Investigating the global drivers of earthworm species diversity on islands

By

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Abstract

Large gaps exist in knowledge of the global patterns and drivers of biodiversity, particularly in belowground systems and island environments. Earthworms are a key group of soil invertebrates in many systems due to their ability to act as ecosystem engineers, yet our understanding of their distributions globally is limited. To investigate the drivers of earthworm species diversity on islands, I conducted literature searches to obtain lists of earthworm species on 379 islands. Earthworm species records were found for 99 of the searched islands, with many of the islands for which no species records were found comprising entire archipelagos. The relationship between earthworm species richness and each island's underlying geology, latitude, distance from the mainland, temperature, precipitation, area, and plant species richness were analyzed using a zero-truncated negative binomial regression model. As predicted, earthworm species richness was positively correlated with island area, plant species richness, and mean annual precipitation and negatively correlated with distance from the mainland. Less expected results were a strong correlation between earthworm species richness and oceanic island geology, and temperature and latitude having no effect on earthworm species richness. Species composition on islands was also explored, and the most widespread species across islands was found to be *Pontoscolex corethrurus*, a dominant invader in the tropics. Overall, it is clear that earthworm species data is severely lacking for a great number of islands, and future research should focus on further sampling of islands chosen by model predictions. In addition, future work should investigate whether drivers differ for the diversity of native versus non-native species of earthworms on islands.

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Table of Contents

1. Introduction

2. Methods

3. Results

4. Discussion

1. Introduction

1.1 Global Patterns of Biodiversity

Biodiversity encompasses the total number of species existing in various ecosystems around the world, from the tiniest organisms such as bacteria to more familiar groups such as animals (Pereira et al., 2012). Biodiversity is critical for maintaining multiple ecosystem functions (Wagg et al., 2014) and supports ecosystem services which are considered essential to human well-being, such as timber production, pollination, water purification, and pest regulation (Bennett et al., 2016; Harrison et al., 2014).

The global patterns of biodiversity are a subject which continues to be explored. At the global level, there is huge spatial variability in species richness (Kerr, 2001). Global biodiversity varies based on a multitude of factors, such as latitude, climate, elevation, and habitat heterogeneity (Kerr, 2001). In terms of latitude, biodiversity follows a general global pattern known as the latitudinal diversity gradient (LDG), in which species richness is greatest at the equator and decreases with growing proximity to the poles (Pianka, 1966). However, there are discrepancies within the LDG, such as greater rates of decline in species richness in the Northern hemisphere than the Southern hemisphere (Gaston, 2000) and peaks of species richness existing some distance from the Equator (Condamine et al., 2012). For these reasons, it is important to remember that the LDG is only a general explanation of the global patterns of species richness, and in order to fully understand its complexities we need to answer the underlying question of why biodiversity is greater in some regions and lesser in others.

The question of what is causing biodiversity to vary across Earth is one researchers have been trying to answer for a long time. Possible explanations range from total chance, to variations in temperature, to levels of ecosystem productivity (Gaston, 2000). Most hypotheses are rooted in the 'species richness-energy hypothesis' (also called the 'species richness-climate hypothesis') which predicts that regional species diversity increases with greater heat and water availability (Kerr, 2001). This hypothesis supports the fact that species richness is greater in the tropics compared to anywhere else on Earth (Kerr, 2001). Two major arguments that further explain why there is greater species richness in the tropics include: 1) the time and area hypothesis, which postulates that the greater size and longer history of tropical ecosystems allow for greater diversity in these regions, and 2) the diversification rate hypothesis, which proposes that lower rates of extinction and higher rates of speciation cause tropical regions to diversify more quickly and thus have higher levels of biodiversity (Mittelbach et al., 2007). However, the most widely accepted reasoning is that, rather than a sole primary factor or hypothesis, it is likely that several of these factors contribute to globally observed patterns of biodiversity (Condamine et al., 2012).

1.2 Biodiversity on Islands

Island ecosystems have their own unique drivers and patterns of biodiversity. Islands contribute a disproportionate amount of total global biodiversity, accommodating 15 to 20% of all terrestrial species yet comprising only 3.5% of the Earth's area (Whittaker et al., 2017). These biodiversity hotspots also support many endemic and threatened species; however, the smaller population sizes and greater vulnerability to disturbance events associated with island ecosystems also make these species more prone to extinction (Werden et al., 2020). A thorough understanding of island ecology and the drivers of biodiversity in these unique environments is thus essential to protecting biodiversity at the global scale.

Island ecology has greatly influenced evolutionary theory and allowed researchers to study and understand various ecological relationships (MacArthur & Wilson, 1967). Classic island biogeography theory maintains that there are three main features of islands that affect their ecology: size, climatic variability, and barriers to dispersal (MacArthur & Wilson, 1967). Generally, smaller islands will have reduced habitat variation and higher extinction rates and therefore support lower levels of biodiversity (MacArthur & Wilson, 1967). Furthermore, larger islands have a greater possibility of experiencing speciation, which also contributes to increased biodiversity (MacArthur & Wilson, 1967). Climatic variability affects island biodiversity by altering population stability; generally, areas with less climatic variation, such as islands located closer to the Equator, will have greater stability and thus be more efficient and arguably able to support more diversity (MacArthur & Wilson, 1967).

Barriers to dispersal, as described by MacArthur & Wilson (1967), are a range of barriers which reduce immigration rates and govern the mechanisms over which dispersal can occur. These barriers include geographical barriers such as distance from the mainland and distance from other islands, also referred to as island isolation (MacArthur & Wilson, 1967). Such barriers reduce immigration to islands which are more isolated, thus resulting in less species diversity on islands which are further from the mainland and other islands (MacArthur & Wilson, 1967). Other barriers relate to physiological factors, such as temperature and salinity, which may decrease the dispersal ability of certain taxa and prevent them from reaching and colonizing an island (MacArthur & Wilson, 1967).

Another characteristic which has the potential to affect an island's ecology is its geologic history. In general, species richness is greater on islands with a history that involves a connection to the mainland at some point in time, such as continental fragment islands (separated by tectonic movement) or continental shelf islands (potentially connected to the mainland during the last glacial maximum), than oceanic islands which have no geologic history of being connected to the mainland (Blackburn et al., 2016). Geologically older islands also often have higher species richness than younger islands, although very old islands may experience declines in species richness (Blackburn et al., 2016).

1.3 Soil Biodiversity

Our limited knowledge of aboveground biodiversity pales in comparison to the knowledge gaps that exist in the study of belowground biodiversity (Bardgett & van der Putten, 2014). What we do know about soil biodiversity is that it is very diverse, with belowground habitats often supporting a much higher proportion of biodiversity per unit area compared to aboveground habitats (Bakker et al., 2019). There are a few widely accepted explanations for why soil habitats are often more diverse than their aboveground counterparts (Thakur et al., 2020). The first is that soil organisms lack trophic specialization, meaning that a greater variety of species are needed to carry out ecosystem services across all trophic levels (Thakur et al., 2020). Secondly, it is believed that the heterogeneity of small-scale abiotic components in the soil contributes to the overall diversity of soil biota (Thakur et al., 2020). Finally, soil organisms are heterogeneous not only taxonomically, but also in size, with body widths ranging from micrometers up to millimeters (Barrios, 2007).

Although we know that soil biodiversity is vast and highly beneficial to life on Earth, its structure, global patterns, and many of the species which contribute to it are still largely unknown (Guerra et al., 2020). The knowledge gaps in soil biodiversity can be explained by two main factors. The first of these is a lack of cohesive, global-scale soil biodiversity data (Cameron et al., 2018). This limited availability of data makes it difficult to construct general global patterns, as well as to understand how soil biodiversity may be responding to global change (Nielsen et al., 2015). A second factor contributing to the knowledge gaps in soil biodiversity is the taxonomic and methodological challenges faced by researchers in the study of these belowground systems (White et al., 2020). With so many soil species still undiscovered, the lack of a clear and universal hierarchy in the organization of species, communities and ecosystems is a severe hindrance to belowground macroecological research (White et al., 2020).

1.4 Earthworm Biodiversity

Earthworms make an excellent candidate for furthering our understanding of soil biodiversity on islands for a variety of reasons. First, the relatively large size of earthworms compared to other soil organisms makes them much easier to collect and study (Nielsen et al., 2015). As a result, there is a substantial amount of published research available on earthworms, with species lists existing for most major geographic regions in the literature (White et al., 2020). Secondly, as ecosystem engineers, earthworms greatly influence soil fertility and ecosystem function through the fragmentation of litter, contribution of their casts and other wastes to soil organic matter, and integration of this organic material into deeper soil horizons via burrowing (Nielsen et al., 2015; Blouin et al., 2013). Such functions make earthworms essential to soil health and biodiversity. Other benefits to soil provided by earthworms include improved water regulation (Blouin et al., 2013), increased crop yields (van Groeningen et al., 2014), and improved soil carbon sequestration, which plays a role in climate regulation (Blouin et al., 2013). Finally, earthworms make an excellent subject for island studies due to island dispersal barriers, such as poor dispersal over ocean due to an intolerance to saltwater (Zhang et al., 2012). This limits their diversity on islands and maintains the geographical separation of populations, making earthworms on islands easy to study and allowing further research and exploration of the biogeographic processes driving island diversity (Zhang et al., 2012). Although island earthworm populations may be rarer and less diverse than mainland populations, earthworms are still distributed widely across the globe, with islands being no exception - another contributing factor which makes them an ideal candidate for global studies (Zhang et al., 2012).

Earthworms are an extremely diverse taxon at the global level (Reynolds, 1994). In 1992, there were about 3600 known species of terrestrial earthworms (Reynolds, 1994). This number has continued to increase over the years, with estimates reaching almost 6,000 species in 2009 (Blakemore, 2009). These numbers consist of only “true” terrestrial earthworm species, which makes up all terrestrial megadriles under the class of Oligochaeta in the Annelida phylum (Blakemore, 2009). Despite there being a huge number of earthworm records, a lack of consolidation across these studies from different regions of the world makes it difficult to provide an accurate, updated count of earthworm species and genera on a global scale. Other factors contributing to this challenge include some country lists being incomplete, especially in regions such as South America, Africa and the Middle East (Blakemore, 2009), and ongoing disagreements in taxonomic classification, particularly when it comes to differentiating newly discovered species from synonyms of already discovered species.

Our knowledge of patterns of earthworm diversity is limited but growing. On a local scale, earthworm diversity is known to be driven by properties of the soil, such as soil carbon concentration and pH, which constrain calcium availability and other resources in the soil required to support earthworm diversity (Phillips et al., 2019). Aside from soil properties, patterns of earthworm diversity can also be affected by habitat and plant cover, and on an even larger scale, climate (Phillips et al., 2019). On a continental scale, earthworm studies in Europe have found that habitat, geologic history, and climatic variables are among the most significant environmental drivers of earthworm species diversity (Rutgers et al., 2016). According to the analyses of these studies and other published literature, grassland habitats have higher earthworm species diversity while cropland, vineyard, forest and heathland habitats have lower earthworm diversity (Rutgers et al., 2016). Looking at terrestrial invertebrates more broadly, studies have found plant species richness to be a significant predictor of insect richness and to potentially have more influence on local insect diversity than abiotic variables (Kemp & Ellis, 2017). However, no large-scale studies have confirmed such a relationship between earthworms and plant species richness.

The effect of climate on earthworm species diversity can be observed on not only continental, but also global scales. Interestingly, patterns of earthworm diversity contrast significantly with the patterns observed in aboveground communities (Phillips et al., 2019). For example, studies have shown that local earthworm diversity is greatest at mid-latitudes, which is in direct opposition to the global patterns of aboveground biodiversity outlined earlier in this review, where species diversity generally decreases with increasing latitude (Phillips et al., 2019). Particular hotspots are believed to exist in the Southern parts of South America, Australia and New Zealand (Phillips et al., 2019) and additional mid-latitude areas where earthworm species diversity was estimated to be high included the Northeastern United States and parts of Europe north of the Black Sea (Phillips et al., 2019). In contrast, areas projected to have low earthworm diversity include subtropical, tropical, and subarctic regions (Phillips et al., 2019). Therefore, earthworm species diversity does not appear to follow the latitudinal diversity gradient. (Phillips et al., 2019).

Climatic variables such as temperature and precipitation appear to have a significant effect on earthworm species diversity (Phillips et al., 2019). One study along an elevation gradient of eight forest types in Northeastern Puerto Rico found that earthworm species richness was positively correlated with annual rainfall and negatively correlated with air temperature (González et al., 2007). Precipitation is believed to influence earthworm species richness because it affects soil moisture; moist conditions are generally required for earthworms to carry out normal functioning and prevent them from drying out and dying (Zorn et al., 2008). Evidence in the literature shows that earthworm abundance, distribution and diversity are often controlled by soil moisture – however, too much moisture can also impact earthworms, with overly wet soils causing most earthworm species to die within a given period of time (Singh et al., 2019). Increases in temperature can also impact soil moisture and result in dry conditions unfavourable for earthworm survival, thus negatively impacting species richness (Singh et al., 2019). Aside from affecting soil moisture, increased temperature alone can also impact earthworm species survival, with upper lethal temperatures generally falling between 25-35 ° C but varying for species in temperate zones versus the tropics (Singh et al., 2019). In contrast, extremely cold temperatures can be detrimental to earthworms as well, although the range of these lower lethal temperatures are not as well-established (Singh et al., 2019).

Research focusing specifically on drivers of earthworm species diversity on islands is limited. However, studies have found that smaller islands tend to host less earthworm species richness than larger islands (Enckell & Rundgren, 1988), and that island populations of earthworm species tend to have a larger mean length and diameter when compared to mainland populations of the same species (Ng et al., 2017). Other studies of island earthworm populations have also observed a positive relationship between island size and earthworm genetic diversity through correlation analysis (Zhang et al., 2012). In the Philippines, research has found that the rapid diversification of earthworm species occurring in this region over time, as determined by phylogenetic trees, was most likely due to changing climate, volcanism, changes in sea level, geological transformation, and other ecological factors (Aspe & James, 2018).

1.5 Objectives

Many questions remain regarding what drives earthworm species distribution on islands and on a global scale. While there are a large number of potential drivers of earthworm species diversity on islands, such as geographic variables, climatic variables, and ecological variables, these factors can also vary in different geographic areas around the world (Guerra et al., 2020). Currently, no known analyses of global island earthworm diversity patterns have been completed despite the fact that much of the data required to make an analysis already exists. Such research has the potential to facilitate further research on and contribute to our understanding of island biogeography, earthworm species distribution, and soil biodiversity as a whole.

The primary objective of this study is to assess the factors driving earthworm diversity on islands around the globe. This will be accomplished by analyzing how the earthworm species diversity on different islands is affected by island size, distance from the mainland, latitude, climate (namely temperature and precipitation), plant diversity, and the island's geological history. It is predicted that earthworm species richness will be positively correlated with island size, latitude, precipitation, and plant diversity; negatively correlated with temperature and distance from the mainland; and that islands with an oceanic geologic history will experience lower species richness than islands with geology that once connected them to the mainland, such as fragment or shelf islands.

2. Methods

2.1 Data Collection

2.1.1 Earthworm Species Data

I conducted a literature search for records of earthworm species on islands using a list of 394 islands obtained from Weigelt et al.'s island dataset (2015). Searches were limited to islands with an area under 100,000 square kilometers, leaving a total of 379 islands to be searched. First, a Web of Science literature search was performed using the following search terms: [island name] AND (earthworm*) AND (“species list*” OR “check-list*” OR “check list*” OR “survey*”). Next, a Google Scholar search using Publish or Perish software was performed for the same islands using the following search terms: [island name] AND (earthworm*) AND (“species list” OR “check-list” OR “check list” OR “survey”). The maximum number of results for Google Scholar searches was set to 50.

The titles of all returned literature were assessed for suitability, with suitable papers saved and used to compile species lists for each island. For each island, the scientific name, possible synonyms, country, genus, family, geographical origin, distribution status, and ecological category of each species was recorded in a spreadsheet if this information could be found in the paper. Additionally, the reference lists of suitable papers were reviewed for additional potential island earthworm species lists. This data was used to determine the species richness of each island. ArcGIS Pro (Esri Inc., 2020) was used to visualize this data as a global map of earthworm species richness, including the islands where no species records were found.

2.1.1 Island Characteristics Data

Other data relating to the islands was also collected to be used as explanatory variables in the analysis. Obtained from the aforementioned Weigelt et al. (2015) spreadsheet, this data included each island’s underlying geology (with possible options being fragment, oceanic, or shelf), latitude, distance from the mainland, temperature, precipitation, area, and an isolation metric of surrounding land mass proportion (SLMP). Additionally, plant species richness data from the islands grouped into angiosperms, ferns and palms was obtained from Schrader et al. (2020), and the values for each group were added together to create an overall plant richness variable.

2.2 Data Analysis

First, I tested the explanatory variables for collinearity by calculating the correlation between all possible pairs of variables. As outlined by Dormann et al. (2013), a correlation coefficient above 0.7 is a good indicator that the correlation between two variables is enough to potentially distort model estimation and prediction. The variables SLMP and distance (from the mainland) were found to be significantly correlated (with a correlation coefficient of 0.74) and the decision was made to drop SLMP as an explanatory variable in favor of the more conventional and less ambiguous distance variable.

Boxplots were used to examine the distribution of the potential explanatory variables. Next, the continuous explanatory variables were standardized and centered. A histogram was used to explore the distribution of the earthworm species richness data (see Appendix A). The data was first fit to a negative binomial regression model which showed the data was overdispersed (theta = 2.532), meaning the conditional variance is greater than the conditional mean (Ver Hoef & Boveng, 2007). However, since the data only consisted of positive values over zero, the data was then fit to a zero-truncated negative binomial regression model instead. Model fit was assessed using a rootogram, which is a graphical technique used to assess the goodness of fit of a model based on how closely the bottom of the data's frequency bars are to a reference line (Yee, 2020) (see Appendix B). Finally, the predicted earthworm species richness values from the regression model were plotted against each variable, grouped by island geologic history. All of the above statistical analyses were conducted using R 4.0.2 (R Core Team, 2021). The MASS package was used for the negative binomial regression (Venables & Ripley, 2002) and the VGAM package was used for the rootogram and zero-truncated negative binomial regression model (Yee, 2020).

3. Results

3.1 Spatial Distribution

Earthworm species records were found for 99 of the 379 islands (Figure 1). Many of the 280 islands for which no earthworm species records were found consisted of entire archipelagos, such as the Svalbard archipelago, islands in the Gulf of California, the Galápagos islands, the South Sandwich Islands, the Cape Verde archipelago, and the archipelagoes of French Polynesia. Figure 1 also shows that overall, the East Pacific Ocean had the greatest number of islands with no species records. In general, islands for which no species records were found occurred across virtually all latitudes, within all biogeographic realms, and did not appear to follow any patterns in terms of distance from the mainland.

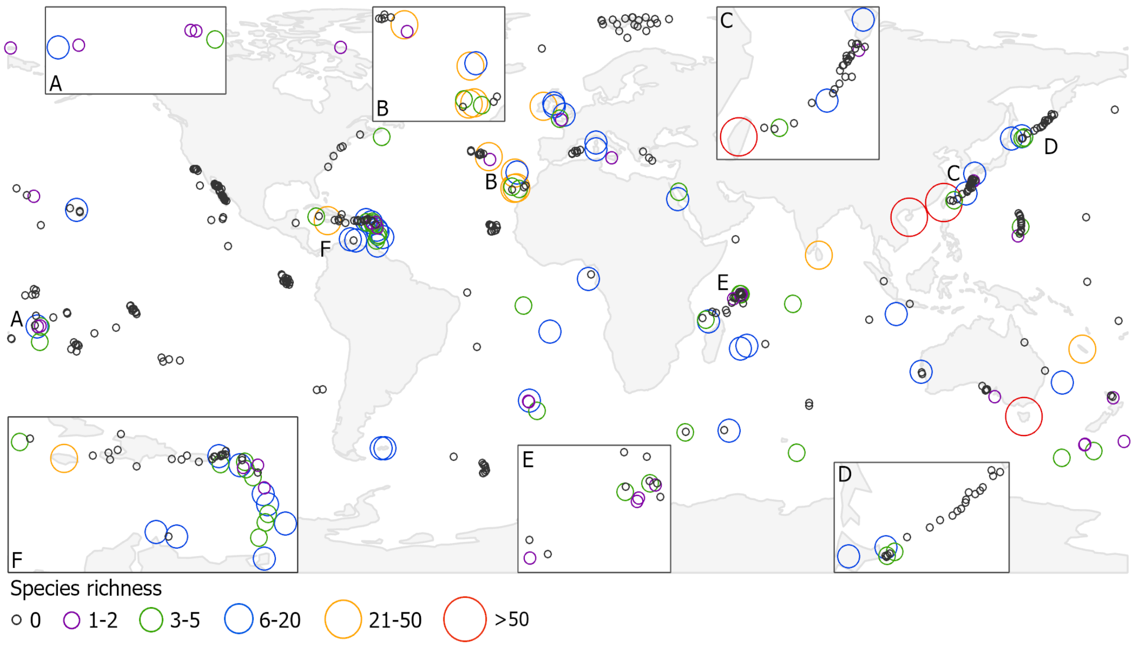

Figure 1. Global distribution of earthworm species richness on islands. The size and color of points is proportional to the number of species found. Inserts A-F provide a detailed view of areas where symbols directly overlap.

Higher species richness counts appear to occur on islands closer to the mainland (Figure 1), especially for those with species counts over 20, and all of the islands with a species richness greater than 50 were only a short distance from the mainland (< 350 km). The islands of Tasmania, Taiwan, and Hainan had the highest earthworm species richness with counts of 230, 137, and 55 species respectively. Other areas of moderate to high earthworm species richness counts included the Caribbean islands (Figure 1, inset map F), Macaronesia (Figure 1, inset map A), the British Isles, the Coral Sea, and the Indian Ocean. Notable areas of low species richness were the Kuril Islands (Figure 1, inset map D), Micronesia, Seychelles (Figure 1, inset map E), and most of the Pacific Ocean (excluding islands off the coasts of Australia and China). There was also very low species richness in the Arctic and Antarctic circles; however, there are also very few islands within the dataset that fall in these regions, with the majority making up the Svalbard archipelago. Overall, species richness appears to be greatest in the middle latitudes, with some notable areas of moderately high species richness in the tropics (Figure 1).

3.2 Species Richness Analysis

Earthworm species richness was strongly correlated with island area and distance from the mainland (Table 1). Earthworm species richness increased with island area (coefficient = 0.42, $p < 0.001$) and decreased with distance from the mainland (coefficient = -0.39, $p = 0.003$), as can be seen from the relationships in Figure 2 (a) and (b). There was also a positive relationship between earthworm species richness and annual mean precipitation (Figure 2 d). Earthworm species richness was also positively and strongly correlated to plant species richness (Figure 2 (f); coefficient = 0.54, $p < 0.001$). Overall, islands with an oceanic geologic history were associated with consistently higher earthworm species richness across each of the other six explanatory variables, followed by shelf and then fragment islands (Figure 2).

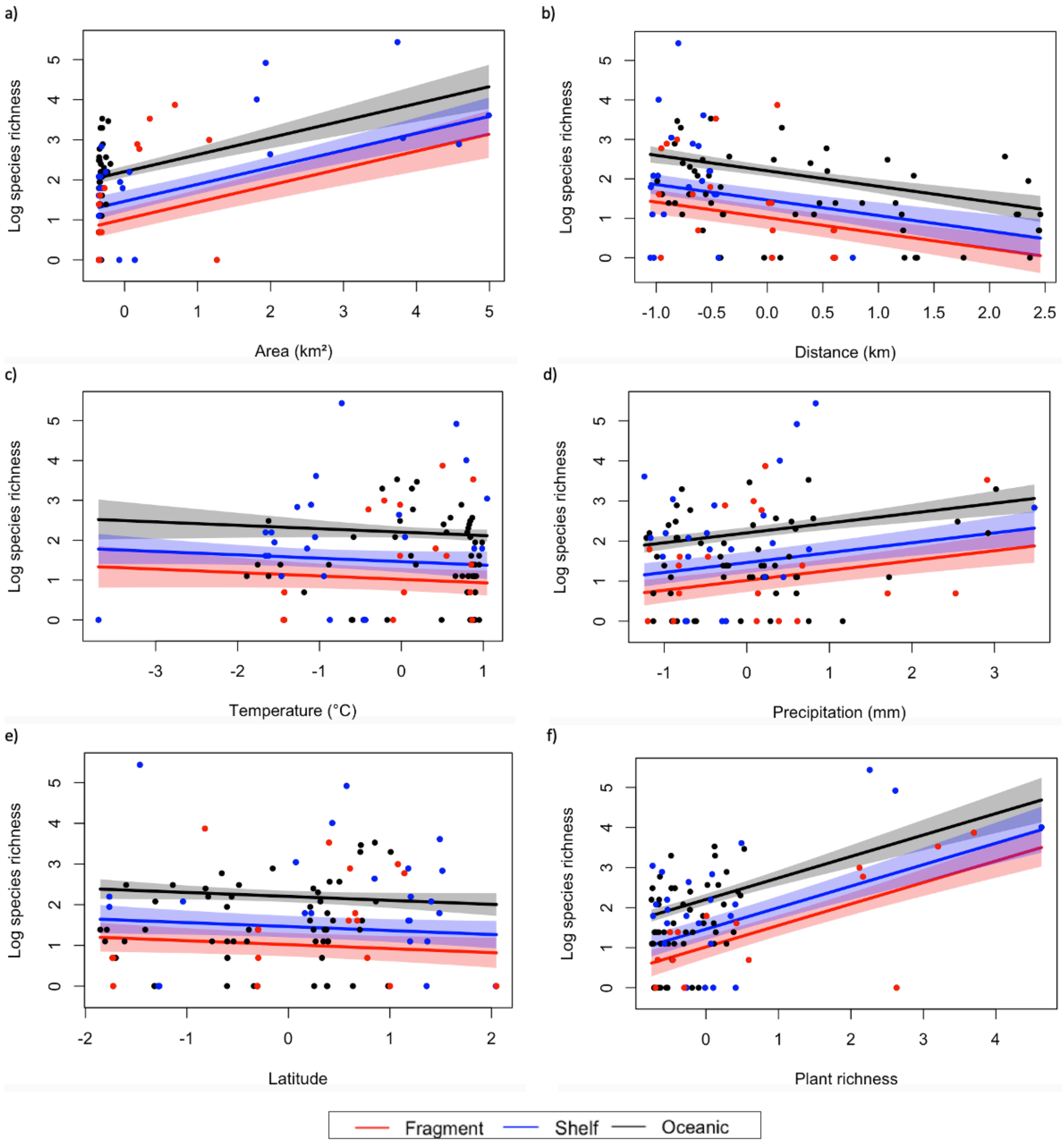

Figure 2. Relationships between island characteristics and earthworm species richness by geology type. Red indicates islands with a fragmented geologic history; blue indicates islands with a shelf geologic history; and black indicates islands with an oceanic geologic history. Variables in plots (a)-(f) are standardized values and refer to island area (km^2), distance from the mainland (km), mean annual temperature (°C), mean annual precipitation (mm), latitude, and plant species richness.

Earthworm species richness was most strongly correlated with island area, plant species richness, and oceanic geologic history (Table 1). To a lesser extent, earthworm species richness was also significantly correlated to annual mean precipitation (coefficient = 0.25, p-value = 0.008) and distance from the mainland (Table 1). In terms of island geology, earthworm species richness was significantly higher on islands with oceanic geologic history (coefficient = 1.19; p-value < 0.001) compared to those with a shelf or fragment history, which did not have an effect on earthworm species richness. The variables of latitude and temperature also did not affect earthworm species richness (Table 1).

Table 1. Zero-truncated negative binomial model examining the relationships between island characteristics and earthworm species richness. Variables are standardized values and refer to latitude, distance from the mainland (km), island area (km^2), mean annual temperature (°C), mean annual precipitation (mm), plant species richness, and underlying island geology.

Variable	Estimate	SE	*Z*	*P*
(Intercept): 1	1.02	0.29	3.54	<0.001
(Intercept): 2	0.55	0.26	2.12	0.034
Latitude	-0.10	0.11	-0.87	0.385
Distance	-0.39	0.13	-3.02	0.003
Area	0.42	0.10	4.21	<0.001
Temperature	-0.09	0.12	-0.72	0.470
Precipitation	0.25	0.09	2.64	0.008
Plant richness	0.54	0.11	4.80	<0.001
Geology (oceanic)	1.19	0.33	3.64	<0.001
Geology (shelf)	0.44	0.38	1.18	0.240

3.3 Species Composition

The peregrine species *Amynthas rodericensis*, *Bimastos rubidus*, *Dichogaster bolaui*, *Lumbricus rubellus*, and *Pontoscolex corethrurus* were all found on 19 or more different islands, representing 5% of all islands searched, or 19% of islands where earthworm species records were found (Table 2). The most commonly occurring earthworm species was *Pontoscolex corethrurus*, found on 9% of all islands searched and 36% of islands where earthworm species records were found (Table 2). The species with the second highest occurrence was *Bimastos rubidus*, occurring on a total of 31 islands which represents 8% of all islands searched and 31% of islands where earthworm species records were found (Table 2).

Table 2. Most commonly occurring earthworm species on islands. Occurrence refers to the number of islands a given species was found on.

Species name	Occurrence
Allolobophora chlorotica	15
Amynthas rodericensis	19
Aporrectodea caliginosa	14
Aporrectodea rosea	15
Bimastos rubidus	31
Dichogaster bolaui	21
Eiseniella tetraedra	16
Eudrilus eugeniae	16
Lumbricus rubellus	19
Pontodrilus litoralis	14
Pontoscolex corethrurus	36

4. Discussion

4.1 Spatial Patterns

This study provides evidence that earthworms are widely distributed not only across continents, but also on islands, and follow spatial patterns that are unique when compared to aboveground organisms. Patterns of earthworm species richness on islands do not appear to follow traditional patterns of aboveground biodiversity such as the latitudinal diversity gradient, with the islands of highest species richness (namely Tasmania and Taiwan) and many other areas of high species richness (such as northern Macaronesia and the British Isles) occurring in the middle latitudes. This directly contrasts with patterns of biodiversity aboveground, where species richness generally decreases with increased latitude (Gaston, 2000). This contrasting pattern in belowground biodiversity is consistent with the results of other studies looking at global patterns of earthworm species diversity, which found high local earthworm species richness in the mid-latitudes (Phillips et al., 2019). Other groups of small aboveground and belowground invertebrates such as aphids, bees and nematodes have also been found to have peak species richness in the mid- to high latitudes (De Deyn & Van der Putten, 2005).

Another spatial pattern which was evident from Figure 1 was that species richness was typically higher on islands closer to the mainland. This is supported by the observation that every island with a species richness greater than 50, and most with a species richness greater than 20, were located a relatively short distance from the mainland. In addition to this, even moderate to high species richness was rarely seen on islands a great distance from the nearest continent. This spatial observation of higher species richness on islands closer to the mainland was expected, given classic island biogeography theory which states that islands further from the mainland will have less species diversity (MacArthur & Wilson, 1967).

There were also spatial patterns with respect to the islands for which no earthworm species records were found. In many cases, entire archipelagos were found to have no earthworm species records, and this appeared to be a large contributor to the 280 of 379 searched islands (almost 74%) for which no species lists were returned. There also appeared to be a high occurrence of islands in the tropical latitudes of the East Pacific Ocean which lacked earthworm species richness counts. Given these spatial patterns, I would suspect that in most cases, these islands do not completely lack earthworm species, but instead have simply not been surveyed at length. It is a well-known fact that island biodiversity is among the most poorly recorded (Churchyard et al., 2016), and combined with the huge knowledge gaps that exist between belowground and aboveground biodiversity (Bardgett & van der Putten, 2014), it is safe to assume that many of the 280 islands where no species were found are more reflective of gaps in the literature than a lack of earthworm species. However, for some archipelagos such as the Galápagos islands, which are known to be relatively well-studied, it was surprising to find no earthworm species lists. In these cases, it is also possible that either the species lists exist but were not found in our extensive literature review; or published species lists were compiled for the entire archipelago, making it impossible to determine which earthworm species came from which island and thus the species lists had to be excluded from this study.

4.2 Drivers of Species Richness

As predicted, earthworm species richness was strongly correlated with the size of the island and its distance from the mainland. The island species-area relationship, which describes how species richness increases with increasing island area, is well established in the literature and thus it comes as little surprise that our findings also support a strong positive relationship between earthworm species richness and island area (Liu et al., 2019).

Other studies have also found island area to be the greatest predictor of ant species richness, followed by distance to the nearest continent (Roura-Pascual, Sanders, & Hui, 2016). Although research focused specifically on earthworm species richness and islands is rare, there are instances in the literature where the number of earthworm species was greater on larger islands compared to smaller ones (Enckell & Rundgren, 1988). The effects of distance to the mainland on island species diversity is also well examined as a common barrier to dispersal in classic island biogeography theory (MacArthur & Wilson, 1967). This pattern has been found with invertebrate groups such as Macaronesian spiders, for which species richness was negatively and significantly related to distance from the mainland (Cardoso et al., 2010). Therefore, a strong negative correlation between earthworm species richness and distance from the mainland was also anticipated.

In my results, earthworm species richness was also found to be strongly and positively correlated with plant species richness. Although the strength of this result was less expected, it is reasonable that islands with greater plant diversity would have greater earthworm diversity due to the observed links between aboveground and belowground biodiversity (De Deyn & Van der Putten, 2005) and the relationship between greater habitat heterogeneity and increased soil fauna species richness (Vanbergen et al., 2007). Furthermore, other studies have reported a positive correlation between lumbricid species richness and vascular plant species richness (Vanbergen et al., 2007), as well as positive correlations between insect richness and plant species richness (Kemp & Ellis, 2017).

Another predicted result of this study was the positive correlation between precipitation and earthworm species richness. This result was expected because precipitation increases soil moisture, which is essential to earthworm survival, and can increase litter fall, which provides more habitat, nutrients, and protection to earthworms which will in turn facilitate greater species diversity (Singh et al., 2019). This result is also supported in the literature by studies which have found that precipitation was among the most important drivers of global earthworm species richness (Phillips et al., 2019) and that earthworms share a positive relationship with precipitation on local, regional and global scales (Singh et al., 2019). A less expected result was that temperature had no effect on earthworm species richness, despite my prediction that they would be negatively correlated. This could be due to the fact that different species in different parts of the world experience varying levels of resistance to extremely cold and extremely hot temperatures, both of which can be detrimental to earthworm function and survival, making it difficult to establish a consistent pattern across all islands at the global level (Singh et al., 2019).

Another result which was not anticipated was the lack of effect of latitude on earthworm species richness, despite Figure 2 appearing to show that earthworms species richness increases with latitude, in direct contrast to aboveground patterns. This pattern also agrees with other studies which have found that earthworm species richness increases with latitude (Phillips et al., 2017). A potential reason that a positive relationship was not found between latitude and earthworm species richness in this study could be the low proportion of islands at high latitudes, resulting in a less representative sample for this region. Furthermore, it is important to note that latitudinal diversity gradients have typically been examined on continents, which usually have more area towards the tropics. This might also help to explain why patterns of species richness on islands do not show similar trends with latitude.

Perhaps the most surprising result of the species richness analysis was that earthworm species richness was predicted to be highest on islands with an oceanic geologic history compared to fragment and shelf islands. Research in the literature generally finds that species richness is greater on islands with a land-bridge geologic history, such as the fragment and shelf island categories used in this analysis, versus oceanic islands which have no geologic history of being connected to the mainland (Blackburn et al., 2016). A potential reason for this could be higher earthworm species establishment outside of what can be predicted by classic island biogeography theory due to introductions facilitated by human activity. Even the most remote and seemingly pristine islands can be affected by species introduction, with one example being the oceanic Gough Island, for which 71 of its 99 recorded species are established introductions (Gaston et al., 2003).

4.3 Species Composition

All of the most commonly occurring species on islands (Table 2) were peregrine species, meaning that they are known to be distributed outside of their native range, and thus it comes as no surprise that they are also widely distributed across islands (DriloBASE, 2021). When these species are introduced outside of their native range, their subsequent biological invasion can have a variety of negative impacts on soil structure, function, plant growth and more (Hendrix et al., 2008). *Pontoscolex corethrurus*, which was found to be the most commonly occurring earthworm species across islands in this study, is a dominant invader in the tropics and has been shown in the literature to impact soil structure, nutrient cycling, litter decomposition, and plant species composition (Hendrix et al., 2008). The second most commonly occurring earthworm species across islands was *Bimastos rubidus*, which has infiltrated practically every biogeographic realm around the world (Blakemore, 2009). Previously known as *Dendrodrilus rubidus*, which is now considered a junior synonym of *Bimastos rubidus* (Csuzdi et al., 2017), this species is an excellent colonizer because it is frost tolerant, acid-tolerant, and has been found on remote rocky islands which suggests it can be transported by water (Addison, 2009). This could have implications for further spread across islands and archipelagos. Due to these negative impacts, a high occurrence of potentially invasive peregrine species across islands could be a cause for concern and highlights the importance of determining whether these species are native or non-native in order to assess how they may be impacting island environments.

4.4 Limitations and Future Research

There are some potential limitations in this study that could be addressed in future research. Pertaining to the literature search, multiple names for the same island, islands with the same name, and the searches only being conducted in English all might have affected the number of records found. Therefore, more insight into the languages used in an island's region, common names for an island, history of name changes on an island, and whether or not the island has a different name in the region's native language may reduce the potential for bias associated with monolingual searches (Nuñez & Amano, 2021). Another potential limitation to this study could be failing to constrain the literature search results by time period, which may have resulted in outdated records and the counting of species which no longer exist on an island or have experienced a name change. This also relates to the limitation of the use of synonyms, a common issue in earthworm species taxonomy which may have affected the accuracy of the species counts. Another way the island species richness counts may have been impacted was through the grouping of species lists for groups of islands or even an entire archipelago, making it impossible to separate which species originated from each island. One example of this occurred in the state of Hawaii, where the most detailed records of earthworm species were listed by county or even without a specific location at all (Reynolds, 2015). Thus, species lists were unable to be completed for many islands of Hawaii. To a lesser extent, this also impacted the Auckland Islands and the Channel Islands, where some species lists were grouped for the entire archipelago, but others were not.

Other potential limitations of this study arise from the availability of island data and earthworm species information. Originally, it was planned to use island age as a potential explanatory variable, but the amount of data for this variable was insufficient. Island age is considered a predictor of species richness in classic island biogeography theory, which is why it would have been interesting to see its effect on earthworm species richness given the strength of other classic island variables in predicting earthworm richness in this study, such as island area and distance from the mainland (MacArthur & Wilson, 1967). Another potential limitation could be the number of islands searched in this study, as a list of only 394 islands was used. This was further reduced to 379 due to there being so few islands with an area over 100,000 square km that model fit was affected, and thus these larger islands had to be excluded. Another data constraint of this study was the lack of information on the native vs. non-native status of earthworm species for each island. Such information could have important implications for biological invasions on islands and would allow for the assessment of whether drivers differ for native vs non-native species on islands, as has been found in recent research of ant species on islands (Roura-Pascual, Sanders, & Hui, 2016).

The results of this study provide many opportunities for future research. One example would be determining if the drivers of island species diversity differ for native vs. non-native species, which would allow further insight into island ecosystem health, as well as evaluation of the impact of human activity and species introductions on belowground island species diversity. Examining historical trade routes may also contribute to our understanding of human-driven species introductions on islands. Additional variables that could be explored in future research as potential drivers of earthworm species richness on islands include soil properties, such as soil moisture or pH, and other climatic variables, such as aridity and seasonality. Another avenue for future research would be exploring the overall distributions of different earthworm species to assess the relationship between island proximity and similarities in species composition. Future research could also further explore the relationship between earthworm diversity and plant species richness on islands, which was found to be strongly correlated in this study and could provide further insight on the complex aboveground-belowground interactions between soil organisms and plants, and whether or not these relationships differ on islands versus the mainland. Finally, model predictions could be used in future research to determine which islands are likely to harbour high earthworm species richness and therefore where future sampling efforts should be focused.

5. Conclusion

Earthworm species diversity on islands is a largely understudied area of research which has the potential to greatly contribute to our global understanding of belowground biodiversity. Overall, the results of this study show that the main drivers of earthworm species diversity on islands are island size, distance to the mainland, and plant species richness. Earthworm species richness is higher on islands with an oceanic geologic history, and many of the species with the highest rates of occurrence across islands, especially the most commonly found species *Pontoscolex corethrurus*, are widespread species that are potentially invasive in the areas where they were found. This study also supports other findings in the literature that belowground biodiversity follows unique patterns compared to aboveground biodiversity (Phillips et al., 2017). This research has provided important insight into what drives belowground species diversity at the global level and the composition of earthworm species on islands, allowing future studies to focus on how drivers may differ for native vs. non-native species and where future sampling efforts should be focused.

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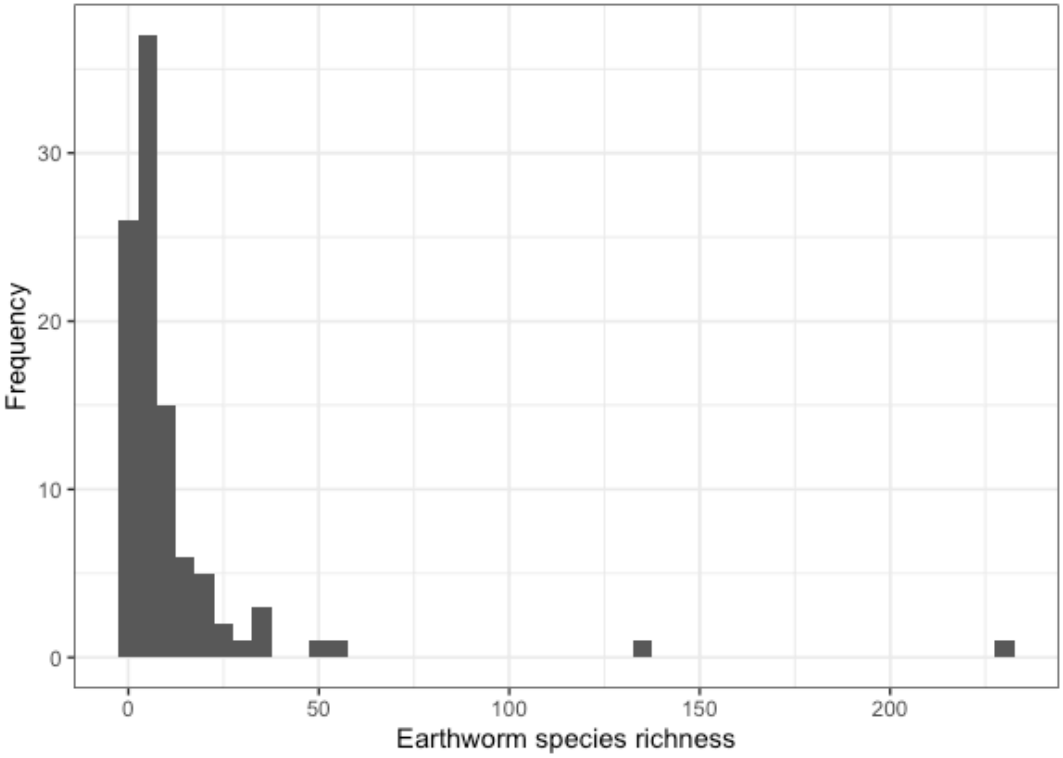
Appendix A - Histogram showing distribution of earthworm species richness data



Appendix B - Rootogram showing appropriate fit of zero-truncated negative binomial regression model