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Opposing island biogeographic effects of turnover and nestedness on beta-diversity of soil faunal communities between woodland and deforested grassland

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ABSTRACT

Human land use intensification is increasing biodiversity loss worldwide through fragmenting contiguous natural habitats into spatially isolated patches of varying sizes. However, it is poorly known as to how the area and isolation of patches operate to jointly alter biological community composition for contrasting land use types, particularly for belowground organisms. Oceanic islands that vary in human activities provide an ideal model system for examining how patch area and isolation affects community dissimilarity resulting from land use change. We conducted a paired sampling design that included both natural woodland (i.e. land covered with woody plants, including trees and shrubs) and degraded grassland for each of 20 islands differing in area and remoteness in the largest archipelago of Eastern China. We used this design to investigate how island area and remoteness shape the community dissimilarity of soil fauna between woodland and grassland directly and indirectly through changing climatic and habitat properties. The dissimilarity of soil fauna communities for each island was estimated by measuring total beta (β) diversity and its turnover and nestedness components between woodland and grassland. We found that land use change did not decrease taxa richness but did alter community composition overall. There was no relationship of island area with community dissimilarity when it was estimated by total β-diversity, due to contrasting responses of its turnover and nestedness components to island area. Soil faunal compositional dissimilarity between woodland and grassland along the area gradient was mainly related to the gain and loss of unique taxa in grassland. On small islands, nestedness was the primary contributor to total β-diversity, due to a loss of soil fauna taxa as habitats shifted from woodland to grassland, and suggests that natural habitats serve as refuges for soil organisms. Meanwhile on larger islands, turnover was the main contributor to total β-diversity, suggesting that diverse land uses can increase biodiversity across habitats. Additionally, high habitat differences combined with favorable climatic conditions (such as low wind speed) on larger islands facilitated species turnover but diminished nestedness. Meanwhile island remoteness did not affect total β-diversity or its components, but it did significantly enhance the negative impact of land-use conversion on the abundance of larger-bodied taxa. These findings suggest that island area, and therefore landscape patch area, play a crucial role in shaping the dissimilarity of soil faunal communities that stem from human land use change. Our results highlight that partitioning total β-diversity into its turnover and nestedness components is essential for understanding the impact of land use change on soil faunal community composition in fragmented habitats.

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1. Introduction

Deforestation has led to the loss of more than a third of forest cover worldwide and it continues at high rates (Hansen et al., 2013; Silva-Junior et al., 2021). Historical deforestation continues to have profound consequences on ecosystem structure and function, and thereby poses a severe threat to biodiversity (Haddad et al., 2015; Maxwell et al., 2016; Sodhi et al., 2010). The conversion of natural forests to agriculture or grassland can greatly change habitat quality, thus reshaping diversity both within local habitats (α diversity) and among habitats or land use types (β diversity) (McGoff et al., 2013; Nowakowski et al., 2018). Deforestation can homogenize biological assemblages across locations, through promoting common species and causing the decline of rarer or more specialized species (Arroyo-Rodríguez et al., 2013; Gong et al., 2023; Rodrigues et al., 2013), and thereby causes a decrease in β diversity across land use types. Further, forest fragmentation resulting from deforestation is a widespread phenomenon, in which large and contiguous forested landscapes are fragmented into small forest patches separated by an agricultural matrix (Melo et al., 2013; Tabarelli et al., 2010). As a result of this landscape reorganization, patch area and spatial isolation are crucial for determining differences in species assemblages between forest patches and the surrounding agricultural matrix (Zhao et al., 2024). However, the role that patch area and isolation play in impacting community dissimilarity across human influenced landscapes remains poorly understood.

Oceanic islands, which vary greatly in area and isolation, can serve as ideal model systems for investigating the fundamental processes of the community compositional changes induced by human land use change. Marine islands sustain an important portion of global biodiversity, and they have experienced a disproportionate loss of it through human activities (Tershy et al., 2015). During the Anthropocene, island biodiversity has changed substantially with some species becoming extinct and others spreading across islands through immigration and invasions (Helmus et al., 2014; Moser et al., 2018; Russell and Kueffer, 2019). This has led to the changing of historical island biogeographical patterns through the increasing contribution of anthropogenic factors. A common outcome is the strengthening of the species–area relationship, and the weakening of the species–isolation relationship (Helmus et al., 2014; Moser et al., 2018). In adapting island biogeography theory to the Anthropocene (Helmus et al., 2014), it is recognized that higher human land use intensity on large and less remote islands can dramatically reshape the original plant community structure and functional composition (Xu et al., 2023). This process involves a reduction in endemic and specialist species and a significant increase in generalist and invasive species, which collectively contribute to a more homogenized plant community composition (Arroyo-Rodríguez et al., 2013; Gong et al., 2023; Rodrigues et al., 2013). These vegetation changes in response to land use is likely to have cascading effects on the belowground subsystem (Wardle et al., 2004, 2012), including the structure and activity of soil faunal communities (i.e., brown food webs) resulting from shifts in litter quality (Bardgett and van der Putten, 2014; Mori et al., 2015; Potapov et al., 2020). However, little is known about how land use change determines soil faunal community dissimilarity on island ecosystems and how these effects may be impacted by variation among islands in their area and remoteness.

One of the major consequences of land use conversion from forest to grassland for soil fauna involves changes in community composition, which is mainly caused by habitat modifications that facilitate species gain and loss (McCune and Vellend, 2013; Nowakowski et al., 2018; Rodrigues et al., 2013). Beta diversity can be the result of two processes, i.e., species replacement between sites (turnover) and 'nestedness' (Baselga, 2010). Here, the turnover component derives from the loss and gain of unique species, and the nestedness component derives from differences in species richness between nested assemblages, i.e., the extent to which the species composition of the poorest site is a subset of that of the richest site. Component partitioning of the β diversity enables us to determine the extent to which community dissimilarity derives from an increase in species turnover, an increase in species nestedness, or both. It can also provide additional insights into the drivers of spatial variation in biotic communities when climatic, environmental, or species characteristics are taken into account (Haslem et al., 2015; Soininen et al., 2018).

Island area and remoteness are likely to play a mediating role in determining the extent, structure and, source of soil faunal community dissimilarity through land use change. Large islands with high resident human populations may suffer a high degree of deforestation because of greater land demand for agriculture and construction (Helmus et al., 2014; Xu et al., 2023). Deforestation may also be higher in less remote islands due to their accessibility to transportation. This intensive deforestation on larger or less-remote islands may create a pool of species that are more tolerant of deforestation through anthropogenic filtering (Hua et al., 2024). That is, deforestation can cause a great loss of ecological specialists that are adapted for forested areas but promote generalists and opportunistic species overall (Filgueiras et al., 2021), and we would expect these effects to be greater on larger and less isolated islands. As a result, we hypothesize that, during the land conversion of forest to grassland, compositional changes (i.e., total β-diversity) for soil faunal communities should be lowest on large and less remote islands.

The turnover and nestedness components of soil faunal β diversity between forests and adjacent deforested grasslands may be influenced by island biogeographic properties. Large and less remote islands often support high species biodiversity due to high immigration rate and low extinction rates (MacArthur and Wilson, 1963), greater variety of habitats (Hortal et al., 2009), and greater efforts from humans in protecting natural vegetation (Xu et al., 2023). Therefore, in comparison with small and remote islands, large and less remote islands tend to have more disturbance-tolerant or grassland-affiliated taxa that can utilize converted habitat. Consequently, we predict that land use changes should lead to a higher turnover between forest and grassland on larger and less remote islands. Further, on small and remote islands, we predict that as a consequence of the loss of specialists during land use conversion from forest to grassland, and the low number of grassland-affiliated taxa in grassland due to small species pools, there will be higher species nestedness between forest and grassland.

Soil and plant litter properties are important for structuring soil faunal communities (Mori et al., 2015; Potapov et al., 2020). Changes in resource availability resulting from land use change are key factors affecting soil faunal community composition (Potapov et al., 2020; Supp and Ernest, 2014; Yan et al., 2008). Typically, the higher the habitat differences, the larger the community dissimilarity (Song et al., 2024). Furthermore, climate factors can also influence the impacts of land use on soil faunal community composition which shows more pronounced responses under harsh environmental conditions (Frishkoff et al., 2016; Hua et al., 2024; Marta et al., 2021). Therefore, in addition to the direct effects of island attributes, other factors that are mediated by island attributes such as microclimate, microhabitat resource quality, and other microhabitat properties might also be important drivers of soil fauna community composition (Gong et al., 2023; Wardle et al., 2003). However, few studies have explored or disentangled the role of biotic and abiotic factors that vary among islands in driving soil faunal community composition changes in the context of land use change in island ecosystems.

Here, we explore how island area and remoteness influences soil faunal community composition during woodland-grassland conversion in the Zhoushan Archipelago, China. We chose woodland-grassland pairs as a proxy of deforestation effects within each of 20 islands that vary with size and remoteness. We used this study system to examine the direct effects of island biogeographic attributes, and indirect effects of these factors via changes of climatic and habitat properties on soil faunal community composition between woodland and grassland. Specifically, we tested: i) how island area and remoteness impacts changes in the soil faunal community composition caused by deforestation (i.e., conversion of woodland to grassland); ii) whether variation among islands of the soil faunal community composition resulting from deforestation is driven by turnover or nestedness; and iii) how other biotic and abiotic habitat factors that may vary among islands influence the biogeographic pattern of soil faunal community composition change caused by deforestation.

2. Materials and methods

2.1. Study region and land use history

The Zhoushan Archipelago (29°31′–31°04′N, 121°30′–123°25′E), located in Zhejiang Province, is the largest archipelago in China, and comprising 1390 islands with an area larger than 500 m^2. The largest island is Zhoushan Main Island, with an area of 515.38 km^2 (including the tidal zone). This land-bridge archipelago was isolated from the mainland 7000 to 9000 years ago (Xu et al., 2017). The climate is typically subtropical monsoon, and the mean annual temperature and mean annual precipitation is 15.6–16.5 °C and 936.3–1330.2 mm, respectively. Temperature and humidity decreases with island remoteness (Xu et al., 2023).

In this studied archipelago, land use intensity (i.e., the proportion of land under human land use) over the period from 1991 to 2017 has been shown to increase with island area but be unrelated to island remoteness (Xu et al., 2023). Historically, deforestation on the islands for wood, fuel and other land uses was very common (Yan et al., 2018). But about 35 years ago, the project of relocating people from small islands to larger ones resulted in a gradual halt to deforestation activities on the small islands. The remaining forests and shrublands (hereafter named woodlands) have since been protected from logging and clear cutting, and the previously cultivated agricultural land was abandoned. This project also led to the gradual expansion of construction areas and agricultural land on the larger islands. With recent rapid socioeconomic development and the convenience of transportation, an increasing number of people from rural areas have been migrating to cities on the large islands. This has resulted in the total urban area on the large islands having expanded (from 97 km^2 to 438 km^2 during 1986–2017) and concomitant widespread abandonment of agricultural land on them (Cao et al., 2021). Thus, in our study area, land use conversion is widespread, and land use intensity varies among islands.

2.2. Experimental design

To examine the effect of deforestation on the community composition of soil fauna, we selected grasslands that are regenerated from agricultural land, and corresponding areas of intact woodlands (forest and shrubland), for each of 20 islands that vary in size and remoteness (Supplementary Fig. S1 and Supplementary Table S1). For each island, three woodland plots, and three adjacent grassland plots that were previously abandoned, have been set up. The distance between the paired woodland and grassland plots does not exceed 300 m. The selected woodland types (forest or shrubland) were consistent within each island and representative of the dominant community type on that island. The plots were randomly selected in each vegetation type and all plots were separated by at least a 50 m buffer from the island edge. The six plots were located on the similar position of the slope, had the same original vegetation historically, and were on soils developed from the same quartzitic parent material. This sampling design allows to quantitatively evaluate how island attributes mediate the effects of deforestation on soil faunal community composition. The plot size was 20 m × 20 m for forest, 10 m × 10 m for shrubland, and 10 m × 10 m for grassland.

The differing plot sizes across forests, shrublands, and grasslands was due to the fact that some of the woodland plots used in this study were based on permanent plots previously established in the study area (Xu et al., 2023). The woodland plot sizes were determined based on the minimum area needed to capture plant community structure and diversity, as indicated by species-area relationships in comparable subtropical regions (Song et al., 2013), where 20 m × 20 m is the minimum size for forest and 10 m × 10 m for shrubland. Ultimately, forest plots were established on 9 islands, and shrubland plots on 11 islands. To maintain consistency with the majority of woodland plot sizes, and because grasslands have a more homogeneous environment than forests, grassland plots were set at 10 m × 10 m. In total, there were 60 woodland plots (27 forest plots + 33 shrubland plots) and 60 grassland plots.

2.3. Soil fauna sampling and identification

In this study, we sampled microarthropods and macrofauna to represent soil animal communities. Soil microarthropods and macrofauna were sampled from May to July, in 2020 and 2022 respectively. In each plot, we randomly selected three locations for sampling soil fauna. In a given location, we excavated soil sample (50 × 50 × 20 cm, length × width × depth) to collect macrofauna by hand sorting in the field. All collected macrofauna were preserved in 95 % alcohol. A metallic tube (20 cm height and 5 cm in diameter) was used to collect soil samples to extract the microarthropods. These collected materials were immediately packed into plastic bags and then sealed to avoid escape of soil animals. For each of the soil samples from three locations were combined to give one composite sample per plot. In total, there were 120 samples (20 islands × 2 land use types (woodland and grassland) × 3 plots). We extracted soil microarthropods within three days after samples were transported to the laboratory. For each composite sample, soil microarthropods were extracted by using a Tullgren funnel for 3 days and then preserved in 75 % ethanol. Finally, all collected soil fauna were identified to the class or order level (Yin, 1998) by using stereoscopic microscopes (Leica DVM6, Germany).

Soil fauna were classified into 26 taxonomic groups, including Oribatida, Astigmata, Prostigmata, Mesostigmata, Pseudoscorpions, Symphyla, Pauropoda, Diplura, Protura, Collembola, Araneae, Diplopoda, Chilopoda, Isopoda, Dermaptera, Blattodea (except Isoptera), Isoptera, Thysanoptera, Hemiptera, Psocoptera, Formicidae, Coleoptera, Lepidoptera, Diptera, Lumbricina, and Gastropoda, which can represent trophic or functional groups roughly (Potapov et al., 2022; Zhou et al., 2023). An overview of body sizes and food resources for the groups mentioned above is provided in Supplementary Table S2.

2.4. Quantification of habitat properties and climate variables

Plant litter and soil samples were sampled in three locations in each plot in the summer (May to July) of 2020. Plant litters were collected using a 0.2 × 0.2 m frame above the soil surface and taken back to the laboratory with the paper bags. We combined the three samples into a composite sample per plot, oven-dried at 65 °C to the constant weight, and then weighed it to represent litter biomass (LB). Three soil samples from the same locations were collected by using a 0–20 cm metal core (diameter is 2.5 cm, five repetitions). In the laboratory, three samples were combined per plot and roots were sorted out immediately with tweezers to prevent root decomposition. Then, the roots smaller than 2 mm in diameter were washed, oven-dried (65 °C), and weighed to calculate fine root biomass (RB). The remaining soil sample material was air-dried for 30 days after roots and stones were removed, and then passed through a 2 mm sieve. A subsample was used to measure soil total carbon (TC) and total nitrogen (TN) concentrations, using a dry combustion automated elemental analyser (Vario EL, Elementar). Another subsample was used to determine soil electrical conductivity (EC), using a conductometer (DDS-SO7A, INESA, China) after shaking the soil water (1:2.5, H_2O) suspension for 30 min.

Soil fauna are highly sensitive to humidity and disturbance, and so we sought to characterize climatic properties separately for each island.

We obtained climate variables for each plot from the WorldClim 2.0 database (Fick and Hijmans, 2017) at 30-arcsec (~1 km^2 spatial resolution). We selected annual precipitation and wind speed to examine how water availability and natural disturbance shape patterns of soil faunal diversity across islands. The extraction process for this data was conducted using the tool of Extract Multi Values to Points in ArcGIS 10.1.

2.5. Data calculation and statistical analysis

For each variable on a given island, we combined the data from three grassland plots and three woodland plots on that island to provide a single data point for grassland and another for woodland, as recommended by Schrader et al. (2019). For each island, we assessed soil faunal diversity in woodlands and grasslands, considering abundance, the number of common (a, present in both woodland and grassland) and unique (b, present only in woodland; c, present only in grassland) taxa, and taxa richness (total number of taxa in woodland (a + b) or grassland (a + c)). We also assessed community dissimilarity (total β-diversity, β) and its components—turnover (β_{tu}) and nestedness (β_{ne})—between woodland and grassland, along with climate factors, and litter and soil properties. For each island the β diversity and its components between woodland and grassland were calculated using the R package *betapart* (Baselga et al., 2021), by employing Jaccard's incidence-based metric. The specific calculation formula is as follows (Baselga, 2012):

$$\beta = \frac{b+c}{a+b+c} \tag{1}$$

$$\beta_{tu} = \frac{2min(b,c)}{a+2min(b,c)} \tag{2}$$

$$\beta_{ne} = \frac{max(b,c)-min(b,c)}{a+b+c} \times \frac{a}{a+2min(b,c)} \tag{3}$$

where a is the number of taxa shared by both woodland and grassland, b is the number of taxa that only occur in woodland and c is the number of taxa that only occur in grassland. We utilized presence and absence data rather than abundance data because, for soil fauna, the large dissimilarities in overall individual numbers among taxa (for example, Oribatida versus Coleoptera) would result in extremely biased patterns. The effect size of land-use conversion on abundance was calculated as the natural logarithm of the response ratio (lnRR), where lnRR = ln(Abundance in woodland / Abundance in grassland). lnRR > 0 indicates that land-use conversion has a negative effect on taxa abundance. For each litter and soil property on each island, we calculated the dissimilarity between woodland and grassland as a proxy for habitat differences (Song et al., 2024).

Specialization can be defined as either taxa that are narrowly distributed on only a few islands, or that are primarily found in one habitat. In this study, taxa that can utilize both woodland and grassland habitat and occur in no less than four-fifths of the islands are defined as generalist taxa, while those found in no more than one-fifth of the islands are defined as specialist taxa. Additionally, as the classification level in this study is at the class or order, the habitat preferences of the taxa might not be as evident as the species level. Thus, we define a group as forest-affiliated taxa if the frequency of its occurrence in woodlands exceeds that in grasslands by 20 % across all islands, and as grassland-affiliated taxa if the frequency of its occurrence in grasslands exceeds that in woodlands by 20 %.

To compare the differences in soil fauna abundance, taxa richness, and in each habitat property between woodland and grassland, two-tailed paired *t*-tests were conducted. For soil faunal abundance, we compared total abundance, the combined abundance of specialist taxa, and the abundance of other groups between woodlands and grasslands. Abundance data was natural log-transformed before analysis to reduce the impact of extreme values. Prior to the t-test, the normal distribution of differences between paired samples was checked, and all tests met the assumption. To investigate how soil faunal community composition varied between land use type, non-metric multidimensional scaling (NMDS) based incidence data and Jaccard distance were implemented to test community dissimilarity. The analysis of similarities (ANOSIM) was used to test the multi-dimensional differences between land use type. We conducted NMDS and ANOSIM analyses by using the *vegan* package (Oksanen et al., 2022).

To assess the relationships between island attributes and each diversity index, general linear models (GLMs) were applied. We also used linear mixed-effects models (LMMs), with plot size as a random effect, to account for the influence of variation in plot size among vegetation types on the relationships involving taxonomic richness or the numbers of unique taxa in woodlands and island attributes. Given the consistency of the results between GLMs and LMMs (Supplementary Table S3), and in order to facilitate comparison with grassland, GLMs were used in the final analysis and visualization. GLMs were also used to examine the relationships between island attributes and predictor variables (i.e. TC, TN, EC, litter biomass, root biomass, wind speed, and annual precipitation), as well as between these predictors and diversity indices. We used the Shapiro-Wilk test and the Breusch-Pagan test to validate the assumptions of normality and homoscedasticity of the model residuals, respectively, and data were transformed by natural logarithms or Box-Cox to improve this whenever needed.

Further, multiple linear regression models were used to evaluate effects of multiple predictors on soil faunal total β-diversity, turnover, and nestedness. The variables were standardized (mean = 0, SD = 1) prior to conducting the statistical analyses. We made multi-model inferences and evaluated ΔAIC for all possible combinations of predictors, and selected the best model with the lowest AIC value. We conducted this analysis using the *dredge* function from the *MuMIn* package (Bartoń, 2022). All analyses were conducted using R version 4.2.3 (R Core Team, 2022).

3. Results

There were 26 taxonomic groups of soil fauna found across the 20 studied islands. The average taxa richness in woodlands and grasslands was 14.35 (ranging from 11 to 17 taxa per island) and 13.65 (ranging from 7 to 18 taxa per island), respectively. The taxa richness showed no difference between woodlands and grasslands (Supplementary Fig. S2, paired *t*-test $P = 0.25$). Total soil faunal abundance in woodlands and grasslands averaged 23,929 ± 3996 and 23,747 ± 4193 ind.m^{-2} (mean ± SE), respectively. Among the taxonomic groups, only Coleoptera and Isoptera exhibited significantly higher abundances in woodlands than in grasslands (Supplementary Table S4). Meanwhile, soil faunal community composition differed significantly between woodland and grassland (Fig. 1a, ANOSIM $P < 0.05$). Overall total β-diversity between woodland and grassland varied widely across these islands, and turnover accounted for 62 % of the total β-diversity, which is higher than the proportion of nestedness (Fig. 1b).

Total β-diversity between woodland and grassland did not statistically change with island area (Fig. 2a), but its components exhibited contrasting patterns with island area (Fig. 2b, c). Specifically, turnover significantly increased and nestedness significantly decreased with island area. On smaller islands, many taxa established in woodlands did not occupy grasslands, leading to a lower number of unique taxa in grassland (Fig. 3). The number of unique taxa increased with island area in grassland, and both land use types—woodlands and grasslands—harbored a comparable number of unique taxa and taxa richness on larger islands (Fig. 3b, Supplementary Fig. S2b). Additionally, the abundance of Chilopoda, Isoptera, and Lumbricina significantly decreased with increasing island area in woodlands, while specialist abundance significantly increased with increasing island area in grasslands (Supplementary Fig. S3a).

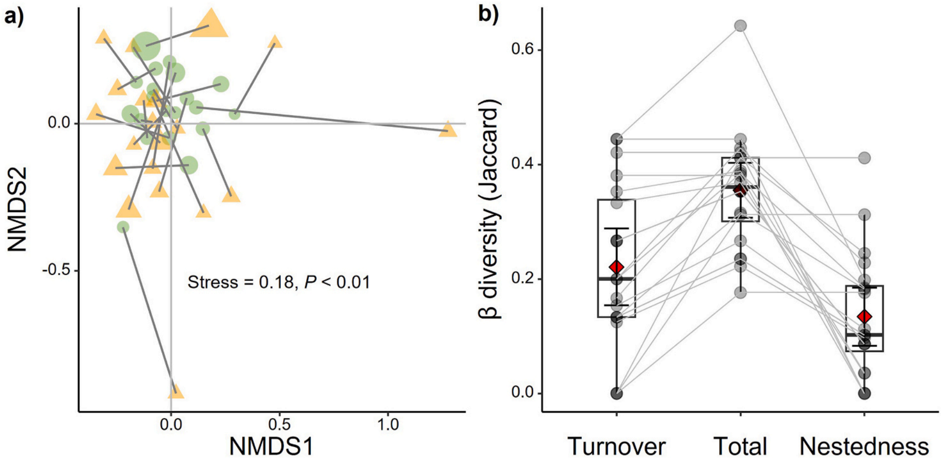


Fig. 1. Comparison of community composition (a) and average β diversity between woodland and grassland (b). In Figure a, the solid green circles and yellow triangles represent woodland and grassland samples, respectively, with the size of the shapes corresponding to the size of the islands. Thin lines connect the woodland and grassland samples from the same island. Box plots show the medians, interquartile ranges, and full ranges, with a red dot indicating the mean.

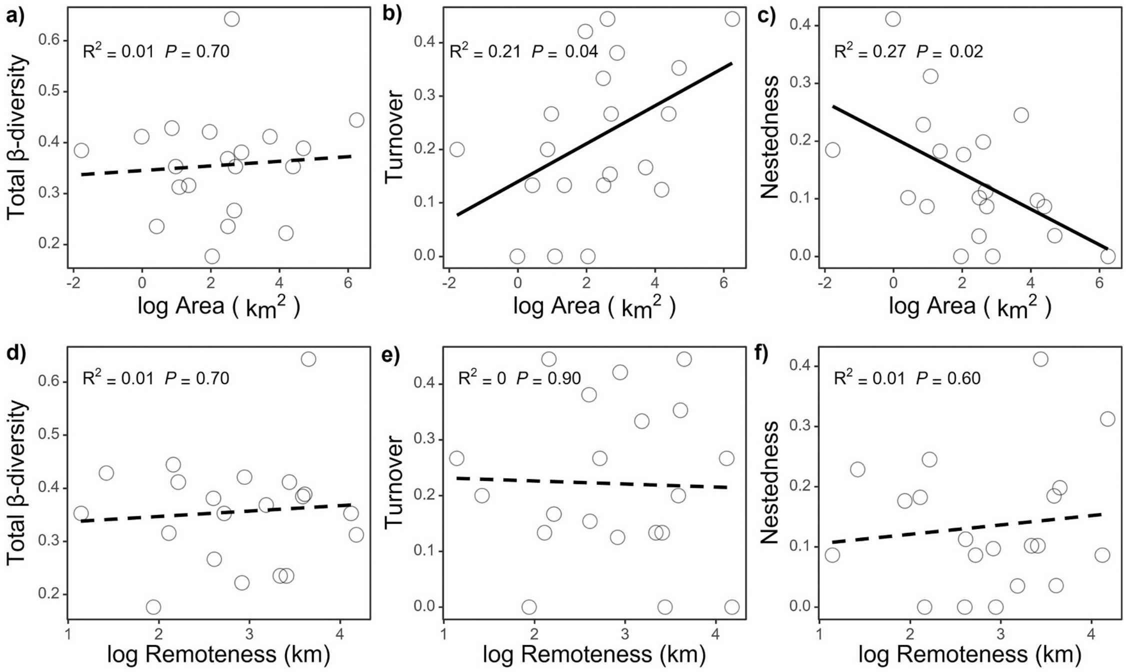


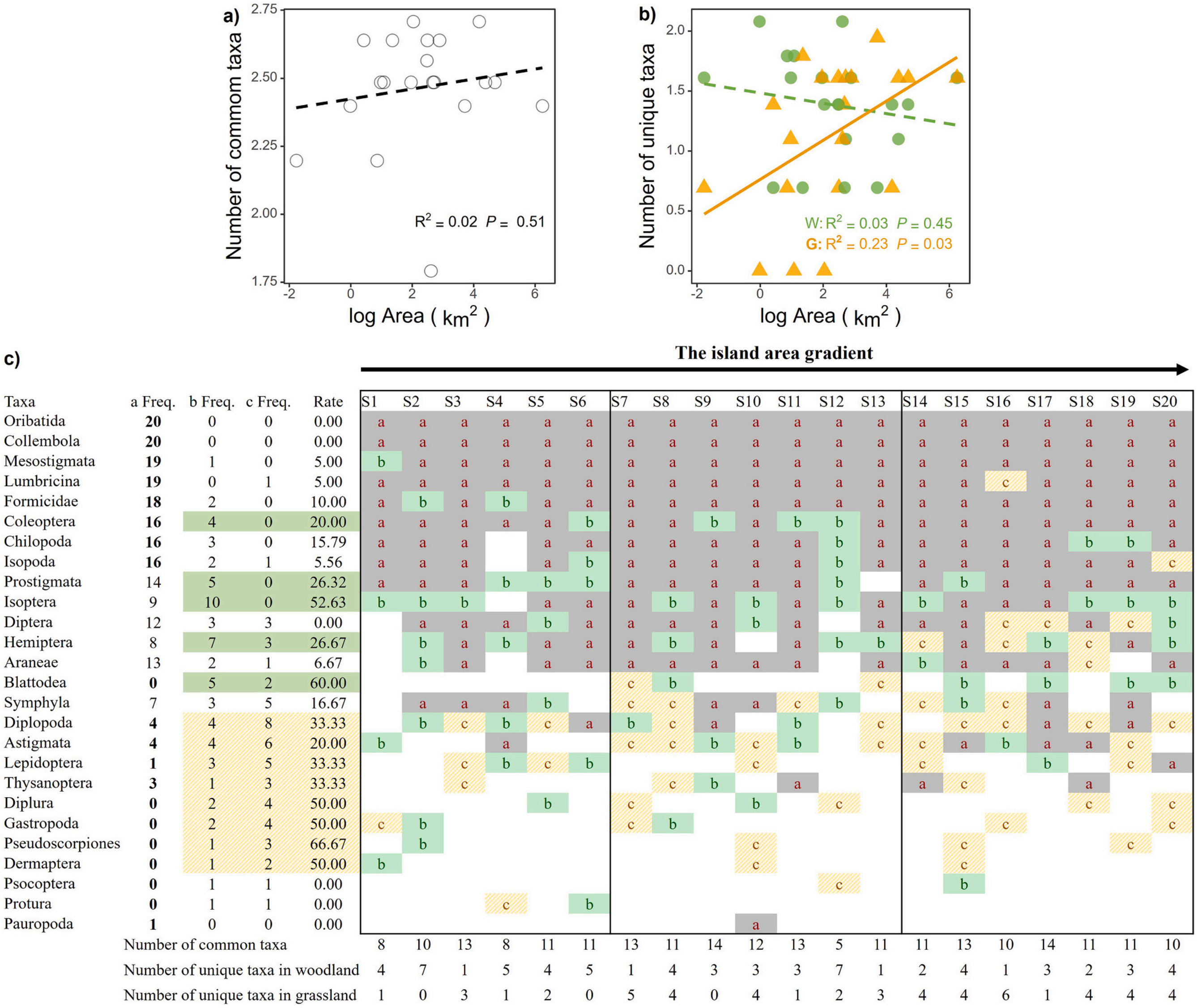
Fig. 2. Relationships of total β-diversity between grassland and woodland, and its components (turnover and nestedness) with island area and remoteness. The solid lines represent significant linear regressions ($P \leq 0.10$).

Total β-diversity and its components did not change with island remoteness (Fig. 2d, e, f). Island remoteness did not affect the number of common or unique taxa, or taxa richness (Fig. 4, Supplementary Fig. S2c). However, the abundance of smaller-bodied groups like Oribatida and Mesostigmata decreased with increasing remoteness in woodlands, while larger-bodied groups such as Chilopoda, Isoptera, and Lumbricina increased significantly (Supplementary Fig. S3b). In grasslands, remoteness led to a significant decrease in the abundance of specialist taxa. Additionally, remoteness increased the negative effects of land-use conversion on the abundance of Isopoda and Lumbricina (Supplementary Fig. S4).

For environmental variables, TC and litter biomass were higher in woodland than in grassland (Supplementary Fig. S5). In woodland, litter biomass increased with island area, and TC decreased with remoteness (Supplementary Fig. S6). In grassland, both TC and TN decreased with island area. Wind speed decreased with island area, and annual precipitation decreased with remoteness (Supplementary Fig. S7). Habitat differences of EC increased with island area, while TC decreased with remoteness (Supplementary Fig. S6). Turnover increased with habitat differences of EC and root biomass but decreased with wind speed (Table 1 and Supplementary Table S5). Nestedness decreased with habitat differences of root biomass and TN but increased with habitat differences of TC. Wind speed increased nestedness, while annual precipitation decreased it.

4. Discussion

We found that land use conversion from woodland to grassland caused significant changes in soil faunal composition across 20 islands, and that island area is a critical driver of the dissimilarity in soil faunal communities resulting from land use change. In partial support of our hypotheses, although the overall community difference (total



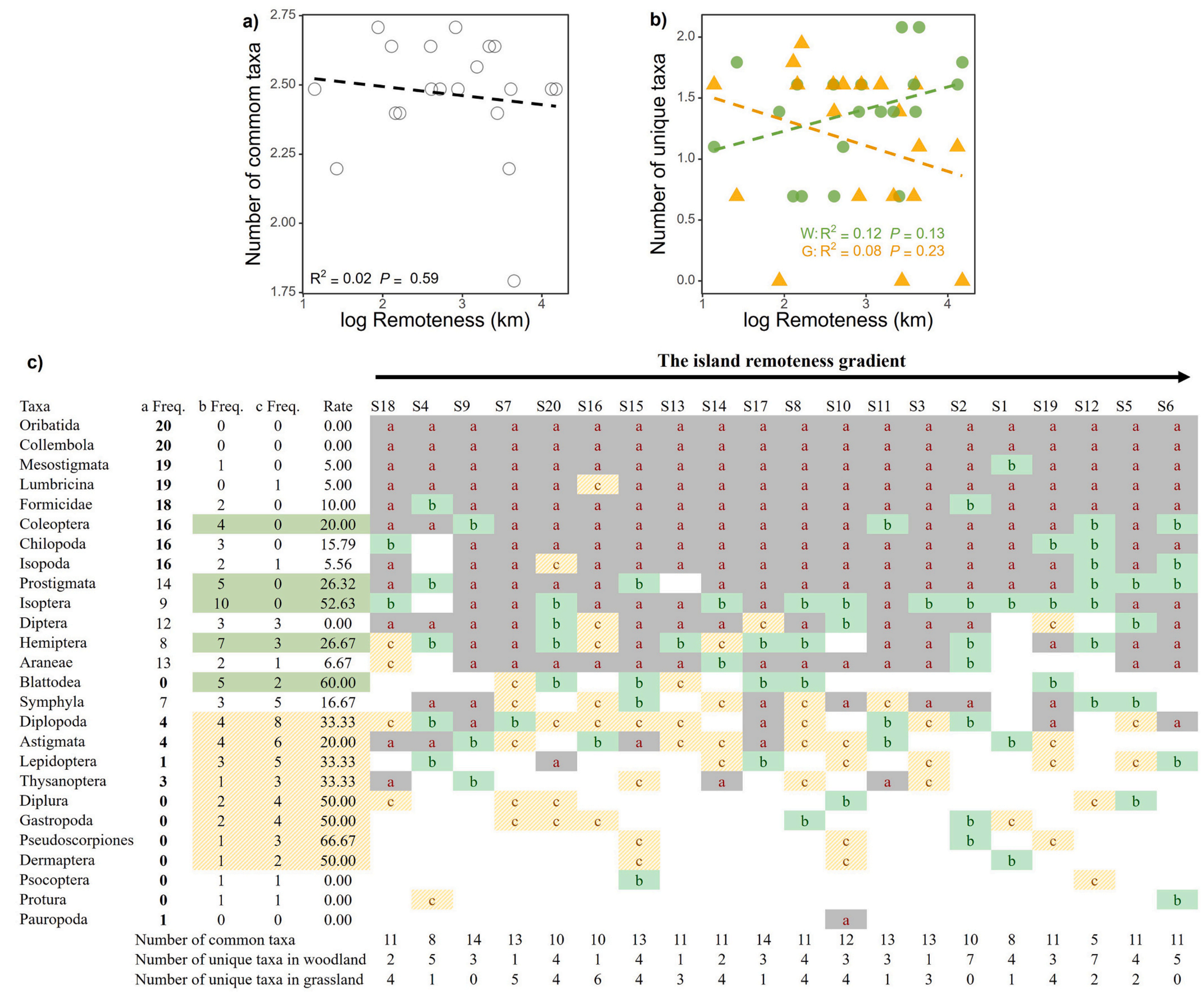
Taxa	a Freq.	b Freq.	c Freq.	Rate	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20
Oribatida	**20**	0	0	0.00	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Collembola	**20**	0	0	0.00	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Mesostigmata	**19**	1	0	5.00	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Lumbricina	**19**	0	1	5.00	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	c	a	a	a	a
Formicidae	**18**	2	0	10.00	a	b	a	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Coleoptera	**16**	4	0	20.00	a	a	a	a	a	b	a	a	b	a	b	b	a	a	a	a	a	a	a	a
Chilopoda	**16**	3	0	15.79	a	a	a		a	a	a	a	a	a	a	b	a	a	a	a	a	b	b	a
Isopoda	**16**	2	1	5.56	a	a	a		a	b	a	a	a	a	a	b	a	a	a	a	a	a	a	c
Prostigmata	14	5	0	26.32	a	a	a	b	b	b	a	a	a	a	a	b		a	b	a	a	a	a	a
Isoptera	9	10	0	52.63	b	b	b		a	a	a	b	a	b	a	b	a	b	a	a	a	b	b	b
Diptera	12	3	3	0.00		a	a	a	b	a	a	a	a	b	a		a	a	a	c	c	a	c	b
Hemiptera	8	7	3	26.67		b	a	b	a	a	a	b	a		a	b	b	c	a	c	b	c	a	b
Araneae	13	2	1	6.67		b	a		a	a	a	a	a	a	a		a	b	a	a	a	c		a
Blattodea	**0**	5	2	60.00							c	b					c		b		b		b	b
Symphyla	7	3	5	16.67		a	a	a	b		c	c	a	a	c	b		c	b	c	a		a	
Diplopoda	**4**	4	8	33.33		b	c	b	c	a	b	c	a		b		c		c	c	a	c	a	c
Astigmata	**4**	4	6	20.00	b			a			c	c	b	c	b		c	c	a	b	a	a	c	
Lepidoptera	**1**	3	5	33.33			c	b	c	b				c				c			b		c	a
Thysanoptera	**3**	1	3	33.33			c					c	b		a			a	c			a		
Diplura	**0**	2	4	50.00					b		c			b		c						c		c
Gastropoda	**0**	2	4	50.00	c	b					c	b								c				c
Pseudoscorpiones	**0**	1	3	66.67		b								c					c				c	
Dermaptera	**0**	1	2	50.00	b									c					c					
Psocoptera	**0**	1	1	0.00												c			b					
Protura	**0**	1	1	0.00				c		b														
Pauropoda	**1**	0	0	0.00										a										
Number of common taxa					8	10	13	8	11	11	13	11	14	12	13	5	11	11	13	10	14	11	11	10
Number of unique taxa in woodland					4	7	1	5	4	5	1	4	3	3	3	7	1	2	4	1	3	2	3	4
Number of unique taxa in grassland					1	0	3	1	2	0	5	4	0	4	1	2	3	4	4	6	1	4	4	4

Fig. 3. Relationships of the number of taxa common to grassland and woodland (a) and taxa unique to (b) woodland (green circles) and grassland (yellow triangles) with island area. W: woodland, G: grassland. The solid line represents significant linear regression ($P \leq 0.10$). Distribution of common and unique taxa for both woodland and grassland along the island area gradient (c). From the second to fifth column, 'a Freq' represents the number of islands (out of 20) where soil faunal taxa occur in both woodland and grassland; and 'b Freq' and 'c Freq' represent the number of islands where species occur only in woodland and only in grassland, respectively. 'Rate' represents the percentage at which each taxa appears more frequently in woodland than in grassland (green background, forest-affiliated taxa) and vice versa (yellow background, grassland-affiliated taxa). For individual taxa, gray (a), green (b) and yellow (c) indicates presence in both woodland and grassland, only woodland, and only grassland, respectively. S* represents the code of 20 studied islands.

β-diversity) of soil faunal communities between woodland and grassland did not directly relate to island biogeographic attributes, the turnover component of β diversity increased while the nestedness component decreased significantly with increasing island area. On small islands, there were not only fewer unique taxa in grassland compared to woodland, but many unique taxa present in woodland were absent in grassland. This indicates that the soil faunal community composition in grassland tends to be the nested subset of that in woodland. On large islands, the number of unique taxa in woodland and grassland was comparable, resulting in two distinct communities. Island remoteness did not significantly affect soil faunal community dissimilarity between woodlands and grasslands but it did increase the negative impacts of land-use changes on certain larger-bodied groups. Moreover, increased habitat differences and decreased environmental stress on larger islands promoted turnover but decreased nestedness. Altogether, our findings contribute to an understanding of the island biogeography of the Anthropocene (Helmus et al., 2014), by highlighting how the interplay of island biogeographic properties and human land use impacts soil faunal communities.

4.1. Effect of island area on community dissimilarity between woodland and grassland

Our finding of island area effects on turnover and nestedness between woodland and grassland suggests that island size is a powerful mediator of how land use conversion impacts the soil faunal community. On smaller islands, nestedness drove changes in community composition between woodland and grassland to a larger extent than did turnover. Specifically, land use conversion led to the loss of more forest-affiliated taxa and the gain of fewer grassland-affiliated taxa, with only generalists persisting in grasslands (Arroyo-Rodríguez et al., 2013; McCune and Vellend, 2013). This is further supported by the lower



Taxa	a Freq.	b Freq.	c Freq.	Rate	S18	S4	S9	S7	S20	S16	S15	S13	S14	S17	S8	S10	S11	S3	S2	S1	S19	S12	S5	S6
Oribatida	**20**	0	0	0.00	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Collembola	**20**	0	0	0.00	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Mesostigmata	**19**	1	0	5.00	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	a	a	a	a
Lumbricina	**19**	0	1	5.00	a	a	a	a	a	c	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Formicidae	**18**	2	0	10.00	a	b	a	a	a	a	a	a	a	a	a	a	a	a	b	a	a	a	a	a
Coleoptera	**16**	4	0	20.00	a	a	b	a	a	a	a	a	a	a	a	a	b	a	a	a	a	b	a	b
Chilopoda	**16**	3	0	15.79	b		a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a	a
Isopoda	**16**	2	1	5.56	a		a	a	c	a	a	a	a	a	a	a	a	a	a	a	a	b	a	b
Prostigmata	14	5	0	26.32	a	b	a	a	a	a	b		a	a	a	a	a	a	a	a	a	b	b	b
Isoptera	9	10	0	52.63	b		a	a	b	a	a	a	b	a	b	b	a	b	b	b	b	b	a	a
Diptera	12	3	3	0.00	a	a	a	a	b	c	a	a	a	c	a	b	a	a	a		c		b	a
Hemiptera	8	7	3	26.67	c	b	a	a	b	c	a	b	c	b	b		a	a	b		a	b	a	a
Araneae	13	2	1	6.67	c		a	a	a	a	a	a	b	a	a	a	a	a	b				a	a
Blattodea	**0**	5	2	60.00				c	b		b	c		b	b						b			
Symphyla	7	3	5	16.67		a	a	c		c	b		c	a	c	a	c	a	a		a	b	b	
Diplopoda	**4**	4	8	33.33	c	b	a	b	c	c	c	c		a	c		b	c	b		a		c	a
Astigmata	**4**	4	6	20.00	a	a	b	c		b	a	c	c	a	c	c	b			b	c			
Lepidoptera	**1**	3	5	33.33		b			a				c	b		c		c			c		c	b
Thysanoptera	**3**	1	3	33.33	a		b				c		a		c		a	c						
Diplura	**0**	2	4	50.00	c			c	c							b						c	b	
Gastropoda	**0**	2	4	50.00				c	c	c					b				b	c				
Pseudoscorpiones	**0**	1	3	66.67							c					c			b		c			
Dermaptera	**0**	1	2	50.00							c					c				b				
Psocoptera	**0**	1	1	0.00							b											c		
Protura	**0**	1	1	0.00		c																		b
Pauropoda	**1**	0	0	0.00												a								
Number of common taxa					11	8	14	13	10	10	13	11	11	14	11	12	13	13	10	8	11	5	11	11
Number of unique taxa in woodland					2	5	3	1	4	1	4	1	2	3	4	3	3	1	7	4	3	7	4	5
Number of unique taxa in grassland					4	1	0	5	4	6	4	3	4	1	4	4	1	3	0	1	4	2	2	0

Fig. 4. Relationships of the number of taxa common to grassland and woodland (a) and taxa unique to (b) woodland (green circles) and grassland (yellow triangles) with island remoteness. Distribution of common and unique taxa for both woodland and grassland along the island remoteness gradient (c). Detailed descriptions of the figure are presented in Fig. 3.

Table 1
Best-fit multiple regression models for the effects of habitat heterogeneity and climatic factors on β diversity. EC: electrical conductivity; TN: total nitrogen; TC: total carbon.

Variable	Estimate	Std. error	t value	*P*
Total β-diversity	$R^2_{adj} = 0.17$, $P = 0.04$			
Litter biomass	0.12	0.05	2.22	0.04
Turnover	$R^2_{adj} = 0.57$, $P < 0.01$			
EC	0.05	0.02	2.10	0.05
Root biomass	0.07	0.02	2.92	0.01
Wind speed	−0.08	0.02	−3.09	<0.01
Nestedness	$R^2_{adj} = 0.74$, $P < 0.01$			
Root biomass	−0.06	0.01	−4.07	<0.01
TN	−0.07	0.02	−3.54	<0.01
TC	0.06	0.02	2.78	0.02
Wind speed	0.11	0.02	7.31	<0.01
Annual precipitation	−0.03	0.01	−2.05	0.06

abundance of specialist taxa in grasslands on smaller islands (Supplementary Fig. S3a). Generalist taxa, which have high adaptability to various environments and resources, can survive in both woodland and grassland. For example, ubiquitous earthworms, and diverse and abundant groups such as Oribatida, Mesostigmata, and Collembola, along with generalist detritivores like Isopoda and generalist predators such as Chilopoda and Formicidae (Potapov et al., 2022), which are widespread in many terrestrial ecosystems, are less affected by land use change (Supplementary Table S2, S4). However, forest-affiliated taxa are more sensitive to land use changes (Arroyo-Rodríguez et al., 2013; Nowakowski et al., 2018; Rodrigues et al., 2013), because land use conversion typically decreases the availability of resources (Li et al., 2021; Potapov et al., 2020). For example, Isoptera, which prefer highly humified organic matter (Potapov et al., 2022), are always lost due to the low soil carbon concentration and litter biomass in grasslands. The low number of unique taxa in grasslands on small islands might primarily be due to a limited species pool on these islands. Overall, the soil fauna community in grasslands represents a subset of that in woodlands, with woodlands on small islands serving as refuges.

On larger islands, turnover was the primary contributor to total β-diversity between woodland and grassland, consistent with many previous studies (Nowakowski et al., 2018; Soininen et al., 2018). This turnover involves the concurrent decline of disturbance-sensitive taxa that depend on woodlands and the proliferation of disturbance-adapted taxa that can exploit grasslands (Filgueiras et al., 2021). The proliferation of unique taxa in grasslands on large islands is related to the size and composition of the species pool. On the one hand, a larger species pool on larger islands can increase the probability of grassland-affiliated taxa appearing. On the other hand, high land use intensity on larger islands in this study system (Xu et al., 2023) may reshape the species pool by ecological filtering, resulting in a pool of species more tolerant of deforestation (Hua et al., 2024). However, these unique taxa gained in grassland are generally characterized by their small size (e.g. Astigmata, Diplura, Pseudoscorpiones) or low trophic status (e.g. Diplopoda) (Fig. 3c, Supplementary Table S2), which might be a consequence of the changing spectrum of available abiotic and biotic resources (Potapov et al., 2020; Supp and Ernest, 2014; Yan et al., 2008). For example, on larger islands, grasslands exhibit lower levels of soil total carbon, total nitrogen, and litter biomass compared to woodlands, thereby failing to support taxa that require high organic matter content and shelter (Lopezosa et al., 2023). These results demonstrate positive relationships between land-cover type diversity and biodiversity (Priyadarshana et al., 2024). Simultaneously, they underscore the importance of identifying which taxa are replaced and the characteristics of these taxa, and thus ecosystem functions (Li et al., 2021; Marichal et al., 2014).

4.2. Effect of island remoteness on community dissimilarity between woodland and grassland

Total β-diversity and its two components were not affected by island remoteness directly. This could be related to strong human activities on both near and far islands, such as the development of convenient transportation and tourism, which may weaken the pattern of species-isolation relationship (Helmus et al., 2014; Xu et al., 2023). Additionally, the complex interactions between climatic factors and habitat properties may also contribute to these results. For example, the low annual precipitation, indicating high drought stress, coupled with high differences of soil carbon concentrations between woodland and grassland on remote islands, contributed to increased nestedness. This indicates that even with high habitat differences, under harsh conditions, some taxa can only occur in a subset of the available habitats (Frishkoff et al., 2016). Consequently, along with global climate change, significant alterations in land use may pose serious threats to biodiversity.

Interestingly, in woodlands, with increasing island remoteness, the abundance of smaller-bodied groups (e.g. Oribatida and Mesostigmata) significantly decreased, while larger-bodied groups (e.g. Formicidae, Isoptera, and Lumbricina) significantly increased. This size-based response may be related to the greater resistance of larger-bodied groups to adverse environmental conditions, which allows them to play a more significant role in maintaining ecosystem functioning (Sagi and Hawlena, 2024). However, the negative effects of land-use changes on the abundance of these taxa (e.g. Isopoda, Lumbricina) increased with remoteness, which may be associated with the harsher environmental conditions on remote islands such as lower precipitation (Supplementary Fig. S7). This change may impair multiple ecosystem functions (Berlinches de Gea et al., 2023; Marichal et al., 2014). These results suggest that not only taxa richness but also taxa abundance warrant attention, especially for generalist or common taxa, which play an important role in maintaining ecosystem functionality (Grime, 1998). Moreover, our results suggest that on remote islands characterized by harsh environments, woodlands are particularly crucial for sustaining soil animal abundance, especially for larger-bodied groups.

4.3. Mediation of habitat differences by island attributes on community dissimilarity between woodland and grassland

Habitat differences have often been shown to be an important driver of β-diversity (Song et al., 2024). Consistent with this expectation, we found that the differences of litter biomass, root biomass, and soil TN, enhanced total β-diversity and turnover but decreased nestedness. These properties play an important role in determining variation in soil faunal diversity and community composition as resources or as a physical protective layer (Sayer et al., 2006; Zhou et al., 2023). Further, the differences of soil electrical conductivity were higher on larger islands and exhibited a positive relationship with turnover. High soil electrical conductivity, indicative of high soil salinity, is characteristic of island ecosystems, particularly on smaller islands due to their increased exposure to sea spray (Vitousek et al., 2004). Because of this, there are lower differences of soil electrical conductivity on small islands compared to large islands. These results collectively above suggest that the effect of environmental filtering on soil fauna leads to high β diversity on larger islands (Song et al., 2024).

Wind speed decreased with island area, exhibiting a negative relationship with turnover and a positive correlation with nestedness, while annual precipitation decreased with remoteness and showed a negative relationship with nestedness. This indicates that the impact of land use change on soil faunal community composition depends on climatic factors, and under harsh conditions (i.e., high speed wind and low annual precipitation), land use conversion will lead to a greater taxa losses. This is consistent with the findings of Frishkoff et al. (2016), which showed that species in drier regions prefer forests, and that forest-dependent species may reduce their habitat range to avoid agricultural land. Due to higher wind speeds on smaller islands and low annual precipitation on remote islands, the woody vegetation and its associated thick litter layer in woodlands may offer greater protective effects for soil fauna compared to grasslands, leading to a high nestedness and low turnover between woodland and grassland. In contrast, the high turnover and low nestedness observed under the low wind speeds on larger islands indicates that stable environmental conditions can lead to distinct community structures (Chase, 2003).

4.4. Uncertainties and limitations

Our study shows that island area drives soil faunal compositional dissimilarity between woodland and deforested grassland by simultaneously increasing turnover and decreasing nestedness components. This extends island biogeographic principles to enable understanding of community composition changes in the Anthropocene, and offers valuable insights into the conservation of belowground biodiversity. While the study presents novel findings, there are some limitations. First, the results are based on order-level data, which may to some extent obscure ecological insights, especially when changes occur only at finer levels of taxonomic resolution and involvec certain functional groups and specialists. Future research could focus on representative groups at the species level to better explore the current topic. We also acknowledge that the larger plot size in forest compared to shrubland and grassland may introduce some uncertainties. However, our supplementary analysis (Supplementary Table S3) suggests that the conclusion that the number of unique taxa is higher in woodlands than in grasslands on small islands, while comparable between woodlands and grasslands on large islands (Fig. 3b), is robust. For this reason, we maintain that the difference in plot size is unlikely to have a substantial influence on the patterns that we found.

5. Conclusions

Our results emphasize that the island biogeographical attributes strongly impacted soil faunal community composition. We found that the direction of effects of island area on β-diversity of soil fauna communities is opposite for their turnover and nestedness components, meaning that they cancel each other out to a certain extent. We therefore propose that, when examining the change patterns of community dissimilarity along biogeographic or environmental gradients, there is a need to partition β-diversity into its turnover and nestedness components. Additionally, along the gradient of island area, land use conversion led to taxa loss from woodland to grassland on small islands and taxa replacement by grassland-affiliated taxa in grassland on large islands. Additionally, although for island remoteness it did not significantly affect the soil faunal compositional dissimilarity between woodlands and grasslands, it did enhance the negative impacts of land-use changes on the abundance of larger-bodied soil fauna. Thus, protecting woody plants and promoting reforestation grassland-to-forest succession is necessary to prevent the extirpation of soil faunal specialists or the decline in the abundance of key taxa, especially on environmentally stressed islands.

CRediT authorship contribution statement

Zengyan Li: Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Zengke Zhang:** Writing – review & editing, Visualization, Investigation, Conceptualization. **Anna Yang:** Writing – review & editing, Visualization, Investigation. **Sufeng Pan:** Writing – review & editing, Methodology, Formal analysis. **Junyong Zheng:** Writing – review & editing, Visualization, Investigation. **Ling Mou:** Writing – review & editing, Investigation. **Wensheng Chen:** Writing – review & editing, Investigation. **Tian Zhang:** Writing – review & editing, Investigation. **Liyi Zhou:** Writing – review & editing, Investigation. **Wenhui You:** Writing – review & editing, Resources. **David A. Wardle:** Writing – review & editing, Methodology, Conceptualization. **En-Rong Yan:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2025.105966.

Data availability

The authors do not have permission to share data.

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