survive (Carlson & Whitford, 1991; Eldridge & Whitford, 2014; Ladegaard-Pedersen et al., 2005). Because of that, in such climates, bioturbators prefer digging next to the occurring sparse vegetation which may serve as food or shelter. In the process of burrowing, they incorporate plant parts into the soil enriching it with C and N (Faiz et al., 2018; Platt et al., 2016; Yurkewycz et al., 2014). Contrary to the bioturbation-enriched more resistant C and N on the near-surface soil, I found P remained stable since bioturbation activity might accelerate the leaching of the more susceptible macronutrient P (Garkaklis et al., 2003; Mohr et al., 2005). As bioturbation increases the macronutrients C and N in especially resource-limited arid climate zones, this might significantly improve these ecosystems through fertilization of near-surface soils and promotion of plant growth which might increase biodiversity (Eldridge & Rath, 2002; Gervais et al., 2010; Kurek et al., 2014; Mulder & Keall, 2001; Whitford & Steinberger, 2010; Yu et al., 2017). In addition, C input due to bioturbation can lead to an increased C sequestration by plants contributing to the mitigation of climate change (Ciais et al., 2008; Pregitzer et al., 2008; Reay et al., 2008; Thomas, 2010).

5.4 Conclusion

In this thesis, I found mostly positive but weak links between geo- and biodiversity. To improve the prediction of biodiversity through geodiversity, more studies combining several elements of geodiversity are needed. In addition, I depicted the additional important drivers such as the taxon, scale and climate zones of these correlations. My findings may facilitate data acquisition in the future making it more time- and cost-efficient.

As an example of a positive link between geo- and biodiversity, I expanded the overall understanding of the impact of bioturbation on ecosystem functioning considering a climate gradient ranging from arid to humid. I found bioturbation activity is mainly driven by climate, vegetation and the abundance of vertebrates. I highlighted the dominant role of vertebrates excavating up to 300-fold larger amounts of soil than invertebrates.

In addition, I showed that one important contribution of the bioturbators to ecosystem functioning is their effect on chemical soil properties. In particular, the enrichment of C (20%) and N (25%) on the near-surface soil by bioturbators in the arid climate zone is prominent and thereby enhances soil quality and contributes to mitigating climate change. Here, my thesis provides thresholds for the incorporation of the macronutrients C and N in different climate zones (arid, semi-arid, Mediterranean) that may serve as estimates for other regions within the

same climate zones. As bioturbation had beneficial effects on ecosystem functioning such as nutrient availability, my thesis supports the positive link between geo- and biodiversity.

Chapter 6: Perspectives

Chapters 2-4 offer several possibilities for additional studies which I discuss in the following.

6.1 Manual on appropriate assessment of geodiversity elements and the inversion of the concept

Since I found there is no recommendation on how to standardize the assessment of geodiversity elements to serve as the best predictor for biodiversity, a detailed manual setting standards is needed. This manual should list all geodiversity elements and their definitions as well as how to easiest gather them. For such a manual, it would also help to expand knowledge on different spatial scales by comparing geo- and biodiversity scales. Chapter 2 and previous research showed that there is an optimum on intermediate to large scales, where geodiversity indices are more suitable surrogates for biodiversity (Bailey et al., 2017; Hjort et al., 2012; Parks & Mulligan, 2010) providing sufficient data to be able to estimate species richness without extensive biological surveying (Müller et al., 2004). Further, investigating which taxa can be assessed at which scales is useful since this thesis and previous research found that certain taxa, e.g. invertebrates, operate on smaller spatial scales than vertebrates (Kremen et al., 1993). In addition, biodiversity measures, especially for species richness, work best at scales from 1 km² or more which should also be considered for data assessments (Wolters et al., 2006). Aside from spatial scales, temporal scales are also important to consider while assessing geodiversity because temporally variable areas permit the coexistence of species without competition which might promote specialization and endemism (Dufour et al., 2006; Parks & Mulligan, 2010). In contrast, less temporally variable resources permit a greater niche width and increased specialization within this niche for coexistence to occur (Parks & Mulligan, 2010). However, just like spatial scales, temporal scales were not investigated thoroughly at especially larger magnitudes (Parks & Mulligan, 2010). Accordingly, research on the impact of spatially varying seasonality on biodiversity is lacking (Dufour et al., 2006). This is why more investigation on larger spatial as well as temporal scales would provide a better insight into the effect of scales on the geo- and biodiversity links accomplishing the manual setting standards for geodiversity measurements.

In previous studies, geodiversity was used as a surrogate for biodiversity (Alahuhta et al., 2018; Hjort et al., 2012; Tukiainen et al., 2019) but this feedback between these two concepts was never turned around. In chapter 4 I showed that biodiversity through bioturbation can also reflect geodiversity as soil macronutrient enrichment. This raises the question if biodiversity may serve as a surrogate for geodiversity. To answer this question, a first hint is given through

the forest plot in the meta-analysis from chapter 2 (Fig. 2.4) which shows that the Shannon index serves as the best surrogate to depict the correlation between geo- and biodiversity. However, it is important to find more studies that use the Shannon index as a biodiversity measure to have a sufficient amount of available studies. Then, we could repeat the meta-analysis investigating if the Shannon index appropriately predicts the geo-biodiversity correlations. If this approach works, in some cases, already existing biodiversity data might be used to reduce the labor to assess geodiversity data (Hjort et al., 2012).

6.2 Expansion of the climate gradient, additional analysis on prevention of fire events and redistribution of microplastic via bioturbation

Since I found that especially climate determines bioturbation patterns in the investigated climate zones (arid, semi-arid, Mediterranean, humid) in chapter 3, it would help to expand the knowledge on bioturbation patterns in all existing climate zones. This would enable to expand the research on bioturbation patterns all over the world. Therefore, the methods developed in this thesis, i.e. hole number and excavated soil volume, can be applied to further climate zones that were not investigated up until now. Another possibility to represent bioturbation patterns worldwide might be the use of additional existing data on traits of bioturbating mammals (Krug, 2021). With that, certain taxa might be assigned to bioturbation activity and quantity for each climate zone since in chapter 3 I found this relation is proportional to their body size. With this, we could provide a better understanding of bioturbation activity and quantity of burrowing mammals worldwide which is important considering the driving force of vertebrates as bioturbators impacting crucial ecosystem services.

Since in chapter 4, we found bioturbation differently affects soil fertility depending on the climate zones, it would be useful to estimate soil fertilization through bioturbation worldwide. Therefore, additional soil sample collections from soil affected and unaffected by bioturbating animals in sparsely observed climate zones are needed. In chapter 4 I started compiling existing literature in different climates (chapter 4, Table S4.10). With this and my thresholds on macronutrient enrichment from chapter 4 (Table S4.2), a threshold of, for instance, C input due to bioturbation all around the world can be established. In addition, there is existing literature on other nutrients such as iron or magnesium affected by bioturbation which can also be incorporated to create additional nutrient input thresholds (Platt et al., 2016). Through the combination of the knowledge of bioturbation activity, the amount of excavated soil and such thresholds from all climate zones, an approximation for soil macronutrient enrichment via bioturbation worldwide would be possible.

In addition, previous studies showed that bioturbation can prevent fire events through either grazing or deposition of plant material and thereby reduction of flammable vegetation cover which is the dry vegetation of the previous season that can easily be inflamed (Foster et al., 2020; Richards et al., 2011). However, such feedbacks were not yet investigated thoroughly. This is why I suggest combining the data of excavated soil volume and vegetation cover from the plots I created for chapters 3 and 4 and comparing it to data from plots unaffected by bioturbation. With this, first, it is possible to calculate how much flammable vegetation cover was removed through bioturbation and then to calculate how much soil was excavated during burrowing. Combining the two previous calculations, the effect on grazing (calculation of flammable vegetation cover removal) and vegetation turn-over through bioturbation (excavated soil volume through bioturbation) reducing flammable vegetation cover can be approximated as a transfer function.

Further, bioturbators may influence microplastic redistribution along the soil column since they vertically redistribute different soil compartments which might incorporate microplastic (Phillips, 2001; Phillips & Lorz, 2008). However, so far, there is no research on the effect of bioturbation on microplastic in nature but just in laboratory greenhouse experiments (Huerta Lwanga et al., 2016; Rillig et al., 2017). These experiments showed that earthworms may transport microplastic in deeper soil horizons where it may negatively affect soil microbial processes, plant growth and litter composition (Rillig et al., 2019, 2021). However, due to the increased mixing of the vertical soil column via bioturbation (Eldridge, 2004; Hagenah & Bennett, 2013; Yurkewycz et al., 2014), the transport of microplastic just as the transport of fine soil compartments might go in both directions. This is why bioturbators may also bring microplastic upward to the soil surface where it then may be eroded through wind (Rezaei et al., 2022) or rainfall events (Han et al., 2022). In addition, the microplastic redistribution might also depend on the taxon since only earthworms were taken for the greenhouse experiments. It is important to also include other taxa in the greenhouse experiments such as ants which bring large soil amounts and, with this, possibly microplastic up to the surface (Debruyn & Conacher, 1994). Further, such experiments should also be performed with vertebrates, i.e. mice, excavating larger soil amounts (Vleck, 1981). As a result, such additional experiments with different taxa might show that certain bioturbators protect deeper soil horizons by transporting microplastic to the soil surface.

Finally, since so far, there is no overview of bioturbation patterns incorporating global estimations, all previously mentioned data evaluating bioturbation and its' effect on a global

scale can be combined to write a review. Therefore, my thesis offers data on soil excavations (chapter 3) and macronutrient inputs (chapter 4) which can be complemented with additional existing data on further effects of bioturbation such as fire prevention, microplastic redistribution or additional information such as erosion rates (Yair, 1995).

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Supplementary material

Appendices chapter 2

Table S2.1: Author, year, study area, DOI and taxon of the 90 studies incorporated in the analysis.

Author	Year	Study area	DOI	Taxon
Alahuhta et al.	2018	Finland	10.1016/j.ecolind.2018.03.068	Plants
Alahuhta et al.	2018	Finland	10.1016/j.ecolind.2018.03.068	Plants
Alahuhta et al.	2018	Finland	10.1016/j.ecolind.2018.03.068	Plants
Alahuhta et al.	2018	Finland	10.1016/j.ecolind.2018.03.068	Birds
Alahuhta et al.	2018	Finland	10.1016/j.ecolind.2018.03.068	Birds
Alahuhta et al.	2018	Finland	10.1016/j.ecolind.2018.03.068	Birds
Alahuhta et al.	2018	Finland	10.1016/j.ecolind.2018.03.068	Invertebrates
Alahuhta et al.	2018	Finland	10.1016/j.ecolind.2018.03.068	Invertebrates
Alahuhta et al.	2018	Finland	10.1016/j.ecolind.2018.03.068	Invertebrates
Hjort et al.	2022	Norway, Finland	10.1111/1365-2664.14183	Plants
Hjort et al.	2012	Finland	10.1007/s10531-012-0376-1	Plants
Hjort et al.	2012	Finland	10.1007/s10531-012-0376-1	Plants
Hjort et al.	2012	Finland	10.1007/s10531-012-0376-1	Plants
Hjort et al.	2012	Finland	10.1007/s10531-012-0376-1	Plants
Fernández et al.	2020	Spain	10.1007/s12371-020-00447-6	Other vertebrates
Fernández et al.	2020	Spain	10.1007/s12371-020-00447-6	Other vertebrates
Fernández et al.	2020	Spain	10.1007/s12371-020-00447-6	Other vertebrates
Tukianen et al.	2019	Finland	10.1111/jbi.13569	Plants
Tukianen et al.	2019	Finland	10.1111/jbi.13569	Plants
Tukianen et al.	2019	Finland	10.1111/jbi.13569	Plants
Recher	1969	USA	10.1086/282583	Birds
Recher	1969	Australia	10.1086/282583	Birds
Böhning-Gaese	1997	Germany, Austria, Switzerland	https://doi.org/10.1111/j.1365-2699.1997.tb00049.x	Birds
Firbank et al.	2008	Great Britain	10.1098/rstb.2007.2183	Plants
Firbank et al.	2008	Great Britain	10.1098/rstb.2007.2183	Birds
Shen et al.	2018	China	10.1556/168.2018.19.1.5	Plants
Shen et al.	2018	China	10.1556/168.2018.19.1.5	Plants
Lehman	2004	Guayana	10.1023/B:IJOP.0000014646.82182.51	Other vertebrates
Honnay & Coppin	1999	Belgium, France	10.1016/S0006-3207(98)00038-X	Plants
Celada & Bogliani	1993	Italy	10.1080/11250009309355794	Birds
Choi	2004	South Korea	10.1046/j.1365-2699.2003.01007.x	Invertebrates
Honnay et al.	1998	Belgium	10.2307/3546872	Plants
Lengyel et al.	2016	Hungary	10.1371/journal.pone.0149662	Invertebrates
Lengyel et al.	2016	Hungary	10.1371/journal.pone.0149662	Invertebrates
Lengyel et al.	2016	Hungary	10.1371/journal.pone.0149662	Invertebrates
Lengyel et al.	2016	Hungary	10.1371/journal.pone.0149662	Birds

Cushman & McGarigal	2003	USA	10.1890/0012-9615(2003)073[0259:LPOADI]2.0.CO;2	Birds
Rueda & Pizarro	2007	Spain	10.1016/j.actao.2007.03.006	Other vertebrates
Rueda & Pizarro	2007	Spain	10.1016/j.actao.2007.03.006	Other vertebrates
Rueda & Pizarro	2007	Spain	10.1016/j.actao.2007.03.006	Other vertebrates
Rueda & Pizarro	2007	Spain	10.1016/j.actao.2007.03.006	Birds
William & Walker	1997	Canada	10.1139/b97-889	Plants
Massada & Wood	2014	USA	10.1111/j.1600-0587.2013.00590.x	Birds
Balvanera & Aguirre	2006	Mexico	10.1111/j.1744-7429.2006.00161.x	Plants
Song & Cao	2017	China	10.3390/f8090344	Plants
Song & Cao	2017	China	10.3390/f8090344	Plants
Song & Cao	2017	China	10.3390/f8090344	Plants
Ramos et al.	2018	Argentina	10.1111/aec.12579	Invertebrates
Ribas et al.	2003	Brazil	10.1046/j.1442-9993.2003.01290.x	Invertebrates
Ribas et al.	2003	Brazil	10.1046/j.1442-9993.2003.01290.x	Invertebrates
Fraser	1998	USA	10.2307/2997377	Other vertebrates
Fraser	1998	USA	10.2307/2997377	Other vertebrates
Wang et al.	2015	China	10.1007/s10980-013-9955-0	Plants
Helbach et al.	2022	Germany	10.1002/ece3.8534	Plants
Peterson & Reich	2008	USA	10.1007/s11258-007-9270-4	Plants
López-Gonzáles et al.	2015	Mexico	10.1111/ecog.00813	Other vertebrates
Leveau	2019	Argentina	10.1016/j.ufug.2019.05.011	Birds
Lundholm & Larson	2003	Canada	10.1111/j.0906-7590.2003.03604.x	Plants
Chen & Su	2020	China	10.1016/j.pld.2020.03.003	Plants
Dupré et al.	2002	Sweden	10.1658/1100-9233(2002)013[0505:SRIDFE]2.0.CO;2	Plants
Dupré et al.	2002	Sweden	10.1658/1100-9233(2002)013[0505:SRIDFE]2.0.CO;2	Plants
Cao et al.	2021	worldwide	10.1098/rspb.2020.3045	Plants
Tukianen et al.	2016	Finland	10.1111/cobi.12799	Plants
Tukianen et al.	2016	Finland	10.1111/cobi.12799	Invertebrates
Tukianen et al.	2016	Finland	10.1111/cobi.12799	Invertebrates
Tukianen et al.	2016	Finland	10.1111/cobi.12799	Plants
Tukianen et al.	2016	Finland	10.1111/cobi.12799	Other vertebrates
Tukianen et al.	2016	Finland	10.1111/cobi.12799	Plants
Tukianen et al.	2016	Finland	10.1111/cobi.12799	Plants
Hofer et al.	2008	Switzerland	10.1111/j.2007.0906-7590.05246.x	Plants
Velázquez & Gómez-Sal	2009	Nicaragua	10.1007/s12224-009-9031-3	Plants
Vetaas et al.	2020	Nepal	10.1111/avsc.12545	Plants
Rotem et al.	2020	Israel	10.1007/s10980-020-01091-9	Other vertebrates
Jauni & Hyvönen	2012	Finland	10.1007/s10530-011-0163-z	Plants
Ewald & Freising-Weihenstephan	2002	Germany	10.1127/0340-269X/2002/0032-0085	Plants
Scott & Baer	2019	USA	10.1111/oik.05877	Plants

Scott & Baer	2019	USA	10.1111/oik.05877	Plants
Cabette et al.	2017	Brazil	10.1016/j.rbe.2016.10.004	Invertebrates
Zhang et al.	2011	China	10.1007/s11284-011-0825-4	Plants
Martins et al.	2022	Brazil	10.1016/j.baae.2022.02.008	Invertebrates
Davis et al.	2015	USA	10.1111/jvs.12302	Plants
Perelman et al.	2007	Argentina	10.1111/j.1365-2745.2007.01255.x	Plants
Bergholz et al.	2017	Israel	10.1016/j.ppees.2017.01.001	Plants
Déak et al.	2021	Hungary	10.1016/j.biocon.2021.109372	Plants
Déak et al.	2021	Hungary	10.1016/j.biocon.2021.109372	Invertebrates
Déak et al.	2021	Hungary	10.1016/j.biocon.2021.109372	Invertebrates
Seifan et al.	2010	Germany	10.1016/j.actao.2010.08.005	Plants
Gupta et al.	2018	Canada	10.1007/s10021-018-0277-6	Plants
Desalegn & Beierkuhnlein	2010	Africa	10.1111/j.1654-1103.2010.01177.x	Plants
Musila et al.	2005	Africa	10.1007/0-387-24320-8_40	Plants

Table S2.2: Number of correlations used in the analysis on geo-biodiversity links. The classification is divided into links found by each of the three different search strings (geodiversity, habitat diversity and environmental heterogeneity), different biodiversity measures (Shannon index, species richness, GI biodiversity indicator), different elements of geodiversity (climate, geodiversity, geomorphology, habitat, rock richness, soil richness, vegetation), different climate zones (Mediterranean, polar, subpolar, temperate, subtropical, cross-zonal, tropical) and different taxa (plants, birds, other vertebrates, invertebrates) analyzed in this review.

Classification	Used moderator	Amount of found studies
Search string for geodiversity	Geodiversity	22
	Habitat diversity	17
	Environmental heterogeneity	51
Biodiversity measure	Shannon index	7
	Species richness	80
	GI biodiversity indicator	3
Geodiversity element	Geodiversity	10
	Geomorphology	14
	Soil richness	14
	Rock richness	3
	Climate	7
	Vegetation	19
	Habitat	21
Climate zone	Polar	2
	Subpolar	25
	Temperate	27
	Mediterranean	8
	Subtropical	10
	Cross-zonal	10
	Tropical	7
Taxon	Plants	48
	Birds	13
	Other vertebrates	12
	Invertebrates	17

Table S2.3: Summary of the meta-regression model involving all studies and moderators.

logLik	deviance	AIC	BIC	AICc
-24.5	49.0	53.0	58.0	53.1

tau² (estimated amount of total heterogeneity):		0.0887 (**SE** = 0.0150)			
tau (square root of estimated tau^2 value):		0.298			
I² (total heterogeneity / total variability):		98.8			
H² (total variability / sampling variability):		80.4			
Q(df = 89) = 4083, p < 0.0001					

Estimate	**SE**	**z**	**ci.lb**	**ci.ub**	**p**
0.276	0.0335	8.22	0.21	0.34	< 0.001 ***

Table S2.4: Results of the meta-regression for the full model. Depicted are the moderators, the estimate, the standard error se, the z-value, the lower and upper 95% confidence interval outputs ci.lb and ci.ub and the p-value. Significant effects are labeled with asterisks: .:<0.1, *:<0.05, **:<0.01, ***:<0.001.

	Estimate	SE	z	ci.lb	ci.ub	p
Intercept	-0.443	0.953	-0.47	-2.3	1.4	0.6
Latitude	0.00520	0.0115	0.45	-0.017	0.028	0.7
Climate zone Mediterranean	0.0871	0.510	0.17	-0.91	1.1	0.9
Climate zone polar	-0.101	0.403	-0.25	-0.89	0.69	0.8
Climate zone subpolar	0.0859	0.325	0.26	-0.55	0.72	0.8
Climate zone subtropical	0.119	0.376	0.32	-0.62	0.86	0.8
Climate zone temperate	0.293	0.236	1.2	-0.17	0.76	0.2
Climate zone tropical	0.400	0.541	0.74	-0.66	1.5	0.5
Grain	-0.00190	0.0355	-0.054	-0.072	0.068	1
Extent	0.0294	0.0289	1.0	-0.027	0.086	0.3
Geodiversity	-0.0775	0.0638	-1.2	-0.20	0.048	0.2
Geomorphology	0.0296	0.0545	0.54	-0.077	0.14	0.6
Geomorphology/ soil richness	0.213	0.317	0.67	-0.41	0.84	0.5
Habitat	0.0498	0.190	0.26	-0.32	0.42	0.8
Rock richness	-0.295	0.0577	-5.1	-0.41	-0.18	<0.001 ***
Soil richness	0.152	0.0547	2.8	0.044	0.26	<0.01 **
Soil richness/ vegetation	-0.161	0.481	-0.33	-1.1	0.78	0.7
Vegetation	-0.0831	0.0278	-3.0	-0.14	-0.029	<0.01 **
Vegetation/ habitat	0.0859	0.569	0.15	-1.0	1.2	0.9
Shannon index	0.164	0.641	0.26	-1.1	1.4	0.8
Species richness	0.191	0.594	0.32	-0.97	1.4	0.7
Invertebrates	-0.0546	0.0548	-0.10	-0.16	0.053	0.4
Other vertebrates	0.194	0.0541	3.6	0.088	0.30	<0.001 ***
Plants	0.0769	0.0541	1.4	-0.029	0.18	0.2

Geodiversity element(s) — Correlation [95% CI]

Geodiversity element(s)	Correlation [95% CI]
vegetation 1	0.94 [0.87,1.01]
vegetation 2	0.9 [0.71,1.09]
geomorphology 14	0.9 [0.79,1.01]
geomorphology 17	0.89 [0.84,0.94]
geomorphology 9	0.84 [0.67,1.01]
vegetation 3	0.68 [0.49,0.86]
habitat 11	0.66 [0.49,0.83]
geomorphology & soil richness 2	0.59 [0.34,0.85]
geomorphology & soil richness 1	0.59 [0.49,0.69]
geodiversity 9	0.59 [0.57,0.61]
vegetation 5	0.58 [0.33,0.84]
geodiversity 8	0.58 [0.56,0.6]
habitat 2	0.55 [0.46,0.63]
habitat 6	0.54 [0.28,0.8]
soil richness 6	0.53 [0.37,0.7]
geomorphology 6	0.53 [0.46,0.6]
soil richness 1	0.52 [0.47,0.56]
soil richness 13	0.52 [0.16,0.89]
geomorphology 5	0.52 [0.44,0.6]
vegetation 17	0.5 [0.38,0.62]
soil richness 2	0.5 [0.46,0.55]
geomorphology 13	0.5 [0.16,0.84]
vegetation 15	0.49 [0.32,0.65]
geodiversity 1	0.49 [0.41,0.57]
geomorphology 10	0.48 [0.24,0.72]
vegetation 13	0.46 [0.18,0.74]
vegetation 10	0.46 [-0.16,1.09]
habitat 9	0.45 [0.33,0.57]
geodiversity 10	0.44 [0.42,0.46]
soil richness 7	0.43 [0.28,0.57]
geomorphology 3	0.42 [0.37,0.48]
geodiversity 2	0.42 [0.34,0.5]
habitat 10	0.39 [0.26,0.52]
geomorphology 1	0.39 [0.33,0.44]
climate 2	0.38 [-0.13,0.88]
soil richness 4	0.37 [0.26,0.47]
soil richness 3	0.37 [0.31,0.42]
soil richness 9	0.36 [-0.15,0.88]
habitat 1	0.36 [-0.04,0.76]
habitat	0.34 [-0.11,0.79]
climate 7	0.34 [0.2,0.48]
geodiversity 6	0.33 [0.31,0.35]
vegetation & habitat 1	0.32 [0.09,0.56]
geomorphology 7	0.31 [0.2,0.42]
vegetation 8	0.27 [0.14,0.4]
habitat 8	0.27 [0.12,0.42]
geomorphology 16	0.27 [0.03,0.52]
vegetation 6	0.24 [-0.15,0.62]
vegetation 4	0.24 [-0.02,0.51]
geomorphology 2	0.24 [0.18,0.3]
vegetation 19	0.23 [-0.05,0.5]
vegetation 16	0.23 [-0.12,0.58]
soil richness 12	0.23 [-0.74,0.29]
geodiversity 7	0.22 [0.2,0.24]
climate 4	0.22 [0.03,0.41]
vegetation 7	0.2 [-0.08,0.47]
geomorphology 4	0.2 [-0.02,0.42]
climate 5	0.2 [0.13,0.27]
habitat 7	0.19 [0.04,0.34]
soil richness 8	0.17 [-0.04,0.37]
soil richness 5	0.16 [0.06,0.25]
habitat 3	0.15 [0,0.3]
geodiversity 5	0.14 [-0.04,0.32]
soil richness 14	0.13 [-0.11,0.37]
climate 3	0.13 [0.09,0.16]
soil richness & vegetation 1	0.11 [-0.09,0.3]
soil richness 15	0.1 [-0.48,0.69]
soil richness 11	0.1 [-0.44,0.64]
vegetation 18	0.08 [-0.14,0.3]
geodiversity 4	0.06 [-0.08,0.2]
vegetation 9	0.04 [-0.33,0.41]
vegetation 11	0.04 [0,0.08]
rock richness 1	0.04 [-0.02,0.1]
rock richness 2	0.03 [-0.03,0.09]
geomorphology 11	0.02 [-0.18,0.23]
geodiversity 3	0.02 [-0.1,0.15]
rock richness 3	0.01 [-0.05,0.07]
climate 6	-0.02 [-0.53,0.49]
climate 1	-0.04 [-0.14,0.06]
geomorphology 12	-0.05 [-0.26,0.16]
geomorphology 8	-0.1 [-0.2,-0.01]
habitat 4	-0.19 [-0.34,-0.04]
soil richness 10	-0.23 [-0.41,-0.05]
soil richness 16	-0.33 [-0.99,0.33]
vegetation 20	-0.34 [-0.58,-0.1]
habitat 5	-0.38 [-0.52,-0.24]
vegetation 12	-0.4 [-0.72,-0.08]
vegetation 14	-0.44 [-0.67,-0.22]
soil richness 17	-0.5 [-0.94,-0.06]
geomorphology 15	-0.53 [-0.69,-0.37]

Correlation coefficient

Fig. S2.1: Forest plot on the effect size of correlation coefficients of geodiversity-biodiversity links across 90 studies after a meta-analysis. The correlation coefficients for the different studies are sorted in a decreasing order. The bars denote 95% confidence intervals. The colors represent the different taxa (blue=birds, grey=invertebrates, pink=other vertebrates, green=plants).
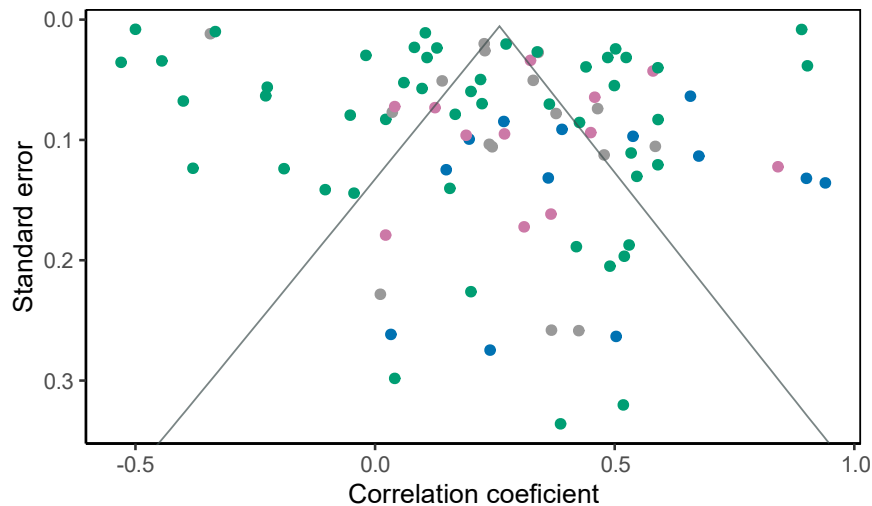
Fig. S2.2: Funnel plot for a meta-analysis on correlation coefficients of geodiversity-biodiversity links across 90 studies analyzed in the present review. The colors represent the different taxa (blue: birds, grey: invertebrates, pink: other vertebrates; green: plants).

Table S2.5: Results of the meta-regression for the interaction between geodiversity elements and taxa. Depicted are the moderators, the estimate, the standard error se, the z-value, the lower and upper 95% confidence interval outputs ci.lb and ci.ub and the p-value. Significant effects are labeled with asterisks: .:<0.1, *:<0.05, **:<0.01, ***:<0.001.

	Estimate	SE	z	ci.lb	ci.ub	p
Intercept	0.657	0.0548	12	0.55	0.76	<0.001 ***
Geodiversity	0.304	0.0264	12	0.25	0.36	<0.001 ***
Geomorphology	-0.417	0.0623	-6.7	-0.54	-0.29	<0.001 ***
Geomorphology/ soil richness	0.435	0.0550	7.9	0.33	0.54	<0.001 ***
Habitat	-0.259	0.0683	-3.8	-0.39	-0.13	<0.001 ***
Rock richness	-0.624	0.0632	-9.9	-0.75	-0.50	<0.001 ***
Soil richness	-0.154	0.0596	-2.6	-0.27	-0.037	<0.01 **
Soil richness/ vegetation	-0.0472	0.103	-0.46	-0.25	0.15	0.6
Vegetation	0.115	0.0477	2.4	0.022	0.21	<0.05 *
Vegetation/ habitat	0.199	0.122	1.6	-0.041	0.44	0.1
Invertebrates	-0.279	0.264	-1.1	-0.80	0.24	0.3
Other vertebrates	-0.532	0.0583	-9.1	-0.65	-0.42	<0.001 ***
Plants	-0.501	0.0483	-10	-0.60	-0.41	<0.001 ***
Geodiversity: invertebrates	-0.354	0.260	-1.4	-0.86	0.16	0.2
Geomorphology: invertebrates	0.467	0.267	1.7	-0.057	0.99	<0.1 .
Habitat: invertebrates	0.222	0.352	0.63	-0.47	0.91	0.5
Rock richness: invertebrates	0.257	0.268	0.96	-0.27	0.78	0.3
Soil richness: invertebrates	0.144	0.267	0.54	-0.38	0.67	0.6
Vegetation: invertebrates	-0.325	0.269	-1.2	-0.85	0.20	0.2
Geodiversity: other vertebrates	0.142	0.0341	4.2	0.075	0.21	<0.001 ***
Geomorphology: other vertebrates	0.769	0.0808	9.5	0.61	0.93	<0.001 ***
Habitat: other vertebrates	0.456	0.0821	5.5	0.30	0.62	<0.001 ***
Soil richness: other vertebrates	0.396	0.0834	4.7	0.23	0.56	<0.001 ***
Vegetation: other vertebrates	-0.191	0.0555	-3.4	-0.30	-0.082	<0.001 ***
Geomorphology: plants	0.785	0.0582	13	0.67	0.90	<0.001 ***
Habitat: plants	0.312	0.0714	4.4	0.17	0.45	<0.001 ***
Rock richness: plants	0.509	0.0657	7.8	0.38	0.64	<0.001 ***
Soil richness: plants	0.397	0.0568	7.0	0.029	0.51	<0.001

Table S2.6: Results of the meta-regression for the climate zones. Depicted are the moderators, the estimate, the standard error se, the z-value, the lower and upper 95% confidence interval outputs ci.lb and ci.ub and the p-value. Significant effects are labeled with asterisks: .:<0.1; *:<0.05, **:<0.01, ***:<0.001.

	Estimate	SE	z	ci.lb	ci.ub	p
Intercept	0.0242	0.170	0.14	-0.31	0.36	0.9
Mediterranean	0.280	0.256	1.1	-0.22	0.78	0.3
Polar	0.148	0.319	0.46	-0.48	0.77	0.6
Subpolar	0.260	0.206	1.3	-0.14	0.66	0.2
Subtropical	0.0724	0.219	0.33	-0.36	0.50	0.7
Temperate	0.360	0.185	1.9	-0.0030	0.72	<0.1 .
Tropical	0.275	0.216	1.3	-0.15	0.70	0.2

Table S2.7: Results of the meta-regression for the grain and extent. Depicted are the moderators, the estimate, the standard error se, the z-value, the lower and upper 95% confidence interval outputs ci.lb and ci.ub and the p-value. Significant effects are labeled with asterisks: .:<0.1, *:<0.05, **:<0.01, ***:<0.001.

	Estimate	se	z	ci.lb	ci.ub	p
Intercept	0.0260	0.0809	3.2	0.10	0.42	<0.01 **
Grain	-0.00150	0.0268	-0.056	-0.054	0.051	0.9
Extent	0.0203	0.0227	0.89	-0.024	0.065	0.4

Table S2.8: Results of the regression tree for geodiversity and biodiversity measures. Depicted are the subgroup (c: climate; r: rock richness; v: vegetation; h: habitat; g: geodiversity; gm: geomorphology; Shannon: Shannon index; spr: species richness; GI: GI biodiversity indicator), number of studies K, the within-subgroup Q-statistic in each subgroup Qw , the subgroup summary effect size based on Hedges'g g, the estimate, the standard error se, the z-value, the lower and upper 95% confidence interval outputs ci.lb and ci.ub and the p-value. Significant effects are labeled with asterisks: .:<0.1, *:<0.05, **:<0.01, ***:<0.001.

Subgroup	K	Qw	g	se	z	ci.lb	ci.ub	p
c; r; v; * spr	26	200.6	0.098	0.010	10.2	0.079	0.12	<0.001 ***
h; s/v; v/h * spr	13	200.9	0.30	0.021	13.9	0.25	0.34	<0.001 ***
c; h; r; s/v; v, v/h * GI; Shannon	5	109.0	0.79	0.028	28.3	0.74	0.85	<0.001 ***
g; gm; s; gm/s * GI; Shannon	46	2102	0.47	0.0040	126.4	0.46	0.47	<0.001 ***

Table S2.9: Results of the validation of the importance of the different moderators. Depicted are the moderators, the estimate, the standard error se, the z-value, the lower and upper 95% confidence interval outputs ci.lb and ci.ub and the p-value.

	Estimate	SE	z	ci.lb	ci.ub	p	importance
Intercept	0.279	0.0958	2.9	0.092	0.47	0.004	1
Grain	0.0146	0.0146	0.99	-0.014	0.043	0.3	0.9
Latitude	0.000100	0.0110	0.13	-0.0020	0.0023	0.9	0.3
Extent	0.00100	0.00870	0.12	-0.016	0.018	0.9	0.3
Shannon index	0.000500	0.0746	0.0073	-0.146	0.147	1	0.1
Species richness	0.00340	0.0571	0.060	-0.011	0.12	1	0.1
Invertebrates	-0.00970	0.0479	-0.20	-0.10	0.084	0.8	0.1
Other vertebrates	-0.00380	0.0389	-0.097	-0.080	0.073	0.9	0.1
Plants	-0.0116	0.0494	-0.24	-0.11	0.085	0.8	0.1
Geodiversity	0.000300	0.00910	0.032	-0.018	0.018	1	0.002
Geomorphology	0.000400	0.0104	0.038	-0.020	0.021	1	0.002
Geomorphology/ soil richness	0.000900	0.0221	0.041	-0.043	0.044	1	0.002
Habitat	0.000200	0.00740	0.023	-0.014	0.015	1	0.002
Rock richness	-0.000500	0.0132	-0.034	-0.026	0.025	1	0.002
Soil richness	0.000200	0.00700	0.023	-0.014	0.014	1	0.002
Soil richness/ vegetation	-0.000200	0.0660	0.017	-0.013	0.029	1	0.002
Vegetation	0.000100	0.00660	0.017	-0.013	0.013	1	0.002
Vegetation/ habitat	0.000200	0.0151	0.015	-0.029	0.030	1	0.002

Appendices chapter 3
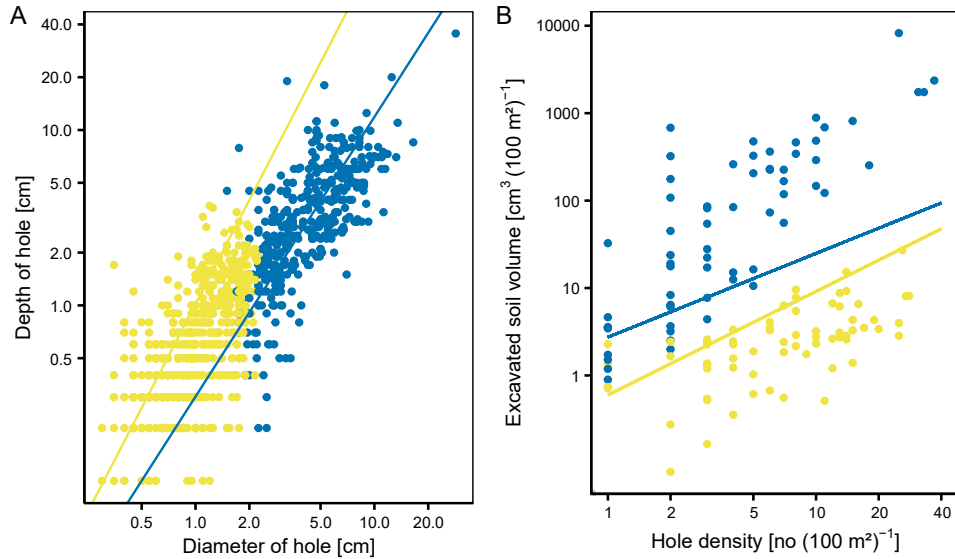
I Raw data of bioturbation parameters

For comparison with published studies, in the following we report the mean, standard deviation and range of the raw data. For the same reason, we converted our results on excavated soil volume [100 cm³ * (100 m²)$^{-1}$] to m³ ha^{-1}. We did not include the annual excavated soil volume since the observed differences in bioturbation quantity were seasonal and burrows from previous seasons were not sampled.

Table S3.1: Raw data of the bioturbation parameters hole density and excavated soil volume. Mean, SD = standard deviation and range of raw data of hole density and calculated excavated soil volume. NP = National Park. Data from the field campaign from September to November were used.

Parameter	Site	Animal group	Mean	SD	Range
Hole density [no (100 m²)$^{-1}$]	NP Pan de Azúcar	vertebrate	2.8	2.9	0 - 10
		invertebrate	14	7.8	3 - 28
	Santa Gracia	vertebrate	9.1	9.7	1 - 37
		invertebrate	7.6	6.5	0 - 26
	NP La Campana	vertebrate	5.6	8.7	0 - 33
		invertebrate	6.8	5.1	0 - 16
	NP Nahuelbuta	vertebrate	2.2	2.1	0 - 6
		invertebrate	2.8	3.1	0 - 10
Excavated soil volume [m³ ha^{-1}]	NP Pan de Azúcar	vertebrate	0.01	0.021	0 - 0.089
		invertebrate	0.000 31	0.0002	0.00005 - 0.00081
	Santa Gracia	vertebrate	0.034	0.063	0.00017 - 0.24
		invertebrate	0.00056	0.00064	0 - 0.0027
	NP La Campana	vertebrate	0.06	0.18	0 - 0.82
		invertebrate	0.00019	0.00016	0 - 0.00065
	NP Nahuelbuta	vertebrate	0.012	0.02	0 - 0.068
		invertebrate	0.00015	0.00022	0 - 0.00096

II Relationships between measured hole variables

We performed regressions between hole depth and diameter as well as between excavated soil volume and hole density for only one season (Chilean spring in September, October, November) to compare seasonal patterns and overall patterns. We chose this season because it consisted of more plots (20) than established in the preceding autumn (12).

Fig. S3.1: Relationships between burrow characteristics and bioturbation parameters created by burrowing invertebrates (yellow) and vertebrates (blue). (A) Relationship between the depth and mean diameter of the holes, (B) relationship between the excavated soil volume and hole density. The regression lines are from the reduced major axis analysis. Note that both axes in (A) and (B) were $\log_{10}$-scaled. Data from the field campaign from September to November and all sites were used.

Table S3.2: Ordinary least squares (OLS) and reduced major axis (RMA) regression analyses of the relationships between the depth and mean diameter of the holes and between the excavated soil volume and hole density for vertebrates and invertebrates (all variables log$_{10}$-transformed). A slope of one represents an isometric relationship. The same was applied in the OLS analysis with plot number as a random factor. Depicted are statistical method, correlation coefficient, slope, standard error (SE) and p-value (p) of the offset. Significant effects are labelled with asteriks: *:<0.1, **:<0.01, ***:<0.001. Data from the field campaign from September to November and from all sites were used. Further information on the statistical analysis is provided in the Methods section.

		invertebrate				vertebrate			
Relation	method	r	slope	SE	p	r	slope	SE	p
Depth and diameter	OLS (mixed model)	0.40	1.04	0.053	<0.001***	0.49	1.12	0.057	<0.001***
	OLS	0.61	1.03	0.053	0.62	0.7	1.12	0.057	0.0332*
	RMA	0.57	1.68	0.053	<0.001***	0.56	1.59	0.057	<0.001***
Excavated soil volume and hole density	OLS (mixed model)	0.35	0.712	0.12	0.017*	0.66	1.91	0.17	<0.001***
	OLS	0.59	0.712	0.12	0.017*	0.82	1.91	0.17	<0.001***
	RMA	0.22	1.2	0.12	<0.001***	0.86	2.34	0.17	<0.001***

III Results of GLMMs and the relationships between bioturbation parameters and vegetation cover

We performed GLMMs followed by Chi-squared tests to compare the different models with hole density and excavated soil volume as the predictor variables. For clarity, the relationship between hole density and excavated soil volume against vegetation cover was then plotted.

Table S3.3: Results of the GLMM for hole density at each site (Pan de Azúcar, Santa Gracia, La Campana, Nahuelbuta) for both seasons (autumn: March-April/ spring: September-November) and both animal groups (invertebrates/ vertebrates). Depicted are the fixed effects for the predictors, the estimate, the standard error SE and the z- and p-value. Data from both field campaigns were used. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

Fixed effects	Estimate	SE	z	p
(Intercept)	2.80	0.117	23.9	<0.001 ***
Site Santa Gracia	-0.454	0.194	-2.34	0.019 *
Site La Campana	-1.32	0.238	-5.53	<0.001 ***
Site Nahuelbuta	1.88	0.801	2.34	0.019 *
Hillslope	0.0245	0.00404	6.05	<0.001 ***
Animal group vertebrate	-1.56	0.0993	-15.7	<0.001 ***
Season September-November	-0.381	0.0795	-4.8	<0.001 ***
Hillside elevation	-0.00495	0.0421	-0.118	0.91
Vegetation cover	-0.0702	0.0101	-6.92	<0.001 ***
Site Santa Gracia: Taxon vertebrate	0.726	0.141	5.14	<0.001 ***
Site La Campana: Taxon vertebrate	-0.969	0.259	-3.74	<0.001 ***
Site Nahuelbuta: Taxon vertebrate	-2.81	0.393	-7.15	<0.001 ***
Site Santa Gracia: Season September-November	-0.0673	0.112	-0.602	0.55
Site La Campana: Season September-November	0.643	0.137	4.70	<0.001 ***
Site Nahuelbuta: Season September-November	-0.0911	0.175	-0.521	0.6
Site Santa Gracia: Hillslope	0.026	0.0073	3.56	<0.001 ***
Site La Campana: Hillslope	0.00371	0.0069	0.538	0.59
Site Nahuelbuta: Hillslope	0.0445	0.0151	2.94	0.0033 **
Site Santa Gracia: Hillside elevation	-0.099	0.0586	-1.69	0.09
Site La Campana: Hillside elevation	0.158	0.076	2.07	0.038 *
Site Nahuelbuta: Hillside elevation	0.719	0.138	5.21	<0.001 ***
Animal group vertebrate: Vegetation cover	0.045	0.00389	11.6	<0.001 ***
Site Santa Gracia: Vegetation cover	0.0292	0.011	2.66	0.0078 **
Site La Campana: Vegetation cover	0.0583	0.0104	5.63	<0.001 ***
Site Nahuelbuta: Vegetation cover	0.0205	0.0126	1.62	0.1

Table S3.4: Results of the GLMM for the excavated soil volume (log$_{10}$-transformed) at each site (Pan de Azúcar, Santa Gracia, La Campana, Nahuelbuta) for both seasons (autumn: March-April/ spring: September-November) and both animal groups (invertebrates/ vertebrates). Depicted are the fixed effects for the predictors, the estimate, the standard error (SE) and the t- and p-value. Data from both field campaigns were used. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

Fixed effects	Estimate	SE	t	p
(Intercept)	-0.322	0.205	-1.57	0.12
Animal group vertebrate	1.08	0.231	4.66	<0.001 ***
Season September-November	-0.233	0.0607	-3.84	<0.001 ***
Vegetation cover	0.003	0.0134	0.224	0.82
Hillside elevation	-0.107	0.0534	-1.99	0.048 *
Site Santa Gracia	0.374	0.198	1.89	0.06
Site La Campana	-0.274	0.204	-1.34	0.18
Site Nahuelbuta	-2.02	1.06	-1.9	0.059
Animal group invertebrate: Hole density	0.988	0.134	7.36	<0.001***
Animal group vertebrate: Hole density	1.82	0.107	17.0	<0.001***
Animal group vertebrate: Vegetation cover	-0.0112	0.0187	-0.602	0.55
Animal group vertebrate: Site Santa Gracia	-0.598	0.281	-2.13	0.034 *
Animal group vertebrate: Site La Campana	1.1	0.339	3.25	0.0014 **
Animal group vertebrate: Site Nahuelbuta	4.19	1.46	2.87	0.0045 **
Hillside elevation: Site Santa Gracia	0.169	0.0756	2.23	0.027 *
Hillside elevation: Site La Campana	0.198	0.0789	2.51	0.013 *
Hillside elevation: Site Nahuelbuta	0.172	0.107	1.61	0.11
Vegetation cover: Site Santa Gracia	-0.00509	0.0147	-0.347	0.73
Vegetation cover: Site La Campana	0.00121	0.0135	0.089	0.93
Vegetation cover: Site Nahuelbuta	0.0208	0.0174	1.19	0.23
Animal group vertebrate: Vegetation cover: Site Santa Gracia	0.0179	0.0208	0.862	0.39
Animal group vertebrate: Vegetation cover: Site La Campana	-0.000534	0.0193	-0.028	0.98
Animal group vertebrate: Vegetation cover: Site Nahuelbuta	-0.0327	0.024	-1.36	0.18

Table S3.5: Chi-squared tests to compare different models of fixed predictors in GLMMs for the response variable hole density. Depicted are the different combinations of the GLMM (Null: tests the null hypothesis against 1 without any fixed predictor), npar: model parameters; AIC, BIC, logLik: log-likelihood for the model; deviance, Chisq: Chi-square-statistic, Df: degrees of freedom and p: p-value. S=site, Sl=hillslope, E=hillside elevation, V=vegetation cover, Se=Season, A=animal group, Pn=plot number. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

GLMM	npar	AIC	BIC	logLik	deviance	Chisq	Df	p
Null	2	2267.1	2274.2	-1131.57	2263.1			
S:Se + S:V:A + (1|Pn)	17	2052.1	2112.4	-1009.04	2018.1	144	4	<0.001 ***
S:Se + S:E + (1|Pn)	13	2185.6	2231.7	-1079.8	2159.6	104	11	<0.001 ***
S:Se + S:Sl + (1|Pn)	13	2188.3	2234.4	-1081.16	2162.3	0	0	
S:Se + S:V:A + S:E + (1|Pn)	21	2046.4	2120.9	-1002.22	2004.4	36.9	3	<0.001 ***
S:Se + S:V:A + S:Sl + (1|Pn)	21	2050	2124.4	-1004	2008	0	0	
S:V:A + S:E + S:Sl + (1|Pn)	18	2077.3	2141.2	-1020.67	2041.3	98.09	1	<0.001 ***
S:Se + S:E + S:Sl + (1|Pn)	17	2173.4	2233.7	-1069.71	2139.4	0	0	
S:Se + S:V:A + S:E + S:Sl + (1|Pn)	25	2030.7	2119.3	-990.34	1980.7	27.3	4	<0.001 ***

Table S3.6: Chi-squared tests to compare different models of fixed predictors in GLMMs for the response variable excavated soil volume. Depicted are the different combinations of the GLMM (Null: tests the null hypothesis against 1 without any fixed predictor), npar: model parameters; AIC, BIC, logLik: log-likelihood for the model; deviance, Chisq: Chi-square-statistic, Df: degrees of freedom and p: p-value. Hd=hole density, S=site, Sl=hillslope, E=hillside elevation, V=vegetation cover, Se=Season, A=animal group. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

GLMM	npar	AIC	BIC	logLik	deviance	Chisq	Df	p
Null	3	612.19	622.23	-303.09	606.19			
Se + S:V:A	12	472.1	512.27	-224.05	448.1	0	2	1
Se + A:Hd	6	330.71	350.79	-159.35	318.71	287	3	<0.001 ***
Se + S:E	8	610.36	637.14	-297.18	594.36	0	2	1
Se + S:V:A + A:Hd	14	296.67	343.53	-134.34	268.67	179	2	<0.001 ***
S:V:A + A:Hd + S:E	17	309.87	366.77	-137.93	275.87	171	1	<0.001 ***
Se + A:Hd + S:E	10	330.55	364.02	-155.28	310.55	284	2	<0.001 ***
Se + S:V:A + S:E	16	478.63	532.19	-223.32	446.63	0	2	1
Se + S:V:A + A:Hd + S:E	18	296.67	356.92	-130.34	260.67	15.2	1	<0.001 ***
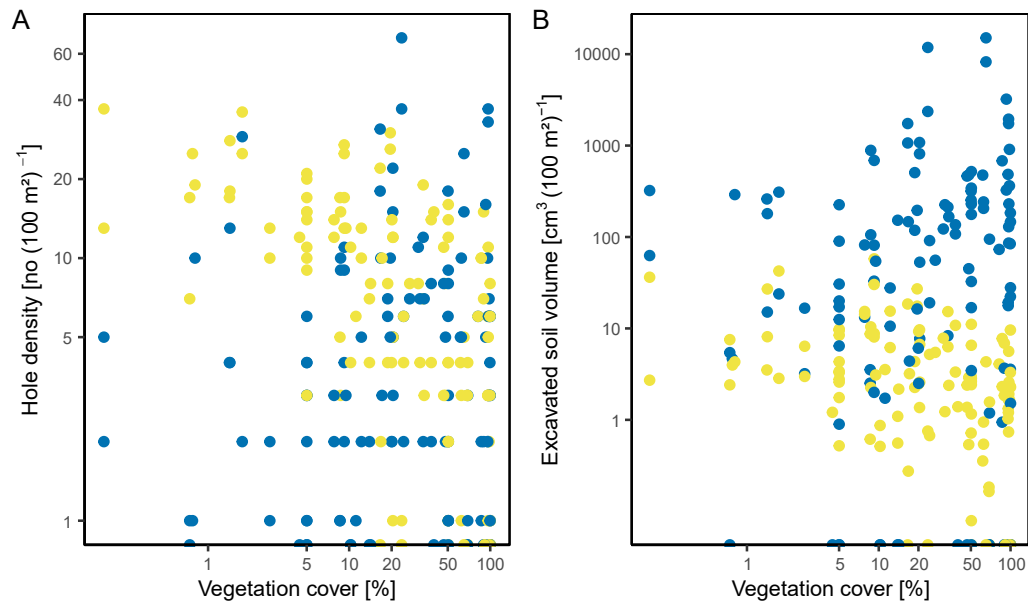
Fig. S3.2: Relationships between bioturbation parameters and vegetation cover. (A) Relationship between hole density (log$_{10}$-transformed) and vegetation cover (log$_{10}$-transformed), (B) relationship between excavated soil volume (log$_{10}$-transformed) and vegetation cover of invertebrates (yellow) and vertebrates (blue). Note that both axes in (a) and (B) were log$_{10}$-scaled. Data from both campaigns were used.

Appendices chapter 4

I Raw data of soil property variables and their correlation

Table S4.1: WGS84 coordinates of the soil sampling locations Pan de Azúcar, Santa Gracia, La Campana.

Research Site	Plot number	Latitude	Longitude
Pan de Azúcar	PdA1	-26.08611	-70.61611
Pan de Azúcar	PdA2	-25.98861	-70.81500
Pan de Azúcar	PdA3	-26.05333	-70.83416
Pan de Azúcar	PdA4	-25.97277	-70.84611
Pan de Azúcar	PdA5	-26.09555	-70.86166
Pan de Azúcar	PdA6	-26.10777	-70.86916
Pan de Azúcar	PdA7	-25.97423	-70.61663
Pan de Azúcar	PdA8	-25.98505	-70.44626
Pan de Azúcar	PdA9	-25.98366	-70.61336
Pan de Azúcar	PdA11	-25.98053	-70.61653
Pan de Azúcar	PdA12	-25.97907	-70.61585
Pan de Azúcar	PdA13	-25.97122	-70.61438
Pan de Azúcar	PdA14	-25.97183	-70.61430
Pan de Azúcar	PdA17	-25.98270	-70.61353
Pan de Azúcar	PdA18	-25.98251	-70.61229
Santa Gracia	SG1	-29.88277	-71.16500
Santa Gracia	SG2	-29.75825	-71.16712
Santa Gracia	SG3	-29.75653	-71.16605
Santa Gracia	SG4	-29.75736	-71.16531
Santa Gracia	SG5	-23.76303	-71.16536
Santa Gracia	SG6	-29.76216	-71.16406
Santa Gracia	SG8	-29.76081	-71.16535
Santa Gracia	SG9	-29.76086	-71.16605
Santa Gracia	SG10	-29.75783	-71.16521
Santa Gracia	SG11	-29.75648	-71.16661
Santa Gracia	SG12	-29.75631	-71.16545
Santa Gracia	SG13	-29.76319	-71.16510
La Campana	LC2	-32.93113	-71.09121
La Campana	LC3	-32.93068	-71.09068
La Campana	LC5	-32.93133	-71.09030
La Campana	LC7	-32.95216	-71.06231
La Campana	LC8	-32.95170	-71.06205
La Campana	LC10	-32.93924	-71.08601
La Campana	LC11	-32.93987	-71.08579
La Campana	LC14	-32.93045	-71.09193
La Campana	LC19	-32.93954	-71.08597

Table S4.2: Raw data of the physical (clay, silt, sand) and chemical (C, N, P) soil properties. The mean and standard deviation (SD) of the total amount (in both mound and control samples) of the measured soil properties clay, silt, sand, C, N, P as well as the mean and SD of the amount of soil properties of mound and unaffected control samples separately and the percentual input of all properties in all research sites are listed.

Soil properties	Site	Mean and SD of total amount (mound and control)	Mean and SD of mound samples	Mean and SD of control samples	% Input (mound - control)
Clay [%]	Pan de Azúcar	0.10 ± 0.09	0.10 ± 0.09	0.10 ± 0.09	0
	Santa Gracia	0.20 ± 0.11	0.20 ± 0.09	0.19 ± 0.13	5
	La Campana	0.21 ± 0.10	0.18 ± 0.11	0.23 ± 0.09	-28
Silt [%]	Pan de Azúcar	0.38 ± 0.13	0.38 ± 0.12	0.39 ± 0.14	-3
	Santa Gracia	0.14 ± 0.08	0.13 ± 0.08	0.15 ± 0.09	-15
	La Campana	0.25 ± 0.17	0.25 ± 0.18	0.26 ± 0.16	-4
Sand [%]	Pan de Azúcar	0.51 ± 0.12	0.52 ± 0.11	0.51 ± 0.14	2
	Santa Gracia	0.66 ± 0.11	0.67 ± 0.10	0.66 ± 0.12	1
	La Campana	0.54 ± 0.21	0.57 ± 0.23	0.52 ± 0.19	26
C [%]	Pan de Azúcar	2.98 ± 2.66	3.32 ± 2.78	2.64 ± 2.51	20
	Santa Gracia	1.49 ± 0.99	1.74 ± 1.17	1.25 ± 0.71	28
	La Campana	6.65 ± 6.70	8.95 ± 8.74	4.34 ± 2.07	52
N [%]	Pan de Azúcar	0.31 ± 0.33	0.36 ± 0.39	0.27 ± 0.24	25
	Santa Gracia	0.19 ± 0.11	0.20 ± 0.11	0.18 ± 0.11	10
	La Campana	0.57 ± 0.44	0.73 ± 0.55	0.41 ± 0.21	44
P [ppm]	Pan de Azúcar	0.73 ± 0.40	0.78 ± 0.43	0.69 ± 0.37	12
	Santa Gracia	0.74 ± 0.30	0.80 ± 0.31	0.69 ± 0.27	14
	La Campana	0.59 ± 0.26	0.67 ± 0.19	0.53 ± 0.31	21

Table S4.3: Correlation coefficients and p-values for all dependent variables. Pearson correlation test was applied. Depicted are the correlation coefficients (cor) and the belonging p-values (p) for the differences between mound and unaffected control of all possible combinations of the physical (clay, silt, sand) and chemical (C, N, P) soil properties. Significance level: $p < 0.05$ is printed in bold.

Dependent variables	P		N		C		Sand		Silt	
	cor	p	cor	p	cor	p	cor	p	cor	p
Clay	0.057	0.5	0.11	0.2	0.12	0.1	**-0.49**	**<0.05**	**-0.43**	**<0.05**
Silt	-0.0019	1	-0.13	0.1	-0.2	0.02	**-0.57**	**<0.05**		
Sand	-0.05	0.5	0.026	0.8	0.079	0.3				
C	**0.2**	**<0.05**	**0.74**	**<0.05**						
N	0.12	0.1								

II Results of GLMMs

We performed GLMMs followed by Chi-squared tests to compare the different models for physical (clay, silt, sand) and chemical (C, N, P) soil properties as the predictor variables.

Table S4.4: Results of the GLMM for clay at each site (Pan de Azúcar, Santa Gracia, La Campana). Depicted are the fixed effects for the predictors, the estimate, the standard error SE and the t- and p-value. Data from both field campaigns were used. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

Fixed effects	Estimate	SE	t	p
(Intercept)	-0.0021	0.0116	-0.18	0.857

Table S4.5: Results of the GLMM for silt at each site (Pan de Azúcar, Santa Gracia, La Campana). Depicted are the fixed effects for the predictors, the estimate, the standard error SE and the t- and p-value. Data from both field campaigns were used. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

Fixed effects	Estimate	SE	t	p
(Intercept)	-0.0407	0.0684	-0.595	0.553
Slope	0.00328	0.0015	2.19	<0.1 *
Mound density	-0.170	0.105	-1.62	0.109
Site Pan de Azúcar	-0.102	0.0732	-1.40	0.164
Site Santa Gracia	-0.000157	0.077	-0.002	0.998
Mound density: Site Pan de Azúcar	0.256	0.114	2.24	<0.1 *
Mound density: Site Santa Gracia	0.109	0.112	0.971	0.333

**Table S4.6: Results of the GLMM for sand at each site (Pan de Azúcar, Santa Gracia, La Campana).** Depicted are the fixed effects for the predictors, the estimate, the standard error SE and the t- and p-value. Data from both field campaigns were used. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

Fixed effects	Estimate	SE	t	p
(Intercept)	0.0185	0.0128	1.45	0.149

Table S4.7: Results of the GLMM for C at each site (Pan de Azúcar, Santa Gracia, La Campana).
Depicted are the fixed effects for the predictors, the estimate, the standard error SE and the t- and p-value. Data from both field campaigns were used. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

| Fixed effects	Estimate	SE	t	p
(Intercept)	-1.38	2.39	-0.576	0.566
Site Pan de Azúcar	1.97	2.57	0.767	0.444
Site Santa Gracia	2.08	2.61	0.767	0.427
Mound density	-12.7	2.7	-4.72	<0.001 ***
Vegetation cover	-0.0571	0.0327	-1.75	<0.1 *
Hillslope	0.459	0.0982	4.68	<0.001 ***
Site Pan de Azúcar: Mound density	11.8	2.80	4.21	<0.001 ***
Site Santa Gracia: Mound density	13.2	2.87	4.59	<0.001 ***
Site Pan de Azúcar: Vegetation cover	0.145	0.0580	2.50	<0.1 *
Site Santa Gracia: Vegetation cover	0.0468	0.0457	1.02	0.308
Site Pan de Azúcar: Hillslope	-0.445	0.103	-4.32	<0.001 ***
Site Santa Gracia: Hillslope	-0.477	0.108	-4.39	<0.001 ***

Table S4.8: Results of the GLMM for N at each site (Pan de Azúcar, Santa Gracia, La Campana).
Depicted are the fixed effects for the predictors, the estimate, the standard error SE and the t- and p-value. Data from both field campaigns were used. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

Fixed effects	Estimate	SE	t	p
(Intercept)	0.908	0.231	3.93	<0.001 ***
Site Pan de Azúcar	-0.862	0.237	-3.64	<0.001 ***
Site Santa Gracia	-0.862	0.254	-3.40	<0.001 ***
Vegetation cover	-0.00933	0.00315	-2.97	<0.01 **
Hillside elevation	-0.203	0.0741	-2.74	<0.01 **
Site Pan de Azúcar: Vegetation cover	0.0178	0.00691	2.58	<0.1 *
Site Santa Gracia: Vegetation cover	0.00839	0.00524	1.60	0.112
Site Pan de Azúcar: Hillside elevation	0.225	0.0836	2.69	<0.01 **
Site Santa Gracia: Hillside elevation	0.218	0.0854	2.55	<0.1 *

Table S4.9: Results of the GLMM for P at each site (Pan de Azúcar, Santa Gracia, La Campana).
Depicted are the fixed effects for the predictors, the estimate, the standard error SE and the t- and p-value. Data from both field campaigns were used. Significant effects are labelled with asterisks: *:<0.1, **:<0.01, ***:<0.001.

Fixed effects	Estimate	SE	t	p
(Intercept)	0.104	0.0331	3.13	<0.01 **
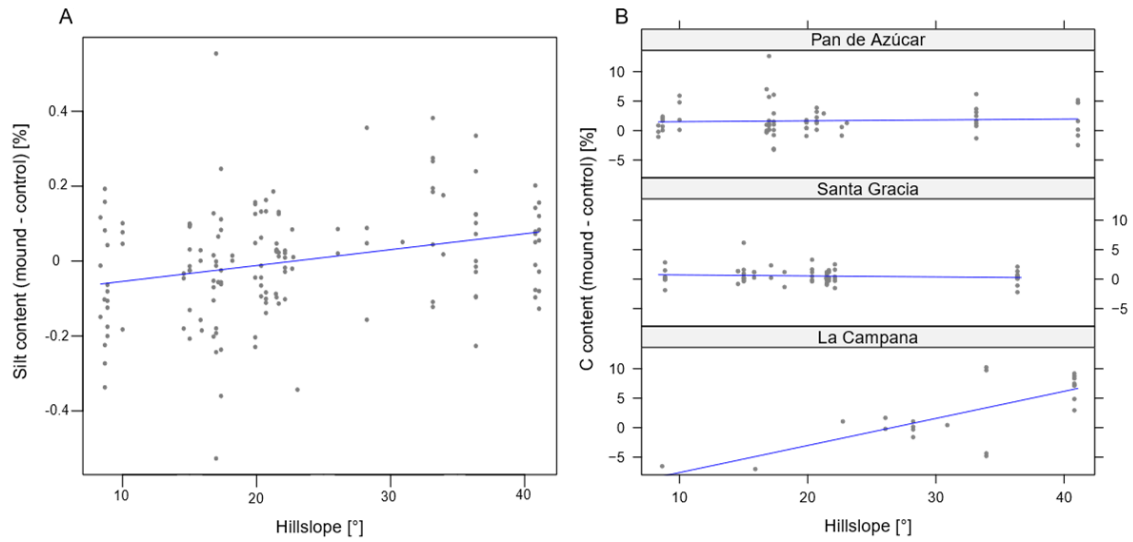
Figure S4.1: Effect plots for the fixed effect hillslope. (A) Fitted relationships between hillslope [°] and silt content [%], (B) fitted relationship between hillslope [°] and C content [%] at each research site (Pan de Azúcar, Santa Gracia, La Campana).
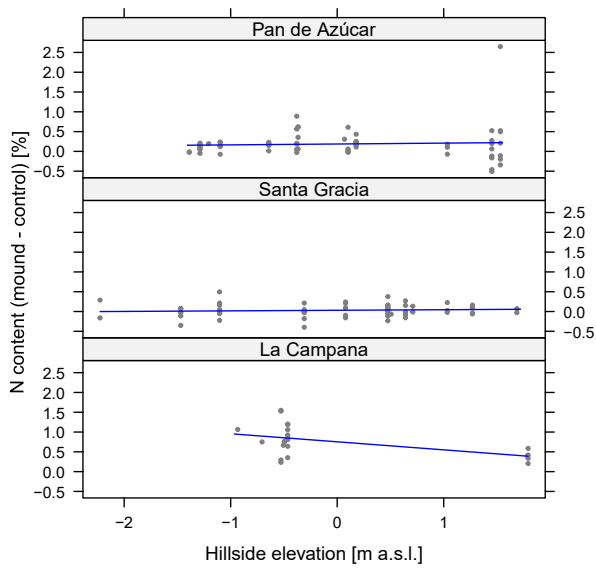
Figure S4.2: Fitted relationship between N content and the fixed effect hillside elevation [m a.s.l.] at each research site (arid Pan de Azúcar, semi-arid Santa Gracia, Mediterranean La Campana). Note that the x-axis was standardized.

III Literature survey

We compiled a survey of literature on the effects of bioturbation on physical (clay, silt, sand) and chemical (C, N, P) soil properties analyzed in our study.

Table S4.10: Literature survey of clay, silt, sand, C, N and P contents of mound and undisturbed soils as well as the impact of bioturbation on ecological processes. We give the mean of the different soil properties (clay, silt, sand, C, N, P), the reference, the contents of the soil properties for mound and undisturbed soil samples and the impacts of bioturbation. If necessary, the units were converted to ppm for P and % for all other soil properties. Significantly different values between mound and undisturbed soil are printed bold.

Soil property	Reference	(Zono-) Biome	Mean of mound samples	Mean of control samples	% Input (mound - control)	Impact
Clay [%]	Nkem et al., 2000	III	**29**	**52**	**-79**	Increase of soil porosity
	Eldridge & Koen, 2008	III	23	22	4	Structuring desert landscapes; providing sediment for mobilization
	Mujinya et al., 2010	II	46	39	15	Mixed charge system with higher permanent and variable charges
	Clark et al., 2016	II	7.5	5.4	28	Altering spatial patterning of competitive interactions, plant diversity and productivity; producing ecological ecosystem functioning
	Jouquet et al., 2017	II	**36**	**32**	**11**	Concentration of clay particles below-ground into nests
	Carlson & Whitford, 1991	VII	**1.2**	**2.7**	**-25**	Large gravel mounds heat up quickly due to the lower thermal capacity of coarse fragments and provide insulation

Silt [%]	Nkem et al., 2000	III	**21**	**16**	**24**	Increase of soil porosity; Differential transport of sand-sized particles for the protection of nest entrances
	Eldridge & Koen, 2008	III	65	68	-5	Structuring desert landscapes; providing sediment for mobilization
	Mujinya et al., 2010	II	27	28	-4	Mixed charge system with higher permanent and variable charges
	Clark et al., 2016	II	17	18	-6	Altering spatial patterning of competitive interactions, plant diversity and productivity; producing ecological legacies that affect ecosystem functioning
	Carlson & Whitford, 1991	VII	**16**	**23**	**-44**	large gravel mounds heat up quickly due to the lower thermal capacity of coarse fragments and provide insulation
Sand [%]	Nkem et al., 2000	III	**50**	**32**	**36**	Increase of soil porosity
	Eldridge & Koen, 2008	III	12	11	8	Structuring desert landscapes; providing sediment for mobilization
	Mujinya et al., 2010	II	27	33	-22	Mixed charge system with higher permanent and variable charges
	Clark et al., 2016	II	76	77	-1	Altering spatial patterning of competitive interactions, plant diversity and productivity; producing ecological legacies that affect ecosystem functioning; C and N dynamics function much like surface soil when soil moisture is not limiting
	Jouquet et al., 2017	II	58	56	3	Selection and concentration of clay particles below-ground into nests

	Carlson & Whitford, 1991	VII	**82**	**74**	**10**	large gravel mounds heat up quickly due to the lower thermal capacity of coarse fragments and provide insulation
C [%]	Nkem et al., 2000	III	**0.00039**	**0.00032**	**18**	Increase of plant diversity and abundance
	Dostál et al., 2004	VI	**4.2**	**6.4**	**-39**	Support of plant growth and below-ground plant parameters; removal of organic matter from the nests
	Eldridge & Koen, 2008	III	1.5	1.9	-27	Structuring desert landscapes; providing sediment for mobilization; establishment of indigenous plant species
	Clark et al., 2016	II	**0.66**	**1**	**-52**	Altering spatial patterning of competitive interactions, plant diversity and productivity; producing ecological legacies that affect ecosystem functioning; C and N dynamics function much like surface soil when soil moisture is not limiting
	Jouquet et al., 2017	II	**2.7**	**0.79**	**71**	C and N are incorporated into termite construction
	Yurkewycz et al., 2014	IV	0.00064	0.00058	9	Soil development is enhanced due to increased C and N, progressing soil and vegetation heterogeneity at small scales
N [%]	Dostál et al., 2004	VI	**0.30**	**0.58**	**-93**	Support of plant growth and below-ground plant parameters; removal of organic matter from the nests
	Eldridge & Koen, 2008	III	0.11	0.16	-45	Structuring desert landscapes; providing sediment for mobilization; establishment of indigenous plant species
	Clark et al., 2016	II	0.07	0.11	-57	Altering spatial patterning of competitive interactions, plant diversity and productivity; producing ecological legacies that affect ecosystem functioning; C and N dynamics function much like surface soil when soil moisture is not limiting

	Jouquet et al., 2017	II	**0.21**	**0.09**	**57**	C and N are incorporated into termite construction	
	Yurkewycz et al., 2014	IV	0.051	0.047	8	Soil development is enhanced due to increased C and N, progressing soil and vegetation heterogeneity at small scales	
P [ppm]	Nkem et al., 2000	III	**100.2**	**27.9**	**72**	Increase of plant diversity and abundance	
	Dostál et al., 2004	VI	23.37	15.46	34	Support plant growth and below-ground plant parameters; increased decomposition rate	Support plant growth and below-ground plant parameters; increased decomposition rate
	Eldridge & Koen, 2008	III	**137.5**	**171.5**	**25**	Structuring desert landscapes; providing sediment for mobilization	Structuring desert landscapes; providing sediment for mobilization
	Carlson & Whitford, 1991	VII	**19.3**	**1.5**	**92**	relative nutrient enrichment	relative nutrient enrichment

Deutsche Zusammenfassung

Heutzutage führen Klimawandel, Umweltverschmutzung oder die übermäßige Ausbeutung natürlicher Ressourcen zu einem weltweiten Rückgang der Biodiversität. Um diese zu erhalten, ist das Management von Ökosystemen von entscheidend. Dafür ist zunächst ein allgemeines Verständnis der vorherrschenden Biodiversität erforderlich, um geeignete Naturschutzmaßnahmen zu entwickeln, die den Biodiversitätsverlust verhindern. Neueste Forschungsarbeiten haben gezeigt, dass leicht verfügbare Geodiversitätsdaten als Ersatz für Biodiversitätsdaten verwendet werden können. Dabei kann Geodiversität die Verfügbarkeit und Vielfalt ökologischer Bedingungen und Ressourcen bestimmen, welche die Koexistenz von Arten erleichtern. Ein Beispiel für eine solche positive Verbindung zwischen Geo- und Biodiversität sind Bioturbationsmuster entlang eines Klimagradienten.

Bioturbation stellt dabei einen wichtigen Mechanismus für das Ökosystem-Engineering dar, da wühlende Tiere Böden und Sedimente biologisch verändern und so die Umwelt für sich selbst und für andere Arten umgestalten. Auf diese Weise beeinflussen Bioturbatoren wichtige Ökosystemprozesse wie Sedimenttransport, Bodenbildung, Nährstoffverfügbarkeit und Bodenwasserkreislauf. Infolgedessen fördert die Bioturbation die Geodiversität durch Verbesserung der Lebensraum- und Bodenbedingungen für die Bioturbatoren sowie für andere Arten.

In dieser Arbeit habe ich eine Meta-Analyse mit 90 Studien aus 51 Veröffentlichungen durchgeführt, in der ich die Beziehung und die Einflussfaktoren der Verbindung zwischen Geo- und Biodiversität untersucht habe. Zur Ergänzung meiner Forschung über den positiven Zusammenhang zwischen Geo- und Biodiversität habe ich zusätzlich die bestimmenden Faktoren der Bioturbationsmuster entlang eines Klimagradienten in Chile untersucht. Dafür legte ich 80 Plots an vier Forschungsstandorten an (in ariden, semiariden, mediterranen und feuchten Klimazonen). Darüber hinaus analysierte ich die Auswirkungen von Bioturbatoren auf die Ökosystemprozesse Bodenbildung und Nährstoffverfügbarkeit unter Einbeziehung von Daten aus den ariden, semi-ariden und mediterranen Untersuchungsgebieten.

Meine Arbeit zeigt, dass (i) die Geodiversität positiv mit der Biodiversität verbunden ist. Diese Beziehung wird jedoch von vielen komplexen Merkmalen beeinflusst, wie z. B. der räumlichen Ausdehnung, der Klimazone oder den Taxa, die berücksichtigt werden sollten, um Biodiversität anhand Geodiversität angemessen vorhersagen zu können. Bei den Bioturbationsmustern sind (ii) das Klima, die Vegetation und die Abundanz von Wirbeltieren die wichtigsten Einflussfaktoren. Hier variiert (iii) das Ausmaß der Bioturbation entlang des Klimagradienten

mit dem stärksten Effekt in ariden Regionen, wo sie eine Makronährstoffanreicherung bewirkt und die Bodenfruchtbarkeit verbessert.

Diese Arbeit erweitert unser Verständnis der positiven Zusammenhänge zwischen Geodiversität und Biodiversität und schärft gleichzeitig das Bewusstsein für die komplexen Beziehungen zwischen den beiden Konzepten. Darüber hinaus stelle ich Bioturbationsmuster und -effekte in verschiedenen Umgebungen dar, indem ich einen breiten klimatischen Gradienten abdecke. Dabei wird insbesondere die Rolle der Bioturbation als wichtiger Mechanismus zur Verbesserung der chemischen Bodeneigenschaften durch den Eintrag von Makronährstoffen hervorgehoben. Somit unterstützt diese Arbeit die Rolle der Bioturbation als potenziellen Treiber der lokalen Geodiversität.

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Kraus D, Chi J, Boenigk J, Beisser D, Graupner N, Dunthorn M. Putatively asexual chrysophytes have meiotic genes: Evidence from transcriptomic data. PeerJ. 2019;2019: e5894. doi:10.7717/PEERJ.5894/SUPP-1

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Kraus D, 2021; Bioturbation along a climate gradient in Chile: Relationships between abiotic and biotic conditions and burrowing animals; poster, 50th annual meeting of Ecological Society/ online/ 30. August -1. September.

Kraus D, 2021; The interplay of climate and vegetation and the abundance of vertebrates or invertebrates determine bioturbation patterns across Chile; poster, Ecology across borders conference, British Ecological Society/ online/ 12. -15. Dezember.

Kraus D, 2022: The potential of in-situ and remote sensing datasets on the analysis of impacts of bioturbation on vegetation in Chile; talk, European Conference of Tropical Ecology/ in Person/ 7 - 9 Juni.

Kraus, D, 2022: Effect of animal bioturbation on chemical and physical soil properties and sediment redistribution across climate gradients; talk, The World Congress of Soil Science/ in Person/ 31. Juli – 5. August.

Declaration/ Erklärung

Ich versichere, dass ich meine Dissertation mit dem Titel „The positive link between geo- and biodiversity reflected in bioturbation patterns along a climate gradient" selbstständig ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfsmittel bedient habe. Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg, den 14.02.2023

Diana Kraus