

Anthropogenic actions shape biodiversity change and ecosystem functioning

Dissertation to fulfil the Requirements for the Degree of

„doctor rerum naturalium“ (Dr. rer. nat.)

Submitted to the Council of the Faculty of Biological
Sciences of the Friedrich Schiller University Jena

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Jena, 2023

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Date of defense: 2.10.2023

— *Estive lendo um dia um filósofo, sabe. Uma vez segui um conselho dele e deu certo. Era mais ou menos isso: é só quando esquecemos de todos os nossos conhecimentos é que começamos a saber.*

Clarice Lispector – 1969: Uma Aprendizagem ou O Livro dos Prazeres

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Summary

Humans do not only depend on living nature, we are part of it. Still, human actions are causing the sixth mass extinction of species, with irreversible changes to the ecosystem and all the essential contributions biodiversity provides us. While much of the lost biodiversity has not been described by scientists yet, we continue to lose new species at impressive rates. To sustain the dominant social-economic system existing today, direct and indirect actions were taken, including unsustainable development, intense landcover change and increasing rates of carbon emission, with inevitable environmental degradation. Still, a joint effort of governments, academia, and civil society warns about the risks and threats to biodiversity and other human societies, in case the scenario does not change. While projections for future climate indicate an increase in temperature and a decrease in precipitation rates for most areas in the world, regionally and locally this scenario might differ, as well as the impacts on the associated biodiversity. Moreover, extreme climatic events such as floods, hurricanes, droughts and temperature extremes will become more often and intense. Simultaneously, humans also altered about three-quarters of the globe's land surface, mainly through agricultural land use changes, such as transitions to cropland or pasture/ rangeland. Climate and land use alterations disrupt ecosystems, but the expected effects on biodiversity are not completely understood. Expected effects may vary from species extinctions, the spread of diseases, changes in species physiology, abundance and growth, shifts in species interactions, and space use by the species, among others. However, the effects will vary according to the ecosystem type, the species involved, and the resilience of both to changes.

In my first chapter, I compile a large dataset for vertebrate assemblages in the Amazon forest. Known for its extensive biodiversity, the Amazon forest, as well as tropical forests in general, remains relatively understudied when compared to ecosystems in higher latitudes in the world. For this reason, a collaborative effort between researchers was fundamental to make this database available. The database englobes camera trap data from mammals, birds and reptile species. In that way, I believe I took a small but important step further in the direction of filling the gap in biodiversity information for the Amazon forest and creating new opportunities to study

biodiversity changes in this biome. And that was my aim with my second chapter. Using the dataset compiled in chapter one, in chapter two I investigated the effects of human modifications on vertebrate communities in the Amazon, and the results were impressive: even within the gradient of low to moderate human modification, we detected a decrease in the richness of vertebrate species. This raises a red flag for the vulnerability of species under our current scenario of changes in climate and land use. Moreover, it opens new doors to investigate the mechanisms underlying the change in species richness.

Understanding the human-nature relationship is a critical step to informing decision-making and support the development of environmental and conservation policies. Living nature provides humans with both positive and negative contributions that are critical for our existence, including food provision, water purification, disease transmission, control of pests, among others. Because the functioning of the ecosystems involves complex processes and interactions of different species, understanding the relationship between biodiversity change and the contribution of biodiversity to the provision of nature's contribution to people (NCP) is a challenge. In my third chapter, I propose a macroecological framework that integrates biodiversity models and energy flux theory to link biodiversity, ecosystem function and NCP. This novel approach allows the incorporation of different aspects (such as species interactions and environmental data) to evaluate biodiversity-based NCP. Moreover, despite the flexibility of this framework, when trying to apply it to belowground ecosystems, I identified the gap for my last and fourth chapter: the need for abundance data or models to predict abundance data for belowground invertebrates. In that way, I worked to aggregate data from different parts of the world that were sampled using similar methods, so I could develop a biodiversity model to predict species abundance based on their body mass. Additionally, I also used the compiled database to explore the effects of environmental conditions on the community-abundance distribution of the communities.

Zusammenfassung

Wir Menschen sind nicht nur von der Natur abhängig, wir sind auch ein Teil von ihr. Dennoch verursachen wir durch unser Handeln das sechste Massensterben von Arten mit damit einhergehenden irreversiblen Veränderungen des Ökosystems und all der wichtigen Dienstleistungen, die die biologische Vielfalt für uns zur Verfügung stellt. Obwohl ein Großteil der Artenvielfalt von den Wissenschaftlern noch nicht einmal beschrieben wurde, verlieren wir weiterhin in beeindruckendem Tempo neue Arten. Um unser heute vorherrschendes sozioökonomisches System aufrechtzuerhalten, wurden direkte und indirekte Maßnahmen ergriffen, die unweigerlich zu einer Verschlechterung der Umwelt führen, darunter eine nicht nachhaltige Entwicklung, intensive Landnutzungsveränderung und zunehmende Kohlenstoffemissionen. Allerdings warnt eine gemeinsame Initiative von Regierungen, Wissenschaft und Zivilgesellschaft vor den Risiken und Bedrohungen für die biologische Vielfalt und der Gesellschaft für den Fall, dass sich die aktuelle Situation nicht ändert. Die Prognosen für das künftige Klima deuten auf einen Temperaturanstieg und einen Rückgang der Niederschlagsmengen in den meisten Gebieten der Welt hin, doch könnte dieses Szenario regional und lokal unterschiedlich ausfallen, ebenso wie die Auswirkungen auf die damit verbundene Artenvielfalt. Außerdem werden extreme klimatische Ereignisse wie Überschwemmungen, Wirbelstürme, Dürren und Temperaturextreme häufiger und intensiver auftreten. Gleichzeitig hat der Mensch etwa drei Viertel der Landoberfläche der Erde verändert, vor allem durch die veränderte landwirtschaftliche Nutzung, z. B. durch die Umwandlung in Ackerland oder Weideland. Klima- und Landnutzungsänderungen stören die Ökosysteme, aber die zu erwartenden Auswirkungen auf die biologische Vielfalt sind nicht vollständig bekannt. Zu den erwarteten Auswirkungen gehören u. a. das Aussterben von Arten, die Ausbreitung von Krankheiten, Veränderungen in der Physiologie, der Anzahl und den Wachstumsraten von Arten, Verschiebungen bei den Interaktionen zwischen den Arten und der Raumnutzung durch die Arten. Die Auswirkungen werden jedoch je nach Art des Ökosystems, der beteiligten Arten und der Widerstandsfähigkeit beider gegenüber Veränderungen variieren.

Im ersten Kapitel meiner Doktorarbeit trage ich einen großen Datensatz für Wirbeltiergruppen im Amazonaswald zusammen. Der Amazonaswald, der für seine große Artenvielfalt bekannt ist, sowie tropische Wälder im Allgemeinen sind im Vergleich zu Ökosystemen in höheren Breitengraden der Welt noch relativ wenig erforscht. Aus diesem Grund war eine enge Zusammenarbeit zwischen Forschern auf diesem Gebiet von grundlegender Bedeutung, um diese Datenbank verfügbar zu machen. Die Datenbank beruht auf den Daten von Kamerafallen, mit Hilfe derer Säugetiere, Vögel und Reptilienarten beobachtet werden können. Ich glaube, dass ich auf diese Weise einen kleinen, aber wichtigen Schritt in Richtung Schließung der Lücke bei den Informationen über die biologische Vielfalt des Amazonaswaldes gemacht habe. Dies schafft auch neue Möglichkeiten zur Untersuchung der Veränderungen der biologischen Vielfalt in diesem Biotop, was das Ziel des zweiten Kapitels meiner Doktorarbeit war. Auf der Grundlage des in Kapitel eins zusammengestellten Datensatzes untersuchte ich dort die Auswirkungen menschlicher Eingriffe auf Wirbeltiergemeinschaften im Amazonasgebiet, und die Ergebnisse waren beeindruckend: Selbst innerhalb des Gradienten von geringer bis mäßiger menschlicher Beeinflussung stellten wir einen Rückgang der Vielfalt an Wirbeltierarten fest. Dies ist ein Warnsignal für die Verwundbarkeit von Arten gegenüber dem derzeitigen Szenario von Klima- und Landnutzungsänderungen. Außerdem eröffnet es neue Möglichkeiten, die Mechanismen zu untersuchen, die der Veränderung des Artenreichtums zugrunde liegen.

Das Verständnis der Beziehung zwischen Mensch und Natur ist ein wichtiger Schritt zur Entscheidungsfindung und zur Unterstützung der Entwicklung von Umwelt- und Naturschutzmaßnahmen. Die Natur liefert dem Menschen sowohl positive als auch negative Beiträge, die für unsere Existenz von entscheidender Bedeutung sind, wie z. B. die Bereitstellung von Nahrungsmitteln, die Reinigung von Wasser, die Übertragung von Krankheiten, die Bekämpfung von Schädlingen usw. Da das Funktionieren der Ökosysteme auf komplexen Prozessen und Interaktionen verschiedener Arten beruht, ist es eine große Herausforderung, die Beziehung zwischen der Veränderung der biologischen Vielfalt und diesen Ökosystemleistungen zu verstehen. Im dritten Kapitel meiner Doktorarbeit stelle ich einen makroökologischen Ansatz vor, der Biodiversitätsmodelle und Energieflusstheorie integriert,

um Biodiversität, Ökosystemfunktion und Ökosystemleistungen miteinander zu verbinden. Dieser neuartige Ansatz ermöglicht die Einbeziehung verschiedener Aspekte (z. B. Interaktionen zwischen Arten oder Umweltdaten) in die Evaluierung biodiversitätsbasierter Ökosystemleistungen. Trotz der Flexibilität dieses Ansatzes habe ich bei dem Versuch, ihn auf unterirdische Ökosysteme anzuwenden, eine Lücke identifiziert, die ich im vierten Kapitel meiner Doktorarbeit versuche zu schließen: Das Fehlen von Abundanz-Daten oder Modellen zur Vorhersage von Abundanzen im Boden lebender Wirbelloser. So habe ich Daten aus verschiedenen Teilen der Welt zusammengetragen, die mit ähnlichen Methoden erhoben wurden, um ein Biodiversitätsmodell zu entwickeln, mit dem sich die Abundanz von Arten auf der Grundlage ihrer Körpermasse vorhersagen lässt. Außerdem nutzte ich die zusammengestellte Datenbank, um die Auswirkungen von Umweltbedingungen auf die Abundanz-Verteilung innerhalb von Lebensgemeinschaften zu untersuchen.

General Introduction

1. How the Anthropocene shaped the Earth-System

All organisms can change (intentionally or not) the environmental conditions in their surroundings. However, humans have been changing Earth so intensely and permanently, that this new epoch, which began at some point in the mid-20th century, is identified as the “Anthropocene” (Waters et al. 2016). Even a new sphere of Earth has been formed — the “Technosphere” — encompassing all technical systems and infrastructures created by humans, from automated agriculture and transportation systems (e.g. roads and highways) to atmospheric pollution and deforestation (Renn 2020). Although we clearly see these human-Earth-system interactions nowadays, a much earlier human activity with a significant impact on nature might probably be associated with megafaunal extinctions during the Pleistocene so that the low diversity of large mammals we observe today in some areas of the globe might be a consequence of past human action (Sandom et al. 2014). Moreover, food production associated with agriculture led to a dramatic landcover change about 6,000 years ago. Since then, changes started to reach higher proportions and cover larger spatial scales. Increasing urbanism, followed by European colonialism were also important drivers of the global extent of human effects that we see today (Roberts et al. 2023). Furthermore, the changes in climate and land use we observe are shaping biodiversity and impacting the functioning of ecosystems, with severe consequences for the delivery of nature’s contributions to people (NCP). Within the next pages, we will understand how those changings are taking place.

To start this journey, I believe it is important to first clarify how and why human society changed and continues changing the environment. Lands are vital for the provision of resources (food, energy, shelter, fibers) and other contributions from nature to human societies. During the Anthropocene, more than 50% of Earth’s land had been modified for human use, with consequent impacts also for areas distant from the ones directly affected (Hooke et al. 2012). It is estimated that, by the year 2000, 12 and 22% of the Earth's ice-free land surface were covered by cropland and pasture, respectively (Ramankutty et al. 2008). Most reliable data quantifying past land use are from 1950-on and show that the main drivers of land use change include

tropical deforestation, reforestation, dryland degradation, agricultural intensification, and urbanization, among others (Ruddiman 2013, van Vliet et al. 2016). Although land use is essential for meeting human needs, we have to discuss the negative consequences associated with the extreme changes in land cover. We are witnessing a substantial decrease in global air quality, with significant impacts on the local and global climate (Heald and Spracklen 2015). Food security and land productivity might be affected by accelerated soil erosion caused by land modifications such as deforestation, overgrazing, tillage and unsuitable agricultural practices (Borrelli et al. 2013). Moreover, biogeochemistry (natural cycles, e.g. carbon cycle), biogeophysics, biodiversity and the climate of our planet are affected (Hurt et al. 2020).

Simultaneously with land cover, the climate is also being impacted by human actions. Changes in the climate naturally occur over geological eras, but especially over the last 50 years, humans are the dominant influence on climate change (Benner et al. 2021). This fast change is mainly related to the burning of fossil fuels and deforestation, which have released an enormous amount of greenhouse gases (such as carbon dioxide) into the atmosphere, increasing the global average temperature (Houghton et al. 2001). Although this process became popularly known as “global warming”, the climatic changes involved are much more complex and the increasing temperature is only one of the consequences. Natural climatic events such as the El Niño and the North Atlantic Oscillation, which affect precipitation and temperature rates globally, are presenting unusual behaviors, apparently linked to global warming (Trenberth and Hoar 1997, Hoerling et al. 2001). With increased temperatures, loss of snow and ice volume cause ice-albedo feedback, which makes the planet darker and causes changes in ocean circulation (Karl & Trenberth, 2003). In general, depending on the region, increased intensity of droughts, wildfires, or heavy precipitation events might occur (Begum et al. 2022). Moreover, scientists are worried that we might be close to achieving a climatic tipping point: when a critical threshold is achieved and self-perpetuate without a turnback, causing substantial Earth system impacts. A joint international effort aims to keep the global mean surface temperature increase between 1.5-2.0°C within the next decades, but this might be enough to put us at risk of triggering some climate tipping points around the globe (McKay et al. 2022). Together, human-induced changes

in climate and land cover are shaping Earth-System drastically (Figure 1), but what are the consequences of these changes for biodiversity?

Human changes on Earth System

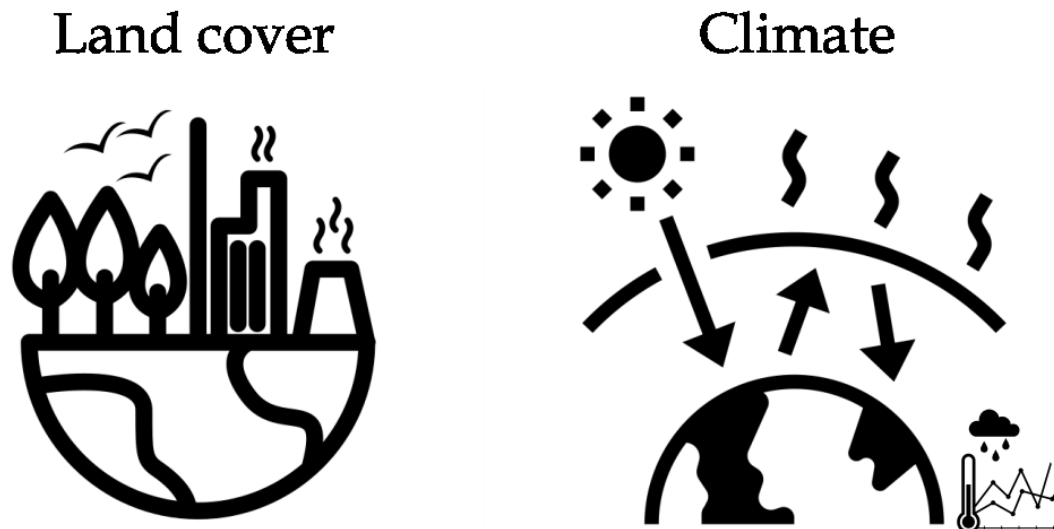


Figure 1: Land cover and climate changes are two important drivers of alterations to the Earth System during the Anthropocene, and will be further investigated in this thesis. Source: Nesialoo Creator and Kamin Ginkae from Noum Project.

2. What are the impacts on biodiversity

Earth biodiversity encompasses all living organisms, at all levels of organizations, humans included. Although for me as an ecologist it seems clear that biodiversity matters, it is possible to look at its importance through multiple lenses. From economic (e.g. harvesting of fish and timber) to recreational (e.g. hiking or bird watching) and cultural values (expression of identity and spirituality), biodiversity provides us with multiple contributions. Moreover, biodiversity is essential for the healthy functioning of the ecosystem, which provides us oxygen, clean water,

pollination of plants, and control of pests, among other contributions which humans deeply depend on. As we maintain our biodiversity, we support our ecosystems to keep working, especially under the context of environmental changes we are observing today. For those reasons, scientists are working on increasing the monitoring of biodiversity, as well as investigating species' responses to ongoing changes. Change in biodiversity is a topic of great debate among specialists, with most studies showing a global trend of decline of species populations, while some researchers believe there is no mean global change, or even a positive one (Leung et al. 2020, van Klink et al. 2020, Murali et al. 2022). Furthermore, it seems that global patterns in biodiversity change are highly dependent on regional and local environmental conditions, and detecting these trends on global scale is a complicated challenge (Valdez et al. 2023). Still, any conclusions in this respect should be taken carefully, especially due to the various bias existing in the available datasets used for the analysis. As an important example, the scarcity of biodiversity data for tropical regions in comparison to higher latitude ones (e.g. Figure 2) undermines most predictions for global biodiversity trends (Collen et al. 2008).

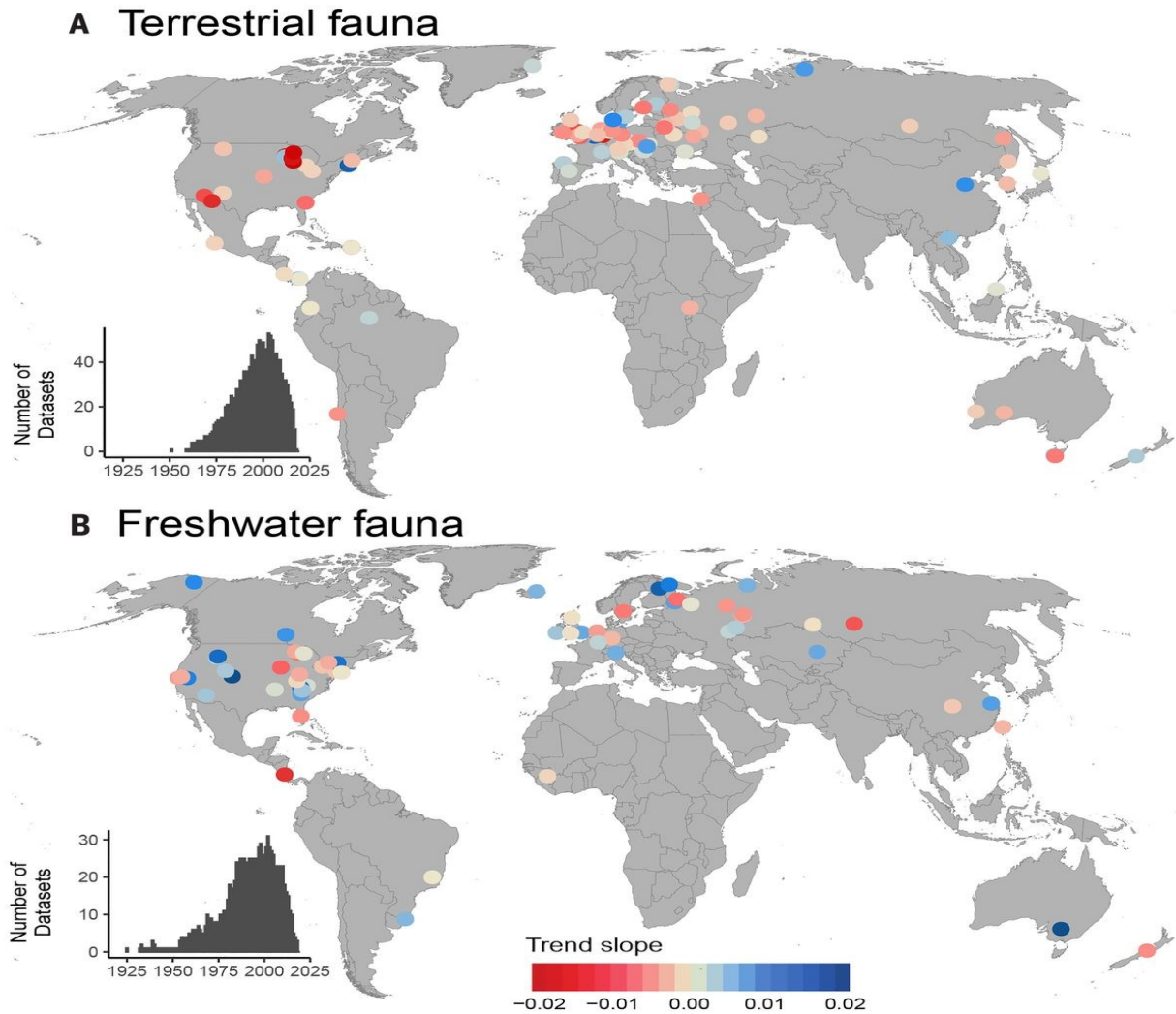


Figure 2: Example extracted from van Klink et al. (2020) showing the bias on the availability of biodiversity data. Any trends observed are driven by North America and European regions, with almost no information from tropical ecosystems. Source: Klink et al. (2020), figure 1.

Tropical forests are not only critical for Earth's biodiversity but also for regulating the global climate and maintaining local well-being and livelihoods. These forests are highly dynamic systems, that changed intensively across ecological and evolutionary timescales, but the ongoing alterations in the forests' structure and composition during the Anthropocene might have profound and determinant effects on the fate of tropical forest biodiversity and functioning (Malhi et al. 2014). The main threats to these forests include an intense process of fragmentation

of the forest (driven by agriculture expansion, timber and wood extraction), unsustainable defaunation, wildfires and changes in the climate (e.g. altered temperature and precipitation patterns, increased CO₂ concentration) (Malhi et al. 2014, Lapola et al. 2023). One of the first steps to investigate trends in biodiversity is to have adequate data on hand but, for tropical areas such as the Amazon, this might be a major challenge. Although access to data is advancing, we are still far from having tropical biodiversity monitored, with data still fragmented and scarce. As I experienced myself during fieldwork expeditions in the Amazon forest, many regions can be remote, logistically challenging and expensive, or subjected to local economic and social conflicts, which makes it very difficult to develop scientific work. However, I believe we can stay optimistic about the data access. More and more researchers are working together to compile, standardize and share biodiversity data, making it freely available. That was my inspiration when I initiated my research chapters, and helping to fill this lack of information about biodiversity in tropical forests by compiling existing data for vertebrate species in the Amazon forest was my aim when developing **chapter 1**. For the Amazon, existing data on vertebrates is often neither published nor accessible, which makes the work of compiling and standardizing it highly valuable, and allows future researchers to work with it too. Furthermore, the scarcity of biodiversity data for vertebrate species reduces our understanding of how this group respond to forest degradation in the Amazon.

Beyond detecting changes in biodiversity on different spatial and temporal scales, it is crucial to understand what are the drivers of these changes. Biodiversity data englobes different types of information about specimens in an ecosystem (e.g. species identification, morphological or genetic data) and allows us to access the impacts of human actions on ecosystems and identify the main threats to the species (Figure 3). This information is essential and can be used in studies to both predict species responses to human changes, as well as to mitigate future impacts on biodiversity and ecosystem functionality. For the Amazon, the largest tropical forest, anthropogenic disturbances were mostly studied through the impact of deforestation, and it is only recently that other types of human disturbances (such as selective logging, fire and extreme droughts) began to be considered. Although we might expect forest disturbances to increase the negative impact of forest degradation on biodiversity, there are only a few studies so far

measuring that on the Amazon-biome scale (e.g. see Bogoni et al. 2020), mainly due to scarcity of data for the area. While deforestation and human actions affect most species, within vertebrates, some species are more susceptible than others. For example, jaguars (*Panthera onca*) tend to avoid unforested/ deforested areas, while the lowland tapir (*Tapirus terrestris*) appears to be tolerant to some habitat degradation, but to avoid burned areas (Quintero et al. 2023). Forest-dependent species seem to avoid crossing roads, with consequent negative impacts for those species, that might have their habitat, feeding behaviors, and even population parameters (e.g. age structure and gender) changed by the presence of roads (Pinto et al. 2020). Such alterations in the occurrence and/ or presence of the species directly reflect on the local species richness of an area, a metric that is commonly used in ecology to analyze changes in biodiversity. Importantly, vertebrate species play an essential role in ecosystem functioning (for example as seed predators, dispersers, or top-down control on herbivores), so it is critical to comprehend how human actions impact vertebrate biodiversity. Therefore, by investigating changes in vertebrate species richness across a gradient of human modification in the Amazon, in **chapter 2**, I aim to understand the consequences of these changes on a biome scale and for a large assemblage of vertebrates.

Impacts on biodiversity

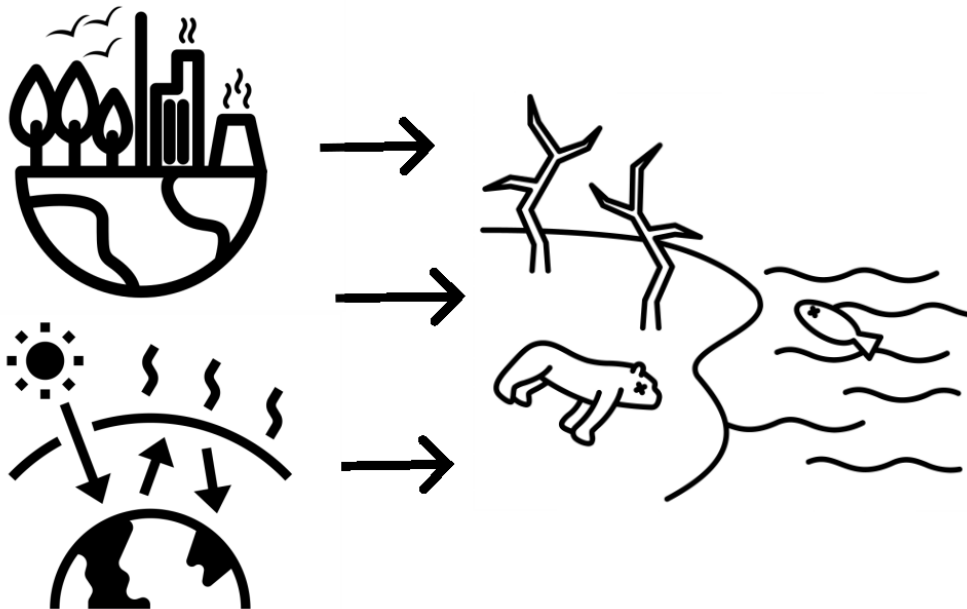


Figure 3: Biodiversity data can be used to understand the impacts of human changes on ecosystems. Source: Tom Fricker, Nesialoo Creator and Kamin Ginkae from Noum Project.

3. Assessing the consequences for ecosystem functioning and Nature's contribution to people

So far, we have navigated around some of the human changes on the Earth System, and how that affect biodiversity. My next and final step is to investigate how anthropogenic changes reflect on entire ecosystems' functionality, directly impacting the contributions we have from nature. For an ecosystem to maintain life, numerous physical, chemical and biological processes must continuously occur. In ecology, those processes are known as ecosystem functions, and some examples are the flow of nutrients and energy through a food chain, the cycling of nutrients in nature, net primary productivity (the amount of biomass produced by primary producers), herbivore control, among many others. A more practical example is the role of carnivores preying on herbivore species and regulating their populations, therefore avoiding the overexploitation of plants. Although there is a clear relationship between biodiversity and ecosystem functions, the exact mechanisms driving this relationship are rooted in complex interactions between species and, of course, which species are present in the ecosystem (Cardinale et al. 2006). If climate and land use changes are impacting biodiversity, it is expected that there will be consequences on the functioning of the ecosystems. In fact, the loss of ecological interactions seems to affect ecosystem functionality in faster rates than the loss of species, which emphasizes the importance of understanding all components of biodiversity change (Valiente-Banuet et al. 2015). In order to survive the environmental changes, species are moving to other locations, which causes shifts in their distributions, and leads to new biotic interactions (Pecl et al. 2017). Species responses may vary, but relative abundances, habitat use and distribution are usually affected, as well as predation and competition dynamics, herbivory and other interactions (Williams et al. 2008, Pecl et al. 2017).

The effect of human impact on the disruptions of ecological interactions and ecosystem functions is now well documented. From previous experiences with megafauna, we know that

large-scale extinctions might significantly restructure plant communities and alter seed dispersion and nutrient availability (Janzen and Martin 1982, Gill et al. 2009, Doughty et al. 2013). More recently, in the last decades, human-induced climate change is causing a shift in the spatial distribution of plant and animal species worldwide, with species moving to colder areas and disrupting key interactions among species (Pecl et al. 2017). Furthermore, for belowground communities, changes in land cover might also impact soil animal biomass, with an uneven loss within size classes and trophic levels, causing shifts in soil communities and threatening ecosystem functioning (Potapov et al. 2019, Yin et al. 2020). From below-ground to aboveground ecosystems, species are threatened, and the impacts can be alarming. The loss of biodiversity we are witnessing today, besides affecting the functioning of the ecosystems, has cascade effects on our society, by negatively impacting the supply of goods and services by nature.

Nature's contributions to people are all the positive and negative contributions of nature (from organisms to entire ecosystems) to human society and quality of life. Those contributions include: i) regulation processes (e.g. pest control and access to fresh air and potable water), ii) material goods (e.g. provision of food and energy resources), iii) non-material values (e.g. learning and inspiring experiences, support of identities) (Brauman et al. 2019). Since 1970, NCP related to the production of goods (such as food, medicine and fiber) had an increase in their provision (although there is a decrease in the long-term ability of nature to continue providing those), while the other NCP are experiencing a decline in their potential capacity, caused by changes in land use and climate (Brauman et al. 2019). For example, the increasing demand for food caused a shift from extensive to intensive agriculture in many countries, which indeed increased food production, but with the cost of biodiversity losses, increased pest pressure, soil erosion and pollution of water bodies (Rehman et al. 2022). However, not only terrestrial ecosystems are threatened. In marine ecosystems, the warming of the ocean is disrupting nutrient cycles and depleting biodiversity (e.g. by changing the abundance and distribution of species), and directly impacting the provision of NCP related to harvesting fish (Smale et al. 2019).

The link between biodiversity and the provision of NCP is complex and remains a challenge to be tackled (Figure 4), which hinders our ability to estimate the capacity of an ecosystem to provide NCP. Most approaches to estimating NCP capacity are based on biophysical

data, for example, land cover, soil properties, and climate, or apply at local or regional spatial scales (Isbell et al. 2017, Verhagen et al. 2017, Brauman et al. 2019, Le Provost et al. 2022). However, to properly capture the components of biodiversity that are relevant for biodiversity-based NCP, it is essential to include both biotic (e.g. species presence, abundance and interactions) and abiotic (e.g. land use type, temperature, precipitation) data in the approach, since ecological interactions vary along environmental conditions. On **chapter 3**, we propose a new framework that integrates biodiversity, ecosystem functioning and NCP, to evaluate the capacity to provide NCP through a macroecological perspective. The key to integrating them is to use tools available from food web ecology associated with biodiversity models. In an ecosystem, the existing species are connected by feeding links that are described by a flux of energy between the different trophic levels (Barnes et al. 2018). One way to estimate NCP is by quantifying those energy fluxes and associating them with ecosystem functions that can be used as indicators for NCP (Barnes et al. 2018). For that, predicting species abundance, distribution and interactions through biodiversity models becomes an intermediate and essential step. For example, to access the NCP related to pest control in an agricultural field, we could quantify the total amount of energy to all predator species (pest control) consuming the pest. In this case, mapping the network topology and accessing species occurrence and respective abundances is necessary to evaluate the fluxes.

Although this approach is flexible and possible to be applied to different organisms, ecosystem types, and scales (temporal and spatial), I came across a limitation when trying to apply it to below-ground communities. The main step in this framework is to estimate energy fluxes, and for that, we need access to biodiversity data, including species abundance. While for vertebrate species there are biodiversity model options available to estimate species abundance (Santini et al. 2018, 2022), such models were not developed so far for invertebrate species. To fill this gap, in **chapter 4** I generated an allometric model to assess the abundance of soil invertebrates for large-scale projections. Abundance is a metric commonly used in ecology to measure biodiversity and consists of the total number of individuals per species found in a given area. In general, the species' body size is the most important biological predictor to estimate species abundance, due to the higher metabolic demand larger species have in comparison to

smaller ones (White et al. 2007, Santini et al. 2018). This body size-abundance relationship follows a negative three-quarter power law and is very consistent across all living organisms (Damuth 1981, 1987, Allen et al. 2002). However, environmental conditions and the availability of resources also play a role and should be considered when estimating species abundance (Santini, 2018, 2022). For below-ground invertebrates, it is expected that edaphic conditions, together with land use intensity, affect species abundance (Johnston and Sibly 2020). For example, higher soil temperature increases species' metabolic demand (especially smaller ones) and consequently their resource uptake. When this higher demand for resources cannot be supported, a decline in population abundance is expected, which might be problematic considering the future projections of global warming. Overall, our abundance model can be used in future research, to predict the impacts of human change on soil communities, as well as integrated with our framework proposed in **chapter 3**, to investigate the impacts on NCP provided by soil ecosystems.

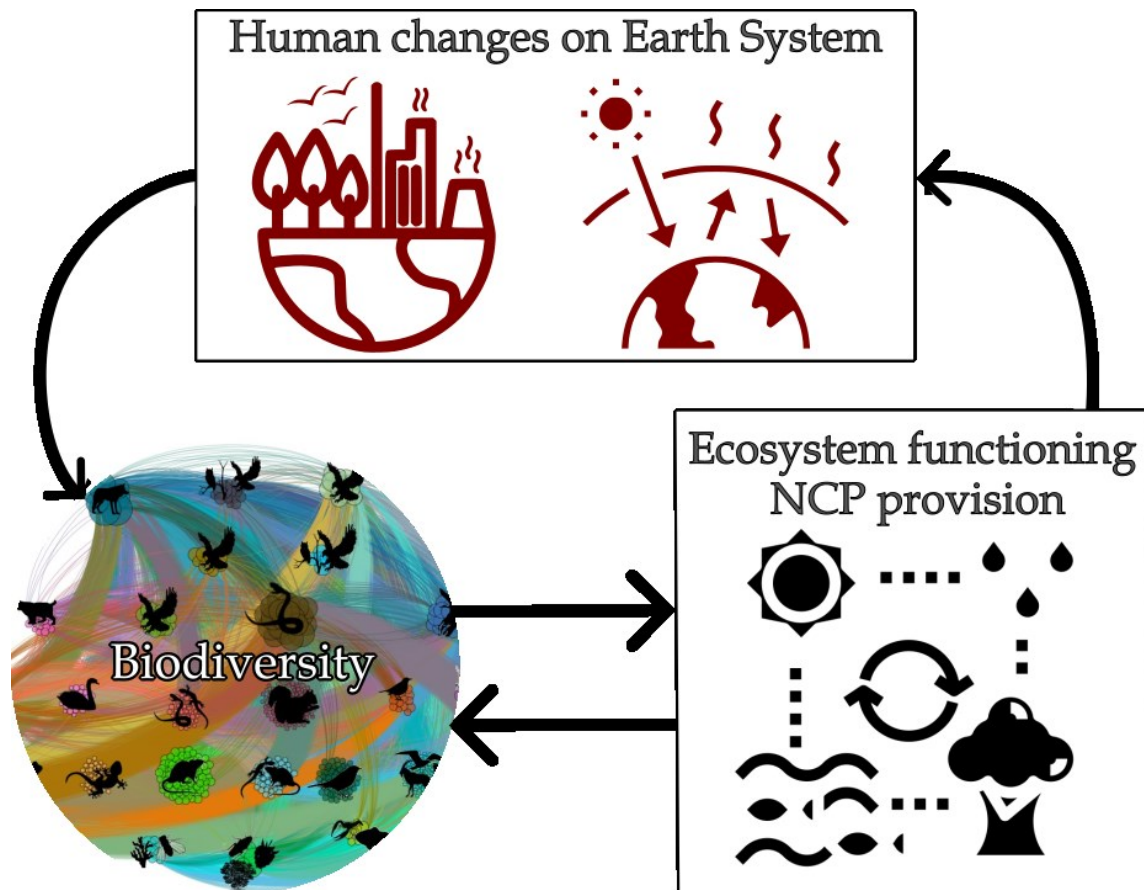


Figure 4: The link between biodiversity, ecosystem functioning and NCP provision is complex and challenging to disentangle. Moreover, it is an important step to understand their relationship with human societies and respective changes in Earth System. Source: Louise O'Connor, Nesialoo Creator, Kamin Ginkae and nareerat jaikaew from Noun Project.

Study outline

As a Brazilian researcher who spent four years working in the Amazon forest, I wanted to dedicate part of my doctoral research to study the human impacts on this biome I am passionate about, and on (some of) the species I had the opportunity to see in the field. Moreover, I was intrigued by how changes impact from below to aboveground communities, also affecting the functioning of ecosystems and the NCP they provide. Thus, I decided to focus my study on the effects of human modifications on vertebrate species in the Amazon biome. During the development of the research, two challenges triggered new questions that led me to the two final chapters of this thesis: first, there are no tools developed so far to evaluate NCP produced through the contribution of biodiversity, and, second, there is no biodiversity model to predict the abundance of invertebrate species, which hinders the possibility of assessing NCP for belowground ecosystems using the framework we propose.

In **Chapter 1**, I compiled and standardized a database containing camera trap records from the Amazon forest. The complete database includes 317 species gathered from 43 surveys developed in eight countries (Brazil, Bolivia, Colombia, Ecuador, French Guiana, Peru, Suriname and Venezuela). Due to its extension, the Amazon forest comprises a great variability of environmental conditions and ecosystem types, which differ in relation to the level of resilience to human alterations, and land-use intensity it is subjected to. Camera traps that photograph animals as they pass by sensors are an efficient and less invasive method to monitor biodiversity over relatively large areas. By summarizing this data, which aggregates a series of information on a local level, I want to answer ecological questions on an Amazonian level (which is the aim of **Chapter 2**). Moreover, it is possible to use this database to estimate species diversity, occupancy

and relative abundance, as well as to understand how vertebrate species respond to different gradients of temperature, precipitation, and human pressure on an Amazon level.

In **Chapter 2**, I use the camera trap data compiled in Chapter 1 to investigate the impacts human modifications on terrestrial landscapes have on the richness of vertebrate species across the Amazon forest. In this biome, forest degradation acts on many fronts, from selective logging, edge effects, fires and extreme drought at regional scales, to deforestation at continental/ global scales. Within this context, I found that vertebrate species richness tends to decrease with increasing human modifications in the Amazon. Moreover, the complex biogeographical history of the area also explains the high heterogeneity, species diversity and richness across the Amazon forest. Therefore, we highlight that increasing anthropogenic threats in the Amazon forest might decrease vertebrate species richness in a way that, preventing further deforestation and disturbances became critical for preserving biodiversity and the associated ecological processes.

In **Chapter 3**, I conceptualize an innovative framework to evaluate and map the provision of NCP over long temporal and large spatial scales. By using this framework, it will be possible to determine how NCP might be affected by future changes in climate and land use. The advantage of this approach is that it offers the potential to explore different time and spatial scales, address species interactions, and incorporate climatic and land use variables. With a case study, I showed how the workflow can be applied using data from terrestrial vertebrates in the European continent. I chose an agricultural rodent pest and demonstrated how to evaluate pest control provided by vertebrate predators on this vole species (*Microtus arvalis*) across the continent. By integrating approaches from food web ecology and macroecological modeling of biodiversity, we gain access to trophic interactions and, ultimately, can monitor and predict NCP' capacity under different climatic conditions.

In **Chapter 4**, I synthesized the so-far largest dataset on abundances and body masses in soil invertebrate communities across different continents, using the same methodologies across all sites. Thus, I developed an allometric model to predict species abundances based on species traits, environmental conditions and resource availability (productivity). In addition, I tested the influence of climatic and edaphic variables on the local body mass-density relationship of the

communities. Decreasing precipitation and increasing temperatures (measured by local soil temperature and water content on the soil) alter the slopes of the body mass-abundance relationship in soil communities, which means that we might expect a shift in the biomass distribution of soil invertebrates, from smaller to larger species in the areas studied. Considering the future climatic scenarios for many global regions, this alteration in biomass might have several implications for the functioning of ecosystems. Moreover, due to the association between species biomass and the flux of energy in the communities, the models we provide can be integrated into food-web approaches, with great potential for predicting the community-level consequences of future warming and drought.

Research chapters

Overview

Chapter 1: AMAZONIA CAMTRAP: A dataset of mammal, bird, and reptile species recorded with camera traps in the Amazon forest

Bibliographic information: Antunes A.C., Montanarin A., Gräbin D.M., Monteiro E.C., Pinho F.F., Alvarenga G.C., Ahumada J., et al. 2022. "AMAZONIACAMTRAP: A Data Set of Mammal, Bird, and Reptile Species Recorded with Camera Traps in the Amazon Forest." *Ecology* 103(9): e3738. Available from: <https://doi.org/10.1002/ecy.3738>

Short summary: In the first chapter, I organized and standardized camera trap records from different Amazon regions to compile a data set of inventories of mammal, bird, and reptile species ever assembled for the area. The complete data set comprises 154,123 records of 317 species. The information detailed in this data paper opens up opportunities for new ecological studies at different spatial and temporal scales.

Chapter 2: Human modifications in terrestrial lands decrease vertebrate species richness across the Amazon forest

Bibliographic information: Ana Carolina Antunes, Benoit Gauzens, Emilio Berti, Fabricio Beggiato Baccaro, Ulrich Brose (*in prep.*). Human modifications in terrestrial lands decrease vertebrate species richness across the Amazon forest.

Short summary: In the second chapter, I analyzed data from chapter 1 to evaluate how human landscape modifications impact vertebrate species richness. In total, I considered 3798 camera trap stations, almost 81,580 occurrence records from 301 species (193 birds, 141 mammals and 13 reptiles). The results showed that, within the gradient of low to moderate human modification observed in our study areas in the Amazon forest, increasing human modification results in decreasing species richness.

Chapter 3: Linking biodiversity and nature's contributions to people (NCP): a macroecological energy flux perspective

Bibliographic information: Antunes A.C., Emilio Berti, Ulrich Brose, Hirt M.R., Karger D.N., O'Connor L.M.J., Pollock L. Thuiller, W., Gauzens, B. (under review on Trends in Ecology & Evolution). Human modifications in terrestrial lands decrease vertebrate species richness across the Amazon forest.

Short summary: In the third chapter, I propose a framework that combines biodiversity models with food web energy flux approaches to evaluate and map NCP at large spatio-temporal scales. While energy fluxes traditionally links biodiversity to NCP locally, biodiversity models permit to extend these predictions across extensive spatial and temporal scales. Moreover, this framework addresses ecological interactions, and incorporate climatic and land use variables.

Chapter 4: Environmental drivers of local abundance–mass scaling in soil animal communities

Bibliographic information: Antunes A.C., Gauzens B., Brose U., Potapov A.M., Jochum M., Santini L., Eisenhauer N., Ferlian O., Cesarz S., Scheu S., Hirt M.R. Environmental drivers of local abundance–mass scaling in soil animal communities. *Oikos* 2022(2): e09735. Available from: <https://doi.org/10.1111/oik.09735>

Short summary: In the fourth chapter, I compiled a dataset comprising 155 invertebrate soil–animal communities across four countries (Canada, Germany, Indonesia, USA), all sampled using the same methodology. I developed an allometric model to predict species abundances based on species traits, environmental conditions and resource availability (productivity). In addition, I showed that soil temperature and water content in the soil have positive and negative net effects, respectively, on soil communities.

Chapter 1: AMAZONIA CAMTRAP: A dataset of mammal, bird, and reptile species recorded with camera traps in the Amazon forest

Manuscript No. 1

Manuscript title: AMAZONIA CAMTRAP: A dataset of mammal, bird, and reptile species recorded with camera traps in the Amazon forest

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The candidate is (Please tick the appropriate box.)

First author, Co-first author, Corresponding author, Co-author.

Status: published

Authors' contributions (in %) to the given categories of the publication

Author	Conceptual	Data analysis	Writing the manuscript	Provision of material (data)
Ana Carolina Antunes	35%	30%	80%	2%
Anelise Montanarin	15%	5%	5%	2%
Diogo Gräbin	15%	5%	5%	2%
Erison Monteiro	15%	30%	5%	2%
Guilherme Alvarenga	15%	30%	5%	2%
Others	5%	0%	0%	90%
Total:	100%	100%	100%	100%

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Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Numbers: 132510/2019-7, 142352/2017-9, 150123/2018-3, 201475/2017-0, 300057/2017-2, 300087/2016-0, 300444/2019-2, 307084/2013-2, 312539/2016-9, 441443/2016-8, 441703/2016-0; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Numbers: 88881.128140/2016-01, 88882.184240/2018-01; Darwin Initiative for the Survival of Species, Grant/Award Number: 20-001; Division of Environmental Biology, Grant/Award Number: 1146206; Programa Petrobras Ambiental, Grant/Award Number: 88881.314420/2019-01; Rufford Foundation, Grant/Award Numbers: 12231-1, 16299-1, 20754-1

Handling Editor: William K. Michener

Abstract

The Amazon forest has the highest biodiversity on Earth. However, information on Amazonian vertebrate diversity is still deficient and scattered across the published, peer-reviewed, and gray literature and in unpublished raw data. Camera traps are an effective non-invasive method of surveying vertebrates, applicable to different scales of time and space. In this study, we organized and standardized camera trap records from different Amazon regions to compile the most extensive data set of inventories of mammal, bird, and reptile species ever assembled for the area. The complete data set comprises 154,123 records of 317 species (185 birds, 119 mammals, and 13 reptiles) gathered from surveys from the Amazonian portion of eight countries (Brazil, Bolivia, Colombia, Ecuador, French Guiana, Peru, Suriname, and Venezuela). The most frequently recorded species per taxa were: mammals: *Cuniculus paca* (11,907 records); birds: *Pauxi tuberosa* (3713 records); and reptiles: *Tupinambis teguixin* (716 records). The information detailed in this data paper opens up opportunities for new ecological studies at different spatial and temporal scales, allowing for a more accurate evaluation of the effects of habitat loss, fragmentation, climate change, and other human-mediated defaunation processes in one of the most important and threatened tropical environments in the world. The data set is not copyright restricted; please cite this data paper when using its data in publications and we also request that researchers and educators inform us of how they are using these data.

KEYWORDS

Amazonia, data paper, tropical forest, vertebrates

ACKNOWLEDGMENT

Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Associated data are provided as Supporting Information and are also available in Zenodo at <https://doi.org/10.5281/zenodo.6325578>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Antunes, Ana Carolina, Anelise Montanarin, Diogo Maia Gräbin, Erison Carlos dos Santos Monteiro, Fernando Ferreira de Pinho, Guilherme Costa Alvarenga, Jorge Ahumada, et al. 2022. "AMAZONIA CAMTRAP: A Data Set of Mammal, Bird, and Reptile Species Recorded with Camera Traps in the Amazon Forest." *Ecology* 103(9): e3738. <https://doi.org/10.1002/ecy.3738>

For data paper publications in Ecology, the main text is added as a supplementary material. Therefore, the main text of chapter 1 can be found in the Appendix A of this thesis.

Chapter 2: Human modifications in terrestrial lands decrease vertebrate species richness across the Amazon forest

Manuscript No. 2

Manuscript title: Human modifications in terrestrial lands decrease vertebrate species richness across the Amazon forest

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Bibliographic information: Ana Carolina Antunes, Benoit Gauzens, Emilio Berti, Fabricio Beggiato Baccaro, Ulrich Brose (in prep.). Human modifications in terrestrial lands decrease vertebrate species richness across the Amazon forest.

The candidate is (Please tick the appropriate box.)

First author, Co-first author, Corresponding author, Co-author.

Status: in preparation

Authors' contributions (in %) to the given categories of the publication

Author	Conceptual	Data analysis	Writing the manuscript
Ana Carolina Antunes	55%	45%	70%
Benoit Gauzens	15%	15%	10%
Emilio Berti	15%	30%	10%
Fabricio Beggiato Baccaro	0%	5%	5%
Ulrich Brose	15%	5%	5%
Total:	100%	100%	100%

Human modifications in terrestrial lands decrease vertebrate species richness across the Amazon forest

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ABSTRACT

The Amazon forest is recognized for its high biological diversity, responsible for the provision of critical ecosystem services. Despite its importance, its biodiversity is currently threatened by increasing rates of deforestation and forest degradation. Large-scale studies investigating the impact of human modifications on vertebrate species are still scarce, therefore, we analyzed data from an extensive database compiled for the Amazon forest to evaluate how human landscape modifications impact vertebrate species richness. In total, we considered data from 3798 camera trap stations, almost 81,580 occurrence records from 301 species (193 birds, 141 mammals and 13 reptiles). Our results showed that, within the gradient of low to moderate human modification observed in our study areas, increasing human modification results in decreasing species richness. We also highlighted that biogeographical differences, captured by the random effects in our model, explain a large proportion of the variation in species richness across our sites. Moreover, our findings contribute to understanding the influences of human-induced changes in vertebrate assemblages and reinforce the need for more research to investigate the mechanisms underlying this change in species richness.

INTRODUCTION

Species richness is declining at the global scale due to anthropogenic actions and climate change (Ceballos et al. 2015). Still, there is no consistent pattern of biodiversity change at the regional and local scales, where trends in species richness vary substantially (Blowes et al. 2019, Chase et al. 2019). Human activities directly impact biodiversity on many fronts, altering species physiology (Somero 2012), population traits (Zheng et al. 2023), interactions (Tylianakis et al. 2007, Geslin et al. 2013), temporal and spatial behavioral patterns (Veldhuis et al. 2019, Hirt et al. 2021), thus leading to changes in their occurrences, densities and distributions (Barlow et al. 2016, Santini and Isaac 2021, Antunes et al. 2022a). Hence, it is crucial to understand the drivers and consequences of these disturbances so that it is possible to develop ecological models to describe and/or predict biodiversity responses to the threats, and the necessary conservation policies to mitigate them.

Within the tropics, the Amazon forest hosts a remarkable share of the world's biodiversity, with high numbers of endemic species and more groups being described by scientists daily (Science Panel for the Amazon 2021). This biome is the world's most diverse rainforest and the primary source of species lineages in the Neotropics (Antonelli et al. 2018). The outstanding species richness found today is a consequence of Amazonia's complex biogeographic history, mainly a combination of the long existence of lowland tropical forests, and their historical disturbances (Antonelli et al. 2010, Rocha and Kaefer 2019). Nevertheless, this biodiversity is currently threatened by human expansion, and the forest might be close to achieving a tipping point, where the Amazon forest might switch to an ecosystem similar to the savannah, with devastating climatic and social consequences at local and regional scales (Wuyts et al. 2018, Amigo 2020).

Forest degradation in the Amazon acts at several scales and is associated with different factors (Silva et al. 2022). Agricultural expansion is the major driver of regional deforestation and is usually associated with infrastructure activities such as forest clear-cut, roads, logging and burning, causing significant losses to animal communities (Franco-Solís and Montanía 2021, Lapola et al. 2023). From local to regional scales, human-induced disturbances such as edge

effects, selective logging, fires and extreme drought threaten species, which may respond differently depending on their functional characteristics (Peres et al. 2010, Albert et al. 2023, Lapola et al. 2023). At continental scales, deforestation and climatic changes cause long-term impacts on the terrestrial carbon cycle, ecosystem functions and services provided by the species (Malhi et al. 2008, Albert et al. 2023). In general, land use alterations induced by anthropogenic actions disturb multitrophic processes by reducing species biomass and richness, triggering cascading effects through biotic interactions, with increasing effects at higher trophic levels (Barnes et al. 2017). Therefore, assessing species at high trophic levels and with large body sizes, such as vertebrate species, which are often most affected by external stressors, is critical to understanding the ecosystem health of the Amazon forest.

While most studies have focused on the impacts of anthropogenic modifications on Amazon biodiversity for restricted taxonomic groups or at local scales (but see Peres and Lake 2003, Quintero et al. 2023), we aim to understand what are the consequences of these changes at a subcontinental scale and for a large assemblage of vertebrate species. More specifically, we developed a subcontinental-scale analysis (macro-scale), comparing data from defined regional areas (meso-scale) to investigate the effects of human modifications on the vertebrate species richness across the Amazon forest. We used a comprehensive camera trap dataset compiled for the Amazon forest (Antunes et al. 2022b) to analyze the impact of human modifications on terrestrial landscapes across the meso-regions defined.

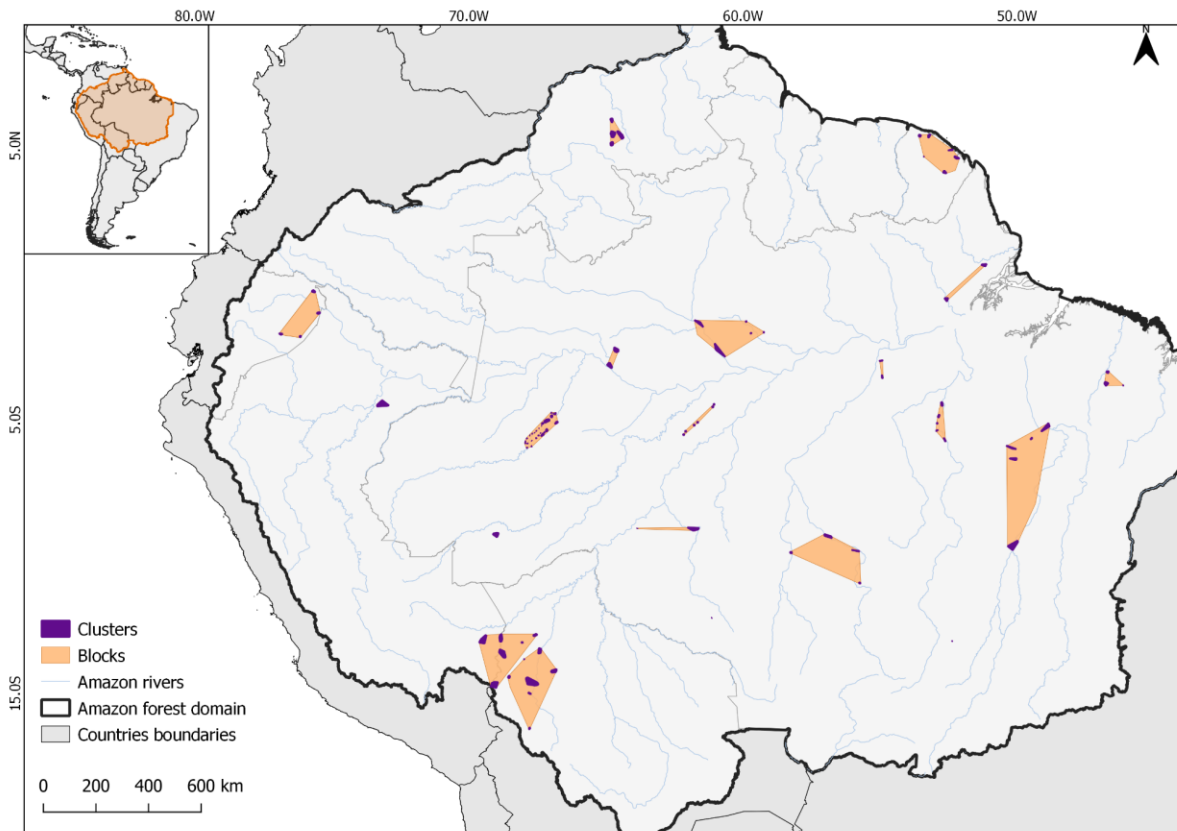
METHOD

Dataset

Camera traps are a consistent method to detect terrestrial vertebrates (Rovero et al. 2010). In this study, we used the largest camera trap database currently available for the Amazon Forest (available from Antunes et al. 2022, at: <https://doi.org/10.5281/zenodo.6325578>). The database compiles 43 datasets and comprises 154,123 records of birds, mammals and reptile

species, recorded by camera traps from 2001 to 2020. The final dataset comprises the spatial range of the original database inside the Amazon forest limits (RAISG, Rede Amazónica de Información Socioambiental Georreferenciada 2020) (Fig. 1). From flooded forests such as *igapós* and *várzeas* to upland forests, our samples are widely spread across different forest and land use types. We filtered the original data to keep only the studies developed on the ground floor (e.g. no canopy sampling), and designed to sample community data (e.g. we excluded studies strictly focused on single species).

Fig. 1: Distribution of the clusters and blocks along the study area. Small purple polygons represent the clusters and orange polygons the blocks.



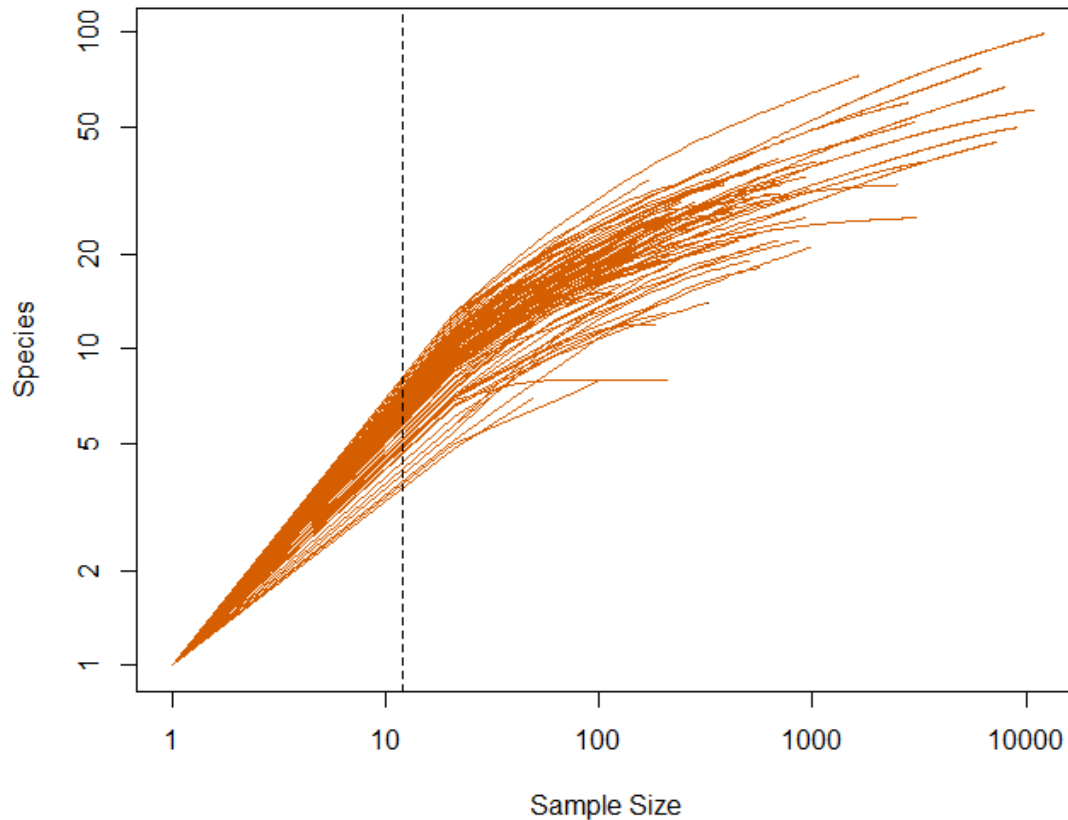
Prior to the analysis, we implemented a two-step approach to prepare the data. Step I: to account for large-scale biogeographical variation that might influence species richness across our sites, we defined unique regions at a macro-scale, in which we aggregated all camera trap

stations present (hereafter: blocks). For that, we combined the camera locations in regions, by grouping the camera trap stations based on their geographic coordinates, and generated 30 blocks using k-means clustering in QGIS 3.6 (Figure 1). The blocks define macro-scale regions for which macroecological and biogeographical processes may influence species composition more homogeneously. In step II, to assess species richness at a finer spatial scale, within each block, we defined a mesoscale spatial level (hereafter: clusters). We manually defined clusters within the blocks by grouping each camera trap within the blocks. In total, we generated 115 clusters, in which we aggregated species richness data on a meso-scale, from the grouped camera trap stations, to reduce associated errors in species detection compared to individual camera-level analysis. Clusters represent our sampling units, and all our variables were calculated at the cluster level.

Estimation of species richness

The sampling effort is the total sum of the days across all cameras that were operational in a cluster. Since the number of observed species was dependent on the sampling effort, we rarefied all estimates of species richness to the smallest sampling effort. The rarefied species richness was estimated (hereafter referred to as “species richness”) for each cluster using sample-based rarefaction curves with the rarefy function (vegan package ver. 2.6-4) (Oksanen et al. 2022) in R (Fig. 2). We discarded 7 clusters that were within the lower sampling effort 10% quantile, and 2 outlier clusters that recorded less than 6 species in total, a very low level of species richness compared to the others (mean species richness considering all clusters was 24.6 ± 15). The results obtained without removing the 9 outliers are shown in the Supplementary Information (SI1) and are overall consistent with what is obtained with the selected dataset. As a final step, we removed 13 clusters (and respective blocks) located outside the Amazon forest limits (RAISG 2020) so that, for the subsequent analysis, we used 20 blocks and 93 clusters.

Fig. 2: Species accumulation curve of terrestrial vertebrate assemblages across the clusters. The lines represent the cumulative number of species as a function of the records sampled. The dashed line represents the cut-off at the sample size of the smallest sample (12 registers).



Human-modification

We used human modification data from (Kennedy et al. 2019) at a 1-km resolution. They developed a continuous metric based on 13 anthropogenic stressors and their estimated impacts on the landscape. Five major categories of human activity are considered: human settlement (population density and built-up areas), electrical infrastructure (powerlines, nighttime lights), agriculture (cropland and livestock), mining and energy productions (mining, oil wells, wind turbines), and road transportation (major and minor roads, two tracks and railroads) (Kennedy et al. 2019). The median and mean from 2016 and 2014, respectively, were used to capture each stressor (for more details, see Kennedy et al. 2019). Values range from 0.00 to 1.00, with four modification classes: “low” ($0.00 \leq HM_c \leq 0.10$), “moderate” ($0.10 < HM_c \leq 0.40$), “high” ($0.40 <$

$HM_c \leq 0.70$), and “very high” ($0.70 < HM_c \leq 1.0$). For each cluster, we created the minimum convex polygon (hulls) including all camera trap stations, so that we can define unique regions and extract the human modification data. For each convex hull, we extracted the mean value of human modification based on all 1-km² resolution pixels.

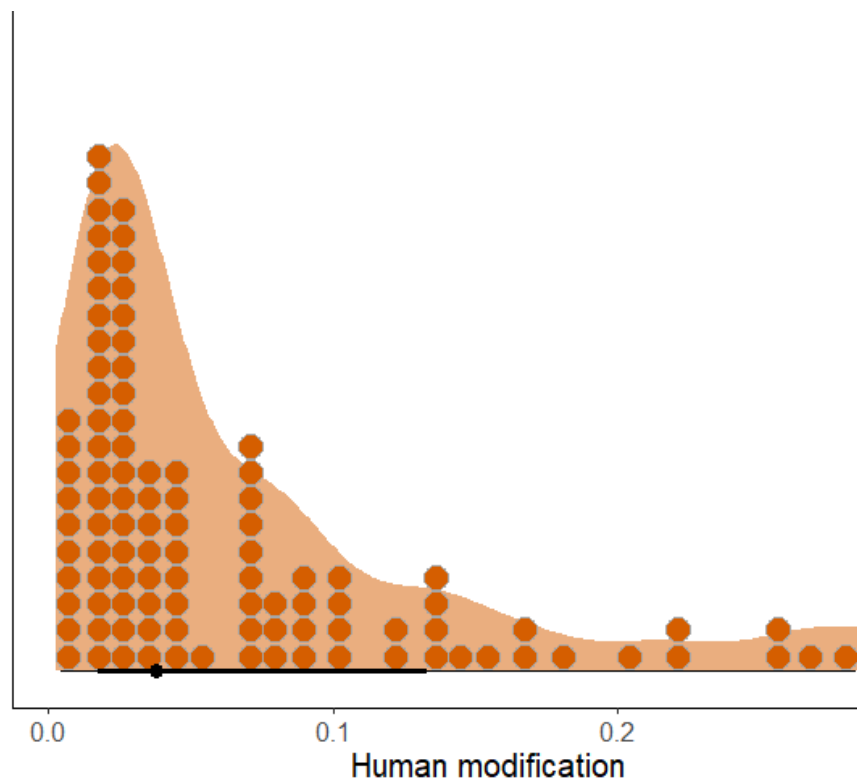
Statistical analyses

To evaluate if human modifications impact species richness across the clusters, we used a Linear Mixed Effect Model that relates species richness for each cluster to the human modification variable. The block ID was assigned as a random intercept effect, to account for macroecological and biogeographical processes that may act across the whole studied area. To assess if the size of the defined clusters has an effect on the relationship between human impact and species richness, we also tested two additional statistical models that include the area of the clusters. Still, the area did not have a significant effect after a model comparison, and the most parsimonious model included only human impacts. It is likely that, after the rarefaction procedure, any biases associated with the cluster size were also corrected (for details, see Supplementary Information - SI2). All statistical analyses were performed using R ver. 4.0.0. We used lme4 ver. 1.1-28 (Bates et al. 2015) to perform the Linear Mixed-Effects Model.

RESULTS

In total, we analyzed data from 3798 camera trap stations, totaling almost 81,580 occurrence records for 301 species (193 birds, 141 mammals and 13 reptiles). The final data source used in the analysis is available as Supplementary Information (S3). The resulting values for human modification within the 93 clusters analyzed ranged from 0.0009 to 0.33 (Fig. 3), within the “low” and “moderate” classes defined by Kennedy et al. (2019).

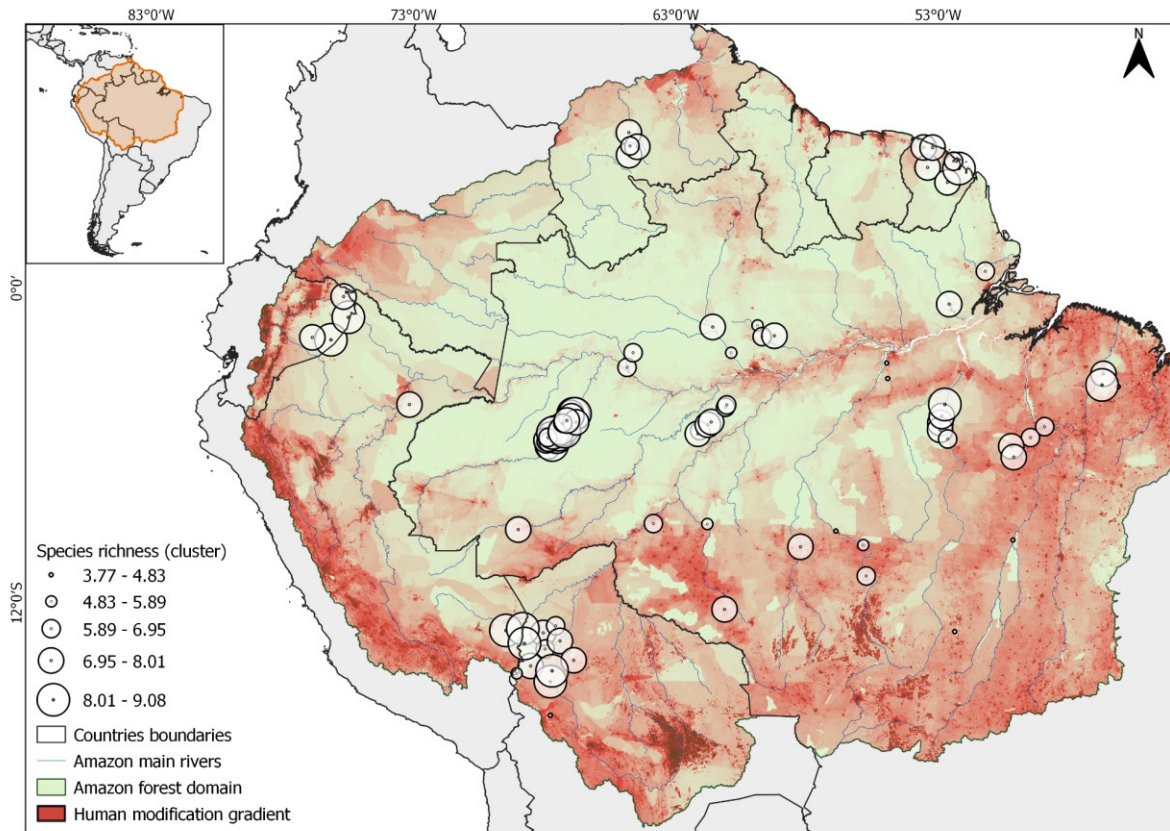
Fig. 3: Distribution of human modification values across the sites (clusters). Frequency of distribution of human modification data with quantiles and median (black line).



The main stressors are the presence of human settlements (especially dense human population), and agriculture (mainly livestock). Most of the clusters with higher values of human modification are located in the area commonly known as the “arc of deforestation”, a crescent shape belt along the southern and eastern borders of the forest (Fearnside 2017) (Fig. 4). Deforestation in this area is mainly related to the expansion of soy cultivation and extensive livestock ranching, in a way that the landscape is mainly covered with pasture (Santos et al. 2021). Within the clusters located in the southeastern Peruvian Amazon bordering Brazil and Bolivia, forest cover is being lost mostly to the expansion of agriculture, mining, and the development of urban areas and roads network (Sánchez-Cuervo et al. 2020).

Fig. 4: Map showing species richness in the clusters across the gradient of land human modification. The circles represent the 93 clusters used in the analysis and are sized proportionally to the rarefied species

richness. Red areas indicate the human modification gradient within the limits of the Amazon forest (RAISG 2020).



The general relationship between species richness and human modification is illustrated in Fig. 5. Our model reveals linear decreases in species richness with increasing human modification (Table 1). The model also shows that there is variation in species richness among blocks. Mean species richness ranged from 3.77 to 9.07.

Fig. 5: Relationship between species richness and human modifications (\log_{10}). Each point represents one cluster across the blocks (different colors) ($y = 8.1 - 1.6x$, $R^2 = 0.12$) along the Amazon forest. The grey area represents the 95% confidence interval.

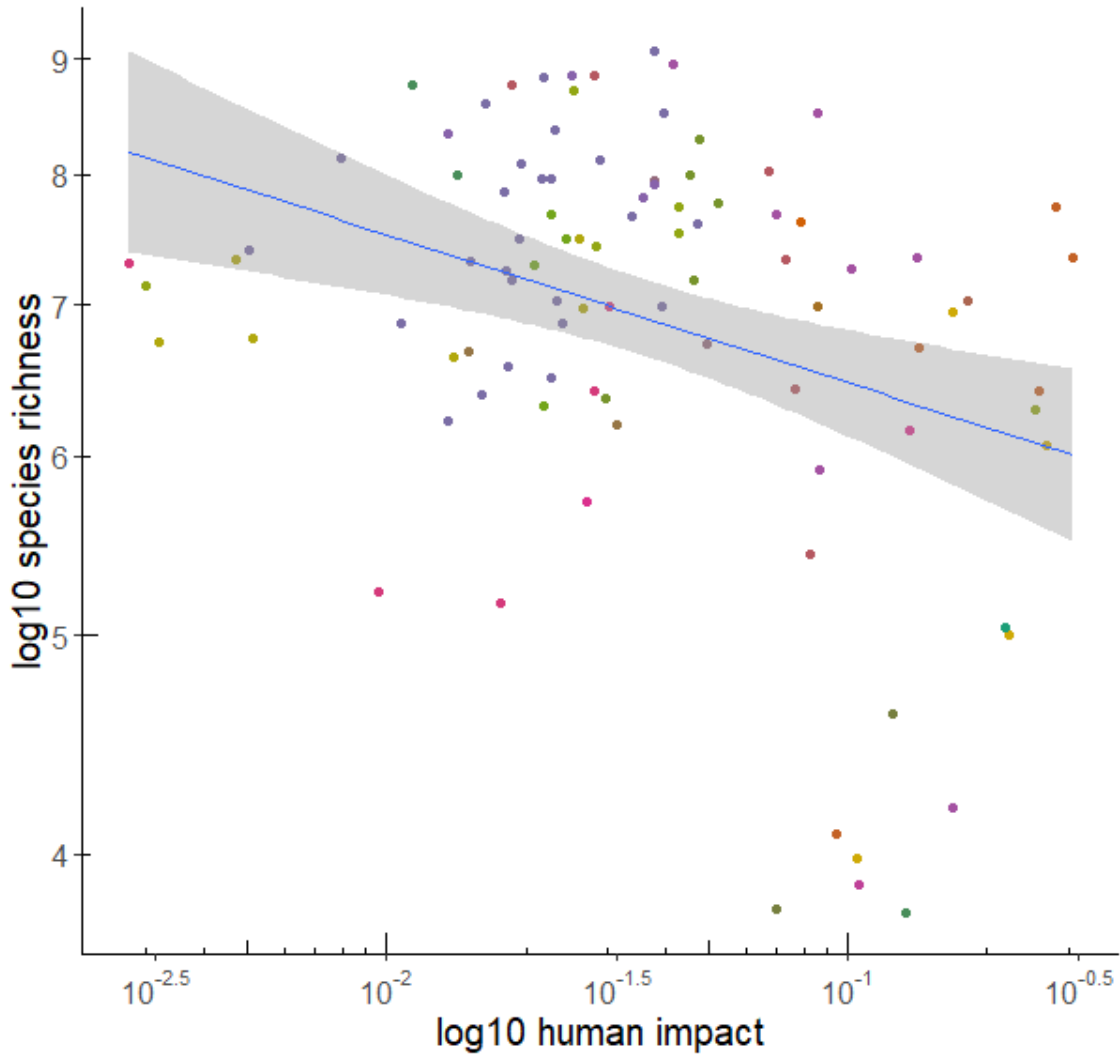


Table 1: Summary of the parameter estimates and random effect of the Mixed-Effect Model for species richness prediction.

Species richness (rarefied)			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	5.77	4.82 – 6.72	< 0.001
Human impact [log10]	-0.78	-1.41 – -0.14	0.017
Random Effects			
SD	0.89 – 1.25		
SD blocks	0.12 – 1.07		
N blocks	20		
Marginal R ² / Conditional R ²	0.076 / 0.327		

DISCUSSION

In this study we examined the effect of human disturbances on vertebrate communities across the Amazon forest. We found that even in areas within a gradient of low to moderate human modification, increasing human modification decreases vertebrate species richness, with individual differences in the mean richness across blocks. This finding complements other studies that show that anthropogenic processes directly impact species distribution, abundance and site use patterns (Li et al. 2022, Quintero et al. 2023). Under critical ranges of habitat loss and fragmentation, such as in the moderate class observed, shifts in biodiversity and the provision of ecosystem services are expected (Dobson et al. 2006, Kennedy et al. 2019). Therefore, we

highlight that increasing anthropogenic threats in the Amazon forest tend to decrease vertebrate species richness in a way that preventing further deforestation and disturbances is critical for preserving biodiversity and the associated ecological processes.

Kennedy et al. (2018) provided a global measurement of human modification to terrestrial land based on multiple stressors and estimated that 52% of the lands are now in a state of moderate modification. Our study areas were classified within low to moderate levels of human modification. Besides deforestation, moderate levels of human modification also include other anthropogenic disturbances such as fires, timber extraction and edge effects have been intensified in the last decades, reducing the number of species (Lapola et al. 2023). This is aggravated by habitat fragmentation, where species richness in isolated forest fragments changes accordingly to the size of the fragment, with smaller patches usually harboring a limited number of species (Michalski and Peres 2007). The presence of roads, even narrow ones, also negatively impacts species richness and abundance, disrupting movement patterns and isolating sub-populations, with amphibians and reptile species being more affected, followed by mammals and birds (Pinto et al. 2020). In that way, the local fauna can take many decades to recover after a disturbance, a threat especially to the many rare species occurring in the tropics (Ferraz et al. 2003, Peres et al. 2010). When impacted species become too small to support viable populations, they are likely to face extinction in the long term (Allan et al. 2019).

Substantial changes in species richness may also result from a substantial reorganization of ecosystem structure and dynamics, altering ecosystem processes and flux of energy and material (Brown et al. 2001). Vertebrate species might develop behavior mechanisms such as altered temporal and spatial patterns in response to human disturbances (e.g. human presence, movement barriers such as roads), leading to increased co-occurrence and rewiring of species interactions (Gilbert et al. 2022, Thu et al. 2022). Alterations on site-use patterns are species-specific (e.g., some species avoid urban areas or areas affected by fire or vegetation cover loss) and usually related to changes in the availability of food resources and shelter, with some species more susceptible to habitat degradation than others (Quintero et al. 2023). Our study sites are located in areas with low to moderate levels of human modification, where forest degradation is an important driver of biodiversity loss, with large negative effects on species of high

conservation and functional value (Barlow et al. 2016). Moreover, degraded areas have larger spatial extensions than deforested areas, in a way that different types of disturbances must be considered jointly when studying anthropogenic impacts on biodiversity in the Amazon forest (Silva et al. 2022, Lapola et al. 2023).

Biogeographical differences, captured by the random effects, also explain a relatively large proportion of the variation in species richness across sites in the Amazon. The east-western gradient of species richness, from the Andes foot downstream the Amazon River Amazonian, is a known biogeographical pattern in the Amazon (Sales et al. 2017). Although the intrinsic mechanisms driving these processes are complex and still debated (Gomes & Kaefer, 2019, Antonelli et al. 2010), historical biogeography helps us understand the high heterogeneity, species diversity and richness across the Amazon forest. Important processes happening throughout the geological times including Andean uplift, riverine barriers, vegetation shifts, but also domestication and different habitat gradients, seem to have contributed to the current species distribution and richness patterns across the Amazon forest (Gomes & Kaefer, 2019). Besides climatic factors (e.g. temperature and precipitation), soil and river characteristics are important determinants of the forest structure and dynamics (e.g. vegetation type and associated biota) (Quesada et al. 2012, Hofhansl et al. 2020). Across our study area, each block is likely subjected to different conditions, which explain the variation in species richness, and reinforces the complexity of these ecosystems' functionality. Despite these differences, we still see a subcontinental-scale impact of human modifications on species richness across the Amazon forest. This opens new venues to investigate how these variations on macro-scale conditions interact with different human disturbances and affect species diversity.

CONCLUSION

Areas with a low degree of human impact are expected to hold high biodiversity levels and resilient ecological functions. Nevertheless, our findings point to a threat to biodiversity due to a reduction in species richness, even in areas under low to moderate gradients of human modifications, with possible cascading impacts on ecosystem functionality and provision of

ecosystem services. Furthermore, as a next step to understand how human actions affect biodiversity, we need to disentangle the contribution of the different disturbances and investigate the main drivers of this lower richness of vertebrate species across different regions of the Amazon. Although species richness should not be used as a unique metric to analyze changes in biodiversity, it can be associated with other information (e.g. species turnover indices, relative abundance distributions) to capture dominance and identify shifts in communities over time (Hillebrand et al. 2017), improving our assess to biodiversity changes across the space and time. As the Amazon might be close to reaching an irreversible tipping point, preventing further forest degradation is a pressing need. Moreover, practical broad-scale conservation actions involve the prevention and punishment of illegal activities such as logging and mining, but also the support of the global community.

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Chapter 3: Linking biodiversity and nature’s contributions to people (NCP): a macroecological energy flux perspective

Manuscript No. 3

Manuscript title: Linking biodiversity and nature’s contributions to people (NCP): a macroecological energy flux perspective

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Bibliographic information: Antunes A.C., Emilio Berti, Ulrich Brose, Hirt M.R., Karger D.N., O’Connor L.M.J., Pollock L. Thuiller, W., Gauzens, B. (*under review on Trends in Ecology & Evolution*). Human modifications in terrestrial lands decrease vertebrate species richness across the Amazon forest.

The candidate is (Please tick the appropriate box.)

First author, Co-first author, Corresponding author, Co-author.

Status: Under review

Authors’ contributions (in %) to the given categories of the publication

Author	Conceptual	Data analysis	Writing the manuscript
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Total:	100%	100%	100%

Linking biodiversity and nature's contributions to people (NCP): a macroecological energy flux perspective

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Keywords

Ecosystem services, biodiversity models, ecosystem function, food web

Abstract

Linking biodiversity and the provision of nature's contribution to people (NCP) remains a challenge. This hinders our ability to properly cope with the decline in biodiversity and the provision of NCP under global climate and land use changes. Here, we propose a framework that combines biodiversity models with food web energy flux approaches to evaluate and map NCP at large spatio-temporal scales. While energy fluxes traditionally links biodiversity to NCP locally,

biodiversity models permit to extend these predictions across extensive spatial and temporal scales. Importantly, this novel approach has the potential to assess the vulnerability of NCP to the climate crisis and support the development of multiscale mitigation policies.

Current trends in evaluating Nature's contributions to people (NCP)

Nature's contributions to people (see Glossary) (e.g., plant pollination, carbon sequestration, food provision, and water purification) are highly sensitive to changes in biodiversity due to species invasion, extreme and long-term climatic changes, and anthropogenic disturbances [1,2]. Uncertainty about the future of NCP resulting from biodiversity change and their importance to human societies worldwide requires reliable models capable of predicting future NCP changes at large spatial scales [3,4]. Due to the complexity of processes and interactions that determine ecosystem functioning in response to biodiversity change [5], most approaches that aim to assess NCP provision are often very context-specific (but see [4,6]) and usually applied at regional spatial scales [7,8]. This hinders progress toward estimating the capacity to provide different types of NCP across larger spatial scales and highly dynamic landscapes, with changing species compositions of communities [9,10]. Although useful tools for assessing NCP have been developed over the last 20 years, they mostly rely on statistical modeling using biophysical (e.g. land cover, soil properties, climate, [11]), social or species-based (e.g. [12]) data [13]. In this way, most NCP produced by biophysical processes and anthropogenic assets can be assessed and quantified, while valuable NCP produced through specific components of biodiversity are not adequately captured, remaining highly uncertain [4]. As an example, a critical and well-studied service, pollination, is often estimated at the global scale in terms of the area of habitat suitable for pollinators around crops or by correlations with pollinator diversity and abundance [14]. In contrast, pollination in nature is the outcome of a set of ecological interactions between pollinator and plant communities. It can be measured through the amount and quality of pollen on the stigma [14], or the number and diversity of pollinators [15,16], nevertheless these measurements are usually restricted to local spatial scales [17]. Similarly, biodiversity underpins the provision of many essential NCP (e.g. fruit and seed

dispersion, crop damage, pollination, and pathogen control), but the complexity of its relationships with NCP requires consideration of the species interactions that determine ecosystem functions to predict future NCP responses to changes in biodiversity (but see [4,6]).

Integrating biodiversity forecasts into NCP at large spatial scales is a complex challenge that should be properly addressed, and directly associating declines in biodiversity with the lower provision of ecosystem services may lead to biases in spatial conservation planning, e.g., by overlooking species interactions or underestimating the contribution of common species [17–19]. At the same time, changes in land use in different landscapes directly influence ecosystems, species composition and interactions, making it difficult to quantify the biodiversity-NCP relationship [20,21]. Some initiatives propose approaches to integrate biodiversity into NCP, but those focus on conservation purposes and assess a limited number of NCP (e.g. [22,23]). Here, we introduce an approach to integrate biodiversity data and species interactions into models, estimating NCP at macroecological scales -e.g. for continental or global analyses- using allometric scaling laws (Box 1, Figure 1). This approach can integrate future predictions from biodiversity scenarios, enabling forecasting of the future of NCP on a global scale. It will prove particularly useful for quantifying how NCP respond to environmental and anthropogenic drivers across long temporal and large spatial scales, as well as for assessing the vulnerability of NCP to the climate crisis and supporting the development of multiscale environmental policies [7].

Linking biodiversity to NCP: lessons from local scales

Biodiversity plays a central role in regulating the fluxes of energy and matter that determine ecosystem functions and ultimately NCP [24]. Energy fluxes represent the amount of energy flowing through the links connecting species and trophic levels and describe the energetic structure of communities [25]. These **trophic links** can be used as proxies to quantify multiple NCP driven by trophic interactions (Box 2), due to their direct relationship to ecosystem functions [25]. Thus, understanding how to calculate fluxes of energy opens up new opportunities for better evaluation and predictions of NCP. For example, by quantifying all energy fluxes between an agricultural pest species and its predators, we can assess the strength of pest control in an ecosystem. In a broader sense, energy fluxes provide an opportunity to link ecosystem

functioning and NCP evaluation with **food-web ecology**, which addresses the underlying network of species interactions [26]. Factors such as the sensitivity of food webs to disturbances (network stability), and limitations on the transfer of biomass within trophic levels have a massive influence on the functionality of the ecosystem and should be considered when predicting future scenarios for NCP [26]. Despite its potential applications, this framework is tailored to estimate energy fluxes only at small spatial scales, typically for areas where experiments or individual measurements (e.g. species metabolic rates, species abundance) can be performed. Moreover, this framework relies on a set of ecological variables that are often accessible to ecologists locally: the list of occurring species, species biomasses and body masses, and the set of trophic interactions between the taxa of the focal community. However, for regional or continental scales, these input data can't be experimentally sampled, which hinders the application of this energy-flux framework to predicting macroecological NCP. There are, instead, alternative ways to predict these variables needed for flux calculations at macroecological scales. Here, we propose a method for applying this approach at larger scales, where most conservation efforts take place.

Scaling up local estimations of NCP: biodiversity models as valuable tools

To evaluate energy fluxes and associate them with NCP at large spatial scales, a few challenges related to data acquisition must be overcome (see Box 1 for details): the low availability of data on species abundance and the identification and establishment of the trophic links. Despite significant gaps in biodiversity knowledge (e.g. for many tropical regions), significant progress has been made in predicting current and future species ranges and distributions. These biodiversity models (i.e. here referred to as any model that predicts biodiversity data, like abundance, interactions, distribution) can fill in gaps in biodiversity data, providing a comprehensive representation of biodiversity, and their predictive capabilities (including species occurrence, abundance, traits and interactions) at regional, continental and global scales are becoming better and more precise [27]. Three types of biodiversity models are needed to scale up local estimations of NCP through fluxes: **species distribution models**, **abundance models and interaction models**. Distribution (predicting species occurrences) and

abundance (predicting species abundance) models generate predictions in plots, communities, or grid cells as a function of a set of environmental covariates. These predictions can be extrapolated across space (e.g. to make a map) or time (e.g. project forward for the climate or land-use scenarios). Interaction models that predict the interactions between species, essential data for building the **network topologies** across space, are traditionally based on traits such as body mass [28] and recently started to incorporate abiotic variables [29,30]. Species interaction data can also be retrieved from global databases (e.g. Globi [31] or GATEWAY v.1.0 for trophic interactions [32]) containing information on various ecosystems and interaction types. While these databases may not document all the potential interactions of any given species, they provide a first and easily accessible source of data. Finally, algorithmic methods can reconstruct the missing parts of a network as soon as a reasonable amount of links were primarily identified [33–35]. A detailed protocol to infer species links for terrestrial ecosystems can be found in [36]. Together, these biodiversity models provide the information needed to calculate fluxes and therefore allow us to integrate biotic (e.g. species interactions, species distributions) and abiotic (e.g. environmental variables) factors into a spatially explicit assessment of NCP. Moreover, we can apply this framework also across different time scales, for example, to predict future scenarios of NCP under different climatic and land use conditions.

The potential to integrate biodiversity models and energy fluxes

Global estimation of NCP remains quite coarse when compared to the advances made in evaluating biodiversity data at the same scale. By combining biodiversity information with energy fluxes, we expand our ability to predict NCP for the vast majority of areas where data is missing. As an example, abundance measurements, needed to evaluate the flux of energy between species, are usually rare and sparse [37], but trait-based biodiversity models are being developed to estimate average population abundances [38–40] and can account for bioclimatic/ biophysical factors, making their use with species distribution models highly consistent. A key advantage of this integration is that the resulting flux calculation connects NCP to biodiversity and local environmental conditions through a predictive framework based on accessible biological and biophysical information. In our case study (Box 3) we focus on trophic links, but similar workflows

can be developed for NCP resulting from non-trophic interactions (see Box 2). This approach can be implemented starting from a local grid cell (local ecological network), up to regional and continental scales. Besides exploring different time and spatial scales, the inclusion of species interactions, which can drastically alter NCP provision [26], allows circumventing a limitation from current studies. Factors such as invasive species and their interactions, responses of ecological networks to climatic conditions, species interactions within assemblages through time, and many others are crucial and should be considered.

Our approach also creates a bridge to the large set of theoretical methods offered by food web ecology that can be incorporated to further test the effect of various perturbations. It is, for instance, relatively straightforward to estimate how communities would respond to punctual disturbances (pulse perturbations) by calculating the resilience of the community based on the fluxes [41] or to assess the robustness of the estimated functions of species extinctions [42]. The loss of a species can trigger secondary extinctions, critically affecting not only the ecosystem functionality but also the robustness of the NCP provided [43]. The approach could also be used to anticipate and prioritize conservation actions by identifying key species supporting the entire future or present communities [44]. As such, the food web framework underlying our macroecological projection of NCP provides a valuable tool to connect theoretical ecology and conservation planning.

Opportunities for future scenarios

Over the past 50 years, most NCP have declined globally as a consequence of climate and land use alterations [17]. The integration of macroecological models (e.g. species distribution models) with energy flux modeling allows us to disentangle the long-term impacts of these alterations on the capacity to provide NCP and to project future scenarios. Although different future scenarios for climate and land use change are projected in macroecological models, we tend to overlook projections for NCP [45]. Our framework enables the integration of projections of environmental conditions to estimate what the future of NCP will be in a global context. For instance, increasing temperatures consistently impact local abundances of species [46], ecological network structure and trophic interactions [47,48]. Simultaneously, land-use change

is causing a general decline in the abundance, diversity, and health of species and ecosystems [49]. Together, land use and climate change are thus likely to be key drivers of variety, quantity and spatial distribution of NCP throughout time. Pollination contribution, for example, is facing a decline due to factors such as land-use change, pesticides, invasive species and climate change [50].

At local spatial and short temporal scales, impacts of human activities on biodiversity are usually associated with a decrease in ecosystem functions and stability, therefore reducing the provision of important NCP. Due to cascading effects, those impacts might increase at larger spatial and longer temporal scales, leading to complex cross-scale interactions [7]. In that way, the relationship between biodiversity, ecosystem functioning and NCP across different scales must be better understood to avoid poor forecasts of future supplies of NCP [7]. By using energy flux to access NCP, it is possible to monitor and predict the sources of changes (both in space and time), while disentangling the influence of ecological processes e.g. secondary extinctions and invasion of species.

Concluding Remarks

Quantifying NCP on large spatial and long temporal scales is an urgent matter and, to address that, a detailed understanding of the relationship between biodiversity, ecosystem functioning and NCP is needed. Here, we propose an applied framework to integrate biodiversity models and energy fluxes approaches, to improve our abilities to evaluate NCP through a macroecological perspective. This approach allows accounting for both biotic (e.g. species presence and interactions) and abiotic (e.g. environmental characteristics) factors when estimating NCP. We also show examples of how this integration opens new venues to address unresolved questions (see Outstanding Questions), as well as to improve conservation policies, by helping us identify and predict future scenarios for areas of NCP provision.

Acknowledgements

We acknowledge funding by the ERA-Net BiodivERSA - Belmont Forum call (project FutureWeb); the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) project no. BR 2315/22-1.

Box 1: General workflow

Our workflow is divided into 7 steps:

Step 1: Obtain the **metaweb** with potential species interactions.

Step 2: Obtain species distributions for the study area.

Step 3: Predict species density for each grid cell of the region of interest.

Step 4: Obtain the local ecological network by subsetting the metaweb based on estimated species occurrences.

Step 5: Calculate energy flux across the ecological network using species metabolic rates.

Step 6: Associate fluxes of energy and/or species densities to NCP.

The local network must be known to estimate fluxes. In general, local networks are obtained by subsetting the species list and interactions that occur within the region of interest, i.e. the metaweb. For the species list, different sources are available and can be used (e.g. IUCN - <https://www.iucnredlist.org>, GBIF - <https://www.gbif.org>). The metawebs can be obtained directly from primary sources (e.g., TETRAEU - [51]) or by extracting from aggregated databases (e.g., GLOBI - [31]) the interactions for the taxonomic groups and the region of interest (Step 1). In order to subset the metaweb, local species occurrences need to be estimated from their large-scale distributions. Geographic limits based on expert opinion can be used to achieve this, possibly combined with species distribution models using occurrence data to further improve accuracy (Step 2). To calculate energy fluxes, and hence evaluate NCP, it is necessary to build predictive models for species abundance in order to obtain local estimates of species' biomasses. In contrast to estimations based on small-scale experiments, data such as species' biomasses and distribution can be derived at macroecological scales only through modeling. In particular, species' biomass, which can be predicted using species' body mass and environmental conditions

[39,40] (Step 3). Local networks are assigned by combining the metaweb of species interactions with the occurrence of species on the grid cell (Step 4). Fluxes throughout the network are calculated based on species' metabolic rates (using allometric regressions) and biomasses. Fluxes of energy can be calculated for single species or an entire trophic level (e.g. herbivores or species feeding on specific prey), depending on the NCP of interest (Step 5). The NCP to be evaluated should be associated with an individual flux of energy or summed network fluxes. By summing all fluxes of energy across the grid cells we evaluate NCP across large spatial scales (Step 6).

Box 2: Energy fluxes to NCP

A diversity of contributions delivered by nature to people can be directly related to individual energy fluxes or to summed network fluxes. Associating NCP to specific trophic links is straight forward and it is a way to determine the amount of energy necessary for the ecosystem to sustain the contribution from nature. To illustrate how NCP can be associated with energy fluxes in ecological networks webs, we identified and listed a few examples in Table 1:

NCP	Link indicator (sum of energy fluxes)
Pollination	plant - pollinator
Seed dispersal	seed - disperser
Pest regulation	pest - predator
Species invasion	invasive species - resource
Disease control (vector-control)	vector - predator
Fish production	prey - fish

Carcass removal	abundance of scavengers
Hunting	abundance of hunted species
Nutrient cycling (mineralization)	assimilation efficiency per link
Nutrient cycling (decomposition)	influx to decomposers
Carbon sequestration	metabolic demand of species

Table 1. Potential associations between NCP and trophic links in ecological networks.

Box 3: Case study: control of an agricultural pest in Europe

To demonstrate how the workflow described in the previous section can be applied, we show how to derive energy fluxes for vertebrates in Europe and, from this, how to obtain access to pest control provided by vertebrate predators on a vole species (*Microtus arvalis*) across the continent. The species checklist as well as the network topology for European vertebrates was obtained from the TETRA-EU database [51]. To obtain local communities, we used species distribution ranges from Maiorano et al. 2013 (which combined species' extent of occurrence with their habitat requirements). To estimate species biomass density, we used a macroecological model similar to the one developed by Santini et al. [40]. We trained this model on the TetraDENSITY database [37] using as predictors macro-climatic (i.e. precipitation, temperature, primary productivity) and species-specific variables (i.e. body mass and phylogeny) to estimate species biomass densities locally. Climatic variables were obtained from CHELSA [52], whereas species body mass was from [53–55].

Using the network topology and the species' density predictions from the species distribution models, we obtained, for each pixel, the local network as well as the local densities of species. From this, we settled metabolic losses using allometric equations [56] and estimated

energy fluxes using the R package *fluxweb* [41]. From the matrix describing the fluxes among species, we then evaluated the NCP of interest. Pest control was calculated as the (standardized by mass) sum of all influxes (vole-predators) from each pixel (Figure I). More details about each step of the workflow for this case study can be found in Supplementary Material. Analyses were performed in the R programming language [57], with the code being available at: <https://github.com>.

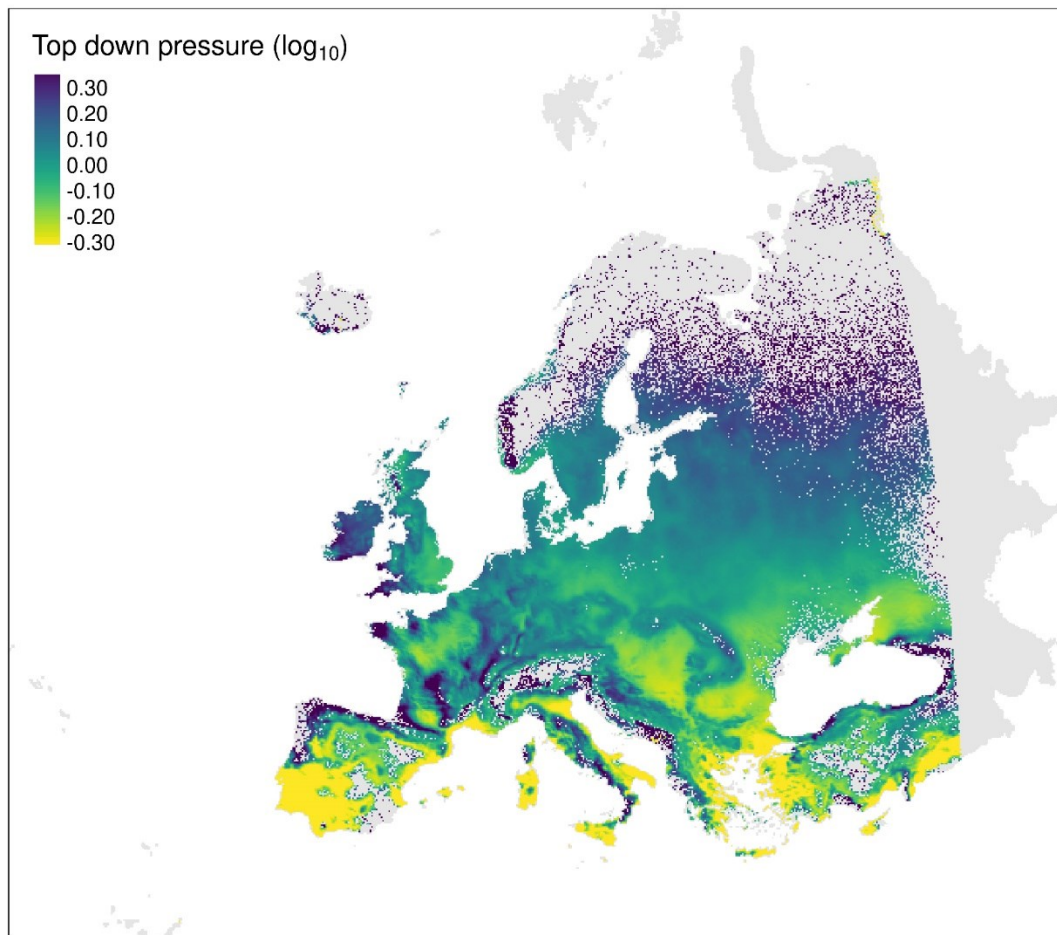


Figure I. Agricultural pest (Common Vole - *Microtus arvalis*) control contribution provided by vertebrate species mapped across the European continent. Map of the top-down pressure (associated with pest control) on *M. arvalis*, a rodent pest for agricultural fields across Europe.

Outstanding Questions

1. How do NCP capacity change across spatial scales?
2. How will NCP capacity be impacted in future scenarios, under climatic and land use alterations?
3. Which NCP provision we are overlooking because we don't properly consider biodiversity data when estimating it?
4. What are the consequences of diversity loss or gain to different NCP provisions? Do cascading effects on energy fluxes across ecological networks play a role in determining NCP?
5. How can we best integrate biodiversity and NCP capacity into conservation plans?

Glossary

Abundance models: predictive models to estimate population abundance of species. Mostly based on species' body mass, such models can also include species' biological traits and environmental conditions.

Food-web theory: area from ecology that describes the trophic links between species in an ecosystem, defined by the flow of energy between different trophic levels.

Interaction models: Models that use species traits (e.g. body mass, diet) and abiotic variables to predict the existence of interactions between species.

Metaweb: an ecological network containing all the species that occur within the study area and all of their potential interactions.

Nature's contributions to people (NCP): all the positive and negative contributions of nature to people's quality of life. There are 18 categories of NCP used in IPBES assessment.

Network topology: Structure of a network that connects links and nodes. In ecology, species usually represent the nodes that are connected through the links (e.g. energy links).

Species distribution models: Models to predict or infer species distribution patterns across spatial scales, accounting for biotic (e.g. species interactions) and abiotic (e.g. environmental) factors.

Trophic links: feeding interactions between species in an ecological network.

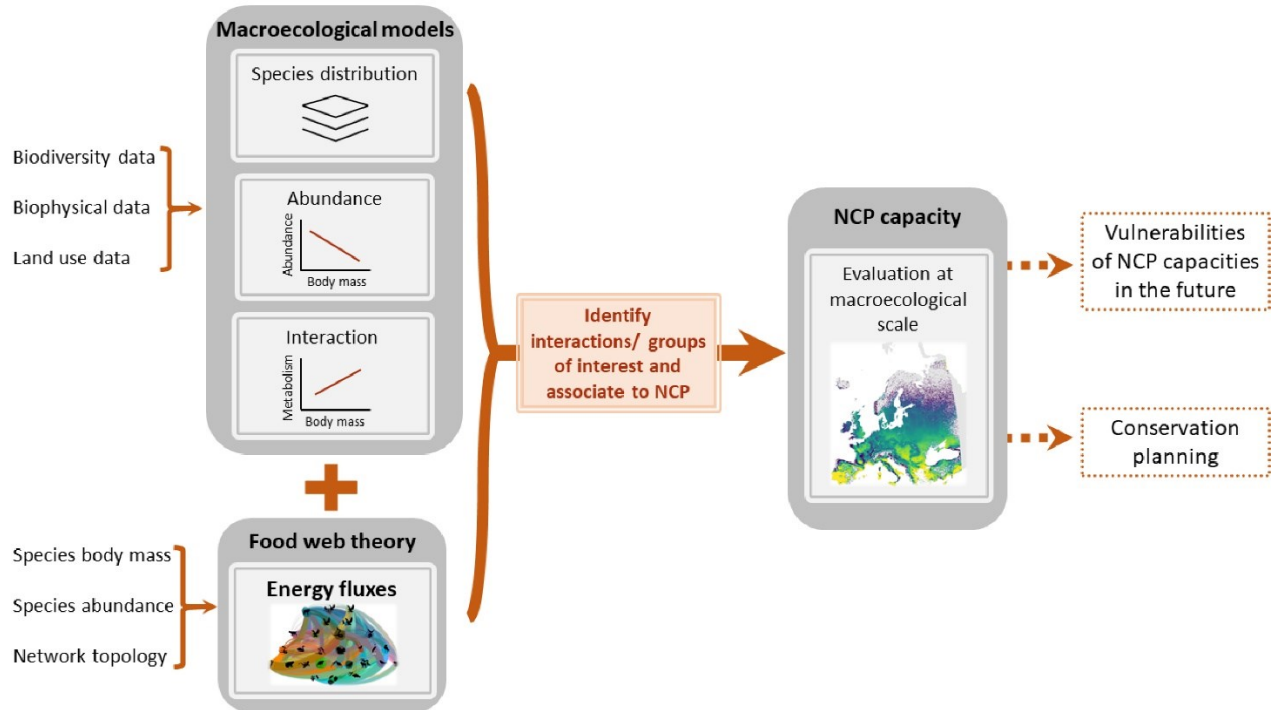


Figure 1: How biodiversity models and food web tools can be integrated to access the provision of NCP at macroecological scales. Macroecological models and food web theory tools use different input data. The integration of these approaches allows the evaluation of NCP capacity, through the identification of relevant taxa or interactions between species, and their association with specific NCP. Moreover, the use of this approach can be applied to conservation planning and future predictions in terms of vulnerabilities of NCP capacities.

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Chapter 4: Environmental drivers of local abundance–mass scaling in soil animal communities

Manuscript No. 4

Manuscript title: Environmental drivers of local abundance–mass scaling in soil animal communities

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Bibliographic information: Antunes A.C., Gauzens B., Brose U., Potapov A.M., Jochum M., Santini L., Eisenhauer N., Ferlian O., Cesarz S., Scheu S., Hirt M.R. Environmental drivers of local abundance–mass scaling in soil animal communities. *Oikos* 2022(2): e09735. Available from: <https://doi.org/10.1111/oik.09735>

The candidate is (Please tick the appropriate box.)

First author, Co-first author, Corresponding author, Co-author.

Status (if not published; "submitted for publication", "in preparation".):

Authors' contributions (in %) to the given categories of the publication

Author	Conceptual	Data analysis	Writing the manuscript	Provision of material (data)
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Benoit Gauzens	10%	15%	5%	0%
Ulrich Brose	10%	5%	20%	20%
Myriam Hirt	40%	30%	20%	0%
Others	0%	0%	0%	80%
Total:	100%	100%	100%	100%

Research article

Environmental drivers of local abundance–mass scaling in soil animal communities

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Oikos

2022: e09735

doi: 10.1111/oik.09735

Subject Editor: Richard Michalet

Editor-in-Chief:

Gerlinde B. De Deyn

Accepted 11 September 2022



The relationship between species' body masses and densities is strongly conserved around a three-quarter power law when pooling data across communities. However, studies of local within-community relationships have revealed major deviations from this general pattern, which has profound implications for their stability and functioning. Despite multiple contributions of soil communities to people, there is limited knowledge on the drivers of body mass–abundance relationships in these communities. We compiled a dataset comprising 155 soil–animal communities across four countries (Canada, Germany, Indonesia, USA), all sampled using the same methodology. We tested if variation in local climatic and edaphic conditions drives differences in local body mass–abundance scaling relationships. We found substantial variation in the slopes of this power-law relationship across local communities. Structural equation modeling showed that soil temperature and water content have a positive and negative net effect, respectively, on soil communities. These effects are mediated by changes in local edaphic conditions (soil pH and carbon content) and the body-mass range of the communities. These results highlight ways in which alterations of soil climatic and edaphic conditions interactively impact the distribution of abundance between populations of small and large animals. These quantitative mechanistic relationships facilitate our understanding of how global changes in environmental conditions, such as temperature and precipitation, will affect community–abundance distributions and thus the stability and functioning of soil–animal communities.

Keywords: body mass, density, invertebrates, precipitation, temperature

Introduction

Global alterations in environmental conditions are expected to have severe impacts on species communities and their contribution to our society (IPBES 2019). In



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particular, soil–animal communities have important functions in many of nature's contributions to people (NCP), including the decomposition of dead organic material, the recycling of nutrients, carbon sequestration and pest control (Blankinship et al. 2011, Bardgett and Van Der Putten 2014, Pereira et al. 2018). Many of these contributions can be quantified using fluxes of energy and material through the food webs, which strongly depend on both the distribution of body masses (i.e. the weight of an individual) and abundances (no. of individuals per unit area) across species (De Ruiter et al. 1995, Neutel et al. 2002, Barnes et al. 2016, 2018, Jochum et al. 2021a). Therefore, fluctuations in the community composition and species' relative densities in soil communities affect the flux of energy through the trophic levels (Schwarz et al. 2017) and, consequently, trophic multifunctionality (Potapov et al. 2019). Despite increasing evidence of direct effects of global warming and altered precipitation on soil biota (Blankinship et al. 2011, Yin et al. 2020), we know little about how these changes in environmental conditions modify the distributions of body masses and abundances within communities, which have strong indirect effects on ecosystem stability and functioning (Winfree et al. 2015, Wang and Brose 2018, Potapov et al. 2019, 2021). This knowledge gap hampers our ability to predict future NCP of soil communities.

Body size is a fundamental trait that regulates species' biological rates, such as metabolism, biomass production and feeding, and thus ultimately abundances (Peters and Wassenberg 1983, Woodward et al. 2005, White et al. 2007). Generally, the body mass–abundance relationship is very consistently described, with density (N) decreasing with population-level body mass (M) following a negative three-quarter power law (Damuth 1981, 1987, Allen et al. 2002). Four body mass–abundance patterns are described in the literature: 1) global size–density relationship (GSDR) pooling data to obtain one relationship at global scale, 2) cross-community scaling relationship (CCSR) pooling data to obtain one relationship for a set of communities, 3) local size–density relationship (LSDR) estimating one relationship per local community and 4) individual size distribution (ISD) calculating abundances for size classes of individuals irrespective of species identity (White et al. 2007). Studies using global or cross-community datasets that aggregate body masses and abundances from different local communities have provided ample empirical support for this relationship (White et al. 2007, Hatton et al. 2019). However, studies describing this body mass–abundance relationship in local communities found deviations from the general negative three-quarter power-law scaling (Currie et al. 1993, Cyr et al. 1997, Cohen et al. 2003, Reuman et al. 2009, Gjon and Glazier 2020), possibly related to gradients of human impact (Munn et al. 2013, Santini and Isaac 2021). This variation implies that local factors can modify the globally stable distribution of abundances across the size classes of species and therefore change local community structures, energy flux and NCP. Addressing the effect of environmental conditions on the local body mass–abundance structure of soil communities will improve our knowledge of the functioning

of these communities and consequently, predictions for future scenarios under different conditions.

There is extensive evidence for the general importance of environmental conditions, such as soil temperature, carbon content or litter stoichiometry, for soil–animal abundances at different spatial scales (Ehnes et al. 2014, Ott et al. 2014, Phillips et al. 2019, Johnston and Sibly 2020). As these studies lump data across individual communities to derive a single body mass–abundance scaling relationship, we still know little about how these factors drive the scaling relationships within local communities, as described, for example, by the slope of the relationship. Yet, this is critical to understand how changes in the environment affect the biomass distribution in communities and thereby ultimately the provision of ecosystem functions. Few comparisons of body mass–abundance slopes among soil communities showed variation depending on land-use types, soil acidity and stoichiometry, and the communities' range in body masses (Mulder and Elser 2009, Ulrich et al. 2015). However, two important aspects of local abundance–mass relationships have remained untapped: 1) effects of climatic variables such as temperature and 2) the relative importance of direct and indirect pathways of environmental variables on the local body abundance–mass relationships.

We addressed this topic by synthesizing the so-far largest dataset on abundances and body masses in 155 soil invertebrate communities across different continents (Canada, Germany, Indonesia, USA). Inconsistent sampling methods at different sites may affect the body mass–abundance relationships, mainly due to differences in species density estimation (Currie et al. 1993). For that reason, all local communities were sampled using the similar methodologies to assess meso- and macrofauna (soil invertebrates in the body size range from ca 0.5 mm to ca 5 cm), and the resulting body mass–abundance relationships are community-specific. We hypothesized that soil temperature and soil water content, which are strongly dependent on climatic factors, have a major impact on body mass–abundance relationships in local soil communities (Johnston and Sibly 2020). We expected that these environmental variables exert a direct effect on edaphic conditions, such as soil pH and soil carbon content (Onwuka 2018, Hartley et al. 2021), thereby indirectly affecting the slopes of the local body mass–abundance relationships. Additionally, we also expected indirect effects on the body abundance–mass slopes mediated via changes in the body-mass range realized in the local communities (Ulrich et al. 2015). Overall, our study thus aims at disentangling the direct and indirect pathways of how climatic and edaphic conditions affect the local distribution of abundances across size classes of soil animals.

Material and methods

Study sites

We investigated forest soil invertebrate communities from four globally-distributed geographic locations covering

diverse environmental conditions (Fig. 1). We compiled data from three large-scale projects: 1) the biodiversity exploratories project is located in the south-west, center and north-east of Germany (Fischer et al. 2010). A total of 45 plots were sampled between 2008 and 2011. The habitats comprise beech and coniferous forest sites, and different land-use types: from intensively managed coniferous monocultures to nearly natural beech forests (see Ott et al. 2014 for a detailed description). The mean percentage of water content in the soil is 28% (in wet weight) and the mean annual soil temperature is 6.6°C. 2) The ECOWORM project was conducted across four northern North American forests in Canada and the USA between 2016 and 2017 (Eisenhauer et al. 2019), and a total of 80 plots were sampled. The forests in Canada (Barrier Lake North, Barrier Lake South and Bull Creek Hills) are situated in the Canadian Rocky Mountains, Kananaskis Valley, and are dominated by aspen tree species. The mean soil water content and temperature are 31% and 5.4°C, respectively. The US forest is located in northern Minnesota and has a mean soil water content of 26%, and a mean soil temperature of 8.1°C. The sites are covered by mesic forests and are dominated by sugar maple species. 3) 30 research plots of the

collaborative German–Indonesian research project CRC990/ EEFoRTS were set up in Jambi province in 2013, Sumatra, Indonesia (Drescher et al. 2016); the sites cover different land-use systems, from rainforest to monoculture rubber and oil palm plantations. Mean soil water content was 40% and mean soil temperature 24.6°C. A detailed description of the sampling methods applied can be found in the original studies (Ott et al. 2014, for sites in Germany, Barnes et al. 2014, Potapov et al. 2019, for sites in Indonesia, Jochum et al. 2021b, for sites in USA and Canada).

Sampling method

Soil samples were collected from litter and mineral soil layers from each study site. Standard sampling methods were applied in all study sites. For assessing the mesofauna, small soil cores and soil quadrats (16 × 16 cm, 5 cm depth) were taken followed by heat extraction. For assessing the macrofauna, sieving of leaf litter (0.5 m²), large soil cores (20-centimeter diameter) with heat extraction, and mustard extraction (0.5 m², only if necessary to cover deep-burrowing species) were conducted. Invertebrates were either identified to the

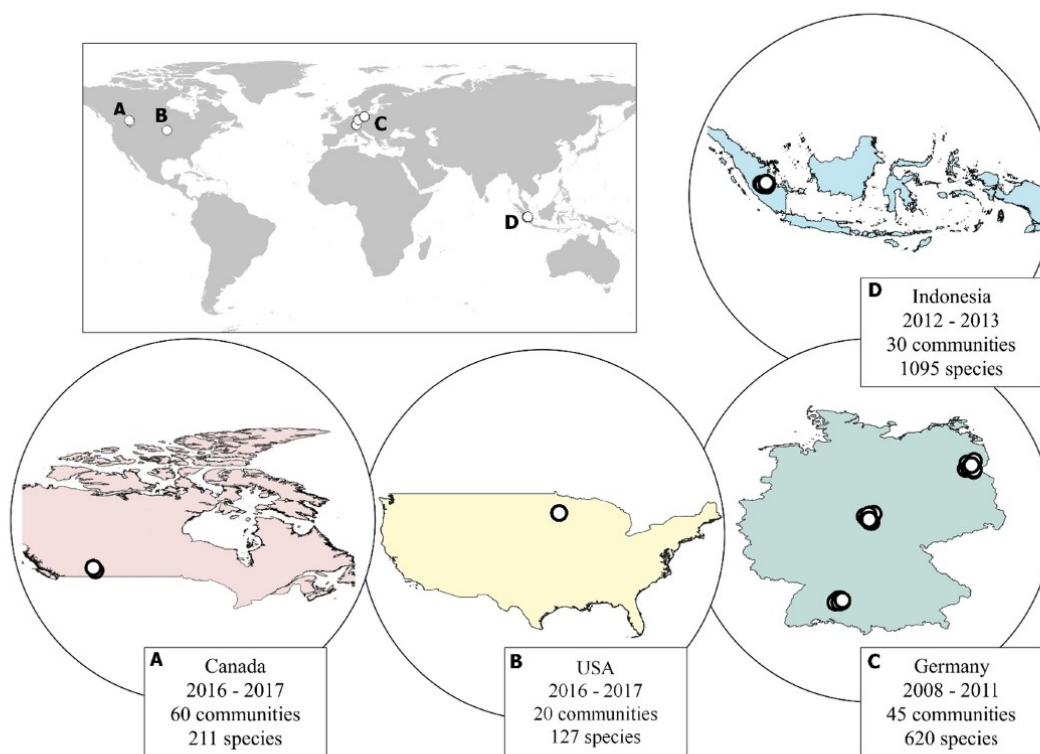


Figure 1. Distribution of study sites where 155 local soil communities were sampled to assess the site-specific body mass–abundance relationships.

species level or classified as morphospecies. A detailed description of sampling methods at each site is provided in the Supporting information. The respective methods provide a representative sample of the soil meso- and macrofauna community. Species abundances, population body masses and the average body masses were calculated for each community (i.e. plot). Abundances were standardized and expressed as (individuals m^{-2}). For sites covering different sampling years, we averaged the abundances across sampling dates. Despite the three-dimensionality of the soil habitat, most of the animals are concentrated in the litter and topsoil; therefore, we calculated the abundances in relation to the surface area, according to the conventionally used approach (Petersen and Luxton 1982, Ehnes et al. 2014).

Environmental factors

We used the georeferences of the communities' location and study year unit to extract soil annual mean temperature at a 1-km² resolution for 0–5 cm soil depth (Lembrechts et al. 2022). Additionally, other edaphic variables were used from the respective projects for each community: soil pH was measured using a digital pH meter, in CaCl₂; water content in the soil was measured by comparing masses of dry and wet soil samples and expressed in % fresh weight; and carbon content was measured in the soil dry weight; Indonesia, USA and Canada: elemental analyser; Germany: automated CHNSO analyser. Data have been reported in detail in Ott et al. (2014), for Germany, Krashevskaya et al. (2015), for Indonesia and Jochum et al. (2021b) for USA and Canada sites.

Statistical analyses

Prior to analyses, we excluded all larval or juvenile individuals from the data due to the complexity of identification to the species or genus level for juveniles. Subsequently, body mass and species–abundance data were log₁₀-transformed to satisfy the assumptions of linearity of the analyses. After this log-transformation, the slope of their linear relationship equals the exponent of the power–law relationship in the untransformed data. In preparation of our further analyses, we independently ran linear regressions of the dependence of log₁₀ abundance on log₁₀ body mass for each of the 155 communities using the `lm` function in R (<www.r-project.org>). This resulted in a secondary dataset containing the 155 slopes of the local, within-community body mass–abundance relationships. Subsequently, we will refer to this data as the 'slopes'. Additionally, we also calculated the log₁₀ body-mass range for each community as the difference between the maximum and minimum body masses. By analyzing the local body mass–abundance slopes, we can address the drivers of variation in slopes across communities to gain an understanding of how they affect the community–abundance distribution. This is a different perspective compared to the global size–density relationship (GSDR) approach described by White et al. (2007), where data from all local sites are pooled together and the number of data points per site gains much more importance.

Thereafter, we used the 'piecewise' approach, based on confirmatory path analysis, to structural equation modeling (SEM) (Lefcheck 2016) to test the relative importance of the environmental variables and the body-mass range for the slopes of the local body mass–abundance relationships. This provides a mechanistic understanding of the direct and indirect pathways by which environmental conditions affect local body mass–abundance slopes and thus the distribution of abundances across small and large animals. We fitted the estimates within our SEM using linear mixed effects models (Supporting information), and we accounted for potential spatial autocorrelation by using the correlation function from `nlme` package (Pinheiro et al. 2020). This type of spatial autocorrelation is only available for mixed-effects models that require a random effect variable. As we did not have any random effects in our models, we used a randomly parameterized dummy variable. The initial model included the communities' body-mass range, soil–carbon content and soil pH as direct effects on the slope, the soil temperature and soil water content as indirect effects, mediated by the local edaphic conditions and species body-mass range. While most of our prior hypotheses were confirmed, the test of direct separation indicated a missing causal path from the soil temperature to the slope. The adequacy of this final model (after adding the missing path) was determined by non-significant χ^2 tests ($p > 0.05$).

As a sensitivity analysis, we also tested if other environmental characteristics have an impact on the abundance–mass slopes. In addition to the independent variables of our SEM analysis (soil temperature, soil water content, soil carbon content, soil pH and body-mass range), we also included additional independent variables (land-use intensity, human footprint index, litter layer mass and depth, C:N rate in the soil; see the Supporting information for detailed description of variables) in a linear mixed effects model. This analysis indicated that none of the additional independent variables contributes to explaining variation in slopes.

To facilitate comparisons with prior studies, we also added an analysis of the general body mass–abundance relationship in a dataset pooling all local communities. This analysis shows the relative role of environmental and edaphic drivers (all independent variables as described in paragraph above) for species densities (dependent variable of the model instead of the slopes, Supporting information). All statistical analyses were performed using R ver. 4.0.0 (<www.r-project.org>). We used `lme4` ver. 1.1-30 (Bates et al. 2015) and the `piecewiseSEM` ver. 2.1.0 (Lefcheck, 2016) package to perform the structural equation model.

Results

In the 155 local communities analyzed, body mass ranged from 0.000267 mg (*Liochthonius* sp. (Brachychthoniidae), Indonesia) to 6055 mg (*Lumbricus terrestris* (Lumbricidae), Germany) and species abundance ranged from 0.33 (*Uroballus koponeni* (Salticidae), *Carrhotus sannio* (Salticidae), Indonesia,

among others) to 138 448 individuals m^{-2} (*Micropoppia minus* (Ophiidae), Germany). We found substantial variation in body mass–abundance slopes across the 155 local scaling relationships, ranging from -1.23 to -0.29 (Fig. 2). Across all of the local communities' slopes concentrated around the mean of -0.759 (Fig. 2, $SD=0.158$, median = -0.770) (for R^2 and p -values of the local community scaling relationships, and graphical description of the body mass–abundance for some communities, see the Supporting information). Together, these findings indicate a stable global scaling relationship whose slope can be strongly modified locally.

Our SEM model adequately fit the data (Fisher's $C=2.412$; p -value = 0.661 ; effects of spatial autocorrelation have been accounted for in the model, Fig. 3) and reveals direct positive effects of soil pH (path coefficient = 0.18), soil temperature (path coefficient = 0.21) and the body mass range (path coefficient = 0.52) as well as a direct negative effect of soil carbon content on the slope (path coefficient = -0.26). Positive and negative effects on the slope indicate shallower and steeper body mass–abundance–scaling relationships, respectively. Additionally, the SEM highlights important indirect effects of soil temperature (overall compound coefficient = 0.09) and water content (overall compound coefficient = -0.07) on the slope. Soil water content increased the pH as well as the carbon content of the soil. Higher soil pH in turn had a positive effect on the slope. In contrast, higher carbon content decreased the slope value. Consequently, soil water content had an indirect positive effect on the slope mediated by pH (compound path coefficient = 0.03) and an indirect negative effect on the slope mediated by carbon content (compound path coefficient = -0.10). Soil temperature decreased soil pH and carbon content, as well as the body mass range. Hence, it has indirect negative effects on the slope via pH (compound path coefficient = -0.12) and the body mass

range (compound path coefficient = -0.16), and an indirect positive effect via carbon content (compound path coefficient = 0.18). Additionally, the soil temperature has a direct positive effect on the slope (path coefficient = 0.21). Overall, our SEM analysis highlighted that the body mass range of the local communities has the strongest direct effect on the slope of the body mass–abundance relationship and reveals that soil temperature has much stronger indirect effects on the slope than soil water content.

Discussion

Our study disentangled the direct and indirect effects of environmental conditions on the body mass–abundance relationships of local soil–animal communities. Despite a global average abundance–mass scaling slope of -0.759 , in line with theoretical expectations (Damuth 1981, 1987, White et al. 2007) and prior empirical analyses of global relationships across communities (White et al. 2007), we found substantial variation in these slopes across the 155 communities when analyzed separately (ranging between -1.23 and -0.29). Consistent with our hypothesis, we found that this variation in slopes can be explained by climatic conditions (soil water content and soil temperature) that exert strong direct and indirect effects via local edaphic (soil carbon content and soil pH) conditions and the body-mass range of the community. These results reinforce the importance of soil temperature and soil water content as strong environmental drivers of soil community structure (Phillips et al. 2019, van den Hoogen et al. 2019, Johnston and Sibly 2020), and illustrate how they influence the body mass–abundance structure of soil communities in concert with edaphic conditions. Our quantifications of these direct and indirect effects provide an important first step towards a mechanistic understanding of how soil communities respond to different environmental and edaphic conditions. These results also facilitate our understanding regarding future climatic scenarios, as shifts in the body-mass ranges and the altered distribution of abundances across size classes can have strong effects on population dynamics, community stability and ecosystem functioning (Emmerson 2012, Brose et al. 2017a).

Our analysis revealed that the body mass range of the community is the strongest source of variation in the slopes of the body mass–abundance relationship of local communities (Fig. 2). Research has shown that slope values vary widely when a narrow range of body mass is considered (White et al. 2007, Hayward et al. 2010). However, these narrow body mass ranges are usually associated with smaller geographic scales or incomplete taxonomic samples, and may thus yield an artifactual component in the study's results, mainly because it could indicate that the local communities are only partially included due to differences in sampling across sites. Moreover, even in cases where rare populations are under-represented in global analysis, that does not exactly bias the estimated slope (Currie 1993), especially considering that our study used directly measured data and not literature-based

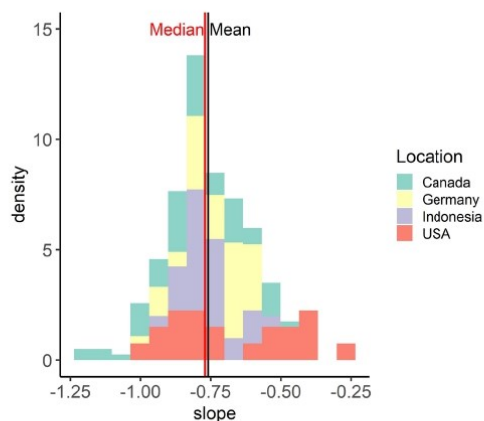


Figure 2. Frequency distribution of the slopes of the relationship between \log_{10} body mass and \log_{10} abundance for 155 local forest communities across three continents (mean = -0.759 , $SD=0.158$, median = -0.770).

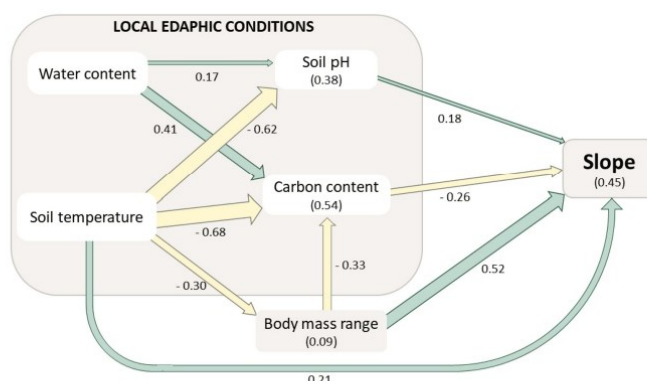


Figure 3. Structural equation model showing the direct and indirect effects of environmental variables on the local body mass–abundance slopes (Fisher’s $C=2.412$; p -value= 0.661). Green and yellow arrows denote significant positive and negative effects respectively. The widths of arrows reflect standardized path coefficients (i.e. the relative strength of the individual effects) and indicate each predictor’s relative effect sizes. Numbers in parentheses inside the boxes indicate R^2 values. Spatial autocorrelation effects are accounted for by the model.

information to estimate the local slopes. By contrast, our study comprised data of comprehensive belowground invertebrate communities that have all been sampled by the same combination of methods. Therefore, sampling biases are unlikely to be responsible for the variance in local body-mass ranges across communities and its effect on the body mass–abundance scaling slopes in our study. Instead, these ranges vary with shifts in the minima and maxima of the body masses in the communities (Supporting information).

Our study also showed that the edaphic conditions, soil pH and carbon content, have important direct effects on the slopes of the body mass–abundance relationships. Both edaphic factors have been shown to be important factors driving the general abundance of soil animals (Johnston and Sibly 2020). We show that a higher carbon content in the soil leads to steeper, more negative slopes, indicating relatively higher abundances of small compared to large animals. This matches research showing that soil systems with higher carbon contents are usually dominated by small soil animals, while the opposite is true for larger species (e.g. Chilopoda, Coleoptera, Clitellata) that occur in soils with lower carbon content (Johnston and Sibly 2020). Additionally, we found that increasing soil pH (i.e. soils becoming less acidic) leads to shallower slopes and thus benefits the large species in terms of abundance. Soil acidity is often associated with multiple nutrient availability (Binkley and Vitousek 2000), and the species’ optimal pH ranges differ across phylogenetic groups. The soil macrofauna is usually restricted to soils with pH values above 3.5. Under the impact of acidification, soil-fauna individuals move downwards trying to mitigate the surface stress, altering the community composition and impacting ecosystem functions (e.g. organic-matter decomposition and greenhouse-gas emissions) (Wei et al. 2017). Catalase activity, the enzyme responsible for decomposing hydrogen peroxide into water and oxygen, decreases significantly with pH 6.5–4.0. The malfunction of this enzyme is lethal

for organisms due to animal intoxication from the accumulation of H_2O_2 , and injury of the cell structure membrane (Vitória et al. 2001). These findings of prior studies provide mechanistic explanations for our result that abundance–mass slopes are more steeply negative at the lower soil pH of the ecosystem. Overall, our study thus extends previous findings on the importance of pH and carbon content for soil animals by quantifying the distribution of abundance across different size classes.

We showed that soil temperature has a direct positive effect on the slope, which can be translated into a shift in relative densities from smaller to larger animals. The influence of soil temperature is directly related to species metabolism and resource requirements, which vary depending on the species size (Allen et al. 2002). An increase in temperature has a greater impact on smaller species, due to their relatively higher metabolic demands with increasing temperature, in comparison to larger species (Johnston and Sibly 2018, 2020). When experiencing higher metabolic demands, species are expected to increase resource uptake or, if this is not possible, exhibit declines in their population densities. Consistent with our results, Johnston and Sibly (2020) found that, under higher temperatures, smaller soil animal abundances declined, while, under low temperatures, larger soil animals experienced a decrease in their abundances. Our results extend this finding to within-community patterns and highlight that warming can cause a substantial reshuffling of abundance and thus biomass to the benefit of large species.

Furthermore, we show for the first time that the climatic variables soil temperature and water content exert important indirect effects on the local body mass–abundance scaling relationships. First, temperature leads to steeper slopes by decreasing the body mass range. While body masses generally decrease with warming, the maxima of body masses decrease more steeply than the minima, which is responsible for the decrease in range (Supporting information). Second,

temperature and water content both indirectly affect the body mass–abundance relationship of the communities by influencing soil pH and carbon content. Soil temperature is known to have a negative effect on the carbon content in the soil (Schimel et al. 1994), mainly by increasing soil carbon decomposition rates (Smith et al. 2008). Increasing soil temperature acts as the activation energy for the processes that effectively increase the carbon mineralization rate (Ågren and Wetterstedt 2007). In this context, rising temperatures will constrain the abundance of smaller species also by decreasing the carbon content in the soil. Overall, we showed that the dominant effects of both soil temperature and water content on the biomass distribution across size classes within local communities are indirectly mediated via changes in edaphic conditions and the body-mass range realized in the community.

Conclusions

Our study confirmed a three-quarter power-law scaling of population abundance with body mass when averaged across soil animal communities of four locations of the globe. However, we also found substantial variation in the power-law exponents along environmental gradients. Specifically, we addressed the consequences of variation in soil temperature and water content. Our study showed a net positive effect of soil temperature on the slope of the body mass–abundance relationship, which is mainly due to the combination of the direct positive effect with the indirect positive effect via soil carbon content and the indirect negative effect via body mass range. This implies that warming generates a less negative slope, resulting in a relative redistribution of biomass from small to large species. Furthermore, the negative indirect effect of soil water content via soil carbon content is roughly three times stronger than the positive indirect effect via soil pH, which yields a negative net effect on the body mass–abundance slopes. This implies that increasing soil water content yields steeper, more negative slopes and thus favors small over large species in the communities. Together, these results reveal the important indirect constraints of soil-climatic variables on the distribution of abundances across size classes, which explains the substantial variation in local body mass–abundance relationships.

Future climate projections suggest a scenario of decreasing precipitation rates and increasing temperatures for most global regions (IPCC 2022). Therefore, lower contents of water in the soils and increased soil temperatures are expected. In combination with our results, this implies that belowground communities will experience a shift in the biomass distribution from smaller to larger species, a reflex of the shallower slopes observed in this study. While our study also corroborates an overall decrease in average body mass with warming (Daufresne et al. 2009), our results suggest that abundance, and thus biomass distribution, is shifting from the smaller to the largest species in the community. Together, these findings imply that warming benefits the small when

analyzed across communities (i.e. the shift to lower body masses) but it also benefits the larger species within communities (shifts in biomass to the larger species of the community). Such increasing dominance of large species in the community has several implications, including the increasing top–down control as densities of large predators increase. Increasing densities of large predators with their high per capita feeding rate can be indicative of increasing feeding rates (Rall et al. 2012, Schneider et al. 2012), which yields higher interaction strength and energy fluxes through the food webs. An increased top–down control have the potential to destabilize community dynamics (Johnson et al. 2014, Jacquet et al. 2016, Wolkovich 2016, Brose et al. 2017b, Zhou et al. 2022). However, this could be offset by the generally stabilizing effect of large species on food-web dynamics (Brose et al. 2006, 2017b, Heckmann et al. 2012). Similarly, increases in the biomass of large species may promote ecosystem functioning at the base of the food web if maximum trophic levels and omnivore rates are increased (Schneider et al. 2012, Wang and Brose 2018, Wang et al. 2019). Interestingly, this suggests that integrating our findings on biomass distribution shifts with food-web approaches offers great potential for predicting the community-level consequences of future warming and drought.

Overall, our study revealed the complex interplay between soil temperature and soil water content and their effects on the body mass–abundance structure of soil communities, which facilitates future modeling approaches to predict the consequences of global change on soil communities and their functioning. Together, this will be an important step towards a mechanistic and predictive understanding of how soil community dynamics and functioning are expected to respond to global change.

Acknowledgements – We thank Vojsava Gjoni for discussing ideas with us. Open Access funding enabled and organized by Projekt DEAL.

Funding – We acknowledge funding by the ERA-Net BiodivERsA - Belmont Forum call (project FutureWeb); the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) project no. BR 2315/22-1; and project no. 192626868 – SFB 990 in the framework of the collaborative German–Indonesian research project CRC990/EFForTS; the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant no. 677232), the German Research Foundation (DFG) in the frame of the Gottfried Wilhelm Leibniz Prize. Further support came from the German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118), and by the DFG Gottfried Wilhelm Leibniz Prize to NE (Ei 862/29-1).

Conflict of interest – The authors declare no conflict of interest.

Author contributions

Ana Carolina Antunes: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Investigation (lead); Project administration (lead); Writing – original draft (equal); Writing – review and editing (lead). **Benoit**

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.2jm63xssm>> (Antunes et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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General Discussion

Humans shaped the Earth System and will continue altering the landscape, climate, biodiversity, the functioning of ecosystems and, ultimately, NCP provided. In my thesis, I dive into this theme and fill gaps in biodiversity data accessibility, knowledge of the consequences of human-induced modifications on biodiversity, evaluation of NCP capacities provided by biodiversity contribution, and availability of abundance data for invertebrates. In the first chapter of this thesis, I contribute to filling the gap on the scarcity of biodiversity data for the tropics, more specifically, by compiling camera trap data for the Amazon forest. Although tropical forests harbor the greatest species richness in the globe, biodiversity data is mostly concentrated in higher latitude regions (Collen et al. 2008). This disparity between tropical and temperate regions is mainly accounted for by insufficient funding, the absence of adequate infrastructure and equipment and political or social conflicts. Unfortunately, the lack of such data compromises the efficiency to describe biodiversity changes in the tropics, with serious implications for conservation. It is not uncommon that existing data are inaccessible, or available only in the form of theses or technical reports. In that way, collaborative approaches with local scientists are the best alternative to explore this type of information. The compilation of the dataset provided in **chapter 1** involved a collaboration between more than 150 researchers from 122 institutions and encompasses data from eight countries. This massive effort resulted in the compilation of the so far largest camera trap dataset for the Amazon forest. The database comprises data from 317 species (185 birds, 119 mammals and 13 reptiles), and most part of the surveys (59%) were conducted in Brazil. The dataset provides basic information about vertebrate species' presence, number of registers and other important details (e.g. presence of bait to attract species, sampling effort, camera trap brand and model), and can be used to investigate species responses to different variables (e.g. temperature, precipitation, or human pressure) on an Amazon scale.

Vertebrate species are key contributors to the ecosystem's functioning, and their loss might cause cascading effects. Therefore, **in chapter 2**, I use the data compiled in chapter 1 to study how anthropogenic impacts on the land affect species richness in the Amazon forest.

Species richness is a metric frequently used to measure biodiversity change, and can also be used in association with other community data (e.g. turnover of species) to identify shifts in communities over time, improving the mechanistic understanding of how biodiversity is changing. Given that the Amazon is well preserved in comparison to other areas of the globe, one might expect that its biodiversity has not yet been impacted by human actions. However, the analysis of our data shows that, for vertebrate communities, even low to moderate levels of human modifications have a significant negative impact on the richness of species. A few mechanisms are known to regulate species richness, including the availability of energy (limiting resources) in the system, which for many vertebrate species means plant availability (or vegetation cover), and a regional species pool to provide for potential species exchange and settlement (Brown et al. 2001). Together with deforestation, other anthropogenic disturbances are important drivers of land cover change in the Amazon forest, such as edge effects, timber extraction, fires and extreme droughts (Lapola et al. 2023). Moreover, increasing habitat fragmentation can lead to the isolation of systems, for example, patches of forests completely isolated by agricultural fields, that species are not able to cross. The size of these isolated fragments influences the richness of species, with smaller fragments able to shelter a limited number of species (Michalski and Peres 2007). Altogether, these human-induced modifications are leading to a decrease in vertebrate species richness, yet, it is important to mention here another result I found in my analysis: the relevance of biogeographical differences across the Amazon. There is a known east-western Amazon pattern on the gradient of species richness (Sales et al. 2017) that can be explained by different processes happening throughout the geological times, for example, the uplift of the Andes and barriers created by the rivers. The mechanistic explanation for this is complex and still debated, therefore this opens new doors for future studies to disentangle the relationships between macroecological patterns and human disturbances, and their impacts on biodiversity.

While in chapter 2 I focus on the threat human actions represent for biodiversity, in the third chapter I moved forward to comprehend human influences on the functioning of ecosystems and the associated NCP. For this, I needed to establish a link between biodiversity change, ecosystem functions and NCP. **In chapter 3**, I propose a new framework that integrates

different fields of Ecology (food web ecology, energy flux approaches and biodiversity modeling) to link biodiversity data and NCP capacity. The concept is based mainly on using specific ecosystem functions as proxies to access NCP. For example, seed dispersion is an essential NCP provided by many species, and it can be associated with the feeding link between the plant species (seed) and the predator (seed disperser) while also considering how abundant they are in the system. Once the link or proxy is defined, the next step is to quantify it. For that, we use metabolic theory to evaluate the amount of energy needed to support that ecosystem function, or, in other words, we calculate the energy flux through the links connecting species and trophic levels. Fluxes of energy are calculated based on the energy demand (metabolism) of the community or species, combined with the efficiency of resource assimilation and loss of energy to predation. Additionally, species' body size and environmental temperature are important information since smaller body sizes and higher temperatures increase the metabolic demand. Finally, the abundance of individuals is also needed to upscale the energy demand evaluation from species to community and ecosystems-level.

As I mentioned earlier in this thesis, the availability of biodiversity data is not homogeneous, therefore in many cases, the input data to proceed with the approach may become challenging to acquire. In the previous example of seed dispersion, data on the occurrence and abundance of the species, as well as the presence of interaction between plant-disperser is essential. In this case, if part of the data is not available, biodiversity models should be used to fill the gaps and predict missing biodiversity data (Pollock et al. 2020). In this chapter, I suggest 3 types of models that might be needed to estimate NCP through fluxes: species distribution models, abundance models and interaction models. Moreover, I provide a case study to illustrate how to apply the framework. The example evaluates and maps the biological control of the agricultural pest (common vole, *Microtus arvalis*) provided by vertebrate species in Europe, using as a proxy the top-down pressure of the predators on the prey (*M. arvalis*). Thus, this conceptual framework has the potential to explore different time and spatial scales, address species interactions, and incorporate climatic and land use variables, while assessing the vulnerability of NCP capacity to the anthropogenic crisis. Moreover, it might be a valuable tool connecting theoretical ecology and conservation planning.

When developing the framework, I realized that, although flexible and possible to apply to different contexts, for invertebrate communities, input abundance data could be hard to access. For vertebrate species, despite the scarcity of data on species abundance, allometric models were developed and can be used to fill gaps where there is no data available (Santini et al. 2018, 2022). For invertebrate species, those models were not developed until the moment. In **chapter 4**, I compiled a large dataset for invertebrate species and developed an allometric model to predict species abundance. The methods used to sample the individuals were consistent across the different studies compiled and, the final database comprises comprehensive belowground invertebrate communities, from four countries (Canada, Germany, Indonesia and the USA). Since abundance data may vary according to the methodology used, using standardized methods was important to guarantee that the results were comparable. Moreover, a large range of body sizes was examined, from meso to macrofauna species (0.000267 mg – *Liochthonius* sp. (Brachychthoniidae), Indonesia – to 6055 mg – *Lumbricus terrestris* (Lumbricidae), Germany. Although body size is a known trait to drive species abundance (due to its relationship with species metabolism, as explained earlier), I fitted a model that also includes other important variables that are known to affect the abundance of soil fauna, such as soil temperature, precipitation, land-use intensity, soil pH, the carbon content in the soil, and other edaphic properties.

Species traits (e.g. body size) and environmental conditions play an important role in determining species abundance. In Ecology, body size-abundance relationships have been extensively studied, and follow a general pattern across communities in which smaller species will be more abundant, while larger ones tend to be less abundant (Damuth 1981, 1987, Allen et al. 2002). However, this pattern is not so clear within communities, where the relationship varies and can show the opposite trend (White et al. 2007). In chapter 4, I used the compiled database also to explore how environmental and edaphic properties influence the body-mass abundance relationship and, consequently, the distribution of abundance between invertebrate soil communities. I was excited to notice that, following the theoretical expectations, the average abundance-mass scaling slope across our soil communities was -0.75. Yet, as I also expected, there was a considerable variation within the slope values across the 155

communities studied (ranging between -1.23 and -0.29). Respectively, soil temperature and water content in the soil (a variable related to precipitation rate) have positive and negative effects on the belowground communities we analyzed, mainly mediated by changes in local edaphic conditions (soil pH and the content of carbon in the soil). Temperature positively affects the slope of the relationship, which can be translated as an increase in the abundance of larger species and a decrease in smaller ones under increasing temperatures. The explanation for this is possibly associated with the metabolic demand of the species, and their energy requirements, which increase under higher temperatures, impacting smaller species strongly in comparison to larger ones (Johnston and Sibly 2018, 2020). The water content in the soil directly influences the pH of the soil and the carbon content, important factors known to drive the abundance of soil animals (Johnston and Sibly 2020). For example, because of their physiological adaptations, larger species are usually restricted to less acidic soils, with pH values above 3.5. Moreover, besides gaining access to a model that predicts invertebrate abundances, in the last chapter of my thesis, I also explore how variation in soil-climatic variables might shift the distribution of abundances across size classes in belowground invertebrate communities.

Considering the current scenario of climate and land use change we are witnessing, I believe the research I present in this thesis can help address the mechanisms species are developing to survive these changes. The use of biodiversity data is essential to understand the drivers of biodiversity loss, but also to estimate changes in biodiversity-related NCP capacity, as it serves as the primary information source to estimate energy fluxes. Nevertheless, these data might not be always available, so biodiversity models (e.g. allometric models to estimate species abundance) are highly valuable. Overall, I explore and move forward to better understand the effects human actions have on biodiversity, ecosystem functioning and the provision of NCP, from belowground to aboveground ecosystems.

Outlook

Biodiversity has many positive effects on the provision and maintenance of ecosystem functions. Although the scenario might be alarming, there are still alternatives to prevent further loss of biodiversity and deeper impacts on the provision of NCP. As I outlined previously in this thesis, a big challenge when studying changes in biodiversity is exactly the lack or scarcity of biodiversity data for specific areas of the globe and taxonomic groups. Thereby, I aim to continue working on filling this gap in my future research, either by compiling existing datasets or organizing and implementing fieldwork campaigns to sample new areas. The Amazon Camtrap (first chapter of this thesis) is part of a bigger initiative that I greatly admire and would be happy to help expand in the future. In Brazil, the *Cerrado* is a vast tropical and subtropical savannah biome that is deeply threatened by land use change (mainly agriculture and pasture). Considering that this is a global biodiversity hotspot, this ecosystem remains understudied in terms of biodiversity change and potential human impacts on ecosystem functioning. In this context, compiling available data for the biome would be a great advance. A deep literature search and a net of collaborations between researchers in the area would allow for gathering valuable data on community composition and distribution of plant and/ or animal species and allow a deeper understanding of how biodiversity changes. Moreover, with standardized biodiversity data from the Amazon forest and Cerrado, large spatial-scale analyses could be developed, for example by comparing the vulnerabilities of the two biomes to climate and land use change. I would be very interested in analyzing biodiversity dynamics and, using the framework proposed here, investigate how it reflects the potential to supply NCP across space and biomes.

As I have proposed a new framework to evaluate biodiversity-related NCP supply, another next step is to apply this approach to real scenarios. There are many possibilities to do that, but the one I am already involved with is the European scenario. In the study case developed for my third chapter, I evaluated biocontrol through predation over agricultural fields in the European continent. I would first like to improve this measurement, for example by considering only the agricultural areas for the energy fluxes calculation. Although the species *M. arvalis* is common to almost the entire continent, they are considered pests only where the

land is covered by agriculture. Furthermore, I will include forecast predictions for the supply of this pest control-NCP, by re-calculating the associated energy fluxes considering different future predictions of climatic scenarios for Europe. By comparing present and future predictions for this NCP supply, we assess how environmental conditions might affect pest control by vertebrate species, and identify areas at higher risk of the NCP not being delivered. By identifying the areas, I would be curious to disentangle the mechanisms driving the decrease in the supply of pest control in specific regions. For example, it could be driven by alterations in the density relation between predator and prey, or by the direct effect of environmental changes (such as temperature and precipitation) on the food supply of the prey (*M. arvalis*). Moreover, this NCP framework in a general way can generate information related to the vulnerability of NCP supply, and help identify areas to be considered as priorities for conservation.

In my thesis, I analyze some of the influence human actions have on biodiversity and propose a way to evaluate and link the changes in biodiversity to ecosystem functionality and the capacity of an ecosystem to provide biodiversity-related NCP. Elucidating the threats to biodiversity together with its ecological implications is an essential step to cope with conservation challenges and reshape human effects on the Earth System. However, generating information has to be part of a larger initiative. Conservation ecology and biodiversity preservation involve a broader context and many different actors, including civil society, stakeholders, and policymakers. When nature is seen only as an explorable natural resource, biodiversity becomes commodified. Therefore, a deep civilizational change, with coordinated international action, is crucial to overcome the obstacles of global change (Fernandes, 2020). As a Latin American woman ecologist, I believe giving voice and autonomy to “minorities” and underrepresented groups is also part of the solution. In that way, I’m glad to see several initiatives recognizing the need for a more inclusive system. For example, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), a joint global effort by governments, academia, and civil society emphasizes the importance of incorporating local and indigenous knowledge into environmental assessment frameworks, environmental governance and associated policies. Sustainable pathways vary according to the

regional context (which reinforces the need for inclusive participation of different actors), and providing information on each context (for example by compiling biodiversity data or evaluating critical NCP) is key to moving forward with conservation actions.

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Appendix A: Supplementary – Chapter 1

AMAZONIA CAMTRAP: A dataset of mammal, bird, and reptile species recorded with camera traps in the Amazon forest

INTRODUCTION

The Amazon is the largest and most biodiverse tropical rainforest on Earth, with 34 million people (RAISG 2009; ARA 2011), and half of the stored terrestrial carbon from tropical forests on the planet, a total of 100 billion tons of carbon in biomass (Feldpausch et al. 2012). This hyper-diverse region has more than 15,000 tree species (ter Steege et al. 2020) distributed in a variety of habitats, such as savannas, white sand forests (campinaranas), flooded and unflooded forests (Maretti et al. 2014). Intersecting these habitats, the Amazon river is the world's largest river basin in length and volume (Venticinque et al. 2016), holding 12 to 20% of global freshwater (Goulding et al. 2003). This complex and immense mosaic of habitats shelters more than 5520 vertebrate species (Da Silva, Rylands, and Da Fonseca 2005), and together, provides the world with essential ecosystem services (Fearnside 2018; Strand et al. 2018).

Despite the importance of this forest, the Amazon is currently facing the highest rates of deforestation and non-natural fire events in the last decade (Escobar 2019; INPE 2020). Increased human pressure comes on many fronts, such as land-grabbing, illegal mining, logging, infrastructure projects (e.g. roads and dams), and agricultural expansion (Richards, Walker, and Arima 2014; Lees et al. 2016; Sonter et al. 2017; Azevedo-Ramos and Moutinho 2018; Brancalion et al. 2018; Fearnside 2017). Despite numerous NGOs and scientists' warnings (Ferrante and Fearnside 2018; Lovejoy and Nobre 2018), few governmental actions have been taken to mitigate the impacts of these anthropogenic pressures. Moreover, some politicians seem to have opposing and contrary agenda, encouraging resource exploitation in Protected Areas (PAs), including the invasion of indigenous lands (ISA 2020; Andrade, Ferrante, and Fearnside 2021) and discrediting scientific information (Escobar 2019).

In this context, gathering data and generating scientific information on species occurrence and distribution patterns are pressing needs (Maestre et al. 2012) to support effective conservation measures (Jambari et al. 2019; De Marco et al. 2020). Among these, vertebrates play a crucial role in maintaining the essential ecosystem services provided by the Amazon forest (Brockhoff et al. 2017). Herbivores contribute to the dispersal of a wide variety of plant species (Moreira-Ramírez et al. 2016; Regolin et al. 2020), so supporting both natural forest regeneration (Paolucci et al. 2019) and the long-term maintenance of above-ground carbon storage (Peres et al. 2016). Predators such as jaguars provide top-down pressure on their prey species, thereby regulating herbivore populations and preventing overexploitation of plants (Terborgh et al. 2001). Nevertheless, scientific knowledge of vertebrate species richness and composition is strongly spatially biased (Oliveira et al. 2016), and valuable data are usually scattered within peer-reviewed publications or grey literature, or in many cases neither published nor accessible.

Over the past two decades, the increasing use of camera traps for wildlife detection and monitoring has expanded our understanding of vertebrate species distributions and ecological relationships (O'Connell, Nichols, and Karanth 2011; Ahumada, Hurtado, and Lizcano 2013). Camera trapping is a non-invasive and cost-effective survey method that allows the detection of low density and elusive species that might otherwise be underestimated when monitoring studies and inventories using other methods are applied (Ahumada et al. 2011). Furthermore, studies using different methods to monitor biodiversity are usually hard to compare and integrate for broader biodiversity analysis (Steenweg et al. 2017). In this sense, camera traps have the potential to provide a more standardized tool for monitoring terrestrial vertebrate biodiversity (Steenweg et al. 2017), because human influence and error are limited to placement and

maintenance of traps, evaluation of model effectiveness, and identification of the photographs (Ahumada et al. 2013). Despite such benefits, camera trap data is still fragmented and unavailable for many areas of the world (Ahumada et al. 2020). There is a current need for more collaborative networks, to increase coordination of camera trap surveys, and to make ecological data more freely available.

Considering the importance of the Amazon forest and the immediate threat to its ecosystems and species, this study aims to unify and summarize existing camera trap data by creating a large-scale repository of such data from within the Amazon. In this AMAZONIA CAMTRAP data paper, we summarize information from camera trap inventories conducted in the Amazon forest, including published and raw and unpublished data. This study represents the largest camera trap dataset ever organized for the Amazon forest.

METADATA

CLASS I – DATA SET DESCRIPTORS

A. Data set identity

Title: AMAZONIA CAMTRAP: *A dataset of mammal, bird, and reptile species recorded with camera traps in the Amazon forest*

B. Data set and metadata identification code

Data S1.zip

Metadata S1

C. Data set description

Originators:

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Abstract:

The Amazon forest has the highest biodiversity on earth. However, information on Amazonian vertebrate diversity is still deficient and scattered across the published, peer-reviewed and grey literature and in unpublished raw data. Camera traps are an effective non-invasive method of surveying vertebrates, applicable to different scales of time and space. In this study, we organized and standardized camera trap records from different Amazon regions to compile the most extensive dataset of inventories of mammal, bird and reptile species ever assembled for the area. The complete dataset comprises 154,123 records of 317 species (185

birds, 119 mammals and 13 reptiles) gathered from surveys from the Amazonian portion of eight countries (Brazil, Bolivia, Colombia, Ecuador, French Guiana, Peru, Suriname and Venezuela). The most frequently recorded species per taxa were: mammals - *Cuniculus paca* (11,907 records); birds - *Pauxi tuberosa* (3,713 records); and reptiles - *Tupinambis teguixin* (716 records). The information detailed in this data paper opens-up opportunities for new ecological studies at different spatial and temporal scales, allowing for a more accurate evaluation of the effects of habitat loss, fragmentation, climate change and other human-mediated defaunation processes in one of the most important and threatened tropical environments in the world. The dataset is not copyright restricted; please cite this data-paper when using its data in publications and we also request that researchers and educators inform us of how they are using this data.

D: Keywords

Data paper, Vertebrates, Tropical forest, Amazonia

E: Description

The complete database includes camera trap data from 43 data sets, from 155 study areas, and contains a total of 154,123 records from 317 species (185 birds, 119 mammals and 13 reptiles). However, for our analysis, we considered only records from studies conducted within the Amazon forest limits (as defined by RAISG 2020 - Fig. 1) and where animals could be identified to the species level.

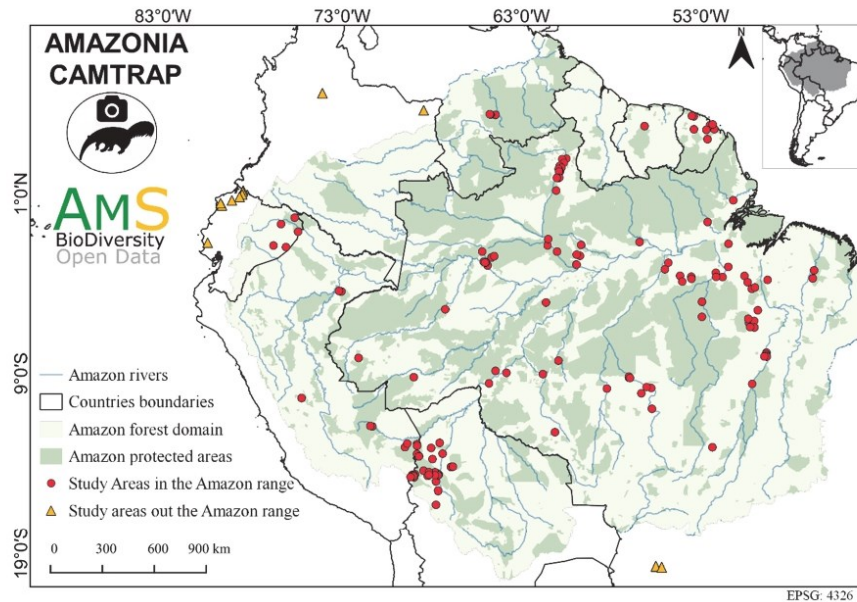


Fig. 1. Distribution of camera trap studies. Red and yellow dots represent study areas within and outside the Amazon Forest limits from this study, respectively. Each red dot represents one study area that englobes multiple sampling units (or camera trap stations).

Considering the filtered dataset, for our analysis, we used data from 42 data sets, 143 study areas, and a total of 122,534 records, from which we identified 289 species (166 birds, 111 mammals and 12 reptiles), from 196 genera, 77 families, and 31 orders (Fig. 2). The most frequent species recorded per taxa were: mammals - *Cuniculus paca* (10,495 records); birds - *Pauxi tuberosa* (3,713 records); reptiles - *Tupinambis teguixin* (708 records). Baits were used in 21% of the data sets. On average, the minimum distance between stations was 1270 ± 714 meters (mean \pm SD). The time interval established for determining independent detections varied

between studies: 37% of studies used 30 minutes, 15% 1 hour, 6% 24 hours, 22% used both 30 minutes and 24 hours (for *Panthera onca*), 16% used other time intervals, while 4% did not report this criterion. For most studies, the time interval was determined by the ecological question and the species studied (Sollmann 2018). The mean sampling effort among study areas was 2127 traps/days (min 3 – max 18,566), with more intense effort in Central Amazonia. The effort was evaluated by multiplying the number of sampling units by the number of days these units were operational. The number of study sites also varied per country, with 59% of the surveys conducted in Brazil, 25% in Bolivia, 3% in Ecuador, 6% in French Guiana, 4% in Peru, 2% in Venezuela, and 0.6% in Suriname.

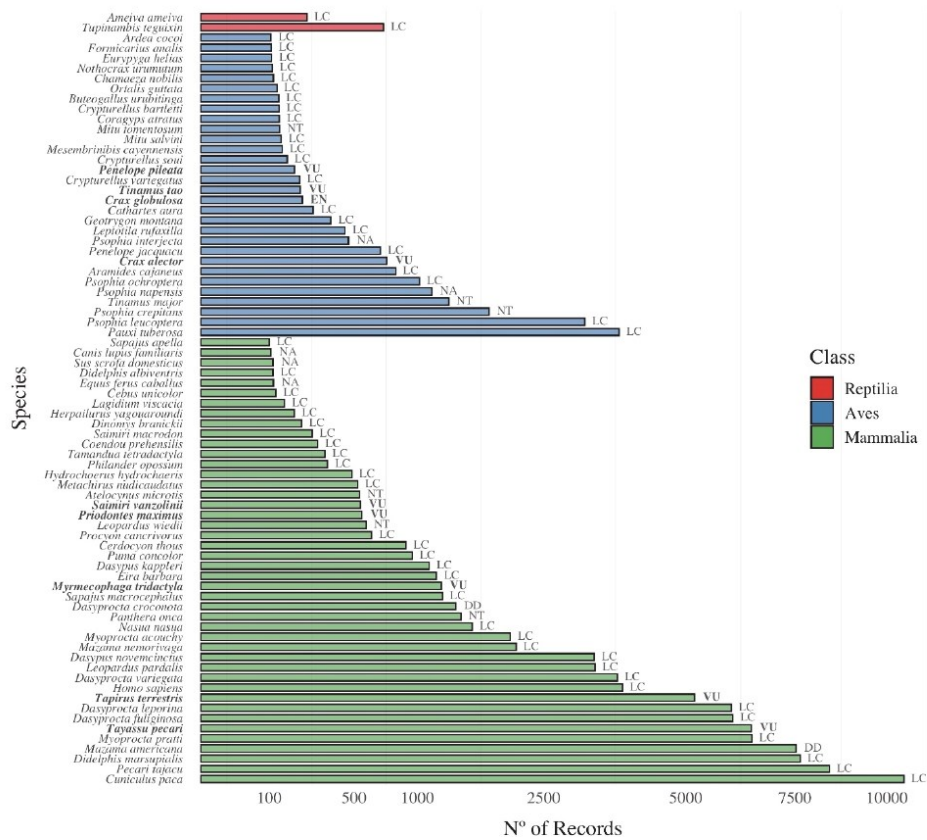


Fig. 2. Number of records of species with more than 100 records. The symbols from the global assessment were: LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, DD = Data Deficient, NA = Data Not Available. Vulnerable and endangered species are shown in bold.

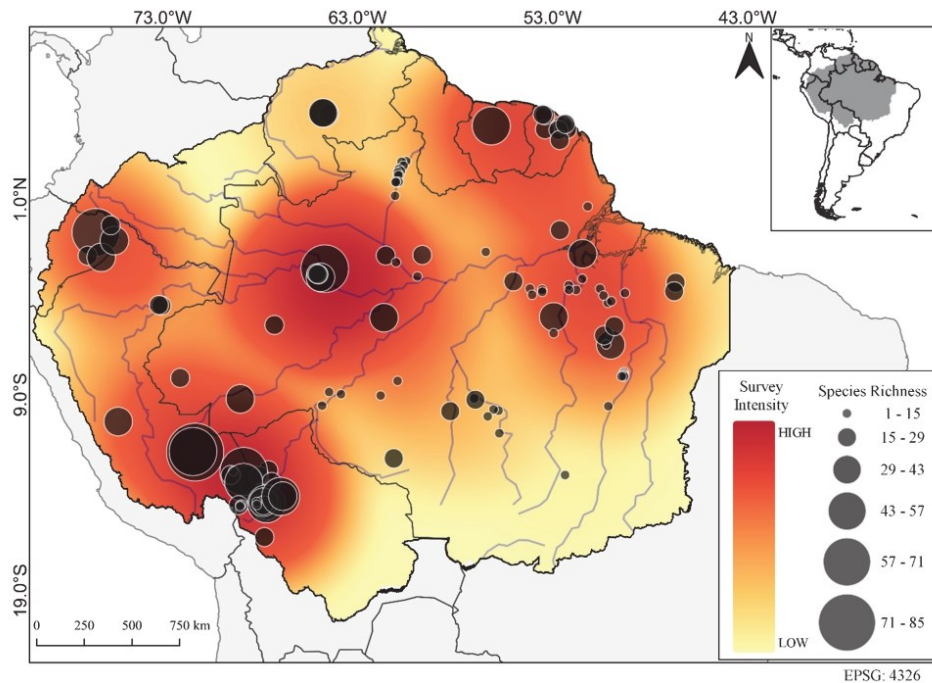


Fig. 3. Species richness and sampling effort per study area. Species richness was higher in areas with more intense sampling effort.

The average detected species richness per site was 18.8 ± 15.6 species (mean \pm SD), with the highest recorded richness in southwestern Amazon, between northwestern Bolivia and southeastern Peru (Fig. 3). About 88% of records occurred inside PAs, while the remaining 9% were in non-protected areas. For 3% of the records the information was not specified. Both species richness and sampling effort were higher in Protected Areas with sustainable use of natural resources, when compared to other classes of protected and non-protected areas (Fig. 4). The sampling effort varied widely among and within PA classes: Ia - 1765.3 ± 2655.8 cameras*day (mean \pm SD); Ib - 1721.9 ± 3270.9 cameras*day; II - 1579.2 ± 3847.9

cameras*day; V - 2104.8 ± 4356.1 cameras*day; VI - 1660.4 ± 3356.4 cameras*day; NA - 1669.5 ± 2759.8 cameras*day.

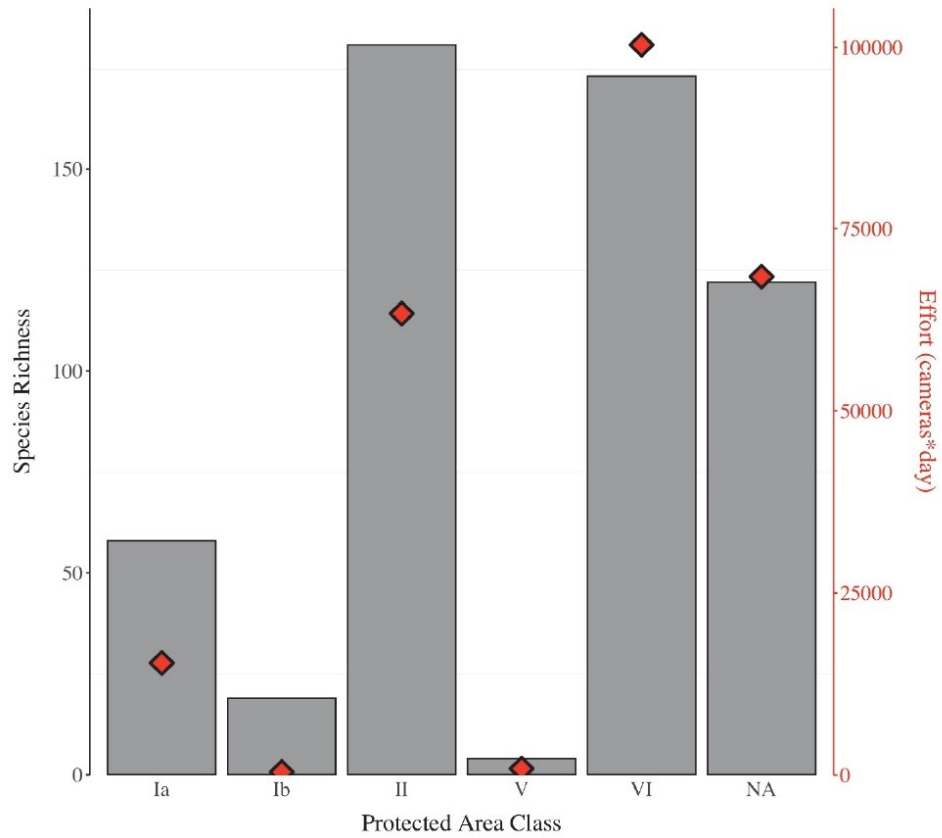


Fig. 4. Species richness (gray bars) and sampling effort (red diamonds) per class of Protected Area. IUCN Protected Area Management Categories were: Ia – Strict Nature Reserve; Ib – Wilderness Area; II – National Park; V – Protected Landscape/Seascape; VI – Protected Area with sustainable use of natural resources; and NA - Non-protected Area (not an IUCN category).

CLASS II – RESEARCH ORIGIN DESCRIPTORS

A. Overall project description

1. Identity

A dataset compilation with information on terrestrial mammals, birds, and reptile species from camera trap records in the Amazon forest.

2. Originators

The AMAZONIA CAMTRAP project was coordinated by Ana Carolina Antunes, Guilherme Costa Alvarenga, Anelise Montanarin, Erison Carlos dos Santos Monteiro, Fernando Ferreira de Pinho and Diogo Maia Gräbin. The following collaborators were part of the support team:

Graphs and statistics: Guilherme Costa Alvarenga, and Fernando Ferreira de Pinho

Dataset standardization: Ana Carolina Antunes, Guilherme Costa Alvarenga, Anelise Montanarin, Erison Carlos dos Santos Monteiro, Diogo Maia Gräbin, and Fernando Ferreira de Pinho

Co-authorship coordination: Anelise Montanarin and Ana Carolina Antunes

Map generations: Fernando Ferreira de Pinho and Ana Carolina Antunes

Manuscript writing: Ana Carolina Antunes, Guilherme Costa Alvarenga, Anelise Montanarin, Erison Carlos dos Santos Monteiro, Diogo Maia Gräbin, Fernando Ferreira de Pinho, Robert B. Wallace, Emiliano Esterci Ramalho, and Milton Cezar Ribeiro.

Species distribution range and taxonomy validation: Daniel Lane, Jean Boubli, Marcélia Basto, Mario Cohn-Haft, Rafael N. Leite, and Ronaldo G. Morato

3. Period of study

Species records range from 2001 to 2020.

4. Objectives

Our main objectives were: (1) To summarize information from camera trap inventories conducted in the Amazon forest, exploring raw, unpublished, and published data; (2) to identify species distribution, richness, the spatial pattern of sampling effort, and knowledge gaps.

Therefore, we provide a database with information that can be used in further macroecological studies.

5. Sources of funding

The compilation of this dataset was supported by grants, fellowships, and scholarships from: Amazon Region Protected Areas Program (ARPA); Brazilian National Council for Scientific and Technological Development (CNPq - Grant numbers 150123/2018-3; 142352/2017-9; 201475/2017-0; 441443/2016-8; 441703/2016-0; 307084/2013-2; bolsa PCI-D; processos individuais número 300087/2016-0, 312539/2016-9, 300057/2017-2, 300444/2019-2 e 132510/2019-7); Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES - Grant numbers 88882.184240/2018-01; Doutorado Pleno no Exterior/ nº:88881.128140/2016-01); Darwin Initiative for the Survival of Species (Grant number 20-001); DEAL Guyane (French Ministry of Environment); Dean Amadon Grant from the Raptor Research Foundation; Disney World Conservation Fund; Ecopetrol; EERC University of Salford internal grants; ERDF

Funds; Fundação Grupo Boticário de Proteção à Natureza; Fundação Monsanto; Fundação Pantanal Com Ciência; Fundación Mario Santo Domingo; Idea Wild; Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio); Instituto de Desenvolvimento Sustentável Mamirauá (IDSM); Instituto Nacional de Pesquisas da Amazônia (INPA - FDB/Vale S.A.); Jaguar Conservation Program (Wildlife Conservation Society – WCS); Leme Engenharia; Liz Claiborne Art Ortenberg Small Grant (Panthera Foundation); National Science Foundation (Division of Environmental Biology - Grant number 1146206); Norte Energia; People’s Trust for Endangered Species (PTES); Phoenix Herpetological Society; Projeto Conservação de Vertebrados Aquáticos Amazônicos (Aquavert) – Programa Petrobras Ambiental; PROCAD-AM, (Grant number 88881.314420/2019-01); The Explorers Club; The Gordon and Betty Moore Foundation; The International Osprey Foundation Endowment; The Rufford Foundation Small Grants (Grant numbers 12231-1; 16299-1; 20754-1); USAID; Wildlife Research; Woodland Park Zoo; World Wide Fund for Nature (WWF).

B. Specific Subproject description

1. Site Description

The Amazon is the largest rainforest in the world. This study is focused on an area of 8,414,085 km² encompassing eight countries: Brazil, Bolivia, Colombia, Ecuador, French Guiana, Peru, Suriname, and Venezuela (RAISG 2020). Dominated by rivers, the Amazon forest mainly consists of lowland plains, however along the frontiers among Venezuela, Brazil, and Guiana, the highlands of Guiana Shield have peaks that can reach up to 3,000 m (Lujan and Armbruster 2011). Rainfall ranges from 1,500 to 3,000 mm annually (Salati and Vose 1984), resulting in extensive seasonally-flooded areas (Junk et al. 2011). Combined with a marked

annual flood pulse, the wide range of soil profiles covering the Amazon forest drives vegetation composition and structure (Quesada et al. 2010).

The Amazon forest comprises a complex mosaic of 53 major ecosystems and over 600 different types of land and freshwater habitat (Salati et al. 2012). Most of the Amazon consists of upland forests, or *terra firme* forests, which occur at well-drained sites above the high-water levels (Melack and Hess 2010). Wetlands cover between 14 - 30% of the Amazon basin and result from the heavy annual rainfall, unevenly distributed between seasons, and consequent rising river levels and inundation of adjacent floodplains of up to 230 days per year (Junk et al. 1989, Melack and Hess 2010, Junk et al. 2011).

The physical and chemical parameters of the major Amazonian floodplain rivers characterize the three dominant habitats in these wetlands: the *várzea* forests, flooded by sediment-rich white-water rivers originating in the Andes; the paleo-*várzeas* formed from ancient Andean sediments and therefore with intermediate fertility; and the *igapós*, associated with nutrient-poor black and clearwater rivers (Prance 1979; Irion et al. 2010; Sioli 1956; Junk et al. 2011). *Campinas* and *campinarianas*, the Amazonian savannahs, are associated with sandy, very nutrient-poor soils, often subject to periodic flooding (Pires and Prance 1985). Other vegetation types are also present and cover small areas, but are quite distinct. Those include mangrove forest, restinga, and swamps (for more details on each vegetation type, see Pires and Prance 1985, Junk et al. 2011).

These ecosystems are interconnected and have different levels of resilience to anthropogenic alterations. In the Amazon Basin, PAs are considered a viable way to conserve biodiversity and reduce deforestation and forest degradation (Sobral-Souza et al. 2018). In, for

example, the Brazilian Amazon, PAs cover 2.2 million km², with 44% comprised of forests (Verissimo et al. 2011). Nevertheless, PA effectiveness as a conservation tool may vary depending on the type, size, administrative level, and exposure to deforestation (Nogueira et al. 2018). Amazonian deforestation is concentrated mainly in the “arc of deforestation”, an area located on its southern and eastern limits, along the Andean piedmont (Malhi et al. 2008). It is estimated that, for the entire Amazon Basin, around 100Gt (gigatons = billion tons) of carbon, as above-ground live biomass, roots, dead trees and soil stocks, could be released into the atmosphere if the forest is converted to non-forest vegetation (Fearnside 2008).

2. Data Compilation

A collaborative network of researchers shared their published and unpublished camera trap data for the Amazon forest. The invitation was open; therefore, we tried to reach every potential collaborator and invited them to contribute and participate as a co-author in the AMAZON CAMTRAP data paper.

3. Research Methods

This data paper is part of the AMAZONIA, NEOTROPICAL, ATLANTIC, and BRAZIL series initiative, which aims to compile information on the biodiversity of these regions, making data available publicly. Until now, the following data papers of these series have been published: NEOTROPICAL – GPS jaguar movements (Morato et al. 2018), Xenarthrans (Santos et al. 2019), Carnivores (Nagy-Reis et al. 2020), Alien mammals (Rosa et al. 2020); BRAZIL: Road kills (Grilo et al. 2018), ATLANTIC: Plant-animal frugivory (Bello et al. 2017), Terrestrial mammals (Lima et al. 2017; Bovendorp et al. 2017; Souza et al. 2019), Bats (Muyllaert et al. 2017), Birds (Hasui et al. 2018), Amphibians (Vancine et al. 2018), Frugivorous butterflies

(Santos et al. 2018), Mammal and bird traits (Gonçalves et al. 2018; Rodrigues et al. 2019), Epiphytes (Ramos et al. 2019) and Primates (Culot et al. 2019).

In this data paper, we compiled records of mammals, birds, and reptiles obtained from camera trap records. Most of these records occurred on or near the ground; however, we also included arboreal sampling efforts. The records were subdivided into two-scale categories: sampling unit and study area. For each study area, we used centroid coordinates of each respective sampling units. All the geographic coordinates are expressed in decimal degrees, using the WGS 84 datum. We focused our data paper on the Amazon forest, and the precise limits of which were defined using RAISG 2020. We maintained records from outside the Amazon forest limits in the dataset, but they were not included in the analysis, graphs, and figures. Data was compiled mostly from unpublished data, but also included data from Negrões et al. 2011; Zapata-Ríos and Araguillin 2013; Benchimol and Peres 2015; Campos et al. 2016; Isasi-Catalá et al. 2016; Abrahams, Peres, and Costa 2017, 2018; Aguiar-Silva et al. 2017; Torralvo, Botero-Arias, and Magnusson 2017; Alvarenga et al. 2018; Costa, Peres, and Abrahams 2018; Antunes et al. 2019; Wang et al. 2019; and Rocha et al. 2020.

4. Taxonomic Data

Each collaborator was responsible for identifying the species recorded in the data shared. After we received the data, the verification and standardization used the following steps: first, the Amazon Camtrap Core Team identified errors in species nomenclature and synonymies species, and standardized all names according to IUCN (2020), Catalog of Life (Roskov et al. 2019), Reptile Database (Uetz et al. 2020), and Patton et al. (2015). After this standardization, we generated maps for the distribution of records of each species and sent them for verification by

specialists of each taxonomic group (reptiles - Marcélia Bastos; birds - Mario Cohn-Haft and Daniel Lane; primates - Jean Boubli; rodents and marsupials - Rafael Leite; medium and large mammals - Ronaldo Morato). Finally, the specialists evaluated whether records needed double-checking. In positive cases, we asked collaborators for photos or videos of the specific species records. After this double-checking, collaborators were informed of the specialist's conclusion. Taxonomic uncertainties were retained at the genus level or excluded from the dataset.

C. Data Limitations and Potential Enhancements

Our dataset compiles information on mainly terrestrial Amazon mammals, birds, and reptiles. Since each study had a different objective, additional care is required when comparing the data, as the study design may influence the detectability of target species (Meek et al. 2014). It is also necessary to consider the time interval independence and the sampling effort per study, both of which can directly influence the number of records and species richness (Fig. 5). Some studies also used baits, which may bias the detection and number of records of some species (e.g., Rocha et al. 2016). In addition, different camera trap brands and models may influence species detection (Meek et al. 2014).

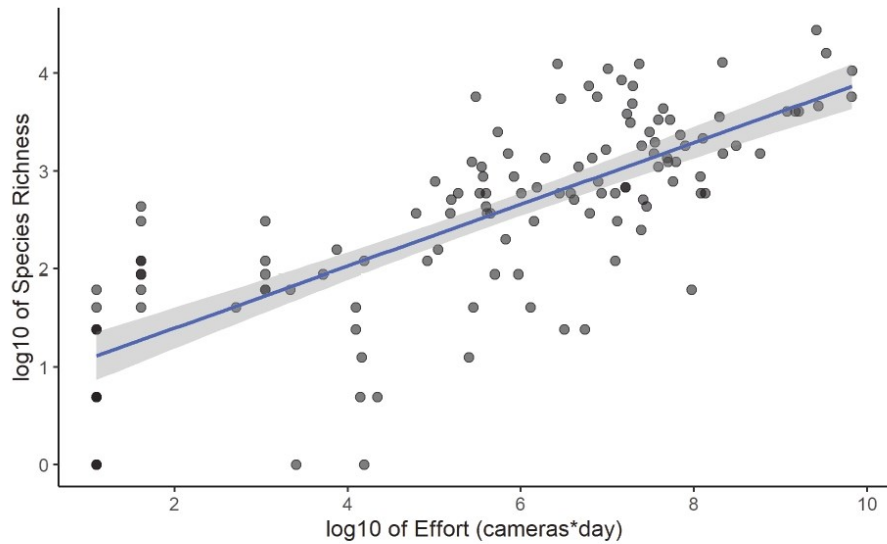


Fig. 5. Positive effect of sampling effort on species richness in the AMAZON-CAMTRAP database.

The slope for the effort-richness relationship was 0.32. Gray area represents the 95% confidence interval (0.27-0.36) and each dot represents one study area. Overlapped dots are represented by a darker color. $R^2 = 0.604$, $p < 0.001$.

Spatial and temporal sampling efforts varied considerably across studies and should be considered when using this dataset. While on a local scale, animal trait, camera specifications, and vegetation type might affect animal detection, on a broader scale, it is important to consider processes such as animal density and movement, sampling unit size, number of cameras, and survey duration (Burton et al. 2015). Abundance data should be carefully used and interpreted. It is not recommended to use the number of records as a measure of abundance, doing so only if the study has specified this (e.g., accounting for individual identification) (Burton et al. 2015). We suggest researchers check the “data type” in our data file prior to using data in this manner.

It is also important to highlight that, even though the Amazon Camtrap Core Team and taxon-specific experts checked the taxonomy and distribution of the species involved, species identification was made independently by the groups who collected the data. Finally, we also highlight the variation in sampling effort, as well as the uneven sampling across the different regions of the Amazon. Similarity of species composition is known to decrease with the distance from access infrastructure (Oliveira et al. 2016). This might be an important issue in the Amazon forest since many regions are remote or hard to access, dangerous, logistically challenging or simply too expensive to receive studies. Additionally, local economic and social conflicts can make it highly challenging to conduct scientific activities in some areas.

Notwithstanding these limitations, this study contributes to the large-scale perspective of research into macroecological processes, and helps answer questions related to anthropogenic impacts on Amazonian biodiversity. This data paper represents a massive effort, and has resulted in the compilation of the largest-ever camera trap dataset for the Amazon forest. In doing so, we provide information that was never accessible before, such as reports and non-published data, and explore data on broad spatial and temporal scales.

CLASS III – DATA SET STATUS AND ACCESSIBILITY

A. Status

Latest update: 20/08/ 2021

Latest Archive data: 20/08/ 2021

Metadata Status: Latest update on 20/08/2021 refers to the submitted version of the revision process.

B. Accessibility

Original AMAZONIA CAMTRAP dataset can be accessed on the GitHub Inc. repository (https://github.com/LEEClab/Amazon_camtrap). All the data – both the updated version and complementary material – are fully available for public use and research purposes. The dataset will be updated on a regular basis on the GitHub Inc. repository and the acquisition of new data is possible by contacting the authors of this manuscript.

1. Storage location and medium

The dataset and its future updates can be accessed on the GitHub Inc. repository (https://github.com/LEEClab/Amazon_camtrap) in .CSV format, as well as its metadata. A mirror of this repository will also be available at https://github.com/LEEClab/Amazon_series, where all the other data-papers of AMAZON SERIES are available.

2. Contact people

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3. Copyright restrictions:

None.

4. Proprietary restrictions

Please cite this data-paper when using its data in publications. We also request that
researchers and educators inform us of how they are using this data.

5. Costs:

None.

CLASS IV – DATA STRUCTURAL DESCRIPTORS

A. Data Set File

1. Identity

AMZ_CAMTRAP_AREA.csv

AMZ_CAMTRAP_UNIT.csv

2. Size

1.5 KB

21.7 KB

3. Format and storage mode

Comma-separated values (.csv).

4. Data anomalies

If no information is available for a given record, this is indicated as 'NA'.

B. Variable Information

Tab Name	Column Abreviation	Column Full Name	Description	Example
All tabs	DATASET	Dataset responsible(s)	Your name and/or team name.	RosaClarissa_LECOM/ UFLA
All tabs	DATA_TEAM	Data owners	Names of data owners.	Rosa, C.; Ribeiro, M.
All tabs	RECORD_ID	Record id	Your own record id.	INV1
All tabs	REFERENCE	Reference	Add complete reference if data has already been published. Otherwise, add "unpublished".	Unpublished
All tabs	TYPE_REF	Reference type	Type of reference (e.g., master's dissertation, unpublished, etc).	Published peer reviewed
All tabs	DATA_TYPE	Type of data	Record type (Presence-only, Presence-absence, Abundance).	Presence_absence
All tabs	DATA_AIM	Aim of data collection	Please specify if data are "primary" (your study was designed to collect this specific information on this species) or "secondary" (your main objective was not to collect data on this specific species).	Primary
All tabs	SITE	Study site	Name of your study area (e.g., remnant name, protected area, etc).	Serra do Japi
All tabs	AREA_HA	Study area size	Size of study area (total in hectares).	35000
All tabs	MUNICIPALITY	Municipality	Name of the nearest city where the study area is located.	Jundiai

32

All tabs	STATE	State	Name of the state/province where the studied area is located.	SP
All tabs	COUNTRY	Country	Name of the country where the studied area is located.	Brazil
Study_area	LONG_X_AREA	Longitude of the study area	Longitude of the study area in decimal degrees (centroid). Use 5 digits if possible.	-46.97554
Study_area	LAT_Y_AREA	Latitude of the study area	Latitude of the study area in decimal degrees (centroid). Use 5 digits if possible.	-23.27613
Sampling_u nit	LONG_X_POINT	Longitude of the sampling unit	Longitude of the record in decimal degrees. Use 5 digits if possible.	-46.97554
Sampling_u nit	LAT_Y_POINT	Latitude of the sampling unit	Latitude of the record in decimal degrees. Use 5 digits if possible.	-23.27613
Study_area	ALTITUDE	Altitude	Altitude of your sampling unit (i.e., point where species was recorded). If not available, use average altitude of study area.	900
Study_area	ANNUAL_RAIN	Annual rain precipitation	Total annual precipitation for your study area.	1424
Study_area	VEG_LANDUSE_T YPE_AREA	Study area's main vegetation or land cover type	Main vegetation or land cover type of study area.	Semidesciduous forest
Study_area	VEG_LANDUSE_T YPE_AREA_BUFFE R5KM	Vegetation or land cover surrounding study area	Vegetation or land cover around your study area (5 km buffer around the entire study area). One or more.	Forest
Sampling_u nit	VEG_LANDUSE_T YPE_POINT	Point's vegetation or land cover type	Vegetation or land cover type of your sampling unit (i.e., point where you recorded the species).	Semidesciduous forest
Sampling_u nit	VEG_LANDUSE_T YPE_POINT_BUFF ER5KM	Vegetation or land cover surrounding sampling unit	Vegetation or land cover around your sampling unit (5 km buffer around the point where data was collected).	Forest
All tabs	PROTECT_AREA	Protected area	Is the sampling unit where you recorded the species located within a protected area? Yes or no.	Yes
All tabs	PROTECT_AREA_T YPE	Type of protected area	If the sampling unit where you recorded the species is located within a protected area, add here the protected area management category according to IUCN: Ia, Ib, II, III, IV,	Ia

			V, VI (Please see guidelines or https://www.iucn.org/theme/protected-areas/about/protected-area-categories).	
All tabs	ORDER	Order	Order of the species.	Carnivora
All tabs	FAMILY	Family	Family of the species.	Felidae
All tabs	GENUS	Genus	Genus of the species.	<i>Leopardus</i>
All tabs	SPECIES	Species	Most recent name of the species.	<i>Leopardus pardalis</i>
All tabs	COL_START_MO	Data collection start month	Month in which data collection started.	Mar
All tabs	COL_START_YR	Data collection start year	Year in which data collection started.	2015
All tabs	COL_END_MO	Data collection end month	Month in which data collection ended.	Apr
All tabs	COL_END_YR	Data collection end year	Year in which data collection ended.	2017
All tabs	METHOD	Method for data collection	Method used to collect data (Camera trap, Paired Camera trap).	Camera trap
All tabs	CAM_TYPE	Camera type	Camera-trap model used in the study.	Reconyx
All tabs	BAIT	Baiting	Presence or absence of bait.	Yes
All tabs	OCCUR	Occurrence	Occurrence (zero or 1).	1
All tabs	N_RECORDS	Number of records	Number of records (number of photos, number of individuals counted).	4
Study_area	TOTAL_EFFORT	Total sampling effort	Total sampling effort: Camera trap/night.	5000
Sampling_unit	EFFORT	Sampling effort	Sampling effort: Camera trap/night.	120
All tabs	IND_CAM	Independence for camera records	Time interval (in min) for independence between records.	60
All tabs	MIN_DIST_CAM	Minimum distance between cameras	Minimum distance (in m) between camera traps.	2000
All tabs	MAX_DIST_CAM	Maximum distance between cameras	Maximum distance (in m) between camera traps.	3000

All tabs	OBS	Observations	Any important observation that users should know to better understand your data.	NA
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Acknowledgments

We would like to thank to Parque Nacional Serra da Bodoquena/ICMBio-MS, Floresta Nacional do Tapajós/ICMBio-PA, Floresta Nacional de Carajás/ICMBio-PA, Área de Relevante Interesse Ecológico PDBFF/ICMBio-AM, Reserva Adolpho Ducke-AM, RESEX Cazumbá-Iracema/ICMBio, the curators and technical team of the Birds and Mammals Collections at INPA, Vandir F. da Silva, José A. Costa Filho, and Tiago G. Junqueira for their help in the field, Dilson E.B. Insfran, Roberto Massafra, Pedro Meloni Nassar, Iury Valente Debien and Ivan Junqueira, for the help with species identifications. We are also grateful to the riverine households, community leaders, and the managers of the Extractive Reserve Riozinho da Liberdade. We would like to thank the communities from Mamirauá sector of the SDR Mamirauá and the communities from Amanã lake of the SDR Amanã, specially, Lázaro, Almir, Socorro, Washington da Silva, Igson, Moisés Levernny, Áquila da Silva e Maria do Carmo. To Instituto de Desenvolvimento Sustentável Mamirauá (IDSM-OS/MCTI), Jairo Silva, André Silva, Erivan Castro, Erinaldo Fragoso. We would like to thank also to Arcadis Logos, Energia Sustentável do Brasil S/A (ESBR), D. Nunes, R.M. Quintino, S.A. Nascimento, E.P. Nascimento, R.L. Pereira, J.M. da Rocha, Grupo AMAGGI, Yasuni Research Station, PUCE, AMCEL (Amapá Florestal e Celulose S.A.), Ibama, ICMBio, Instituto Vida Verde, WCS team and landowners, CNPq (individual process n° 300087/2016-0, 312539/2016-9, 308040/2017-1, 300057/2017-2, 300444/2019-2, 306345/2019-6, and 132510/2019-7). PELD/CNPq (n° 441703/2016-0; site TANG), the Max Planck Institute for Biogeochemistry, the Gordon and Betty Moore Foundation (n° 5483), NSF (DEB-1457602), Local Staff Biocev Smart Projects Group, Interligação Elétrica do Madeira S/A (IEMAD), Parque Nacional Campo Amazônicos and Parque Nacional Mapinguari for logistical support. Sébastien Barrioz, Eddy Poirrier Instituto

de Pesquisas Cananéia, IPeC “Carbon Sink Project”, Peugeot-Citroën, Office National des Forêts (ONF-International and ONF-Brasil) for logistic support in the Fazenda São Nicolau (FSN), Parque Nacional do Jaú/ICMBio and communities of Jaú river, AMCEL (Amapá Florestal e Celulose S.A.), Earthwatch volunteers and interns Dr. Rodolfo Jaffé - Vale Institute of Technology Vale S/A. All people involved in the field on the armadillo density study in French Guiana. Benoit de Thoisy for his help with mammal identification, Olivier Claessens for his help with bird identification, and Benoit Villette for his help with amphibia and reptile identification. Daniel Martins, Reginey Gomes, Roberto da Costa, Elenilson Silva, Fernando Costa, Sebastião Gama and Rosilene Gutierrez. To all lovers of Amazon biodiversity and those who believe the world can be better with shared scientific data.

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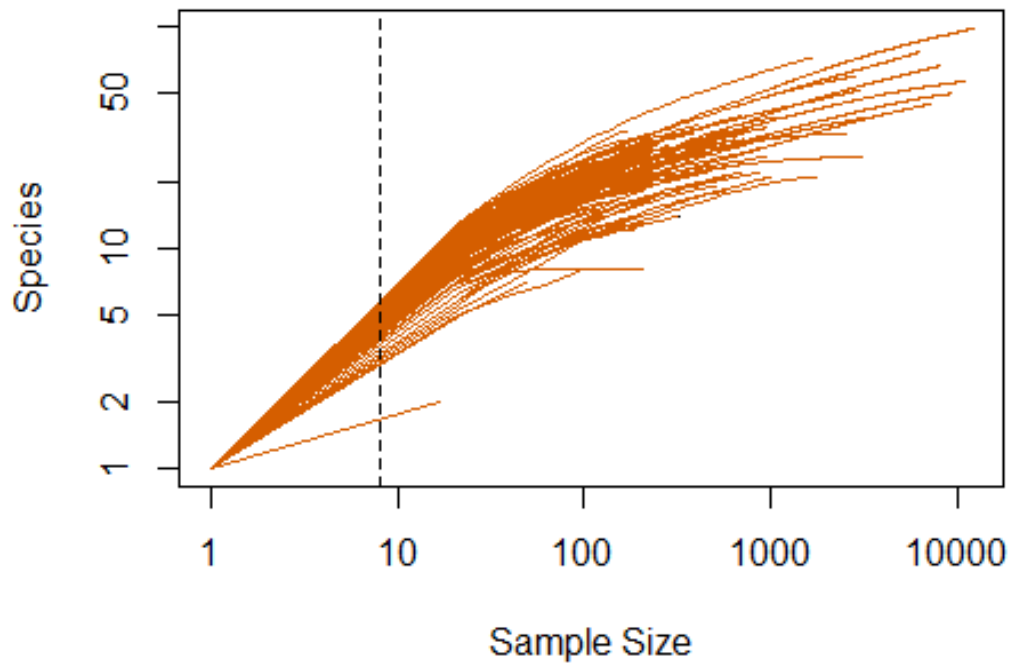
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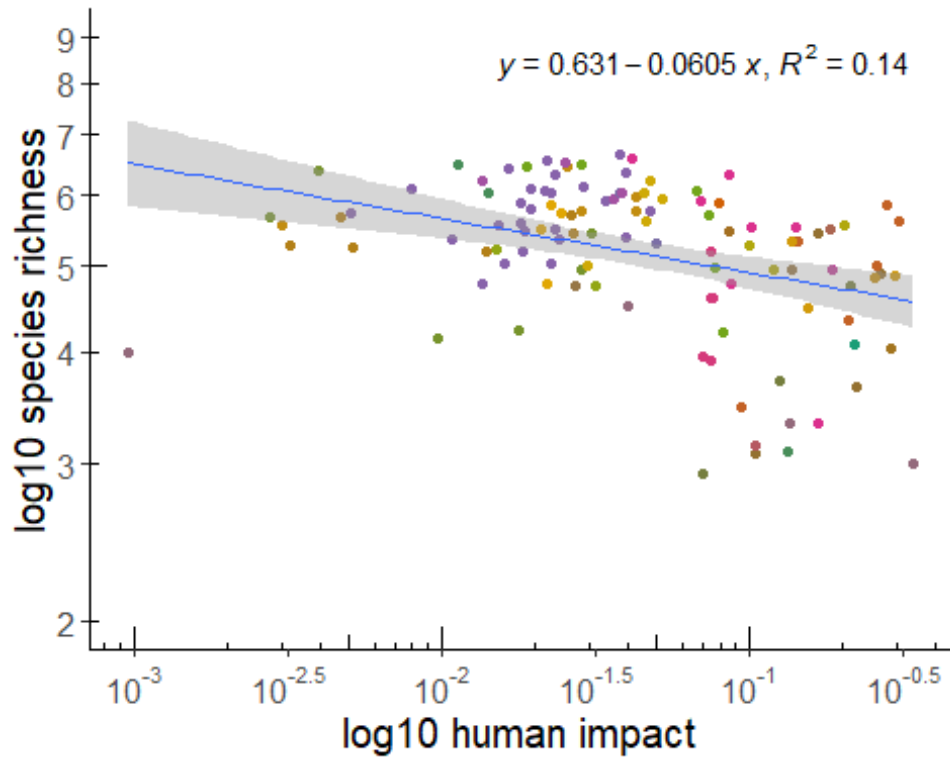
Appendix B: Supplementary – Chapter 2

Supplementary information 1

In order to show that the results obtained without removing the 9 outliers are overall consistent with what is obtained with the selected dataset, we re-ran our analysis with the outliers. The rarefied species richness was estimated and the cut-off at the sample size of the smallest sample was equal to 8 registers.



Even when we keep the outliers, we still see a negative trend on species richness.

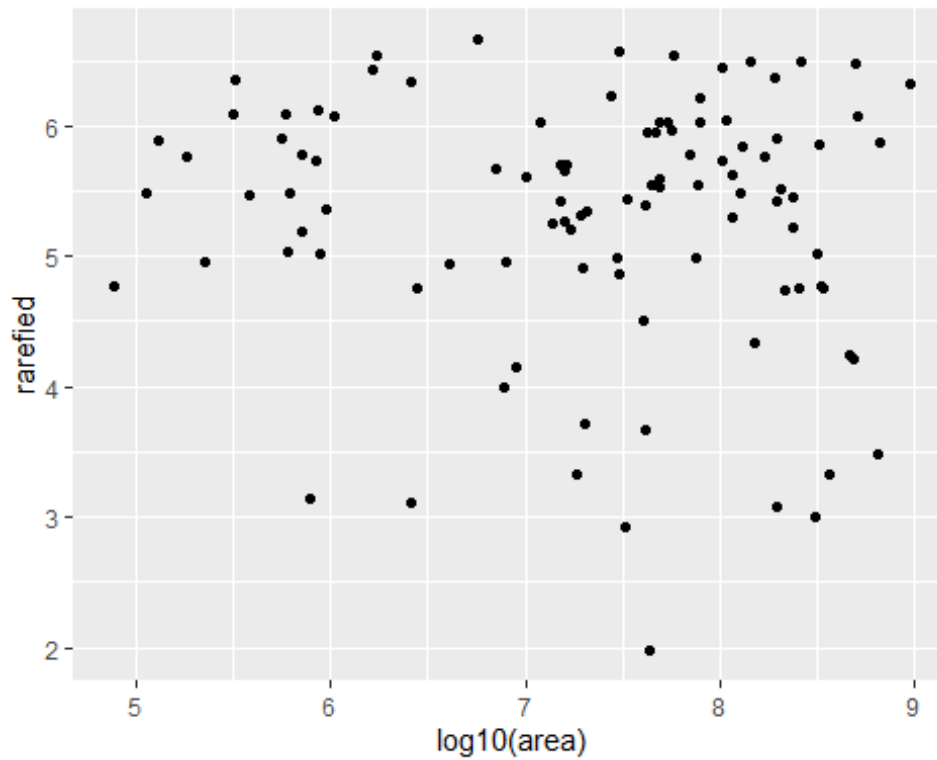


The result from the Linear Mixed Effect Model relating species richness to human modification shows a significant negative relationship, with lower species richness across the gradient of landscaper modification.

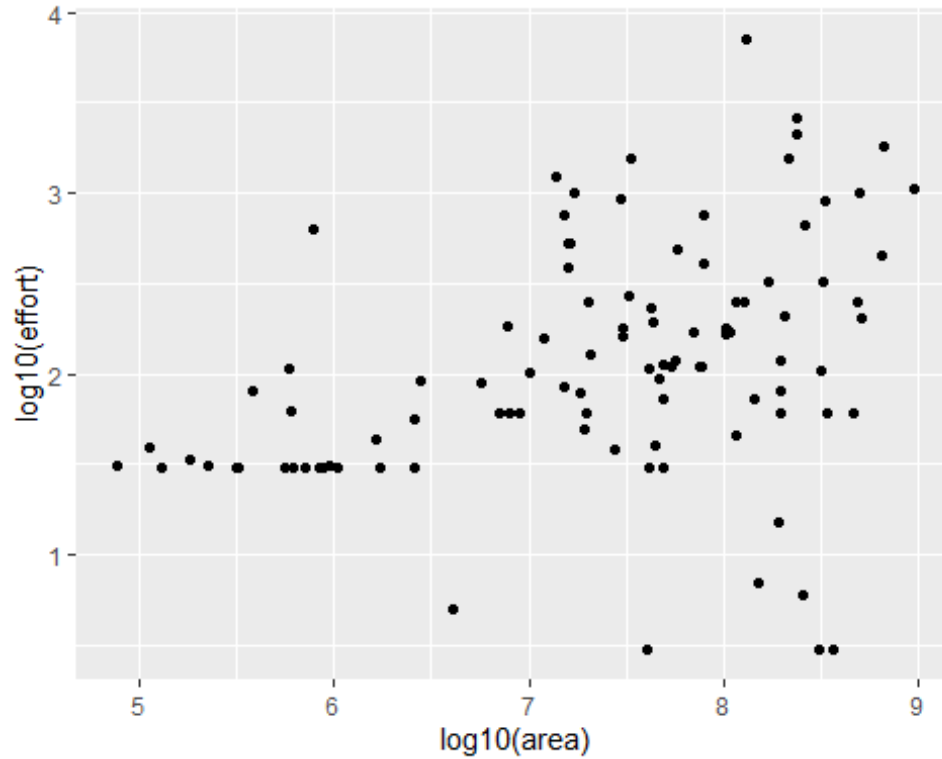
	rarefied		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	4.51	3.90 – 5.12	<0.001
human [log10]	-0.48	-0.87 – -0.09	0.016
Random Effects			
σ^2	0.54		
τ_{00} blocks	0.37		
ICC	0.41		
N_{blocks}	22		
Observations	102		
Marginal R^2 / Conditional R^2	0.059 / 0.444		

Supplementary information 2

We here assess the effect of cluster sizes on the relationship between human pressure and species richness. We can see that there is no direct correlation between cluster area and the estimated species richness after the rarefaction procedure:



This result is mostly explained by the relationship between cluster size and the sampling effort associated to clusters:



As such, this result suggests that the rarefaction procedure done on the effort was also correcting potential biases associated to cluster size. We investigate that further by comparing incorporating cluster size in our statistical models. We considered two new statistical models: an additive model in which the potential interaction between area and human modification is not considered, and one including this interaction effect. In all models (including the one with human modification only, variables were re-scaled).

First, model with interaction:

```
inter.n <- lmer(rarefied ~ log.human*log.area + (1 | blocks), data = res.normalised)
tab_model(inter.n)
```

<i>Predictors</i>	rarefied		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	5.17	4.85 – 5.49	<0.001
log human	-0.25	-0.44 – -0.05	0.014
log area	0.13	-0.07 – 0.32	0.205
log human × log area	-0.10	-0.31 – 0.11	0.357

Random Effects

σ^2	0.54
τ_{00} blocks	0.38
ICC	0.41
N_{blocks}	22
<hr/>	
Observations	102
Marginal R^2 / Conditional R^2	0.072 / 0.457

Then model without interaction:

```
add.n <- lmer(rarefied ~ log.human+log.area + (1 | blocks), data = res.normalised)
tab_model(add.n)
```

<hr/> <hr/>			
	rarefied		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
<hr/>			
(Intercept)	5.17	4.85 – 5.50	<0.001
log human	-0.24	-0.44 – -0.05	0.015
log area	0.12	-0.08 – 0.31	0.231
Random Effects			
σ^2	0.53		
τ_{00} blocks	0.39		
ICC	0.42		
N_{blocks}	22		
<hr/>			
Observations	102		
Marginal R^2 / Conditional R^2	0.062 / 0.457		

and model with human impact only:

```
rand.n <- lmer(rarefied ~ log.human + (1 | blocks), data = res.normalised)
tab_model(rand.n)
```

rarefied			
<i>Predictors</i>	<i>EstimatesCI</i>		<i>p</i>
(Intercept)	5.20	4.88 – 5.51	<0.001
log human	-0.24	-0.44 – -0.04	0.016
Random Effects			
σ^2	0.54		
τ_{00} blocks	0.37		
ICC	0.41		
N _{blocks}	22		
Observations	102		
Marginal R ² / Conditional R ²	0.059 / 0.444		

Now if we compare the different models using AIC and BIC criteria:

```
AIC(rand.n, add.n, inter.n)
```

```
##    df    AIC
## rand.n  4 264.3682
## add.n   5 267.7234
## inter.n 6 271.5198
```

```
BIC(rand.n, add.n, inter.n)
```

```
##    df    BIC
## rand.n  4 274.8681
## add.n   5 280.8483
## inter.n 6 287.2697
```

We can see that in both cases the most parsimonious model is the one with human impact only, confirming the conclusion from the visual inspection of the data

Supplementary information 2

blocks	cluster	effort	richness	human	rarefied	area
2	4	56	7	0.132887	3.771042	2557486
2	2	73	27	0.014225	8.000634	49434911
2	3	73	29	0.011334	8.765209	1.43E+08
3	6	248	21	0.124871	4.617978	20469504
3	7	273	22	0.069982	3.783087	32657289
4	9	2110	50	0.086004	6.992809	2.39E+08
5	10	1797	33	0.078951	7.620677	6.61E+08
6	15	49	14	0.14235	6.702008	19210363
6	16	105	19	0.258363	6.414591	3.18E+08
6	14	251	27	0.306364	7.34758	1.16E+08
6	11	453	8	0.093884	4.085272	6.5E+08
6	13	7110	52	0.280536	7.744743	1.31E+08
7	17	39	19	0.181539	7.033049	113281.6
9	23	46	14	0.049287	6.724071	1.16E+08
9	24	170	19	0.037977	7.9495	1.07E+08
10	26	30	18	0.021737	7.963035	1037236
10	27	30	20	0.028982	8.121198	865416.3
10	28	30	15	0.033796	7.661364	565185.3
10	29	30	21	0.021816	8.837227	1716600
10	30	30	14	0.023148	8.371078	2557438
10	31	30	21	0.01808	7.246838	48797562
10	38	30	16	0.039649	8.513297	319402.9
10	39	30	13	0.005005	7.404839	841268.5
10	42	30	17	0.017965	7.864121	130590.2
10	45	30	11	0.007982	8.137513	311982.5
10	47	30	17	0.023245	7.03606	610624.4
10	49	30	18	0.019398	7.495318	714073.4
10	50	30	17	0.016043	6.394792	874788.7
10	51	30	15	0.018216	6.574193	717241
10	43	31	19	0.013552	6.224465	76437.43
10	44	31	15	0.010776	6.874702	946530.1
10	34	40	17	0.01517	7.324483	44898791
10	46	44	13	0.016327	8.602609	1653516
10	48	62	16	0.022593	6.50492	598658.4
10	32	81	17	0.018568	7.183148	386294.9
10	37	90	21	0.037941	9.075254	5679220
10	33	106	21	0.019544	8.089382	585117.3
10	36	107	22	0.039524	6.987773	41334185
10	35	109	22	0.02274	7.966621	53676749

10	41	128	28	0.023942	6.87873	20588090
10	40	324	31	0.047305	7.606104	1.7E+08
11	55	38	34	0.013577	8.33188	27357498
11	56	93	24	0.035867	7.811895	46985952
11	54	491	40	0.025056	8.845284	58480333
11	53	752	27	0.038114	7.924691	78206791
13	69	79	19	0.167606	4.194946	18251712
13	65	91	13	0.086668	5.918077	2771908
13	62	114	34	0.101749	7.257762	49575197
13	66	119	24	0.069622	7.685565	1.94E+08
13	68	162	34	0.041656	8.954252	30287142
13	67	211	60	0.140179	7.346528	2.06E+08
13	64	1061	99	0.085772	8.518143	9.4E+08
16	76	638	18	0.105016	3.878214	774029.7
17	77	31	10	0.135958	6.167142	227266.2
17	78	60	8	0.027153	5.730376	3.36E+08
18	79	60	12	0.030432	6.99417	1.96E+08
18	82	60	13	0.017645	5.162118	4.63E+08
18	83	60	22	0.009623	5.230755	9035107
18	84	60	22	0.028254	6.408742	7910576
18	85	60	24	0.002766	7.303547	7012792
19	89	84	18	0.073118	7.328139	15340129
19	90	110	20	0.07663	6.425463	75403839
19	86	203	46	0.067486	8.023233	5.07E+08
19	91	247	39	0.082201	5.427049	4.88E+08
19	87	670	73	0.028228	8.850595	2.59E+08
19	88	991	77	0.018724	8.763923	5.02E+08
20	92	1537	45	0.031394	6.202612	2.18E+08
20	93	2625	57	0.015054	6.678912	2.36E+08
23	102	102	23	0.046194	7.179477	10138525
23	103	159	29	0.045331	7.994232	11921622
23	101	229	28	0.051975	7.772732	42430147
23	100	406	33	0.047581	8.292598	79435245
23	104	936	13	0.029712	6.370681	29341006
24	105	181	29	0.024402	7.488868	1.03E+08
24	108	247	34	0.020948	7.296291	1.29E+08
24	107	324	29	0.022677	7.675219	3.21E+08
24	106	911	35	0.021838	6.313682	3.32E+08
26	114	33.2	23	0.042946	7.540217	184025.9
26	117	110	26	0.003018	7.135804	78034070
26	112	120	18	0.042802	7.741545	56711050
26	116	167	36	0.025307	8.710139	1.03E+08
26	113	170	19	0.028533	7.427602	69513625
26	115	180	31	0.254903	6.28833	30679843

27	120	392	26	0.003212	6.743232	15778807
27	119	529	28	0.004705	7.328038	16108287
27	121	534	26	0.026157	7.488231	16289950
27	122	753	19	0.026558	6.972735	15304123
27	123	998	27	0.013952	6.643067	16923691
27	124	1236	30	0.005111	6.772426	13932758
30	129	30	5	0.223381	5	41306730
30	131	60	15	0.268387	6.070269	19675576
30	128	81	21	0.104173	3.983702	1.97E+08
30	127	1546	26	0.167685	6.957596	33541864

Metadata:

blocks Blocks ID
cluster Cluster ID
effort Camera trap/ night
richness Sampled species richness per cluster
human Human modification gradient
rarefied Rarefied species richness per cluster
area Area of the cluster in m²

Appendix C: Supplementary – Chapter 3

Supplementary Material

Network topology

Our study area contained the whole of continental Europe and was divided into 395,219 equal-area cells (pixels) of 10 x 10 km². We obtained the network topology for European vertebrates from the TETRA-EU database (S Maiorano et al. 2020). TETRA-EU already provides the checklist of native or naturalized vertebrate species in Europe and their predator-prey interactions. During preliminary analyses, we detected several pixels for which flux calculation failed, most likely due to trophic loops i.e., in the local network. Therefore, every time we encountered a cycle in the local network, we randomly removed one of the two links involved in the cycle.

Species distributions

We extracted the distributions of the species occurring in the study area from (S Maiorano et al. 2013). These distributions were obtained by combining the extent of occurrence for each species with their habitat requirements. Species distributions were mapped in a regular grid of 300 m resolution, where cells had values of zero for unsuitable habitat, one for marginal habitat (habitat where the species can be present, but does not persist in the absence of primary habitat) and two for primary habitat. Here, we treated the primary habitat only as 'suitable habitat', which provides a better prediction of the actual species distribution (S Ficetola et al. 2015). We upscaled distribution maps to a 10 × 10 km equal-size area grid (ETRS89). We considered the species potentially present in a 10 × 10 km cell if the grid cell contained at least one suitable habitat.

Species biomass density

To estimate species biomass densities (D), we employed a model similar to the one developed by (S Santini et al. 2018b). In particular, we fitted vertebrate densities using the TetraDENSITY database (S Santini et al. 2018a), after keeping only records within Europe, and, as predictors, species body mass, net primary productivity (NPP), precipitation seasonality (PCV), temperature, and taxonomic order. As some species didn't have body mass information, we performed a multiple imputation by chained equation using the package *mice* (S van Buuren and Groothuis-Oudshoorn 2011) and the taxonomic family and order as covariates. All chains had similar mean and standard deviation, the influence of missing data on estimate uncertainty was low (0.077), and the average relative efficiency was high (0.993), all indicating robust imputations. NPP, PCV, and temperature were obtained from the CHELSA database (S Karger et al. 2017), using the normalized difference vegetation index (NDVI), the precipitation coefficient of variation, and the average annual temperature averaged from 1981-2005. Body mass of species was obtained from (S Trochet et al. 2014, S Wilman et al. 2014, S Slavenko et al. 2016). We also included as predictors the quadratic terms of body mass, NPP, and PCV, as these were shown to play an important role in determining vertebrate densities (S Santini et al. 2018b).

From the full model, we used a multi-model averaging approach using the package MuMIn (S "Barton, K. (2022) MuMIn 1.46.0: Multi-Model Inference. R package version. <https://CRAN.R-project.org/package=MuMIn>" n.d.). In particular, we averaged coefficient estimates across all models that had $\Delta AIC \leq 2$ from the best model; we used the full average, i.e. including a coefficient as zero when it was not present in a model, as conditional average can lead to overestimates of model parameters (S Grueber et al. 2011). Each taxonomic class (i.e. birds, mammals, reptiles, and amphibians) was modeled separately, resulting in four total sets of

averaged estimates that were used to predict vertebrate densities in Europe. Importantly, we also mapped where linear models extrapolated in geographic space, which can be used as a proxy for the confidence we have in our results (Fig. S1). We used these models to estimate the biomass density for all European vertebrates in the study area. A potential issue here is inaccuracies in the density estimates originating from extrapolation outside the body mass range of the linear models. Moreover, as some taxonomic orders were present in TETRA-EU, but not in TetraDENSITY (e.g. Chiroptera), our models lacked coefficient estimates for such orders. To solve this problem, we calculated these coefficients as the average across all other taxonomic orders that were available; despite solving the practical computational issues, we acknowledge that this approach may introduce several biases in the calculation of fluxes.

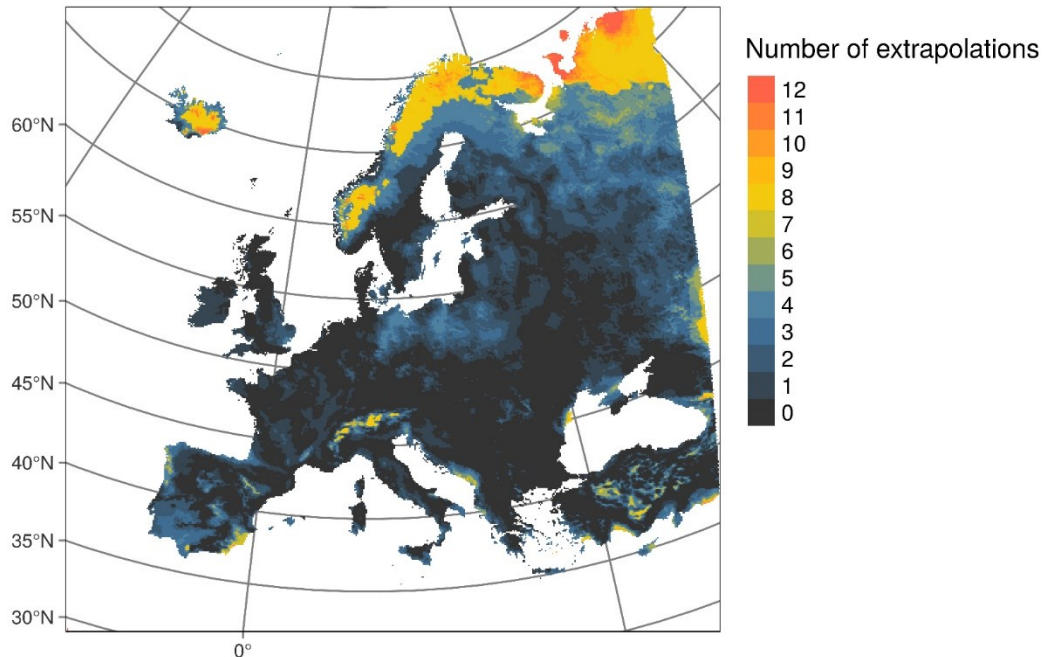


Figure S1: Extrapolations from the linear models used to estimate densities of vertebrate species, mapped across the European continent.

We then used the geographic distribution of species as obtained from (S Maiorano et al. 2013), which combines the extent of occurrence of each species with their habitat requirements. In particular, we upscaled the original data from $1 \times 1 \text{ km}^2$ to our resolution of $10 \times 10 \text{ km}^2$; to each upscaled cell, we assigned a new value that was computed as the fraction (F) of the cells where the species occurred at the higher resolution. This layer was then used in two ways: on one side, it was converted to a binary occurrence distribution for the species, i.e. we assumed the species was present if $F > 0$; on the other, we weighted the expected species densities (calculate at $10 \times 10 \text{ km}^2$) by the fraction of area that was suitable, hence correcting species densities for the fraction of suitable area: $D = D \cdot F$.

Taxonomic harmonization

As original sources for taxonomic names were different across datasets, we harmonized the species names against a common taxonomic backbone. As datasets comprised multiple taxonomic groups and had regional to global scope, we chose GBIF, a multi-taxa, global backbone, to harmonize taxonomic names (S Grenié et al. 2022). GBIF was accessed through package *rgbif* (3.6.0) in December 2021. We first appended all taxonomic names from all datasets into one list of 25,688 unique species names, which were then queried in GBIF to obtain the accepted taxonomic name. When the first iteration on GBIF (using *name_backbone()*) did not return an accepted name, we ran a second step (using *name_usage()*) where we used the GBIF

key for the taxonomic name to query the database. A total of 2,243 species names were re-assigned, including changes in taxonomic families.

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Appendix D: Supplementary – Chapter 4

Supporting Information – S1

Table S1: description of sampling methods in each site

Site Location	Group	Sampling method	Number of plots	Area per plot m ²	Soil core	Sampling date	Body mass estimation
USA, Canada	Macrofauna	litter sieving, hand sorting	80	0.5	NA	2016 - 2017	length-mass regressions from Wardhaugh 2013, Sohlström et al. 2018
USA, Canada	Mesofauna	1 soil core, heat-extraction	80	0.00196	5cm diameter, 10 cm depth	2016 - 2017	length-mass regressions for specific taxa from Mercer et al. 2001
Germany	Macrofauna	2 soil cores, heat-extraction	48		20cm diameter, two samples per plot	2008 - 2011	measured or estimated with mass-length regressions from Ehnes et al. 2014
Germany	Macrofauna	litter sieving, mustard extraction	48	0.25	NA	2008 - 2011	measured or estimated with mass-length regressions from Ehnes et al. 2014
Germany	Mesofauna	2 soil cores, heat-extraction	48		5cm diameter, two samples per plot	2008 - 2011	measured or estimated with mass-length regressions from Ehnes et al. 2014
Indonesia	Mesofauna	2 soil cores, heat-extraction	32	0.0256	litter + 5cm depth	2013	length-mass regressions were used for Collembola: dry weight (Peterson 1975)
Indonesia	Macrofauna	litter sieving, heat-extraction	32	3	NA	2012	length-body mass regressions were used to estimate spp body mass (Sohlström et al. 2018)

Supporting Information – S2

Additional environmental variables descriptors

In order to explore the effect of additional environmental and edaphic variables on our analysis, we extracted the human footprint index based on data on human pressures at 1 km² resolution (from 1993 and 2009) (Venter et al. 2016). Current global scale land-change classifications were extracted from van Asselen and Verburg (2012) at a 5-arcminute resolution (Table S2). Original land-use maps were converted to numerical data, following Pouzols et al. (2014) and Eitelberg (2018), with values imputation for the missing categories (Table 1 - S2). Other environmental variables were available from the respective projects for each community: litter layer was measured (cm) and weighted (g/m²); carbon and nitrogen content were measured in the soil (dry weight), and used to calculate C: N ratio. We used the georeferences of the communities' location and study years in a 0.05 degrees unit to extract NDVI (from 2000 to 2018) (MOD13C2 Series – Didan, 2015).

Table S2: Current global scale land-change classifications were extracted from Van Asselen & Verburg (2012) and Eitelberg (2018)

Land System	Pouzols et al. (2014)	Eitelberg (2018)	Imputation	Final intensity value
Cropland; extensive, few livestock	0.4	0.4		0.4
Cropland; extensive, bovines, goats & sheep		0.4		0.4
Cropland; extensive, pigs & poultry			0.45	0.45
Cropland; medium intensive, few livestock	0.3	0.3		0.3
Cropland; medium intensive, bovines, goats & sheep		0.3		0.3
Cropland; medium intensive, pigs & poultry			0.35	0.35
Cropland; intensive, few livestock	0.2	0.2		0.2
Cropland; intensive, bovines, goats & sheep		0.2		0.2
Cropland; intensive, pigs & poultry			0.25	0.25
Mosaic cropland and grassland; bovines, goats & sheep		0.8		0.8
Mosaic cropland and grassland; pigs & poultry			0.85	0.85
Mosaic cropland (ext.) and grassland; few livestock	0.7	0.7		0.7
Mosaic cropland (med. int.) and grassland; few livestock	0.6	0.6		0.6
Mosaic cropland (int.) and grassland; few livestock	0.5	0.5		0.5
Mosaic cropland and forest; pigs & poultry			0.55	0.55
Mosaic cropland (ext.) and forest; few livestock	0.7	0.7		0.7
Mosaic cropland (med. int.) and forest; few livestock	0.6	0.6		0.6
Mosaic cropland (int.) and forest; few livestock	0.5	0.5		0.5
Dense forest	1	1		1
Open forest, few livestock	0.9	0.9		0.9
Open forest, pigs & poultry			0.95	0.95

Mosaic grassland and forest	1	1	1
Mosaic grassland and bare	1	1	1
Grassland, natural	1	1	1
Grassland, few livestock	0.9	0.9	0.9
Grassland, bovines, goats & sheep		0.9	0.9
Bare	0.1	1	1
Bare, few livestock	0.9	0.9	0.9
Peri-urban & villages	0.1	0.1	0.1
Urban	0.1	0	0

Supporting Information – S3

To evaluate if additional environmental variables affect body mass-abundance relationships across local communities, we used Linear Mixed Effects Models that relate the previously evaluated slopes of the body mass-abundance relationship for each soil animal community to the local community's body mass range and environmental variables (soil temperature, precipitation, land-use intensity, soil pH, human footprint index, the carbon content in the soil, litter layer mass and depth, C: N rate in the soil, water content in the soil). Based on a correlation analysis of all environmental variables, we removed NDVI from the model due to its high correlation with soil temperature. The mixed-modeling approach was used to account for potential spatial autocorrelation by using the `corGaus` function from `nlme` package (Pineiro et al. 2020), which required the use of a randomly parameterized dummy variable as a random effect (note that the `corGaus` function is only available for mixed-effects models that require a random effect variable). Each of the independent variables was added as a linear term, without interactions. We started with the full model comprising all independent variables and selected the best-fitting model by the 'dredge' function of the `MuMIn` package (Barton 2022), using the Bayesian information criterion (BIC) for model comparison ($\Delta\text{BIC} < 2$).

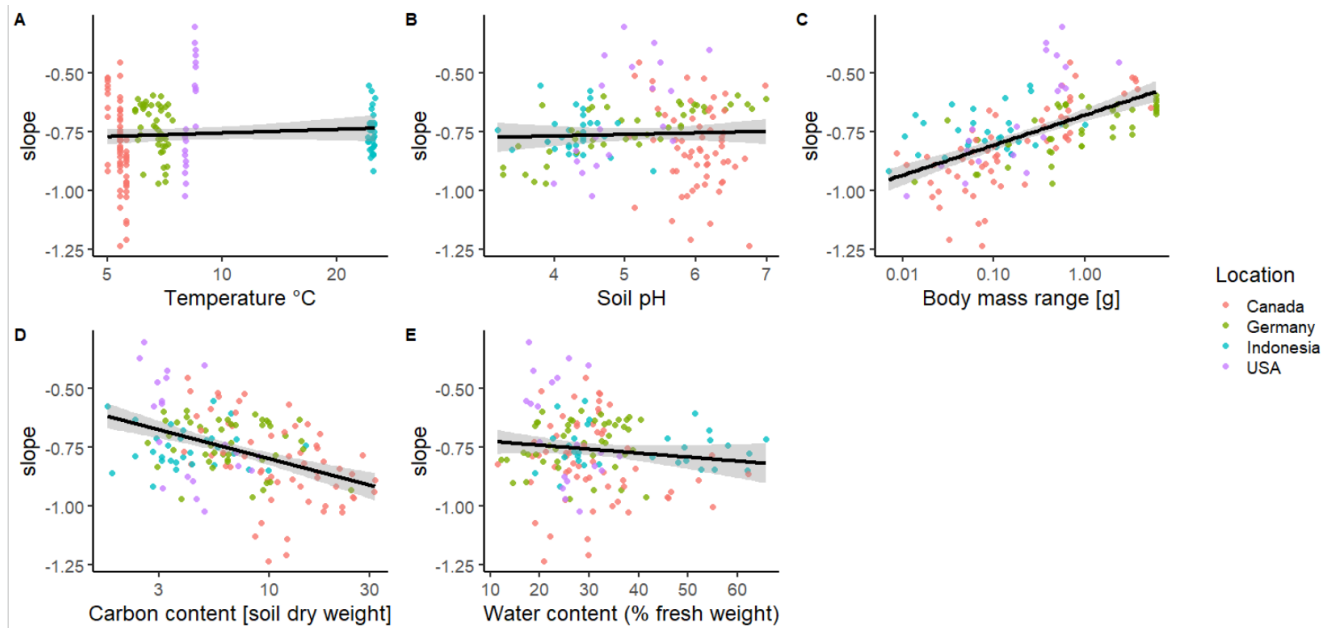
The two most supported models ($\Delta\text{BIC} < 2$) were used to generate model-averaged estimates of the parameters using the 'model.avg' function from the `MuMIn` package. Model-averaged estimates from the top models ($\Delta\text{BIC} < 2$) included the body-mass range, water content in the soil, soil carbon content and temperature. This final model reveals linear increases in the slope with increasing body-mass range, soil temperature and water content and decreases with increasing

soil carbon content (Table 1 - S3). The general relationships between the slopes and the variables selected in the final model were illustrated in Figure 1 (S3).

Table S3: Summary of the parameter estimates of the final Mixed-Effect Model (conditional average) for slope prediction. Estimates, standard errors and p-value for the Z-statistic are indicated.

Predictors	Estimates	Std. Error	Pr(> z)
(Intercept)	-0.63931	0.15688	4.72 x 10 ⁻⁵
log body mass range	0.10926	0.01452	< 2 x 10 ⁻¹⁶
log carbon content	-0.16443	0.03951	3.61 x 10 ⁻⁵
log soil temperature	0.13989	0.05617	0.0135
soil pH	0.03220	0.01321	0.0156

Figure S3: Relationships between the slopes of the body mass-abundance relationship in the communities in each location (colored symbols) with **A.** mean soil temperature (\log_{10}), ($y = -0.81 + 0.051x$, $R^2 = 0.0063$), **B.** soil pH, ($y = -0.79 + 0.0066x$, $R^2 = 0.0015$), **C.** body mass range of the communities (\log_{10}), ($y = -0.68 + 0.13x$, $R^2 = 0.35$), **D.** soil carbon content (\log_{10}), ($y = -0.56 - 0.24x$, $R^2 = 0.18$) and **E.** water content in the soil (% fresh weight), ($y = -0.71 - 0.0017x$, $R^2 = 0.0014$).



Supporting Information – S4

To describe general body mass-abundance relationships across communities, we fitted a linear model pooling the abundance and mass data of the species for all sites. We ran a linear regression of the dependence of each species \log_{10} abundance on the \log_{10} body mass and edaphic variables (soil temperature, precipitation, land-use intensity, soil pH, human footprint index, the carbon content in the soil, litter layer mass and depth, C: N rate in the soil, water content in the soil). Based on a correlation analysis of all environmental variables, we removed NDVI from the model due to its high correlation with soil temperature. Each of the independent variables was added as a linear term, without interactions. We started with the full model comprising all independent variables and selected the best-fitting model by the 'dredge' function of the MuMIn package (Barton 2022), using the Bayesian information criterion (BIC) for model comparison ($\Delta\text{BIC} < 2$).

The two most supported models ($\Delta\text{BIC} < 2$) were used to generate model-averaged estimates of the parameters using the 'model.avg' function from the MuMIn package. Model-averaged estimates from the top models ($\Delta\text{BIC} < 2$) included body mass, human footprint index, land-use intensity, litter layer depth, soil temperature, soil pH and water content in the soil). This final model reveals linear increases in the species abundance with increasing human footprint index and land-use intensity and decreases with increasing species body mass, litter layer depth, soil temperature, soil pH and water content in the soil (Table 2 - S2). Our model can be used in future predictions to assess the abundance of soil species for large-scale projections.

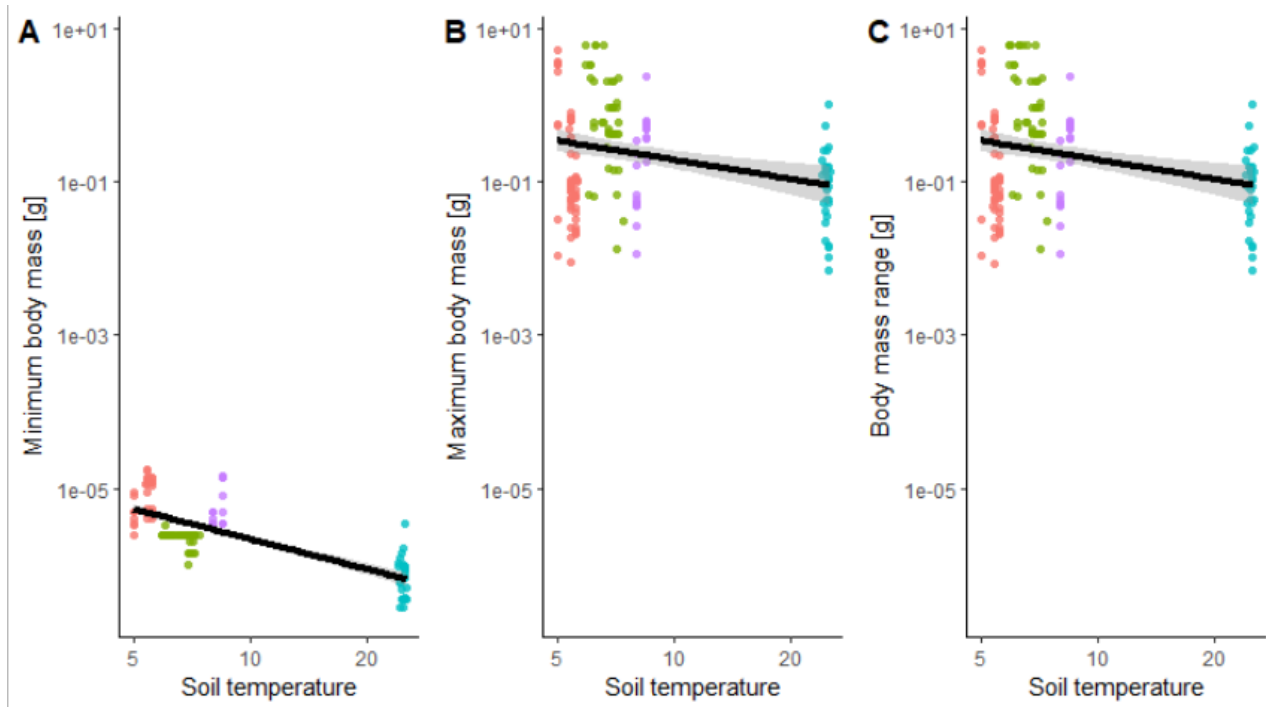
Table S4: Summary of the parameter estimates of the final Mixed-Effect Model for species abundances prediction. Estimates, standard errors and p-value for the Z-statistic are indicated.

Predictors	Estimates	Std Error	Pr(> z)
(Intercept)	1.882579	0.124495	< 2 x 10 ⁻¹⁶
human footprint index	0.006876	0.001473	3.07 x 10 ⁻⁶
land-use intensity	0.246828	0.038845	< 2 x 10 ⁻¹⁶
litter layer depth	-0.020904	0.006052	0.000553
log soil temperature	-2.818322	0.050278	< 2 x 10 ⁻¹⁶
log body mass	-0.743859	0.006296	< 2 x 10 ⁻¹⁶
soil pH	-0.090023	0.011250	< 2 x 10 ⁻¹⁶
log water content	-0.162260	0.058978	0.005945

Supporting Information – S5

To evaluate how the body-mass range of the communities varies along the gradient of temperature, we ran linear regressions of the dependence of **A.** \log_{10} minimum body mass (g), **B.** \log_{10} maximum body mass (g) and **C.** \log_{10} body-mass range (g) (difference between maximum and minimum body masses) on soil temperature ($^{\circ}\text{C}$) for each of the 155 communities using the `lm` function in R (R Core Team, 2020).

Figure S5: Relationships between the soil temperature (\log_{10}) in each location (colored symbols) with **A.** minimum body mass (\log_{10}) ($y = -4.4 - 1.3x$, $R^2 = 0.63$) **B.** maximum body mass (\log_{10}) ($y = 0.12 - 0.83x$, $R^2 = 0.078$) and **C.** body mass range (\log_{10}) ($y = 0.12 - 0.83x$, $R^2 = 0.078$) in each community.



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Appendix E – Declaration forms

Contribution to figures

Manuscript No. 1

Short reference: Antunes et al. 2022, Ecology

Contribution of the doctoral candidate

Contribution of the doctoral candidate to figures reflecting experimental data (only for original articles):

Figure(s) # 1	<ul style="list-style-type: none"><input checked="" type="checkbox"/> 100% (the data presented in this figure come entirely from experimental work carried out by the candidate)<input type="checkbox"/> 0% (the data presented in this figure are based exclusively on the work of other co-authors)<input type="checkbox"/> Approximate contribution of the doctoral candidate to the figure: 20% Brief description of the contribution: <i>(Figure 1 – map with points distribution)</i>
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Figure(s) # 2-5	<ul style="list-style-type: none"><input type="checkbox"/> 100% (the data presented in this figure come entirely from experimental work carried out by the candidate)<input checked="" type="checkbox"/> 0% (the data presented in this figure are based exclusively on the work of other co-authors)<input type="checkbox"/> Approximate contribution of the doctoral candidate to the figure: ____% Brief description of the contribution:
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Manuscript No. 2

Short reference: Antunes et al. 2023 (in prep.)

Contribution of the doctoral candidate

Contribution of the doctoral candidate to figures reflecting experimental data (only for original articles):

Figure(s) # 1-4	<input checked="" type="checkbox"/>	100% (the data presented in this figure come entirely from experimental work carried out by the candidate)
	<input type="checkbox"/>	0% (the data presented in this figure are based exclusively on the work of other co-authors)
	<input type="checkbox"/>	Approximate contribution of the doctoral candidate to the figure: _____% Brief description of the contribution: <i>(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)</i>

Figure(s) # 5	<input type="checkbox"/>	100% (the data presented in this figure come entirely from experimental work carried out by the candidate)
	<input checked="" type="checkbox"/>	0% (the data presented in this figure are based exclusively on the work of other co-authors)
	<input type="checkbox"/>	Approximate contribution of the doctoral candidate to the figure: _____% Brief description of the contribution: <i>(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)</i>

Figure(s) # S1-S4	<input type="checkbox"/> 100% (the data presented in this figure come entirely from experimental work carried out by the candidate)
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	<input type="checkbox"/> Approximate contribution of the doctoral candidate to the figure: _____% Brief description of the contribution: <i>(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)</i>

Manuscript No. 3

Short reference: Antunes et al. 2023 (under review – TREE)

Contribution of the doctoral candidate

Contribution of the doctoral candidate to figures reflecting experimental data (only for original articles):

Figure(s) # 1	<ul style="list-style-type: none"><input checked="" type="checkbox"/> 100% (the data presented in this figure come entirely from experimental work carried out by the candidate) <input type="checkbox"/> 0% (the data presented in this figure are based exclusively on the work of other co-authors) <input type="checkbox"/> Approximate contribution of the doctoral candidate to the figure: _____% Brief description of the contribution: <i>(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)</i>
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Figure(s) # I, S1	<ul style="list-style-type: none"><input type="checkbox"/> 100% (the data presented in this figure come entirely from experimental work carried out by the candidate) <input checked="" type="checkbox"/> 0% (the data presented in this figure are based exclusively on the work of other co-authors) <input type="checkbox"/> Approximate contribution of the doctoral candidate to the figure: _____% Brief description of the contribution: <i>(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)</i>
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Manuscript No. 4

Short reference: Antunes et al. 2022, Oikos

Contribution of the doctoral candidate

Contribution of the doctoral candidate to figures reflecting experimental data (only for original articles):

Figure(s) # 1-3, S3, S4	<input checked="" type="checkbox"/>	100% (the data presented in this figure come entirely from experimental work carried out by the candidate)
	<input type="checkbox"/>	0% (the data presented in this figure are based exclusively on the work of other co-authors)
	<input type="checkbox"/>	Approximate contribution of the doctoral candidate to the figure: _____% Brief description of the contribution: <i>(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)</i>

Ehrenwörtliche Erklärung

Ich versichere, dass mir die geltende Promotionsordnung bekannt ist (Promotionsordnung der Fakultät für Biowissenschaften der Friedrich-Schiller-Universität Jena vom 23.09.2019), ich die Dissertation selbstständig und ohne unerlaubte Hilfe Dritter angefertigt habe, keine Textabschnitte Dritter oder eigener Prüfungsarbeiten ohne Kennzeichnung übernommen habe und alle benutzten Hilfsmittel, persönlichen Mitteilungen und Quellen in der Arbeit angegeben habe. Alle Stellen, die inhaltlich oder wörtlich aus Veröffentlichungen stammen sind kenntlich gemacht. Ich habe keine Hilfe einer kommerziellen Promotionsvermittlung in Anspruch genommen und Dritte haben weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Folgende Personen haben mich bei der Auswahl und Auswertung des Materials sowie bei der Herstellung der einzelnen Manuskripte unterstützt: Ulrich Brose, Benoit Gauzens, Myriam Hirt, Emilio Berti, Louise M.J. O'Connor, Wilfried Thuiller, Dirk N. Karger, Laura J. Pollock, Anelise Montanarin, Diogo Maia Gräbin, Erison dos Santos Monteiro, Fernando Ferreira de Pinho, Guilherme Costa Alvarenga, Fabricio Baccaro, Anton M. Potapov, Malte Jochum, Luca Santini, Nico Eisenhauer, Olga Ferlian, Simone Cesarz, Stefan Scheu. Nähere Angaben sind den *Author Contributions* und Forschungskapiteln zu entnehmen.

Diese Dissertation lag noch nicht als staatliche oder andere wissenschaftliche Prüfungsarbeit einer Prüfungsbehörde vor und wurde bisher noch nicht veröffentlicht. Ich habe die gleiche, eine in wesentlichen Teilen ähnliche oder eine andere Abhandlung bei keiner anderen Hochschule oder anderen Fakultät als Dissertation eingereicht.

Leipzig, den 15.04.2023

Ana Carolina Antunes